USING AN ECOLOGICAL LAND HIERARCHY TO PREDICT SEASONAL-WETLAND ABUNDANCE IN UPLAND FORESTS

Brian J. Palik,[1] Richard Buech, and Leanne Egeland

USDA Forest Service, North Central Research Station, 1831 Highway 169 E, Grand Rapids, Minnesota 55744 USA

Abstract. Hierarchy theory, when applied to landscapes, predicts that broader-scale ecosystems constrain the development of finer-scale, nested ecosystems. This prediction finds application in hierarchical land classifications. Such classifications typically apply to physiognomically similar ecosystems, or ecological land units, e.g., a set of multi-scale forest ecosystems. We speculated that hierarchical constraint also controls the development of small, nested ecosystems that are structurally distinct from the constraining matrix. We tested this hypothesis using seasonal wetlands in upland forest. Specifically, we related seasonal-wetland abundance in upland forest stands to multi-scale terrestrial ecological units, as defined by hierarchical combinations of regional physiography, glacial landform, soils, and forest cover. Moreover, we determined the spatial scale of terrestrial ecological unit that is the best predictor of seasonal-wetland abundance. Our study area is mapped into a set of nested terrestrial ecological units, including two subsections (differing in physiography), four land-type associations (glacial landforms), and 11 land types (forest vegetation, soil). We used a geographic information system to determine seasonal wetland densities in 16-ha plots located within the nested terrestrial ecological units.

Cumulative plot frequency distributions of wetland density did not differ between subsections; 50% of plots contained no wetlands, 38% contained 1–3 wetlands, and 12% contained ≥4 wetlands. Frequency distributions differed among land-type associations (LTA). Ninety percent of plots on a glacial lake plain contained no wetlands, compared to 63%, 42%, and 38% for outwash, end moraine, and ground moraine LTAs, respectively. Ten percent of plots on the lake plain contained 1–3 wetlands, compared to 32%, 48%, and 43% for the outwash, end moraine, and ground moraine, respectively. The remaining plots on the latter three LTAs contained >3 wetlands. Frequency distributions rarely differed among land types. Compared to occurrence, identity and scale of the ecological unit were poorer predictors of actual wetland densities. Regression tree analysis, while significant, explained only 11.6% of variation in wetland density among plots. Still, the leaves of the regression tree differed in densities primarily based on LTA.

Our results demonstrate that identity of constraining upland forest ecosystem explains significant amounts of variation in seasonal wetland abundance. We identify glacial landform as the scale of ecological unit having the greatest control over seasonal wetland abundance. We focus on seasonal wetlands in forests, yet our approach should apply to other small, nested ecosystems. This approach may facilitate conservation management of small, nested ecosystems by providing likelihood estimates of occurrence within mapped terrestrial ecological units.

Key words: conservation management; GIS; Great Lakes forest; hierarchical land classification; landscape hierarchies; Minnesota, USA; nested ecosystems; predicting wetland abundance; regression tree analysis; seasonal-wetland development; seasonal wetlands; wetland management.

INTRODUCTION

One can view a landscape as a set of nested hierarchical ecosystems (Fig. 1). Tenets of hierarchy theory (Allen and Starr 1982, O'Neill et al. 1986) readily apply to this set of nested ecosystems and are useful for making predictions about ecosystem structure and function. For example, when applied to landscapes, hierarchy theory predicts that broad-scale matrix ecosystems constrain the development of finer-scale nested

ecosystems (Rowe and Sheard 1981, O'Neill et al. 1986).

Application of hierarchy theory in natural resource management is most evident in the area of land classification. Although there are many approaches to land classification, those developed and applied by Bailey (1980), Barnes (Barnes et al. 1982), and others (Palik et al. 2000, Goebel et al. 2001) explicitly view landscapes as a set of nested ecosystems, commonly termed "hierarchical ecological units" (Keys et al. 1995). Users of this approach describe hierarchical ecological units based on combinations of regional physiography, meso-scale geomorphology, and site-scale typography
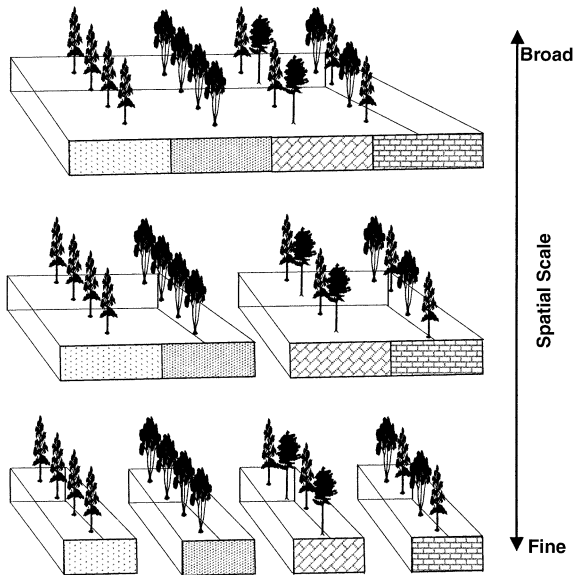
FIG. 1. Conceptual representation of nested hierarchical ecosystems. Broader-scale ecosystems encompass greater variation in biophysical characteristics, e.g., plant communities and soil properties. At finer spatial scales, this same variation is divided into a greater number of distinct ecosystems.

and soil, within which organisms live and interact (Rowe and Barnes 1994).

One promising, but unexplored area of application is the use of hierarchy theory and hierarchical land classifications to guide management of small, nested ecosystems. Specifically, we refer to ecosystems that stand in sharp structural and functional contrast to the broader-scale matrix in which they occur, but may be overlooked during mapping and management due to their size. Seasonal wetlands (i.e., small wetlands with a seasonally fluctuating water level) nested in upland forest are a good example (see Plate 1). As with structurally similar ecosystems (e.g., a hierarchical set of upland forest ecosystems), one might predict that the larger-scale landscape matrix also constrains the occurrence and function of nested, seasonal wetlands (Palik et al. 2001).

