ARTICLE

Plant community development of Isle Royale's moose-spruce savannas

Michael C. Rotter and Alan J. Rebertus

Abstract: In Isle Royale National Park, heavy moose browsing over the past 100 years has suppressed the regeneration of many tree species, gradually resulting in a shift towards more open forests and savannas. By 1996, 16% of the forests at the southwestern end of Isle Royale had become savanna and another 20% of forests were starting to have canopy breakup. The changes in understory vegetation brought about by savanna formation have received little attention, even though the future of moose and wolf populations on Isle Royale is tied to these vegetation changes. This study examined the vegetation of savannas ranging in age (date since formation) from <10 years to 80 years to examine how the ground flora changes over time from initial forest canopy breakup, to extensive grassland, and finally to a zootic subclimax dubbed "moose-spruce savanna." Ordination techniques were used to describe plant communities and to identify environmental variables that influence vegetation development. Nonparametric multiplicative regression was used to predict how these variables influenced individual plants and structure within the communities. Plant communities had a notable shift from forest herbs to ruderal species, especially non-native plants. This succession was influenced strongly by the underlying bedrock and hydrology-altering moisture regimes and plant communities. *Picea glauca* (Moench) Voss. and *Poa pratensis* L. competed in a dynamic inhibitory relationship. The former facilitated forest plants while the latter out-competed other plants and promoted open swards. These interactions are dramatically changing the character of Isle Royale's upland plant communities and will have important trophic consequences for the island.

Key words: Isle Royale National Park, *Poa pratensis*, *Picea glauca*, herbivory, plant communities.

Résumé : Le broutement intensif des orignaux du Parc National de l'Isle Royale au cours des 100 dernières années a éliminé la régénération de plusieurs espèces d'arbres, ce qui a graduellement résulté en un changement de végétation vers des forêts à couvert ouvert et des savanes. En 1996, 16 % des forêts du sud-ouest de l'Isle Royale étaient devenues de savanes et 20 % de plus commençaient à montrer un morcellement du couvert forestier. Les changements de la végétation de sous-étage amenés par la formation de la savane ont reçu peu d'attention, même si l'avenir des populations d'orignaux et de loups de l'Isle Royale est lié à ces changements de végétation. Cette étude s'est penchée sur la végétation des savanes d'âges variés (date depuis leur formation) allant de 10 ans à 80 ans afin d'examiner comment les changements de la flore du sol en fonction du temps, du morcellement du couvert forestier de la forêt initiale à la prairie généralisée et finalement à un sous-climax zootique définissaient la « savane orignal-épinette ». Des techniques d'ordination ont été utilisées afin de décrire les communautés végétales et d'identifier les variables environnementales qui influencent le développement de la végétation. Une régression multiplicative non paramétrique a été utilisée afin de prédire comment ces variables influençaient les plants individuels et la structure à l'intérieur des communautés. Les communautés végétales présentaient des changements notables, allant d'herbes forestières à des espèces rudérales, particulièrement des plantes non indigènes. Cette succession était fortement influencée par le substrat rocheux et l'hydrologie sous-jacents modifiant les régimes d'humidité et les communautés végétales. *Picea glauca* (Moench) Voss. et *Poa pratensis* L. compétitionnaient dans une relation inhibitoire dynamique. Le premier favorisait les plantes forestières alors que le deuxième supplantait les autres végétaux et favorisait les peuplements ouverts de graminées. Ces interactions changent dramatiquement le caractère des communautés végétales des hautes terres de l'Isle Royale et elles auront des conséquences trophiques importantes pour l'ile. [Traduit par la Rédaction]

Mots-clés : Parc National de l'Isle Royale, *Poa pratensis*, *Picea glauca*, herbivorisme, communautés végétales.

Introduction

The impact of ungulate browsing in structuring plant communities is well known (Bergström 1992; Hobbs 1996; Côté et al. 2004). These impacts include changes to the vegetation structure and species composition (Pastor and Naiman 1992; McLaren and Peterson 1994; Ritchie et al. 1998; Gill and Beardall 2001). Grubb (1986) emphasized the importance of so-called "third-party" effects in succession, whereby animals or other organisms shift the relative success of different plant species by creating gaps, alter-

ing light regimes, and influencing litter. Browsing systems have generally been shown to increase biomass and the cover of ground flora (Snyder and Janke 1976; Augustine and McNaughton 1998). Such third-party effects can modify both the rate and pathways of succession. In northern forest ecosystems, for example, preferential browsing of early successional, deciduous tree species often leads to accelerated succession to coniferous, and later successional species (Bryant and Chapin 1986; Johnston and Naiman 1990; Pastor and Naiman 1992). Where herbivore densities are high, they can have particularly strong influences on plant

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Fig. 1. Map of the study area at the western end of Isle Royale. Savannas, based on 2005 aerial photographs, are shaded black. Inset shows the location of the study area on Isle Royale in the Lake Superior Region.
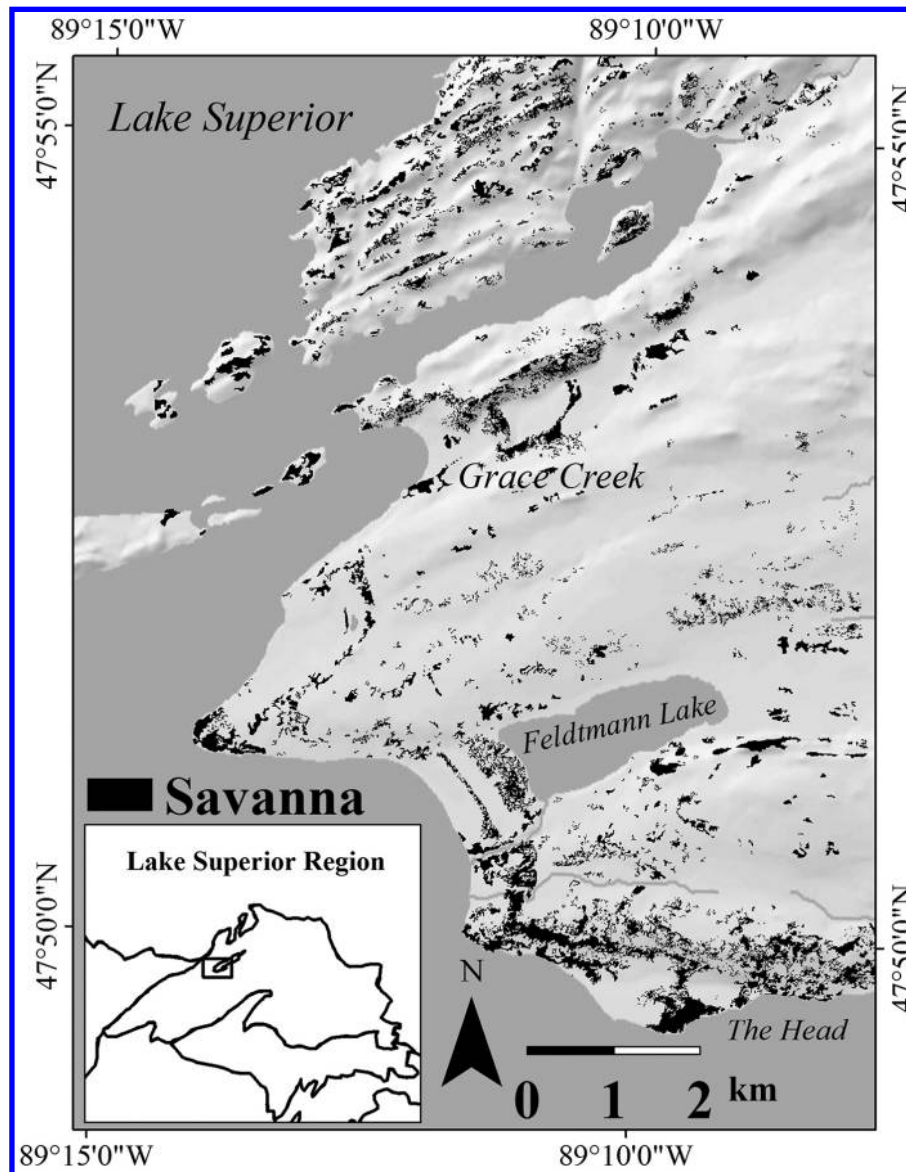
communities (Ripple et al. 2001), potentially creating unique stable states (Augustine et al. 1998; Kotanen and Abraham 2013) or through altering disturbance regimes (e.g., Savage and Swetnam 1990).

Isle Royale National Park, Keweenaw County, Michigan, USA, (Fig. 1) has a long history of botanical and ecological study (Cooper 1913; Nelson et al. 2011), particularly the trophic dynamics of the island's moose (*Alces alces* Linnaeus) and wolf (*Canis lupis* Linnaeus) populations. The isolated nature of the island (located 24 km from the nearest mainland) and relative simplicity of the food web (one large ungulate with one predator) make it an ideal place for studying trophic relationships. Moose colonized the island in the early 1900s and, without any predators, the population grew almost exponentially to 1000–5000 animals in the late 1920s and early 1930s (reviewed by Mech 1966). Over-browsing and starvation caused the population to plummet from 1933 to 1943. As the moose population started to recover in 1945, wolves became established on the island and kept the moose herd relatively low for two decades. The past 30 years, however, have seen major fluctuations in both moose and wolf populations, largely driven by disease and (or) pests, bad winters, and reproductive problems among the remain-

ing wolves (Peterson et al. 1984; Peterson 1999; Vucetich and Peterson 2004). As of 2012, the moose herd had recovered to around 750 animals (Vucetich and Peterson 2013).

Moose on Isle Royale preferentially browse *Populus* spp., *Betula* spp., *Sorbus decora* (Sarg.) C.K.Schneid, and *Abies balsamea* (L.) Mill. (Pastor et al. 1988; Snyder and Janke 1976; Brandner et al. 1990; McInnes et al. 1992; Hodgson 2010). Some species, including the once common *Taxus canadensis* Marshall, were almost eliminated by the first wave of over-browsing in the 1920s and 1930s (Murie 1934; Brown 1935). Many browsed species have been more resilient, persisting as heavily pruned, hedge-like saplings for decades (e.g., *Abies balsamea*, McLaren 1996), but recent studies have emphasized the progressive loss and regeneration failure of *Abies balsamea* (Campbell 2002; De Jager and Pastor 2009; De Jager et al. 2009). Heavy browsing of tree saplings has created a demographic bottleneck in which young trees fail to replace any losses of mature trees in the canopy (Risenhoover and Maass 1987; Pastor et al. 1988; McInnes et al. 1992). The result has been a gradual conversion of forest to open woodlands and savannas, particularly at the western end of the island. The earliest recognized savannas

formed during the 1930s (Gorkiewicz 2006). Since then, savanna coverage has steadily increased and, by 1996, 16.1% of the upland habitat at the western end of the island had been converted to savanna and another 20% was starting to break up with canopy cover in the 40%–60% range (Gorkiewicz 2006). Unbrowsed *Picea glauca* (Moench) Voss. has increased, creating a unique zootic disclimax known as "spruce-moose savanna" (Johnston et al. 1993).

The magnitude of these changes will no doubt affect ground vegetation and have important trophic implications for the island. Several long-term exclosure studies have demonstrated that long-term browsing has not only altered vegetation, but also litter quantity and quality. These alterations have "cascaded" downward to microbial processes and soil properties (McInnes et al. 1992; Pastor et al. 1993). Shifting biotic processes have serious implications for the ecological systems on Isle Royale and may be important drivers of changes to plant communities.

