

Alternative Metrics for Evaluating Forest Integrity and Assessing Change at Four Northern-tier U.S. National Parks

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ABSTRACT.—Measures of forest integrity often focus on only one or a small number of metrics (*e.g.*, regeneration, soil organic layer depth). It is possible, however, to view forest integrity more holistically, using the species assemblages present as phytometers, or integrative measures of the complete set of drivers, stressors, and filters acting on the ecosystem. Thus, the species themselves express forest integrity. We collected extensive data on the overstory, understory, and groundlayer from 158 long-term vegetation monitoring plots in four U.S. national parks, within the Great Lakes basin. From these data, we calculated species richness and the modified Floristic Quality Index (mFQI), a measure of species' conservatism and habitat faithfulness. We also determined the proportion of species within categories of each of four separate ecological traits: growth form, life history, pollination mode, and nativity. In general we found lower mFQI values in parks with greater species richness. The proportions of species in categories within the life history and nativity ecological traits varied little among all four parks; proportions in categories for the growth form and pollination mode traits at Apostle Islands differed from the other parks, in having more woody species than any other growth form and more species pollinated abiotically than by other strategies. Across all four parks, our results are consistent with other assessments of species richness on islands and species richness in relation to habitat variability. Both the mFQI values and the taxa groupings in each of the four ecological traits are expected to be responsive to ongoing stressors of forest integrity. Because these techniques are both intuitive and relatively easily assessed, their application as effective gauges of change can apply not only in these four parks, but more broadly, throughout most natural areas.

INTRODUCTION

Metrics to characterize forests often focus on one or a few aspects, such as stand structure (McCarthy and Weetman, 2006; Bradford and Kastendick, 2010), regeneration dynamics (Brudvig and Asbjornsen, 2008; Buchanan and Hart, 2012), or size and abundance of target understory species (McGraw and Furedi, 2005; Knight, 2007). Changes in these metrics are often caused by environmental drivers such as altered disturbance regimes, which can be due to climate change (Anderson-Teixeira *et al.*, 2013), deer (Côte *et al.*, 2004), insects (Morin *et al.*, 2007), or invasive species, such as earthworms (Bohlen *et al.*, 2004). Understanding the processes affecting each aspect of forest dynamics is critical for active forest management. Ultimately, however, the most efficient metrics to characterize forests may be the forests themselves, specifically, the species present and what these species assemblages convey about the integrity of the system.

Ecological integrity has been variously described as the degree to which an area is unimpaired, sound, or complete (Tierney *et al.*, 2009), the degree of impairment across a range of characteristics through both time and space (De Leo and Levin, 1997) and the ability of an ecosystem to maintain composition, diversity, and function, within a range that is similar to the natural habitats of the region (Karr and Dudley, 1981; Parrish *et al.*, 2003). Here, we adopt the definition proposed by both Czech (2005) and Tierney *et al.* (2009) and recognize that systems, and species assemblages, are dynamic. We consider high integrity to

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be where the interreliance of these species on one another (whether for food, development, reproduction, or otherwise) are intact.

Clements (1916) and Clements and Goldsmith (1924) introduced the idea of plants as “phytometers,” gauges that directly measure the integrity of ecosystems. For example Canada yew (*Taxus canadensis* Marshall) is a coniferous shrub that is extremely slow to recover from browse (Windels and Flaspohler, 2011) and other disturbance, such as fire (De Grandpre *et al.*, 1993). The simple presence of Canada yew in a stand conveys important information about the integrity of that stand. Other species are more commonly observed under conditions typical of impaired forests. Invasions of Pennsylvania sedge (*Carex pensylvanica* Lam.) are often manifested when the soil organic layer is absent, typically in the presence of anecic earthworms (Hale *et al.*, 2006; Holdsworth *et al.*, 2007). One may make inferences about the soil quality in that stand based on the extent of the Pennsylvania sedge invasion. In summary the species that are present in a given stand serve as an integrated measure of the complete suite of stressors, drivers, and filters for that stand and are the ultimate manifestation of forest integrity.

One way forest integrity can be quantified using phytometers is with the Floristic Quality Index (FQI). This index was developed by Swink and Wilhelm (1979; 1994) and has been widely used to assess site quality in wetlands (Bourdaghs *et al.*, 2006; Matthews *et al.*, 2009; Johnston *et al.*, 2010), though its application in forested habitats has been limited (for an exception, see Andreas *et al.*, 2004). The index ranges from 0 to 10 and reflects the degree of habitat faithfulness of the species present. Sites with lower FQIs will have more generalist species that are found in a range of habitat types; lower FQIs may be more commonly observed in early successional forests, where the species present tend to be opportunistic. Sites with higher FQIs indicate that the species present are more specialists. Example areas could include swamps and fens, pine barrens, and marl communities.

The FQI, as well as other quantitative metrics of communities based on composition, can be calculated from forest inventory and monitoring data. The information gleaned from these can be especially meaningful if the inventories and monitoring efforts are designed effectively. The Great Lakes Inventory and Monitoring Network of the U.S. National Park Service (hereafter, Great Lakes Network) implemented a long-term forest monitoring program at nine national parks within the Great Lakes ecoregion. The general goals of this program include detecting and assessing forest change to inform management decisions. Because this is a long-term program, we did not pre-select target indicators to assess forest integrity; rather the monitoring methods were developed to be robust to forest change. Our design allows the detection of change due to both current and foreseeable stressors (climate change, impending invasions of exotic insects) as well as potential future impacts, currently unforeseen. A collateral feature of this sampling design is that it allows for assessment of forest integrity simply by knowing the species, and suites of species, that are present. Essentially, we are using species as phytometers – integrative measures of forest integrity – from an idea first espoused by Clements nearly 100 years ago.

In this current study, we assessed the forest integrity for four of the nine national parks within the Great Lakes Network. These four were selected because they have similar latitude, environment, land use history, and threats. We assessed forest integrity using two methods: (1) we applied a modification of the Floristic Quality Index, both across a broad geographic scale and in a novel ecosystem (forests), and we estimated this index along with species richness, for multiple forest types within the parks; (2) we also examined forest integrity by grouping species into ecologically relevant plant traits. We feel the classifications presented here will be especially useful in illuminating environmental change in the coming decades.

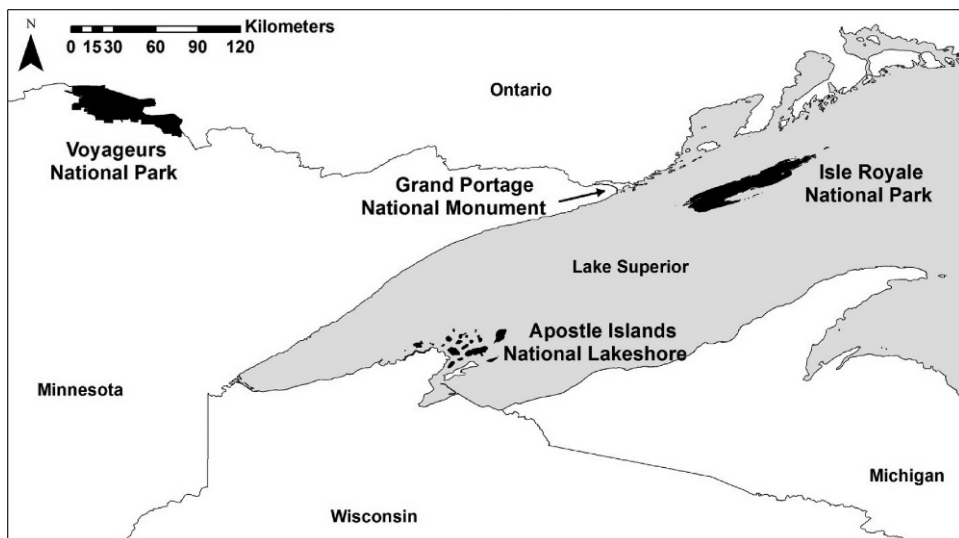


FIG. 1.—The western Lake Superior basin and locations of the four study areas: Apostle Islands National Lakeshore, Grand Portage National Monument, Isle Royale National Park, and Voyageurs National Park

We contend that these two assessments of forest integrity will be as meaningful as other, more computationally challenging measures. As such they may be especially useful for preserves, natural areas, or other forested lands managed with limited staffs and resources.

