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USING LANDSCAPE HIERARCHIES TO GUIDE RESTORATION OF DISTURBED ECOSYSTEMS

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Abstract. Reestablishing native plant communities is an important focus of ecosystem restoration. In complex landscapes containing a diversity of ecosystem types, restoration requires a set of reference vegetation conditions for the ecosystems of concern, and a predictive model to relate plant community composition to physical variables. Restoration also requires an approach for prioritizing efforts, to facilitate allocation of limited institutional resources. Hierarchy theory provides a conceptual approach for predicting plant communities of disturbed ecosystems and, ultimately, for prioritizing restoration efforts. We demonstrate this approach using a landscape in southwestern Georgia, USA. Specifically, we used an existing hierarchical ecosystem classification, based on geomorphology, soil, and vegetation, to identify reference plant communities for each type of ecosystem in the landscape.

We demonstrate that ecosystem identity is highly predictable using only geomorphic and soil variables, because these upper hierarchical levels control the development of vegetation, a lower hierarchical level. We mapped the potential distribution of reference ecosystems in the landscape and used GIS (geographic information systems) to determine relative abundance of each ecosystem, as a measure of its historical rarity. We joined the reference ecosystem map with a current cover map to determine current abundance of each reference ecosystem, and percentage conversion to different disturbance classes. We show that over half of the landscape supports something other than reference plant communities, but degree of rarity varies widely among ecosystems. Finally, we present an index that integrates information on historical and current rarity of ecosystems, and disturbance levels of individual polygons, to prioritize restoration efforts. The premise of the index is that highest priority be given to restoring (1) currently rare ecosystems that were also historically rare and (2) the least disturbed examples of these ecosystems, as these will require the least effort to restore. We found that 80% of high-priority sites occur within just three (of 21) ecosystems. Moreover, the high-priority ecosystems all occur within stream valleys. Our approach provides managers with a straightforward methodology for determining potential distribution of reference ecosystems and for allocating efforts and resources for restoration in complex landscapes. Development of a priority index for a specific landscape requires an understanding of the hierarchical relationships among geomorphology, soil characteristics, and plant communities, in addition to well-defined restoration objectives.

Key words: Coastal Plain (Georgia, USA); ecosystem classification; ecosystem development, geomorphology vs. vegetation; ecosystem identity, predicting; ecosystem restoration and resource allocation; geographic information systems (GIS); hierarchy theory; landscape hierarchies; restoration of ecosystems, prioritizing.

INTRODUCTION

Identifying reference vegetation conditions for ecosystem restoration is an important, but contentious, issue (Simberloff 1990, Pickett and Parker 1994, Aronson et al. 1995, Fulé et al. 1997). Successional pathways and plant community composition can be highly variable even within a particular type of ecosystem. This suggests that it is problematic to identify vegetation targets for restoration based solely on specific comparisons to historical plant communities (Sprugel 1991, Wyant et al. 1995). We use the term "historical" in a sense similar to Morgan et al. (1994), to describe potential plant communities "over a time frame relevant to understanding" changes in contemporary plant communities due to past management.

Still, the need for a reference target to use as a metric for assessing restoration is obvious (Aronson et al. 1995). Pickett and Parker (1994) suggest a conceptual approach for dealing with the dynamic reference states of plant communities during restoration. Their idea of

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contingency recognizes that site history (e.g., natural and human disturbances), along with the site itself, influence plant community development. Other contingencies include peculiarities of dispersal events and the nature of the system's interaction with the surrounding landscape. For a manager interested in restoring plant communities to disturbed ecosystems, contingency means that a range of potential reference states exists for any particular type of ecosystem. Further, the choice of a reference condition may be appropriate even if the resultant plant community differs over time from other restored sites for the same type of ecosystem.

Ultimately, the restorationist requires a tool for identifying at least one of the potential plant communities, or reference conditions, of disturbed ecosystems. To be useful the tool must discern when reference vegetation conditions should differ because of inherent differences in physical site characteristics, rather than contingent ecosystem development. This need is particularly important in complex landscapes, where variation in physiography and soil characteristics result in a diverse array of plant communities within small spatial scales (e.g., 10–1000 ha). Each of these communities has a unique array of potential successional pathways leading to mature vegetation states. Each of these states, in turn, may serve as reference vegetation targets in a restoration effort.

Restoration also requires prioritization of efforts. Prioritization depends as much on economic issues as ecological concerns (Wyant et al. 1995). An organization may prioritize restoration efforts based on current and historical abundance of an ecosystem, giving highest priority, for example, to restoring historically abundant ecosystems that are currently rare. The effort (cost) to restore a particular site is another factor in prioritization; effort depends on degree of similarity to a reference condition. Highly disturbed sites require greater effort to restore than minimally disturbed sites (following the idea of thresholds of irreversibility; Aronson et al. 1993). Effective prioritization of restoration efforts requires information that integrates conservation status of ecosystems with effort to restore individual examples of these ecosystems.

Hierarchy theory (Allen and Starr 1982, O'Neill et al. 1986) provides a conceptual framework for identifying potential reference plant communities of disturbed ecosystems and for prioritizing restoration efforts. As applied to landscapes, hierarchy theory predicts that geomorphology and soil characteristics constrain the development of plant communities at the scale of stands (Rowe and Sheard 1981, Host and Pregitzer 1992). Used in this way, hierarchy theory is an effective way of understanding interrelationships among plant communities and multiscale environmental constraints. Indeed, viewing landscapes as hierarchical systems is the basis for multifactor ecosystem classifications (e.g., Barnes et al. 1982, Spies and Barnes 1985*a*, Grossman et al. 1998). Such classifications usually define ecosystems from a geomorphic perspective, as hierarchically structured volumes of earth, air, and water, having particular developmental histories within which organisms live and interact with each other (Rowe and Barnes 1994, Barnes et al. 1998).

Typically, hierarchical classifications describe vegetation communities of minimally disturbed ecosystems (Pregitzer and Barnes 1984, Hix and Pearcy 1997). We are not aware of their use for predicting plant communities of highly altered ecosystems, yet they are appropriate for this purpose. This is because anthropogenic factors that alter vegetation have less influence on geomorphology and soil, the physical factors that constrain vegetation development.

We demonstrate the use of landscape hierarchies for predicting potential plant communities of disturbed ecosystems using an 11 400-ha landscape in southwestern Georgia, USA. Specifically, we show how to combine an existing hierarchical classification of reference ecosystems with spatial-data layers on geomorphology, soil characteristics, and land use to derive reference ecosystem distributions and to predict potential plant communities of disturbed sites. Second, we present an approach for prioritizing restoration efforts in a landscape using information on conservation status of reference ecosystems and the effort required to restore individual examples of these ecosystems.

Methods

Study area

We applied our approach at Ichauway, an 11 400-ha reserve of the Jones Ecological Research Center in southwestern Georgia, USA. The Ichauway landscape includes large areas of mature second-growth longleaf pine (*Pinus palustris* Mill.), along with wetland and stream-valley ecosystems, all with no history of agriculture. These include some of the regions best examples of native ecosystems. However, they all have altered fire regimes, including near-annual dormant-season burning of longleaf pine (Wright and Bailey 1982), instead of the historical regime of growing-season fires every 2–10 yr (Ware et al. 1993). Additionally, plowed breaks prevent the spread of fires (natural and human-caused) from the longleaf pine uplands into wetlands and stream-valley ecosystems. Historically, these ecosystems likely burned infrequently (Marks and Harcombe 1981, Ware et al. 1993), particularly during drought. The Ichauway landscape also contains substantial land area supporting greatly altered plant communities, including active agricultural fields, old-fields in various stages of succession, and forest plantations.