Although numerous studies have demonstrated the large-scale impacts of moose browsing on the island's plant communities, little work has been done on savannas and the successional pathways that are initiated in the ground flora once the canopy is removed. The first objective of this study was to document how the composition of savannas change over a roughly 80 year period using a chronosequence approach, i.e., substituting savannas of different ages for an assumed temporal sequence. Because savannas form gradually, we selected only discrete, well-developed savannas that showed up on aerial photographs of the following years: 1930, 1957, 1978, and 2005. We were particularly interested in how long forest groundcover species persisted in savannas, and whether there were consistent trends in the colonization of other functional types (e.g., graminoids, old-field herbs and shrubs, invasive species).

A second, related objective was to determine whether any physical environmental (e.g., soil type) biotic (e.g., particular plant species), or landscape factors (e.g., savanna size, isolation from other savannas or other communities with ruderal species) influenced successional patterns both within and between savannas, possibly leading to alternate plant communities. Loss of canopy cover can strongly influence soil temperature and moisture regimes (reviewed by Bhatti et al. 2000). In general, canopy removal tends to increase soil moisture (via reduction of evapotranspiration), particularly after high precipitation events, but soil moisture can become low following dry weather owing to evaporation. These effects are influenced by soil characteristics (Bhatti et al. 2000), so we predicted that more heterogeneous plant communities might develop both within and between savannas depending on soil depth, presence of a fragipan, and water-holding capacity.

On the biotic side, we hypothesized that an increase of *Picea glauca* in these savannas might play an important role in determining community patterns, particularly in relationship to graminoid species like the abundant *Poa pratensis* L. Interactions between trees and grass species have been shown to be important in the development of savanna communities elsewhere (Scholes and Archer 1997). We also hypothesized that *Picea glauca* could favor the re-development of patches of forest vegetation by providing shade and reduced grass competition for understory herbs.

Methods

Study area

The study area encompassed 6100 ha at the western end of Isle Royale National Park (47°54′48″N; 89°09′36″W) (Fig. 1). Savannas were located in upland forests classified as balsam fir – aspen – paper birch, aspen–birch boreal coniferous forest, white spruce woodland alliance, and yellow birch – spruce forest (ESRI 2000). The western end of Isle Royale was chosen for several reasons. First, during the 1930s, this end of the island was densely forested, and there have been no major fires during the past 70 years (Hansen et al. 1973). Second, unlike the rocky outcrops of the eastern end of

the island, glacial deposits provide for deeper soils that can support a more continuous forest canopy (Huber 1975), so it was much easier to distinguish moose-generated savannas from edaphic openings such as rock outcroppings or bog meadows.

The chronosequence approach requires careful consideration of site differences (e.g., soil and stand history) that could potentially confound interpretation of temporal trends. Savannas from the 1930, 1957, and 1978 age classes were all located on very similar soil types: principally glacial till over coarse gravel and sand associated with ancient beach deposits (e.g., Minocqua – Copper Harbor – Bete Gris complex and Waiska – Feldtmann – Copper Harbor complex) and very rocky and stony, coarse loamy till over basalt and conglomerate (e.g., Michigame–Peshekee complex). About 40% of the plots from the 2005 age class were found on the Arcadian–Nipissing Complex, which was not associated with older savannas. However, this soil type is similar to the Michigame–Peshekee complex and supports similar vegetation. The formation of recent savannas appeared to be driven, in part, by dieback of *Betula papyrifera* Marshall, possibly the result of a regional outbreak of bronze birch borer (*Agrilus anxius* Order Coleoptera) that began in 1979 and lasted into the 1990s (Millers et al. 1989; Jones et al. 1993).

Sampling design

Historical aerial photos from 1930, 1957, 1978, and 2005 were used to identify savannas based on year of first appearance. It should be emphasized that savannas probably formed gradually during the 21–27 year periods between photographs. Within each age class, 10–11 savannas were chosen. Within each of these savannas, a minimum of 15 randomly located 5 m radius plots, separated by at least 20 m, were sampled. For savannas that expanded over time, plots were located within the oldest, original boundaries. We were unable to develop a large enough pool of savannas for random selection. Instead, we prioritized savannas using the following criteria: (1) size large enough to accommodate 15 plots, (2) unambiguous age, and (3) representation from all parts of the study area. Within this selection criteria, we selected a spread of savannas within each age class that represented various spatial relationships to other savannas (i.e., isolated and connected) and size (Table 1). Five reference stands with predominantly closed canopy (>60%) were also sampled in the same manner. Based on vegetation maps (ESRI 2000), the reference stands were located within the same general stand types as the savannas. Reference areas were much larger than sampled savannas owing to their indiscreet boundaries.

Landscape level variables were processed in ArcGIS (ESRI 2011). Savannas were digitized as patches and total area and core area (area of savanna >10 m from forest edge) were calculated. Distances between neighboring savannas were measured to determine isolation. For this purpose, savannas <10 m away from each other, but in different age classes, were considered linked (connectivity). Distance from Lake Superior was included because coastal communities were a likely source population for many ruderal species. Soil and bedrock data were accessed from the NRSC Soil data mart (Soil Survey Staff 2011).

Field sampling took place June–August 2012. Within each plot, we visually estimated cover for each vascular plant species, mosses, lichens, bare ground, woody debris, rock, and litter using a modified Braun-Blanquet scale: + = <1%, 1 = 1%–5%, 2 = 5%–10%, 3 = 10%–20%, 4 = 20%–40%, 5 = 40%–60%, 6 = 60%–80%, 7 = 80%–100%. Tree and shrub cover were recorded at two different heights: 1.3 m (diameter at breast height was measured) and <1.3 m (measured in the Braun-Blanquet scale). Vascular plant taxonomy follows Voss and Reznicek (2012) and fern and fern relatives follow Cobb et al. (2005). Plant species and their abbreviation codes are listed in Appendix A.

Soil depth was operationally defined by pushing a 6.3 mm diameter steel rod into the soil until hitting bedrock, boulders, or a gravel layer. Measurements were taken at 10 locations within each

Table 1. Total richness of all age classes with estimated 1st order Jackknife. Mean (±SE) richness of plots for each age class.

Age class	Mean (±SE) savanna size (km²)	Richness	Jackknife	Mean (±SE) richness per plot
Ref	—	86	101.78	21.49±0.47
2005	1.70±0.4	138	164.83	23.33±0.30
1978	1.69±0.5	121	152.85	23.72±0.37
1957	2.72±0.41	129	159.77	22.03±0.40
1930	2.31±1.0	149	179.8	22.23±0.47
All age classes	2.13±3.2	202	261.89	22.70±0.86

plot and averaged. Litter depth was measured by allowing a 22 g, 3.0 cm diameter washer to slide down the steel rod until the washer was supported by litter, and then using a ruler to measure the height above the O horizon. This was repeated five times in each plot to obtain a mean. Canopy openness (%), diffuse light, total direct beam, and total radiation were determined from hemispherical photos taken with a Nikon Coolpix 990 with a FC-E8 fisheye converter. Photos were taken at a height of 1.3 m at plot center, and then processed using Gap Light Analyzer version 2 (Fraser et al. 1999).

Data analysis

Nonparametric multidimensional scaling, performed using PC-ORD version 6 (McCune and Mefford 2011), was used to examine differences in species composition among savanna age classes (objective 1). We used Sorensen distance as the similarity measure, and the program was run on "Autopilot" mode under the "slow and thorough" method, with principal axes rotation. The program converged on a three-dimensional solution with a final stress of 20.1, stable after 85 iterations. Significance of the ordination was based on a Monte Carlo test with 250 iterations.

Canonical correspondence analysis (CCA) community tested which physical and biotic variables modified the proposed temporal sequence (objective 2). This approach also helped differentiate between physical site differences and age-related trends. CCA analyses were conducted for (1) all plots ($n = 687$) and (2) across savanna sites and reference stands ($n = 46$) to examine within and between savanna compositional trends, respectively. In the site-level ordination, mean cover for each species was input into the species matrix, and landscape metrics (e.g., savanna size, isolation) were added to the environmental matrix. One hundred iterations of the Monte Carlo randomization tests were used to determine significance for each CCA. We also used nonparametric multiplicative regression (NPMR, HyperNiche version 2.2) to model individual species response to important environmental variables identified by CCA (McCune and Mefford 2009). NPMR avoids the unrealistic assumptions of simple linear or nonlinear responses to environmental variables. Models were evaluated using cross-validated r^2 (xr^2), which is similar to r^2 but uses a cross validation of the residual sum of squares in relation to the total sum of squares (McCune 2006). Model significance was assessed with Monte Carlo randomization tests.

Finally, we graphed the relative cover and species richness of different functional groups, including non-native species, across the chronosequence. All species were grouped as either old field, forest, or edge based on published flora accounts (Voss 1996; Voss and Reznicek 2012).

Results

Vegetation composition across age classes

Overall, 202 species were recorded, with the lowest richness (86 species) in the reference areas and the highest in the 1930 age class (149 species) (Table 1). A secondary peak in richness occurred in the 2005 savannas. These differences were despite the similarity in mean savanna size between age classes (Table 1). In contrast,

mean richness at the plot level (21–23 species) was remarkably consistent across age classes.

Plot and site-level ordinations confirmed major shifts in vegetation composition across savanna age classes (Fig. 2, Fig. 3). At the plot scale (Fig. 2), reference stands were tightly clustered on the right side of axis 1. Plots from 2005 and 1978 overlapped strongly in the middle. Older savannas (1957 and 1930) were highly variable in composition: most plots were shifted far to the left (i.e., composition maximally different than closed forest), but some plots from 1930 also overlapped with reference plots, and 1957 overlapped with 2005 plots.

Forest species (e.g., *Oxalis acetosella* L., *Coptis trifolia* Salisb., *Huperzia lucidula* (Michx.) Trevis.) were poorly represented in all savannas; even in the 2005 age class, forest species comprised just 10% of the relative cover (Fig. 4). Forest species were slightly more abundant in older age classes but their relative cover never completely rebounded. *Oxalis acetosella* and *H. lucidula* were examples of this trend.

Edge species such as *Rubus parviflorus* Nutt., *Diervilla lonicera* Mill., and *Eurybia macrophylla* (L.) Cass. were overwhelmingly dominant in the youngest savannas. Relative cover of edge species dropped in older savannas, especially *E. macrophylla*, but *R. parviflorus* was well represented in even the oldest savannas.

Relative cover of old-field species increased with savanna age, reaching a maximum of nearly 40% in the 1930 age class, led by *Poa pratensis* and *Hieracium* sect. *Pilosella*. Relative cover of *Poa* peaked in 1978 savannas, whereas *Hieracium* sect. *Pilosella* and *Clinopodium vulgare* L. peaked in 1957 and 1930 savannas, respectively. Non-native species were almost nonexistent in the reference stands, but were increasingly common in older savannas. In the 1930 age class, non-native species made up 18% of the relative cover and 14% of the total species richness (Fig. 5).

Environmental factors related to chronosequence trends

CCA revealed several of the key variables related to compositional variation among savanna age classes. CCA of all savanna plots (Fig. 6) indicated that solar radiation was highly correlated with the first axis ($r = 0.60$). Savanna age classes were also aligned somewhat sequentially along the first axis; but, as expected, many plots in the older savannas were shaded and had understories more indicative of closed forest (see Appendix B, Fig. B2). A plethora of old-field species were associated with older savannas in high light situations, especially *Poa* spp., *Phleum pratense* L., *Bromus ciliatus* L. *Hieracium* sect. *Pilosella*, *Clinopodium vulgare*, and *Taraxacum officinale* F.H.Wigg. Shrubs characteristic of these areas included *Sambucus racemosa* L., *Prunus virginiana* L., *Crataegus douglasii* Lindl., *Rubus strigosus* Michx., and *Ribes oxyacanthoides* L. Interestingly, several forest herbs (e.g., *Maianthemum canadense* Desf., *Streptopus lanceolatus* (Aiton) Reveal, *Pyrola elliptica* Nutt.) were common under high solar radiation. Field observations confirmed that these species were common in open savanna and not just under isolated trees.