METHODS

STUDY AREAS

This study was conducted at four National Park Service units (hereafter, “National Parks”) in the Great Lakes Network: Apostle Islands National Lakeshore (APIS; 677973E, 5203631N), Grand Portage National Monument (GRPO; 297294E, 5318863N), Isle Royale National Park (ISRO; 359142E, 5316583N), and Voyageurs National Park (VOYA; 512021E, 5369873N). Apostle Islands National Lakeshore is an archipelago of 21 islands, plus a mainland unit, arising from the Bayfield Peninsula in northern Wisconsin and extending into western Lake Superior (Fig. 1). The islands range in size (1.2–3993 ha), distance to mainland (1.5–24 km), deer density (varies), recreational use by humans, and logging and fire histories. There is one additional island within the archipelago, Madeline Island, which is not part of the national park. Grand Portage National Monument is a 13.6 km trail in far northeastern Minnesota, extending from Lake Superior to the Pigeon River, which forms the boundary between the United States and Canada. National Park Service land includes approximately 100 meters on each side of the trail and larger tracts at both the Lake Superior and Pigeon River termini. This park commemorates the historic portage used by fur traders to circumvent a series of waterfalls on the Pigeon River. As such the vegetation is somewhat homogeneous; the route stamped out by the fur traders preferentially included areas of locally higher topography, while avoiding wetter, more low-lying areas. Isle Royale National Park is an archipelago of one main island and over 400 smaller islands in northern Lake Superior. The main island is 72 km long and consists of a series of parallel ridges of

erosion-resistant basalts interlaid with sandstone that creates a series of ridges separated by low-lying, often wet swales. The eastern third of the island is lower in elevation and intersected by numerous bays and inlets, while the western third is generally higher and more cohesive. The island is well-known as the location of a 50+ y study of the population dynamics of moose (*Alces alces* L.) and wolves (*Canis lupus* ssp. *lupus* L.) (Post *et al.*, 2002). Voyageurs National Park lies at the northern boundary of Minnesota and is adjacent to both the Boundary Waters Canoe Area Wilderness in the United States and Quetico Provincial Park in Canada. Voyageurs contains all of Kabetogama Lake (104 km²) and portions of three large lakes along the United States-Canadian border: Namakan (50 km²), Sand Point (21 km²), and Rainy lakes (147 km²). In addition to the large lakes, Voyageurs encompasses 26 smaller lakes and hundreds of wetlands.

At all parks, northern hardwood and southern boreal forest types predominate (Judziewicz and Koch, 1993; White and Host, 2003; Faber-Langendoen *et al.*, 2007; Sanders and Grochowski, 2013). Mesic areas are dominated by paper birch (*Betula papyrifera* Marshall) and trembling aspen (*Populus tremuloides* Michx.) on early to mid-successional sites and yellow birch (*B. alleghaniensis* Britton) and balsam fir (*Abies balsamea* (L.) Mill.) on later successional sites. On more coarse-textured soils, red pine (*Pinus resinosa* Aiton) and jack pine (*P. banksiana* Lamb.) are common, while black ash (*Fraxinus nigra* Marshall) is generally present in moist pockets. Other common overstory species within these parks include white spruce (*Picea glauca* (Moench) Voss), eastern white cedar (*Thuja occidentalis* L.), and red maple (*Acer rubrum* L.). Three notable species have distribution limits within, or near, the study area. Eastern hemlock (*Tsuga canadensis* (L.) Carrière) is found only at APIS, while basswood (*Tilia americana* L.) is located at three of the four parks, with the exception being ISRO. Sugar maple (*A. saccharum* Marshall) is located at all parks, although its presence is only known in a few locations at VOYA. Understory species vary greatly but widespread and common species include wild sarsaparilla (*Aralia nudicaulis* L.), false lily of the valley (*Maianthemum racemosum* (L.) Link), bunchberry (*Cornus canadensis* L.), and starflower (*Trientalis borealis* Raf.).

FIELD TECHNIQUES

Plots were established at all four parks as part of the National Park Service's Inventory and Monitoring Program (Fancy *et al.*, 2009). All four parks lie within the Great Lakes Network and are sampled as part of its forest monitoring protocol (Sanders *et al.*, 2008). Sampling was initiated at GRPO in 2007 (20 plots), followed by VOYA in 2008 (38 plots), ISRO in 2010 (52 plots), and APIS in 2011 (48 plots).

At each park, plot locations were selected using a generalized random-tessellation stratified design (Stevens and Olsen, 2004). This design ensures that the sites are both randomly placed and spatially balanced within the sampling frame. This sampling frame consisted of all forested (or potentially forested) areas of the park. The "potentially forested" caveat ensured areas experiencing a recent burn or blowdown were included. At each sampling site, three parallel 50 m east-west transects were established, with each successive transect placed 50 m south of the previous one (Fig. 2). Data were collected on all overstory species within a 6 m wide swath at each transect (3 m on either side); the diameter at breast height (DBH) of all living and standing dead trees ≥ 2.5 cm DBH was recorded. Under this design, tree data were collected within a 300 m² area for each transect, corresponding to a 900 m² area for each plot. Groundlayer species were recorded from 1 m² quadrats placed every 5 m along each transect ($n = 10$ per transect, or 30 per plot). Within each quadrat, we recorded all species of herbs, shrubs, and overstory species < 2.5 cm DBH

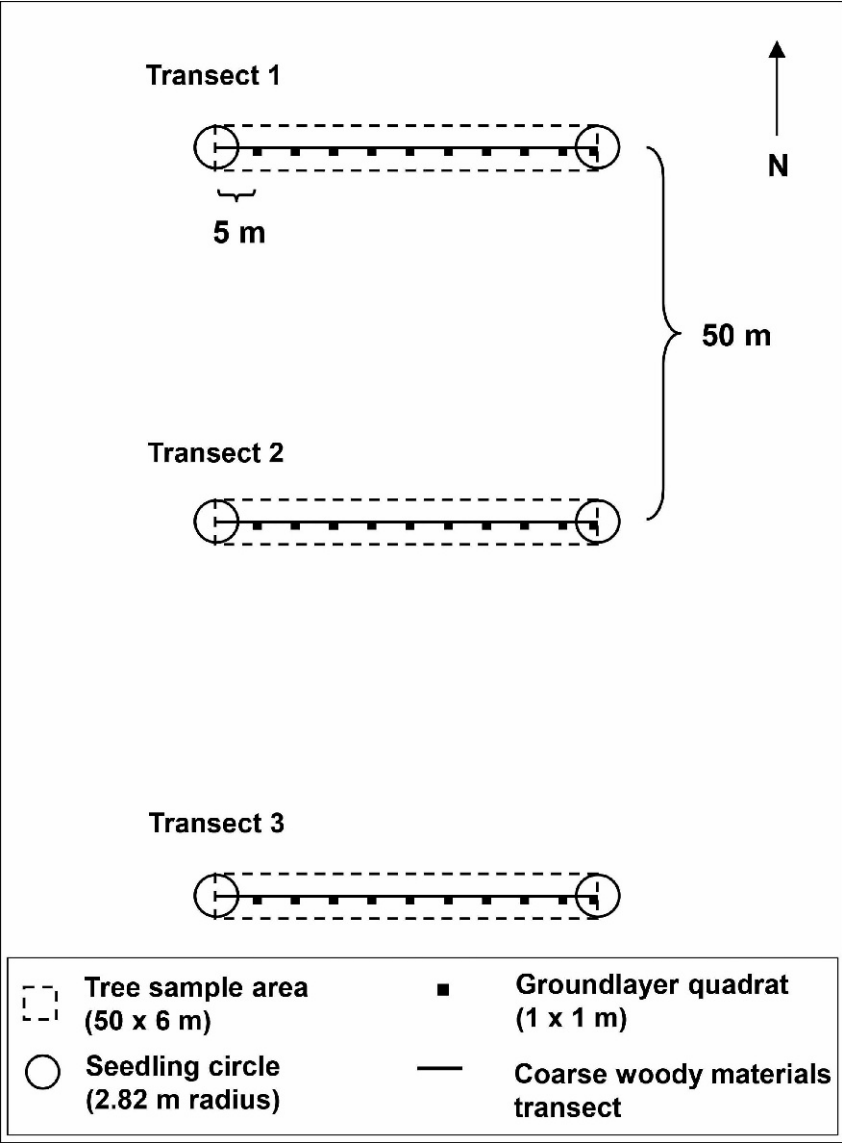


FIG. 2.—Sampling plot layout, showing areas where trees, shrubs, and groundlayer were sampled

(provided they were ≥ 15 cm in height and exhibited second year growth) present. We chose to quantify the groundlayer by presence/absence rather than measures of abundance to fit better with the needs of a long-term monitoring program. Assessments of species cover are highly subjective and as such, vary greatly among observers (Helm and Mead, 2004; Symstad *et al.*, 2006). In a long-term monitoring program, where multiple observers collect data in any given field season and any one observer is usually only present for one to two field seasons, any analyses of change based on percentage cover estimates would be highly

questionable. In addition to observer bias, cover also changes throughout the growing season. We felt that the frequency of occurrence in quadrats would approximate abundance, provided enough quadrats were included (Johnson *et al.*, 2008). We also felt that frequency would be less subject to observer bias and more time-efficient in the field. Shrub cover was assessed within each of six 2.82 m-radius circles, each located at a transect end. Finally, after all measures were taken, we performed a time-delimited walkthrough survey of each plot to document any species not already recorded.

