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IDENTIFYING POTENTIAL INDICATORS OF CONSERVATION VALUE USING NATURAL HERITAGE OCCURRENCE DATA

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Abstract. Conservation planning based on the occurrence of rare species has been criticized as being too limited in scope to conserve biodiversity as a whole. Conversely, planning based on indicator taxa may lack sufficient focus to conserve those species in greatest need of conservation. An alternative approach is to identify a variety of species at risk that are associated with areas of conservation value, which is defined based on species-independent characteristics. We identified potential indicators of conservation value using occurrence data on species at risk and independent information on conservation value that incorporated indices of ecosystem integrity. We propose a taxonomically diverse group of indicator species that are strongly associated with areas of exceptional ecosystem integrity, to serve as a focus for further research and in planning for biodiversity conservation.

We identify potential indicator species by defining a null model in which species at risk are equally associated with areas of high ecosystem integrity, then by conducting randomization tests to identify noncompliant species in the state of Michigan, USA. Areas of high ecosystem integrity are selected using criteria to flag (1) secure biotic communities with structural integrity and few exotic species, (2) natural areas subjected to expert review, (3) contiguous relict areas of forest interior, (4) contiguous areas of unmodified wetland, and (5) all these areas combined. We determine the spatial occurrence of species at risk using data from Michigan's statewide Natural Heritage database.

The potential indicators include plants, insects, and birds. Their species identity and distribution of occurrences varies with the five scenarios, and together the species broadly cover the entire state. These species at risk, many of which occur throughout the Great Lakes region, may be used to identify additional areas potentially high in conservation value and to monitor their conservation. The ecological criteria and numerical methods we employ may be broadly applicable as Heritage Program databases in North America and parts of Latin America grow to become representative of species distributions.

Key words: adaptive management; conservation planning; conservation priority; endangered species; heritage program; inventory; monitoring; null model; randomization test; rarity; reserve selection; surrogate species.

Introduction

The current rates of fragmentation and habitat loss, usurpation of primary productivity for human purposes, and resulting loss of populations indicate a pressing need for establishment of reserve networks, restoration of ecosystems, and management of these areas for biodiversity conservation (Robinson et al. 1995, Dobson et al. 1997, Hughes et al. 1997, Vitousek et al. 1997). Evaluating all of biological diversity as a basis for reserve selection would be a mammoth undertaking (Raven and Wilson 1992). Thus, identification of indicators for systematically choosing locations with high conservation value, then managing and monitoring for biodiversity conservation are principal tasks for conservation biologists (Noss 1990, Kremen et al. 1993, 1994, Margules and Pressey 2000). These tasks are complicated because the richness of species in a single taxon is often not indicative of richness in other taxa or larger groups (Prendergast et al. 1993, Flather et al. 1997, Kerr 1997, Lawton et al. 1998, van Jaarsveld et al. 1998, Vessby et al. 2002). Further, few proposed indicators may fulfill multiple criteria that have been established for indicator species (Hilty and Merenlender 2000, Lindenmayer et al. 2000), suggesting the importance of considering ecological function and requirements of suites of species in selecting indicators for conservation planning (Lambeck 1997, Simberloff 1998, Soulé et al. 2003). Nonetheless, debate surrounds the relative importance of information on species distributions and environmental variation across landscapes for conserving both biodiversity and the ecosystem services it provides (Brooks et al. 2004*a*, *b*, Higgins et al. 2004, Molnar et al. 2004, Pressey 2004). These issues suggest the collective importance of data on species distributions, species environmental dependencies, and the spatial distribution of land types for

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guiding the conservation of biodiversity (Cowling et al. 2004).

Species with pressing conservation needs can fall outside hotspots of species richness of well-studied taxa (Prendergast et al. 1993, Panzer and Schwartz 1998, Chase et al. 2000), and protecting conservation-dependent species may involve large investment compared to that needed for protecting biodiversity (Kintsch and Urban 2002). While protection of rare species may provide substantial benefits for other species (Mikusinski et al. 2001, Lawler et al. 2003), some studies suggest that few species benefit from efforts directed at rare species because of their restricted distribution and idiosyncratic habitat needs (Andelman and Fagan 2000, Chase et al. 2000, Fleishman et al. 2000, Possingham et al. 2002). Nonetheless, rare and listed species may be useful as indicators of forest conservation value (Thor 1998, Gustafsson 2000, Sillett et al. 2000, Uliczka and Angelstam 2000). Identification of additional rare species to serve as indicators could broaden accessory benefits obtained by directing limited resources toward their conservation. To facilitate this we identify potential indicators of conservation value in pools of species at risk (listed species and additional watch-list species) by investigating their relationship with ecosystem integrity (Karr 1991, Woodley et al. 1993). The potential positive relationships between ecosystem integrity, ecosystem services, and the occurrence of species at risk (Costanza et al. 1997, Rapport et al. 1998, Balmford et al. 2002) suggest focusing on ecosystem integrity to evaluate conservation value. We employ data on current and historical land cover and occurrence of species at risk to evaluate the conservation value of all 1900 93.2-km^2 townships in Michigan, USA.

Natural Heritage Program data—a source for identifying rare species indicators?

Species needing conservation attention are identified by nongovernmental organizations and governmental bodies to help prioritize conservation efforts (Master 1991). Occurrence data on these species in North America and elsewhere are available from Natural Heritage Program databases, a set of resources with immense geographic scope that form the basis for numerous public–private conservation partnerships (Jenkins 1988, Groves et al. 1995, Stein and Davis 2000). These records contain information that has been collected from surveys on federal, state, and private land, from literature and museum records, and from a variety of reports sent to Natural Heritage Program participating organizations. Additionally, data may be included on the type, degree of anthropogenic impact, and geographic extent of biotic communities having conservation value due to ecosystem integrity and potential for viability (Groves et al. 1995, Stein and Davis 2000). Nonetheless, while the usefulness of inventories and lists of species at risk as tools for planning and monitoring is unclear (Andelman and Fagan 2000, Possingham et al. 2002), quantitative analysis of Heritage Program data has seen little exploration.

Efforts to identify indicator species for biodiversity conservation and management have previously taken two approaches. Taxonomic groups, functional groups, or individual species may be identified a priori as part of an indicator scheme for studying potential reserve networks. The scheme is then tested for correspondence and correlation between the indicator group and a broader group of species using incidence and distribution data (Ryti 1992, Prendergast et al. 1993, Andelman and Fagan 2000). Alternatively, indicator groups may be inferred from empirical patterns in data obtained from statistically valid field sampling (Kremen 1992, Dufrene and Legendre 1997). Statistical analysis of Heritage Program databases is complicated because information is unavailable on unsurveyed areas and locations where tracked species were not observed. Statistically valid sampling designs are generally lacking. Natural Heritage and other species databases are often biased geographically due to differential access to private and public lands, and by focus on vertebrates and vascular plants (Margules et al. 1994). Natural Heritage Program occurrence data are, thus, not well suited for the ordination, classification, and correlation approaches used with data from randomly sampled units.

An alternative approach would be to define a null model for association of species at risk with areas of high ecosystem integrity that are recognized by employing species-independent criteria, then to test for deviations from the model using a randomization test (Rebelo and Siegfried 1992, Gotelli and Graves 1996). We develop this approach, clarifying assumptions and providing caveats that must be considered when employing these methods using Natural Heritage data or similar information. The existence of Heritage Program databases in North America and much of Latin America (Deblinger and Jenkins 1991, Groves et al. 1995) suggests that as these databases become increasingly representative of regional species occurrence, the methods developed here may be useful for identifying potential indicators for locating and managing areas with high ecosystem integrity and conservation value.

Methods

Identification of areas of high ecosystem integrity

We identified high ecosystem integrity based on four criteria in order to develop a broad set of indicators reflective of this aspect of conservation value. We defined five land types with high ecosystem integrity as: (a) areas containing biotic communities ranked as having high ecosystem integrity and conservation value following documented Natural Heritage Program methodology (Stein and Davis 2000), (b) formally designated and administratively recognized state natural areas that are managed for biodiversity conservation, (c) large contiguous blocks of remnant forest cover, (d) large contiguous blocks of remnant wetlands or wetland complexes, and (e) pooled area represented by the union of the preceding four criteria. We focused on areas within the state of Michigan (USA) because the state has a system of biotic-community classification for conservation purposes, a state natural-areas program, and access to a Natural Heritage Program database containing over 13 000 occurrences of state and federally listed species, additional species of conservation concern, and biotic-community types. These data have been collected over more than 20 years.

High-ranking biotic communities.—Each community occurrence tracked in Michigan's Natural Heritage database has been categorized based on a classification system consisting of 74 natural terrestrial and wetland community types that were derived from a classification of plant community types in Wisconsin (Curtis 1959). A list of the community types is found in Appendix A. Heritage Programs rank occurrences of communities (i.e., element occurrence or EO ranks) on a qualitative four-point scale with half steps from *A* through *D*, based on expert assessment (Master 1991, Stein and Davis 2000, Groves et al. 2003). The presence of species at risk upon which we focus our study is not a criterion used in conducting this expert assessment. All occurrences of *A*- through *D*-ranked communities in Michigan's Heritage database were digitized into a Geographic Information System (GIS) data layer from their original demarcation on U.S. Geological Survey (USGS) 7.5-minute quadrangle maps. Digitized boundaries were reviewed independently for spatial accuracy by another worker using recent geographically referenced aerial photographs.