The cumulative importance of seasonal wetlands in a landscape may be large. They are abundant in many temperate forests (e.g., Gibbs 1993, Brooks et al. 1998, Kirkman et al. 1999) where they provide primary breeding habitat for several amphibian species, such as blue-spotted salamanders (*Ambystoma laterale*) and wood frogs (*Rana sylvatica*) in northern forests. Small seasonal wetlands may contribute disproportionately to biological diversity of species and ecosystems in regional landscapes because of their abundance and distinctive characteristics, relative to the matrix in which they occur.

A fundamental constraint to developing effective conservation and management policies for seasonal

wetlands, and small nested ecosystems in general, is our inability to predict where and with what abundance the systems occur in a landscape. Apart from extensive ground-based physical inventories or time consuming air-photo inventories of entire management areas (see Brooks et al. [1998] for an example), there is no easy methodology to predict the number and location of seasonal wetlands over large areas. Remote-sensing technologies, e.g., Radarsat synthetic aperture radar (Townsend 2001), may allow better detection and mapping in the future. In the interim, resource managers could benefit from a tool that helps predict seasonal wetland abundance using readily available spatial data layers, combined with limited physical inventories. Moreover, even advanced remote-sensing detection methods might benefit from understanding hierarchical relationships between seasonal wetlands and landscape matrices, if this helps to refine search parameters for wetland detection.

With the need for such a tool in mind, we explore relationships between small seasonal wetlands and hierarchically structured, broader-scale terrestrial ecological units. We focus on seasonal wetlands in forests of northern Minnesota (USA) because of the growing ecological and conservation interest surrounding these systems. However, we believe our approach may apply to a wide array of small ecosystems in other types of landscapes, such as rock outcrops (Wiser et al. 1996), tree islands in tundra (Marr 1977), and oak domes in pine forest (Guerin 1993). Specifically, we addressed two questions: (1) Can we predict wetland abundance in upland forest stands from knowledge of terrestrial ecological units, as defined by hierarchical combinations of regional physiography, glacial landform, soils, and forest cover? and (2) What spatial scale of terrestrial ecological unit is the best predictor of wetland abundance.

METHODS

Study area

We conducted our study on the Chippewa National Forest in northcentral Minnesota, USA. The USDA Forest Service has mapped ecological land units at various spatial scales (Chippewa National Forest 1996), using the hierarchical framework suggested by ECO-MAP (1993). We selected two study areas: the 12 925-ha (10 031 upland hectares) Sucker Lakes study area and the 22 061-ha (14 591 upland hectares) Rice River study area. Both areas fall within the Northern Minnesota Drift and Lake Plains Section (Keys et al. 1995), but they occur within different subsections (differing in subregional physiography) and include different land-type associations and land types (Table 1). In the classification, land-type association (LTA) corresponds largely to glacial landform, whereas land type (LT) corresponds to a combination of soil characteristics and overstory vegetation (Almendinger et al. 2000). The

PLATE 1. A seasonal wetland as seen in spring, summer and winter. The summer (bottom left) and winter (bottom right) photos illustrate the potential difficulty of locating and identifying these ecosystems outside of the spring flooded condition (top). Photos are by Dwight Streblow, USDA Forest Service.

two study areas do not include the total areas of the subsections and LTAs we describe (Table 1). However, they do largely include the entire mapping units for the array of LTs occurring within the larger scale ecological units.

In the classification, different classes of a broader-scale ecological unit overlap in the array of finer-scale ecological units they contain. For instance, in our study area, the outwash plain and end moraine LTAs (Table 1) both contain LT 1 (jack and red pine on sandy soil).

TABLE 1. Hierarchical structure of ecological units for two study areas in northern Minnesota, USA.

Study area	Subsection† (10^3–10^6 ha)	Land-type association, LTA (10^2–10^4 ha)	Land type, LT‡ (10–10^2 ha)
Sucker Lakes	Chippewa Plains	outwash plain (Bemidji Sand Plain)	LT 1
			LT 2
			LT 3
		ground moraine (Guthrie Till Plain)	LT 2
			LT 3
			LT 4
			LT 5
Rice River	St. Louis Moraines	end moraine (Marcell Moraine)	LT 1
			LT 2
			LT 4
			LT 5
		glacial lake plain (Agassiz Lake Plain)	LT 2

† Subsections differ primarily in thickness of glacial drift, which ranges from 65 to 200 m in the Chippewa Plains subsection and from 32 to 65 m in the St. Louis Moraines subsection.

‡ Landtype definitions are as follows: LT 1 = jack and red pine forests on excessively drained sandy soils: LT 2 = mixed pine and hardwood forests on well-drained to moderately well-drained, loamy till and fine-textured soils; LT 3 = boreal hardwood–conifer forests on moderately well-drained to somewhat poorly drained loamy to fine-textured soils; LT 4 = northern hardwood forests on well-drained to moderately well-drained loamy to fine-textured soil; LT 5 = northern hardwood–conifer forests on moderately well-drained to somewhat poorly drained loamy to fine-textured soils.

However, it is the unique combination of characteristics across spatial scales that determine the characteristics of an ecological unit at the smallest spatial scale. As such, LT 1 in outwash and on the end moraine may differ in important ecological characteristics, for example in seasonal wetland density. Our analytical approach (see *Statistical analysis* and *Results*, below) reflects this hierarchical structure.