CLASSIFICATION AND ANALYSIS METHODS

Habitat classification.—At the outset of this program, we assigned plots to forest habitat types using the Kotar classification system (Kotar and Burger, 2000, 2005). Under this system, forest habitat types are largely dependent on soil moisture and nutrient availability and identifiable by distinct assemblages of understory species. Following the field seasons at VOYA and GRPO, we grouped the plots into predefined habitat types, based on the forest type assigned while at the site, as determined by the Kotar system. While this classification system was functional at VOYA and GRPO, we encountered difficulty at other parks, both because forest types at the wetter end of the spectrum (*e.g.*, cedar) were not defined and because, at ISRO, the park forest types had not been included in the original development of the Kotar classification system. Therefore, we grouped APIS and ISRO plots using a post-hoc multivariate cluster analysis based on importance values of the most abundant tree species. These were determined by the sum of the relative density and relative basal area of each species-plot combination (Dyer, 2006; Elliott and Swank, 2008). For the cluster analysis, we used PC-ORD software with a Sørensen distance measure and a flexible beta linkage ($\beta = -0.25$; McCune and Grace, 2002). Because these groups tended to be broadly inclusive, in terms of species associations, we use the term “(forest) habitat type,” rather than “forest (cover) type,” to describe them. Habitat type names were assigned based on the dominant trees in these groups.

Coefficients of conservatism, the modified floristic quality index, and richness.—Coefficients of conservatism (COC) describe the affinities of species to nondegraded habitats. These were presented by Swink and Wilhelm (1979; 1994), in concert with the Floristic Quality Index, to assess site quality in the Chicago region. COC values range from 0 (either nonnative species or generalists with no faithfulness to any particular habitat) to 10 (conservative species found only in high-quality, nondegraded habitats). Because a given species may be conservative in one area of its distribution but a generalist in the center of its range, COC values vary by region. Typically, values are assigned at the state level by experienced botanists and ecologists. For ISRO, we used COC values defined for the state of Michigan (Herman *et al.*, 2001). Although Isle Royale is geographically distant from most of the landmass of Michigan, species affinities for habitats throughout the entire state were taken into consideration (Tony Reznicek, University of Michigan, pers. comm.). For GRPO and VOYA, we used values defined for the province of Ontario (Oldham *et al.*, 1995) because Minnesota does not have defined COC values for terrestrial plant species. Although both parks border northwestern Ontario, the COC values must be interpreted with caution as they were developed for southern Ontario. The COC values for APIS were those defined for the state of Wisconsin (Bernthal, 2003). Because we identified some plants only to the genus level, we objectively assigned COC values for each park-genus combination based on the COC values of the species within that genus that were present at that park. For example both *Agrimonia gryposepala* Wallr. and *A. striata* Michx. are present at ISRO and cannot be distinguished from one another unless a reproductive stalk has formed; hence there were instances where *Agrimonia* sp. was recorded in the data. In Michigan these species have COC values of two

and three, respectively. Our convention was to assign the lower value of the pair to the genus. All nomenclature follows that of the Integrated Taxonomic Information System.

The Floristic Quality Index is an extension of the COC concept; it is a quantified assessment of site health based on the COC values of the species present. While the FQI concept, as described by Swink and Wilhelm (1974; 1994), has been widely used to assess site quality, particularly in wetlands, there has been some concern about bias, whereby larger areas generally have larger FQI values. We used a modified FQI (mFQI; Rooney and Rogers, 2002) that reduced this bias, where mFQI is simply the mean COC values of all species recorded in the area of interest (park, site, *etc.*). In essence mFQI measures conservatism; lower values for a given park, site, *etc.* suggest the species present tend to be generalists, with less affinity for particular habitats, while higher values suggest more specialized species are present. For parkwide mFQI values, we calculated the mean COC of all taxa present in the park; at the habitat level, mFQI is the mean COC for all taxa present in that habitat.

Species richness was determined for each plot. Not all individual plants located within the groundlayer quadrats or time-delimited walkthrough surveys could be identified to species because they were not at the necessary reproductive stage to do so. When this occurred, these individuals were typically identified to genus only, or in rare instances, to the family level (*e.g.*, Poaceae, Asteraceae). These higher level taxa identifications were included in summations of species richness, a practice that introduces some degree of uncertainty into our species richness values. For example a species recorded as “*Carex* sp.” may correctly represent a previously unidentified *Carex* species in that plot or erroneously represent a duplicate, if an individual of that same species was actually fully identified (to species) within that plot. Further, actual species richness could also be underrepresented if not all species are located within the combination of sampling quadrats and timed walkthroughs. Although great care was taken during the walkthroughs to look for species that were not previously noted, it is possible some were missed. The scenarios presented above are realities of field sampling and are largely unavoidable (Archaux *et al.*, 2007). We felt that this ambiguity of species richness was small in comparison to the total number of species present. We also felt that over- and under- estimates of the actual species richness would approximately offset one another. Therefore, in the present work, we are using the term “species richness” as a surrogate for the taxa richness that was actually recorded, as described above. For parkwide mean species richness, we determined the mean of the richness of all plots within that park; at the habitat level, mean richness was calculated from the mean of all plots within that habitat.

Ecological traits.—All taxa (overstory as well as understory) were assigned to a category within each of four key ecological traits: Growth Form, Life History, Pollination Mode, and Nativity (Table 1). Within the Growth Form trait, species were considered to be woody (trees, shrubs, some vines), graminoid (grasses, sedges, rushes), forbs (broad-leaved herbs, including herbaceous vines), or ferns and their allies (horsetails, clubmosses). Within the Life History trait, taxa were annual, biennial, or perennial. Taxa known to exhibit a range of life history strategies were assigned to the suite with the shortest strategy. For example, if a species is known to be either biennial or perennial, we assigned it to the biennial suite. We felt this was valid because the majority of species we encounter are near the northern limit of their ranges, where the life cycle would tend to be shorter. For the Pollination trait, taxa were considered to be abiotically pollinated if the flowers are nonexistent (conifers) or are not showy and not known to produce any sensory attractants. These are typically wind pollinated. Otherwise, taxa were considered to be biotically pollinated. Fern and fern allies were not assigned to suites within this ecological trait group. Within the Nativity trait, taxa were assigned to native, nonnative, or native/nonnative suites. Naturalized taxa (*e.g.*, *Taraxicum officinale*, *Ranunculus*

TABLE 1.—Ecological traits and the suites included in each. All taxa (overstory as well as understory) were assigned to one suite within each trait

Trait	Categories	Example
Growth form	Ferns and allies	Horsetails, clubmosses
	Forb	Broad leaved herbs (including herbaceous vines)
	Graminoid	Grasses, sedges, rushes
	Woody	Trees, shrubs, some vines
Life history	Annual	Many grasses and members of the aster family
	Biennial	Several species in the mustard family
	Perennial	Trees, shrubs, many herbs
Pollination mode	Abiotic	Grasses, most trees and shrubs
	Biotic	Most herbs, several trees and shrubs in the rose family
	Not applicable	Ferns and allies
Nativity	Native	Species whose presettlement distribution includes the park area
	Nonnative	Species with presettlement distributions outside of the park area
	Native/nonnative	Species identified only to genus with both native and nonnative species in the park

acris) were considered nonnative. In some instances taxa were identified only to the genus (or rarely family) level and could not be assigned a nativity as species within these genera are both native and otherwise. Examples include *Hieracium* sp. and *Poa* sp.

RESULTS

Parkwide mFQI mean values ranged from 4.564 to 5.254 (Table 2); there was some variation in mFQI values between habitats within a park, except at GRPO where all plots were classified as the same habitat type. Mean parkwide species richness ranged from 39.52 to 68.63 species per plot, with mean habitat species richness varying greatly within each park.