NPMR models demonstrate response curves of several species to solar radiation (Fig. 7A). *Huperzia lucidula*, a clubmoss commonly found in closed forest, was almost nonexistent in plots with even moderate light. Other forest herbs, such as *Coptis trifolia* and *Spinulum annotinum* (L.) A.Haines, were found in plots with moderate sunlight but absent from the most open plots. Other forest species, such as *Linnaea borealis* L. and *Streptopus lanceolatus*, were tolerant across a wide range of light conditions. *Hieracium* sect. *Pilosella*, *Clinopodium vulgare*, and *Poa pratensis* increased dramatically with higher solar radiation ($xr^2 = 0.114$, 0.090, and 0.279, respectively). These graphs do not represent true physiological responses, because potential confounding variables (e.g., soil moisture, competition, temporal trends in colonization) were not taken into account.

Several soil and (or) bedrock variables were correlated with axis 2 in the plot level CCA (Fig. 6), including presence of basalt

Fig. 2. Nonparametric multidimensional scaling ordination for all sampled plots. Individual plots coded by age class. Final model was a three-dimensional solution with stress = 20.1. For 250 iterations of Monte Carlo test, $p = 0.004$. Axes 1 and 3 accounted for the most variation ($r^2 = 0.23$ and 0.22, respectively). Plots with axis 2 ($r^2 = 0.19$) showed similar trends.
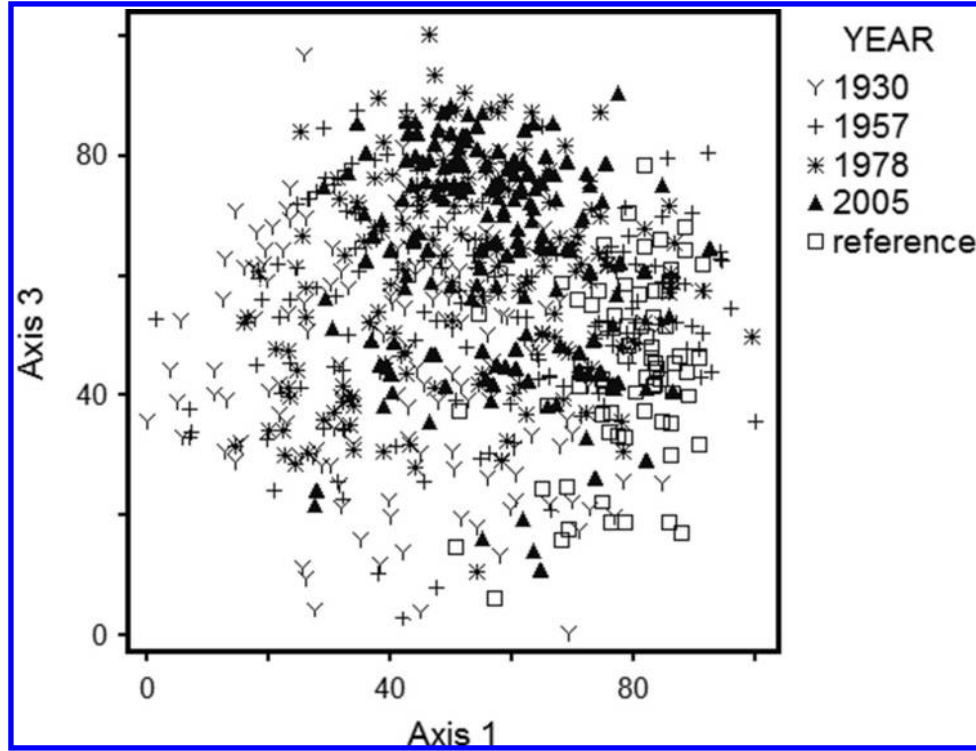

Fig. 3. Canonical correspondence analysis of savannas with all data from plots within each savanna pooled. Eigenvalues for axis 1 and axis 2 were 0.295 (14.4%) and 0.208 (10.1%), respectively. For 100 iterations of Monte Carlo test, $p = 0.010$. Year was a categorical variable. Convex hull polygons enclose all savannas of a given age class to illustrate compositional variability.
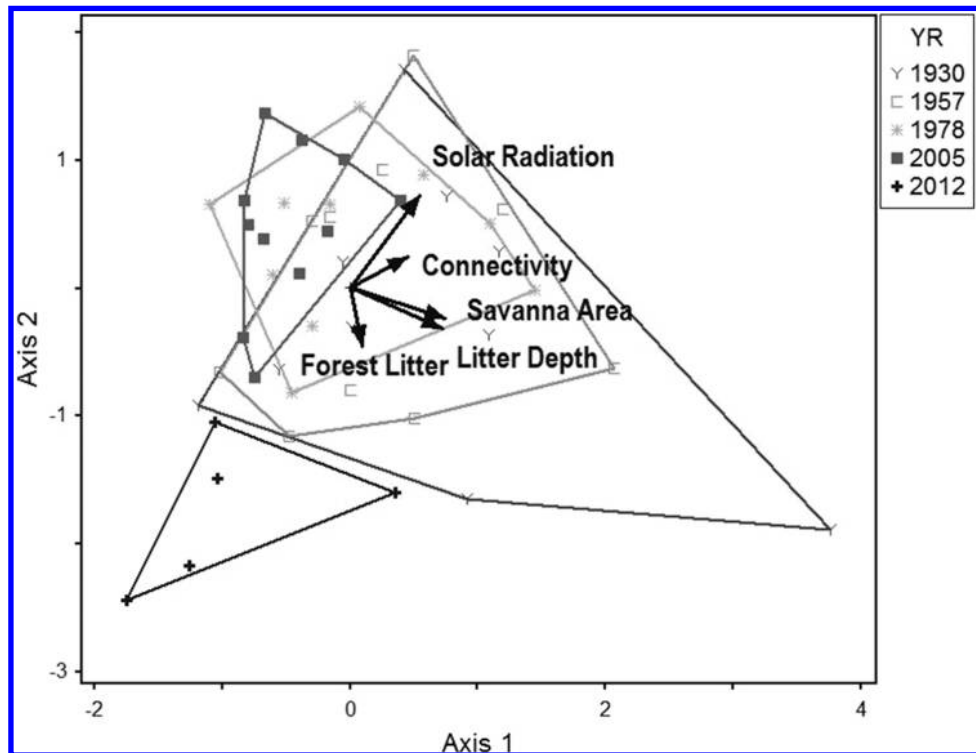
Fig. 4. (*a*) Relative cover of functional groups across age classes. (*b*) Relative cover of select field species across age classes. (*c*) Relative cover of forest species across age classes. (*d*) Relative cover of edge species across age classes. Axis on right is the mean basal area of spruce (m²·ha⁻¹) for each age class.
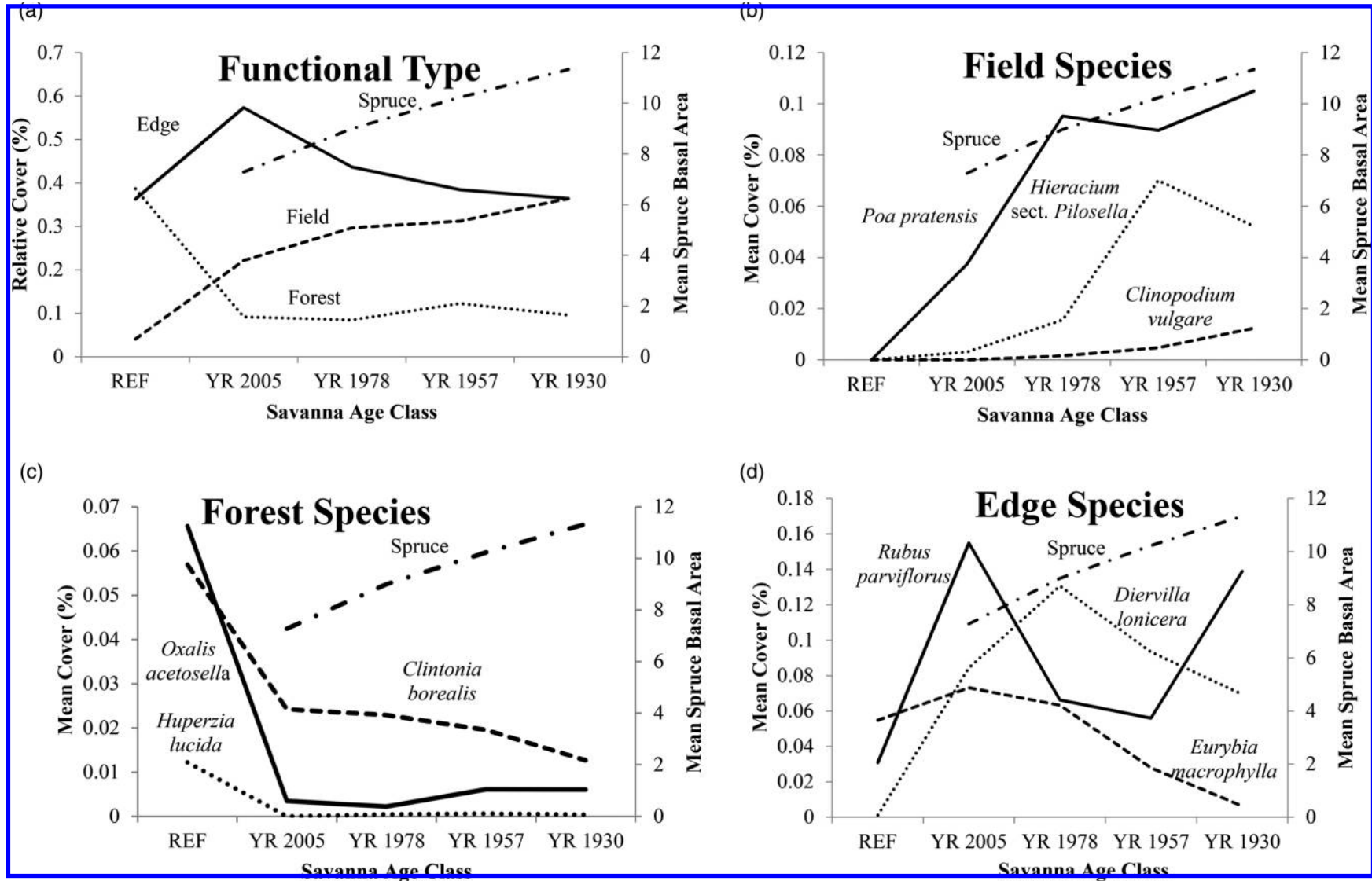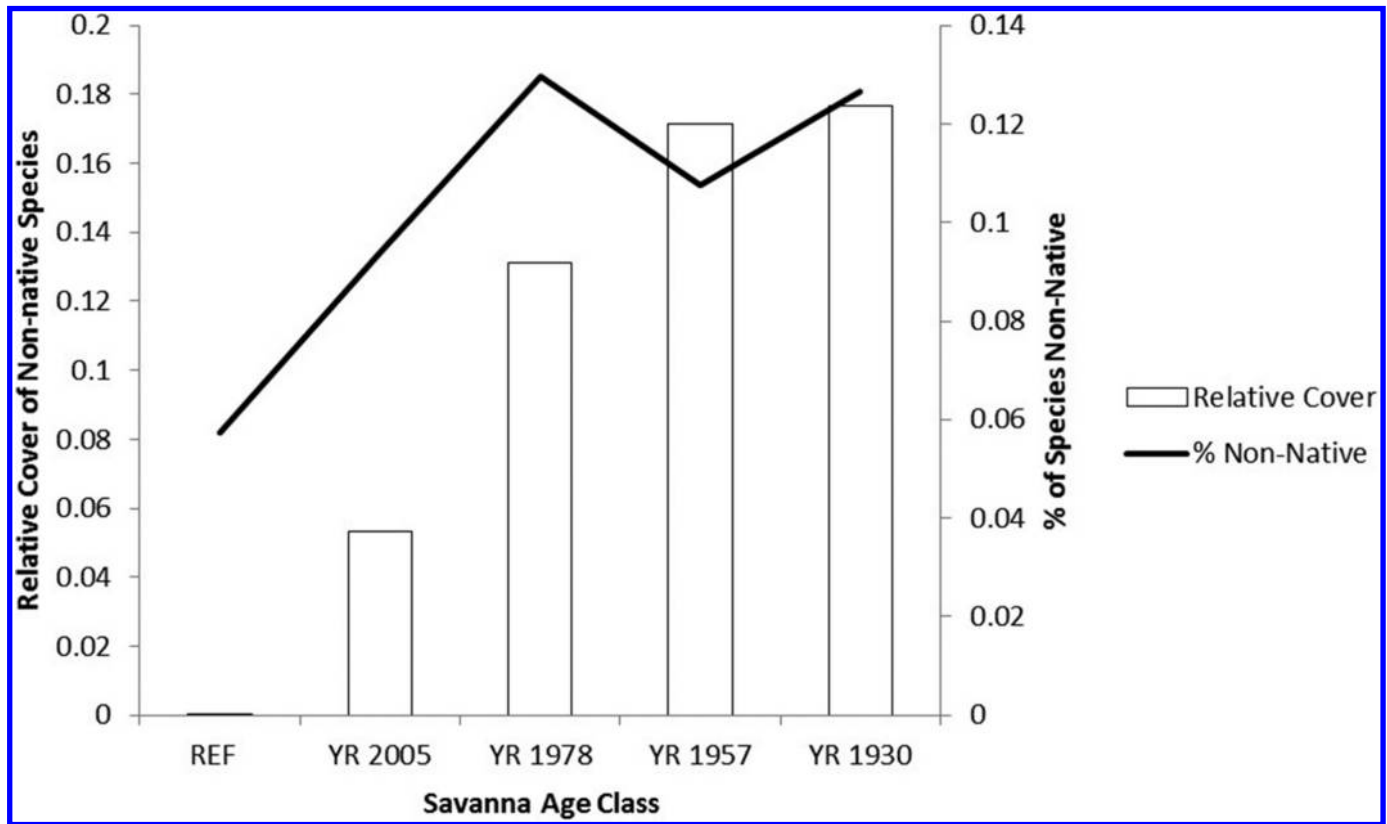
Fig. 5. Relative cover of non-native plant species by age class displayed in bars. Black line indicates the percent of plant species richness composed of non-native species by age class.

