ARTICLE

Multiple developmental pathways for range-margin *Pinus banksiana* forests

Kyle G. Gill, Anthony W. D'Amato, and Shawn Fraver

Abstract: Empirical knowledge of forest structure and development in early successional and range-margin populations is often lacking, limiting our ability to effectively model and manage these forests. Such is the case for jack pine (*Pinus banksiana* Lamb.) in central Minnesota, USA, where it reaches its southwestern range limit. Our objective was to quantify this population's historical range of variability of structural conditions and developmental pathways. We collected structural, spatial, and dendrochronological data on 0.25 ha plots from 10 jack pine dominated sites that initiated and developed outside of active management. Our results revealed a broad range of structural characteristics and developmental pathways, including rapid and protracted recruitment windows (5–50 years), with subsequent even- and uneven-aged structures, and random and clumped stem spatial arrangements. As such, these mature, early successional forests often displayed a degree of complexity more typically associated with old-growth forests. Our findings suggest that this population, like other southern range-margin populations with mostly nonserotinous cones, historically followed a variety of stand development pathways and did not solely follow the rapid establishment, even-aged pathway often attributed to this forest type. We suggest that even- and uneven-aged silvicultural systems should be used to reflect this historical range of developmental pathways and to increase resilience and adaptability.

Key words: dendrochronology, early successional forest, jack pine, marginal population, range of variability.

Résumé : Le fréquent manque de connaissances empiriques sur la structure et le développement des forêts en début de succession et à la marge de leur aire de distribution limite notre capacité à les modéliser et les aménager efficacement. C'est le cas du pin gris (*Pinus banksiana* Lamb.) dans le centre du Minnesota, aux États-Unis, où il atteint la limite sud–ouest de son aire de distribution. Notre objectif était de quantifier l'étendue historique de la variabilité des conditions structurales et des trajectoires de développement de cette population. Nous avons recueilli des données structurales, spatiales et dendrochronologiques dans des placettes de 0,25 ha établies dans 10 peuplements dominés par le pin gris dont l'origine et le développement sont survenus sans aménagement actif. Nos résultats ont mis en évidence un large éventail de caractéristiques structurales et de trajectoires de développement, incluant des périodes rapides et prolongées de recrutement (de 5 à 50 ans) suivies de l'établissement de structures équiennes et inéquiennes avec des arbres dont la distribution spatiale était aléatoire et groupée. Ainsi, ces forêts matures de début de succession avaient souvent un degré de complexité généralement associé aux vieilles forêts. Nos résultats indiquent que cette population, comme d'autres populations avec des cônes généralement non sérotineux et situées à la limite sud de leur aire de distribution, a dans le passé suivi une variété de trajectoires de développement et non la seule trajectoire souvent attribuée à ce type de forêt, soit un établissement rapide et une structure équienne. Nous suggérons d'avoir recours à des systèmes sylvicoles équienne et inéquienne pour refléter cet éventail historique de trajectoires de développement et accroître la résilience et l'adaptabilité de ces forêts. [Traduit par la Rédaction]

Mots-clés : dendrochronologie, forêt de début de succession, pin gris, population marginale, étendue de la variabilité.

Introduction

Plant populations located at their geographic range margins tend to display atypical species traits and population-level dynamics due to their proximity to suboptimal abiotic conditions and ecotonal community associations (Kawecki 2008). These marginal populations represent the dynamic edges of a species' larger central population whose expansion or contraction indicates range or elevation shifts. Conservation of marginal populations — including their connectivity with central populations and their biologically diverse ecotone communities — is seen as a way to maintain migratory and adaptive potential in the face of uncertain future conditions (Lesica and Allendorf 1995). Given their unusual character, as well as their vulnerability to change, there is a great need to document their historical variation and adaptive potential to establish baselines for assessing long-term climate impacts and develop targets for setting conservation priorities (Keane et al. 2009).

Currently, knowledge of the historical range of variability for range-margin populations is limited because the focus has primarily been on nonmarginal populations (e.g., Fraver and Palik 2012). In forested settings, this focus has left key knowledge gaps regarding the variability of structure and developmental pathways associated with these forests. In addition, the behavior of these systems has rarely been included in forest dynamics and species distribution models, despite the fact that they may be the first to face and respond to altered environmental stressors, which limits the current predictive power of such models (Seidl

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et al. 2011). An understanding of the range of variability in marginal populations would not only assist predictions of potential future range distributions and variation, but also provide the foundation for appropriate local adaptive management (D'Amato et al. 2011).

In a similar regard, the range of variability in early successional forest developmental pathways is often unknown but is a topic that is now gaining increased attention (Swanson et al. 2011). Many early successional forests are expected to develop along conventional even-aged pathways with relatively homogeneous structure (e.g., spatial arrangement and age range) and composition (Oliver and Larson 1996). However, given the complex nature of forest systems and their dynamic response to disturbance events (Puettmann et al. 2009), alternative developmental pathways that include more structural complexity should also be expected (Donato et al. 2012). These pathways may include longer periods of herbaceous vegetation and shrub dominance along with protracted tree recruitment windows (period when most recruitment occurs) and time until canopy closure (Nyland 1998). Although different pathways may converge towards similar mature forest conditions (Kashian et al. 2005), understanding the range of variability in potential pathways can have important modeling and management implications.

Jack pine (*Pinus banksiana* Lamb.) is an abundant, early successional tree species of the boreal forest biome that has been studied across much of its natural range, which extends from Canada's Northwest Territories to the Maritime provinces and south to the Great Lakes region of the USA. A southern range-margin population displaying atypical traits such as nonserotinous cones (Schoenike 1976) and community associations with tallgrass prairie species (Aaseng et al. 2003) exists along the prairie–forest ecotone in north–central North America. Neither the structural characteristics nor the associated developmental pathways of this marginal population have been thoroughly documented. Other southern range-margin populations have been investigated in Indiana (Chun and Choi 2012), Michigan (Abrams et al. 1985), and Maine (Barton and Grenier 2008), USA, but no work has examined a full set of structural characteristics, including establishment, development, and spatial patterns. Such data are critical for understanding regional and range-wide variation and potential future conditions for this forest type. In addition, this topic has timely and important regional management implications because both natural and artificial regeneration difficulties in jack pine stands are contributing to a reduction of this forest type. These difficulties may be caused by incongruity between the historical dynamics and contemporary use of even-aged management, the removal of fire from a fire-prone system (e.g., Platt et al. 1988), high levels of herbivory (White 2012), or shifts in suitable climatic conditions (Zhu et al. 2012).

In the current study, we investigated the natural range of variability of structure and development in early successional jack pine dominated forests near their range margin in north–central Minnesota to document reference conditions for monitoring future climate impacts and to inform regional adaptive management (D'Amato et al. 2011). Specifically, we aimed to (*i*) quantify the natural range of variability of stand structure in representative stands and (*ii*) characterize historical stand development patterns that have shaped contemporary, natural jack pine forests in this region. Our results demonstrate varying levels of structural complexity and suggest a range of early development pathways for jack pine forests. These can be reflected in the region through the use of both even- and uneven-aged silvicultural systems, which could also promote stand- and landscape-level resilience.

Methods

Study area

Our study area (Fig. 1) is located within the Northern Minnesota Drift and Lake Plains (MDL) ecological subsection of the Laurentian Mixed Forest Province (Aaseng et al. 2003). The MDL has complex surface geology due to a patchy distribution of glacial deposits such as outwash, lake and till plains, moraines, and drumlin fields (Aaseng et al. 2003). The cold–temperate continental climate in the region is characterized by short, cool summers and long, cold winters with periods of temperature extremes in both seasons. Using monthly PRISM climate data for each study site (www.prism.oregonstate.edu) and the time period 1913–2012, the mean total annual precipitation, over 80% of which fell between April and October, was 632 mm (standard deviation (SD) = 102 mm), the mean minimum winter (December–January) temperature was –19 °C (SD = 4 °C), and the mean maximum summer (June–August) temperature was 25 °C (SD = 2 °C).

Site selection

We focused our site selection on locating mature to decadent jack pine dominated sites older than the recommended commercial forestry rotation lengths (40–70 years; Burns and Honkala 1990) that had regenerated and developed outside of active management. In the attempt to ensure natural stand origin and development, we sought sites with little or no evidence of past management such as cut stumps, uniform (plantation-like) tree spacing, furrows, or logging roads. To capture the oldest sites possible and avoid the influence of known periods of heavy management, we sought out sites that initiated prior to 1950, including jack pine snags, and contained a variety of tree crown and diameter classes. These characteristics also provided the possibility of locating multi-aged jack pine systems that are expected to exist along the southern range-margin (e.g., Barton and Grenier 2008). Potential sites were provided by the Minnesota Department of Natural Resources, along with input from other area professionals. Together, these sources identified 128 potential sites that were first screened for management activity via historical aerial photographs (1939–2012). From this pool, 76 were inspected on the ground. Ten sites ultimately met our criteria and were selected for sampling (Fig. 1; Table 1).