Within all four ecological traits, the relative proportion of species in the respective categories was comparable at GRPO, ISRO, and VOYA (Figs. 3A, B). In the Growth Form trait, approximately half of the species were classified as herbs. Slightly less than half were woody, with graminoids and ferns collectively comprising about 10% of the species encountered. In the Life History trait, nearly all species were classified as perennials, although a small percentage were annuals, with only a handful considered biennials. For the Pollination Mode trait, slightly over half of the species were biotically pollinated, roughly one-third were abiotically pollinated, and approximately 15–20% were ferns or fern allies, which do not have flowers. Across these three parks, species were predominantly native, with native species comprising 99.1%, 96.5%, and 98.8% of the total documented species at GRPO, ISRO, and VOYA, respectively.

At APIS, species proportions in the categories within both the Life History and the Nativity ecological traits were comparable to these at the other three parks, with 99.1% of the species recorded being native. In contrast to the other parks, however, nearly half of the species were pollinated abiotically. Additionally, there were more woody plants than forbs within plots at APIS.

DISCUSSION

One key aspect of our results was anticipated: the ranges of modified FQI values within parks were fairly limited. Use of the standard FQI tends to result in a wider range of values

TABLE 2.—Mean mFQI and species richness for each park and habitat

Park habitat	Number of plots	mFQI	Richness
Apostle Islands NL			
Balsam fir	4	5.252	48.25
Sugar maple-yellow birch-hemlock	18	5.506	32.89
Mountain maple-black ash	7	5.007	47.29
Bigtooth aspen-paper birch	11	5.500	47.27
Eastern white cedar	8	5.804	32.63
Apostle Islands NL (parkwide)	48	5.254	39.52
Grand Portage NM ¹			
Spruce-fir-birch	20	4.774	60.90
Isle Royale NP			
Balsam fir-mixed forest	9	4.675	68.78
Eastern white cedar	10	4.974	68.64
Paper birch-mixed forest	6	4.373	78.17
Sugar maple-yellow birch	8	4.489	54.13
White spruce-trembling aspen-mixed forest	19	4.541	68.64
Isle Royale NP (parkwide)	52	4.564	68.63
Voyageurs NP			
Dry to dry mesic, nutrient poor	12	5.050	48.58
Dry mesic to mesic, poor to medium nutrient	19	5.250	57.37
Mesic to wet mesic, poor to medium nutrient poor	4	4.929	75.50
Wet mesic to wet, poor to medium	3	5.314	74.00
Voyageurs NP (parkwide)	38	5.069	57.50

¹ No parkwide values are presented for Grand Portage NM because all plots fell into the same habitat type

within regions, even within the same general habitat type, such as wetlands (Johnston *et al.*, 2010) or prairies (Taft *et al.*, 1997). This is because the standard FQI is proportional to the number of species sampled and, therefore, indirectly related to the size of the study area (MacArthur and Wilson, 1967). Because we used a modification of this index, our results were less an indication of the size of the study area and more of a reflection of the communities themselves.

Three aspects of the analysis of mFQI and species richness for the four national parks were unanticipated. First, GRPO had the second highest plot species richness despite being considerably smaller than the other parks. In the Border Lakes region of northern Minnesota, the area that lies to the west of GRPO and includes VOYA, shallow, coarse textured soils are common. In contrast GRPO soils are primarily clays, interspersed with sandy loam (Gafvert, 2009). These finer textured soils have greater moisture holding capacity than those to the west. In addition climate gradients exist over the region during the growing season. Temperatures are higher to the west, away from the moderating effects of Lake Superior (Baker *et al.*, 1985); growing season precipitation along the northern Minnesota border is also greater at the western edge of the Border Lakes region, with less precipitation near Lake Superior (Baker *et al.*, 1967). Like most of northern Minnesota, both parks experienced extensive fires during both the initial settlement (1870–1910) and post-settlement (1910–1940) periods (Heinselman, 1973; White and Host, 2003). A mixed mosaic of stand ages and types now exists along the Grand Portage trail (White and Host,

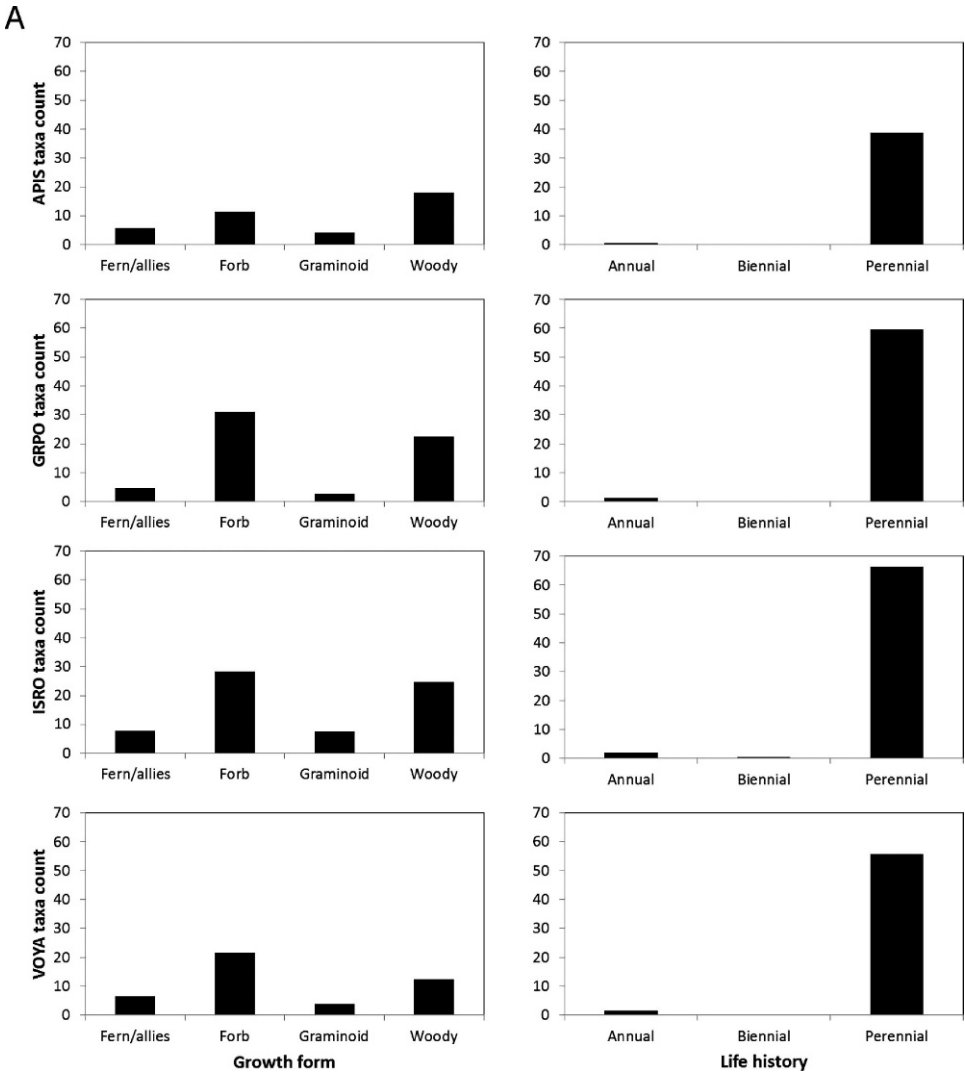


FIG. 3A.—The proportion of species within categories of the Growth Form and Life History traits at each park

2003). Along the half nearest Lake Superior, aspen and paper birch predominate with stand ages generally ranging from <50 y to 100 y: a few isolated pockets of older forest also remain. Farther from Lake Superior, forests are older, typically ranging from 75 to 140 y, with isolated stands >140 y throughout (White and Host, 2003). Collectively, the mesic conditions and mixed stand ages could explain the fairly large number of species at GRPO, in spite of its smaller size.

The second unanticipated result was the relatively low mFQI value at ISRO. White-tailed deer are not present on the island, but it does support a variable population of moose.

