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WHITE SPRUCE (*PICEA GLAUCA*), MOOSE (*ALCES ALCES*) AND THE ORIGIN OF A ZOOTIC DISCLIMAX COMMUNITY ON ISLE ROYALE

By

Stephen Christopher Caird

THESIS

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WHITE SPRUCE (*PICEA GLAUCA*), MOOSE (*ALCES ALCES*) AND THE ORIGIN OF A ZOOTIC DISCLIMAX COMMUNITY ON ISLE ROYALE

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ABSTRACT

WHITE SPRUCE (*PICEA GLAUCA*), MOOSE (*ALCES ALCES*) AND THE ORIGIN OF A ZOOTIC DISCLIMAX COMMUNITY ON ISLE ROYALE

By

Stephen Christopher Caird

Understory herbivory combined with canopy loss alters trajectories of forest succession, and in extreme cases may produce novel landscapes dominated by the groundcover layer. I investigated the response of woody species to savannas which have emerged in Isle Royale National Park as a result of moose herbivory. I used dendrochronological methods and microsite plots to describe the spatial, temporal, and competitive responses of white spruce (*Picea glauca*), a non-palatable species, to the savanna environment. Most tree species had lower densities in savannas, however bird-dispersed species mountain ash (*Sorbus decora*) and chokecherry (*Prunus virginiana*) were increasing in older savannas. White spruce has increased more or less synchronously in both savanna and forest sites, with new establishment favored by sites transitioning from forest to savanna. Spruce seedling density increased with forb cover and plant species richness and decreased with plant litter depth, an effect which intensified with savanna age. Spatial patterns in savannas reflected clustering attributable to seed dispersal and microsite limitation, suggesting long-sustaining patterns of microsite heterogeneity in open savannas.

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STEPHEN CHRISTOPHER CAIRD

2015

DEDICATION

This work is dedicated to my parents, Steve and Gail Caird, to Ryne Rutherford who introduced me to ecological thinking, and to Sara Miller who helps keep me sane.

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PREFACE

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Introduction

A wide range of herbivores impact forest structure and successional dynamics. Insects such as spruce budworm (*Choristoneura spp.*) (Osawa 1994), mountain pine beetle (*Dendroctonus ponderosae*) (Dordel et al. 2008), and beech scale (*Cryptococcus fagi*) (Houston 1975) disproportionately affect taller canopy trees, whereas large terrestrial browsers such as white-tailed deer (*Odocoileus virginiana*) (Frelich and Lorimer 1985), moose (*Alces alces*) Bergerud and Manuel 1968), elk (*Cervus elaphus*) (White et al. 1998), and elephant (*Loxodonta africanus*) (Edkins et al. 2007) mostly impact small understory trees. Beavers (*Castor canadensis*) preferentially harvest small stems, but fell large trees in some situations (Basey et al. 1988), and both elk and elephant damage and sometimes kill large trees by stripping bark (White et al. 1998, Edkins et al. 2007).

Herbivores influence succession by selectively facilitating (e.g. seed dispersal) or reducing (e.g. direct herbivory) species from one or more seral stage. Beaver (Johnston and Naiman 1990), elk (Baker et al. 2005), white-tailed deer (Anderson and Loucks 1979), and moose (Belovsky 1981) tend to accelerate succession by heavy browsing on small early-successional trees, e.g. quaking aspen (*Populus grandidentata*), willow (*Salix spp.*) and paper birch (*Betula papyrifera*). During winter, moose also browse balsam fir (*Abies balsamea*) (Bergerud and Manuel 1968), a late-successional boreal species and important gap colonist (Kneeshaw and Bergeron 1998), and deer browse eastern hemlock (*Tsuga canadensis*), shifting monotypic self-replacing hemlock stands to sugar maple (*Acer saccharum*) (Anderson and Loucks 1979). In some parts of Africa, elephants mostly damage mid-successional species, leading to bifurcated succession of patches

with either early- or late-successional trees (Ssali et al. 2012). In North America's southeastern boreal forest, spruce budworm kills mature balsam fir, which typically self-replace by advance regeneration (Osawa 1994), although may promote growth of aspen where the two species coincide (Nealis and Régnière 2004). In western montane North America, spruce beetles (*Dendroctonus rufipennis*) accelerate succession to subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*) (Veblen et al. 1991).

When understory browsing severely inhibits canopy recruitment, woodland/parkland and savanna (<25% canopy cover) formations may develop. Localized canopy suppression occurs within optimal foraging range of beavers (Johnston et al. 1993) and at tree-line in South America where guanaco (*Lama guanacoe*) browsing is heavy (Rebertus et al. 1997). Savanna formation by browsing is often aided by other disturbances, as with fire in areas browsed by elephant (Beuchner and Dawkins 1961) or elk (Bailey and Whitham 2002), depending on fire severity. Canopy openings created by spruce budworm may be maintained by moose browsing, allowing for grasses to invade and suppress woody stems (Franklin 2013).

Moose herbivory and its effects on Isle Royale

On Isle Royale, a century of heavy moose herbivory, aided somewhat by beavers, has severely limited regeneration of most deciduous trees, especially aspen (*Populus* spp.), birches (*Betula* spp), and mountain ash (*Sorbus* spp). However, instead of rapidly succeeding to later-successional species, heavy winter browsing of balsam fir by moose has led to persistent savannas that have only slowly been colonized by the single remaining player that moose will not eat, white spruce (*Picea glauca*). The resulting

zootic “disclimax” has been dubbed a “moose-spruce savanna.” I used tree rings to reconstruct the historical timing of white spruce invasion, and to document the current age structure and spatial patterns which have developed within savannas.

When moose arrived to the island ~1905-1913 (Murie 1934), balsam fir and yew (*Taxus canadensis*) were abundant as winter browse (Cooper 1913). By ~1930, moose peaked at 1000-3000 animals, stifling balsam fir regeneration, and nearly extirpating yew (Murie 1934). Moose regulation by wolves beginning in the late 1940s has periodically alleviated balsam fir from browsing (McLaren & Peterson 1994), but chronic herbivory has hampered regeneration of most tree species, with the notable exception of white spruce. Although white spruce was apparently not abundant when moose arrived on Isle Royale (Cooper 1913), it has been increasing more recently (Risenhoover & Maas 1987).White spruce is avoided by moose, likely because of its high fiber content (Sauvé & Côté 2007) and camphor (von Rudloff 1972), an antifeedant livestock toxin (Dziba et al 2009). The increase of white spruce in some areas on the island has been sufficient to alter soil chemistry by deposition of its nutrient-poor litter, which slows microbial soil nitrogen cycling (Pastor et al. 1988).

Landscape effects of moose browsing are striking on the west end of Isle Royale, where aerial images from 1930 initially reveal large-scale canopy loss. Successive images illustrate rapid conversion from forest to savanna, with gradual return of some areas to more wooded, spruce-dominated states. At least 16% of former upland forest was savanna in 1996 (Gorkiewicz 2006), and herbaceous cover in savannas has shifted from forest and edge species to grasses and “old field” herbs (Rotter and Rebertus 2015). With the exception of white spruce, most tree species have declined in savannas; however,

some palatable species persist in savannas as heavily-pruned, bonsai-like shrubs, including birch, mountain ash, and balsam fir. Although these stunted fir and mountain ash can become conditioned to browsing and persist as dwarf trees for >50 years (Risenhoover and Maass 1987, McLaren 1996), these species are mostly declining on the southwestern end of the island (Campbell 2002, Rotter and Rebertus 2015).

Factors affecting white spruce regeneration in savannas

As a forest species, the silvics of white spruce are well known, but whether its regeneration and persistence in savannas follows similar principles is not. Post-fire seed beds and treefall gaps present vastly different regeneration niches than among savanna grasses. White spruce is a mast seeding species, producing large cone crops every 2 to 6 years, with seeds not viable past one year (Nienstaedt and Zasada 1990). Seed dispersal of spruce drops precipitously beyond 30 m and rarely beyond 100 m (Dobbs 1976). Rare instances of dispersal past 300 m are possible by wind over snow (Wirth et al. 2008). Establishment is favorable when mast years coincide with temporarily available microsites, e.g. after a soil-exposing fire (Peters et al. 2005). White spruce establishes poorly in grass, and is usually outcompeted by other trees in forest gaps (Arlidge 1967). In older stands, white spruce establishes in large gaps (Kneeshaw & Bergeron 1998) and on decaying wood (Peters et al. 2006), but hardwood litter prevents seeds from contacting the soil (Barras & Kellman 1998), and falling leaves may smother seedlings (Arlidge 1967). Favorable microsite may become limiting in older forests, but its longevity (>300 years) favors its persistence in many communities (Cooper 1913, White et al. 1985, Veblen 1986).