Seasonal wetland detection and definition

We used 1:15 840 color infrared air photography to identify seasonal wetlands in the study areas. The photography was done in the spring of 1994 after snowmelt, but before leaf flush. In these photos, water bodies are black and an experienced interpreter can easily identify small wetlands. We identified 2064 small wetlands in 24 622 ha of upland forest in the combined study areas (0.08 wetlands/ha). We field-checked 10% of the wetlands, selecting samples for verification from across the two study areas. From this sampling we estimated our error of commission (classifying something as a wetland when it was not one) at 20%. Misidentified wetlands were largely anthropogenic openings, such as old log landings or trail intersections, where shallow water pooled on compacted soil in the spring. Through the course of searching for sample wetlands during the field check, we encountered very few additional small wetlands not identified on air photography. We estimate our error of omission at <10%.

The wetlands we identified from air photography largely conform to the definition of ''seasonal wetland'' sensu Cowardin et al. (1979), namely, palustrine, forested, shrub–scrub, or emergent wetlands having a semipermanent or seasonally flooded water regime and a mineral soil substrate. Under this definition, the water regime does not necessarily include a dry period, but water levels are seasonally fluctuating. Based on measurements from a sample of wetlands in our study area, hydroperiods ranged from 10 to 365 d (Palik et al. 2001; B. Palik, *unpublished data*) and wetland size ranged from 0.01 to 0.25 ha. Wetlands types were distributed approximately equally among forested, shrub–scrub, and emergent plant communities. Dominant vegetation included black ash (*Fraxinus nigra* Marshall) in forested wetlands, speckled alder (*Alnus rugosa* (Duroi) Sprengel) in shrub–scrub wetlands, and various sedges (*Carex* spp.) in emergent wetlands.

GIS analysis

We used ArcView 3.2 (ESRI, Redlands, California, USA) to estimate the density of seasonal wetlands in simulated 16-ha plots randomly placed within ecological units of our study areas. We chose 16 ha because it falls at the mid-range of timber-sale sizes in Minnesota (Puettmann et al. 1998). Thus, wetland densities in these virtual plots approximate actual numbers encountered by natural-resource managers when establishing timber sales on the ground.

Our procedure for plot establishment was as follows. First, we generated random points within each LT polygon in the two study areas using *Random Points in Polygon,* a script developed and submitted by Mark Cedeholm to the Environmental Systems Research Institute (ESRI) Internet home page.[2] The number of random points varied in relation to the area of each LT, ranging from 25 to 465 for a total of 1477 points. We excluded LT 3 on the outwash plain LTA (Table 1) from analysis because its cumulative area was too small to include at least 25 16-ha plots. To minimize edge effects, we constrained points to be at least 300 m from LT and study area boundaries, and at least 200 m from the nearest point to reduce overlap in sample plots. Next, we used *Square Buffer Wizard* (script developed by Robert J. Scheitlin) to create square 16-ha (400 × 400 m) plots centered on each random point. We joined the 16-ha plot layers for the two study areas with the digitized seasonal-wetland layers. We then summed the number of wetlands occurring within each 16-ha plot using *Count Points in Polygon* (script developed by Yingming Zhou). Our procedure sampled wetlands with replacement. In other words, plots could overlap partially (a maximum of 50% shared area), so a wetland counted in one plot might also be counted in a second, partially overlapping plot.

Statistical analysis

We used two analyses to assess relationships between seasonal-wetland abundance and characteristics of multi-scale ecological units. First, we compared cumulative frequency distributions of 16-ha plots, having different wetland densities, between and among types of an ecological unit at each spatial scale (i.e., subsection, LTA, LT). For these analyses, we used replicated goodness-of-fit tests (G statistic) (Sokal and Rohlf 1981) to test the hypothesis that all types of ecological unit within a spatial scale (subsection, LTA, LT) had similar cumulative frequency distributions. We first computed G_H (G for heterogeneity) for each hierarchical level to determine if the distributions were significantly different. If G_H was significant (using alpha $\leq$ 0.05), we then used a simultaneous test procedure to compare cumulative frequency distributions for subsets of ecological types within that hierarchical level. We excluded LT 2 in the glacial lake plain LTA (Table 1) from the LT-scale analysis, since it was the sole LT in this landform.