and (or) conglomerate bedrock ($r = 0.47$), presence of a fragipan ($r = -0.52$), and volumetric soil moisture ($r = 0.36$). Species strongly associated with higher soil moisture and fragipan included *Matteuccia struthiopteris* (L.) Tod., *Thalictrum dasycarpum* Fisch. & Ave-Lall., *Heracleum maximum* W.Bartram, and *Carex intumescens* Rudge, particularly in plots from the 1930 savannas. At the other extreme, species associated with drier soils and basalt/conglomerate bedrock included plants typical of open "barrens" (e.g., *Danthonia spicata* (L.) Roem. & Schult., *Diervilla lonicera*, *Anaphalis margaritacea* (L.) Benth.; lower right of Fig. 6B) as well as plants typical of dry, acidic woodland (*Pteridium aquilinum* (L.) Kuhn, *Chimaphila umbellata* (L.) W.P.C.Barton, and *Orthilia secunda* (L.) House; lower left of Fig. 6B). Again, many of the plots associated with this vegetation were from the 1930 age class.

Several representative NPMR species response curves to soil moisture are shown in Fig. 7. *Poa pratensis* ($xr^2 = 0.042$) cover was inversely related to soil moisture. *Cornus canadensis* L. ($xr^2 = 0.033$) was found on all but the wettest plots. *Streptopus lanceolatus* cover did not vary much across a wide range of moisture levels ($xr^2 = 0.07$).

Ordination of older savannas

To better understand the extreme variability in species composition in older savannas, we performed CCA just on plots from the 1957 and 1930 age classes. This ordination confirmed that vegetation in older savannas was segregated along both light and moisture gradients. These vectors were orthogonal, indicating soil moisture was largely independent of site openness (Fig. 8). A third important factor was revealed in this analysis: spruce cover. This was recorded at 1.3 m height, picking up mostly lower tree boughs and saplings. Beneath spruce cover, many woodland species abound, especially those associated with more acidic conditions (*Linnaea borealis*, *Coptis trifolia*, *Cornus canadensis*, and several club mosses). These spruce "gardens" were extremely diverse at a scale

of <1 m² (Appendix B, Figs. B1, B2). The occurrence of *Taxus canadensis* in these gardens is notable because it is highly preferred by moose.

Litter depth also appeared to influence compositional patterns, although only in the site-level ordination (see Fig. 3). In savannas, this litter was composed mainly of dead grasses. *Picea glauca* and *Cornus canadensis* sharply declined with increasing litter depth ($xr^2 = 0.03$ and 0.06, respectively) (Fig. 7). *Streptopus lanceolatus*, another forest species, was not influenced by litter depth ($xr^2 = 0.01$). *Hieracium* sect. *Pilosella*, which tend to grow near *Poa*, were abundant in deeper litter ($xr^2 = 0.226$).

Within versus among savanna trends in composition

Similar to the nonparametric multidimensional scaling (Fig. 2), earlier age class savannas (reference and 2005 age classes) were relatively homogenous in composition (Fig. 4). Older age class savannas (1930 and 1957), in contrast, were far more variable. The convex hull polygons show a striking pattern of expansion (increasing heterogeneity) across age classes (Fig. 3). One key environmental variable that explains this at the savanna level is site openness. Some of the older savannas segregate into ones that are very open ($r = 0.60$ for axis 1) whereas others are more closed in, especially by *Picea glauca*. Savanna core area was the only landscape variable that was important ($r = -0.414$ for axis 1); most of the smaller savannas were from the 2005 age class, whereas the largest savannas were from 1957 and 1930. This could explain the higher representation of edge species in the 2005 savannas.

Discussion

Savanna composition over time: a proposed model

In Fig. 9, we have created a working model interpreting the chronosequence of Isle Royale savanna development. Interpretation of chronosequences can be problematic when site and time variables