We considered occurrences of biotic communities with EO ranks between *A* and *BC* to constitute a category of sites with high conservation value because they have lost few species due to anthropogenic causes, contain few populations of exotic invasive species in comparison to other similar areas, often occur in a relatively stable landscape context, and currently face relatively few threats to their persistence, thus suggesting high ecosystem integrity (Stein and Davis 2000, Groves et al. 2003). While we excluded lower ranked sites from consideration, species composition and vegetation structure distinguish *C*- and *D*-ranked communities from the surrounding anthropogenic landscape matrix. We considered only terrestrial areas and wetlands because a scheme for classifying aquatic communities of Michigan and other Great Lakes states is lacking. Local, regional, and national land conservancies and state natural-resource agencies use a Natural Heritage system for ranking communities to determine conservation and acquisition priorities, thus providing additional justification of these rankings as an operational basis for recognizing sites of high conservation value.

Administered natural areas.—State-administered natural areas are sites recognized as having high conservation value following expert review and achievement of standards required for this legal designation. In order to qualify as a recognized Natural Area in the State of Michigan, according to the State of Michigan Natural Resources and Environmental Protection Act (Act 451 of 1994),[2] an area must be judged during review to have ''retained or reestablished its natural character, . . . but it need not be undisturbed'' (Michigan Compiled Laws, Chapter 324, Section 324.35101(a)(i)). The list of state natural areas maintained by the Heritage Program in the Wildlife Division of the Michigan Department of Natural Resources (MDNR) also includes state-dedicated Wild Areas, state-dedicated Wilderness Areas, state-designated Natural Areas, and selected Natural Areas awaiting formal approval. We included in our analysis all these types of administratively recognized natural area because expert review and subsequent designation has affirmed their perceived conservation value. Boundaries of administered natural areas were digitized into a GIS layer, a total of 245 sites.

Contiguous forest tracts.—We used three criteria to define forest tracts with high conservation value to ensure that interior forest areas would be of sufficient size and structural integrity to support viable populations of forest-interior species. First, we assumed that edge effects penetrate 90 m into forest from the forest–non-forest boundary. While edge effects have been described for a large number of forest systems, most studies suggest that edge effects penetrate less than 150 m (Laurance 2000). Nonetheless, there are no established values for the magnitude of edge effects that would apply to a wide range of animal and plant taxa. We chose a 90-m buffer (three 30-m pixels) as a working value for an altered landscape of the North American Midwest. A 90-m buffer distance is consistent with buffers used previously (Temple 1986). There is also no universally accepted minimum width of forest canopy opening (e.g., a road or power-line cut) below which negative affects on forest communities are absent. While some studies show a correlation between the widths of openings and greater edge effect on avian species (Rich et al. 1994), we found no documented opening size that does not create edge effect. To decrease the possibility of edge effects from roads, highways, railroads, and utility rights-of-way, we buffered them by 90 meters (90 m each side, 180 m total) using an appropriate GIS data set. Second, we included all Michigan forests with interior areas larger than 100 ha. This definition of core area is consistent with suggestions for minimum core-area size for North American forest-dependent avian species (Robinson et al. 1995).

We considered only forest areas that are still compositionally similar to that recorded during the Gov-

[2] ⟨http://www.legislature.mi.gov⟩, specify section 324.35101.

ernment Land Office (GLO) surveys of the 1800s (Hutchison 1988). To identify areas of remnant vegetation (Frelich 1995) we used a statewide map of Michigan's pre-European-settlement vegetation. This map was constructed using transcribed GLO survey notes and township plat maps copied from microfilm records of the Michigan Department of Natural Resources and State Archives of Michigan (Comer et al. 1995). These surveyor notes contained information on vegetation type and tree species along section lines of each Michigan township, wetland boundaries located along each section line, and information on natural disturbances such as wildfires and wind throws (Hutchison 1988). Vegetation cover was interpreted from surveyor information onto USGS 7.5-minute paper maps, digitized, and converted into 30-m resolution raster data sets. A table of land and vegetation cover types used to create these GIS layers is found in Appendix B. Appendix C presents a map of the vegetation that preceded European settlement of Michigan ca. 1800.

A subsequent map layer representing areas with vegetation that has remained essentially unchanged through the late 20th century was made by intersecting the pre-European-settlement data layer with an additional data layer. This 30-m resolution data layer was assembled by directly classifying land cover from aerial photographs (1:24 000 scale) taken in 1978, the latest date of uniform coverage for the entire state of Michigan available at the time. A standard land-cover classification scheme was used (Anderson et al. 1976). Unchanged vegetation was identified in a GIS through supervised comparison of the land-cover types on the two layers. We identified tracts of forest that satisfied the criteria for forest-interior extent using the layer of unchanged vegetation and additional recent aerial photographic imagery. The criteria of unchanged vegetation ensured that selected forest tracts would have ecological continuity (Norden and Appelqvist 2001) extending into the period prior to settlement by Europeans, could conceivably provide refuge for species with little capacity for dispersal, and would exclude otherwise sufficiently large tracts that, while forested currently, had experienced overwhelming anthropogenic influence. Appendix D presents a map of the distribution of unchanged vegetation in Michigan. This and the pre-European-settlement vegetation data layer are available as GIS data sets (Supplement 1).

Contiguous wetland areas.—All wetland classes were subset from the most current land-cover raster data sets of Michigan and merged with National Wetlands Inventory 1:24 000 palustrine classes. Two criteria were used to define contiguous tracts of wetland with high ecosystem integrity. We selected wetlands larger than 100 ha in recognition that larger remnant wetland complexes were more likely to support intact ecological functions and processes. To exclude wetlands differing from the type recorded in the original GLO land surveys we intersected GIS layers of contiguous wetland areas and unchanged land-cover types. This eliminated anthropogenic wetlands and such artificial environments as reservoirs and excavated ponds. Wetland complexes were not buffered for edge effects because many were natural, open-canopy systems and contained wetland–upland ecotones that may harbor rare species.

All areas pooled.—We constructed a pooled data set in which GIS layers representing all four land types were combined to create a single layer. This data set thus represented the application of four criteria for identifying areas with high ecosystem integrity and conservation value within Michigan, providing the most comprehensive statement of the distribution of valuable land types, based on ecosystem integrity, for conservation in the state.

A null model and a test

A proportion p of n total occurrences of all species fell within the geographic limits of a particular land type, as did a proportion p_i of occurrences of each species i. Under a null model, species did not vary in their association with a land type, except for random variation:

$$p_i = p_j = \mathrm{E}(p) \quad \text{for all } i \neq j$$

where $\mathrm{E}(p)$ is the expected proportion of occurrences of species i and j falling within areas of a land type, and is estimated in a real database by p as determined by maximum likelihood (Beard et al. 1999).

Simultaneously for each species in the database, we tested the proposition that some species are more strongly associated with a particular land type than expected. We examined the probability under the null model of observing as many or more occurrences of a species within land type boundaries as actually occur in the data set. These probabilities were equivalent to Type I statistical-error probabilities in a standard statistical test (Manly 2001) and were estimated with a randomization procedure. A data set was created with the same number of occurrences of each species as in the original data set. A proportion pn of the occurrences randomly received a value of 1 (falling within the land type), and the remaining $1 - pn$ occurrences received a value of 0. This procedure was repeated to create 1000 independently randomized data sets. The estimated probabilities for each species were calculated as

$$P_i(N_i \geq n_i) = 1 - \sum_{x=0}^{n_i - 1} r_{ix} \qquad (1)$$

where P_i is the randomization probability of observing as many or more occurrences of a species within land-type boundaries, N_i is the random variable of interest for the ith species, n_i is the number of occurrences of the species within the land type, and r_{ix} is the proportion of randomized data sets in which there are exactly x

occurrences of species *i* within the area defined by the land type.

We intersected species-occurrence data with the GIS layer representing the spatial extent of each land type, in order to determine whether each occurrence lay within land-type boundaries. We determined the number of occurrences that corresponded to a randomization probability of 5% for each species. Some species had many more occurrences in areas corresponding to particular land types than was expected under the null model and determining the randomization P_i directly based on 1000 randomized data sets was not possible. We estimated the randomization P_i for each species by first calculating the mean and standard deviation of the species' randomization distribution, and then calculating the corresponding cumulative frequency using fitted normal distributions. The normal distribution provided a good fit to the randomization distribution of occurrences, as long as there were ~20 or more occurrences of the species in the database. We also estimated randomization P_i using the randomization mean to fit the Poisson distribution. The choice of distribution as a basis for P_i estimation had very little effect on identification of potential indicator species in the statistical selection procedure that we employed. The lists of potential indicator species presented here were based on randomization P_i estimated from the normal distribution.