Second, we used regression-tree analysis (De'ath and Fabricius 2000) to relate variation in wetland abundance to ecological-unit identity at each spatial scale. We used number of wetlands in a 16-ha plot as the response variable and ecological-unit identity at the subsection, LTA, and LT scales (Table 1) as categorical explanatory variables. We calculated impurity of nodes (a measure of homogeneity of selected groups) in the
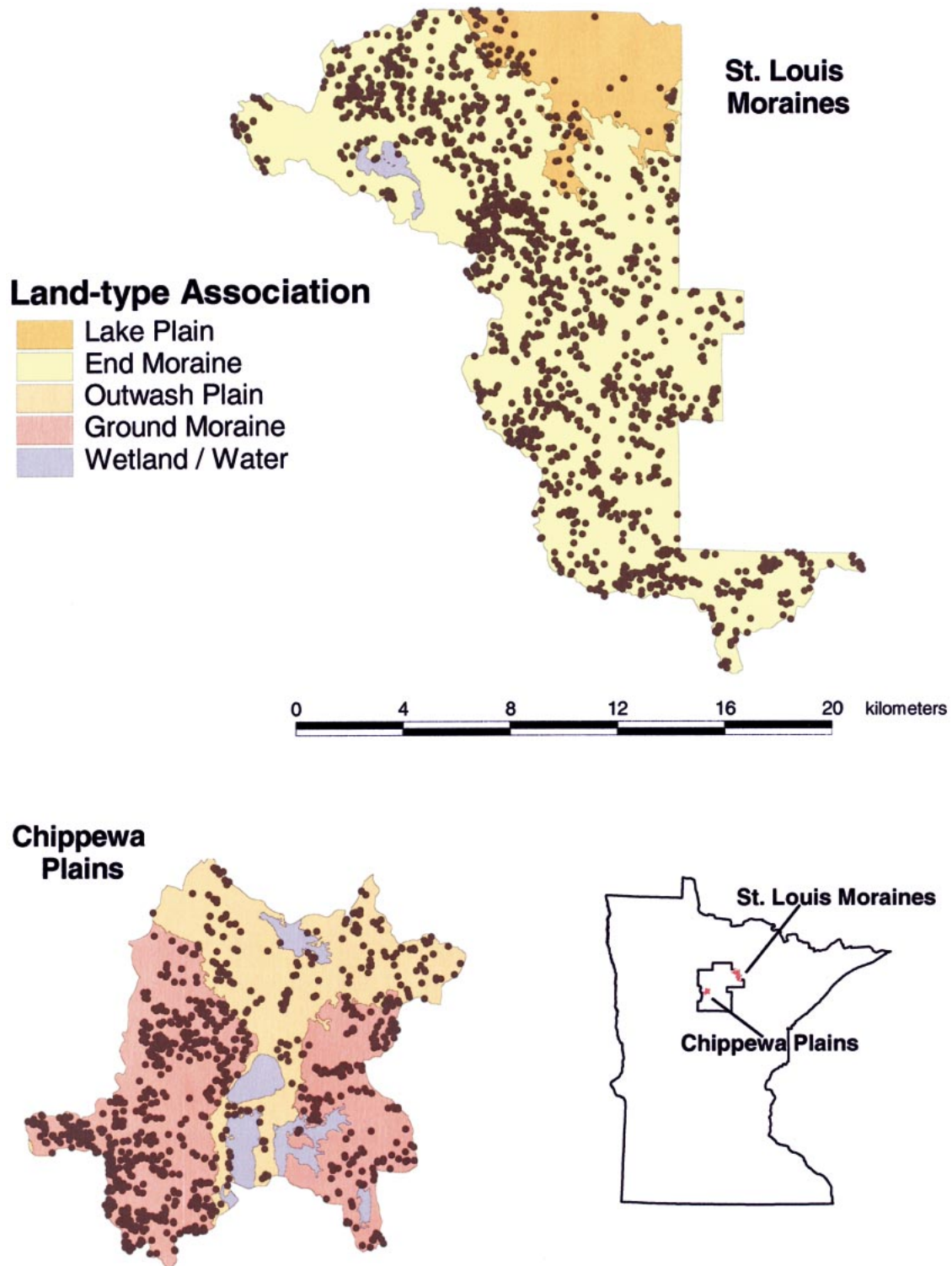
Fig. 2. Seasonal forest wetland distributions in portions of two ecological subsections (St. Louis Moraines, Chippewa Plains) in northern Minnesota, USA, stratified by ecological land-type association (LTA). Each black dot is a seasonal wetland. The map inset shows the location of the Chippewa National Forest in Minnesota and locations of the two study landscapes within the national forest.
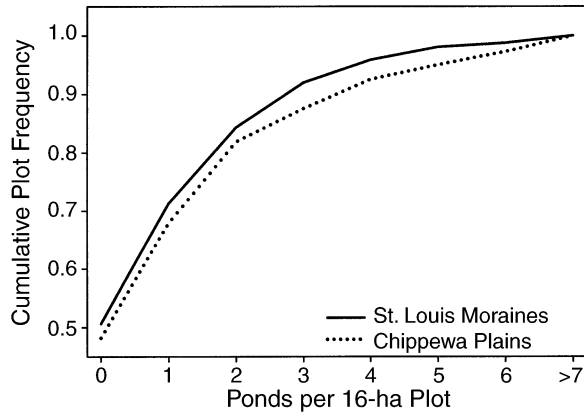
FIG. 3. Cumulative (plot by wetland density) frequency distributions for two ecological subsections in northern Minnesota, USA. Sample sizes (number of 16-ha plots) are 443 and 1035 plots for Chippewa Plains and St. Louis Moraines subsections, respectively.

regression tree using the sums of squares about the group means, with a minimum stopping value of 0.01 for determining a split. We selected optimal tree size through cross validation (De'ath and Fabricius 2000). For this procedure we split the data randomly in half (735 plots and 736 plots) and using one half, grew the tree to an overly large size by maximizing the number of possible leaves. We then pruned the tree through additional analyses that decreased the maximum leaf number progressively until we reached the root tree (one leaf). For each tree we then predicted the response of the second half of the data and calculated the estimated error as the sum of squared differences of the observations and predictions. The optimal tree size is selected by minimizing cross-validation error. Wetland densities were square-root transformed before analysis, with the resultant means and standard deviations back transformed for graphing. We assessed the statistical significance of the selected tree using a Monte Carlo permutation procedure (Rejwan 1999) in which the amount of variance explained by the selected tree (created using the complete data set) is compared with variance explained by trees (pruned to the same size as the selected tree) generated from 100 random associations between wetland density and ecological-unit identity. We considered the selected tree statistically significant if it explained more variation than at least 95% of the randomly generated trees.

RESULTS

Subsection comparison

Wetlands were distributed widely across the two study areas at the scale of ecological subsections (Fig. 2). Overall wetland densities were similar between the two ecological subsections and did not differ from the pooled mean density for the combined study areas (0.08 wetlands/ha). The cumulative (plot by wetland density)

frequency distributions (Fig. 3) did not differ significantly between subsections ($G_H = 13.17$, df = 7, $P \sim 0.07$). For both, about 50% of the 16-ha plots did not contain a wetland, another 35–40% of the plots contained 1–3 wetlands, while the remaining 10–15% of plots contained four or more wetlands (Fig. 3).