An assumption of our approach for identifying targets for restoration is that minimally disturbed ecosystems are the basis for the reference classification. However, plant communities of these ecosystems may not be wholly representative of pre-European-settlement conditions. Rather, they represent the best examples available regionally. At Ichauway, these plant communities will likely change if managed fire regimes better mimic natural fire regimes and, perhaps, as the communities develop old-growth characteristics.

Reference-ecosystem classification

In prior work, we developed a hierarchical classification of Ichauway reference ecosystems (P. C. Goebel, B. J. Palik, L. K. Kirkman, and L. West, *unpublished report* to Jones Ecological Research Center [Newton, Georgia, USA]). The classification includes 21 hierarchically structured ecosystems (Table 1). The first level of the hierarchy differentiates major physiographic zones (fluvial vs. upland). The next level separates ecosystems by landform (10's–100's ha), while the third level differentiates based on terrain shape (e.g., undulating). The fourth level separates ecosystems by several soil characteristics that reflect moisture regime. The final two levels identify ecosystems based on overstory and ground-flora plant communities. For the current study, we used data collected for the classification to demonstrate our approach to identifying reference conditions for disturbed sites and for prioritizing restoration efforts.

Ecosystem predictability

The basis for our restoration approach is that a potential plant community for a disturbed ecosystem is identifiable using only physiographic and soil variables. We assessed this predictability using linear discriminant analysis (LDA). We used LDA to quantify misclassification probabilities that result from assignment of a known ecosystem to the classification, using only physical variables. This analysis excludes ecosystems 1 and 3 (Table 1), from which we did not collect detailed soil data.

There are few formal statistical assumptions for LDA when used to address classification questions (James and McCulloch 1990, Kent and Coker 1992). However, because of small sample sizes within groups (ecosystems), we used a nonparametric version of LDA based on nearest-neighbor distances. We selected the nearest-neighbor group size, k, by minimizing the overall estimate of misclassification error (SAS Institute 1990). We derived prior probabilities for the LDAs using the percentage of land area for each ecosystem in the current landscape (see *GIS analyses* . . . , below). We assessed misclassification rates using cross-validation (Kent and Coker 1992). In a nearest-neighbor, nonparametric LDA, cross-validation excludes the classified observation from the k nearest neighbors of that observation (SAS Institute 1990).

We ran the LDAs separately for fluvial (EC 1–8, 15), upland (EC 9–14, 16, 17), and wetland (EC 18–21) ecosystems. The original soil and landform data sets collected for the classification contained 18 variables each for fluvial and upland ecosystems, and 21 variables for wetland ecosystems (P. C. Goebel, B. J. Palik, L. K. Kirkman, and L. West, *unpublished report* to Jones Ecological Research Center). We reduced the number of physical variables used in the LDAs by including: (1) only those variables having factor loadings >0.8 in principal-component analyses (PCA results not shown) and (2) only uncorrelated physical variables ($r < 0.8$). For pairs of correlated variables, we retained only the variable with the highest loading in the PCA. Because of its importance in distinguishing several ecosystems, we included landform as a variable in all LDAs, even if it did not have a high factor loading in the corresponding PCA. The resulting three subsets of physical variables used in the LDAs are listed in Table 2. The majority of these are standard descriptors of soil morphology and physiography. We derived two variables from texture and color, namely available water content (AWC) and color-development equivalent (CDE). AWC is an estimate of centimeters of water per centimeter of soil, based on known water-holding capacities of different soil textures. CDE is a measure of hue–chroma interaction on soil color development and indicates drainage conditions (Buntley and Westin 1965). Low CDE values (<10) indicate gray, poorly drained soils; intermediate values (11–20) indicate yellow, moderately well-drained soils; high values (>20) indicate red, well-drained soils. Details of AWC and CDE determination are available on request (P. C. Goebel, B. J. Palik, L. K. Kirkman, and L. West, *unpublished report* to Jones Ecological Research Center). Before analysis, we transformed percentage data with an arcsine transformation. Additionally, we transformed the categorical variables of landform and terrain shape to a semi-continuous scale by ranking them according to relative differences in moisture-retaining potential.

Ecosystem mapping

Using the ecosystem classification, we mapped potential ecosystem across the entire study area. This map served as a baseline against which to compare changes in plant communities, within each ecosystem, due to human disturbance. The mapping procedure was as follows:

1) We delineated major physiographic zones and landforms on 1:12 500 aerial photos.

2) Using a digital elevation model, we determined terrain-shape categories (e.g., nearly level, undulating, slope) within each landform.

3) We inventoried soils in the field within each physiographic unit–landform combination primarily using the subset of variables from the LDAs (Table 2). To expedite mapping, we assessed soil textures in the field, rather than with laboratory determinations. Further, we determined soil drainage class and horizon colors in the field. These serve as surrogate measures for AWC and CDE (continuous variables used in LDA).

4) If possible, we used vegetation to aid in ecosystem mapping. However, in many cases reference plant

TABLE 1. Summary of hierarchically structured fluvial, upland, and wetland ecosystems of Ichauway (southwestern Georgia, USA).

Ecosystem code	Level 1, physiographic zone†	Level 2, landform‡	Level 3, terrain shape§	Level 4, Soil: Drainage‖	Level 4, Soil: Texture¶	Level 5, overstory#	Level 6, ground-flora species groups††
Fluvial ecosystems							
EC 1	F	T	NL	SPD	S to SL over SCL to C	*P. pal., P. tae., Q. nig.*	not sampled
EC 2	F	T	Und.	MD	SCL over FS	*P. pal., P. tae., P. ech.*	*Vaccinium, Ruellia*
EC 3	F	T	NL to Und.	WD	LS over SL to SCL	*P. pal.*	not sampled
EC 4	F	T	NL to Und.	WD to SED	S and LS	*P. pal.*	*Aristida, Andropogon*
EC 5	F	T	NL	SED	S	*Q. hem., C. gla., M. gra.*	*Parthenocissus, Bignonia*
EC 6	F	SR	Und.	ED	S	*P. pal., Q. lae., Q. mar.*	*Aristida, Andropogon*
EC 7	F	FP	Und	MWD	SCL over SL	*Q. vir., L. str., A. sac.*	*Parthenocissus, Bignonia/Dioscorea, Viola*
EC 8	F	FP	Und.	MWD	SL over LS	*Q. vir., L. str., A. sac.*	*Parthenocissus, Bignonia*
EC 15	F	SL	S	WD to SED	LS over SL to SCL	*P. pal., Q. mar.*	*Aristida, Andropogon*
Upland ecosystems							
EC 9	U	T	NL	SPD to PD	SL over SCL to C	*P. pal.*	*Aristida, Dyschoriste/Scleria, Aster*
EC 10	U	T	NL	MWD	LS over SCL to C	*P. pal.*	*Aristida, Dyschoriste/Scleria, Aster*
EC 11	U	T	Und.	WD	LS over SCL to C	*P. pal.*	*Aristida, Dyschoriste/Rhyncosia, Crottolaria*
EC 12	U	T	Und.	WD to ED	LS to SL	*P. pal.*	*Aristida, Dyschoriste/Centrosema, Schrankia*
EC 13	U	SR	Und.	ED	S	*P. pal., Q. lae, Q. mar*	*Aristida, Dyscoriste/Croton, Stylisma*
EC 14	U	WM	S	WD to PD	LS over SL to C	*P. pal., P. ell*	*Aristida, Dyschoriste/Hypericum, Solidago*
EC 16	U	SD	Und.	MWD to PD	S to SL over SCL to C	*Q. vir., Q. nig., Q. lau.*	*Quercus, Campsis*
EC 17	U	SD	Und.	WD to MWD	S over SCL	*Q. gem., P. pal., Q. vir.*	*Aristida, Dyschoriste*
Wetland ecosystems							
EC 18	U	D		VPD	O over C	*N. syl., T. asc.*	*Nyssa, Taxodium*
EC 19	U	D		PD	LS over SC to C	*T. asc.*	*Panicum, Andropogon*
EC 20	U	D		PD to VPD	LS over SCL to SC	none	*Panicum, Leersia*
EC 21	U	FL		PD to VPD	LS over SCL to SC	*P. ell.*	*Sporobolus, Pityopsis*