Using a single real data set to construct multiple statistical tests may result in inflation of Type I error, i.e., the problem of multiple comparisons (Mendenhall et al. 1981). We accounted for this in constructing the lists of potential indicators by first ranking species by increasing value of P_i as estimated from the fitted normal distributions. For each successive species, we employed the Bonferroni criterion (Mendenhall et al. 1981) for a number of comparisons equal to the rank of the species. A species was significantly associated with a land-cover class to a greater degree than expected under the null model if the estimated randomization P_i was smaller than the corresponding Bonferroni critical value. Species with relatively few occurrences in the state were unlikely to be included on the list using this procedure because they were unlikely to have an extremely small estimated randomization P_i.

We evaluated the rank correlation among the five indicator groups in terms of (a) indicator species richness and (b) total number of occurrences of indicator species in the 1900 full mainland townships in Michigan. We then eliminated from consideration all townships that had no occurrence of a potential indicator in any of the five groups, leaving 922 of 1900 townships. We constructed a vector consisting of the number of species occurrences in each of the five indicator groups in each township and evaluated the 922 townships using data from the Michigan Natural Heritage database. We subjected the vector to variable reduction using principal-component analyses (PCA; Morrison 1976) to summarize the variation in number of occurrences of species in the five groups. We then weighted the scores of townships on the principal components by the corresponding eigenvalues in order to reflect the relative contribution of the indicator groups to overall data variability. The weighted scores were then summed. We ranked the townships based on these sums to create a proposed conservation prioritization based on the occurrence of the potential indicators of ecosystem integrity.

Results

Areas of high ecosystem integrity

The areas of high ecosystem integrity corresponding to the five land types varied in terms of the number of areas in the state, the average area size and the total extent comprised by the areas (Fig. 1, Table 1). No definition resulted in consideration of more than 4.5% of the entire area of the State of Michigan (USA). Highly ranked biotic communities were smaller on average than the other three land types, while contiguous forest areas had the largest average size. Administratively recognized natural areas were the least numerous in Michigan, and were outnumbered by a factor of 3.2 by highly ranked communities, a factor of 5.6 by contiguous forest sites, and a factor of 3.6 by contiguous wetlands. A larger percentage of occurrences of at-risk species lay within areas identified under the highly ranked communities criterion than lay within areas identified using the other criteria (Table 1). Five supplemental data sets containing the GIS layers for areas of high ecosystem integrity in Michigan are available as Supplement 2.

Indicator species

Sixteen species were significantly associated with high-ranking occurrences of biotic communities once the Bonferroni criterion was applied (Table 2). In comparison, there were seven species, six species and three species identified as being significantly associated with administered natural areas, contiguous forests and contiguous wetlands, respectively. Potential indicator species (Table 2) that were identified through their association with high-ranking communities included plants associated with fens [e.g., Richardson's sedge (*Carex richardsonii*), Indian-plaintain (*Cacalia plantaginea*), tall beaked-rush (*Rhynchospora macrostachya*), black-fruited spike-rush (*Eleocharis melanocarpa*), small white lady's-slipper (*Cypripedium candidum*)], a plant associated with alvar and wet prairies (northern drop-seed, *Sporobolus heterolepis*), and plants and animals associated with the Great Lakes shoreline [dwarf lake iris (*Iris lacustris*), Houghton's goldenrod (*Solidago houghtonii*), dune thistle (*Cirsium pitcheri*), and the Piping Plover (*Charadrius melodus*)]. These last four species are primarily responsible for the clustering of species occurrences along the margin of the Great

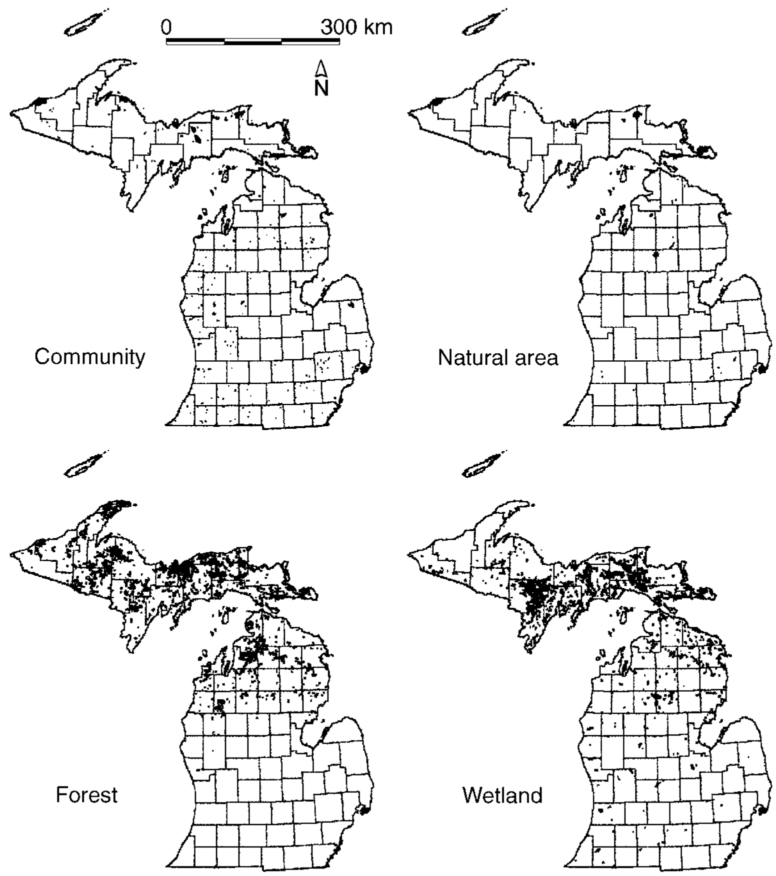

FIG. 1. Distribution of areas of four land types (within Michigan, USA), identified using four criteria for high ecosystem integrity (see *Methods: Identification. . . : High-ranking biotic communities, Administered natural areas, Contiguous forest. . .* , and *Contiguous wetland. . .* for criteria descriptions).

Lakes (Fig. 2). Species associated with administered natural areas were predominantly found in lakeshore habitats or in wet prairies and were essentially a subset of species identified based on association with highly ranked communities. Species that were significantly associated with contiguous forest areas included breeding populations of two raptors (the Osprey, *Pandion haliaetus*, and Red-shouldered Hawk, *Buteo lineatus*), a spleenwort associated with densely shaded, moist rocky outcrops (walking-fern, *Asplenium rhizophyllum*), an orchid of densely shaded forests (fairy slipper, *Calypso bulbosa*) and a grass associated with woody habitats principally near Lake Superior (smooth wild rye, *Elymus glaucus*). Species associated with large contiguous wetlands included breeding populations of the Osprey and Bald Eagle (*Haliaeetus leucocephalus*), and a clubmoss found in wetlands with a marked hydrological cycle (fir clubmoss, *Huperzia selago*). Elev-

TABLE 1. Summary of characteristics of areas of high conservation value (HCV) in the State of Michigan (USA), identified using four criteria.

Criterion	No. areas	Average area size (ha)	Total area in state (ha)	Percentage of state	Occurrences of species at risk within areas (%)
Highly ranked community	776	176	136 148	0.9	18.3
Natural area	245	221	54 038	0.4	4.7
Integral forest area	1377	235	323 942	2.2	4.8
Integral wetlands	872	333	290 606	1.9	5.7
All criteria together†	2764	237	655 589	4.4	26.2

Notes: The total number of areas and total extent of all high-value sites together is less than the sum under the four criteria individually. Some wetlands contained forested areas, for example, and no area was counted more than once.

† A fifth criterion was established by pooling all the areas to create a composite group.

TABLE 2. Potential indicator species associated with areas of high conservation value (HCV) identified using five criteria, together with *P* values, decision values, and ranks.