Fig. 6. (A) Canonical correspondence analysis (CCA) of savanna plots. Eigenvalues for axis 1 and axis 2 were 0.371 (4%) and 0.210 (2.3%), respectively. For 100 iterations of Monte Carlo test, $p = 0.010$. Individual plots labeled by age class. Variable codes in gray: Conglomerate/Basalt, on conglomerate or basaltic bedrock; Solar Radiation, total solar radiation (mol·m^{-2} per day); Savanna Area, savanna core area; Fragipan, over fragipan base; H2O Content, volumetric water content; and Core Area, area (m²) of savanna >10 m from forest edge. (B) CCA of savanna plots. Eigenvalues for axis 1 and axis 2 were 0.371 (4%) and 0.210 (2.3%), respectively. For 100 iterations of the Monte Carlo test, $p = 0.010$. Species codes are the first three letters of the genus and the first three letters of the specific epithet, see Appendix A for scientific names. Scaling was min to max. Conglomerate/Basalt, on conglomerate or basaltic bedrock; Solar Radiation, total solar radiation (mol·m^{-2} per day); Savanna Area, savanna core area; Fragipan, over fragipan base; and H2O Content, volumetric water content; and Core Area, area (m²) of savanna >10 m from forest edge.
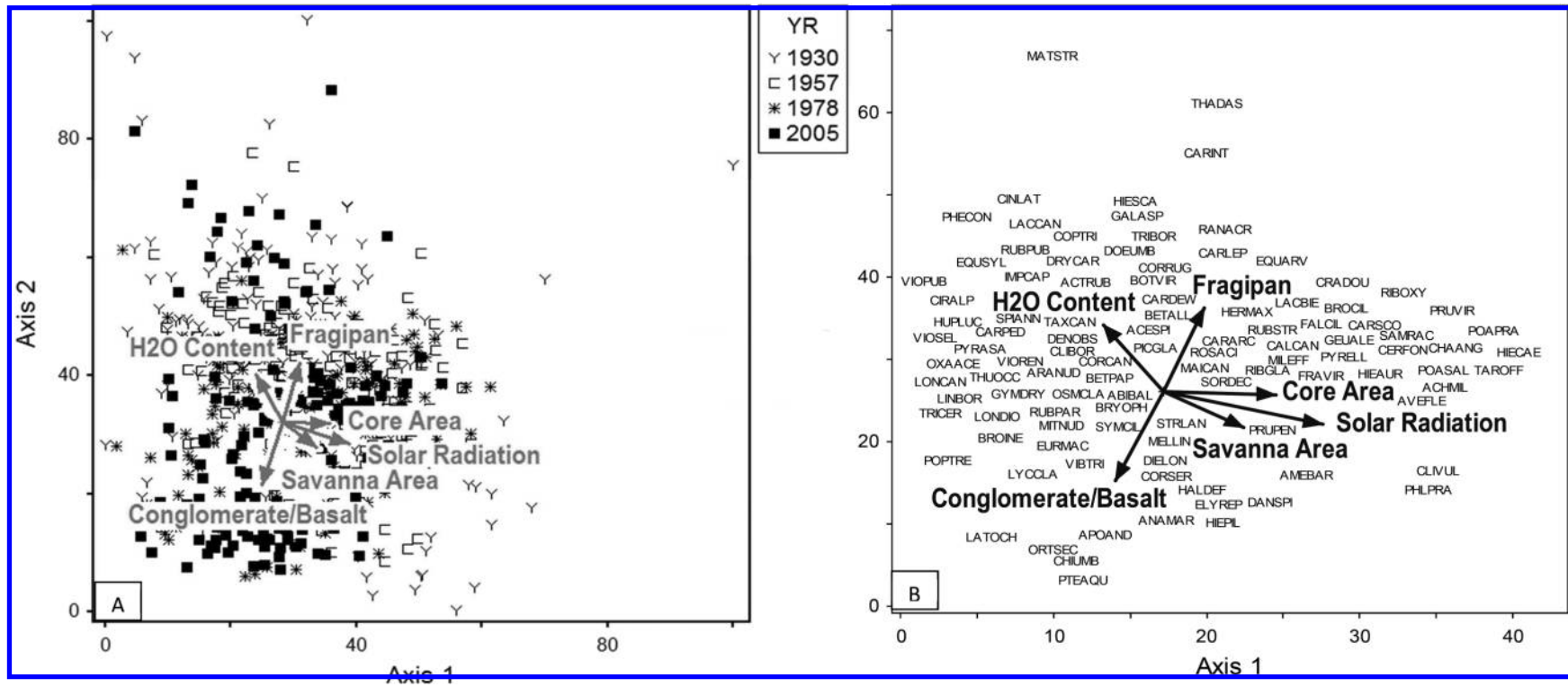
Fig. 7. Response curves of selected species to important environmental variables (total solar radiation, litter depth, and volumetric water content). Curves created from local mean Gaussian models in HyperNiche. (For all models, $p \leq 0.05$).
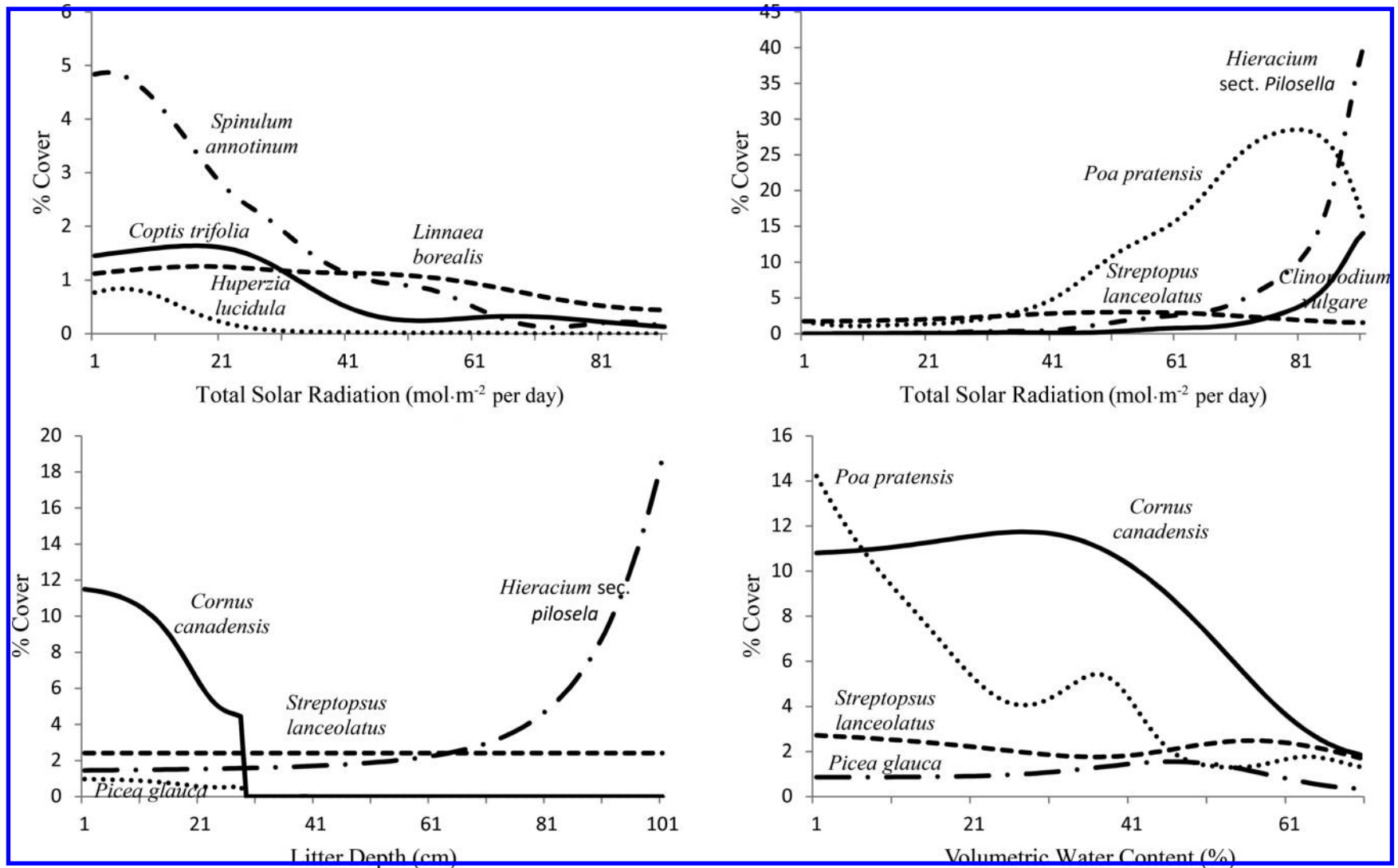
Fig. 8. Canonical correspondence analysis for all savanna plots in the 1930 and 1957 savanna age class groups. Eigenvalues for axis 1 and axis 2 were 0.382 (4.4%) and 0.291 (3.4%), respectively. For 100 iterations of the Monte Carlo test, $p = 0.010$. Variable codes: Solar Radiation, total solar radiation (mol·m^{-2} per day); Savanna Area, savanna core area; Spruce Cover, *Picea glauca* cover at breast height; H2O Content, volumetric water content; Core Area, area (m^2) of savanna >10 m from forest edge; and Connectivity, area of savannas <10 m away. Species codes are the first three letters of the genus and the first three letters of the specific epithet; see Appendix A for scientific names.
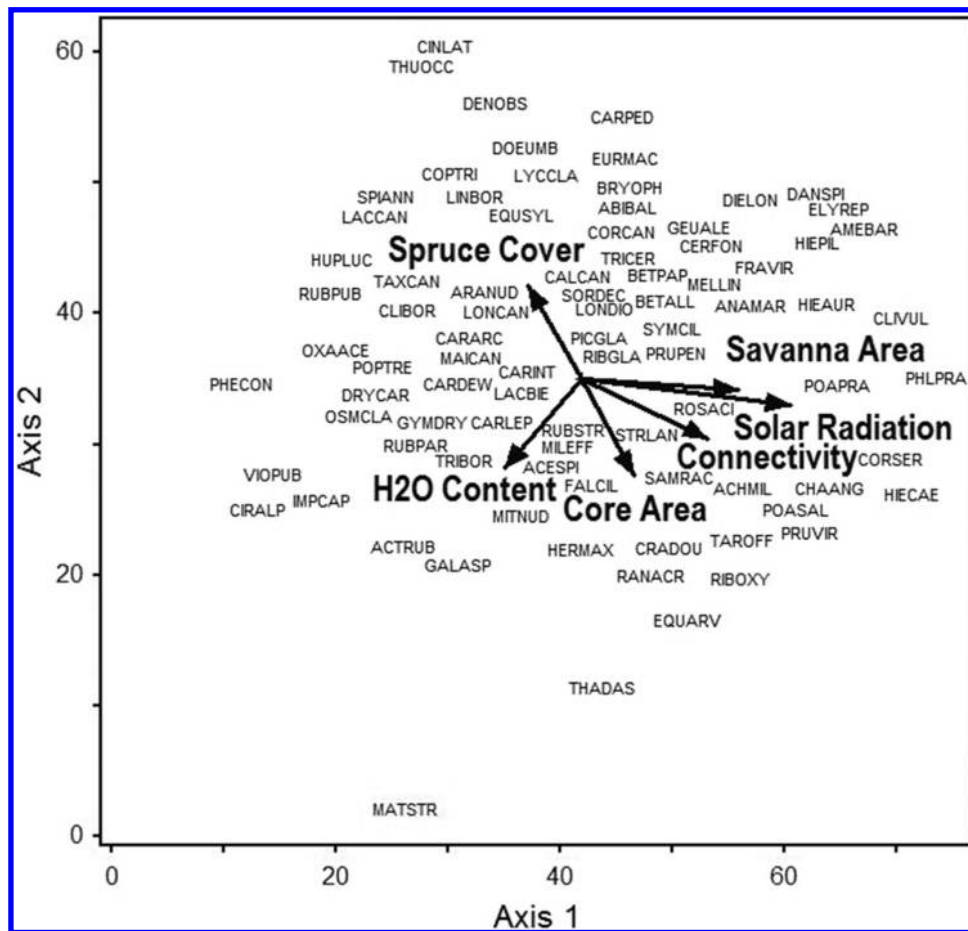
are confounded or when historical legacies are not considered (Johnson and Miyanishi 2008). We have established permanent plots to further test these hypotheses and monitor future trends. Fortunately, Isle Royale has a long history of vegetation research, moose exclosures dating back 65 years, aerial and ground photographs, and eyewitness accounts that are consistent with the general successional trends derived from this chronosequence. Additionally, the CCA approach takes into account soil differences and how they modify vegetation trends partially independent of savanna age.

Historical accounts of the pre-moose forests on Isle Royale portray most areas as densely forested and with thick understories of *Abies* and *Taxus* (Ruthven 1906; Adams 1909; Cooper 1913). Furthermore, aerial photographs confirm that forests in the study area were still intact in 1930. Moose exclosures in the study area, one dating back to 1948 (Krefting 1974), and comparisons with vegetation on islands in the archipelago that are inaccessible to moose, leave no doubt that moose browsing has been the primary force maintaining these openings after canopy decline or loss (Snyder and Janke 1976; Pastor et al 1988; McInnes et al. 1992). For instance, areas hit by birch dieback from bronze birch borer have remained open since the 1990s (Millers et al. 1989; Jones et al. 1993).

The understories of our reference forest stands were very similar to the closed forests ca. 1905 described by Cooper (1913). However, the overstory composition has no doubt shifted, with less *Abies balsamea* and *Betula papyrifera* but more *Picea glauca* (McInnes et al. 1992; Campbell 2002). Closed canopy areas had relatively low

species richness, high abundance of forest herbs, and few non-native plant species. These mixed deciduous conifer forests are the starting point of the chronosequence (Fig. 9A).

As the forests fell apart, through natural senescence and birch dieback (see Study Area), an increase in light started to shift vegetation composition. Initial changes, as exemplified by the 2005 age class, showed increased richness driven by an increase of edge species, a modest influx in old-field species, and the persistence of some forest species. The increase in edge species in young savannas forming in the 1970s is corroborated by eyewitness accounts and photographs by the second author. However, thickets composed of saplings of preferred deciduous tree species (e.g., *Sorbus decora*) were far more common in the past. The steep decline of forest species bottoms out and stabilizes for the 1978 through the 1930 age classes (Fig. 4). Relative abundance of edge species also declined with savanna age, but the abundance of old-field species, especially non-native ones, increased greatly and contributed to higher species richness in older age classes. Indeed, the oldest savannas are overwhelmingly dominated by swards of non-natives *Poa pratensis* and *Hieracium* sect. *Pilosella*.

Forest herbs were poorly represented in the dry open savannas (Fig. 9C), suggesting they were either out-competed or simply could not tolerate open conditions. However, some forest species appeared to be remarkably persistent in savannas, even in some areas densely overgrown with *Poa pratensis*. Persistence of many forest herbs in savannas can be explained by two mechanisms:

Fig. 9. Flowchart of possible savanna vegetation development. Rectangles represent forest states and ovals represent biotic and abiotic processes.
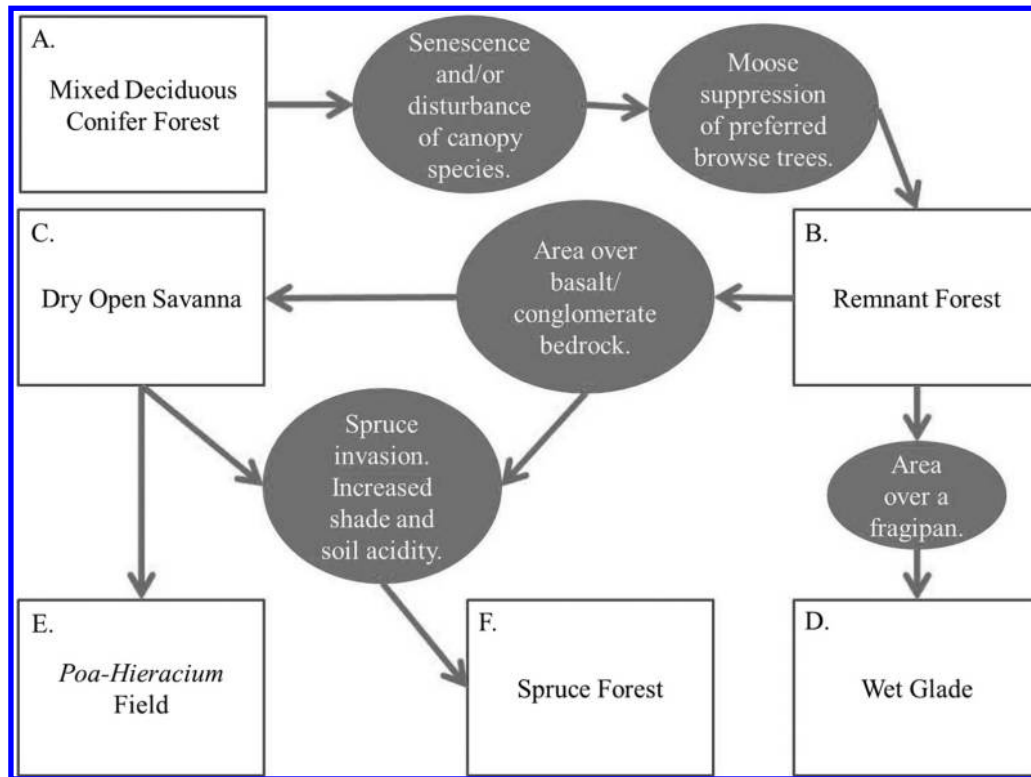
(1) tolerance of open savanna conditions and (2) persistence and (or) colonization of micro-refugia within the savanna matrix. Forest understory species that were especially tolerant of open savanna conditions included *Streptopus lanceolatus*, *Linnaea borealis*, *Maianthemum canadense*, and *Clintonia borealis* (Aiton) Raf. NMPR models show these species were found across a wide range of light, moisture, and litter depths (Fig. 7). The presence of *Maianthemum canadense* in open savannas was unexpected given its previously documented sensitivity to excessive light (Sparling 1967). One likely explanation is that these species enjoy some benefit of shade and extra moisture by growing underneath dense grass cover. Such niche partitioning has been well described for prairie communities (Knapp et al. 1993). However, competition with graminoids for limited moisture and nutrients may hinder the growth of other forb species, so the interactions likely depend on individual life histories. The persistent species above also form extensive clonal networks where water and nutrient sharing may buffer plants from mortality. *Clintonia borealis*, for example, freely shares nutrients through rhizome connection throughout the entire clone (Ashmun et al. 1982). Forest species can also persist in savannas by growing under the shade of isolated trees, especially *Picea glauca* (see Alternate successional sequences).

The general trend of loss of forest herbs and increase in old-field species, including non-native species, has been observed in other situations with large densities of herbivores, most notably with the impacts of white-tailed deer (*Odocoileus virginianus* Zimmermann) in eastern deciduous forests (Knight et al. 2009; Relva et al. 2010). Moose themselves have been implicated in the spread and establishment of non-native plants (Rose and Hermanutz 2004).

Alternate successional sequences

Initially, succession in savannas appeared to be dominated by a precipitous loss of shade-loving forest plants and a dramatic increase in edge, old-field, and non-native plant species. However, the composition of the oldest savannas implies that succession

may eventually become bi- or multi-directional. As the buffering effects of the canopy were lost, divergence in the understory plant communities probably was driven increasingly by underlying geology and its effects on soil moisture (see Figs. 6, 8). Higher soil moisture was found over areas with a fragipan, favoring a wet glade community dominated by *Matteuccia struthiopteris*, *Thalictrum dasycarpum*, *Carex intumescens*, and *Heracleum maximum* (Fig. 9D). Although these sites would normally favor mesic forest understories, we believe that moose, by restricting tree regrowth and reducing evapotranspiration, have created more mesohydric communities. In contrast, savannas overlying well-drained, shallow conglomerate and (or) basalt formations, may have become drier without canopy shading, favoring more xerophytic communities (e.g., *Pteridium aquilinum*, *Danthonia spicata*, *Anaphalis margaritacea*) (Fig. 9C). Such opposing effects of canopy loss on soil moisture are well documented following logging activities on different soil types (Bhatti et al. 2000).

In addition to geology, we believe that the interaction of two key plant species, *Poa pratensis* and *Picea glauca*, created divergent successional pathways. All the ordination results indicate that some open portions of older savannas achieve maximum dissimilarity to closed forest. A good example is the extensive swards that are overwhelmingly dominated by *Poa pratensis* and *Hieracium* spp. (see Appendix B, Fig. B1). Paradoxically, other areas appear to be undergoing a reversion towards forest understories, which is being driven by spruce invasion. The shade of *Picea glauca* acts both as a refuge for persistence of forest herbs and a nucleus for their re-colonization. Higher levels of moisture underneath these isolated trees may allow for persistence of understory herbaceous species (Scholes and Archer 1997). Because moose do not browse *Picea glauca*, it provides a refuge for preferred species such as *Sorbus decora*, *Betula papyrifera*, and *Taxus canadensis* (see Fig. 8). Associational resistance ("defense guilds" sensu Atsatt and O'Dowd

1976) has been shown to effectively defend plants against large generalist herbivores (Olff et al. 1999; Callaway et al. 2005).

The islands of spruce habitat, however, represent a very different environment than the original forests. First, spruce in savannas are mostly open-grown; their dense boughs extend to ground level and block light very effectively. Second, their needle litter, which creates acidic soils and limits many nutrients, also affects species composition (Pastor et al. 1988; McInnes et al. 1992). The groundcover under savanna spruce was largely barren, with many herbs strongly favoring edges.

Historical establishment patterns of *Poa* and *Picea* may have influenced each other in creating the current savanna mosaic. Cooper (1913) remarked on the scarcity of *Picea glauca* at the northern end of the island in the early 1900s. Few spruce in the study area are older than 85 years, and most became established in waves of regeneration starting ca. 1950 (S. Caird and A. Rebertus, unpublished data, 2014). Spruce invasion was not restricted to savannas, because similar age structures were found in forest stands. Although climate and the timing of masting events may have influenced spruce establishment, it is also possible that declining inputs of deciduous litter, increased sunlight, and a competitive edge over declining browse species (especially *Abies*) played a role in the success of spruce. Spruce regenerates best on microsites with bare mineral soil (Purdy et al. 2002), and grass can strongly inhibit its establishment (Chhin and Wang 2002). It is possible that early establishment of spruce in savannas may have preceded the establishment of dense swards of *Poa pratensis*. When *Picea glauca* reaches the canopy, it can inhibit *Poa pratensis* through shading and allow more shade-tolerant forbs and spruce seedlings to establish.

An important question is how resistant *Poa pratensis – Hieracium* fields (Fig. 9E) are to further compositional changes. Does this represent a "plateau" in savanna development? The habits of both species suggest they may be resistant to change. *Poa* has aggressive growth habitats and produces smothering litter that inhibits other plants (Bosy and Reader 1995). Rosette forming species, such as *Hieracium* sect. *Pilosella* are able to create room around themselves and escape litter suppression of *Poa* (Bosy and Reader 1995). *Pilosella* species have allelopathic pollen that may further limit other species capabilities to invade through seed propagules (Murphy 2000). Some shrub species (e.g., *Ribes oxyacanthoides*, *Sambucus racemosa*), however, are able to survive with *Poa pratensis*, most likely through vegetative growth and by escaping the litter through height. *Sambucus racemosa*, which moose strongly avoid, is becoming particularly common in many savannas.

It is highly unlikely that any deciduous species will be able to re-colonize open savanna areas under the current and historical browsing pressure. In the absence of fire, the fate of savannas will depend on the rate of *Picea glauca* invasion, which appears to be highly variable. Figure 3 shows that the composition of 4–5 savannas from the 1957 and 1930 age class overlap strongly with the reference plots; these are rapidly being closed in by spruce forests (Fig. 9F). The rest, however, are being colonized more slowly and may represent an alternate stable state. Alternative stable states as the result of browsing pressure have been previously documented in forests heavily browsed by white-tailed deer (Augustine et al. 1998).

Moose, ecosystems, and the future of Isle Royale

Savanna systems depend on multiple buffering mechanisms to maintain a sparse tree and grass composition (Jeltsch et al. 2000). Continued moose browsing and (or) other disturbances, such as fire or insect outbreaks, may be necessary for the persistence of savannas on Isle Royale. In fact, these biotic and abiotic interactions have been seen as important processes in savanna formation. For instance, the time intervals between fires are important to biotic feedbacks in savanna and forest balances (Hoffmann et al. 2012). On Isle Royale, fires occur infrequently (Krefting 1974; Bergeron 1991), leaving an open question of whether or these

savannas will remain stable over long periods or will succumb to the reinvasion of *Picea glauca*.

The continued long-term recruitment of *Picea glauca* to the overstory may be important for survival of some understory species. If lost, some shade-tolerant forest species may recover very slowly, even under canopy reformation (Duffy and Meier 1992). Savanna formation has already shifted species richness and altered the fundamental composition of large areas of the island. With a persistent or climbing moose population (Vucitech and Peterson 2013), the long term impacts on the island's plant communities could be severe and will alter the landscape of this island wilderness.

References

Adams, C.C. 1909. An ecological survey of Isle Royale, Lake Superior. University of Michigan Museum and State Biological Survey, Wynkoop Hallenbeck Crawford, Lansing, Mich.

Ashmun, J.W., Thomas, R.J., and Pitelka, L.F. 1982. Translocation of photoassimilates between sister ramets in two rhizomatous forest herbs. Ann. Bot. **49**(3): 403–415.

Atsatt, P.R., and O'Dowd, D.J. 1976. Plant defense guilds. Science, **193**(4247): 24–29. doi:10.1126/science.193.4247.24. PMID:17793989.

Augustine, D.J., and McNaughton, S.J. 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. J. Wildl. Manage. **62**(4): 1165–1183. doi:10.2307/3801981.

Augustine, D.J., Frelich, L.E., and Jordan, P.A. 1998. Evidence for two alternate stable states in an ungulate grazing system. Ecol. Appl. **8**(4): 1260–1269. doi:10.1890/1051-0761(1998)008[1260:EFTASS]2.0.CO;2.

Bergeron, Y. 1991. The influence of island and mainland lakeshore landscapes on boreal forest fire regimes. Ecology, **72**(6):1980–1992. doi:10.2307/1941553.

Bergström, R. 1992. Browse characteristics and impact of browsing on trees and shrubs in African savannas. J. Veg. Sci. **3**(3): 315–324. doi:10.2307/3235756.

Bhatti, J.S., Fleming, R.L., Foster, N.W., Meng, F.R., Bourque, C.P.A., and Arp, P.A. 2000. Simulations of pre- and post-harvest soil temperature, soil moisture, and snowpack for jack pine: comparison with field observations. For. Ecol. Manage. **138**(1–3): 413–426. doi:10.1016/S0378-1127(00)00427-8.

Bosy, J.L., and Reader, R.J. 1995. Mechanisms underlying the suppression of forb seedling emergence by grass (*Poa pratensis*) litter. Funct. Ecol. **9**(4): 635–639. doi:10.2307/2390155.

Brandner, T.A., Peterson, R.O., and Risenhoover, K.L. 1990. Balsam fir on Isle Royale: effects of moose herbivory and population density. Ecology, **71**(1): 155–164. doi:10.2307/1940256.

Brown, C.A. 1935. Ferns and flowering plants of Isle Royale, Michigan. U.S. Department of the Interior, National Park Service, Washington, D.C.

Bryant, J.P., and Chapin, F.S., III. 1986. Browsing-woody plant interactions during boreal forest plant succession. *In* Forest ecosystems in the Alaskan taiga: a synthesis of structure and function. *Edited by* K. Van Cleve, F.S. Chapin, III, P.W. Flanagan, L.A. Viereck, and C.T. Dryness. Springer-Verlag, New York. pp. 213–225.