† F = fluvial, U = upland.

‡ T = terrace, SR = sand ridge, FP = floodplain, SL = slope, WM = wetland margin, SD = shallow depression, D = depression, FL = flat.

§ NL = nearly level, Und. = undulating, S = slope.

‖ SPD = somewhat poorly drained, MD = moderately drained, WD = well drained, SED = somewhat excessively drained, ED = excessively drained, MWD = moderately well drained, PD = poorly drained, VPD = very poorly drained.

¶ S = sand, SL = sandy loam, SCL = sandy clay loam, C = clay, FS = fine sand, LS = loamy sand, O = organic, SC = sandy clay.

\# *A. sac.* = *Acer saccharum*, *C. gla.* = *Carya glabra*, *L. str.* = *Liquidambar stryaciflua*, *M. gra.* = *Magnolia grandiflora*, *N. syl.* = *Nyssa sylvatica*, *P. ech.* = *Pinus echinata*, *P. ell.* = *P. elliottii*, *P. pal* = *P. palustris*, *P. tae* = *P. taeda*, *Q. gem.* = *Quercus geminata*, *Q. hem.* = *Q. hemisphaerica*, *Q. lae.* = *Q. laevis*, *Q. lau.* = *Q. laurifolia*, *Q. mar.* = *Q. margaretta*, *Q. nig.* = *Q. nigra*, *Q. vir.* = *Q. virginiana*, *T. asc.* = *Taxodium ascendens*.

†† Diagnostic ground-flora species groups. Each group may contain up to 50 species. Most ecosystems contain one or two additional species groups that are not listed.

TABLE 2. Physiographic and soil variables used in linear discriminant analysis (LDA). The number of samples (n) for each ecosystem class (EC) is given in parentheses. Numerical entries are means with 1 SE in parentheses.

Variable	Fluvial ecosystems						
	EC 2 (n = 5)	EC 4 (n = 3)	EC 5 (n = 8	EC 6 (n = 8)	EC 7 (n = 4)	EC 8 (n = 5)	EC 15 (n = 9)
Landform†	T	T	T	SR	FP	FP	SL
Sand thickness (cm)‡	15 (5)	139 (84)	300 (0)	264 (28)	174 (74)	96 (29)	107 (19)
AWC (cm water/cm soil)	34 (3)	24 (6)	15 (0)	16 (1)	32 (2)	21 (4)	32 (2)
Percentage sand (50–150 cm)	38 (9)	77 (8)	95 (1)	93 (2)	61 (8)	87 (5)	75 (3)

Variable	Upland ecosystems							
	EC 9 (n = 6)	EC 10 (n = 5)	EC 11 (n = 16)	EC 12 (n = 10)	EC 13 (n = 6)	EC 14 (n = 5)	EC 16 (n = 10)	EC 17 (n = 3)
Landform†	T	T	T	T	SR	WM	SD	SD
Terrain shape§	NL	NL	Und.	Und.	Und.	S	Und.	Und.
AWC (cm water/cm soil)	40 (0)	39 (1)	38 (2)	28 (2)	19 (2)	38 (5)	38 (3)	25 (2)
Percentage silt (0–50 cm)	22 (2)	19 (2)	16 (2)	11 (1)	5 (1)	12 (1)	21 (3)	5 (2)
Percentage sand (50–150 cm)	50 (5)	57 (3)	64 (5)	83 (2)	93 (1)	66 (3)	57 (5)	83 (4)
CDE (50–150 cm)	9 (2)	11 (1)	20 (3)	13 (1)	19 (1)	14 (3)	7 (1)	6 (1)

Variable	Wetland ecosystems			
	EC 18 (n = 10)	EC 19 (n = 7)	EC 20 (n = 10)	EC 21 (n = 3)
Landform†	D	D	D	FL
Percentage med. sand (0–50 cm)	2.3 (1.0)	14.0 (1.3)	17.9 (2.4)	25.4 (3.4)
Percentage clay (0–50 cm)	16.1 (6.6)	26.6 (2.7)	24.4 (3.1)	7.2 (1.5)
Percentage clay (50–100 cm)	31.9 (5.1)	46.3 (3.4)	38.7 (4.3)	16.9 (9.4)
Percentage clay (100–150 cm)	36.9 (4.7)	49.9 (6.2)	39.0 (3.7)	30.2 (7.0)

Notes: Two variables were derived from soil texture and color: AWC, available water context, based on water-holding capacities of different soil textures; and CDE, color-development equivalent. See *Methods: Ecosystem predictability* for description.

† D = depression, FL = flat, FP = floodplain, SD = shallow depression, SL = slope, SR = sand ridge, T = terrace, WM = wetland margin.

‡ Thickness of a sandy surface horizon.

§ NL = nearly level, Und. = undulating, S = slope.

communities were not present. Consequently, we delineated most ecosystems using physiographic and soil relationships alone.

During mapping, it is common to detect rare ecosystems missed during earlier development of a classification. We discovered two such ecosystems (ecosystems 1 and 3; Table 1), and after further examination, revised the classification to include these ecosystems. Their physiography, soils, and vegetation characteristics (Table 1) were determined from inventories collected during mapping, rather than detailed plot analysis.

GIS analyses and restoration-priority index

We digitized ecosystem boundaries into a geographic information system (GIS) to produce a reference ecosystem map for the study area. We verified ~20% of the map with independent field observations. We used ARCINFO (Environmental Systems Research Institute, Redlands, California, USA) to determine the potential area of each reference ecosystem from the digitized ecosystem map. We joined the ecosystem map with an existing map of current land cover to determine disturbance conditions of ecosystems. Current land-cover classes (hereafter called "disturbance classes") were ranked according to dissimilarity to the reference condition. These include: (1) mature, fire-maintained forest or herbaceous community (i.e, the reference condition, dissimilarity = 0%); (2) mature, fire-excluded forest or herbaceous community (dissimilarity to the reference condition = 10%); (3) mature old-field forest or old-field herbaceous wetland community (30%); (4) plantation forest (50%); (5) abandoned agricultural field (70%); (6) active agricultural field (90%); and (7) developed land (100%). While the relative ranking of classes was objective, based on observations of degree of disturbance, the assigned percentages were subjectively selected to span the full range of possibilities, from 0 to 100% dissimilarity to the reference condition. From the joined map, we determined (1) the area of reference ecosystems in the current landscape and (2) the area of each disturbance class within each reference ecosystem. Conceptually, this approach is similar to gap analysis (Scott et al. 1993, Kiestor et al. 1996), which uses GIS to identify spatial relationships between the distributions of species or habitats of concern and current protected areas in a region.