Species name (family)	Common name	No. occurrences: Michigan	No. occurrences: HCV areas	No. occurrences: Critical†
Communities criterion				
Carex richardsonii (Cyperaceae)	Richardson's sedge	25	16	7
Cacalia plantaginea (Asteraceae)	prairie Indian-plantain	43	21	11
Rhynchospora macrostachya (Cyperaceae)	tall beaked-rush	53	23	14
Rhexia virginica (Melastomataceae)	Virginia meadow-beauty	41	19	11
Eleocharis melanocarpa (Cyperaceae)	black-fruited spike-rush	46	20	12
Sporobolus heterolepis (Poaceae)	northern dropseed	30	15	8
Solidago houghtonii (Asteraceae)	Houghton's goldenrod	65	25	16
Cypripedium candidum (Orchidaceae)	small white lady's-slipper	79	28	19
Iris lacustris (Iridaceae)	dwarf lake iris	81	28	20
Rotala ramosior (Lythraceae)	toothcup	42	17	11
Valeriana edulis var. *ciliata* (Valerianaceae)	hairy valerian	24	11	7
Oecanthus laricis (Gryllideae)	tamarac tree cricket	42	16	11
Platanthera leucophaea (Orchidaceae)	eastern prairie white-fringed orchid	34	14	9
Cirsium pitcheri (Asteraceae)	dune thistle	155	42	37
Neonympha mitchellii mitchellii (Nymphalidae)	Mitchell's satyr	22	10	6
Charadrius melodus (Charadriidae)	Piping plover	46	16	12
Psilocarya scirpoides (Cyperaceae)	long-beaked baldrush	27	11	8
Trisetum spicatum (Poaceae)	narrow false oats	31	12	9
Trimerotropis huroniana (Acrididae)	Lake Huron locust	82	24	20
Angelica venenosa (Apiaceae)	hairy angelica	31	11	9
Calephelis mutica (Riodinidae)	swamp metalmark	23	9	7
Pterospora andromedea (Monotropaceae)	pinedrops	39	13	10
Castilleja septentrionalis (Scrophulariaceae)	pale Indian-paintbrush	28	10	8
Lycopodium appressum (Lycopodiaceae)	southern bog clubmoss	24	9	7
Tanacetum huronense (Asteraceae)	Lake Huron tansy	111	28	27
Natural-areas criterion				
Platanthera leucophaea (Orchidaceae)	eastern prairie white-fringed orchid	34	11	4
Charadrius melodus (Charadriidae)	Piping Plover	46	12	5
Trimerotropis huroniana (Acrididae)	Lake Huron locust	82	15	7
Iris lacustris (Iridaceae)	dwarf lake iris	81	13	7
Cirsium pitcheri (Asteraceae)	dune thistle	155	19	11
Solidago houghtonii (Asteraceae)	Houghton's goldenrod	65	10	6
Asclepias sullivantii (Asclepiadaceae)	prairie milkweed	20	5	3
Asclepias purpurascens (Asclepiadaceae)	purple milkweed	24	3	3
Sterna hirundo (Laridae)	Common Tern	81	8	7
Orobanche fasciculata (Orobanchaceae)	clustered broomrape	19	3	3
Carex richardsonii (Cyperaceae)	Richardson's sedge	25	3	3
Contiguous-forests criterion				
Pandion haliaetus (Accipitridae)	Osprey	319	63	20
Buteo lineatus (Accipitridae)	Red-shouldered Hawk	309	45	20
Cryptogramma stelleri (Pteridaceae)	fragile rockbrake	41	13	4
Asplenium rhizophyllum (Aspleniaceae)	walking-fern	26	9	3
Elymus glaucus (Poaceae)	smooth wild-rye	19	7	2
Calypso bulbosa (Orchidaceae)	fairy slipper	98	14	8
Vertigo paradoxa (Pupillidae)		20	4	3
Asplenium trichomanes-ramosum (Aspleniaceae)	green speenwort	23	4	3
Pinguicula vulgaris (Lentibulariaceae)	common butterwort	63	7	6
Accipiter gentilis (Accipitridae)	Northern Goshawk	87	8	7
Haliaeetus leucocephalus (Accipitridae)	Bald Eagle	506	30	31
Contiguous-wetlands criterion				
Pandion haliaetus (Accipitridae)	Osprey	319	89	24
Haliaeetus leucocephalus (Accipitridae)	Bald Eagle	506	48	35
Huperzia selago (Lycopodiaceae)	fir clubmoss	23	5	3
Rallus elegans (Rallidae)	King Rail	38	6	5
Appalachia arcana (Acridadae)	secretive locust	45	6	5
All-areas-pooled criterion				
Carex richardsonii (Cyperaceae)	Richardson's sedge	25	18	10
Pandion haliaetus (Accipitridae)	Osprey	319	117	110
Platanthera leucophaea (Orchidaceae)	eastern prairie white-fringed orchid	34	20	13
Rhexia virginica (Melastomataceae)	Virginia meadow-beauty	41	21	15
Cacalia plantaginea (Asteraceae)	prairie Indian-plantain	43	21	15
Solidago houghtonii (Asteraceae)	Houghton's goldenrod	65	29	22
Iris lacustris (Iridaceae)	dwarf lake iris	81	34	27

TABLE 2. Extended.

	Bonferroni		Ranks	
P	P	N‡	G	S
8.70×10^{-9}	0.05	1	G4	S3S4
1.03×10^{-7}	0.025	2	G4G5	S3
2.62×10^{-7}	0.017	3	G4	S3S4
3.56×10^{-6}	0.013	4	G5	S3
5.50×10^{-6}	0.01	5	G4	S3
6.42×10^{-6}	0.0083	6	G5	S3
1.97×10^{-5}	0.0071	7	G3	S3
5.14×10^{-5}	0.0063	8	G4	S2
5.65×10^{-5}	0.0056	9	G3	S3
9.42×10^{-5}	0.005	10	G5	S3
7.85×10^{-4}	0.0045	11	G5T3	S2
1.19×10^{-3}	0.0042	12	G1G2	S1S2
1.40×10^{-3}	0.0038	13	G2	S1
1.42×10^{-3}	0.0036	14	G3	S3
1.69×10^{-3}	0.0033	15	G1G2T1T2	S1
2.06×10^{-3}	0.0031	16	G3	S1
3.22×10^{-3}	0.0029	17	G4	S2
4.06×10^{-3}	0.0028	18	G5	S2S3
4.79×10^{-3}	0.0026	19	G2G3	S2S3
0.0109	0.0025	20	G5	S2
0.0120	0.0024	21	G3G4	S1S2
0.0150	0.0023	22	G5	S2
0.0184	0.0022	23	G5	S2S3
0.0198	0.0021	24	G5	S2
0.0212	0.0020	25	G5T4T5	S3
1.03×10^{-13}	0.05	1	G2	S1
1.57×10^{-10}	0.025	2	G3	S1
9.19×10^{-09}	0.017	3	G2G3	S2S3
1.10×10^{-06}	0.0125	4	G3	S3
2.22×10^{-06}	0.01	5	G3	S3
7.90×10^{-05}	0.0083	6	G3	S3
2.15×10^{-05}	0.0071	7	G5	S2
0.0343	0.0063	8	G5	S3
0.0371	0.0056	9	G5	S2
0.0948	0.005	10	G4	S2
0.2070	0.0045	11	G4	S3S4
0	0.05	1	G5	S4
1.89×10^{-15}	0.025	2	G5	S3S4
9.10×10^{-15}	0.017	3	G5	S3S4
1.63×10^{-11}	0.0125	4	G5	S2S3
1.16×10^{-09}	0.01	5	G5	S3
2.19×10^{-05}	0.0083	6	G5	S2
0.0102	0.0071	7	G3Q	S3
0.0269	0.0063	8	G4	S2S3
0.0289	0.0056	9	G5	S3
0.0430	0.0051	10	G5	S3
0.0828	0.0045	11	G4	S4
0	0.05	1	G5	S4
1.09×10^{-5}	0.025	2	G4	S4
0.0062	0.017	3	G5	S3
0.017	0.0125	4	G4	S1
0.040	0.0100	5	G2G4	S2S3
9.75×10^{-8}	0.05	1	G4	S3S4
1.44×10^{-7}	0.025	2	G5	S4
5.66×10^{-6}	0.017	3	G2	S1
1.07×10^{-4}	0.0125	4	G5	S3
4.39×10^{-4}	0.01	5	G4G5	S3
4.83×10^{-4}	0.0083	6	G3	S3
5.99×10^{-4}	0.0071	7	G3	S3

TABLE 2. Continued.

Species name (family)	Common name	No. occurrences: Michigan	HCV areas	Critical†
Rhynchospora macrostachya (Cyperaceae)	tall beaked-rush	53	24	18
Cryptogramma stelleri (Pteridaceae)	fragile rock brake	41	20	15
Eleocharis melanocarpa (Cyperaceae)	black-fruited spike-rush	46	21	16
Sporobolus heterolepis (Poaceae)	northern dropseed	30	15	11
Trimerotropis huroniana (Acrididae)	Lake Huron locust	82	31	27
Pterospora andromedea (Monotropicaceae)	giant pinedrops	39	17	14
Rotala ramosior (Lythraceae)	toothcup	42	18	15
Charadrius melodus (Charadriidae)	Piping Plover	46	19	16
Cypripedium candidum (Orchidaceae)	small white lady's-slipper	79	28	26
Elymus mollis (Poaceae)	American dune wild-rye	21	10	9
Valeriana edulis var. *ciliata* (Valerianaceae)	hairy valerian	24	11	9
Neonympha mitchellii mitchellii (Nymphalidae)	Mitchell's satyr	22	10	9
Angelica venenosa (Apiaceae)	hairy angelica	31	13	12
Castilleja septentrionalis (Scrophulariaceae)	pale Indian-paintbrush	28	12	11
Oecanthus laricis (Gryllideae)	tamarac tree cricket	42	16	15
Huperzia selago (Lycopodiaceae)	fir clubmoss	23	10	9
Psilocarya scirpoides (Cyperaceae)	long-beaked baldrush	27	11	10
Trisetum spicatum (Poaceae)	narrow false oats	31	12	12

Notes: For descriptions of the criteria, see *Methods: Identification. . . : High-ranking biotic communities*, *Administered natural areas*, *Contiguous forest tracts*, and *Contiguous wetland areas*. Species are compared in terms of the total number of occurrences in Michigan (USA) and in areas of high conservation value (HCV), the number of occurrences in high-value areas needed for a randomization P value of 0.05 (''Critical''), the P value for the species that is estimated from fitting a normal distribution to the randomization results, and the Bonferroni-corrected decision values for a number of comparisons corresponding to the rank of the species in the list. NatureServe G-ranks and Michigan S-ranks are as of date of publication.