Land-type association comparison

The distribution of wetlands differed markedly among land-type associations (LTAs) (Fig. 2). Wetland densities ranged from 0.03 wetland/ha in the lake plain LTA, to 0.05 wetland/ha in the outwash LTA, to 0.10 wetland/ha in both the ground and end moraines LTAs. The cumulative (plot by wetland density) frequency distributions (Fig. 4) differed significantly among the four LTAs ($G_H = 248.4$, df = 21, $P < 0.001$). The six pair-wise comparisons of plot distributions between LTAs were all significant ($P < 0.05$ to $P < 0.001$), indicating that all frequency distributions differed from each other. Ninety percent of the lake plain LTA plots did not contain a wetland, compared to 63% for the outwash plain LTA, 42% for the end moraine LTA, and 38% for the ground moraine LTA (Fig. 4). The remaining 10% of lake plain LTA plots contained 1–3 wetlands, compared to 32% of plots in the outwash plain LTA, 48% on the end moraine LTA, and 43% on the ground moraine LTA (Fig. 4). The remaining 5%, 10%, and 19% of plots on the outwash, end moraine, and ground moraine LTAs, respectively, contained ≥ 4 wetlands.

Land-type comparison

Wetland distribution varied somewhat at the land-type (LT) scale (Fig. 5). Wetland densities ranged from 0.03 wetland/ha to 0.13 wetland/ha among the 12 LTs. (For land-type definitions see footnotes to Table 1.) At
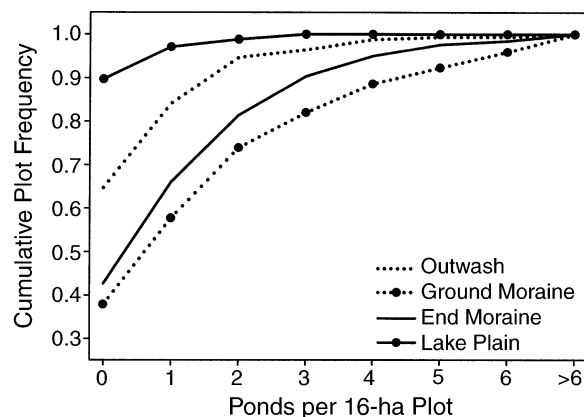

FIG. 4. Cumulative (plot by wetland density) frequency distributions for four ecological land-type associations (LTA) in northern Minnesota, USA. Samples sizes (number of 16-ha plots) are 171, 272, 860, and 175 plots for the outwash plain, ground moraine, end moraine, and lake plain LTAs, respectively.
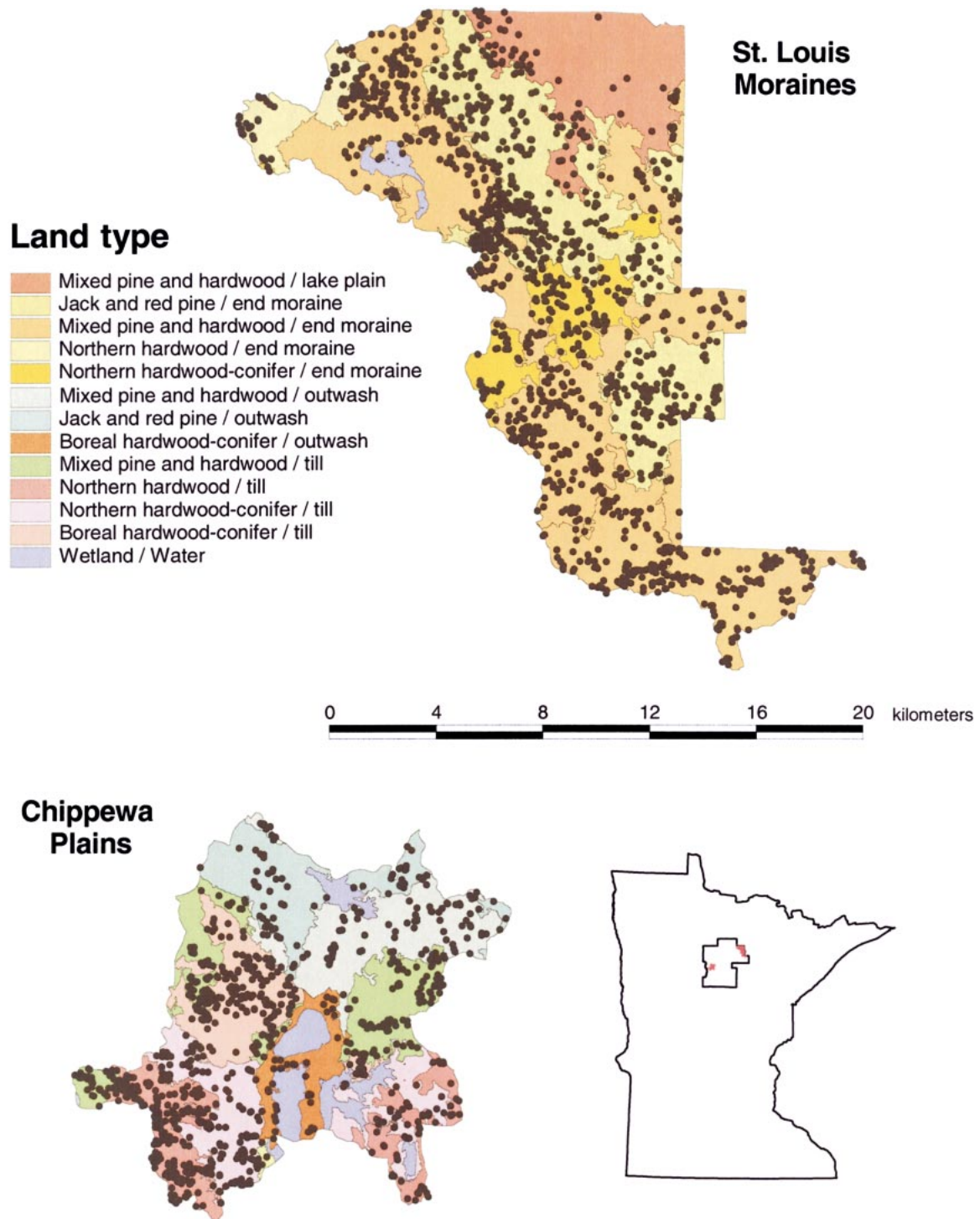
Land type