Field and laboratory methods

Within each site, one 50 m × 50 m study plot was randomly or systematically established along cardinal directions during 2012 (Midge Lake sites) or 2013 (all other sites). For larger sites, a point was randomly selected in a GIS and established as plot center. For two relatively small sites (~4 ha), we placed plot center in the geographic center to avoid edge bias. Within each plot, all trees ≥10 cm diameter at breast height (DBH, 1.37 m) were sampled. Each tree was given a unique number and sampled for species, DBH, crown class (based on the Kraft classification system; Oliver and Larson 1996), mortality class (living or snag), and location (within-plot *x* and *y* coordinates). Saplings, defined as any tree species taller than breast height and <10 cm DBH, were tallied by species in three 5 m × 50 m within-plot transects.

The volume of downed woody debris (DWD) was estimated using the line-intercept method (Van Wagner 1968) to further quantify stand structural conditions. DWD ≥10 cm in diameter at line-intersection point was sampled along eight equiangular line-intercept transects radiating from plot center, for a total of 241 m of transect per plot. Each piece was sampled for species (or genus when precluded by advanced decay), diameter at intersection, and decay class (Sollins 1982). DWD volume per hectare was calculated as per Van Wagner (1968) and reduced to account for collapse of decay class IV and V pieces (Fraver et al. 2013).

Fig. 1. Location of study area and sites within a southern range-margin jack pine (*Pinus banksiana*) population in north–central Minnesota, USA. Jack pine range (grey shading) is from Little (1971).
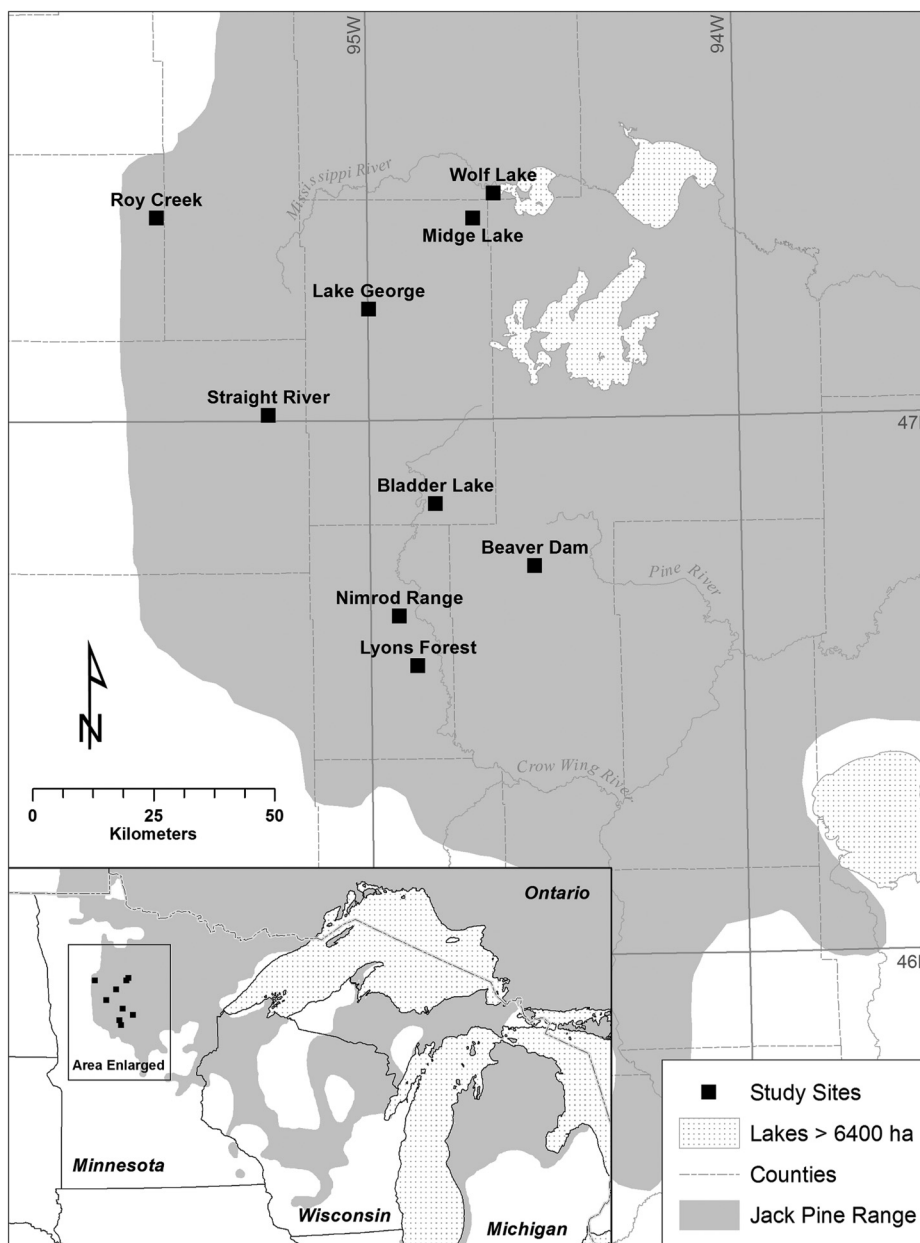
Table 1. Site names, codes, and stand characteristics for the 10 range-margin jack pine study sites.

Site name	Site code	Native plant community[a]	Geomorphic description[b]	Soil texture[c]	Stand size (ha)
Beaver Dam	BD	Northern Dry–Sand Pine Woodland	Hillslopes on moraines	Coarse loamy	4
Bladder Lake	BL	Central Rich Dry Pine Woodland	Outwash plains	Sandy	13
Lyons Forest	LF	Central Dry Pine Woodland	Outwash plains	Coarse loamy	40
Lake George	LG	Central Poor Dry Pine Woodland	Flats on outwash plains, rises on outwash plains	Sandy	15
Midge Lake East	ME	Central Dry Pine Woodland	Outwash plains, valley trains	Sandy	59
Midge Lake West	MW	Central Dry Pine Woodland	Outwash plains, valley trains	Sandy	59
Nimrod Range	NR	Central Rich Dry Pine Woodland	Hillslopes on outwash plains	Sandy	10
Roy Creek	RC	Central Rich Dry Pine Woodland	Hillslopes on outwash plains	Fine loamy	4
Straight River	SR	Central Rich Dry Pine Woodland	Hillslopes on moraines	Sandy	28
Wolf Lake	WL	Central Rich Dry Pine Woodland	Hillslopes on outwash plains	Sandy	31

[a]Aaseng et al. (2003).
[b]SSURGO (data downloaded from www.websoilsurvey.nrcs.usda.gov).
[c]Cummins and Grigal (1980).

To characterize age structures, development patterns, and disturbance histories, increment cores were collected at 30 cm above the forest floor from all living and, when possible, standing dead trees (snags). In the laboratory, increment cores were affixed to wooden mounts and sanded using progressively finer grits (up to 800 grit) to clearly reveal ring anatomy. If the core had not passed directly through the pith, the number of missing rings to pith was visually estimated (Applequist 1958); cores estimated to be greater than 10 years from pith were excluded from age-related analyses. The pith year, or adjusted pith year, was taken as the year of recruitment and used to represent the age of the individual. A Velmex sliding-stage micrometer (Velmex Inc., Bloomfield, New York) was used to measure annual growth rings to the nearest 0.001 mm. All cores were cross-dated visually (Yamaguchi 1991) and statistically confirmed with COFECHA (Lamont-Doherty Earth Observatory, available from www.ldeo.columbia.edu). Cores from snags were cross-dated using marker years from associated site-level live-tree chronologies and statistically confirmed with COFECHA. Stand-wide growth patterns and disturbance events were assessed by creating standardized growth chronologies for jack pine from each site; additional chronologies were developed for any additional species at sites where the species had an importance value (IV; (relative basal area + relative density)/2; Curtis and McIntosh 1951) ≥25%. To this end, each tree-ring series was fit with a horizontal line through the mean ring width, and annual ring widths were divided by fitted values (i.e., mean ring width) to produce a unit-less index (Fritts 1976). These indexed series were then averaged to arrive at a standardized, indexed time series that maintains stand-wide growth trends related to disturbance (Veblen et al. 1991). Chronologies were developed in ARSTAN v44h3 (Lamont-Doherty Earth Observatory) and only interpreted for portions where sample size included 10 or more series. To further refine site disturbance history, cores were collected from on-site trees that displayed fire scars, following the methods of Barrett and Arno (1988).