Callaway, R.M., Kikodze, D., Chiboshvili, M., and Khetsuriani, L. 2005. Unpalatable plants protect neighbors from grazing and increase plant community diversity. Ecology, **86**(7): 1856–1862. doi:10.1890/04-0784.

Campbell, M. 2002. Spatial variation in stand structure of balsam fir (*Abies balsamea*) and the role of moose (*Alces alces*) herbivory on balsam fir at Isle Royale National Park, Michigan, U.S.A. M.Sc. thesis, Michigan Technological University, Houghton, Michigan, USA.

Chhin, S., and Wang, G.G. 2002. Spatial and temporal pattern of white spruce regeneration within mixed-grass prairie in the Spruce Woods Provincial Park of Manitoba. J. Biogeogr. **29**(7): 903–912. doi:10.1046/j.1365-2699.2002.00704.x.

Cobb, B., Farnsworth, E., and Lowe, C. 2005. Ferns of Northeastern and Central North America. 2nd ed. Houghton Mifflin, New York.

Cooper, W.S. 1913. The climax forest of Isle Royale, Lake Superior, and its development. I. Bot. Gaz. **55**(1): 1–44. doi:10.1086/330990.

Côté, S.D., Rooney, T.P., Tremblay, J.P., Dussault, C., and Waller, D.M. 2004. Ecological impacts of deer overabundance. Annu. Rev. Ecol. Evol. Syst. **35**: 113–147. doi:10.1146/annurev.ecolsys.35.021103.105725.

De Jager, N.R., and Pastor, J. 2009. Declines in moose population density at Isle Royle National Park, MI, U.S.A. and accompanied changes in landscape patterns. Landsc. Ecol. **24**(10): 1389–1403. doi:10.1007/s10980-009-9390-4.

De Jager, N.R., Pastor, J., and Hodgson, A.L. 2009. Scaling the effects of moose browsing on forage distribution, from the geometry of plant canopies to landscapes. Ecol. Monogr. **79**(2): 281–297. doi:10.1890/08-0149.1.

Duffy, D.C., and Meier, A.J. 1992. Do Appalachian herbaceous understories ever recover from clearcutting? Conserv. Biol. **6**(2): 196–201. doi:10.1046/j.1523-1739.1992.620196.x.

Environmental Systems Research Institute (ESRI). 2000. Isle Royale National Park Spatial Vegetation Data; Cover Type/Association level of the National Vegetation Classification System: USGS-NPS Vegetation Mapping Program Isle Royale National Park, USGS, BRD, Center for Biological Informatics, Denver, Colorado, USA.

Environmental Systems Research Institute (ESRI). 2011. ArcGIS Desktop: Release 10. Environmental Systems Research Institute, Redlands, Calif.

Fraser, G.W., Canham, C.D., and Lertzman, K.P. 1999. Gap Light Analyzer (GLA), Version 2.0: Imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs, user's manual and program documentation. Institute of Ecosystem Studies, Simon Fraser University, Burnaby, B.C., and Millbrook, New York.

Gill, R.M.A., and Beardall, V. 2001. The impact of deer on woodlands: the effects of browsing and seed dispersal on vegetation structure and composition. Forestry, **74**(3): 209–218. doi:10.1093/forestry/74.3.209.

Gorkiewicz, L.M. 2006. Effects of selective moose herbivory on savanna formation in Isle Royale National Park, Michigan, U.S.A. M.Sc. thesis, Northern Michigan University, Marquette, Mich., USA.

Grubb, P.J. 1986. The ecology of establishment. *In* Ecology and design in landscape. *Edited by* A.D. Bradshaw, D.A. Goode, and E.H. Thorp. Blackwell, Oxford, U.K. pp. 83–97.

Hansen, H.L., Krefting, L.W., and Kurmis, V. 1973. The forest of Isle Royale in relation to fire history and wildlife. University of Minnesota Agricultural Experiment Station St. Paul. Tech. Bull. **294**: 43.

Hobbs, N.T. 1996. Modification of ecosystems by ungulates. J. Wildl. Manage. **60**(4): 695–713. doi:10.2307/3802368.

Hodgson, A.L. 2010. Temporal changes in spatial patterns of moose browse, causes and consequences. Dissertation, Graduate School, University of Minnesota, Duluth, Minn.

Hoffmann, W.A., Geiger, E.L., Gotsch, S.G., Rossatto, D.R., Silva, L.C., Lau, O.L., Haridissan, M., and Franco, A.C. 2012. Ecological thresholds at the savanna-forest boundary: how plant traits, resources and fire govern the distribution of tropical biomes. Ecol. Lett. **15**(7): 759–768. doi:10.1111/j.1461-0248.2012.01789.x. PMID:22554474.

Huber, N.K. 1975. The geologic story of Isle Royale National Park. United States Department of the Interior, United States Geological Survey, Bulletin 1309.

Jeltsch, F., Weber, G.E., and Grimm, V. 2000. Ecological buffering mechanisms in savannas: a unifying theory of long-term tree-grass coexistence. Plant Ecol. **150**(1–2): 161–171. doi:10.1023/A:1026590806682.

Johnson, E.A., and Miyanishi, K. 2008. Testing the assumptions of chronosequences in succession. Ecol. Lett. **11**(5): 419–431. doi:10.1111/j.1461-0248.2008.01173.x. PMID:18341585.

Johnston, C.A., and Naiman, R.J. 1990. Browse selection by beaver: effects on riparian forest composition. Can. J. For. Res. **20**(7): 1036–1043. doi:10.1139/x90-138.

Johnston, C.A., Pastor, J., and Naiman, R.J. 1993. Effects of beaver and moose on boreal forest landscapes. *In* Landscape ecology and GIS. *Edited by* R. Haines-Young, D.R. Green, and S.H. Cousins. Taylor and Francis, London. pp. 237–253.

Jones, E.A., Reed, D.D., Mroz, G.D., Liechty, H.O., and Cattelino, P.J. 1993. Climate stress as a precursor to forest decline: paper birch in northern Michigan, 1985-1990. Can. J. For. Res. **23**(2): 229–233. doi:10.1139/x93-030.

Knapp, A.K., Fahnestock, J.T., Hamburg, S.P., Statland, L.B., Seastedt, T.R., and Schimel, D.S. 1993. Landscape patterns in soil-plant water relations and primary production in tallgrass prairie. Ecology, **74**(2): 549–560. doi:10.2307/1939315.

Knight, T.M., Dunn, J.L., Smith, L.A., Davis, J., and Kalisz, S. 2009. Deer facilitate invasive plant success in a Pennsylvania forest understory. Nat. Areas J. **29**(2): 110–116. doi:10.3375/043.029.0202.

Kotanen, P.M., and Abraham, K.F. 2013. Decadal changes in vegetation of a subarctic salt marsh used by lesser snow and Canada geese. Plant Ecol. **214**(3): 1–14. doi:10.1007/s11258-013-0178-x.

Krefting, L.W. 1974. The ecology of the Isle Royale moose with special reference to the habitat. Available from University of Minnesota Agricultural Experiment Station, St. Paul, Minn.

McCune, B. 2006. Non-parametric habitat models with automatic interactions. J. Veg. Sci. **17**(6)**1**: 819–830. doi:10.1111/j.1654-1103.2006.tb02505.x.

McCune, B., and Mefford, M.J. 2009. HyperNiche: nonparametric multiplicative habitat modeling. Version 2. MjM Software, Gleneden Beach, Ore.

McCune, B., and Mefford, M.J. 2011. PC-ORD for Windows: multivariate analysis of ecological data. Version 6. MjM Software, Gleneden Beach, Ore.

McInnes, P.F., Naiman, R.J., Pastor, J., and Cohen, Y. 1992. Effects of moose browsing on vegetation and litter of the boreal forest, Isle Royale, Michigan, USA. Ecology, **73**(6): 2059–2075. doi:10.2307/1941455.

McLaren, B.E., and Peterson, R.O. 1994. Wolves, moose, and tree rings on Isle Royale. Science, **266**(2): 2059–2075. doi:10.1126/science.266.5190.1555.

McLaren, B.E. 1996. Plant-specific response to herbivory: simulated browsing of suppressed balsam fir on Isle Royale. Ecology, **77**(1): 228–235. doi:10.2307/2265672.

Mech, L.D. 1966. The wolves of Isle Royale. Fauna of the National Parks of the United States, Fauna Series 7. Department of the Interior, National Park Service, Washington, D.C.

Millers, I., Shriner, D.S., and Rizzo, D. 1989. History of hardwood decline in the eastern United States. USDA Forest Service Broomall, Pa. General Technical Report NE-126.

Murie, A. 1934. The moose of Isle Royale. Available from University of Michigan Museum of Zoology, Miscellaneous Publications Ann Arbor, Mich. No. 25.

Murphy, S.D. 2000. Field testing for pollen allelopathy: a review. J. Chem. Ecol. **26**(9): 2155–2172. doi:10.1023/A:1005572516948.

Nelson, M.P., Vucetich, J.A., Peterson, R.O., and Vucetich, L.M. 2011. The Isle Royale wolf–moose project (1958-present) and the wonder of long-term ecological research. Endeavour, **35**(1): 30–38. doi:10.1016/j.endeavour.2010.09.002.

Olff, H., Vera, F.W.M., Bokdam, J., Bakker, E.S., Gleichman, J.M., Maeyer, K.D., and Smit, R. 1999. Shifting mosaics in grazed woodlands driven by the alternation of plant facilitation and competition. Plant Biol. **1**(2): 127–137. doi:10.1111/j.1438-8677.1999.tb00236.x.

Pastor, J., and Naiman, R.J. 1992. Selective foraging and ecosystem processes in boreal forests. Am. Nat. **139**(4): 690–705. doi:10.1086/285353.

Pastor, J., Naiman, R.J., Dewey, B., and McInnes, P. 1988. Moose, microbes, and the boreal forest. BioScience, **38**(11): 770–777. doi:10.2307/1310786.

Pastor, J., Dewey, B., Naiman, R.J., McInnes, P.F., and Cohen, Y. 1993. Moose browsing and soil fertility in the boreal forests of Isle Royale National Park. Ecology, **74**(2): 467–480. doi:10.2307/1939308.

Peterson, R.O. 1999. Wolf-moose interaction on Isle Royale: the end of natural regulation? Ecol. Appl. **9**(1): 10–16. doi:10.2307/2641163.

Peterson, R.O., Page, R.E., and Dodge, K.M. 1984. Wolves, moose, and the allometry of population cycles. Science, **224**(4655): 1350–1352. doi:10.1126/science.224.4655.1350. PMID:17837195.

Purdy, B.G., Macdonald, S.E., and Dale, M.R.T. 2002. The regeneration niche of white spruce following fire in the mixed-wood boreal forest. Silva Fenn. **36**(1): 289–306. doi:10.14214/sf.564.

Relva, M.A., Nuñez, M.A., and Simberloff, D. 2010. Introduced deer reduce native plant cover and facilitate invasion of non-native tree species: evidence for invasional meltdown. Biol. Invasions, **12**(2): 303–311. doi:10.1007/s10530-009-9623-0.

Ripple, W.J., Larsen, E.J., Renkin, R.A., and Smith, D.W. 2001. Trophic cascades among wolves, elk and aspen on Yellowstone National Park's northern range. Biol. Conserv. **102**(3): 227–234. doi:10.1016/S0006-3207(01)00107-0.

Risenhoover, K.L., and Maass, S.A. 1987. The influence of moose on the composition and structure of Isle Royale forests. Can. J. For. Res. **17**(5): 357–364. doi:10.1139/x87-062.