Research objectives

I investigated white spruce dynamics in upland savanna and remnant forest habitat on the southwestern end of Isle Royale. In a chronosequence, savannas of different ages (ranging in date of formation from 1930 to 2005) were assumed to represent a temporal sequence. I supported this approach by using tree rings to reconstruct forest histories in the same savannas to address the following hypotheses and predictions.

Hypothesis 1: Due to moose browsing and regeneration failure of most trees species, the vacant niche in savannas will be dominated by white spruce. The physiognomy of the "spruce-moose savanna" makes this seem like a trivial hypothesis: the open-grown patches of spruce are what first catch the eye, but do they really dominate? And does the savanna really offer an advantage to white spruce compared with closed forests?

Prediction 1: White spruce will dominate savannas and show preferential colonization of these habitats compared to closed forest. White spruce ages will mainly post-date savanna formation.

Hypothesis 2: Older savannas should present a longer window of opportunity for spruce to colonize vacant niche space and develop into more fully treed "spruce woodlands."

Prediction 2: Older savannas (1930 and 1957) will have older spruce (i.e. earlier invasion), and higher densities of spruce than younger savannas (1978-2005).

Hypothesis 3: Broadly even-aged establishment of spruce often follows a major disturbance, such as fire, but the gradual breakup of the canopy associated with savanna formation should produce more continuous, gradual recruitment, similar to trees invading

an old-field environment. This hypothesis assumes that seed sources are readily available near establishing savannas. Modest variation in establishment would be expected due to masting events and favorable climatic windows for seedling establishment. A related question is whether spruce invasion of savannas has remained constant, is accelerating, or has declined.

Prediction 3: Spruce age structures will be all-aged. I also predict that spruce recruitment will increase with time as earlier colonists mature and provides additional local seed sources.

Hypothesis 4: Microsite factors, such as litter depth, light availability, and associated understory vegetation (especially grasses) affect regeneration of white spruce in savannas.

Prediction 4: White spruce seedling densities will be negatively associated with deep litter and competing vegetation, especially *Poa* spp, and most abundant in partial shade.

Hypothesis 5: A final objective concerns the spatial patterns of invading spruce. By casual observation, white spruce in the current savanna landscape on Isle Royale appear clustered (Johnston et al. 1993, Rotter and Rebertus 2015). I used large mapped plots for pattern analysis, and these were not randomly located, so my goals were mainly exploratory and descriptive. Nevertheless, I hypothesized that the life history traits of spruce would create similar spatial patterns in most savannas. Patchiness would be expected given spruce's limited seed dispersal (Dobbs 1976) and poor recruitment in dense grasses (Rotter and Rebertus 2015). Dense shading and thick duff within spruce patches (Rotter and Rebertus 2015) would limit recruitment of spruce and other species

away from established patches at broader scales. Therefore, I predicted that younger spruce cohorts will be locally repulsed by older cohorts (stem exclusion hypothesis), but attracted to older cohorts at broader scales (local seed dispersal hypothesis). I also predicted that preferred browse species will be repulsed by spruce at finer scales (stem exclusion hypothesis) but attraction might occur at scales where they still gain protection by growing near unpalatable spruce (c.f. "defense guild," sensu Atsatt and O'Dowd 1976).

Materials and methods

Study area

Isle Royale National Park (47º50'00" N 89º08'34" W) is an archipelago in northwest Lake Superior, isolated from the mainland by ~24 km. The main island is ~72 km long and occupies 544 km^2. Deep glacial till covers lacustrine gravels on the terraced topography of its southwest end, in sharp contrast with the shallow soils and rugged terrain left by quick glacial retreat on the northeast end (Huber 1975). Mixed spruce-fir-paper birch forest prevails near the lakeshore, lending way to yellow birch-sugar maple (*Betula alleghaniensis-Acer saccharum*) forest further inland (Adams 1909, Cooper 1913). Quaking aspen occurs infrequently, in clones, and northern white cedar (*Thuja occidentalis*) and black spruce (*Picea mariana*) mostly occupy poorly drained sites. Much of Isle Royale was burned in the late 1800's by mining prospectors, and ~31% of the island burned in 1936 near Siskiwit Lake (Krefting 1973), however the areas used in the present study have not been influenced by major fires in recorded history.

Site selection and sampling scheme

Savanna age categories were based on maps made by Gorkiewicz (2006) and Rotter and Rebertus (2015) reflecting the extent of savanna (<25% canopy cover) on Isle Royale, in aerial images from 1930, 1957, 1978, and 2005. "Savanna age" in this study is defined as the year in which the savanna first appeared on aerial images, with the understanding that these are minimum ages, and the savannas opened up at some point between photograph years.

Two sampling schemes were used to address the hypotheses. A total of 399, randomly located nested plots (10- and 5-m radius) were sampled in 27 savannas (10-15 plots per savanna. At least 4 savannas per age class (but ranging up to 8) were randomly selected from a pool meeting several criteria: unambiguous age, size large enough to accommodate 10-15 plots, and representation on major soil types. Four reference stands with 87-94% canopy cover were also sampled. These plots were used to show the extent of spruce and other tree species in savannas (Hypothesis 1) and to test whether any site variables (e.g. light, soil characteristics, ground cover vegetation) could predict recruitment of spruce seedlings (Hypothesis 4). In the second approach, tree locations were mapped in 16 large rectangular plots (averaging around 0.5 ha), 3-4 plots per age class, to examine spatial patterns of spruce and other species (Hypothesis 5). Tree age data were also gathered in these large plots to reconstruct historical patterns of spruce invasion in savannas (Hypotheses 2 and 3) and to address whether spruce pre-dated savanna formation (Hypothesis 1). By collecting age data in mapped stands, I could also address spatial and temporal questions in Hypothesis 5 more effectively. Mapped plots

were chosen opportunistically in representative areas of each savanna age. The large size of the plots insured a mosaic of spruce and open areas were included.

Prediction 1: White spruce will dominate savannas and show preferential colonization of these habitats compared to closed forest.

Species and DBH were recorded for all trees (≥ 5 cm DBH) within a 10-m radius of nested plot centers, including 66 plots in 1930 savannas (n=5), 104 plots in 1957 savannas (n=8), 80 plots in 1978 savannas (n=6), 107 plots in 2005 savannas (n=8), and 42 plots reference stands (n=4). Stem density (individuals per hectare) and basal area coverage (m^2 per hectare) were calculated for all species within each savanna, and the mean and standard deviation of these values were calculated for each savanna age class, and for reference stands. Mean stem density was also calculated for 5-cm size classes, by pooling plot data for each savanna or stand, and calculating the average for each savanna age class.

Predictions 2 and 3: Older savannas will have older spruce and higher densities of spruce than younger savannas, and spruce age structures will show acceleration

Ages of white spruce were sampled in the large, mapped plots, which averaged about 0.5 ha in size (see Methods, Prediction 5). Ages were determined by tree-rings in cores extracted ~0.3 m from the ground, or when possible, by counting annual branch whorls in smaller trees. Sample size varied depending on plot size and spruce density, but a minimum of 30 tree cores/plot were extracted from larger trees (≥5 cm DBH). Sample sizes of smaller trees, where ages were determined from branch whorls, typically ranged from 50-100 per plot. Density of seedlings (<0.2 m) was generally low, and were

individually mapped with age information, however for some sites only seedling density is reported. One site, Grace 1978 B, had an overwhelming seedling density, and all stems < 1.4 m tall were counted rather than mapped.

Increment cores were mounted and sanded until rings were clearly visible. Number of rings to center were counted, aided by 10 to 40X magnification, using a stereoscope, and 5 years were added to account for growth below coring height. For cores missing piths, I matched the approximate mean ring-width of the center-most portion of the core with a template of concentric circles printed on transparency film, and added the number of concentric circles to center. Age histograms included all white spruce of known age, grouped by 5-year age classes. Counts were converted to densities to aid in comparing across sites.

Prediction 4: White spruce seedling densities will be negatively associated with deep litter and competing vegetation, and most abundant in partial shade.

Within 5 m of each plot center, I counted the number of white spruce seedlings (<2.0 cm DBH). Site variables measured included the percent cover of grass, forb, shrub, litter, bare ground, coarse woody debris, and lichen/moss. Cover values by individual species were also measured. To measure litter depth, an 8.3-g, 3-cm- diameter metal washer encircling a steel rod was let to slide down until resting on top of the litter layer, and then using a ruler to measure the height above the top of the O horizon. We used the average of five random measurements for "litter depth" for each plot. Soil depth was operationally defined as the depth a 6-mm diameter steel rod could be pushed into the soil before encountering rock. Measurements were taken at 10 locations within each plot and averaged. 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 (Frazer et al. 1999).