- Mixed pine and hardwood / lake plain
- Jack and red pine / end moraine
- Mixed pine and hardwood / end moraine
- Northern hardwood / end moraine
- Northern hardwood-conifer / end moraine
- Mixed pine and hardwood / outwash
- Jack and red pine / outwash
- Boreal hardwood-conifer / outwash
- Mixed pine and hardwood / till
- Northern hardwood / till
- Northern hardwood-conifer / till
- Boreal hardwood-conifer / till
- Wetland / Water

FIG. 5. Seasonal forest wetland distributions in two ecological subsections (St. Louis Moraines, Chippewa Plains) in northern Minnesota, USA, stratified by ecological land-type (LT). Each black dot is a seasonal wetland. The map inset shows the location of the Chippewa National Forest in Minnesota and locations of the two study landscapes within the national forest.
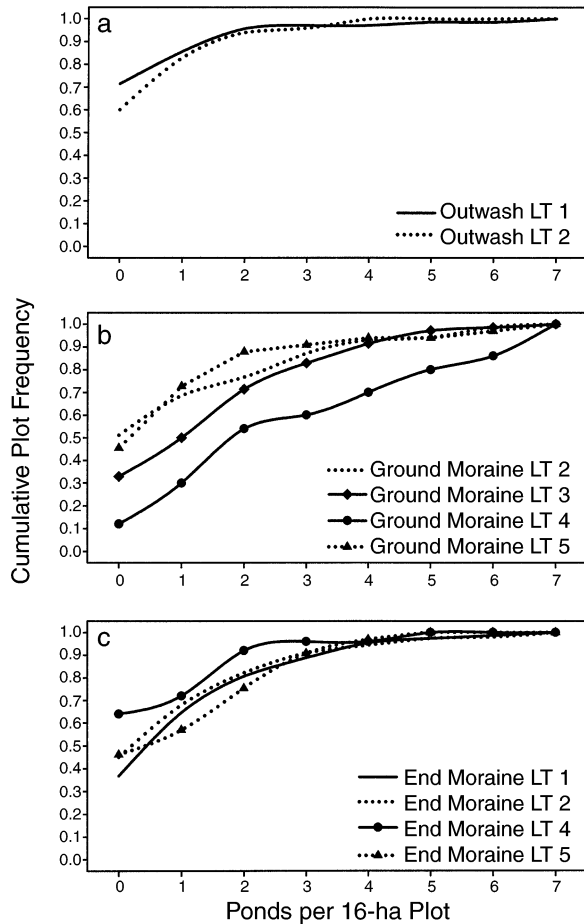
FIG. 6. Cumulative (plot by wetland density) frequency distributions for 10 ecological land types (LT) in northern Minnesota, USA. (For land-type definitions see footnotes to Table 1.) Sample sizes (number of 16-ha plots) are as follows: (a) For outwash plain: LT 1, $n = 70$ plots; LT 2, $n = 100$ plots. (b) For ground moraine: LT 2, $n = 86$ plots; LT 3, $n = 70$ plots; LT 4, $n = 50$ plots; LT 5, $n = 66$ plots. (c) For end moraine: LT 1, $n = 305$ plots; LT 2, $n = 465$ plots; LT 4, $n = 25$ plots; LT 5, $n = 175$ plots.

this scale, we compared cumulative (plot by wetland density) frequency distributions separately within each LTA, because we already knew that many LTs would differ among LTAs, based on a significant G_H at the LTA scale. Within the outwash plain LTA, wetland density was 0.03 wetland/ha for LT 1 and 0.06 wetland/ha for LT 2. Frequency distributions did not differ significantly between the two LTs ($G_H = 15.41$, df = 70, $P > 0.995$). In both, ~65% of the 16-ha plots contained no wetlands, another 27% contained one or two wetlands, while the remaining 8% of plots contained >2 wetlands (Fig. 6a).

On the ground moraine LTA, wetland density was 0.09 wetland/ha in LT 2, 0.11 wetland/ha in LT 3, 0.13 wetland/ha in LT 4, and 0.08 wetland/ha in LT 5. Cumulative (plot by wetland density) frequency distri-

butions for the four LTs differed significantly ($G_H = 92.25$, df = 70, $P < 0.05$). Inspection of the distributions indicated that LT 4 was noticeably different from the remaining LTs (Fig. 6b). We recalculated G_H again while excluding LT 4 and found that the remaining LTs (2, 3, and 5) did not differ significantly ($G_H = 45.60$, df = 70, $P > 0.995$). About 32–45% of the 16-ha plots in LT 2, 3, and 5 did not contain a wetland, 45–48% contained 1–3 wetlands, while the remaining 10–20% of plots contained >3 wetlands. In contrast, only 11% of LT 4 plots did not contain a wetland. Another 49% of plots contained 1–3 wetlands and the remaining 40% of plots contained ≥4 wetlands.

Wetland density among LTs on the end moraine LTA ranged from 0.10 wetland/ha for LT 1 and LT 2, to 0.05 wetland/ha for LT 4, and to 0.12 wetland/ha for LT 5. The plot by wetland density cumulative frequency distributions did not differ significantly among the four LTs ($G_H = 63.29$, df = 70, $P > 0.995$). Approximately 38–64% of plots did not contain a wetland, another 31–47% contained 1–3 wetlands, and the remaining 5–15% of plots contained ≥4 wetlands (Fig. 6c).