B

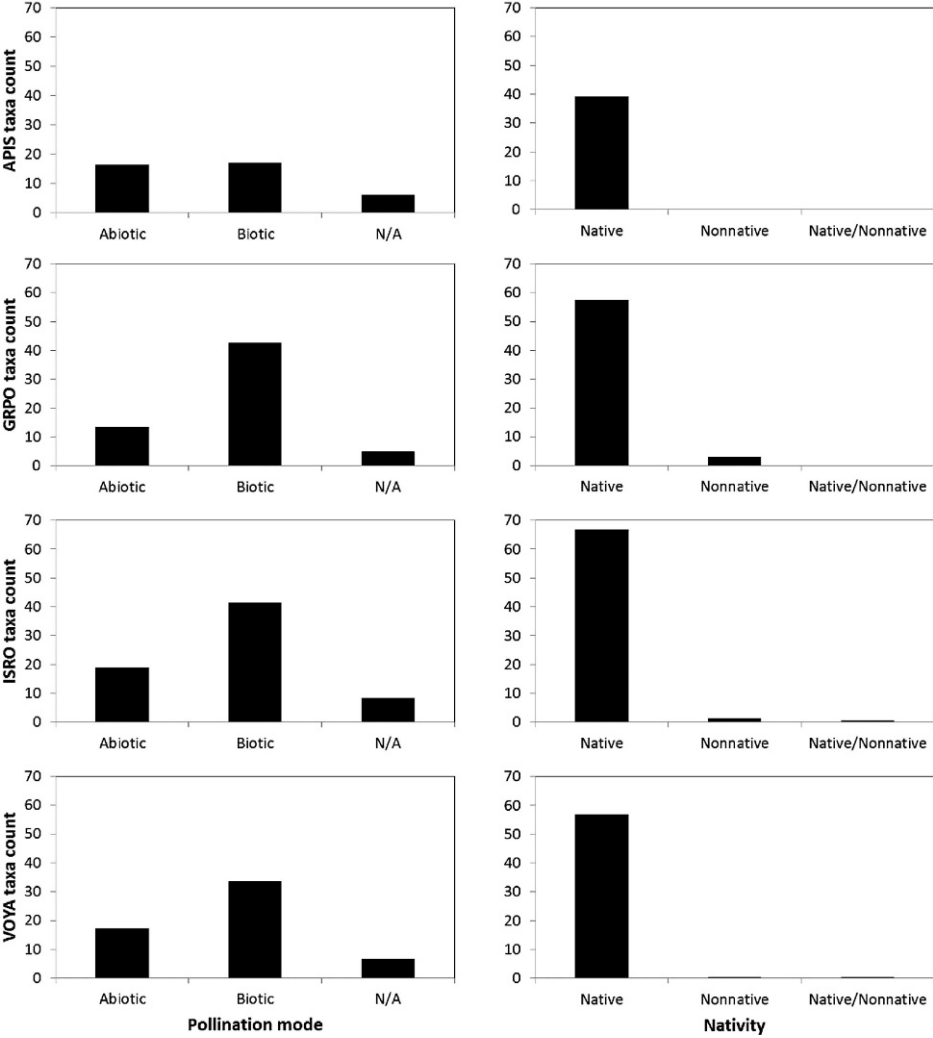


FIG. 3B.—The proportion of species within categories of the Pollination Mode and Nativity traits at each park

Moose tend to focus browsing on woody species in terrestrial areas and herbaceous species in aquatic habitats (Aho and Jordan, 1976). This pattern differs somewhat from white-tailed deer, which can exert considerable browse pressure on understory herbs (Crête *et al.*, 2001). Because of this difference in primary browsers, the understory species assemblage appeared to differ greatly from that of other parks. At ISRO, we commonly encountered numerous orchid species not generally observed at other parks, including ram’s head ladies slipper (*Cypripedium arietinum* W. T. Aiton), roundleaved orchid (*Platanthera orbiculata* (Pursh) Lindl.), and northern green orchid (*Platanthera hyperborea* (L.) Lindl.). Additionally, under

the moderating effects of Lake Superior, the park supports a number of western plant species with disjunct distributions maintained largely on extensive basalt outcrops. These disjunct species include American rockbrake (*Cryptogramma acrostichoides* R. Br.), squashberry (*Viburnum edule* (Michx.) Raf.), and devil's club (*Oplopanax horridus* (Torr. & Gray) Miq.). Finally, Isle Royale supports large populations of numerous state-endangered species. Collectively, these patterns suggest species with strong conservatism may flourish here. We believe the relatively low mFQI value may be related to the high species richness on the island. Isle Royale exhibits a great deal of habitat heterogeneity, even over relatively short distances, a feature that promotes species richness (Wright *et al.*, 2002; Dufour *et al.*, 2006). Nonetheless, many of the species present are generalists; the high COC values of only a few species are easily offset by the relatively lower COC values (*e.g.*, ≤ 4) of several species.

The final unforeseen result was the combination of high mFQI and low species richness at APIS, along with a high proportion of woody taxa. This pattern of species assembly exemplifies two tenets of community ecology. First, a well-documented, positive relationship exists between species richness and area (Lomolino and Weiser, 2001; Turner and Tjorve, 2005). Forty-four of the 48 plots at APIS were on islands; the sizes of the islands on which plots were established ranged from 115 to 3993 ha. Low richness is likely due to a combination of limited habitat variability, low immigration, and minimal disturbance. Indeed, the pattern observed at APIS supports the Intermediate Disturbance Hypothesis (Connell, 1978). Per this hypothesis, species richness is at a maximum in areas with an intermediate disturbance frequency; where disturbance frequency is low, competitive exclusion occurs and dominance of long-lived species will result. Throughout the upper Midwest, the major disturbance arguably results from white-tailed deer (*Odocoileus virginianus* Zimm.), a major ecosystem driver (Rooney, 2001; Augustine and DeCalesta, 2003; Heckel *et al.*, 2010).

In northern Wisconsin, the region where APIS is located, white-tailed are present at densities greatly exceeding historic levels. Although abundant on the mainland, deer density is only high on two of the islands where plots were placed; on the other 16 islands with plots, deer occupation is either minimal or nonexistent. On many of these deer-free islands, dense expanses of Canada yew, a long-lived coniferous shrub, dominate the understories. Where this occurs, only a few other understory species are present. We argue this dominance of Canada yew, in combination with limited habitat variability and limited immigration of plant species, is a primary reason for the low richness at APIS. This scenario of species assembly at APIS, is based on competitive exclusion and the dominance of long-lived species, both of which are central to the Intermediate Disturbance Hypothesis.

GENERAL UTILITY OF THE TWO METRICS FOR FOREST HEALTH

To our knowledge, this work is the first to assess site quality using the modified FQI in upland, forested habitat. As such, it is difficult to place these four parks in context with other natural forested areas. Andreas *et al.* (2004) developed COC values for plant species of Ohio and calculated FQI values for a range of natural areas and natural area types within the state. They present an FQI value of 64.9, corresponding to an mFQI of 3.94, for Fowler Woods State Nature Preserve, a mixed mesophytic forest.

Both the mFQI and the proportion of species in categories within each of the functional traits can be interpreted as measures of forest integrity. The mFQI measures conservatism; lower values for a given habitat suggest the species present tend to be generalists, with less affinity for particular habitats, while higher values suggest more specialized species are present. One should be careful to not equate low mFQI values with low forest integrity. Although to some extent high values may indicate high integrity, the mFQI also reflects

TABLE 3.—Characteristic species of four common forest types in the Upper Great Lakes region and their mean COC value from Michigan, Wisconsin, and Minnesota

Forest type species	Mean COC
Jack pine	
<i>Pinus banksiana</i> (jack pine)	6.3
<i>Deschampsia flexuosa</i> (wavy hairgrass)	6.7
<i>Chimaphila umbellata</i> (pipsissewa)	8.0
<i>Arctostaphylos uva-ursi</i> (bearberry)	7.7
Eastern white cedar	
<i>Thuja occidentalis</i> (eastern white cedar)	5.7
<i>Rhododendron groenlandicum</i> (Labrador tea)	8.3
<i>Coptis trifolia</i> (goldthread)	6.7
<i>Gaultheria hispidula</i> (snowberry)	8.0
<i>Maianthemum trifolium</i> (threeleaf false lily-of-the-valley)	10.0
<i>Huperzia lucidula</i> (shining clubmoss)	6.3
<i>Symplocarpus foetidus</i> (skunk cabbage)	7.0
Aspen-paper birch	
<i>Populus tremuloides</i> (trembling aspen)	1.7
<i>Betula papyrifera</i> (paper birch)	2.3
<i>Maianthemum canadense</i> (Canada mayflower)	4.7
<i>Eurybia macrophylla</i> (bigleaf aster)	4.3
<i>Pteridium aquilinum</i> (bracken fern)	1.3
<i>Diervilla lonicera</i> (bush honeysuckle)	5.0
Sugar maple-yellow birch	
<i>Acer saccharum</i> (sugar maple)	4.7
<i>Betula allegheniensis</i> (yellow birch)	6.5
<i>Clintonia borealis</i> (bluebead lily)	6.3
<i>Dryopteris carthusiana</i> (spinulose woodfern)	5.7
<i>Lonicera canadensis</i> (fly honeysuckle)	6.3

successional state, disturbance, and habitat type. For example among the four common forest types in the upper Great Lakes region the species in the cedar and jack pine types generally have higher COC values than those of aspen-paper birch and sugar maple-yellow birch (Table 3). Of the five habitats at ISRO, the highest mFQI (4.974) was in eastern white cedar. This is not surprising because a number of species are limited to, or preferentially found in, cedar forests (Minnesota DNR, 2003). In contrast to cedar forests, the lowest mFQI at ISRO (4.373) was observed in paper birch forests. The birch forests were transitioning from an early to a midsuccessional sere, with many species present being generalists and pioneers. White cedar and jack pine are specialized forest types, generally occurring in moist pockets and high light environments, respectively, within the study areas. In contrast aspen-paper birch and sugar maple-yellow birch are both mesic forest types; the former is early successional while the latter is late successional. The early successional species identified with aspen-paper birch forests in Table 3 are not undesirable species. Rather, they are species capable of thriving under greater ranges of light, moisture, temperature, and nutrients. One should also use caution when comparing mFQI values between habitats or regions, as the ecological filters regulating species assembly will differ. The real utility of the mFQI is to examine changes for a given region or habitat type over time. Changes could occur via multiple pathways.