Analyses

Age distributions and jack pine recruitment windows were developed to characterize stand establishment and development. For age distributions, individuals at each site were grouped by 5-year age-class intervals. Jack pine recruitment windows were calculated at each site to quantify the time it took for a majority of jack pine trees to recruit into the site and to determine if they met standard criteria for being even aged (tree age ranges around 20% of rotation). Because the recommended jack pine rotation ages are between 40 and 70 years (Burns and Honkala 1990), we used 15 years as the maximum even-aged recruitment window length. Recruitment windows were calculated using the interpercentile range spanning the 5th through 95th percentiles of year of recruitment. The middle 90% was assumed to represent a majority of individuals while excluding potential outliers.

To further elucidate stand establishment and development patterns, the spatial arrangement of jack pine stems at each plot was assessed using the pairwise correlation function (Stoyan and Stoyan 1994). Analyses of the univariate spatial distributions of all jack pine stems (living and standing dead pooled) were conducted for each plot using the spatstat package (Baddeley and Turner 2005) in R (available from www.r-project.org) to test against null hypotheses of complete spatial randomness (CSR) using isotropic edge correction and pointwise significance bands (α = 0.05) produced by 499 Monte Carlo simulations. The pooled group was used because it was thought to provide the most complete picture of patterns from early establishment through maturity (our interest) prior to decadence. However, we recognize that true number of individuals is likely underestimated because of potential early mortality and loss of some stems. Analyses conducted with solely

living jack pine stems revealed comparable results (not shown) with those using all stems; however, we focus on the pooled group given that this better represents stand development prior to decadence. Additionally, four sites that had protracted and continuous jack pine recruitment and sufficient sample depth were further analyzed to assess potential differences in the spatial patterns of trees through time. The same process as above was used to analyze spatial patterns of two age groups ("older" and "younger") at each site. Using only individuals that recruited during the calculated recruitment window, groups were separated at the median tree age (older > median ≥ younger) to provide relatively balanced samples. The spatial arrangement of all individuals included in these latter analyses was first assessed at each site to confirm that the sample was representative of the population (results not shown).

Results

Composition and structure

Jack pines were the predominant species and structural components across the study sites, but other species were present and sometimes abundant. Jack pine IVs ranged from 27% to 89% (mean ± standard error (SE) = 50% ± 6%) across sites (Table 2). Red pine (*Pinus resinosa* Aiton) had lower and more variable IVs across sites, ranging from 0% to 72% (mean ± SE = 25% ± 7%). Paper birch (*Betula papyrifera* Marshall) was absent or a minor component at most sites; however, at Bladder Lake, it constituted a greater portion of the stand basal area than living jack pine (Table 3, see basal area of jack pine snags). Total live tree densities ranged from 376 to 904 trees·ha⁻¹ (species pooled) and from 128 to 696 trees·ha⁻¹ (jack pine) (Table 2). The basal area of living trees ranged from 16.4 to 32.5 m²·ha⁻¹ (species pooled) and from 7.1 to 19.0 m²·ha⁻¹ (jack pine) (Table 3). Stand-level diameter distributions (Fig. 2; note that species are pooled) varied in shape across sites from unimodal (Midge Lake West) and bimodal (Nimrod Range) to negative exponential (Midge Lake East). The DBH distributions of jack pine (Fig. 2, black bars) were primarily unimodal; this shape was wider (e.g., Lake George), or absent (Midge Lake East), in stands with protracted recruitment windows (see below). Mean jack pine diameter at each site ranged from 18.2 to 28.5 cm (mean ± SE = 23.5 ± 1 cm).

Jack pine was most abundant in upper canopy layers (dominant and codominant) and decreased in abundance in lower layers (intermediate and suppressed). Red pine, paper birch, *Populus* species, and *Quercus* species were the primary species in the intermediate and suppressed layers; however, composition varied between sites (Table 3). Total sapling density (species pooled) ranged from 560 to 2187 stems·ha⁻¹ (Table 2). Oak saplings, 84% of which were red oaks (*Quercus rubra* L.), were the most abundant sapling species group. Very few jack pines were found in the sapling layer (Table 2).

Standing and downed deadwood was abundant at all sites, but the causes of mortality were not explicitly determined. Jack pine snags (*N* = 670) occurred nearly as often as living jack pine (*N* = 674); snags of other species were uncommon (*N* = 15). The snag basal area was greater than that of living jack pine at 3 of 10 sites (Table 3; Bladder Lake, Roy Creek, and Wolf Lake); however, snag diameters tended to be smaller than those of living jack pines at all sites (Fig. 2). The mean diameter of jack pine snags per site ranged from 13.9 to 23.3 cm (mean ± SE = 19.2 ± 1.0 cm). The total DWD volume per site ranged from 18.8 to 125.6 m³·ha⁻¹ (Table 2), of which 43%–99% (mean ± SE = 83.2% ± 5.3%) was jack pine. The majority of DWD at many sites was in decay classes II and III, yet distribution among decay classes varied (Appendix Fig. A1).

Table 2. Structural characteristics of range-margin jack pine (JP) study stands including live tree density (trees·ha⁻¹) and importance value (IV), JP snag density, sapling density for JP and for all species (total), and downed woody debris (DWD) volume.

Site code	Live trees (trees·ha⁻¹)	Live JP Trees·ha⁻¹	Live JP IV (%)	JP snags (trees·ha⁻¹)	Saplings JP·ha⁻¹	Saplings Total·ha⁻¹	DWD (m³·ha⁻¹)
BD	800	292	40.5	284	—	1253	72.3
BL	528	128	32.3[a]	212	—	1573	67.2
LF	516	348	64.8	196	27	987	13.9
LG	904	232	27.3[b]	276	—	560	21.3
ME	376	224	57.4	276	67	2187	29.9
MW	780	696	89.1	308	13	1053	18.8
NR	448	236	44.7[c]	208	—	1373	39.8
RC	444	184	45.5	288	—	1227	125.6
SR	408	144	47.2	168	—	1027	60.3
WL	476	212	49.6	464	—	1147	54.6
Mean (SE)	568 (59.3)	270 (51.6)	49.8 (5.6)	268 (26.4)	11 (6.8)	1239 (135)	50.4 (10.7)

Note: JP had the highest live tree IV in a given plot, unless noted. See Table 1 for site codes. SE, standard error.

[a]*Betula papyrifera*, IV = 56.9%.

[b]*Pinus resinosa*, IV = 72%.

[c]*P. resinosa*, IV = 47.5%.

Table 3. Live tree basal area (m²·ha⁻¹) for each species or species group, plus standing dead jack pine trees (snags), by site.

Species	Site codes BD	BL	LF	LG	ME	MW	NR	RC	SR	WL	Mean (SE)
Live trees											
Pinus banksiana	14.5	7.1	11.9	8.7	8.7	19.0	11.1	10.8	9.7	9.3	11.1 (1.1)
Pinus resinosa	11.5	0.0	6.5	21.3	5.3	1.1	18.1	6.9	0.9	1.8	7.4 (2.4)
Betula papyrifera	2.0	9.2	0.7	0.0	0.3	0.0	0.1	0.2	0.6	2.0	1.5 (0.9)
Populus spp.[a]	4.1	0.6	0.0	0.0	0.0	0.0	0.3	2.2	2.4	3.0	1.3 (0.5)
Quercus spp.[b]	0.0	0.6	0.0	0.0	0.8	0.2	0.6	0.7	1.9	0.3	0.5 (0.2)
Other conifers[c]	0.5	0.0	0.0	0.2	0.6	1.0	0.0	0.5	0.0	0.5	0.3 (0.1)
Other deciduous[d]	0.0	0.1	0.0	0.0	0.1	0.0	0.0	0.5	0.9	0.1	0.2 (0.1)
Stand total	32.5	17.5	19.1	30.2	15.8	21.4	30.1	21.8	16.4	17.0	22.2 (2.0)
Snags											
Pinus banksiana	9.9	9.4	4.9	5.5	8.7	5.0	6.2	12.5	6.9	15.2	8.4 (1.1)

Note: See Table 1 for site codes.

[a]*Populus grandidentata* and *Populus tremuloides*.

[b]*Quercus macrocarpa* and *Quercus rubra*.

[c]*Abies balsamea*, *Picea glauca*, *Picea mariana*, and *Pinus strobus*.

[d]*Acer rubrum*, *Alnus incana*, *Prunus serotina*, *Fraxinus pennsylvanica*, and *Ulmus americana*.

Age distributions and stand development

Tree age distributions including all species showed uneven-aged structures at all sites (Fig. 3, bars). Sites tended to have one primary pulse of jack pine recruitment, often protracted, with recruitment of additional jack pine and other species prior, during, and (or) after this period. Most sites displayed varied but usually low levels of non jack pine recruitment concurrent with the primary jack pine cohort (e.g., Straight River). At several sites, small cohorts of red pine recruited 30–80 years prior to the initiation of a majority of other individuals (e.g., Nimrod Range and Roy Creek). These sites also tended to have additional red pine recruitment concurrent with, or slightly delayed from, the primary jack pine pulse. At Bladder Lake and Lake George, cohorts of paper birch and red pine, respectively, occurred after the establishment of most jack pines, and these species constituted a greater live stem importance relative to jack pine at the time of sampling (Table 2; see Disturbance effects on stand development and succession).