We used two statistical approaches for modelling the spruce seedling counts in response to environmental predictors: nonparametric multiplicative regression (NPMR) and negative binomial regression. The advantage of NPMR was its flexibility in modelling complex, non-linear responses to environmental gradients. Nonparametric multiplicative regression (NPMR) was run in HyperNiche (version 2.0, MjM Software, Gleneden Beach, OR, US). NPMR uses a smoothing function with leave-one-out cross validation to estimate response variables (Berryman and McCune 2006). A quantitative model was constructed using a local mean estimator with Gaussian weighting, which was assessed by a cross-validated R^2 (xR^2). NPMR does not fit coefficients in a fixed equation; instead, NPMR fits tolerances used in the Gaussian smoothers (Berryman and McCune 2006). A scree plot of xR^2 versus the number of variables was used to select the final model. Significance of models was evaluated by Monte Carlo tests based on 1000 random permutations of the original data.

We used negative binomial regression analysis in SPSS Statistics ver. 21.0 software (IBM incorporated, 2012) to model the relationship between the dependent variable, seedling count, and most of the environmental variables showing a good fit to this distribution. Savanna year was treated as a nominal categorical variable. A negative binomial model and log link function were used to account for the large number of plots with "zero" seedlings counts, and a "tail" of high-count plots. A scaled deviance model was used, and the Newton-Raphson algorithm was applied to parameterize the model to

scale with the dataset. We manually chose a final model based on a best subsets approach using AIC (Akaike Information Criterion) values.

Spatial patterns

Mapped areas were rectangles ranging from 900 to 8100 m^2, averaging 4594 m^2. With a compass and tape measures, I mapped all stems ≥ 5 cm DBH with a pair of (x, y) coordinates to the nearest decimeter. All white spruce ≥ 0.2 m height were mapped, with the exception Grace 1978B, where it was not practical to map seedlings.

Ripley's L(t) (Diggle 1983) was calculated to detect spatial scales of clumping for individual species (univariate analysis) and clustering and repulsion between species or between white spruce cohorts (bivariate analysis). The age histograms (see Methods, predictions 3-4) revealed distinct "older" and "younger" cohorts (peaks in the graph, see Fig. 3). For example, in Head 1957 I compared the 4- to 36-year cohort to the 37- to 73-year cohort. This method seemed more appropriate than setting arbitrary age cutoff points for all sites. Rotten trees that could not be cored successfully were included in the spatial analysis. In most cases, these trees could easily be placed in a cohort by their DBH and growth form.

All spatial analyses were performed using the SpPack macro for Microsoft Excel (Perry 2003). For each iteration, L(t) was calculated for each 0.5 m increment, up to half the length of the shortest side of a mapped stand, using weighted edge points (Goreaud & Pelissier 1999) and 500 Monte Carlo simulations to acquire 95% confidence intervals. Windigo 1930 was excluded, as white spruce was not locally abundant. L is an index of how clumped or regular tree patterns are plotted across of range of scales (t). I examined

both univariate (single species) and bivariate L(t) patterns (between different species or between different age cohorts of spruce).

Results

Prediction 1: White spruce will dominate savannas and show preferential colonization of these habitats compared to closed forest.

White spruce had the greatest density and basal area compared with other species for savannas of all age classes, and was secondarily dominant only in some reference sites, where yellow birch had comparable density and higher basal area (Table 1, Figure 2). The high density of white spruce in reference stands indicates that white spruce colonization was not unique to savannas.

No trends in spruce density and savanna age were detected (Table 1). Densities of white spruce were actually lowest in 1930 savannas and highest in the 1957 and Reference stands (Table 1). Although the 1930 savannas had lower densities, basal area was comparable to other years because there were more large trees (>40 cm dbh) (Table 1, Fig. 2). "Seedling" densities (trees < 2 cm dbh) were highly variable but lowest in 1930 and highest in the 2005 savannas (Table 2)

Balsam fir, northern white cedar, quaking aspen, paper birch, and yellow birch had higher basal area and density in reference areas and more recent savannas, generally decreasing with savanna age, but with considerable site variation (Fig. 2). For example, elevated densities of yellow birch in 1930 reflect the historical dominance of this species on the southwest coast where 3 of the 1930 savannas were located. Quaking aspen, paper birch, and balsam fir were represented almost exclusively by mature trees, and saplings

were scarce (Fig. 2). Yellow birch was most abundant in small size classes, and northern white cedar was overrepresented by small stems. One of the most striking results was the lack of balsam fir trees in savannas (<1 tree/ha) and low densities in reference stands.

A few bird-dispersed tree species were prominent in savannas, especially mountain ash and chokecherry (*Prunus virginiana*). Mountain ash was most abundant in 1930, 1957, and 1978 savannas, and chokecherry occurred in all savanna ages and reference stands, with saplings restricted to 1930 and 1957 savannas. Other fruit trees were abundant at individual sites, such as serviceberry (*Amelanchier bartramia*), and fire cherry (*Prunus pensylvanicum*), and hawthorn (*Crataegus douglassi*).

Predictions 2 and 3: Older savannas will have older spruce and higher densities of spruce than younger savannas, and spruce age structures will show acceleration

Age structures of white spruce were similar at coarse temporal scales regardless of savanna age (Fig. 3). Reference stands also showed the same general patterns as savannas. In general, low-density regeneration began c. 1930, followed by a second wave beginning c. 1960-1970, exceeding the first wave by at least a four-fold density increase. This basic pattern was most prominent in Feldtmann 1930 A, all 1957 savannas, and Feldtmann Reference (Figs. 3a, d-f, i, n). In the 1978 savannas, the second wave of regeneration was delayed to c. 1975-80.

Young trees and seedlings were rare in the older savannas (1930 and 1957) and reference stands, with the exception of Feldtman 1930 B (Fig. 3b). If un-aged seedlings are included, recent regeneration was much higher in two of the 1978 savannas (Figs.

3g,h) and two from 2005 (Figs. k,l). It should be noted that these plots do not necessarily represent recent regeneration trends throughout the whole savannas.

The initial wave of recruitment roughly coincided with the formation of the first savannas c. 1930. The oldest cohort in Feldtman B (Fig. 3b) was probably underrepresented. The initial wave of regeneration in 1930, however, pre-dates the formation of savannas from 1957, 1978, and 2005. The 1930 aerial photographs indicate these areas were fully forested when this first cohort established.

An apparent association between the second waves of regeneration and savannas first appearing on the 1957 and 1978 aerial photographs (see arrows on x axis, Fig. 3) is complicated by the intermittent photographic record and uncertainty of when canopy breakup occurred. It is noteworthy that the same cohort that shows up shortly after 1957 also occurs in many other plots from 1930, 2005, and in the reference stands (Fig 4).

Two of the 1978 savannas in the Grace Creek area stand out for their high densities of spruce during initial establishment, followed by waves of regeneration far-exceeding densities observed elsewhere (Fig. 3g,h). In Grace 1978 B, the densities in the 50- to 70-year age classes was probably underestimated because many trees of similar size had rotten centers. White spruce was not as prolific in Grace 1978 A (Fig. 3g), however the magnitude of increase was similar.

East 2005, East Reference, and Head 1978 all contained white spruce preceding moose arrival to the island. A period of establishment c. 1880-1910 was observed in the former two sites (Figs. 3l,m), and in Head 1978 a single tree had established c. 1825 (Fig.

3i); nevertheless, substantial density increases did not come until more recently, with similar patterns to other sites.

Prediction 4: White spruce seedling densities will be negatively associated with deep litter and competing vegetation, and most abundant in partial shade.

The best negative binomial regression model of white spruce seedling density included the main effects of litter depth, forb cover, savanna age (as a categorical variable) and the interaction between litter depth and savanna age (Table 3, Fig. 4). Spruce seedlings generally decreased with litter depth (except in the reference stand) and increased with forb cover (Fig. 4). The interaction between litter depth and savanna age was significant, with negative effects of litter depth becoming more severe with savanna age (Table 3 & Fig. 4a).

The best NPMR model included litter depth and groundcover species richness (xR^2= 0.10; P=0.01). Litter depth had higher sensitivity (0.491) compared to species richness (0.313). Predicted spruce seedling counts declined with litter depth, similar to the graphs for savannas (see Fig. 4). Spruce seedling counts increased with groundcover species richness, especially in plots with >25 species (Fig. 5).

Spatial Patterns

The univariate L(t) patterns demonstrated that spruce was significantly clumped at all sites (Fig. 6). At 9 of the 15 sites analyzed, spruce was strongly clumped at scales of 5 to 15 m (varying somewhat among savanna), which indicates a typical patch radius (Fig 6a). At broader scales of 20-40 m, the pattern switches to random or even regular in some sites, indicating the arrangement of patches and their degree of separation. Two

sites showed similar clumping intensity at all scales (Fig. 6b), indicating that patches are merging into progressively larger patches. In four other sites, spruce were clustered at all scales, reflecting that the mapped area contained a single patch (not shown).