In cedar forests at ISRO, an increase in mFQI could occur in the absence of disturbance. Cedar is a climax forest type on moist sites in the region (Bergeron and Dubuc, 1989). As these forests continue to mature, light will become increasingly limited, concomitant with an ongoing, gradual loss of the remaining midsuccessional understory species. Further, immigration and establishment of species characteristic of the cedar habitat could also increase the mFQI in cedar forests (Table 3). A reduction in the mFQI could also occur, particularly as a result of disturbance such as altered soil hydrology. A gradual drying of the soil over time may lead to replacement of cedar-characteristic species with more generalist species better able to compete in the lower moisture conditions. Because of these varied possibilities, interpretation of modified Floristic Quality Index values should be qualified with known recent ecological dynamics.

While use of indices to rate ecosystem integrity is not new (see Karr and Dudley, 1981; Overton *et al.*, 1990), interest in them may be increasing, due largely to their development and adoption by agencies and nonprofit organizations (O'Connell *et al.*, 1998; Guilfoyle *et al.*, 2009). One clear advantage to these approaches is their parsimony. They characterize a suite of metrics or conditions by one or a few values, with changes in these values readily assessed over time. Nonetheless, as demonstrated above, a comprehensive knowledge of the subject matter is helpful to understand the values and why they may be changing. An alternative approach to any one index for evaluating ecosystem integrity is to use multi-metric ecological scorecards. For example Tierney *et al.* (2009) identified 13 metrics of forest integrity and established threshold values of these so that each could be rated as either good, warranting caution, or of significant concern. One advantage of ecological scorecards over a numerical index is that they are an effective way to communicate with park superintendents, administrators, and resource managers whose specialization is in a field other than forest ecology. In addition they concisely identify the status of each component of integrity. Despite this, rating criteria identified *a priori* pose some risks. For example events such as fires or windstorms can impart drastic changes to a forest, leading to ratings warranting caution or significant concern, despite the fact that these events are natural (and beneficial). As such one still must consider the full ecological scope when interpreting the rating of each metric. Ultimately, we feel the two approaches are complimentary; the way the data are summarized and presented depends largely on the audience and any management actions that may be taken as a result. Further examination of the species proportions within selected functional traits could also help sort out these situations.

The four ecological traits were selected, in part, because we anticipate them to be telling indicators of the cascading impacts of change in both long-term climate trends and ecosystem drivers. For example change within the Growth Form trait may reflect the collective impacts of deer and earthworms. Continued high deer densities at some parks will likely lower the proportional contribution of woody species, while ferns and graminoids, two groups generally avoided by deer, will likely have greater representation (Horsley *et al.*, 2003; Rooney, 2009). At the same time, areas where earthworms have invaded will also likely exhibit increases in ferns and graminoids, probably at the expense of forbs (Hale *et al.*, 2006; Corio *et al.*, 2009). Thus, monitoring for change within these groups will provide an integrative measure of these impacts.

Within the Life History trait, we anticipate a shift toward a greater proportion of species with annual life cycles along with a corresponding reduction in perennials. The shorter life cycle of annuals (Harper and White, 1974), coupled with generally much higher seed output, will allow these species to adapt more readily to climate change (Jump and Peñuelas, 2005). This is especially relevant since there is a great deal of concern about the

ability of species' migration rates to keep up with the speed of climate change (Iverson and Prasad, 1998; Scheller and Mladenoff, 2005).

We anticipate a reduction in the proportion of those species that are biotically pollinated with corresponding increases in abiotically pollinated species and those that are not pollinated. Biotically-pollinated species often rely on specific interactions between the plant and the pollinator (Midgley and Bond, 1991). Ongoing climate change, particularly rising temperatures, may result in phenological asynchrony and disrupted interactions. While insects and other pollinators may respond to temperature cues, the signal to initiate flowering can depend on other cues such as moisture levels or day length, the latter of which may not be impacted by climate change. This disruption of coadapted pollination has already been documented (Parmesan, 2006).

Finally, native-to-nonnative species ratios will undoubtedly change over time as a result of both introduction of nonnative species and loss of natives. The results of this study of the four parks revealed high percentages of native species; this is not surprising as our plots are randomly distributed throughout the forested area of the parks and not stratified by accessibility. In addition to nonnative species comprising only a small fraction of the total species richness, few of these nonnatives were species we would classify as invasive within a forest interior. They tended to be naturalized opportunists located on trails and other disturbed areas. Exceptions include species such as *Cirsium vulgare* (Savi) Ten. (bull thistle), *C. arvense* (L.) Scop. (Canada thistle), and *Hieracium aurantiacum* L. (orange hawkweed).

Maintaining the proportions of species in the respective categories of the ecological traits will be important in the coming years. While it has been recognized that the maintenance of species diversity promotes the maintenance of ecosystem processes and, therefore, ecosystem resilience (Hooper *et al.*, 2005; Drever *et al.*, 2006; Bodin and Wimen, 2007), there is growing recognition of the importance of redundancy within the components comprising this diversity (Fonseca and Ganade, 2001; Cadotte *et al.*, 2011). For example stands with high species diversity, but composed exclusively of shallow rooted trees, may experience widespread blowdown and a complete loss of the canopy in the event of a windstorm (Stueve *et al.* 2011). Thus, the lack of functional diversity (tree rooting depth) within that stand limits the resilience. In contrast the same wind event acting on a stand with both shallow and deep rooted species may result in only limited pockets of downed trees. These openings will promote the regeneration of early successional species and contribute to the persistence of a diverse, multi-aged forest. In this case, the diversity of the rooting function contributed to the resilience of the stand. In addition to rooting depth, other ecological traits for which diversity is desired include response to fire, leaf nutrient retention, and dispersal mode.

Obviously, change within northern hardwood and southern boreal forests will be great during the coming decades. The impending arrivals of the emerald ash borer (*Agilus planipennis* Fairmaire) and other exotic insects will have significant consequences for these forests. In addition, species migration induced by climate change may cause even greater stresses, especially if current species assemblages become disrupted. We propose that the mFQI and the assessments of species proportions within selected, key ecological traits will directly reflect these stresses and, ultimately, the health of the parks' forests as a whole. These benefits, plus the relative ease with which these can be applied and calculated, lend credence to their use by land managers in long-term forest monitoring programs.