† Number of occurrences sufficient for significance at the $P = 0.05$ level.

‡ Number of tests upon which Bonferroni correction of critical value is based.

en species were significantly associated with areas of high ecosystem integrity in an analysis that pooled areas identified under each of the four criteria (Table 2).

Spatial distribution of indicators

The spatial distribution of the known occurrences of species at risk identified as potential indicators varied markedly with the criterion used to define high ecosystem integrity (Fig. 2). In general, occurrences of potential indicators were concentrated in the northern portion of Michigan's Lower Peninsula and in the Upper Peninsula. Additionally, species selected using highly ranked terrestrial communities occurred in the south and south-central portion of the Lower Peninsula, and along the margins of the Great Lakes (Fig. 2). Potential indicators selected using the administered natural areas criterion were primarily (five of six species) distributed along the margins of the Great Lakes (Fig. 2). Indicators identified through significant association with contiguous forest and contiguous wetlands (Fig. 2) were conspicuously absent from the areas of arable land throughout the southern portion of the Lower Peninsula of Michigan. Occurrences of potential indicators associated with forest are clumped in two areas of the northern Lower Peninsula, while occurrences of species associated with large wetlands are well distributed across the northern Lower Peninsula. Two nuclei of occurrences of Red-shouldered Hawk in the northern and northwestern portions of Michigan's Lower Peninsula are responsible for the clusters of points seen in the species associated with contiguous forest (Fig. 2). Occurrences of potential indicators identified using the pooled areas of high ecosystem integrity (Table 2) were well distributed throughout the state (Fig. 3).

Two patterns emerged when we evaluated the five groups of potential indicators for correlated patterns across 1900 townships in Michigan. Species richness and number of occurrences of potential indicators of forest and wetland ecosystem integrity were correlated, as were richness and occurrence of indicators identified using biotic communities and administered natural areas. Tables presenting full correlation analysis results for both species richness of potential indictors and number of occurrences in 1900 townships are found in Appendix E. The values for administered natural areas and forest indicators were weakly correlated compared to other significant correlations in the table. The general pattern in the correlations was also observed in PCA of the number of occurrences of potential indicators in 942 Michigan townships where indicator species were present. The first principal component reflected variation in the occurrence of species identified using the pooled land type and the high-ranking community criteria, and accounted for 43% of the occurrence variation. The second principal component accounted for an additional 32% and reflected variation in occurrence of species identified under the forest and wetland criteria. The third principal component explained less variation, 12.5%, and was dominated by the designated natural areas criterion. The remaining principal components were not as easily interpreted (see Appendix F for full

TABLE 2. Extended. Continued.

	Bonferroni		Ranks	
P	*P*	*N*‡	G	S
6.93×10^{-4}	0.0063	8	G4	S3S4
7.22×10^{-4}	0.0056	9	G5	S3S4
1.93×10^{-3}	0.005	10	G4	S3
3.12×10^{-3}	0.0045	11	G5	S3
6.68×10^{-3}	0.0042	12	G2G3	S2S3
6.74×10^{-3}	0.0038	13	G5	S2
0.011	0.0036	14	G5	S3
0.014	0.0033	15	G3	S1
0.021	0.0031	16	G4	S2
0.024	0.0029	17	G5	S3
0.026	0.0028	18	G5T3	S2
0.033	0.0026	19	G1G2T1T2	S1
0.036	0.0025	20	G5	S3
0.042	0.0024	21	G5	S2S3
0.047	0.0023	22	G1G2	S1S2
0.052	0.0022	23	G5	S3
0.056	0.0021	24	G4	S2
0.072	0.0020	25	G5	S2S3

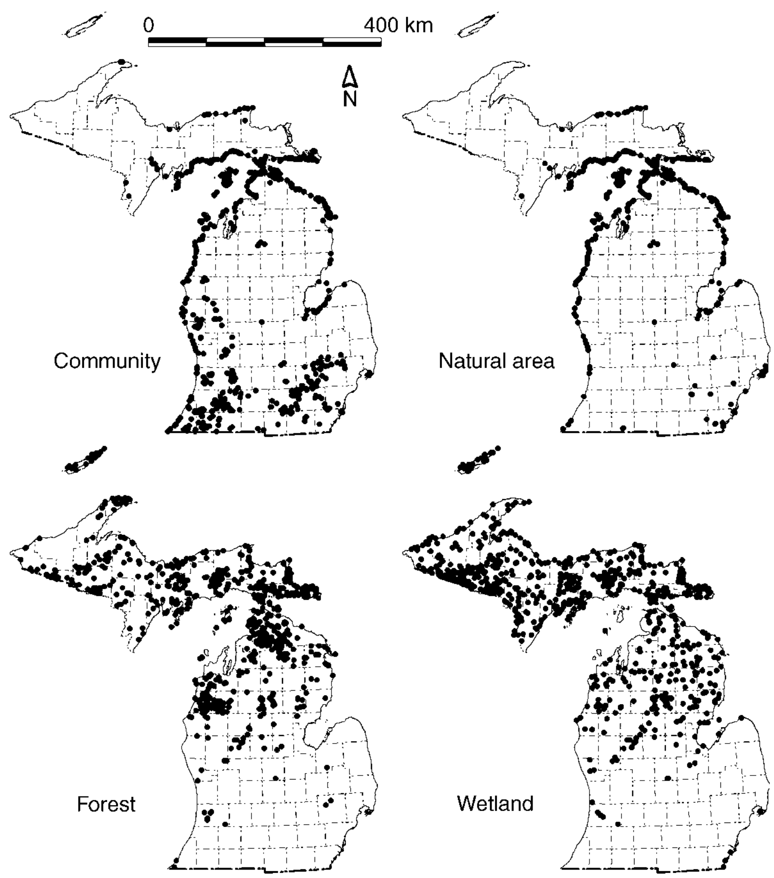

FIG. 2. Distribution of all known occurrences of potential indicator species, as identified in the Michigan Natural Heritage database, using four criteria for defining areas of high ecosystem integrity.

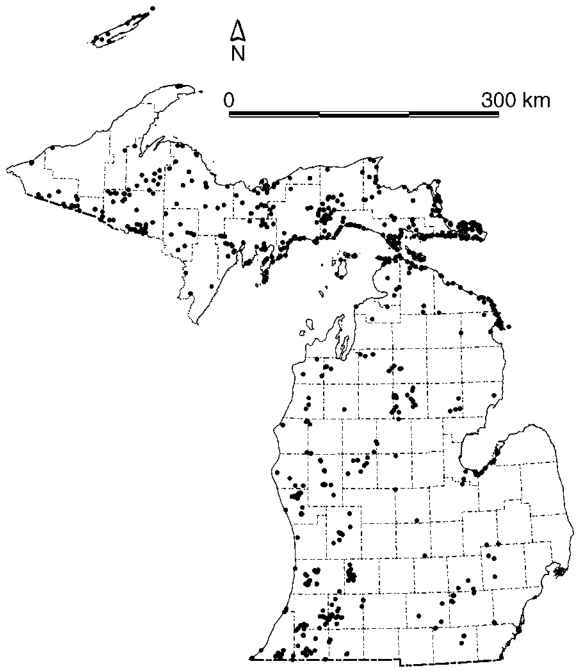

FIG. 3. Distribution of all known occurrences of potential indicator species, as identified in the Michigan Natural Heritage database, using the pooled area of high ecosystem integrity comprising highly ranked communities, administered natural areas, contiguous forest, and contiguous wetlands (for definitions see relevant sections of *Methods: Identification. . .*).

PCA results). We used the summed weighted scores on the first two principal components to rank the 924 townships (Fig. 4). The locations of the top 5% of the townships were widely dispersed across the state and were largely indicative of the geographic pattern that arose upon consideration of additional, lower ranked townships.

DISCUSSION

Indicator species may be useful in conservation planning and in monitoring the efficacy of conservation programs and management strategies (Landres et al. 1988, Noss 1990). Nonetheless, diversity within indicator groups and taxa demonstrates mixed performance as a tool to enable prioritization of areas for conservation because hotspots of diversity in different groups often do not coincide (Prendergast et al. 1993) and few species or groups may meet multiple indicator criteria (Hilty and Merenlender 2000). Further, species in greatest need of attention may not be covered in areas selected by indictor schemes (Lawler et al. 2003). The use of species-occurrence data for conservation planning entails caveats because their collection is not optimized for hypothesis testing and monitoring (Possingham et al. 2002). Nonetheless, Natural Heritage program databases provide information on the local and regional distribution of species at risk in much of North America (Groves et al. 2003). These data are currently used to identify hotspots of conservation need based on level of species endangerment and threats to persistence, and to support environmental review under regulatory frameworks (Stein and Davis 2000). Our study suggests that potential indicators of high conservation value can be selected through their association with ecosystem integrity. Indicators of ecosystem integrity may complement other measures of conservation value (Pressey et al. 1993, Margules and Pressey 2000) and assist in the identification of additional areas of conservation importance.