In the bivariate analysis, white spruce were organized into loose multi-cohort groves in seven savannas, ranging mostly from 8 to 16 m in radial dimension, but ranging from 3 to 22 m. This pattern was strong in five savannas, and weaker in two others (Fig 7a). Young white spruce were repelled from older trees at finer scales but attracted at scales corresponding to full grove size. In some instances, young trees were clustered around the perimeter of older trees. At even broader scales (>20 m) the bivariate pattern again becomes random or slightly repulsed, indicating separation or isolation of groves from each other. Two other savannas show similar finer scale patterns but the broad-scale patterns shows clustering, suggesting that groves are merging with each other and forming larger networks (Fig 7b).

Single-cohort patches dominated the patterns of two savannas, where young and old cohorts were either separated from one another by open savanna groundcover, or in which young white spruce were limited to patches not shaded by the dense growth of their predecessors (Fig 7c). In Grace 1978B, for example, dense, relatively even-aged cohorts enforced wide separation with other cohorts.

In contrast to all savanna sites, the pattern between young and older cohorts was mostly random (or marginally repelled at some scales) in two of the three reference stands (Fig 7d). Young spruce were concentrated in patches with older spruce in the other reference stand and one 2005 savanna (Fig. 7e).

With the exception of mountain ash, preferred browsed species were too rare in the mapped plots to examine spatial patterns. In all mapped savannas where it occurred, mountain ash's univariate pattern was strongly clustered at scales <5 m. Mountain ash clustered strongly with other fruit trees in the 1930 savannas. It clustered with chokecherry in three 1930 savannas, at scales of 2-33 m, 2-10 m, and 1.5-13.5 m, respectively (figures not shown). In one of these, mountain ash also clustered with hawthorn from scales of 0.5-22 m.

I hypothesized that preferred browse species, such as mountain ash, might gain some protection by growing near the unpalatable spruce. Sample size was adequate to test this in only a few sites. The bivariate analysis supported mutual attraction in some savannas but weakly or not at all in others. In one 1978 savanna, attraction occurred at 5-25 m. At this site, mountain ash was intermixed with spruce in large groves of 37- to 83-year old spruce. In two 1930 savannas, both showed coarse scale attraction (>15 m and 25-30 m, respectively), indicating mountain ash growing near the periphery of spruce groves. One of these stands also had spotty, local attraction (e.g. at 2 m) indicating some intermixing. In the third 1930 savanna, mountain ash and white spruce were repelled at scales <5 m.

Discussion

Prediction 1: White spruce will dominate savannas and show preferential colonization of these habitats compared to closed forest.

I predicted that white spruce would favor colonization of savannas over forest due to removal of competitor trees, but my findings imply otherwise. White spruce was

unequivocally the most dominant tree in savannas, however it was comparably abundant in reference sites. In addition, an initial wave of spruce recruitment began in the 1930's at most sites—pre-dating canopy breakup in all but the oldest savannas. Although the reference sites still retained an intact canopy (average canopy cover ranged from 87-94%), this does not imply lack of moose impact. One would expect moose to have impacts on forest structure, herbaceous composition, and litter depth and composition in reference stands and savannas alike (Snyder and Janke 1976, Pastor et al. 1988, McInnes et al. 1992).

Bird-dispersed species had much higher occurrence in savannas, especially chokecherry, than in reference sites but did not assume great dominance. Fruit trees are often recruited into old fields, especially when there are roosting areas for birds (McDonnell and Stiles 1983). McDonnell and Stiles (1983) found that recruitment of bird-dispersed species was correlated with the structural complexity of old fields. Some of the savannas on Isle Royale have exceptional structural complexity; for example, the 1930 Feldtman Lake Savannas have remnant yellow birch (some >100 cm dbh), spruce of all sizes, and scattered thickets of suppressed, over-browsed deciduous species. Once established in a savanna, several species are capable of spreading via suckers (chokecherry, pin cherry, and hawthorn).

The remaining forest dominant species were largely absent from savannas, most often occurring as remnants or over-browsed bonsai forms, as has been reported elsewhere on Isle Royale (Risenhoover and Maass 1986, McLaren 1996). Balsam fir was encountered very infrequently, and most often as mature trees in forest stands, or as saplings damaged by browsing. This supports Campbell (2002), who reported a serious

decline and imminent collapse of balsam fir on the western end of Isle Royale. Similar regeneration problems have been reported in Newfoundland (McLaren et al. 2004). Savannas would also pose a problem for balsam fir seedling regeneration due to excessive grass litter, which is prone to drying out, and competition from grasses and other herbaceous species (Frank 1990 and McLaren et al. 2009).

Predictions 2 and 3: Older savannas will have older spruce and higher densities of spruce than younger savannas, and spruce age structures will show acceleration.

I had predicted that older savannas would contain older white spruce than more recent savannas, however initial establishment was not dependent upon timing of savanna origin. Rather, our age structures reveal more or less synchronous initiation in the 1930's regardless of canopy cover. Moose browsing had reached an historic maximum by 1930 (Murie 1934), which could have created an initial window of opportunity for white spruce establishment. An extensive spruce budworm outbreak pre-1930 reported on Isle Royale by Murie (1934) may have also played a role. Balsam fir and paper birch both tend to surpass white spruce in gaps (Arlidge 1967, Kneeshaw and Bergeron 1998), and Adams (1909) comments in an early account of Isle Royale's vegetation that white spruce seedlings were typically overgrown by dense balsam fir regeneration. Similarly, on the east end of Isle Royale, Snyder and Janke (1976) observed higher white spruce seedling and sapling density in more heavily browsed areas.

The beginning of the second wave of regeneration found in most savannas (1957, 1978, and some 2005) roughly corresponded with the appearance of these savannas on aerial photographs, but canopy breakup undoubtedly preceded these dates so it is difficult to draw any conclusions. The 2005 savannas, for example, can partly be traced back to a

major dieback of mature birch in the 1980-90s from drought and subsequent bronze birch borer infestation (Millers et al. 1989, Jones et al. 1993). Some aspects of a "young" savanna may favor spruce regeneration. Canopy breakup would be associated with coarse woody debris, which can provide suitable microsites for spruce seedling establishment (Peters et al. 2006, Barrette et al. 2014). Coarse woody debris that was somewhat decayed (e.g. punky and moss-covered) would have better moisture retention, less N immobilization, and more potential for mycorrhizae than fresh woody debris. Many white spruce in the study area had established on nurse logs, and linear clusters of young spruce in some sites evoked traces of fallen snags and branches; however, this perceived pattern was not formally evaluated.

The 30-40 years between cohorts could also simply mean the first cohort had started to mature and produce cones (Nienstaedt and Zasada 1990). Since the first cohort ranged from 60 to 80 years, the timing of maturation would account for the wide variation in establishment of the second cohort. As savannas mature further, I believe seedbed rather than seed source would be most limiting, as suggested by my regression model. Lack of young spruce in the 1930 savannas, which have extensive *Poa-Hieracium* patches (Rotter and Rebertus 2015), is also consistent with this hypothesis.

Another aspect favoring establishment of spruce in newly formed savannas is a temporary lack of litter inputs from lost deciduous species, and a delay in inhibition by smothering grasses. Loss of litter input from deciduous species has been noted previously on Isle Royale but attributed mainly to browsing and an increase in spruce relative to other species (Pastor et al. 1988). Spruce is known to be inhibited by deciduous leaf litter (Barras and Kellman 1998). Our study of microsite quality suggests highest seedbed

receptivity in sites which characterize stands breaching from forest to savanna (Fig. 4a) that have forbs but where extensive, dense patches of grass have yet to form (Rotter and Rebertus 2015).

Prediction 4: White spruce seedling densities will be negatively associated with deep litter and competing vegetation, and most abundant in partial shade.

Trends in white spruce seedling density suggest influences by two opposing systems of positive feedbacks in the savanna groundcover. In the first system, grass litter deteriorates seedbed quality, maintaining groundcover that becomes progressively less habitable for white spruce seedlings. Litter depths greater than those recorded in reference plots were almost certainly from grasses (see Fig. 4a), and Rotter and Rebertus (2015) report specific ecological polarity between white spruce and non-native *Poa pratensis* in savannas, consistent with other studies which cite grasses as inhibitory to white spruce seedlings (e.g. Arlidge 1967, Lieffers et al. 1993, Barrette et al. 2014). In the second proposed system, forb cover enhances white spruce seedbed (Fig. 4a), and forest forbs find amenable growing conditions near white spruce (Rotter and Rebertus 2015). Forb cover may simply represent the absence of shrub and grass cover, but may also facilitate seedling establishment by providing bare patches of ground between more sparse growth.