Jack pine age distributions (Fig. 3, black bars) and recruitment windows (Fig. 4) indicate both even-aged and uneven-aged struc-tures but typically display one primary pulse with varying levels of additional jack pine recruitment surrounding the pulse. The duration of jack pine recruitment windows for four sites that met even-aged criteria ranged from 5 years (Fig. 4, Nimrod Range) to 15 years (Fig. 4, Bladder Lake). The other six sites had uneven-aged jack pine with protracted recruitment windows (up to 50 years; Fig. 4, Midge Lake East) and age structures that followed three primary patterns (Fig. 3). At Straight River, two distinct cohorts were separated by just under a decade of no recruitment. At Midge Lake East, Midge Lake West, and Wolf Lake, varying levels of low to nearly continuous recruitment either preceded or followed a primary cohort that had a 5- to 10-year window. A similar trend was observed at Lyons Forest and Lake George but with primary cohorts spanning 10–15 years.

No clear relationship between age structures and disturbance events was observed. Evidence of past fires was rare and only once showed a direct influence on age structures (Fig. 3). In particular, at Nimrod Range, the earliest cohort of red pine recruited shortly after an autumn 1894 or spring 1895 fire (Fig. 3). These trees later (ca. 1945) displayed an abrupt growth increase (Fig. 3, Nimrod Range, grey line) concurrent with the recruitment of the even-

Fig. 2. Diameter at breast height (DBH, 1.37 m) distributions of living trees (*n*, listed below site name) and snags (inset) for 10 range-margin jack pine sites (number of living + snag trees (*N*) = 2105). Diameter classes are labeled by the minimum value of the 5 cm class range.
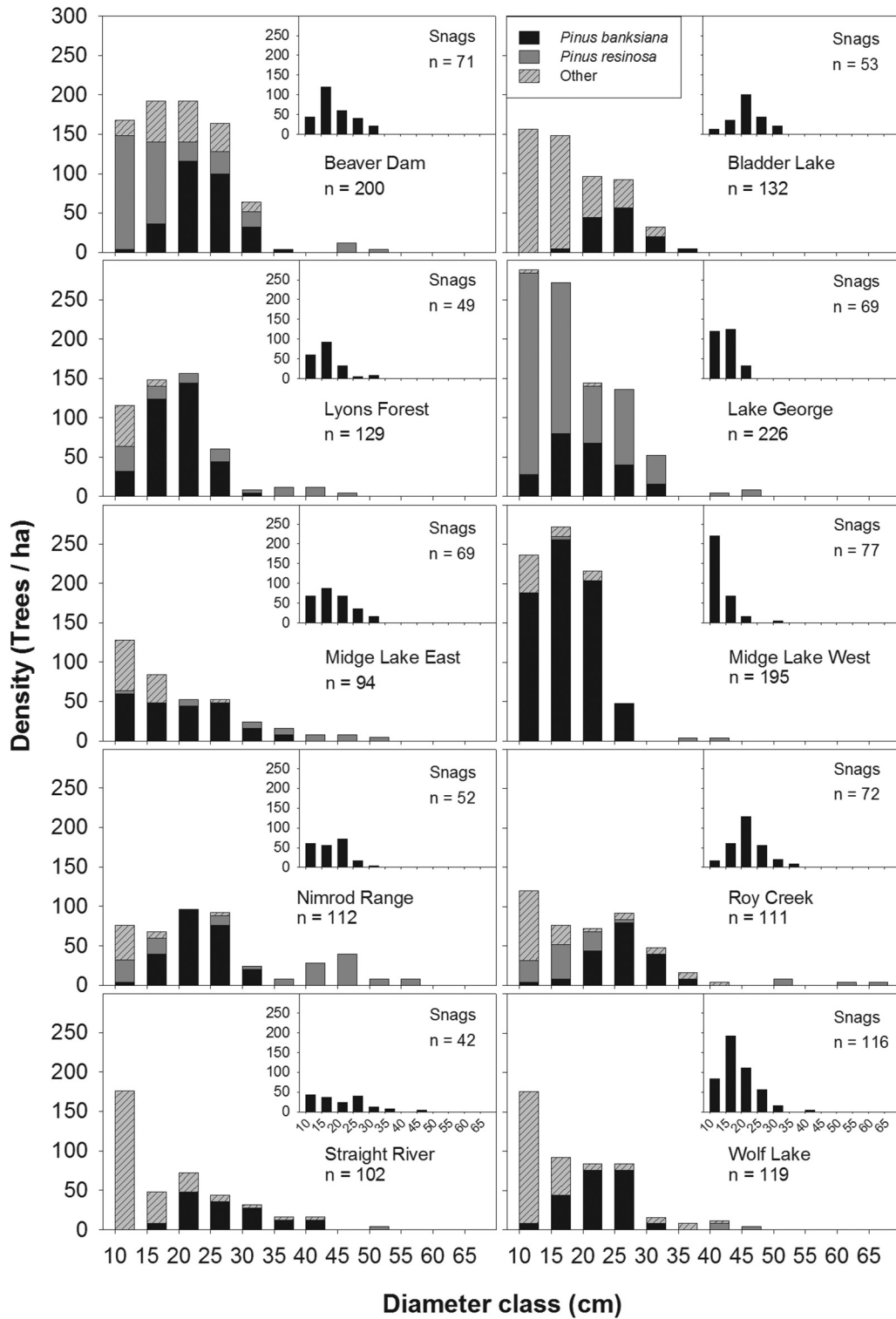

aged jack pine cohort. However, the cause of this event was unclear. The fires documented at Lake George and Roy Creek do not appear to have fostered recruitment (Fig. 3). Some sites showed evidence of a July 2012 regional windstorm, as demonstrated by the high percentage of recent DWD at many sites (Appendix Fig. A1). Additionally, abrupt periods of near zero growth in jack pines (see below) may suggest past intermediate disturbances by

wind or insects that could be contributing to jack pine mortality, although there was no observed linkage with jack pine recruitment.

Site-level mean jack pine growth (Fig. 3, black lines) generally followed a gradually declining pattern, yet growth releases and irregular and parabolic growth patterns were also observed. Most notably, jack pine individuals at Midge Lake West that recruited