We used Eq. 1 as an index for prioritizing restoration of each map polygon in the study area:

$$\mathrm{RPI} = [h\ (\%) + a\ (\%) + d\ (\%)]/3 \qquad (1)$$

TABLE 3. Cross-validation summaries from linear discriminant analysis, showing the range of classifications of ecosystems (both correct and incorrect) based on physical (physiographic and soil) variables.

A) Fluvial ecosystems

Ecosystem	n†	No. of times classified into ecosystem EC2	EC4	EC5	EC6	EC7	EC8	EC15	Misclassification (%)
EC2	5	5	0	0	0	0	0	0	00.0
EC4	3	1	1	1	0	0	0	0	67.0
EC5	8	0	0	8	0	0	0	0	00.0
EC6	8	0	0	0	8	0	0	0	00.0
EC7	4	0	0	0	0	3	1	0	25.0
EC8	5	0	0	0	0	0	5	0	00.0
EC15	9	0	0	0	0	0	0	9	00.0
Overall									7.1

B) Upland ecosystems

Ecosystem	n†	No. of times classified into ecosystem EC9	EC10	EC11	EC12	EC13	EC14	EC16	EC17	Misclassification (%)
EC9	6	0	6	0	0	0	0	0	0	100.0
EC10	5	0	5	0	0	0	0	0	0	0.00
EC11	16	0	0	14	2	0	0	0	0	12.5
EC12	10	0	0	6	4	0	0	0	0	60.0
EC13	6	0	0	0	0	6	0	0	0	00.0
EC14	5	0	0	0	0	0	5	0	0	00.0
EC16	10	0	0	0	0	0	0	10	0	00.0
EC17	3	0	0	0	0	0	0	3	0	100.0
Overall										27.9

C) Wetland ecosystems

Ecosystem	n†	No. of times classified into ecosystem EC18	EC19	EC20	EC21	Misclassification (%)
EC18	10	9	0	1	0	10.0
EC19	7	0	2	5	0	71.4
EC20	10	1	1	8	0	20.0
EC21	3	0	0	3	0	100.0
Overall						36.7

† Number of samples.

where RPI is restoration-priority index, *h* is historical extent of an ecosystem, measured as the potential percentage of the landscape occupied by a reference ecosystem (i.e., all disturbed polygons restored), *a* is area of an ecosystem remaining, measured as the percentage of the historical total of an ecosystem in the current landscape, and *d* is one of the seven disturbance classes, which measure percentage dissimilarity of a selected polygon to the reference condition (e.g., 0% = the reference condition, 100% = developed land).

RPI integrates information on ecosystem conservation status (historical vs. current rarity), with effort to restore a selected polygon to a reference condition. Our assumption for the latter is that cost to restore a disturbed site to the reference condition increases as degree of dissimilarity to the reference ecosystem increases. RPI ranges from zero to 100; the lower the RPI value, the higher the restoration priority. We divided the range of RPI into three categories representing high (0–25), medium (>25–58), and low (>58–100) restoration priority. The divisions are subjective, so for comparison we examined a second scenario in which each priority level has equal class width (high = 0–33, medium = >33–66, low = >66–100). Using this approach, we assigned RPI scores to each polygon of the current cover map, producing a third map that codes the study area by our three prioritization classes (high, moderate, low).

RESULTS

Predicting ecosystem identity

Five of the 21 ecosystems (6, 15, 13, 14, 21) occupy unique combinations of physiographic zone and landform (Tables 1 and 2). Further, ecosystems 7 and 8 (both floodplains) occur in different river valleys (Ichawaynochaway Creek and Flint River, respectively). Consequently, these seven ecosystems were distinguishable during mapping without reliance on additional physical characteristics. The addition of soil variables helped to distinguish those ecosystems occurring on the same landforms. The linear discriminant analyses (LDA) verified this probabilistically. The LDAs suggested generally good predictability of ecosystem identity based on just a small subset of physiographic and soil variables (Table 2). The misclassification rate from cross-validation analysis for all ecosystems combined was 21.1% (Table 3). Among physiographic zones, physical variables were better predictors of fluvial ecosystems (misclassification = 7.1%) than upland ecosystems (misclassification = 27.9%) or wetland ecosystems (misclassification = 36.7%). Ecosystem 4 was the only fluvial system with a high misclassification rate (67%), probably because of small sample size (n = 3).

Within the upland zone, LDA misclassified all ecosystem 9 samples as ecosystem 10 (Table 3), and 60% of ecosystem 12 samples as ecosystem 11. These results reflect the subtle differences we found between these ecosystems in the classification (Table 1). LDA also misclassified all ecosystem 17 samples as ecosystem 16, probably due to small sample size (n = 3).

Among the wetlands, the LDA misclassified 71.4% of ecosystem 19 samples as ecosystem 20 and all ecosystem 21 samples as ecosystem 20 (Table 3). The latter is probably the result of small sample size for ecosystem 21 (n = 3), but is not problematic because this ecosystem occurs on a different landform than ecosystem 20 (Table 1).

Landscape composition

The reference ecosystem map depicts the potential composition of the landscape, given generally predictable relationships among physiography, soils, and plant communities (Fig. 1a). The distribution of land area among ecosystems is highly variable (Fig. 1b). Together, ecosystems 11, 12, and 16 make up 75% of the land base. Ecosystems 2, 3, and 4 each make up about 3.5% of the land base. No other single ecosystem comprises more than 2.5% of the land base.

The current land cover of the study area is a mosaic of reference ecosystems and the seven disturbance classes (Fig. 2a). Nearly half of the 11 400-ha area is in a reference condition (Fig. 2b). Old-field forests and herbaceous wetland communities, along with active agricultural fields, comprise most of the remaining land area. In total, the remaining disturbance classes comprise <8% of the land area (Fig. 2b).

As in the potential landscape, the 21 reference ecosystems do not occupy equal area within the undisturbed portion of the current landscape. However, their relative land areas are similar to the potential landscape. Ecosystems 11, 12, and 16 occupy nearly 70% of the less-disturbed portion of the study area. No other single ecosystem accounts for more than 5% of reference ecosystem area. Ecosystems 1 and 21 are the rarest ecosystems, accounting for 0.1% and 0.2% of reference area, respectively.

Amount of disturbed area (i.e., non-reference condition) is highly variable among ecosystems (Fig. 3). At the extremes, 81% of ecosystem 3 and 1.3% of ecosystem 20 are currently in disturbed cover classes. Additional ecosystems experiencing large conversions (55–69%) include ecosystems 1, 2, 4, 9, 11, and 14 (Fig. 3). Conversely, <10% of ecosystems 5, 7, 8, 17–19, and 21 are in disturbed cover classes (Fig. 3). Distribution of area among disturbance classes is variable among ecosystems (Fig. 3). For instance, land area in forest plantations (14.5%) and agriculture (31.2%) is much higher for ecosystem 3 than for other ecosystems (Fig. 3). Similarly, ecosystem 6 contains more land in abandoned agricultural fields (14%) than do the other ecosystems.