Spatial patterns

Most savannas were characterized by small clusters of old spruce encircled by a second younger cohort. Despite local repulsion by the spreading lower boughs of mature open-grown spruce, later-cohort spruce in 10 of 12 mapped savannas were spatially

associated with older individuals at a range of scales ~8 to 16 m. Two possible explanation are localized seed dispersal (Dobbs 1976) and/or microsites that are buffered by sustained tree cover, except where dense stocking prohibits. Dobbs (1976) reported highest seed rain occurred <30 m from parent trees. Clustering among young white spruce in savannas occurred at scales as small as 0.5 m, demonstrating microsite patchiness at fine scales. In savannas with relatively low density of white spruce, the spatial scale of multi-cohort groves fell within the range of highest seed rain density, < 30 m (Dobbs 1976). In three such savannas, younger spruce were constrained to patches of older trees or remnant paper birch, suggesting preservation of microsite conditions since initial establishment at scales of ~8-16 m. Multi-cohort networked groves were characteristic of savannas with higher establishment density, where tight clusters of younger trees were distributed within 10-15 m of older trees, creating a continuous landscape pattern at scales at least as great as 30 m. Groundcover swards intervened between groves, resulting in large-scale repulsion between patches with spruce. Such patterns are potentially underlain by long-maintained groundcover heterogeneity, possibly reflecting historical traces of browsed forest edges as described by Franklin (2013).

Spatial autocorrelation between mountain ash and both hawthorn and chokecherry may demonstrate a "plant defense guild" effect (*sensu* Atsatt and O'Dowd 1976) through concealment by chokecherry, or physical protection by hawthorn. Intermediate-scale clustering with white spruce may represent either a protective effect, or the reliance of both species on a spatially constrained subset of available savanna microsites. Chokecherry, hawthorn, and mountain ash all have the advantage of bird dispersal,

removing seed source limitation as a constraint to site colonization. Chokecherry appears to be spreading by vigorous asexual regeneration in older savannas, which may profit the increase of mountain ash.

The role of moose in the moose-spruce savanna

Moose browsing on the west side of Isle Royale has interfered with gap-phase regeneration of formerly dominant canopy species, resulting in a release of white spruce from sapling competition, especially balsam fir. Selective browsing of deciduous species and fir has also changed litter composition, quantity and quality (Pastor et al. 1988). The initial loss of deciduous litter, which may strongly inhibit spruce seedling establishment, may also have provided a period of favorable seed bed conditions for white spruce. Currently, most spruce regeneration occurs in microsites with light grass cover and high forb richness. Owing to seed source limitation, white spruce was initially slow to replace a gradually breaking canopy; as such, merging canopy gaps have allowed for establishment of a recalcitrant groundcover layer, producing a savanna physiognomy. Seed source is no longer a major limitation to white spruce, however regeneration is limited in savannas by densely accumulating litter, namely from monodominant swards of *Poa pratensis*. Heavy understory herbivory and canopy loss have produced strikingly similar landscape changes on Anticosti Island, Quebec with deer as the major herbivore (e.g. Hidding et al. 2013, Barrette et al. 2014), and spruce budworm defoliation combined with moose browsing in northern Cape Breton, Nova Scotia (Franklin 2013) has also resulted in grass-dominated openings. White spruce is increasing in both cases, but is less prolific among grasses.

There is little doubt that moose were instrumental in savanna formation, but do moose actively maintain savanna conditions? Over the long term, continual moose browsing may further eliminate seed sources of preferred browse species, however birch, fir, and cedar all have light, wind-dispersed seeds which probably fare as poorly among grasses as does white spruce. I hypothesize that obstruction of potential seed bed by accumulated grass litter is of greatest importance to savanna maintenance compared with moose browsing, especially in older savannas.

The future of white spruce in the moose-spruce savanna

The vegetative dynamics in savannas are unfavorable for white spruce, however facilitative processes may exist within them. Many open-grown spruce in savannas have lower boughs which shade all growth up to 4 m from the bole (see Fig. 7b), and leachates may be allelopathic to competing groundcover species, as those of black spruce are to *Poa pratensis* (Jobidon 1986). Some white spruce groves within the study area were devoid of any growth at the ground layer, especially where needle litter had accumulated. Bird-dispersed species are becoming prevalent in some older savannas, and may continue to increase, possibly creating new groves for spruce and other species to establish in decades to come. Finally, large ant mounds are common in savannas on Isle Royale (pers. obs.), which could provide bare soil microsite amenable to white spruce upon colony abandonment. Vlasáková et al. (2009) found large ant mounds to facilitate the invasion of Norway spruce (*Picea abies*) in Slovakian montane grasslands.

I hypothesize that the intermittent nature of white spruce cone production will continue to offer grasses and shrubs the opportunity to firmly establish, resisting white spruce invasion after canopy loss. Despite this, I predict that remnant forest groves and

novel groves of bird-dispersed species will fill and gradually expand by white spruce regeneration, eventually overcoming the recalcitrant layer by shading.

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Table 1. Mean tree densities and basal areas (±S.D.) for savannas of each age class and reference sites, based on pooled data from 10 m radius plots.

Species	Density (stems/hectare)									
	1930		1957		1978		2005		Reference	
	Mean	± S.D.	Mean	± S.D.	Mean	± S.D.	Mean	± S.D.	Mean	± S.D.
Picea glauca	116.1	±56.6	275.3	±219.3	182.9	±95.3	177.6	±44.6	224.8	±133.3
Betula alleghaniensis	35.0	±31.8	10.9	±23.5	26.3	±37.0	10.5	±21.6	199.6	±322.5
Betula papyrifera	5.9	±4.2	17.3	±9.3	15.0	±18.3	20.2	±20.0	69.3	±65.1
Thuja occidentalis	0.0		12.7	±17.1	4.8	±8.3	30.2	±38.6	41.7	±43.1
Populus tremuloides	0.6	±1.4	1.4	±3.6	0.0		4.4	±5.6	10.2	±20.1
Sorbus decora	10.8	±8.4	13.6	±19.1	13.0	±28.1	2.1	±4.1	4.7	±8.7
Picea mariana	0.0		9.5	±25.3	0.6	±1.6	0.0		8.8	±16.0
Abies balsamea	0.4	±0.9	0.3	±0.9	0.4	±1.1	0.6	±1.6	8.1	±15.1
Prunus virginiana	5.9	±8.1	3.5	±7.6	2.7	±3.6	0.9	±2.4	2.7	±5.0
Prunus pensylvanicum	0.6	±1.4	0.0		3.3	±5.8	0.0		0.4	±1.1
	Basal area (m^2/hectare)									
	1930		1957		1978		2005		Reference	
	Mean	± S.D.	Mean	± S.D.	Mean	± S.D.	Mean	± S.D.	Mean	± S.D.
Picea glauca	8.18	±2.92	10.51	±5.35	7.19	±3.19	6.23	±3.12	7.24	±2.84
Betula alleghaniensis	3.36	±2.25	0.94	±1.64	3.00	±3.68	0.73	±1.68	10.49	±10.78
Betula papyrifera	0.71	±0.86	1.05	±0.67	0.94	±0.93	1.24	±1.03	6.36	±3.24
Thuja occidentalis	0.00		0.52	±0.48	0.46	±1.12	1.64	±1.94	2.33	±2.89
Populus tremuloides	0.00		0.13	±0.25	0.00		1.00	±1.30	2.23	±4.46
Sorbus decora	0.26	±0.29	0.36	±0.63	0.20	±0.24	0.07	±0.17	0.09	±0.18
Picea mariana	0.00		0.26	±0.74	0.02	±0.05	0.01	±0.03	0.34	±0.56
Abies balsamea	0.01	±0.03	0.02	±0.05	0.06	±0.14	0.04	±0.11	0.61	±0.73
Prunus virginiana	0.03	±0.06	0.07	±0.20	0.03	±0.05	0.03	±0.07	0.06	±0.11
Prunus pensylvanicum	0.05	±0.11	0.01	±0.02	0.10	±0.15	0.00		0.00	

Table 2. Mean spruce seedling densities in savannas of different age class and reference plots.

Year	N*	total plots	seedlings/ha ±SD†
1930	4	52	83 ± 205
1957	6	74	284 ± 560
1978	7	88	264 ± 654
2005	9	111	423 ± 571
Ref	4	42	218 ± 542

*Number of savannas

† Means and standard deviations are weighted by sample size in each savanna, which ranged from 9-15 plots.

Table 3. Regression of white spruce seedling density in response to forb cover, litter depth, and year of savanna origin.