Fig. 3. Age distributions (bars) and standardized radial growth indices (lines) for 10 range-margin jack pine sites. Ages are grouped into 5-year classes. Triangles indicate fire-scar dates. Growth indices are shown for each site where *n* ≥ 10 for jack pine (*Pinus banksiana*, black line), and if criteria were met (see Methods), a second species (grey line) was also shown, which was most often red pine (*Pinus resinosa*) but was paper birch (*Betula papyrifera*) at Bladder Lake.
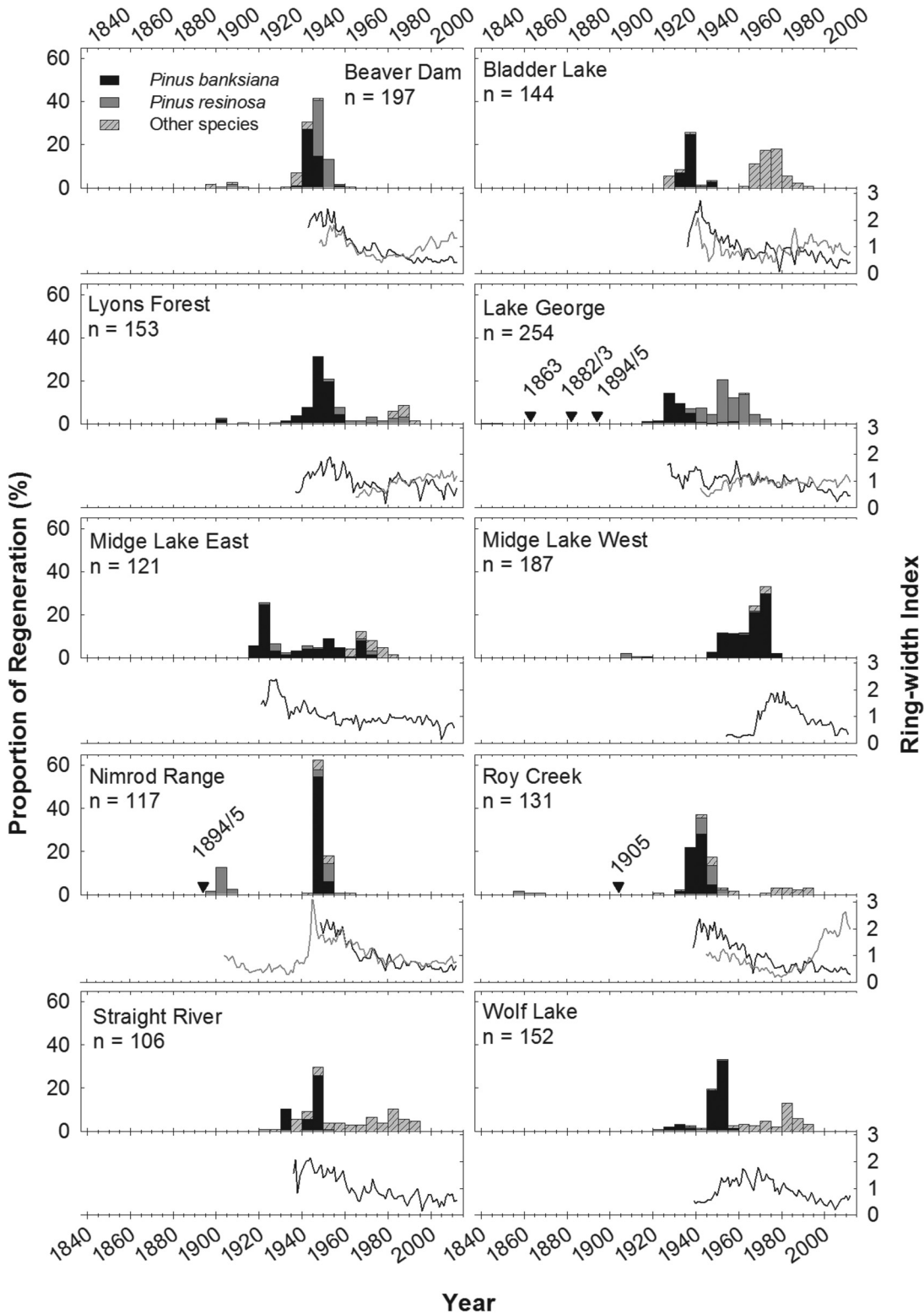
Fig. 4. Jack pine recruitment windows at 10 range-margin jack pine sites. Black dots represent recruitment of at least one individual in a given year at a given site. Recruitment windows (black-lined rectangle) mark the 5th and 95th percentiles of year of recruitment to enclose the middle 90% of recruited trees. The total window length (years) is listed in parentheses beside the site code (code definitions found in Table 1). The threshold for designating sites as even or uneven aged (above or below the grey line, respectively) was 15 years (see Methods). Year of recruitment at each site was standardized by its median year of recruitment for display.
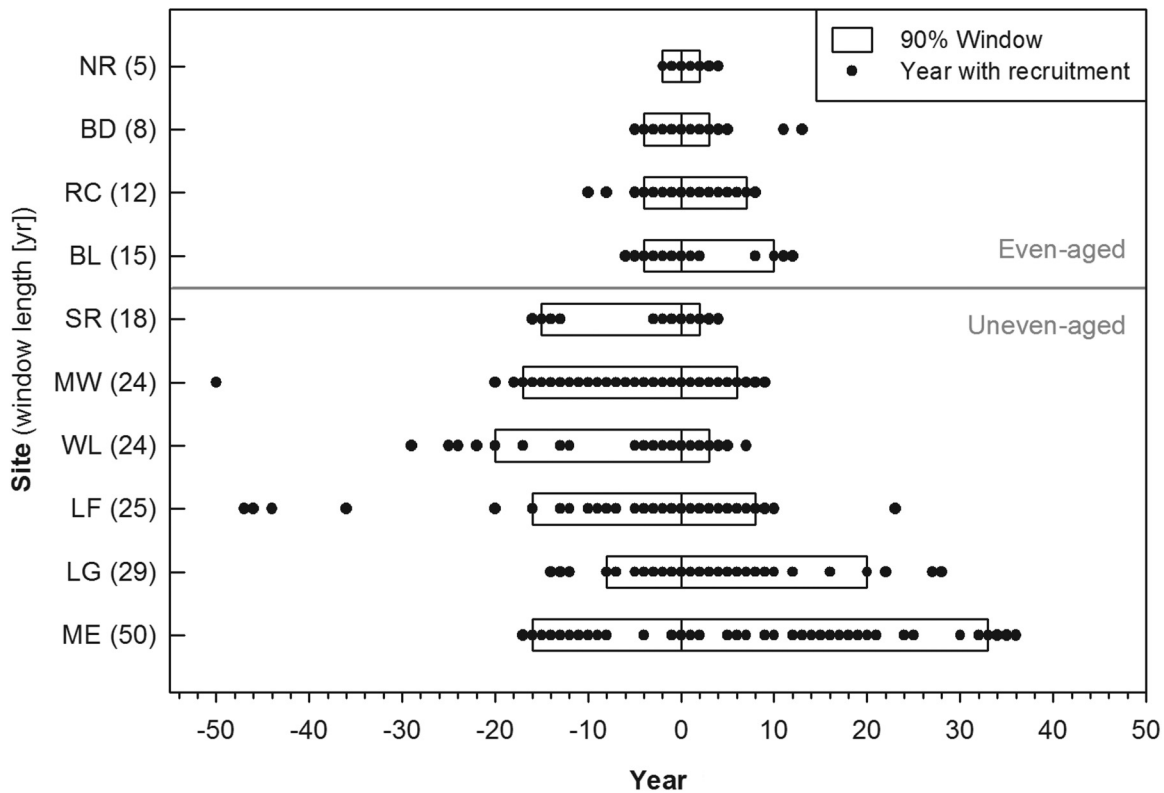
prior to 1967, roughly 35% of total recruitment, showed a period of up to 20 years of suppressed growth followed by an abrupt and sustained growth increase beginning around 1967 (Fig. 3). Concurrent with this release, a new jack pine cohort recruited, individuals of which followed gradually declining growth patterns. Mean growth curves for jack pine also showed years with sharply reduced ring width or nearly zero growth (Fig. 3, black lines; e.g., 1979 at Bladder Lake and Lyons Forest); however, other important species did not show concurrent growth reductions (Fig. 3, grey lines). In fact, these species tended to maintain or increase in growth as stand-wide jack pine growth declined later in stand development (Fig. 3; e.g., Roy Creek, grey line).

Spatial patterning

Analyses of the spatial arrangement of jack pine stems demonstrated significant deviations from complete spatial randomness (CSR) at half of the sites where tree age was not considered and all four sites where tree age was considered. When different from CSR, stems (living stems plus snags) were most often clumped. This was the case at various distances, primarily between 2 and 8 m (Fig. 5; Nimrod Range, Lake George, Beaver Dam, Straight River, and Midge Lake West); Nimrod Range also indicated clumping at larger distances (Fig. 5). Both the older and younger groups of trees at sites with protracted recruitment demonstrated significant clumping. This was evident at many distances in the older age group at all four sites (Fig. 6) and primarily between 2 and 8 m in the younger group at three of four sites (Fig. 6; Lyons Forest, Lake George, and Midge Lake East). At these three sites, the stems

of the age groups were generally segregated spatially (Fig. 7); however, groups at Midge Lake West, where the spatial arrangements were rarely different from CSR, were generally more interspersed (Fig. 7).

Discussion

Collectively, our results indicate that jack pine dominated systems in this region can be structurally complex and may follow a wide range of stand development pathways to maturity, i.e., these systems do not only follow the conventional single-cohort pathway typically expected (Gauthier et al. 1993). The abundance or heterogeneity of structural metrics employed (i.e., tree age, spatial arrangement, deadwood) suggest levels of structural complexity at some sites more often associated with late-successional forests (Donato et al. 2012; Franklin et al. 2002) and further underscore the diversity of postdisturbance stand development pathways for early successional systems (Nyland 1998; Swanson et al. 2011). Moreover, the ability of these systems to progress along various developmental and successional pathways suggests the potential for inherent range-margin system adaptability and resiliency and argues for the use of an equally diverse range of management approaches (D'Amato et al. 2011; Puettmann 2011).