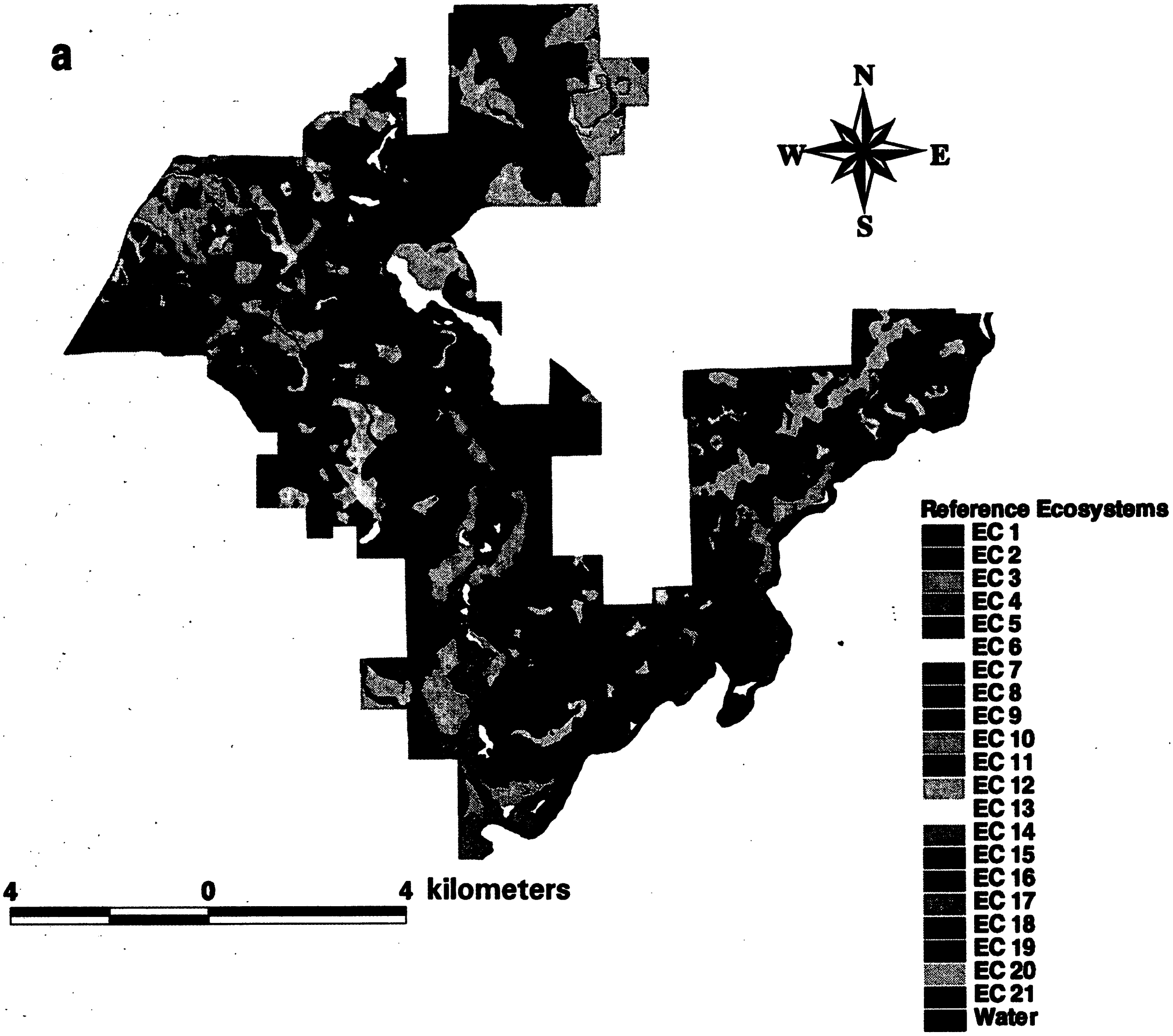
Prioritizing restoration efforts

We used Eq. 1 to assign an RPI (restoration-priority index) to each polygon of the study area (Fig. 4). As an example of how RPI works, consider the polygon labeled A in Fig. 4a. The polygon has the following characteristics: (1) disturbance class is 30% (old-field forest; from Fig. 2a), (2) the reference condition for the polygon is ecosystem 4 (from Fig. 1a), an historically rare ecosystem (potential cover of the landscape = 3.6%; from Fig. 1b), and (3) reduction in reference ecosystem area is moderate (historical area remaining = 35.5%; from Fig. 3). RPI for this polygon is 23, or high restoration priority under scenario 1 (unequal class widths, see *Methods: GIS analyses and restoration-priority index*) and scenario 2 (equal class widths). Now consider polygon B (Fig. 4a) having the following characteristics: (1) disturbance class = 90% (active agricultural field), (2) reference condition is ecosystem 11, an historically abundant ecosystem (potential cover of the landscape = 62.1%), and (3) reduction in historical area is moderate (area remaining of the historical total = 33.3%). This polygon has an RPI of 62, or a low rating under scenario 1 and a medium rating under scenario 2.

Using this procedure, we estimated that 13.0% of the disturbed landscape (excluding developed land, which will never be restored) has high restoration priority under scenario one, while 60.5% has medium priority, and 26.5% has low priority (Fig. 4a, Table 4). Under scenario two, 14.4% of the disturbed landscape has high restoration priority, 85.6% has medium priority, and 0% has low restoration priority (Fig. 4b, Table 4).

Under both scenarios, nearly 80% of high-priority sites occurred in the fluvial physiographic zone, specifically within reference ecosystems 2, 3, and 4 (Table 4). While no wetlands were high-priority sites, ~18% of high-priority sites under both scenarios occurred in ecosystem 14, the wetland margins (Table 4). Under scenario 1, >90% of medium- and low-restoration-priority sites occur in the upland physiographic zone, while under scenario 2, 94% of medium-priority sites occur in the upland (scenario 2 identifies no low-priority sites).