Regression tree

The regression tree selected through cross validation (Fig. 7) had five terminal nodes (or leaves), explained 11.6% of the total sum of squared error, and was highly significant ($P < 0.001$; Monte Carlo procedure). Wetland density per 16-ha plot in the root node was 0.54 ± 0.67 (mean ± 1 SD) wetland/16ha (back transformed from square-root transformed data). The first split explained 7.6% of the total error and was based on LTA, with the outwash and lake plain LTAs in the left branch (0.11 ± 0.37 wetland/16 ha) and the moraine LTAs in the right branch (0.74 ± 0.70 wetland/16 ha). The left branch divided a second time, again based on LTA, with the lake plain LTA forming a leaf on the left (0.02 ± 0.15 wetland/16 ha) and the outwash plain LTA forming a leaf on the right (0.27 ± 0.52 wetland/16 ha). This split explained 1.2% of the total error. The right branch of the tree (containing the moraines) split again based on LT, with LT 1, 2, 3, and 5 forming a leaf on the left (0.69 ± 0.67 wetland/16 ha) and LT 4 forming a node on the right (1.61 ± 0.86 wetland/16 ha). This split explained 1.4% of the total sum of squared error. The LT 4 node split once more based on LTA, with the end moraine LTA forming a leaf on the left (0.47 ± 0.66 wetland/16 ha) and the ground moraine LTA forming a leaf on the right (2.47 ± 0.72 wetland/16 ha). This split explained 1.4% of the total sum of squared error. The last two splits indicate that the ground moraine and end moraine LTAs differed in wetland density largely because wetland densities in LT 4 on the ground moraine LTA were substantially higher than densities for the other LTs in that landform.

DISCUSSION

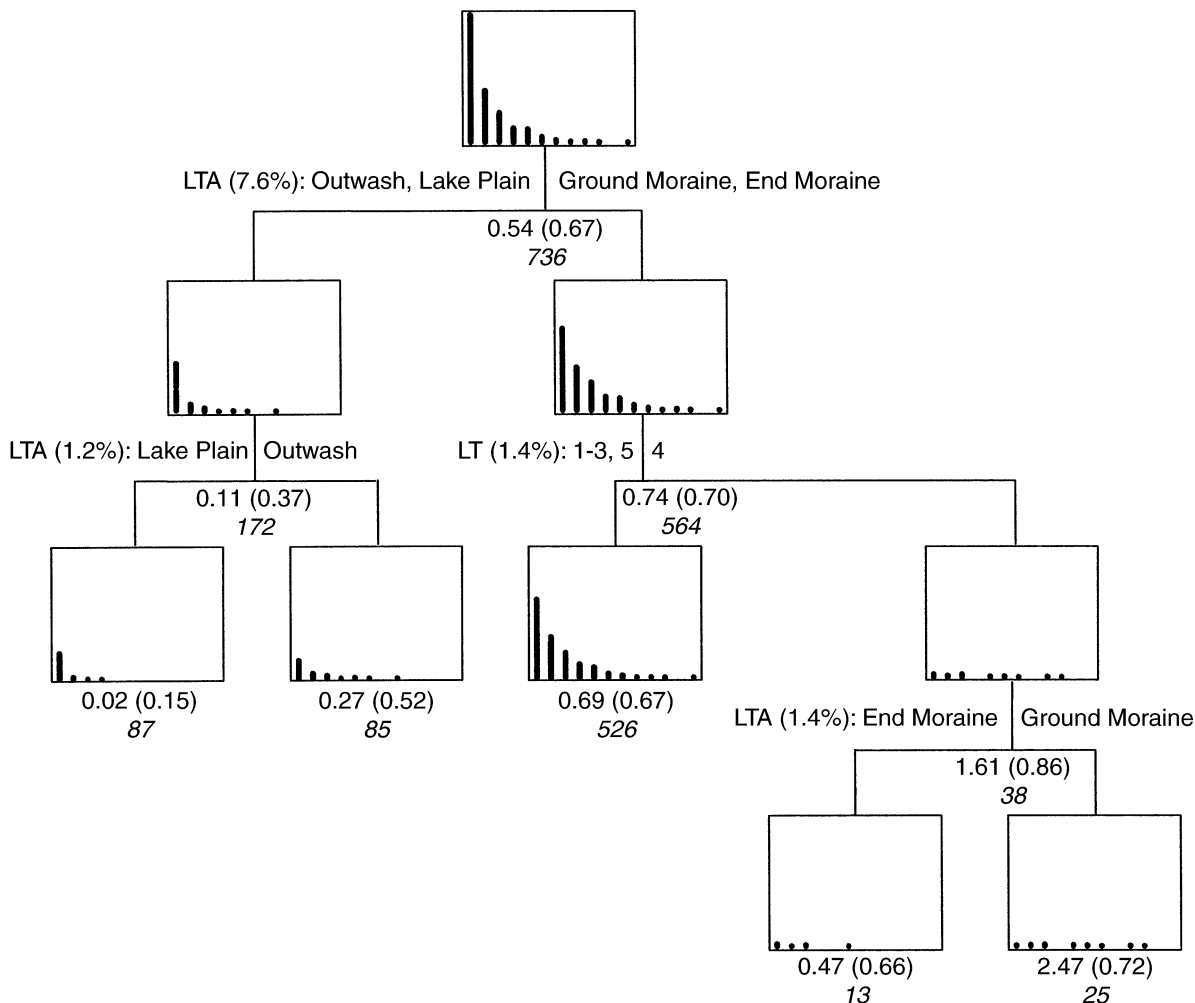Our premise is that the development of small, nested ecosystems is constrained by characteristics of the sur-