Stand composition, structure, and development

Our results show the current abundance and stature of jack pine and associated tree species to be within the ranges of earlier descriptions of these communities in this region (e.g., Spurr 1954). Basal areas and tree densities were on the low end of, or sometimes below, ranges reported from other naturally regenerated jack pine stands (e.g., Schoenike 1976) and recommended in

Fig. 5. Spatial distribution of all living and snag jack pine trees (stems pooled) at each site as a function of distance r. The solid line displays the observed value (g_{obs}) for a given distance, the dashed line displays the theoretical value (g_{theo}) for complete spatial randomness (CSR), and the grey shaded area is a 95% significance band of CSR produced by 499 Monte Carlo simulations. Observed values above or below this band are indicative of clumping or uniformity, respectively. Figure provided in colour online.
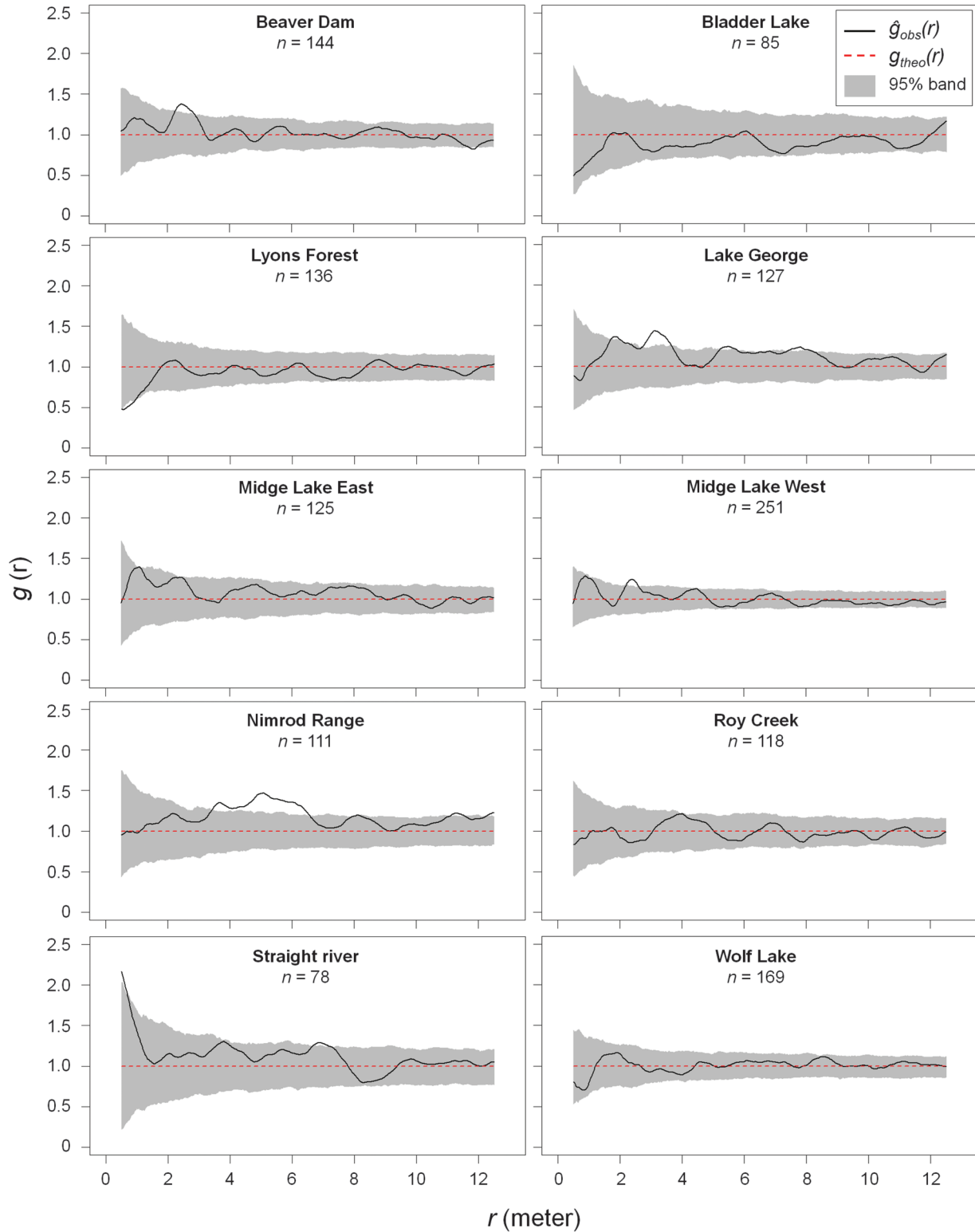
Fig. 6. Spatial distribution as a function of distance (r) of two age groups at four sites that had protracted and continuous recruitment. "Older" and "younger" age groups were separated at the median tree age (older > median ≥ younger). For each, the solid line displays the observed value (g_{obs}) for a given distance, the dashed line displays the theoretical value (g_{theo}) for complete spatial randomness (CSR), and the grey shaded area is a 95% significance band of CSR produced by 499 Monte Carlo simulations. Observed values above or below this band are indicative of clumping (which is observed at many distances in both age groups) or uniformity, respectively. Figure provided in colour online.
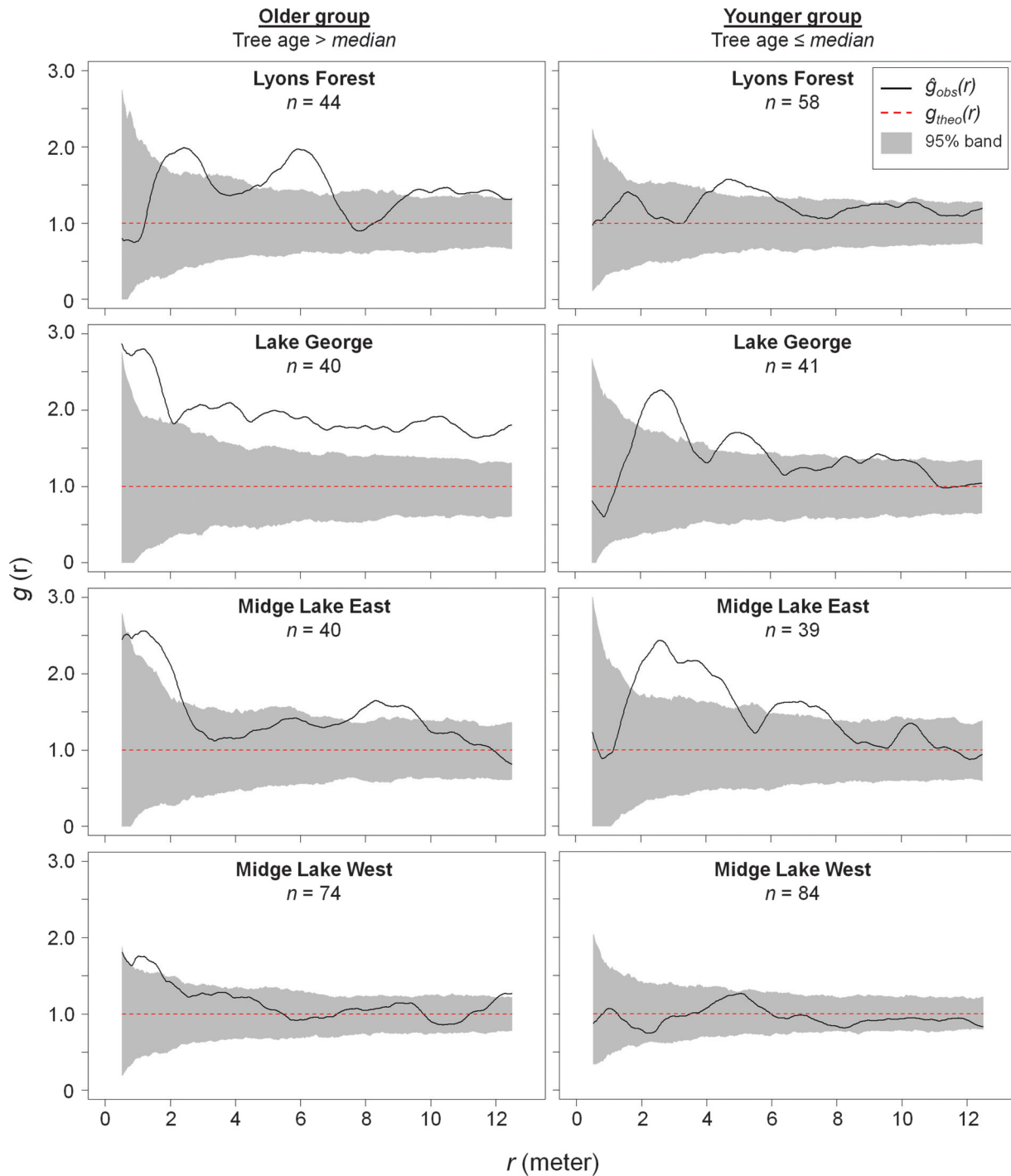
management guides (e.g., Archibald and Bowling 1995), further highlighting the range-wide variation in jack pine systems (Schoenike 1976). This finding, together with the clumped spatial distributions, reflect the heterogeneous and interrupted canopies observed at some sites (Fig. 8). The variation in live-tree size distributions and canopy structures also reflects the diversity of age structures observed.