The randomization method we present compares distribution and occurrence information among species, all of which are of demonstrable conservation interest. It identifies species that are significantly associated with recognized areas of high ecosystem integrity and viability, in comparison with other at-risk species. The potential indicator species identified here are associated to an unusual degree with a very small portion of the total landscape (Table 1), suggesting that the conditions present in these areas contribute to the persistence of the most threatened components of biodiversity. The actual mechanisms responsible for the association have not been studied, but may be as simple as, for example, the presence of topographical features that create favorable wetland hydrology and the parallel destruction of other (previously occupied) habitat types. In contrast, several large raptors have significant associations with large wetland complexes and forest remnants (Fig. 1, Table 2). Successful nesting of large raptors both inside and outside of the high-value areas we identified indicates an adequate prey base, vertical structure sufficiently complex to provide nest sites (often trees), and other requirements for reproduction. Thus, areas outside of the high-value areas we used to select potential indicators can also support processes that actively contribute to the persistence of populations of these species. We emphasize that the species identified here are potentially indicators of areas of conservation value provided by ecosystem integrity. Focused study of areas in which these potential indicators occur may reveal additional sites of existing conservation value in the form of communities with associated native biodiversity, areas with marked ecosystem function and restoration potential, and/or relic populations that, while in areas of diminished habitat quality, may contribute to maintenance of regional distribution and population connectivity.

The use of indicator species has been proposed for adaptive management for preserving ecosystem integrity, function, and levels of biodiversity (Stork et al. 1996). Ideally, indicators for adaptive management provide readily observable metrics that lie intermediate between changing levels of threat and stress, and presage broad responses by complicated and diverse ecological systems (Elzinga et al. 2001, Noon 2003). Data on carefully chosen indicators could provide infor-

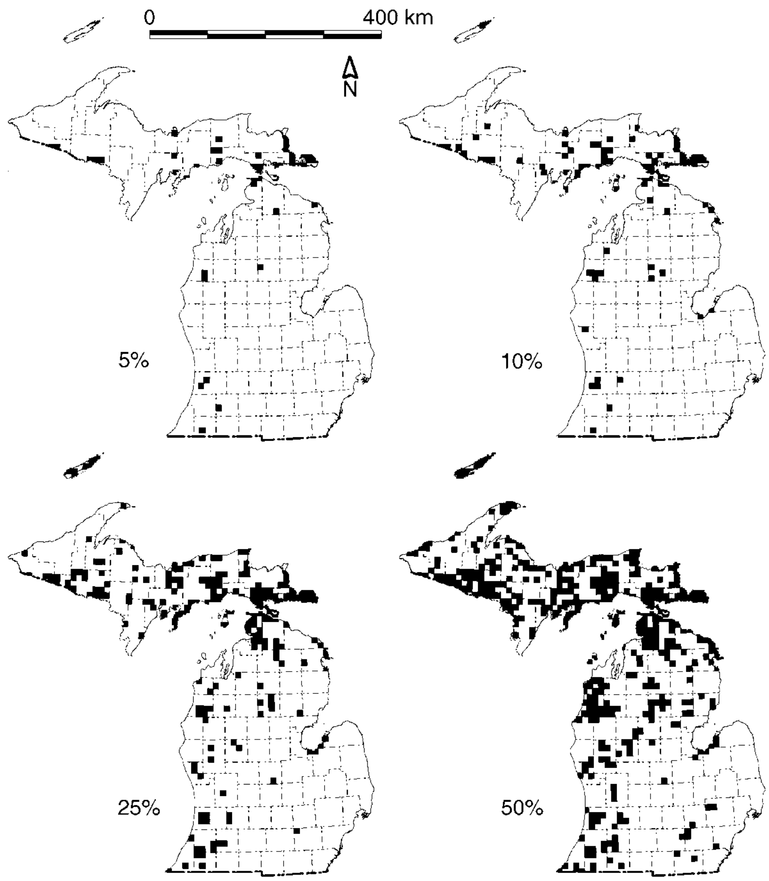

FIG. 4. Distribution of upper percentiles of ranked townships based on the occurrence of potential rare-species indicators of ecosystem integrity. Ranks are based on the weighted sum of the first two principal-component scores from a principal-components analysis of the number of occurrences of potential indicators selected under five criteria.

mation on pending or incipient ecological changes and thus enable timely management responses. Species at risk may prove to be practical indictors for management of anthropogenic impacts and ecological integrity when a regionally distributed pool of species at risk responds to threats and stresses that are also regionally distributed (Frelich 1995). Statewide or regional trends in species exhibiting strong empirical associations with areas of high ecological integrity could alert managers to trends in the ecosystem integrity and function of focal areas before the majority of the components of biodiversity are affected. To be useful in management, these indicators should be easy to identify and sample, cost effective, and provide sufficient sample size for trend analysis (Elzinga et al. 2001).

Definitions of ecosystem integrity

We developed four spatial definitions of high ecosystem integrity with which to search for associated species that may potentially indicate conservation value. Use of these four definitions and a fifth category, the pooled area, influenced the identity (Table 2) and distribution (Fig. 2) of the potential indicators. First, even though the areas with high ecosystem integrity constituted a minute portion of the total land area under consideration (Fig. 1), the occurrences of indicator species were often widely distributed across the entire state. One exception was the species identified through consideration of administered natural areas. These species were primarily distributed along the margins of the Great Lakes. Administered natural areas constitute less total area than was comprised under other criteria (Table 1), and do not include habitats preferred by some of the potential indicators identified under the other definitions of ecosystem integrity. Further, the approval of Michigan's administered natural areas is an ad hoc process, involves an expert committee of varying composition, and operates with much looser guidelines than the quantitative aspects that comprised the other three criteria, thus allowing more opportunity for subjective influence and political motivation. The exact influence and importance of floristic and faunistic composition on the designation of these areas, including the potential influence of the presence of rare species, is difficult to evaluate using available historical information. The influence of the administered natural areas criterion was less than other criteria in identifying broad patterns of indicator species occurrence using PCA (Table 2).

Second, restrictive definitions of ecosystem integrity (i.e., those resulting in fewer hectares of area with high conservation value) may sometimes result in fewer occurrences of at-risk species falling within the defined areas. When restrictive definitions produce a land type with a small footprint, occurrence of species at risk within the footprint is a rare event, and a smaller proportion of the species' occurrences need to fall into the defined area for a statistically significant association to be detected. For example, the critical number for significance at the $\alpha = 0.05$ level for *Lycopodium appresum* (Table 2, communities) and *Asclepias purpurascens* (Table 2, natural areas) were 7 and 3, respectively, even though both species have 24 occurrences within the state. Finally, use of the Bonferroni criteria constrains Type I error, but may inflate Type II error rates (Zar 1999) and contribute to differences in the identity of potential indicators when using various criteria for conservation value. Many species associated with highly ranked communities, for example, had *P* values that exceeded the relevant Bonferroni-adjusted alpha value (0.0029, Table 2) but were well under $P = 0.05$. These species may also merit study as potential indicators.

Potential limitations to the use of rare species as indicators

While we identify species with significantly more recorded occurrences than expected in areas representative of high ecosystem integrity, low existing threats, and physical contiguity, there are potential limitations to our methods. Relationships between most groups of indicators and levels of biodiversity have not generally been well established (Lindenmayer et al. 2000). We emphasize that our results present *potential* indicators whose usefulness for indicating areas of conservation value is a hypothesis that may be confirmed with additional study. Recognition of potential biases in the identification of potential indicators using data on species at risk will contribute to their study and application for conservation planning and adaptive management.

Detection and sampling bias.—Authors have questioned the usefulness of species inventories and lists for biodiversity conservation because of the incompleteness of the data, potential biases that result from ad hoc collection of information, and the possibility that the data do not accurately represent species distribution (Margules et al. 1994, Renner and Ricklefs 1994). Analyses using Heritage Program data may also incorporate bias because statistically valid sampling schemes and data on species absence are generally lacking. The challenge of gaining access to private land leads to a strong bias in favor of conducting surveys on public land. This may lead to the association of species with particularly well-visited and surveyed areas. For example, the larger proportion of species at risk occurrences in highly ranked communities relative to areas identified under other criteria (Table 1) may reflect greater survey effort in these areas, while nevertheless suggesting the association of some species at risk with areas of high ecosystem integrity.