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LITERATURE CITED

- AHO, R. W. AND P. A. JORDAN. 1976. Production of aquatic macrophytes and its utilization by moose on Isle Royale National Park. p. 341–348. *In*: Proceedings of the First Conference on Scientific Research in the National Parks. U.S. Department of the Interior, New Orleans, Louisiana.
- ANDERSON-TEIXEIRA, K. J., A. D. MILLER, J. E. MOHAN, T. W. HUDIBURG, B. D. DUVAL, AND E. H. DELUCIA. 2013. Altered dynamics of forest recovery under a changing climate. *Glo. Chng. Biol.*, **19**:2001–2021.
- ANDREAS, B. K., J. J. MACK, AND J. S. MCCORMAC. 2004. Floristic Quality Index (FQAI) for Vascular Plants and Mosses for the State of Ohio. Ohio Environmental Protection Agency, Division of Surface Water, Wetland Ecology Group, Columbus, Ohio. 219 p.
- ARCHAUX, F., L. BERGES, AND R. CHEVALIER. 2007. Are plant censuses carried out on small quadrats more reliable than on larger ones? *Plant Ecol.*, **188**:179–190.
- AUGUSTINE, D. J. AND D. S. DECALESTA. 2003. Defining deer overabundance and threats to forest communities: from individual plants to landscape structure. *Ecosci.*, **10**:472–486.
- BAKER, D. G., D. A. HAINES, AND J. H. STUBB. 1967. Climate of Minnesota, Part V. Precipitation facts, normals, and extremes. University of Minnesota Agriculture Experiment Station Technical Bulletin, **254**:1–43.
- , E. L. KUEHNAST, AND J. A. ZANDLO. 1985. Climate of Minnesota. Part XV – Normal temperatures, 1951–1980, and their application. University of Minnesota Agruculture Experiment Station AD-SB-2777-1985.
- BERGERON, Y. AND M. DUBUC. 1989. Succession in the southern part of the Canadian boreal forest. *Vegetatio*, **79**:51–63.
- BERNTHAL, T. W. 2003. Development of a Floristic Quality Assessment Methodology for Wisconsin. CD975115-01-0, Wisconsin Department of Natural Resources. 19 p.
- BODIN, P. AND B. L. WIMEN. 2007. The usefulness of stability concepts in forest management when coping with increasing climate uncertainties. *For. Ecol. Mang.*, **242**:541–552.
- BOHLEN, P. J., S. SCHEU, C. M. HALE, M. A. MCLEAN, S. MIGGE, P. M. GROFFMAN, AND D. PARKINSON. 2004. Non-native invasive earthworms as agents of change in northern temperate forests. *Front. Ecol. Envir.*, **2**:427–435.
- BOURDAGHS, M., C. A. JOHNSTON, AND R. R. REGAL. 2006. Properties and performance of the floristic quality index in Great Lakes coastal wetlands. *Wetlands*, **26**:718–735.
- BRADFORD, J. B. AND D. N. KASTENDICK. 2010. Age-related patterns of forest complexity and carbon storage in pine and aspen-birch ecosystems of northern Minnesota, USA. *Can. J. For. Res.*, **40**:401–409.
- BRUDVIG, L. A. AND H. ASBJORNSEN. 2008. Patterns of oak regeneration in a Midwestern savanna restoration experiment. *For. Ecol. Mang.*, **255**:3019–3025.
- BUCHANAN, M. L. AND J. L. HART. 2012. Canopy disturbance history of old-growth *Quercus alba* sites in the eastern United States: examination of long-term trends and broad-scale patterns. *For. Ecol. Mang.*, **267**:28–39.
- CLEMENTS, F. E. 1916. Plant succession: an analysis of the development of vegetation. Publication Number 242. Carnegie Institution of Washington, Washington, D. C.
- AND G. W. GOLDSMITH. 1924. The phytometer method in ecology: the plant and community as instruments. Publication Number 356. Carnegie Institution of Washington, Washington, D. C.
- CADOTTE, M. W., K. CARSCADDEN, AND N. MIROTCHEV. 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. *J. App. Ecol.*, **48**:1079–1087.
- CONNELL, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Sci.*, **199**:1302–1310.
- CORIO, K., A. WOLF, AND M. DRANEY. 2009. Exotic earthworms of great lakes forests: a search for indicator plant species in maple forests. *For. Ecol. and Mang.*, **258**:1059–1066.
- CÔTE, S. D., T. P. ROONEY, J. TREMBLAY, C. DUSSAULT, AND D. M. WALLER. 2004. Ecological impacts of deer overabundance. *Ann. Rev. Ecol. Evol. Syst.*, **35**:113–147.

- CRÉTE, M., J. OUELLET, AND L. LESAGE. 2001. Comparative effects on plants of caribou/reindeer, moose and white-tailed deer herbivory. *Arctic*, **54**:407–417.
- CZECH, B. 2005. A chronological frame of reference for ecological integrity and natural conditions. *J. Nat. Res.*, **44**:1113–36.
- DE GRANDPRÉ, L., D. GAGNON, AND Y. BERGERON. 1993. Changes in the understory of Canadian southern boreal forest after fire. *J. Veg. Sci.*, **4**:803–810.
- DE LEO, G. A. AND S. LEVIN. 1997. The multifaceted aspects of ecosystem integrity. *Conserv. Ecol.*, **1**:3.
- DREVER, C. R., G. PETERSON, C. MESSIER, Y. BERGERON, AND M. D. FLANNIGAN. 2006. Can forests management based on natural disturbances maintain ecological resilience? *Can. J. For. Res.*, **36**:2285–2299.
- DUFOUR, A., F. GADALLAH, H. H. WAGNER, A. GUISAN, AND A. BUTTLER. 2006. Plant species richness and environmental heterogeneity in a mountain landscape: effects of variability and spatial configuration. *Ecog.*, **29**:573–584.
- DYER, J. M. 2006. Revisiting the deciduous forests of eastern North America. *BioSci.*, **56**:341–352.
- ELLIOTT, K. J. AND W. T. SWANK. 2008. Long-term changes in forest composition and diversity following early logging (1919–1923) and the decline of American chestnut (*Castanea dentata*). *Plant Ecol.*, **197**:155–172.
- FABER-LANGENDOEN, D., N. AASENG, K. HOP, M. LEW-SMITH, AND J. DRAKE. 2007. Vegetation classification, mapping, and monitoring at Voyageurs National Park, Minnesota: an application of the U.S. National Vegetation Classification. *Appl. Veg. Sci.*, **10**:361–374.
- FANCY, S. G., J. E. GROSS, AND S. L. CARTER. 2009. Monitoring the condition of natural resources in U.S. national parks. *Envir. Mon.*, **151**:161–74.
- FONSECA, C. R. AND G. GANADE. 2001. Functional redundancy, random extinctions and the stability of ecosystems. *J. Ecol.*, **89**:118–125.
- GAFVERT, U. 2009. Grand Portage National Monument preliminary soil survey. Natural Resource Technical Report NPS/GLKN/NRTR—2009/188. National Park Service, Fort Collins, Colorado.
- GUILFOYLE, M. P., J. S. WAKELEY, AND R. A. FISCHER. 2009. Applying an Avian Index of Biological Integrity to Assess and Monitor Arid and Semi-arid Riparian Ecosystems. ERDC TN-EMRRP-RQ-01. U.S. Army Corps of Engineers.
- HALE, C. M., L. E. FRELICH, AND P. B. REICH. 2006. Changes in hardwood forest understory plant communities in response to European earthworm invasions. *Ecol.*, **87**:1637–1649.
- HARPER, J. L. AND J. WHITE. 1974. The demography of plants. *Ann. Rev. Ecol. Syst.*, **5**:419–463.
- HECKEL, C. D., N. A. BOURG, W. J. MCSHEA, AND S. KALISZ. 2010. Nonconsumptive effects of a generalist ungulate herbivore drive decline of unpalatable forest herbs. *Ecol.*, **91**:319–326.
- HEINSELMAN, M. L. 1973. Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. *Quat. Res.*, **3**:329–382.
- HELM, D. J. AND B. R. MEAD. 2004. Reproducibility of vegetation cover estimates in south-central Alaskan forests. *J. Veg. Sci.*, **15**:33–40.
- HERMAN, K. D., L. A. MASTERS, M. R. PENSKAR, A. A. REZNICEK, G. S. WILHELM, W. W. BRODOVICH, AND K. P. GARDNER. 2001. Floristic Quality Assessment with Wetland Categories and Examples of Computer Applications for the State of Michigan. Michigan Department of Natural Resources. 136 p.
- HOLDSWORTH, A. R., L. E. FRELICH, AND P. B. REICH. 2007. Effects of earthworm invasion on plant species richness in northern hardwood forests. *Cons. Biol.*, **21**:997–1008.
- HOOPER, D. U., F. S. CHAPIN, J. J. EWEL, A. HECTOR, P. INCHAUSTI, S. LAVOREL, J. H. LAWTON, D. M. LODGE, M. LOREAU, S. NAEEM, B. SCHMID, H. SETALA, A. J. SYMSTAD, J. VANDERMEER, AND D. A. WARDLE. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol. Monogr.*, **75**:3–35.
- HORSLEY, S. B., S. L. STOUT, AND D. S. DECALESTA. 2003. White-tailed deer impact on vegetation dynamics of a northern hardwood forest. *Ecol. Appl.*, **13**:98–118.
- IVERSON, L. R. AND A. M. PRASAD. 1998. Predicting abundance of 80 tree species following climate change in the eastern United States. *Ecol. Mon.*, **68**:465–485.
- JOHNSON, S. E., E. L. MUDRAK, E. A. BEEVER, S. SANDERS, AND D. M. WALLER. 2008. Comparing power among three sampling methods for monitoring forest vegetation. *Can. J. For. Res.*, **38**:143–156.