Ritchie, M.E., Tilman, D., and Knops, J.M. 1998. Herbivore effects on plant and nitrogen dynamics in oak savanna. Ecology, **79**(1): 165–177. doi:10.1890/0012-9658(1998)079[0165:HEOPAN]2.0.CO;2.

Rose, M., and Hermanutz, L. 2004. Are boreal ecosystems susceptible to alien plant invasion? Evidence from protected areas. Oecologia, **139**(3): 467–477. doi:10.1007/s00442-004-1527-1.

Ruthven, A.G. 1906. An ecological survey in the Porcupine Mountains and Isle Royale, Michigan. Michigan Geological Survey Annual Report for 1905, pp. 17–55.

Savage, M., and Swetnam, T.W. 1990. Early 19th-century fire decline following sheep pasturing in a Navajo ponderosa pine forest. Ecology, **71**(6): 2374–2378. doi:10.2307/1938649.

Scholes, R.J., and Archer, S.R. 1997. Tree-grass interactions in savannas. Annu. Rev. Ecol. Syst. **28**: 517–544. doi:10.1146/annurev.ecolsys.28.1.517.

Snyder, J.D., and Janke, R.A. 1976. Impact of moose browsing on boreal-type forests of Isle Royale National Park. Am. Midl. Nat. **95**(1): 79–92. doi:10.2307/2424235.

Soil Survey Staff. 2011. Natural Resources Conservation Service, United States Department of Agriculture. Soil Survey Geographic (SSURGO) Database for Isle Royale, Michigan. Available from http://www.nrcs.usda.gov/wps/portal/nrcs/surveylist/soils/survey/state/?stateId=MI. [accessed 29 August 2011].

Sparling, J.M. 1967. Assimilation rates of some woodland herbs in Ontario. Bot. Gaz. **128**(3–4): 160–168. doi:10.1086/336393.

Voss, E.G. 1996. Michigan flora, parts I–III. Cranbrook Institute of Science, Ann Arbor, Mich.

Voss, E.G., and Reznicek, A.A. 2012. Field manual of Michigan flora. University of Michigan Press, Ann Arbor, Mich.

Vucetich, J.A., and Peterson, R.O. 2004. The influence of top–down, bottom–up and abiotic factors on the moose (*Alces alces*) population of Isle Royale. Proc. R. Soc. Biol. Sci. **271**(1535): 183–189. doi:10.1098/rspb.2003.2589.

Vucitech, J.A., and Peterson, R.O. 2013. Ecological studies of wolves on Isle Royale: Annual report 2012-2013. School of Forestry and Wood Products, Michigan Technological University, Houghton, Mich.

Appendix A

Table A1 begins on the next page.

Table A1. Species name and six-letter codes for all species observed, nomenclature follows Voss and Reznicek 2012.

Species name	Code	Species name	Code
Abies balsamea	ABIBAL	*Aralia nudicaulis*	ARANUD
Acer saccharum	ACESAC	*Arctostaphylos uva-ursi*	ARCUVA
Acer spicatum	ACESPI	*Athyrium filix-femina*	ATHFIL
Achillea millefolium	ACHMIL	*Avenella flexuosa*	AVEFLE
Actaea rubra	ACTRUB	*Betula alleghaniensis*	BETALL
Agrimonia striata	AGRSTR	*Betula papyrifera*	BETPAP
Agrostis scabra	AGRSCA	*Botrychium minganense*	BOTMIN
Allium schoenoprasum	ALLSCH	*Botrychium multifidum*	BOTMUL
Alnus incana	ALNINC	*Botrychium simplex*	BOTSIM
Amelanchier arborea	AMEARB	*Botrychium virginianum*	BOTVIR
Amelanchier bartramiana	AMEBAR	*Bromus ciliatus*	BROCIL
Anaphalis margaritacea	ANAMAR	*Bromus inermis*	BROINE
Anemone canadensis	ANECAN	*Bryophyte*	BRYOPH
Anemone cylindrica	ANECYL	*Calamagrostis canadensis*	CALCAN
Antennaria howellii	ANTHOW	*Carex arctata*	CARARC
Apocynum androsaemifolium	APOAND	*Carex brunnescens*	CARBRU
Aquilegia canadensis	AQUCAN	*Carex crinita*	CARCRI
Carex deweyana	CARDEW	*Carex disperma*	CARDIS
Carex gracillima	CARGRA	*Coptis trifolia*	COPTRI
Carex houghtoniana	CARHOU	*Corallorhiza maculata*	CORMAC
Carex hystericina	CARHYS	*Corallorhiza striata*	CORSTR
Carex intumescens	CARINT	*Cornus canadensis*	CORCAN
Carex leptonervia	CARLEP	*Cornus rugosa*	CORRUG
Carex pedunculata	CARPED	*Cornus sericea*	CORSER
Carex pensylvanica	CARPEN	*Corylus cornuta*	CORCOR
Carex scoparia	CARSCO	*Crataegus douglasii*	CRADOU
Carex stricta	CARSTR	*Cynoglossum boreale*	CYNBOR
Cerastium fontanum	CERFON	*Danthonia spicata*	DANSPI
Chamerion angustifolium	CHAANG	*Dendrolycopodium dendroideum*	DENDEN
Chenopodium album	CHEALB	*Dendrolycopodium obscurum*	DENOBS
Chimaphila umbellata	CHIUMB	*Dianthus plumarius*	DIAPLU
Cinna latifolia	CINLAT	*Diervilla lonicera*	DIELON
Circea alpina	CIRALP	*Diphasiastrum complanatum*	DIPCOM
Cirsium arvense	CIRARV	*Doellingeria umbellata*	DOEUMB
Cirsium vulgare	CIRVUL	*Dryopteris carthusiana*	DRYCAR
Clematis virginiana	CLEVIR	*Elymus repens*	ELYREP
Clinopodium vulgare	CLIVUL	*Elymus wiegandii*	ELYWIE
Clintonia borealis	CLIBOR	*Epilobium ciliatum*	EPICIL
Coeloglossum viride	COEVIR	*Equisetum arvense*	EQUARV
Comandra umbellata	COMUMB	*Equisetum hyemale*	EQUHYE
Equisetum palustre	EQUPAL	*Hieracium pilosella*	HIEPIL
Equisetum sylvaticum	EQUSYL	*Hieracium scabrum*	HIESCA
Erigeron strigosus	ERISTR	*Hieracium umbellatum*	HIEUMB
Eurybia macrophylla	EURMAC	*Huperzia lucidula*	HUPLUC
Euthamia graminifolia	EUTGRA	*Impatiens capensis*	IMPCAP
Fallopia cilinodis	FALCIL	*Iris versicolor*	IRIVER
Fragaria vesca	FRAVES	*Juniperus communis*	JUNCOM
Fragaria virginiana	FRAVIR	*Lactuca biennis*	LACBIE
Fraxinus nigra	FRANIG	*Lactuca canadensis*	LACCAN
Galeopsis tetrahit	GALTET	*Lathyrus japonicus*	LATJAP
Galium asprellum	GALASP	*Lathyrus ochroleucus*	LATOCH
Galium boreale	GALBOR	*Linnaea borealis*	LINBOR
Geranium bicknellii	GERBIC	*Lonicera canadensis*	LONCAN
Geum aleppicum	GEUALE	*Lonicera dioica*	LONDIO
Goodyera oblongifolia	GOOOBL	*Lycopodium clavatum*	LYCCLA
Gymnocarpium dryopteris	GYMDRY	*Maianthemum canadense*	MAICAN
Halenia deflexa	HALDEF	*Maianthemum racemosum*	MAIRAC
Hepatica americana	HEPAME	*Matteuccia struthiopteris*	MATSTR
Heracleum maximum	HERMAX	*Melampyrum lineare*	MELLIN
Hieracium aurantiacum	HIEAUR	*Mentha arvensis*	MENARV
Hieracium caespitosum	HIECAE	*Milium effusum*	MILEFF
Hieracium kalmii	HIEKAL	*Mitella nuda*	MITNUD
Moneses uniflora	MOEUNI	*Populus tremuloides*	POPTRE
Monotropa uniflora	MONUNI	*Prenanthes alba*	PREALB

Table A1 (*concluded*).

Species name	Code	Species name	Code
Oenothera biennis	OENBIE	*Prunus pensylvanica*	PRUPEN
Orthilia secunda	ORTSEC	*Prunus virginiana*	PRUVIR
Oryzopsis asperifolia	ORYASP	*Pteridium aquilinum*	PTEAQU
Osmunda claytoniana	OSMCLA	*Pyrola asarifolia*	PYRASA
Osmunda regalis	OSMREG	*Pyrola chlorantha*	PYRCHL
Oxalis acetosella	OXAACE	*Pyrola elliptica*	PYRELL
Phegopteris connectilis	PHECON	*Pyrola minor*	PYRMIN
Phleum pratense	PHLPRA	*Ranunculus acris*	RANACR
Picea glauca	PICGLA	*Ranunculus recurvatus*	RANREC
Picea mariana	PICMAR	*Rhamnus alnifolia*	RHAALN
Pinus strobus	PINSTRO	*Rhododendron groenlandicum*	RHOGRO
Platanthera huronensis	PLAHUR	*Ribes glandulosum*	RIBGLA
Platanthera orbiculata	PLAORB	*Ribes lacustre*	RIBLAC
Poa compressa	POACOM	*Ribes oxyacanthoides*	RIBOXY
Poa palustris	POAPAL	*Rosa acicularis*	ROSACI
Poa pratensis	POAPRA	*Rubus parviflorus*	RUBPAR
Poa saltuensis	POASAL	*Rubus pubescens*	RUBPUB
Polygonum douglasii	POLDOU	*Rubus strigosus*	RUBSTR
Polypodium virginianum	POLVIR	*Rumex acetosella*	RUMACE
Populus balsamifera	POPBAL	*Salix bebbiana*	SALBEB
Salix discolor	SALDIS	*Thuja occidentalis*	THUOCC
Sambucus racemosa	SAMRAC	*Tragopogon pratensis*	TRAPRA
Schoenoplectus pungens	SCHPUN	*Trientalis borealis*	TRIBOR
Scirpus cyperinus	SCICYP	*Trifolium aureum*	TRIAUR
Scutellaria galericulata	SCUGAL	*Trifolium pratense*	TRIPRA
Silene noctiflora	SILNOC	*Trillium cernuum*	TRICER
Solidago altissima	SOLALT	*Urtica dioica*	URTDIO
Sorbus decora	SORDEC	*Vaccinium angustifolium*	VACANG
Spinulum annotinum	SPIANN	*Vaccinium myrtilloides*	VACMYR
Stellaria graminea	STEGRA	*Veronica officinalis*	VEROFF
Streptopus lanceolatus	STRLAN	*Viburnum trilobum*	VIBTRI
Symphyotrichum ciliolatum	SYMCIL	*Vicia americana*	VICAME
Symphyotrichum puniceum	SYMPUN	*Viola blanda*	VIOBLA
Symplocarpus foetidus	SYMFOE	*Viola pubescens*	VIOPUB
Taraxacum officinale	TAROFF	*Viola renifolia*	VIOREN
Taxus canadensis	TAXCAN	*Viola selkirkii*	VIOSEL
Thalictrum dasycarpum	THADAS	*Viola sororia*	VIOSOR

Appendix B

Photographs of the savannas appear on the next page.

Fig. B1. Forest plants underneath a mature *Picea glauca* in an open savanna. *Taxus canadensis* pictured in the middle with *Cornus canadensis* and *Gymnocarpium dryopteris* in the foreground and *Rubus parviflorus* in the background.

Fig. B2. View of an open savanna community near Feldtmann Lake dominated by *Hieracium caespitosum* and *Poa pratensis*, with scattered *Picea glauca* and *Sambucus racemosa*.