Overall, the two scenarios were similar in how they assigned RPI scores to specific ecosystems (Table 4). However, there were several distinctions, beyond the fact that scenario 2 identified no-low priority sites. The one major change involved ecosystem 11. Under sce-



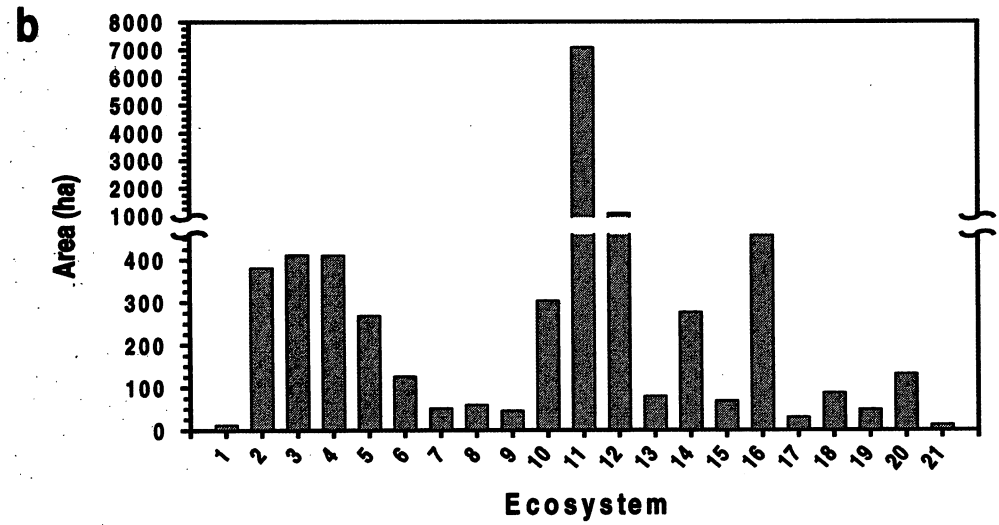


Fig. 1. (a) Potential cover map of the study landscape showing distribution of the 21 reference ecosystems. (b) Potential distribution of land area among reference ecosystems as derived from (a).

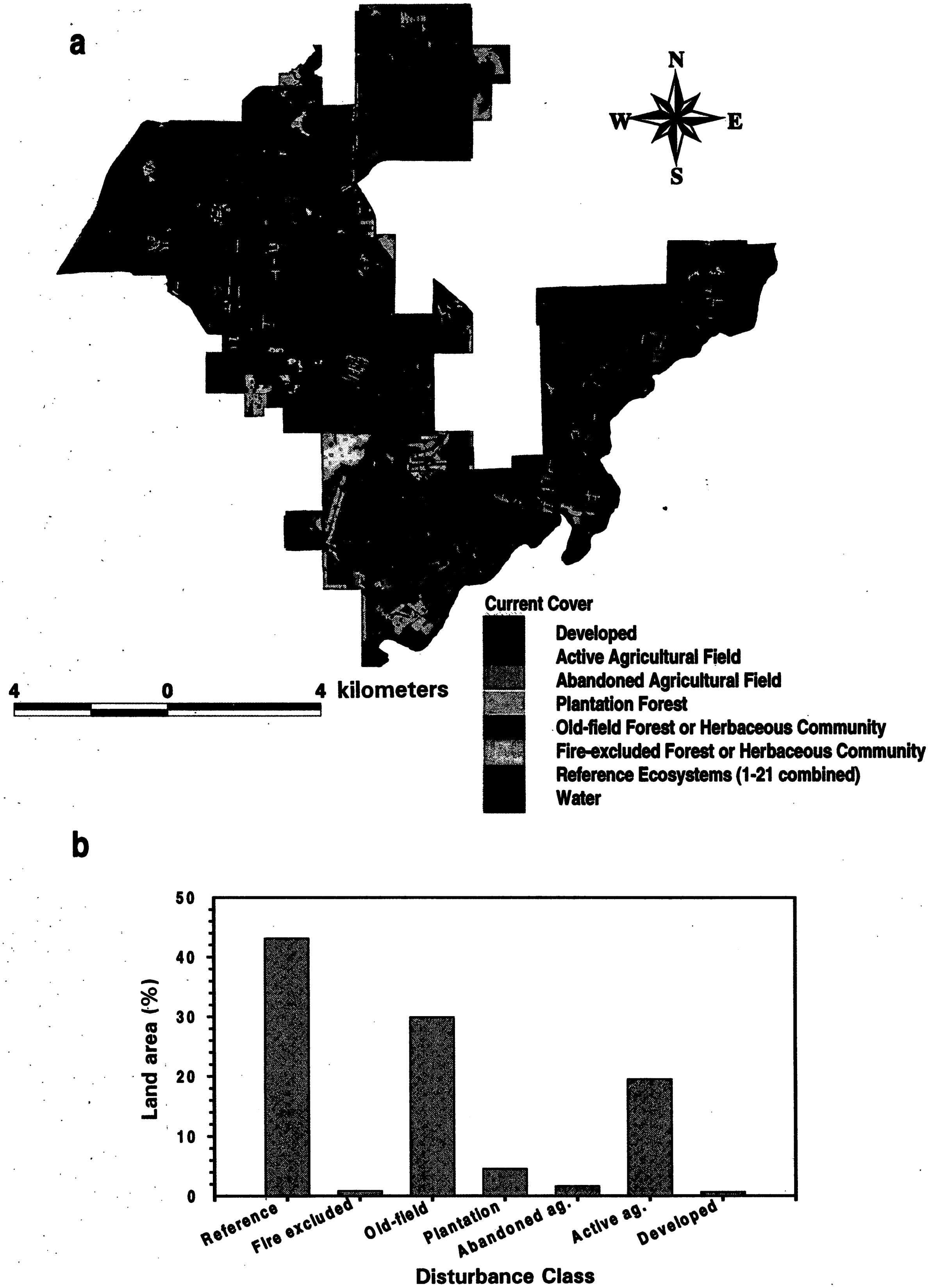


Fig. 2. (a) Current cover map of the study landscape showing distribution of the seven disturbance classes. (b) Distribution of land area among different disturbance classes. Note that disturbance-class labels on the x-axis are abbreviated; complete labels are as in the map legend.