	Variable	Category	Coefficient	Std. Error	Chi-Square	df	*p*
Single Variables	Forb cover (%)	(N/A)	0.014	0.005	8.705	1	0.003***
	Litter depth	(N/A)	0.442	0.311	2.016	1	0.156
	Year	1930	3.472	1.525	5.185	1	0.023*
		1957	3.356	1.365	6.047	1	0.014*
		1978	3.483	1.366	6.502	1	0.011*
		2005	3.104	1.345	5.327	1	0.021*
Interaction Variables	(Year)*(Litter depth)	1930	-1.010	0.367	7.582	1	0.006**
		1957	-0.829	0.333	6.196	1	0.013*
		1978	-0.779	0.327	5.686	1	0.017*
		2005	-0.520	0.321	2.615	1	0.106
Model Effects	Constant				3.382	1	0.066
	Forb cover (%)				8.705	1	0.003***
	Litter depth				5.282	1	0.022*
	Year				6.864	4	0.143
	(Year)*(Litter depth)				14.418	4	0.006**
Omnibus Model					94.326	10	0.000***

*p<0.05, **p<0.01, ***p<0.005

Figure 1. Study area on the west end of Isle Royale National Park.

Figure 2. Size class distribution of select tree species in savanna and forest habitats on the west end of Isle Royale in 2012.

Figure 3. Age structure in mapped stands, derived from tree-ring cores and counts of whorls in 2012. Year numbers correspond with the earliest year that each stand was known to have transitioned from forest (>75% canopy) to savanna (<25% canopy). Additional numbers within panels reflect seedling density per hectare below the specified height class, below which age was not determined. Data are shown for: (a) Feldtmann 1930 A, (b) Feldtmann 1930 B, (c) Rainbow 1930, (d) Head 1957, (e) Fedltmann 1957, (f) Rainbow 1957, (g) Grace 1978 A, (h) Grace 1978 B, (i) Head 1978, (j) Head 2005, (k) Grace 2005, (l) East 2005, (m) East Reference, (n) Feldtmann Reference, and (o) Head Reference. Data are not shown for Windigo 1930, which had only 5 spruce stems.

Figure 4. Count of *Picea glauca* seedlings in 5 m radius plots in savanna and forest habitats on Isle Royale, in response to: (a) percent forb cover and (b) litter depth and year of savanna origin, as predicted by negative binomial regression.

Figure 5. Response of white spruce seedling count to plant species richness in savanna and forest plots on Isle Royale, modelled by non-parametric multiplicative regression.

Figure 6. Univariate spatial patterns of white spruce showing patterns in sites with (a) distinct groves and (b) merging groves. Clustered patterns are indicated by solid lines, random patterns are indicated by small-dotted lines, and regular patterns are indicated by large-dotted lines.

Figure 7. Representative bivariate spatial patterns between white spruce cohorts with corresponding maps showing old (trees) and young (asterisks) white spruce in savanna and reference stands. Stands for which L(t) and sample patterns are displayed are asterisked (*). Patterns included (a) loose multi-cohort groves separated by open treeless patches, (b) networked multi-cohort groves more saturated by spruce regeneration, (c) single-cohort patches, (d) random distribution of cohorts, and (e) highly concentrated multi-cohort patches.

Figure 1.

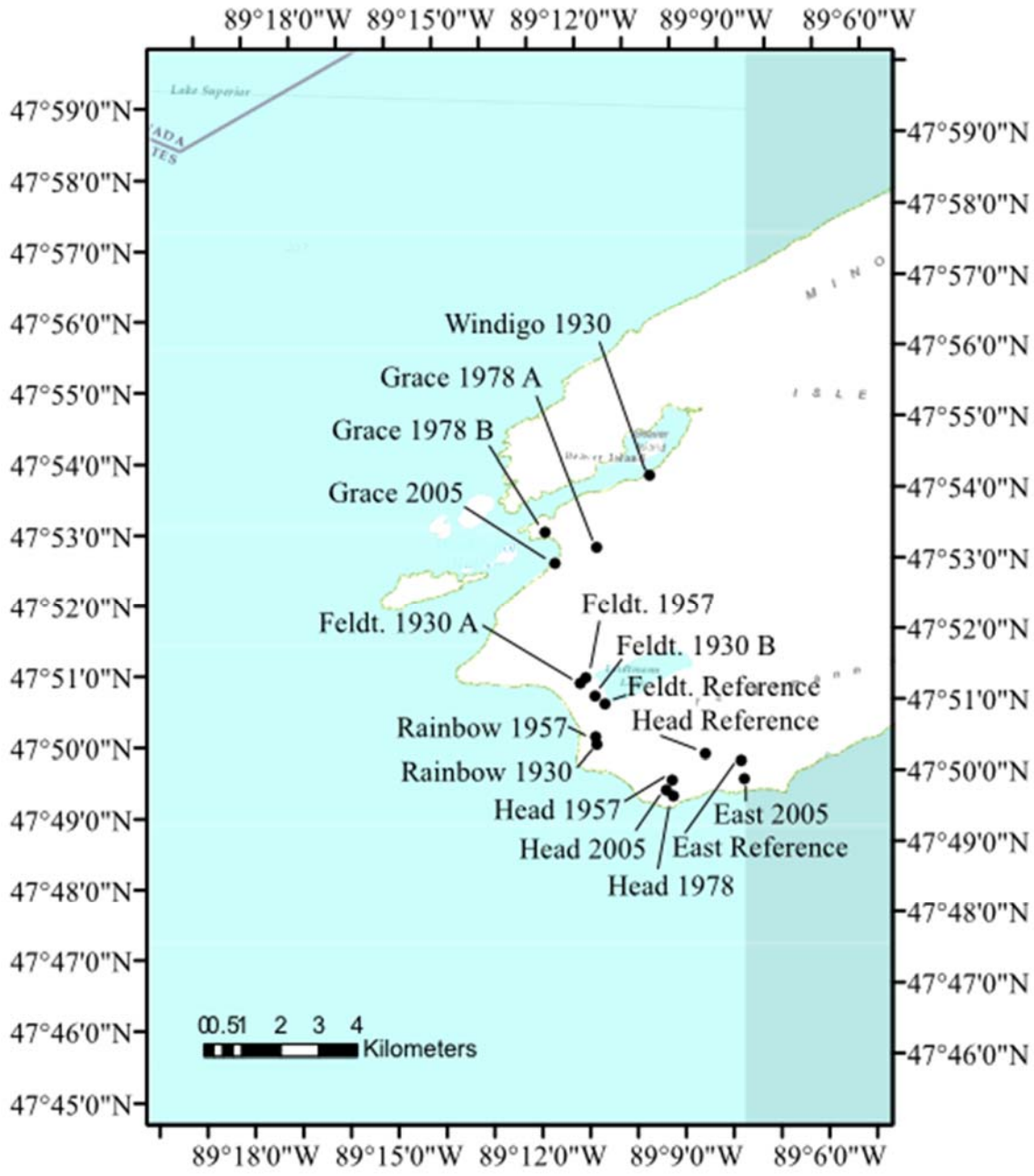

89°18'0"W
89°15'0"W
89°12'0"W
89°9'0"W
89°6'0"W
47°59'0"N
47°58'0"N
47°57'0"N
47°56'0"N
47°55'0"N
47°54'0"N
47°53'0"N
47°52'0"N
47°51'0"N
47°50'0"N
47°49'0"N
47°48'0"N
47°47'0"N
47°46'0"N
47°45'0"N
Lake Superior
Windigo 1930
Grace 1978 A
Grace 1978 B
Grace 2005
Feldt. 1957
Feldt. 1930 A
Feldt. 1930 B
Feldt. Reference
Head Reference
Rainbow 1957
Rainbow 1930
Head 1957
East 2005
Head 2005
East Reference
Head 1978
0 0.5 1 2 3 4
Kilometers

Figure 2.