We believe that sampling bias will be less likely to impact indicator identity when analyses use databases including species that, while arguably at risk at some level, demonstrate a substantial number of occurrences. Of the species identified as potential indicators in this study, some relatively widely distributed species, such as the Osprey (*Pandion haliaetus*), Bald Eagle (*Haliaeetus leucocephalus*), and Pitcher's thistle (*Cirsium pitcheri*) have >100 registered occurrences, are readily recognized by nonspecialists and, thus, their occurrences are well reported. In contrast, extremely rare species are unlikely to be chosen here as potential indicators of conservation value because (1) a high proportion of the occurrences must fall within a very small proportion of the state's total land area and (2) implementation of the Bonferroni criterion further weighs against selection of species with relatively few occurrences within the state. Finally, species with very few occurrences are unlikely to be broadly distributed, may have narrow habitat requirements, and/or may have received a disproportionate amount of attention in inventory efforts and ad hoc reporting because of their extreme rarity. This suggests that development of indicators of ecological integrity may complement strategies involving algorithms to estimate irreplaceability as these may give weight to extremely rare species (Pressey et al. 1993, Margules and Pressey 2000).

We assumed species do not vary systematically in their probability of detection. We believe species with few occurrences and narrow habitat requirements are the most likely to experience this sampling bias. Their observation may result from targeted surveys in appropriate habitat within areas recognized or suspected to have high conservation value. These species are unlikely to be selected as potential indicators in this study because extraordinarily uncommon species cannot present small randomization *P* values. Finally, the statewide distribution of highly ranked townships (Fig. 4) suggests that large-scale geographic biases in Michigan's Heritage Program data are not evident at this scale.

Temporal bias.—Temporal bias may affect analyses based on incidence data obtained through Natural Heritage Program databases because the data on occurrences of species represent observations of species locations at different times. All Natural Heritage Program databases are constantly being updated (Jenkins 1988, Stein and Davis 2000) but observation date does not imply current presence or absence. In analysis, we used all observations on terrestrial and wetland species regardless of time elapsed since a species was last confirmed at a site. Regardless of their relative ages, the observations in Michigan's Heritage database constitute a recent, composite snapshot of the known distribution of species at risk. These observations stand in contrast to the longer history of large-scale habitat disturbance beginning in the 19th century (Frelich 1995).

Utility of rare species as indicators.—Some species with strong fidelity to defined land types may be small and difficult to detect, exhibit sporadic or unpredictable emergence, be difficult to identify (e.g., cryptic species requiring examination by taxonomic specialists) or require specialized capture techniques. For example, *Rhynchospora macrostachya* and *Eleocharis melanocarpa* occur in coastal plain marshes in Michigan (Reznicek 1994) and emerge from seed banks only when seasonal drawdowns attain a specific level (Keddy and Reznicek 1982). Identification may complicate the use of these species of Cyperaceae. *Trimerotropis huroniana*, a locust species endemic to Great Lakes coastal dunes, may also present identification problems. Nonetheless, Natural Heritage Program data on species occurrence and natural communities, when combined with information on land-cover and natural-area boundaries, can be used to identify potential indicators of conservation value in pools of species at risk.

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Literature Cited

Andelman, S. J., and W. F. Fagan. 2000. Umbrellas and flagships: efficient conservation surrogates or expensive mistakes? Proceedings of the National Academy of Sciences (USA) **97**:5954–5959.

Anderson, J. R., E. E. Hardy, J. T. Roach, and R. E. Witmer. 1976. A land use and land cover classification system for use with remote sensor data. Professional Paper 964. U.S. Geological Survey, Reston, Virginia, USA.

Balmford, A. K., et al. 2002. Ecology. Economic reasons for conserving wild nature. Science **297**:950–953.

Beard, K. H., N. Hengartner, and D. K. Skelly. 1999. Effectiveness of predicting breeding bird distributions using probabilistic models. Conservation Biology **13**:1108–1116.

Brooks, T. M., G. A. B. da Fonseca, and A. S. L. Rodrigues. 2004*a*. Protected areas and species. Conservation Biology **18**:616–618.

Brooks, T. M., G. A. B. da Fonseca, and A. S. L. Rodrigues. 2004*b*. Species, data, and conservation planning. Conservation Biology **18**:1682–1688.

Chase, M. K., W. B. Kristan, A. J. Lynam, M. V. Price, and J. T. Rotenberry. 2000. Single species as indicators of species richness and composition in California coastal sage scrub birds and small mammals. Conservation Biology **14**: 474–487.

Comer, P. J., D. A. Albert, H. A. Wells, B. L. Hart, J. B. Raab, D. L. Price, D. M. Kashian, R. A. Corner, and D. W. Schuen. 1995. Michigan's native landscape as interpreted from the General Land Office surveys 1816–1856. Report 1995-07. Natural Features Inventory, Lansing, Michigan, USA.

Costanza, R., R. dArge, R. deGroot, S. Farber, M. Grasso, B. Hannon, K. Limburg, S. Naeem, R. V. ONeill, J. Paruelo, R. G. Raskin, P. Sutton, and M. vandenBelt. 1997. The value of the world's ecosystem services and natural capital. Nature **387**:253–260.

Cowling, R., A. Knight, D. Faith, S. Ferrier, A. Lombard, A. Driver, M. Rouget, K. Maze, and P. Desmet. 2004. Nature conservation requires more than a passion for species. Conservation Biology **18**:1674–1676.

Curtis, J. T. 1959. The vegetation of Wisconsin: an ordination of plant communities. University of Wisconsin Press, Madison, Wisconsin, USA.

Deblinger, R. D., and R. E. Jenkins. 1991. Preserving coastal biodiversity—the private, nonprofit approach. Coastal Management **19**:103–112.

Dobson, A. P., A. D. Bradshaw, and A. J. M. Baker. 1997. Hopes for the future: restoration ecology and conservation biology. Science **277**:515–522.

Dufrene, M., and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs **67**:345–366.

Elzinga, C. L., D. W. Salzer, J. W. Willoughby, and J. P. Gibbs. 2001. Measuring and monitoring plant and animal populations. Blackwell Science, Malden, Massachusetts, USA.

Flather, C. H., K. R. Wilson, D. J. Dean, and W. C. McComb. 1997. Identifying gaps in conservation networks: of indicators and uncertainty in geographic-based analyses. Ecological Applications **7**:531–542.

Fleishman, E., D. D. Murphy, and P. E. Brussard. 2000. A new method for selection of umbrella species for conservation planning. Ecological Applications **10**:569–579.

Frelich, L. E. 1995. Old forest in the lake states today and before European settlement. Natural Areas Journal **15**:157–167.

Gotelli, N. J., and G. R. Graves. 1996. Null models in ecology. Smithsonian Institution Press, Washington, D.C., USA.

Groves, C. R., M. W. Beck, J. V. Higgins, and E. C. Saxon. 2003. Drafting a conservation blueprint: a practitioner's guide to planning for biodiversity. Island Press, Washington, D.C., USA.

Groves, C. R., M. L. Klein, and T. F. Breden. 1995. Natural heritage programs: public–private partnerships for biodiversity conservation. Wildlife Society Bulletin **23**:784–790.

Gustafsson, L. 2000. Red-listed species and indicators: vascular plants in woodland key habitats and surrounding production forests in Sweden. Biological Conservation **92**:35–43.

Higgins, J., T. Ricketts, J. Parrish, E. Dinerstein, G. Powell, S. Palminteri, J. Hoekstra, J. Morrison, A. Tomasek, and J. Adams. 2004. Beyond Noah: saving species is not enough. Conservation Biology **18**:1672–1673.

Hilty, J., and A. Merenlender. 2000. Faunal indicator taxa selection for monitoring ecosystem health. Biological Conservation **92**:185–197.

Hughes, J. B., G. C. Daily, and P. R. Ehrlich. 1997. Population diversity: its extent and extinction. Science **278**:689–692.

Hutchison, M. 1988. A guide to understanding, interpreting, and using the public land survey field notes in Illinois. Natural Areas Journal **8**:245–255.

Jenkins, R. E. 1988. Information management for the conservation of biological diversity. Pages 231–239 *in* E. O. Wilson, editor. Biodiversity. National Academy Press, Washington, D.C., USA.

Karr, J. R. 1991. Biological integrity: a long-neglected aspect of water-resource management. Ecological Applications **1**: 66–84.

Keddy, P. A., and A. A. Reznicek. 1982. The role of seed banks in the persistence of Ontario coastal plain flora. American Journal of Botany **69**:3–22.

Kerr, J. T. 1997. Species richness, endemism, and the choice of areas for conservation. Conservation Biology **11**:1094–1100.

Kintsch, J. A., and D. L. Urban. 2002. Focal species, community representation, and physical proxies as conservation strategies: a case study in the Amphibolite Mountains, North Carolina, USA. Conservation Biology **16**:936–947.

Kremen, C. 1992. Assessing the indicator properties of species assemblages for natural areas monitoring. Ecological Applications **2**:203–217.

Kremen, C., R. K. Colwell, T. L. Erwin, D. D. Murphy, R. F. Noss, and M. A. Sanjayan. 1993. Terrestrial arthropod assemblages—their use in conservation planning. Conservation Biology **7**:796–808.

Kremen, C., A. M. Merenlender, and D. D. Murphy. 1994. Ecological monitoring—a vital need for integrated conservation and development programs in the tropics. Conservation Biology **8**:388–397.