Early successional forests adapted to develop following stand-replacing disturbance are generally expected to display strongly even-aged populations, short recruitment windows, and high initial stand densities (Oliver and Larson 1996). Several sites that we examined displayed such characteristics (Nimrod Range, Beaver Dam, and Roy Creek), although the remnant red pine cohorts suggest that stand-initiating disturbances were not lethal to all

Fig. 7. Jack pine tree locations for four sites that had protracted and continuous recruitment windows and sufficient sample sizes for spatial analyses by age group. For each site, jack pine trees are separated into older (black circles) and younger (light grey circles) age groups based on the median tree age (older > median ≥ younger). For display, icons are sized to reflect intrasite relative diameter at breast height (DBH, 1.37 m); see Fig. 2 for actual DBH ranges at each site. See Fig. 6 for results of spatial pattern analyses.
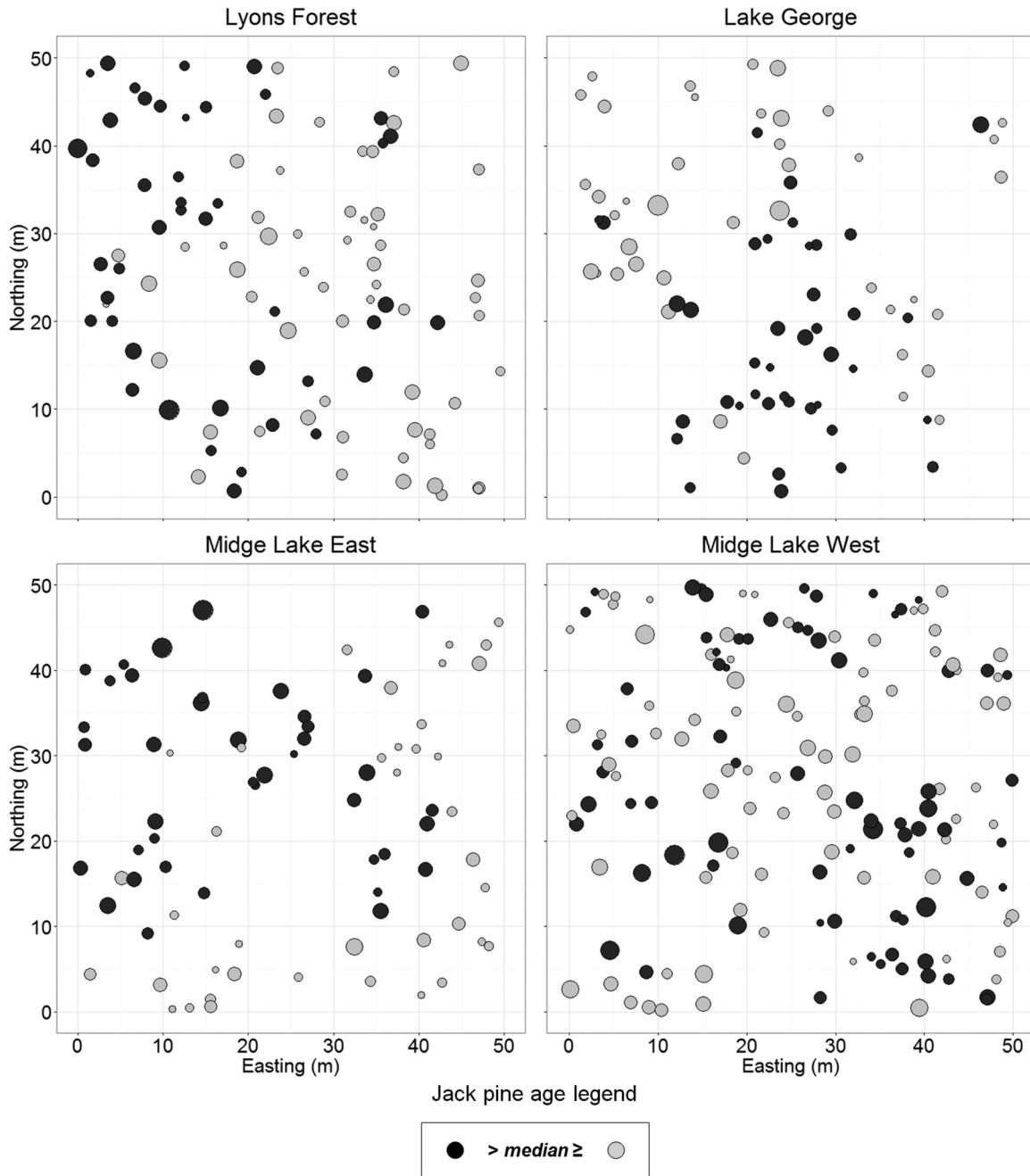
individuals in the predisturbance forest. However, the jack pine age structures more often observed in our study — even where initial stand conditions appear to have been relatively open — indicated protracted recruitment windows (up to 50 years) that are much longer than typically expected. Protracted stand initiation stages have elsewhere been observed in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests of the Pacific Northwest, USA (Freund et al. 2014), as well as montane lodgepole pine (*Pinus contorta* var. *latifolia* (Engelm. ex S. Watson) Critchfield) forests (Kashian et al. 2005; Nyland 1998). These findings have called into question previous notions of ubiquitous rapid, postdisturbance recruitment for these species and suggests that a postdisturbance open

period with spatially heterogeneous seedling establishment might be a typical early successional condition (Swanson et al. 2011).

The protracted recruitment found in our study may have been caused by low initial stand densities and subsequent infilling of new recruits (Nyland 1998). Although density dependent, age-related, and agent-based mortality likely reduced stand densities over time, the observed age and spatial structures, as well as rapid early growth rates (Fig. 3), suggest that stand conditions at initiation were often open and densities were relatively low. These conditions have been shown for this species after abandoned land-conversion attempts (Thomson 1943) and following high-severity fires (Pinno et al. 2013). The observed heterogeneous spa-

Fig. 8. Photo of the *Pinus banksiana* forest at the Lyons Forest study site showing an interrupted low-density canopy, stem clumping (background left), and a range of diameter and canopy sizes in *P. banksiana* (three foreground stems, as well as others with scaly bark). Patchy understory clumps of *Corylus americana* (middle-ground right) are also evident on this site of medium moisture and nutrient quality. The jack pine recruitment window was 30 years. Figure provided in colour online. (Photo by K.G. Gill.)

tial patterns of protracted recruitment suggest that soil and light conditions favorable for germination varied across space and time. Presumably, precocious seed production and dispersal (as early as 5–10 years; Burns and Honkala 1990) and nonserotinous cones at maturity (Schoenike 1976) are expected to have allowed for this spatially and temporally complex pathway (Nyland 1998). Similar opportunistic and protracted recruitment related to open or low-density canopy conditions, moderate to low competition, and minimal intermediate disturbance has been observed in other range-margin jack pine forests (e.g., Barton and Grenier 2008), as well as other early successional forests (e.g., Kashian et al. 2005).

Tree spatial arrangement and growth patterns also suggest that jack pine does not necessarily require fully open conditions for establishment. Spatial patterns in several stands revealed heterogeneous spatial patterns and clumping of stems recruited in sizeable gaps between pre-established trees. This is best demonstrated in the younger group of recruitment at Midge Lake East (Fig. 7, grey circles) and in the even-aged jack pines at Nimrod Range (Appendix Fig. A2, circles). Clumping of conifers has been shown in numerous previous studies and attributed to interspecies repulsion (Beland et al. 2003) or heterogeneous canopy conditions and microsite availability following disturbances (Larson and Churchill 2012; Platt et al. 1988). Both of these likely contributed to the complex spatial structures and establishment patterns observed in this study. The 20 years of recruitment, supression, and eventual release of jack pines at Midge Lake West — establishment and growth patterns that have rarely been observed for this species (Copenheaver and Abrams 2003) — provides additional evidence of this species' unexpected ability to establish and persist through patchy and, potentially, suppressive conditions.

Disturbance effects on stand development and succession

Fire is often put forth as the primary disturbance agent shaping the development of jack pine stands (Gauthier et al. 1993), and its importance is generally manifest during stand initiation (Pinno et al. 2013) due to the preparation of a mineral soil seedbed and release of seeds from serotinous cones. Previous work documenting multi-cohort jack and red pine populations have indicated that surface fires are important for recruiting additional cohorts

over the course of stand development (Bergeron and Brisson 1990; Fraver and Palik 2012; Gauthier et al. 1993), as is the case for pines in other regions (e.g., Platt et al. 1988). We found little direct evidence linking the observed even- and uneven-aged establishment to fires, although physical records of surface fires do not always occur or persist (Piha et al. 2013). However, given the demonstrated positive link between fire frequency and serotiny (Gauthier et al. 1996), the historical occurrence of surface fires in the region can be inferred from the low levels of cone serotiny present (Schoenike 1976). Additionally, age structures displaying clear cohort recruitment, rather than low levels of extended recruitment, may be indicative of past surface fires. If so, the later cohorts at Straight River and Wolf Lake (Figs. 3 and 4) may have been generated by surface fires that left no physical evidence other than age structures. However, the continuous protracted recruitment periods observed (e.g., Midge Lake East, Fig. 3) are more likely related to heterogeneous low-density initial postdisturbance recruitment (Nyland 1998) combined with disturbance quiescence (sensu Brown 2006) or, potentially, to insect or wind disturbances (Svoboda et al. 2010).