- JOHNSTON, C. A., J. B. ZEDLER, AND M. G. TULBURE. 2010. Latitudinal gradient of floristic condition among Great Lakes coastal wetlands. *J. Great Lakes Res.*, **36**:772–779.
- JUDZIEWICZ, E. J. AND R. G. KOCH. 1993. Flora and vegetation of the Apostle Islands National Lakeshore and Madeline Island, Ashland and Bayfield Counties, Wisconsin. *Mich. Bot.*, **32**:43–189.
- JUMP, A. S. AND J. PEÑUELAS. 2005. Running to stand still: adaptation and the response of plants to rapid climate change. *Ecol. Let.*, **8**:1010–1020.
- KARR, J. R. AND D. R. DUDLEY. 1981. Ecological perspective on water quality goals. *Environ. Mang.*, **5**:55–68.
- KNIGHT, T. M. 2007. Population-level consequences of herbivory timing in *Trillium grandiflorum*. *Amer. Midl. Nat.*, **157**:27–38.
- KOTAR, J. AND T. L. BURGER. 2000. Field Guide to Forest Habitat Type Classification for North Central Minnesota. Terra Silva Consultants, Madison, Wisconsin. 252 p.
- AND ———. 2005. A Guide to Forest Habitat Types of the Grand Portage Indian Reservation. Terra Silva, Eau Claire, Wisconsin. 109 p.
- LOMOLINO, M. V. AND M. D. WEISER. 2001. Towards a more general species-area relationship: diversity on all islands, great and small. *J. Biogeog.*, **28**:431–445.
- MACARTHUR, R. H. AND E. E. WILSON. 1967. The Theory of Island Biogeography. Princeton University Press, Princeton, New Jersey. 203 p.
- MATTHEWS, J. W., G. SPYREAS, AND A. G. ENDRESS. 2009. Trajectories of vegetation-based indicators used to assess wetland restoration progress. *Ecol. Appl.*, **19**:2093–2107.
- MCCARTHY, J. W. AND G. WEETMAN. 2006. Age and size structure of gap-dynamic, old-growth boreal forest stands in Newfoundland. *Silva Fenn.*, **40**:209–230.
- MCCUNE, B. AND J. B. GRACE. 2002. Analysis of Ecological Communities. MJM Software Design, Glenden Beach, Oregon, U.S.A. 300 p.
- MCGRAW, J. B. AND M. A. FUREDI. 2005. Deer browsing and population viability of a forest understory plant. *Sci.*, **307**:920–922.
- MIDGLEY, J. J. AND W. J. BOND. 1991. How important is biotic pollination and dispersal to the success of the angiosperms? *Phil. Trans. Biol. Sci.*, **333**:209–215.
- MINNESOTA DEPARTMENT OF NATURAL RESOURCES. 2003. Field Guide to the Native Plant Communities of Minnesota: the Laurentian Mixed Forest Province. Ecological Land Classification Program, Minnesota County Biological Survey, and Natural Heritage and Nongame Research Program. MNDNR St. Paul, Minnesota.
- MORIN, R. S., A. M. LIEBHOLD, P. C. TOBIN, K. W. GOTTSCHALK, AND E. LUZADER. 2007. Spread of beech bark disease in the eastern United States and its relationship to regional forest composition. *Can. J. For. Res.*, **37**:726–736.
- O'CONNELL, T. J., L. E. JACKSON, AND R. P. BROOKS. 1998. The Bird Community Index: A Tool for Assessing Biotic Integrity in the Mid-Atlantic Highlands. 98-4. Penn State Cooperative Wetlands Center Forest Resources Laboratory, University Park, Pennsylvania.
- OLDHAM, M. J., W. D. BAKOWSKI, AND D. L. SUTHERLAND. 1995. Floristic Quality Assessment System for Southern Ontario. Natural Heritage Information Centre, Ontario Ministry of Natural Resources. 17 p.
- OVERTON, W. S., R. D. WHITE, AND D. L. STEVENS. 1990. Design report for EMAP, Environmental Monitoring and Assessment Program. EPA/600/3-91/053. U.S. Environmental Protection Agency, Corvallis, Oregon.
- PARMESAN, C. 2006. Ecological and evolutionary responses to recent climate change. *Ann. Rev. Ecol. Evol. Syst.*, **37**:637–669.
- PARRISH, J. D., D. P. BRAUN, AND R. S. UNASCH. 2003. Are we conserving what we say we are? Measuring ecological integrity within protected areas. *BioSci.*, **53**:851–860.
- POST, E., N. C. STENSETH, R. O. PETERSON, J. A. VUCETICH, AND A. M. ELLIS. 2002. Phase dependence and population cycles in a large mammal predator-prey system. *Ecol.*, **83**:2997–3002.
- ROONEY, T. P. 2001. Deer impacts on forest ecosystems: a North American perspective. *For.*, **74**:201–208.
- . 2009. High white-tailed deer densities benefit graminoids and contribute to the biotic homogenization of forest ground-layer vegetation. *Plant Ecol.*, **202**:103–111.
- AND D. A. ROGERS. 2002. The modified Floristic Quality Index. *Nat. Areas J.*, **22**:340–344.

- SANDERS, S. AND J. GROCHOWSKI. 2013. The forests of Isle Royale: can we preserve this pristine wilderness in the face of climate change? *Nat. Areas J.*, **33**:66–77.
- , S. E. JOHNSON, AND D. M. WALLER. 2008. Vegetation monitoring protocol: Great Lakes Inventory and Monitoring Network. Natural Resource Report NPS/GLKN/NRR—2008/056. National Park Service, Fort Collins, Colorado.
- SCHELLER, R. M. AND D. J. MLADENOFF. 2005. A spatially interactive simulation of climate change, harvesting, wind, and tree species migration and projected changes to forest composition and biomass in northern Wisconsin, USA. *Glob. Chng. Biol.*, **11**:307–321.
- STEUVE, K. M., C. H. PERRY, M. D. NELSON, S. P. HEALEY, A. D. HILL, G. G. MOISEN, W. B. COHEN, D. D. GORMANSON, AND C. HUANG. 2011. Ecological importance of intermediate windstorms rivals large, infrequent disturbances in the northern Great Lakes. *Ecosph.*, **2**:2.
- STEVENS, J. AND A. R. OLSEN. 2004. Spatially balanced sampling of natural resources. *J. Amer. Stat. Assoc.*, **99**:262–278.
- SWINK, F. AND G. WILHELM. 1979. Plants of the Chicago Region. 3rd ed. The Morton Arboretum, Lisle, Illinois. 922 p.
- AND ———. 1994. Plants of the Chicago Region. 4th ed. The Indiana Academy of Science, Indianapolis, Indiana. 932 p.
- SYMSTAD, A. J., C. L. WIENK, AND A. THORSTENSON. 2006. Field-based evaluation of two herbaceous plant community sampling methods for long-term monitoring in northern Great Plains national parks. U.S. Geological Survey Open-File Report 2006-1282, Helena, Montana. 38 p.
- TAFT, J. B., G. S. WILHELM, D. M. LADD, AND L. A. MASTERS. 1997. Floristic quality assessment for vegetation in Illinois: a method for assessing vegetation integrity. Illinois Native Plant Society, Westville, Illinois. 29 p.
- TIERNEY, G. L., D. FABER-LANGENDOEN, B. R. MITCHELL, W. G. SHRIVER, AND J. P. GIBBS. 2009. Monitoring and evaluating the ecological integrity of forest ecosystems. *Front. Ecol. Environ.*, **7**:308–316.
- TURNER, W. R. AND E. TJORVE. 2005. Scale-dependence in species-area relationships. *Ecog.*, **28**:721–730.
- WHITE, M. A. AND G. E. HOST. 2003. Changes in disturbance frequency, age and patch structure from pre-Euro-American to settlement to present in northcentral and northeastern Minnesota. Minnesota Forest Resources Council Report LT-1203a, St. Paul, Minnesota.
- WINDELS, S. K. AND D. J. FLASPOHLER. 2011. The ecology of Canada Yew (*Taxus canadensis* Marsh.): a review. *Bot.*, **89**:1–17.
- WRIGHT, J. P., JONES, C. G., AND A. S. FLECKER. 2002. An ecosystem engineer, the beaver, increases species richness at the landscape scale. *Oecol.*, **132**:96–101.