Lambeck, R. 1997. Focal species: a multi-species umbrella for nature conservation. Conservation Biology **11**:849–856.

Landres, P. B., J. Verner, and J. W. Thomas. 1988. Ecological uses of vertebrate indicator species—a critique. Conservation Biology **2**:316–328.

Laurance, W. F. 2000. Do edge effects occur over large spatial scales? Trends in Ecology and Evolution **15**:134–135.

Lawler, J. J., D. White, J. C. Sifneos, and L. L. Master. 2003. Rare species and the use of indicator groups for conservation planning. Conservation Biology **17**:875–882.

Lawton, J. H., D. E. Bignell, B. Bolton, G. F. Bloemers, P. Eggleton, P. M. Hammond, M. Hodda, R. D. Holt, T. B. Larsen, N. A. Mawdsley, N. E. Stork, D. S. Srivastava, and A. D. Watt. 1998. Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. Nature **391**:72–76.

Lindenmayer, D. B., C. R. Margules, and D. B. Botkin. 2000. Indicators of biodiversity for ecologically sustainable forest management. Conservation Biology **14**:941–950.

Manly, B. F. J. 2001. Randomization, bootstrap and Monte Carlo methods in biology. Second edition. Chapman and Hall/CRC, Boca Raton, Florida, USA.

Margules, C. R., M. P. Austin, D. Mollison, and F. Smith. 1994. Biological models for monitoring species decline—construction and use of data-bases. Philosophical Transactions of the Royal Society of London, Series B **344**:69–75.

Margules, C., and R. Pressey. 2000. Systematic conservation planning. Nature **405**:243–253.

Master, L. L. 1991. Assessing threats and setting priorities for conservation. Conservation Biology **5**:559–563.

Mendenhall, W., R. L. Scheaffer, and D. D. Wackerly. 1981. Mathematical statistics with applications. Second edition. Prindle, Weber and Schmidt, Boston, Massechusetts, USA.

Mikusinski, G., M. Gromadzki, and P. Chylarecki. 2001. Woodpeckers as indicators of forest bird diversity. Conservation Biology **15**:208–217.

Molnar, J., M. Marvier, and P. Kareiva. 2004. The sum is greater than the parts. Conservation Biology **18**:1670–1671.

Morrison, D. F. 1976. Multivariate statistical methods. Second edition. McGraw-Hill, New York, New York, USA.

Noon, B. R. 2003. Conceptual issues in monitoring ecological resources. Pages 27–71 *in* D. E. Busch and J. C. Trexler, editors. Monitoring ecosystems: interdisciplinary approaches for evaluating ecoregional initiatives. Island Press, Washington, D.C., USA.

Norden, B., and T. Appelqvist. 2001. Conceptual problems of ecological continuity and its bioindicators. Biodiversity and Conservation **10**:779–791.

Noss, R. F. 1990. Indicators for monitoring biodiversity—a hierarchical approach. Conservation Biology **4**:355–364.

Panzer, R., and M. W. Schwartz. 1998. Effectiveness of a vegetation-based approach to insect conservation. Conservation Biology **12**:693–702.

Possingham, H. P., S. J. Andelman, M. A. Burgman, R. A. Medellin, L. L. Master, and D. A. Keith. 2002. Limits to the use of threatened species lists. Trends in Ecology and Evolution **17**:503–507.

Prendergast, J. R., R. M. Quinn, J. H. Lawton, B. C. Eversham, and D. W. Gibbons. 1993. Rare species, the coincidence of diversity hotspots and conservation strategies. Nature **365**:335–337.

Pressey, R. 2004. Conservation planning and biodiversity: assembling the best data for the job. Conservation Biology **18**:1677–1681.

Pressey, R. L., C. J. Humphries, C. R. Margules, R. I. Vane-wright, and P. H. Williams. 1993. Beyond opportunism. Key principles for systematic reserve selection. Trends in Ecology and Evolution **8**:124–128.

Rapport, D. J., R. Costanza, and A. J. McMichael. 1998. Assessing ecosystem health. Trends in Ecology and Evolution **13**:397–402.

Raven, P. H., and E. O. Wilson. 1992. A 50-year plan for biodiversity surveys. Science **258**:1099–1100.

Rebelo, A. G., and W. R. Siegfried. 1992. Where should nature reserves be located in the Cape Floristic Region, South Africa? Models for the spatial configuration of a reserve network aimed at maximizing the protection of floral diversity. Conservation Biology **6**:243–252.

Renner, S. S., and R. E. Ricklefs. 1994. Systematics and biodiversity. Trends in Ecology and Evolution **9**:78–78.

Reznicek, A. A. 1994. The disjunct coastal plain flora in the Great Lakes region. Biological Conservation **68**:203–215.

Rich, A. C., D. S. Dobkin, and L. J. Niles. 1994. Defining forest fragmentation by corridor width. The influence of narrow forest-dividing corridors on forest-nesting birds in southern New Jersey. Conservation Biology **8**:1109–1121.

Robinson, S. K., F. R. Thompson, T. M. Donovan, D. R. Whitehead, and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. Science **267**:1987–1990.

Ryti, R. T. 1992. Effect of the focal taxon on the selection of nature reserves. Ecological Applications **2**:404–410.

Sillett, S. C., B. McCune, J. E. Peck, T. R. Rambo, and A. Ruchty. 2000. Dispersal limitations of epiphytic lichens result in species dependent on old-growth forests. Ecological Applications **10**:789–799.

Simberloff, D. 1998. Flagships, umbrellas, and keystones: is single-species management passe in the landscape era? Biological Conservation **83**:247–257.

Soulé, M. E., J. A. Estes, J. Berger, and C. M. Del Rio. 2003. Ecological effectiveness: conservation goals for interactive species. Conservation Biology **17**:1238–1250.

Stein, B. A., and F. W. Davis. 2000. Discovering life in America: tools and techniques of biodiversity inventory. Pages 19–53 *in* B. A. Stein, L. S. Kutner, and J. S. Adams, editors. Precious heritage: the status of biodiversity in the United States. Oxford University Press, New York, New York, USA.

Stork, N. E., M. J. Samways, and H. A. C. Eeley. 1996. Inventorying and monitoring biodiversity. Trends in Ecology and Evolution **11**:39–40.

Temple, S. A. 1986. Predicting impacts of habitat fragmentation on forest birds: a comparison of two models. Pages 301–304 *in* J. Verner, M. L. Morrison, and C. J. Ralph, editors. Wildlife 2000. Modeling habitat relationships of terrestrial vertebrates. University of Wisconsin Press, Madison, Wisconsin, USA.

Thor, G. 1998. Red-listed lichens in Sweden: habitats, threats, protection, and indicator value in boreal coniferous forests. Biodiversity and Conservation **7**:59–72.

Uliczka, H., and P. Angelstam. 2000. Assessing conservation values of forest stands based on specialised lichens and birds. Biological Conservation **95**:343–351.
van Jaarsveld, A., S. Freitag, S. Chown, C. Muller, S. Koch, H. Hull, C. Bellamy, M. Kruger, S. Endrody-Younga, M. Mansell, and C. Scholtz. 1998. Biodiversity assessment and conservation strategies. Science **279**:2106–2108.
Vessby, K., B. Soderstrom, A. Glimskar, and B. Svensson. 2002. Species-richness correlations of six different taxa in Swedish seminatural grasslands. Conservation Biology **16**: 430–439.
Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human domination of Earth's ecosystems. Science **277**:494–499.
Woodley, S., J. Kay, and G. Francis. 1993. Ecological integrity and the management of ecosystems. St. Lucie, Delray Beach, Florida, USA.
Zar, J. H. 1999. Biostatistical analysis. Fourth edition. Prentice Hall, Upper Saddle River, New Jersey, USA.

APPENDIX A

A list of the names of the community types used in the selection of occurrences of highly ranked communities in Michigan, USA (*Ecological Archives* A016-011-A1).

APPENDIX B

A table of land and vegetation cover types used in creating geographic information system data layers of Michigan's land cover ca. 1800 and a coverage of unchanged vegetation (*Ecological Archives* A016-011-A2).

APPENDIX C

A map of Michigan's land cover ca. 1800 (*Ecological Archives* A016-011-A3).

APPENDIX D

A map of Michigan's unchanged land cover ca. 1980 (*Ecological Archives* A016-011-A4).

APPENDIX E

A table presenting the results of two correlation analyses of conservation value across 1900 Michigan townships, determined using the species richness and species occurrences in five groups of potential indicators (*Ecological Archives* A016-011-A5).

APPENDIX F

A table of results from a principal-components analysis of the number of occurrences of potential indicator species in 924 townships in Michigan (*Ecological Archives* A016-011-A6).

SUPPLEMENT 1

Two geographic information system data layers showing Michigan's land cover ca. 1800 and unchanged land cover ca. 1980 (*Ecological Archives* A016-011-S1).

SUPPLEMENT 2

Five geographic information system data layers specifying the size and location of areas of high conservation value that were used in this study (*Ecological Archives* A016-011-S2).