A variety of biotic and abiotic disturbance agents have affected the observed structural conditions but their linkages with stand decadence are more clear than those of stand establishment. Although our study sites were naturally regenerated, it is likely that logging activities ca. 1900–1950 were influential. Historic photographs and rapid early growth in jack pines at some sites indicate that many initiated under relatively open growing conditions. Though we cannot determine the cause of these conditions, the broader regional land-use history suggests that they may have initiated through logging and fire disturbance, the combination of which was prevalent in the region into the 1920s before fire suppression efforts became effective (Spurr 1954), or land-conversion attempts (Thomson 1943). Insect and wind disturbances appear to be having the greatest influence on current stand structure through the creation of snags and DWD. Jack pine budworm (*Archips pinus* (Freeman)) outbreaks are known to have recurred in the study region (2012 Forest Health Annual Report, available from http://files.dnr.state.mn.us/assistance/backyard/treecare/forest_health/annualreports/2012annualReport.pdf), and synchronous decreases in growth (Fig. 3, e.g., Lyons Forest) along

with the high abundance of snags suggest that many of our sites were affected. As well, strong evidence of wind-related mortality, in the form up uprooted trees and splintered stem snaps, was also present at several sites. These and other agents of intermediate disturbance that do little to create mineral soil seedbed and light conditions conducive to pine regeneration appear instead to primarily alter stand structure in a way that promotes succession (Gilliam and Platt 1999).

Many of the jack pine stands that we sampled were succeeding away from dominance by this species. Historically, red and white (*Pinus strobus* L.) pine would be expected to increase in dominance through succession (Aaseng et al. 2003). Results from several stands (e.g., Lake George and Beaver Dam) support this successional trajectory. However, results from other stands (e.g., Bladder Lake and Straight River) suggest that fire suppression has promoted succession towards dominance by deciduous tree and shrub species. Similar trajectories have been observed following fire exclusion in other fire-adapted systems (Nowacki and Abrams 2008). Given the current challenges from competing hardwood species, high levels of herbivory, and fire suppression, pine regeneration and establishment will only occur in these systems through targeted management actions that retain seed availability, create favorable light and seedbed conditions, and protect seedlings from browse damage (White 2012). Prescribed fire has been one effective approach for promoting historical size, age, and spatial structures in pyrogenic forests that face similar biotic and abiotic pressures (e.g., Gilliam and Platt 1999).

Management implications and conclusions

The variation in compositional and structural complexity observed across our sites augments findings from jack pine forests in Indiana (Chun and Choi 2012) and Maine (Barton and Grenier 2008), USA, as well as in Ontario and Quebec, Canada (Gauthier et al. 1993). These findings support the growing body of literature addressing the complexity of postdisturbance developmental pathways — often the result of early open periods and spatially heterogeneous tree establishment (Nyland 1998) — for systems historically believed to follow a simple, single-cohort self-thinning trajectory. Other such systems include *P. contorta* forests in the western USA (e.g., Nyland 1998), *P. menziesii* communities in the Pacific Northwest, USA (Donato et al. 2012; Freund et al. 2014), and *P. sylvestris* forests in northern Europe (Kuuluvainen and Aakala 2011). Conservation and promotion of these early successional forests is critical, as their role in larger ecosystem function has only recently been appreciated (Swanson et al. 2011). Nonconventional management techniques may be required to meet these goals, particularly when the systems also face novel conditions due to their range-margin proximity.

The range of structure and developmental patterns documented in this study suggests that a variety of even- and uneven-aged silvicultural techniques can be ecologically justified to restore, manage, and promote jack pine forests of varying complexities. Our results demonstrated that a range of recruitment window lengths and initial seedling densities should be considered as a normal part of the development processes (Kashian et al. 2005). They also suggest that seed rain, whether from adjacent stands, on-site retention (Franklin et al. 2002), or precocious seedling maturity (Burns and Honkala 1990), can supplement initial tree densities over time (Nyland 1998). Thus, it is important that postharvest or postdisturbance regeneration not necessarily be considered a failure if initial stocking goals are not immediately met (e.g., 5 years). These early processes are likely to be actively or passively influenced by many factors such as cone serotiny level and associated seed availability (Lamont et al. 1991), the abundance and dispersion of suitable mineral soil seedbeds (Burns and Honkala 1990), presence and type of herbaceous competition, and the degree to which herbivory is minimized. Both multi-aged regeneration techniques (i.e., seed tree with reserves and variable retention harvesting) and even-aged systems (i.e., clearcutting and conventional seed tree), along with intermediate treatments (i.e., variable density thinning), should be used across the landscape. Using a range of techniques will promote the historical diversity of conditions by allowing within- and among-stand developmental diversity and complexity (Puettmann et al. 2009). Such a diverse management approach is also thought to increase landscape-level adaptability and resilience (Puettmann 2011), which should be the pre-eminent management goal for range-margin forests.

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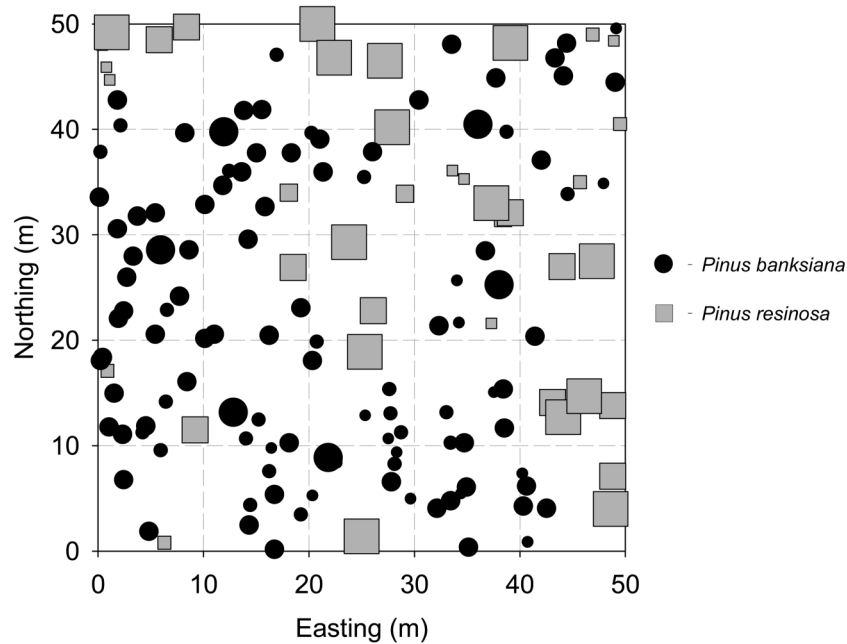
Appendix A

Figures A1 and A2 appear on the following page.

Fig. A1. Percent volume distribution of downed woody debris (DWD, N = 456 intersections) per decay class at each range-margin jack pine site. See Table 1 for full site names and Table 2 for total volume at each site.
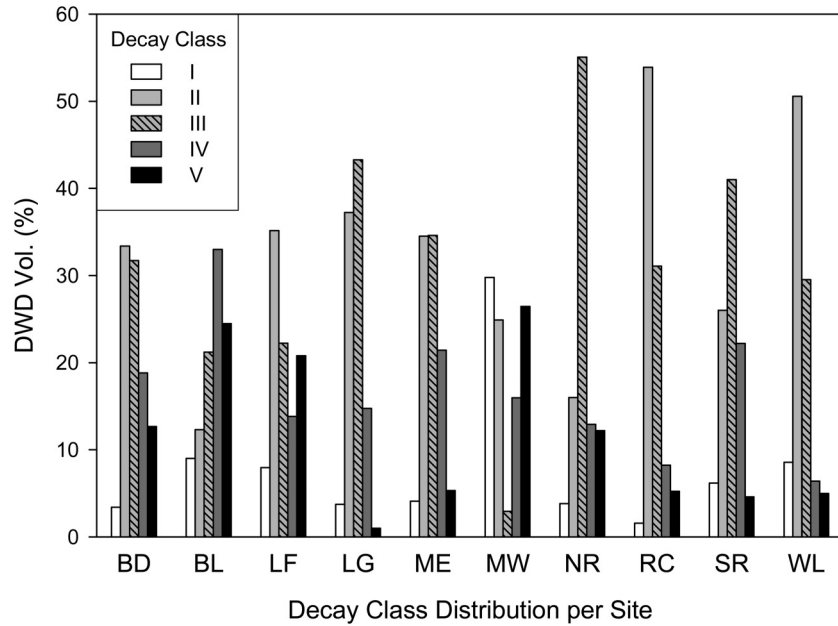
Fig. A2. Tree locations at Nimrod Range showing even-aged jack pine (*Pinus banksiana*) trees (black circles) spatially aggregated between red pine (*Pinus resinosa*) trees (grey squares), most of which were around 50 years old at the time of jack pine recruitment (see Fig. 3). Jack pine stems were clumped at distances between 3.5 and 7 m (see Fig. 5), and red pine stems were clumped at distances between 1 and 3 m (results not shown). The icons are sized to reflect relative diameter at breast height (DBH, 1.37 m); see Fig. 2 for DBH distribution.