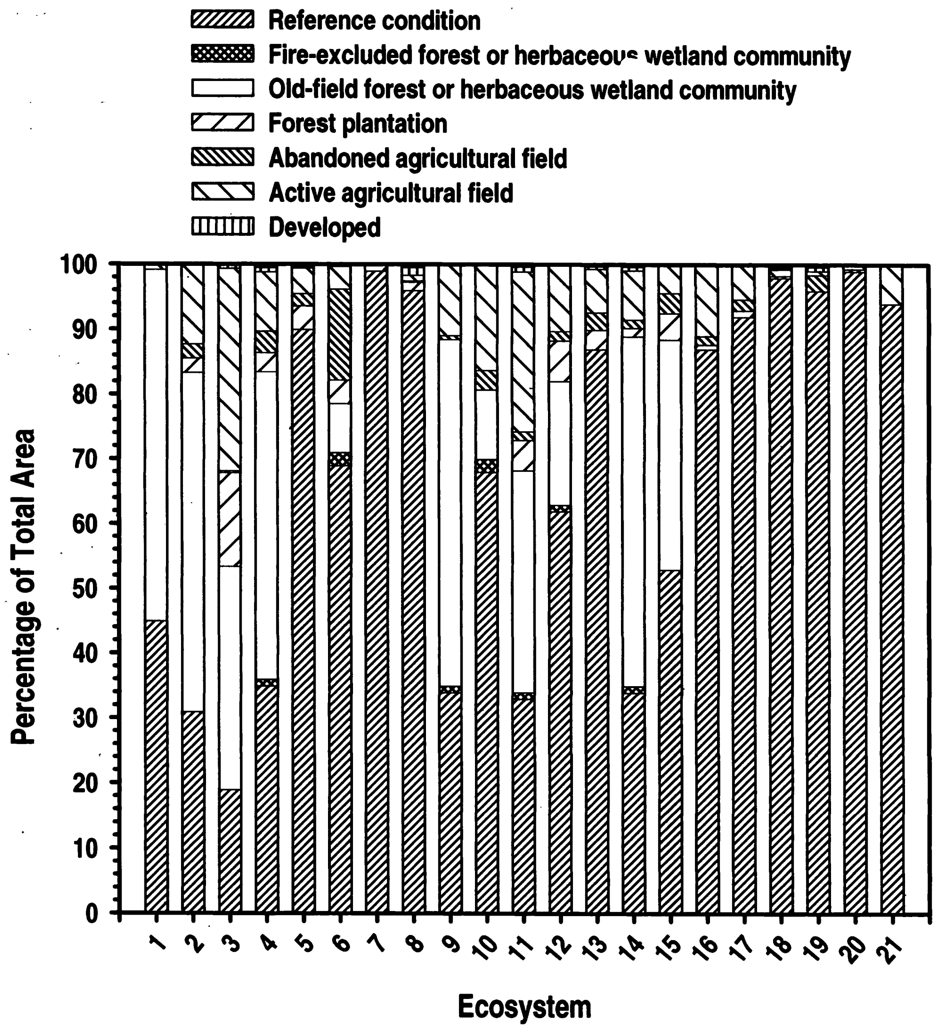


FIG. 3. Relative abundance of the seven disturbance classes (current cover) for each reference ecosystem.

nario 1, 95% of the low-priority sites occurred in ecosystem 11 (Table 4). Under scenario 2, all low-priority area for the ecosystem moved into the medium-priority status. A more interesting, but subtle, change involved high-priority ecosystems. Scenario 1 identified six high-priority ecosystems, including ecosystems 1–4, 9 and 14 (Table 4). The second scenario increased this number by four, adding ecosystems 6, 10, 12, and 15. However, the corresponding increase in percentage area receiving high-priority status was low, totaling <2% (Table 4).

DISCUSSION

Identifying reference targets for restoration

Ecosystem restoration often includes the objective of reestablishing native plant communities (Brown and Bedford 1997, Choi and Pavlovic 1998). Identifying appropriate vegetation for restoration is problematic if the manager does not first understand the relationship between plant communities and physical site characteristics, i.e., having reference targets for restoration. This is particularly important in disturbed landscapes that contain several types of ecosystems that support similar native plant communities. We are aware of few objective approaches for determining reference plant communities of disturbed ecosystems (Allen and Wilson 1991), and none for determining reference conditions for the full array of ecosystems that occur in any one landscape.

Our approach identifies potential plant communities of disturbed ecosystems in a complex landscape based on probabilistic relationships among geomorphology, physical soil characteristics, and vegetation. The predictive ability of our approach is a direct consequence of the hierarchical structure of the study landscape. Large-scale geomorphic features often constrain soil development and, in turn, plant community development. It follows that ecosystem identity is predictable even without vegetation because in hierarchical systems upper levels of the hierarchy (e.g., landform, to-

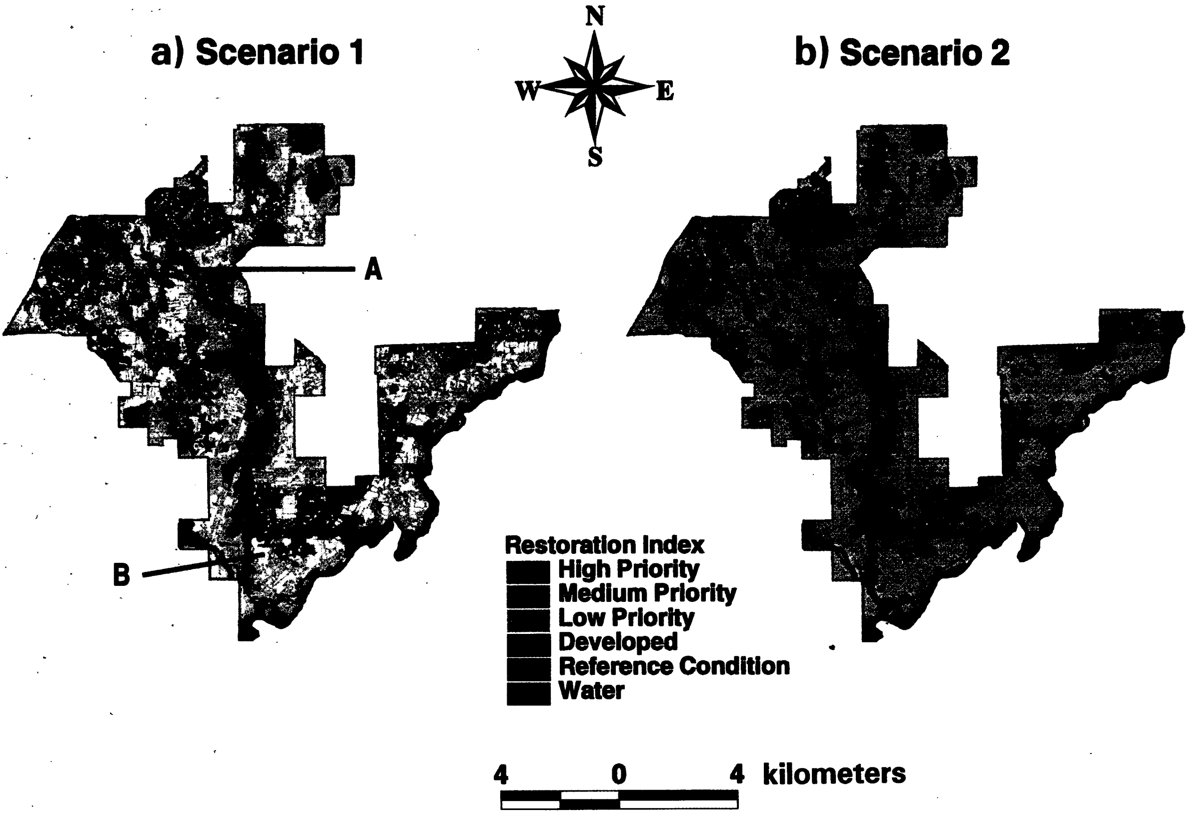


Fig. 4. Cover map of the study landscape identifying areas of high, medium, and low priority for restoration using (a) unequal class widths for RPI (scenario 1, see *Methods: GIS analyses and restoration-priority index*) and (b) equal class widths for RPI (scenario 2). See *Results: Prioritizing restoration efforts* for discussion of points A and B.

TABLE 4. Distribution of ecosystems among three restoration-priority classes using the two scenarios for dividing RPI (restoration-priority index). For each scenario, cell values are percentages of total disturbed area in the landscape.