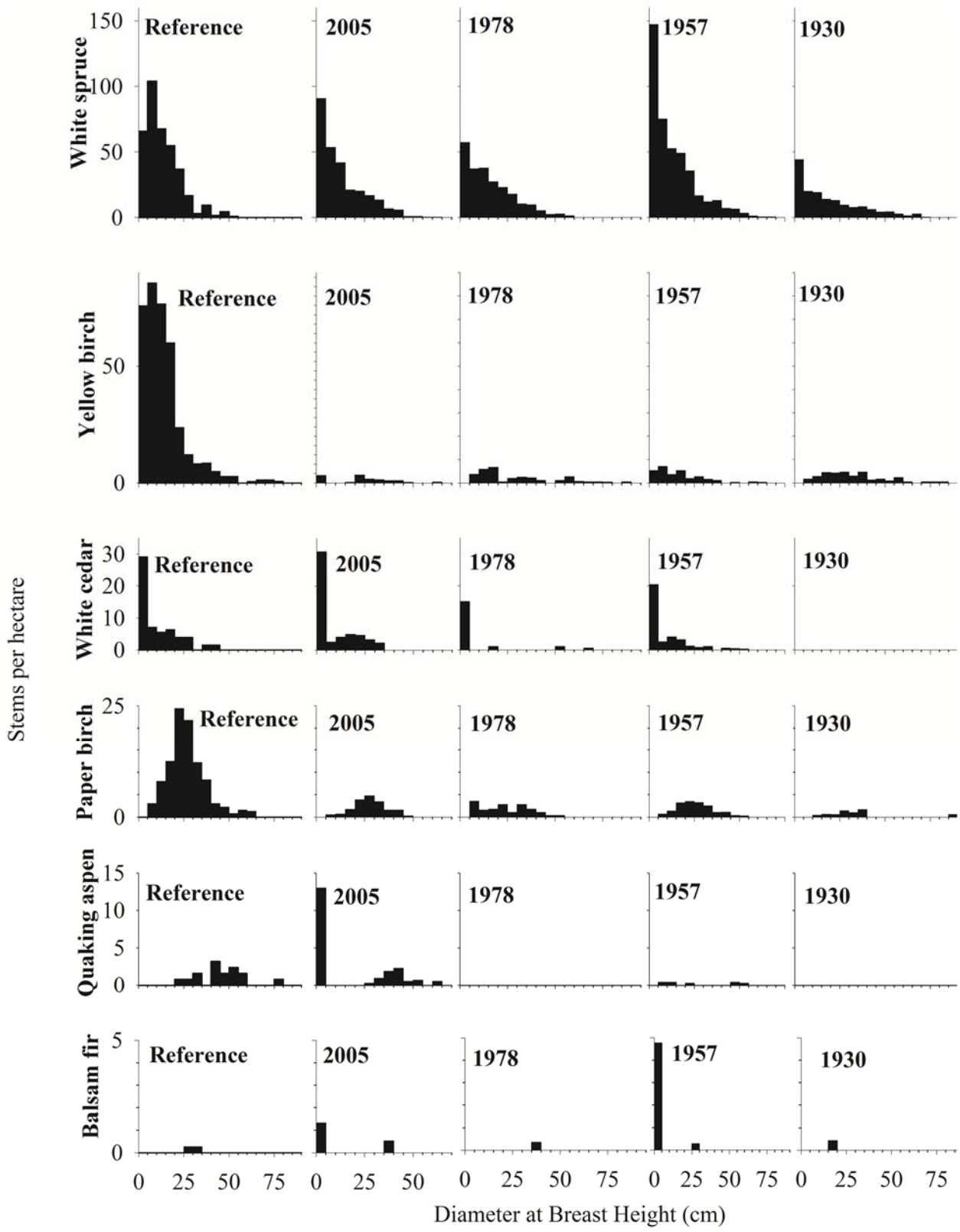

Reference
2005
1978
1957
1930
White spruce
Yellow birch
White cedar
Paper birch
Quaking aspen
Balsam fir
Stems per hectare
Diameter at Breast Height (cm)

Figure 3.

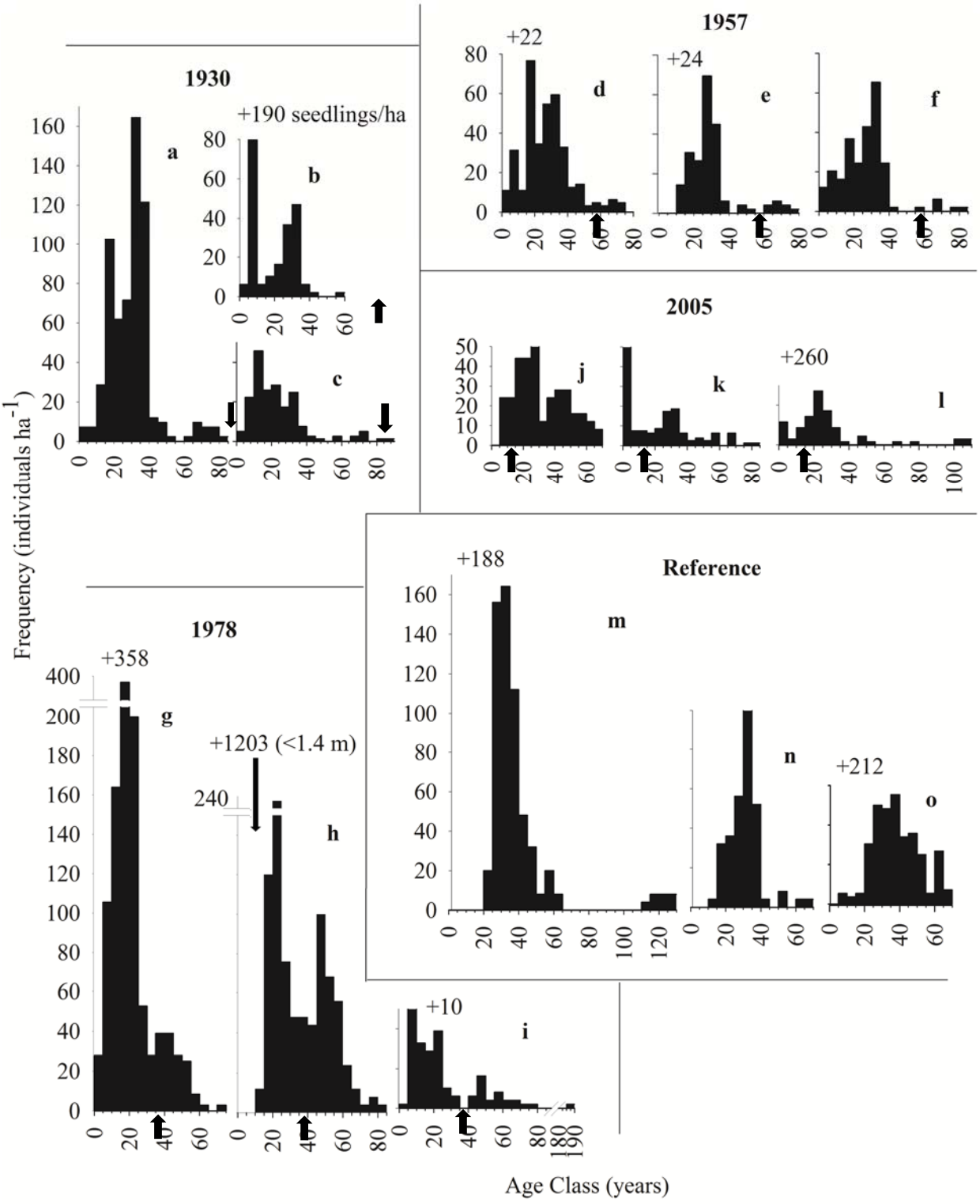

1930
1957
2005
1978
Reference
+190 seedlings/ha
+22
+24
+260
+358
+1203 (<1.4 m)
240
+188
+212
+10
a
b
c
d
e
f
g
h
i
j
k
l
m
n
o
Frequency (individuals ha-1)
Age Class (years)

Figure 4.

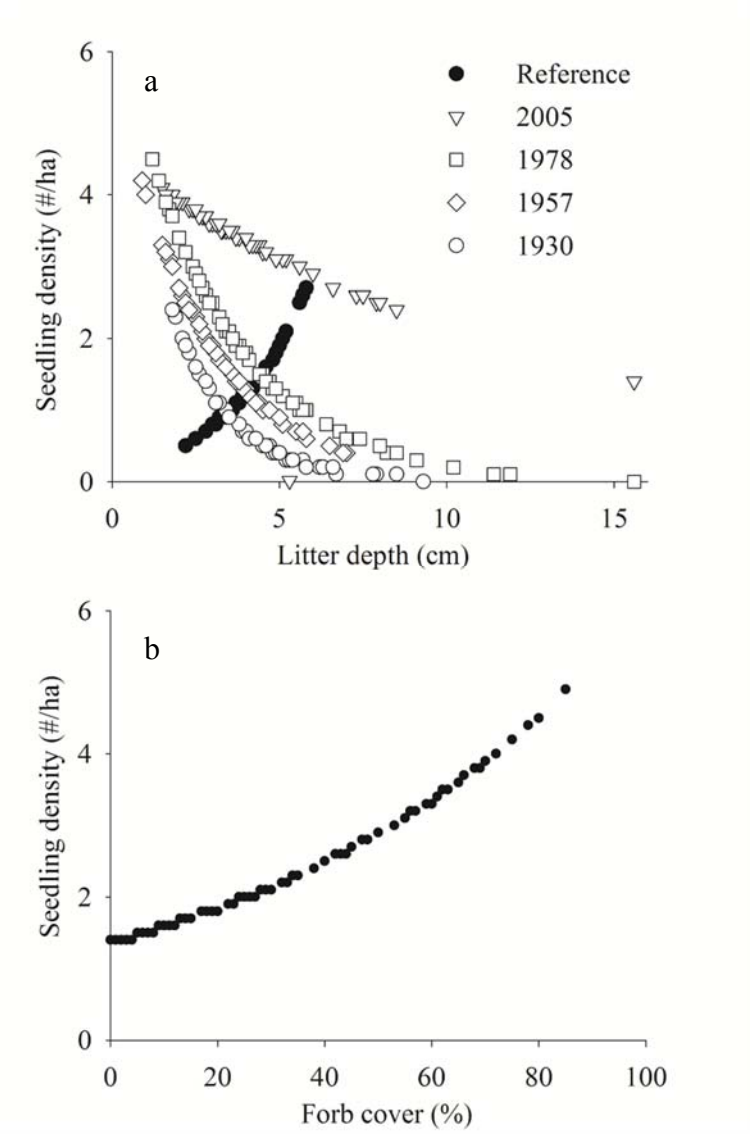

a
Reference
2005
1978
1957
1930
Seedling density (#/ha)
Litter depth (cm)
b
Seedling density (#/ha)
Forb cover (%)

Figure 5.