FIG. 7. Regression-tree analysis of the abundance of seasonal forest wetlands in 16-ha plots in northern Minnesota, USA. Explanatory variables included ecological subsection, ecological land-type association (LTA), and ecological land type (LT) (see Table 1). Each split (nonterminal node) is labeled with the variable that determines the split and the percentage of the total sum of squared error explained by the split (in parentheses). For each of the nonterminal nodes and the leaves (terminal nodes), the distribution of the observed values of wetland abundance per 16-ha plot, ranging from 0 to 12, is shown in a histogram. Finally, each node is labeled with the mean, 1 SD (in parentheses), and number of observations in the group (in italics). See *Results: Regression tree* for detailed explanation of tree results.

rounding landscape matrix, and thus predictable in their abundance based on knowledge of constraining ecosystem identity. This prediction follows from a key tenet of hierarchy theory, namely, that asymmetric relationships occur between levels of a hierarchical system, such that upper hierarchical levels constrain the development of lower levels (Allen and Starr 1982, O'Neill et al. 1986).

Specifically, we addressed two questions related to the occurrence of seasonal wetlands, as a model type of nested ecosystem: (1) Can we predict wetland abundance in upland forest stands from knowledge of terrestrial ecological units, as defined by hierarchical combinations of regional physiography, glacial landform, soils, and forest cover? and (2) What spatial scale

of terrestrial ecological unit is the best predictor of wetland abundance? In fact, seasonal wetland abundance did differ among terrestrial ecological units, particularly at the scale of land-type association (LTA) or glacial landform. Sixteen-hectare plots on a ground moraine LTA were 6 times more likely to contain at least one seasonal wetland than were plots on a glacial lake plain LTA (63% vs. 10%). The probability of at least one wetland occurring in a 16-ha plot on outwash plain and end moraine LTAs was 38% and 58%, respectively. In general, broader and finer spatial-scale ecological units (ecological subsections and land types, respectively) were poor discriminators of wetland abundance. The exception to this was LT (land type) 4 on the ground moraine LTA (a northern hardwood forest type

on well-drained loamy soil), which had a higher probability of at least one wetland occurring in a plot (89%) than other LTs on this landform (50% to 68%). Landtype 4 had low probability of wetland occurrence on the end moraine LTA (36%), so high wetland abundance in the northern hardwood forest type may be unique to ground moraines.

Compared to wetland occurrence (presence/absence), identity and scale of ecological unit were poor predictors of actual wetland densities (number of wetlands per 16-ha plots). The regression tree demonstrates this; although statistically significant, it explained only 11.6% of the total sum of squared error in wetland density among plots. Poor prediction of wetland density reflects high variability in wetland numbers among the plots that actually contained wetlands (Fig. 7). The regression tree, however, was informative because it confirmed our conclusions based on comparisons of cumulative frequency distributions, namely, that glacial landform (LTA) is an important predictor of wetland occurrence in upland forest stands of the study landscape, accounting for 88% of explained variation (see Fig. 7; the 1st, 2nd (left), and 3rd branches of the tree are all based on LTA).

The relationship we demonstrate between glacial landforms and seasonal wetland abundance is suggestive of Class 4 landform effects (Swanson et al. 1988), whereby landform constrains the frequency of geomorphic processes that alter biotic features and processes of ecosystems. In our case, the geomorphic process constrained by glacial landform is variation in the frequency of small ice blocks stranded with glacial retreat (Wright 1972). After melting, these ice blocks formed trapped depressions that persist in the present as kettles occupied by wetlands and lakes (Hamblin 1989).

Our results are important for several reasons. We demonstrate, for the first time, the significant degree of spatial variation that occurs in seasonal-wetland densities across a forest landscape and how characteristics of the constraining landscape matrix explain some of this variation. We identify LTA, or glacial landform, as the hierarchical scale having the greatest discriminating power for predicting wetland occurrence and abundance. More broadly, we demonstrate the utility of our analytical approach, based on predictions stemming from hierarchy theory, for relating small-ecosystem occurrence to larger-scale constraining influences in a landscape. Finally, our research is unique in that we use hierarchy theory to develop a model to predict seasonal-wetland occurrence, as opposed to its more traditional use as metatheory to guide research approaches, e.g., the development of a nested, hierarchical ecosystem classification.

Application to seasonal-wetland management

Forest managers often overlook small seasonal wetlands during inventories and timber-sale layout. Thus,

they are subject to potentially degrading impacts from harvest operations, particularly when covered with snow during winter, or when dry during summer. To the untrained eye, a wetland in these conditions may be indistinguishable from the surrounding upland forest. Impacts can be direct, through tree removal, equipment trafficking, and slash piling within the wetland. They also can be indirect, through changes in ecological inputs (organic matter, shade, sediment) from the surrounding upland forest (Batzer et al. 2000, Palik et al. 2001). The latter impact makes awareness of wetland abundance and proximity important, even if harvest does not occur in the wetland itself.

Inventorying all wetlands from air photography over large areas often is impractical, particularly when they are abundant, as in our example. However, natural-resource managers could use our approach to estimate the likelihood of wetland occurrence and put bounds on the number of wetlands to expect in a particular area. Our approach does not discount the need for increased awareness of seasonal wetlands during on-the-ground management activities. However, by using our approach, wetland abundance can be anticipated and efforts prioritized to avert potentially negative impacts from management operations. Fortunately, most large forest-management organizations already possess the spatial-data layers needed to develop the tool we present, including hierarchical land classifications and air photography. Models to predict seasonal-wetland abundance, or indeed other types of small, but distinct ecosystems, could be developed by combining a land classification with stratified sampling of the system from air photography or limited ground surveys.

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