	Scenario 1			Scenario 2			Percentage change†		
Ecosystem	High	Medium	Low	High	Medium	Low	High	Medium	Low
EC 1	0.1	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0
EC 2	3.0	0.9	0.0	3.1	0.8	0.0	+0.1	−0.1	0.0
EC 3	3.0	1.9	0.0	3.0	1.9	0.0	0.0	0.0	0.0
EC 4	4.1	0.8	0.0	4.2	0.7	0.0	+0.1	−0.1	0.0
EC 5	0.0	0.2	0.2	0.0	0.4	0.0	0.0	+0.2	−0.2
EC 6	0.0	0.8	0.0	0.6	0.2	0.0	+0.6	−0.6	0.0
EC 7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
EC 8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
EC 9	0.4	0.1	0.0	0.4	0.1	0.0	0.0	0.0	0.0
EC 10	0.0	1.9	0.0	0.1	1.8	0.0	+0.1	−0.1	0.0
EC 11	0.0	45.9	25.4	0.0	71.3	0.0	0.0	+25.4	−25.4
EC 12	0.0	6.8	0.0	0.1	6.7	0.0	+0.1	−0.1	0.0
EC 13	0.0	0.1	0.1	0.0	0.2	0.0	0.0	+0.1	−0.1
EC 14	2.4	0.4	0.0	2.4	0.4	0.0	0.0	0.0	0.0
EC 15	0.0	0.5	0.0	0.4	0.1	0.0	+0.4	−0.4	0.0
EC 16	0.0	0.2	0.8	0.0	1.0	0.0	0.0	+0.8	−0.8
EC 17	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
EC 18	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
EC 19	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
EC 20	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
EC 21	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sum	13.0	60.5	26.5	14.4	85.6	0.0	+1.4	+25.1	−26.5

Notes: RPI ranges from 0 to 100; the lower the RPI value, the higher the restoration priority. Scenario 1 represents our subjective division into three categories representing high (0–25), medium (25–58), and low (58–100) restoration priority. Scenario 2 gives each priority level equal class widths: high = 0–33, medium = 34–66, and low = 67–100.

† Change from scenario 1 to scenario 2, in percentage of an ecosystem in each RPI class.

pography, soil morphology) constrain the dynamics of lower hierarchical levels (Allen and Starr 1982).

Our approach for identifying reference vegetation conditions of disturbed ecosystems is consistent with the idea of contingent ecosystem development (sensu Pickett and Parker 1994). Contingency can result in multiple successional pathways and multiple reference vegetation states for any one type of ecosystem (Simberloff 1990). Each of our reference ecosystems displays inherent variability in plant species composition and abundance that likely reflects subtle differences in successional pathways. The idea of ecological species groups (Spies and Barnes 1985*b*), an important feature of the classification used in this study (Table 1), embodies this variability. Ecological species groups consist of those species having high fidelity to a particular type of site. However, it is the group itself, not individual species, that is most diagnostic of a particular ecosystem. Individual group members may be absent at any particular site due to contingencies in plant community development (Archambault et al. 1989).

The foundation of our approach is that within-ecosystem variation in vegetation composition is generally less than variation among ecosystems. The results from the linear discriminant analyses (LDAs) support this distinction. Thus, using our methodology, a restorationist can discern when the reference vegetation targets for a group of disturbed sites should differ because of inherent differences in physical site characteristics, as opposed to natural variation in composition within ecosystems as caused by contingent ecosystem dynamics (Pickett and Parker 1994).

Prioritizing restoration efforts

Enhancement of biodiversity and increased ecosystem goods and services are obvious benefits of restoration. However, a manager must weigh the benefits against financial costs, which can be considerable even for small land areas (Atkinson 1988). Prioritizing restoration, based on costs and benefits, is an essential consideration, particularly in large landscapes that include multiple types of ecosystems and various levels of disturbances among individual sites.

Our approach to prioritization uses the conservation status of an ecosystem, as expressed in current and historical rarity, to assess benefits associated with restoration of that ecosystem. For instance, restoration of ecosystems that were historically abundant, but are now rare, will likely result in high conservation benefit. This approach has similarities to gap analysis (Scott et al. 1993), but on a local scale, whereby we compare the potential distribution of reference ecosystems to the area and distribution of protected areas of each ecosystem. In so doing, we can readily identify ecosystems of concern, as well as the local geographic areas they occupied historically.

We also incorporate the cost of restoration into the prioritization, assuming that the level of disturbance is proportional to the effort required to restore a site to a reference condition. Given equal conservation status, highly disturbed sites receive lower priority for restoration than less-disturbed sites because restoration costs may be prohibitive for the former. However, even highly disturbed sites may be high priorities for restoration if the site represents an ecosystem that has lost substantial area in the landscape.

In practice, identifying goals for restoration and prioritizing restoration efforts are subjective exercises. The actual divisions for the range of the restoration-priority index (RPI) are likely to depend on organizational objectives. For instance, most organizations will probably want sites in their focus landscapes to span the range of RPI; that is, some each in high-, medium-, and low-priority categories. The class widths may require adjustment if the index fails to identify high-priority or low-priority sites (as in our scenario 2).

An interesting result of our study is that using either scenario 1 or 2 (for dividing RPI), the percentages of land area identified as high priority for restoration were similar. Moreover, both scenarios identified fluvial and wetland-margin ecosystems as having highest priority for restoration (Fig. 4). This suggests that our approach is robust to minor subjective differences in calculation of RPI, at least in terms of how it identifies high-priority restoration sites. It is probably desirable that the index assign high-priority scores consistently, and less important if it is not robust in assigning medium- and low-priority scores. In reality, an organization will likely reprioritize their land base after restoration of the high-priority sites, so the exact distribution of sites in the medium- and low-priority classes is not critical.

Disturbance-class rankings also are modifiable to suit organizational needs. In our example, we chose to divide the landscape into seven prominent disturbance classes. However, we could have easily modified these divisions, allowing for more or fewer disturbance classes or different numerical values for the classes. This flexibility, in conjunction with the other benefits of our approach, provides managers with a straightforward methodology for assessing restoration priorities under many different scenarios.

Additional landscape considerations

Our method of prioritizing restoration efforts relies exclusively on conservation status of ecosystems and disturbance level of polygons within the jurisdictional boundaries of the study area. The various cover maps of the study area (Figs. 1, 2, and 4) suggest two landscape considerations that may alter the prioritization. The first of these is the obvious *fragmentation* of the landscape. For instance, even among reference ecosystems, most large polygons contain many small disturbance patches. Most of these disturbance patches have low priority for restoration (Fig. 4). This is because they occur predominantly within ecosystems 11 and 12, relatively abundant ecosystems in the current landscape, and because the disturbance level of the small patches is high.

A manager may choose to place high priority on restoring these small, highly disturbed patches because of the potential to reduce fragmentation within the least disturbed portion of the landscape. The effort needed to restore small embedded patches may be less than their level of disturbance suggests. This would be true if the patches receive substantial ecological inputs (e.g., diaspores, natural disturbances) from the surrounding matrix, as do small oceanic islands near the mainland (Simberloff 1990). There likely are other examples in the study area where judicious focus of restoration efforts, even in low-priority polygons, can decrease landscape fragmentation.

A second landscape consideration is that assessments of ecosystem abundance and diversity, as well as prioritization of restoration efforts, require a *regional perspective*. The efforts of neighboring landowners in restoring or degrading rare ecosystems may influence prioritization decisions in the focus landscape. In the case of Ichauway, the bordering landscapes are largely under intensive agriculture. Consequently, Ichauway assumes regional importance as a center for conservation of biological diversity. In this sense, all the disturbed ecosystems of Ichauway have high-priority status for restoration. In reality, limited budgets and time dictate the need for the multi-level prioritization approach we present. In other regions, rare ecosystems in a focus landscape may be abundant on surrounding ownerships. If this is the case, it may be desirable to prioritize restoration efforts in the focus landscape to better meet objectives not being pursued by other regional ownerships. In either case, cross-ownership planning will facilitate regional restoration efforts by helping to focus priorities and make the best use of limited restoration dollars.

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