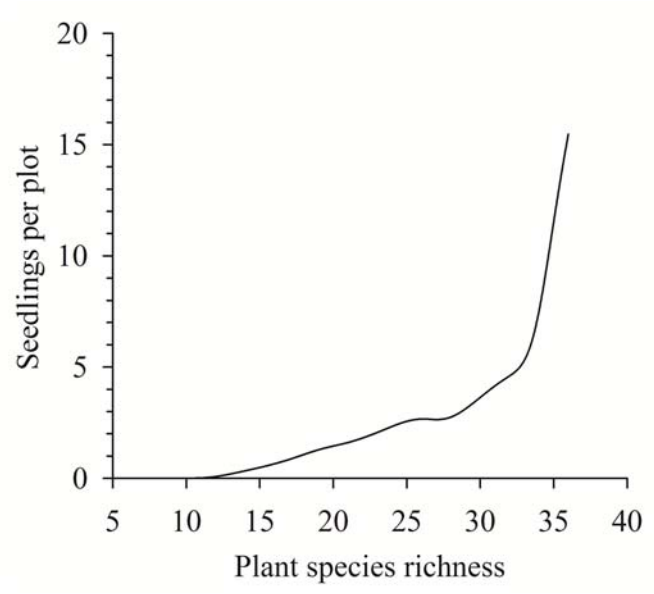

20
15
10
5
0
Seedlings per plot
5
10
15
20
25
30
35
40
Plant species richness

Figure 6.

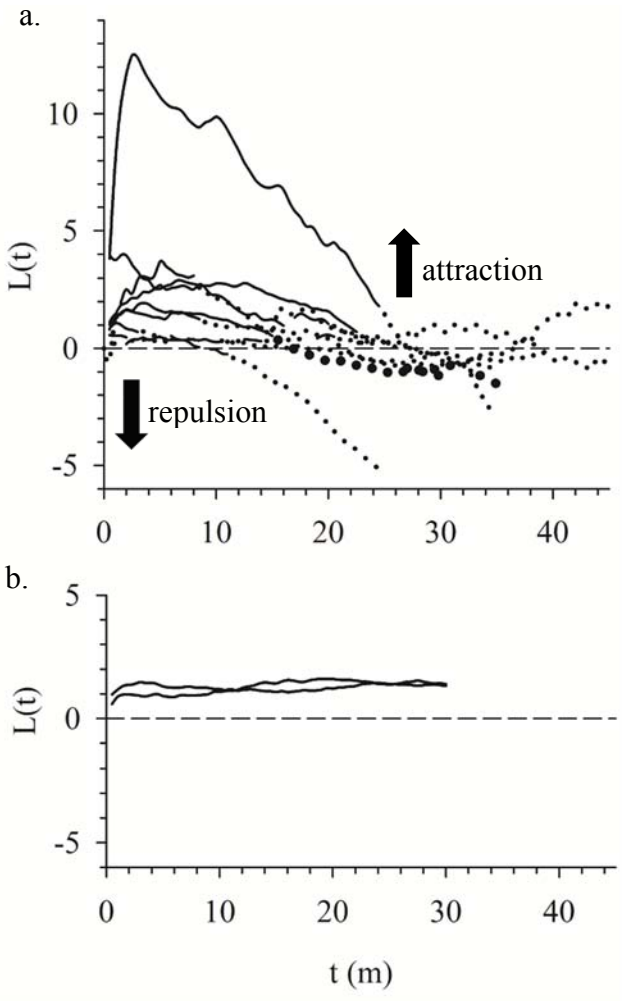
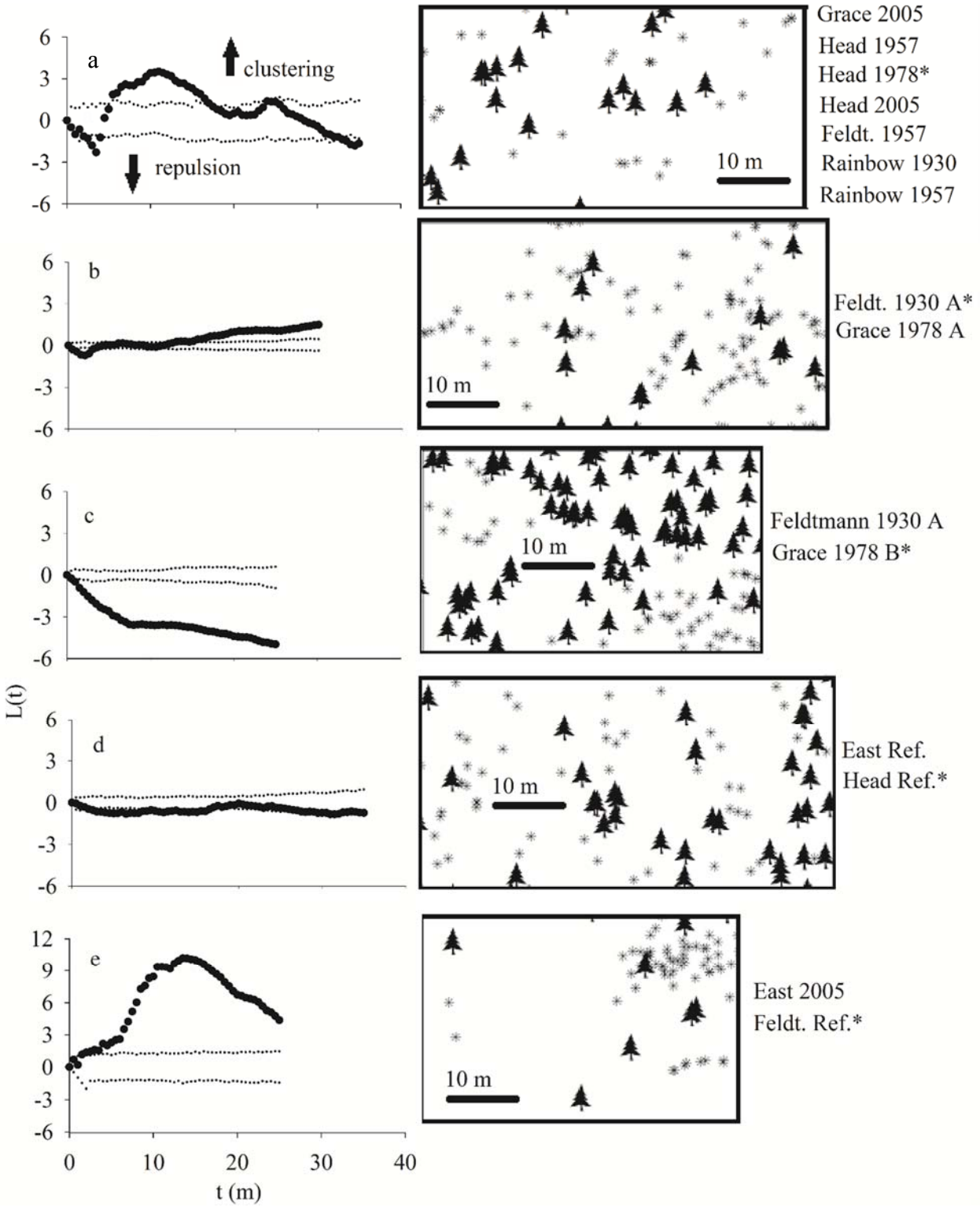

a.
10
5
0
-5
L(t)
attraction
repulsion
0
10
20
30
40
b.
5
0
-5
L(t)
0
10
20
30
40
t (m)

Figure 7.


a
clustering
repulsion
b
c
d
e
L(t)
t (m)
10 m
Grace 2005
Head 1957
Head 1978*
Head 2005
Feldt. 1957
Rainbow 1930
Rainbow 1957
Feldt. 1930 A*
Grace 1978 A
Feldtmann 1930 A
Grace 1978 B*
East Ref.
Head Ref.*
East 2005
Feldt. Ref.*