Ecological Modelling 519 (2026) 111620

Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel

Evaluating an individual-based model's ability to reproduce fine-scale spatial structure in boreal mixed forests

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ARTICLE INFO

Keywords:
Simulation
Modelling
Disturbance
Spatial structure
Fine scale
Spatial pattern
Boreal

ABSTRACT

Process-based forest models are increasingly used to guide management, but few are validated against fine-scale spatial patterns that emerge from neighborhood interactions. We tested whether the spatially explicit individual-based model SORTIE-ND, which simulates growth, mortality, and recruitment as functions of neighbourhood interactions among individual trees, can reproduce observed fine-scale structure in boreal mixedwoods. Using long-term data from the Lake Duparquet Research and Teaching Forest (Québec) station, we initialized simulations from transect plots representing younger post-fire stands and compared simulated outcomes to independent hectare plots of similar ages along a 249-year chronosequence. The spatial structure was quantified with inhomogeneous L-functions for univariate and bivariate patterns, and model performance was assessed by comparing observed curves to simulation envelopes. SORTIE-ND reproduced fine-scale patterns for balsam fir and trembling aspen, showed partial agreement for white spruce, and failed to match the observed clustering of paper birch. Cross-species patterns were captured for fir–aspen but not for pairs involving white spruce. These results indicate that SORTIE-ND can approximate fine-scale spatial patterns for dominant species in boreal mixedwoods, but limitations remain where key processes (e.g., vegetative propagation, substrate dependence) are under-represented. We discuss implications for stand- to landscape-scale management and recommend model extensions and more independent validation to improve generality.

1. Introduction

The spatial configuration of trees at fine scales shapes individual growth, survival, and recruitment, and cumulatively influences stand composition and structure (Wiegand and Moloney, 2014). Tree spacing alters diffuse light and neighbourhood interactions, affecting regeneration and the development of complex vegetation structure (Canham et al., 2004; Kim et al., 2025). In boreal mixedwoods, this fine-scale structure interacts with recurrent disturbances - especially fire and insect outbreaks - which strongly influence productivity and succession (Yataco et al., 2024; Labrecque-Foy et al., 2025). Under climate change, several disturbance regimes are expected to intensify, with implications for regeneration failure and stand composition (Attiwill, 1994; Bergeron et al., 2001; Carrer et al., 2018; Liu et al., 2019; Pureswaran et al., 2015). Gap dynamics are central to these processes as canopy openings favour shade-intolerant species such as trembling aspen (*Populus tremuloides*), whereas smaller gaps can promote balsam fir (*Abies balsamea*); gap number and size influence sapling density and understory composition (Kneeshaw and Bergeron, 1998, 1999; Kneeshaw and Prévost, 2007; de Römer et al., 2007).

Spatial point-pattern statistics offer a rigorous lens to quantify these structures. Summary functions such as Ripley's K, the inhomogeneous L, and the pair-correlation function describe clustering or overdispersion across distances relative to appropriate null models, and inhomogeneous forms control for large-scale intensity gradients to isolate neighbourhood processes (Ripley, 1981; Wiegand and Moloney, 2014; Law et al., 2009; Baddeley et al., 2005, 2015).

SORTIE-ND is a spatially explicit, individual-based model that represents growth, mortality, and recruitment through neighbourhood competition and gap dynamics, with process parameters derived from

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https://doi.org/10.1016/j.ecolmodel.2026.111620
Received 19 September 2025; Received in revised form 11 February 2026; Accepted 20 April 2026
Available online 14 May 2026

field data (Pacala et al., 1996; Busing and Mailly, 2004). It has been widely applied to examine succession, silviculture, and disturbance scenarios- including partial harvesting and post-disturbance trajectories - and in combination with climate scenarios (Ameztegui et al., 2012; Beaudet et al., 2011; Bose et al., 2015; Brown et al., 2018; Yasuda et al., 2013; Dhar and Hawkins, 2011; Maleki et al., 2021a; Ameztegui et al., 2015, 2017). However, while the ability of SORTIE-ND to predict overall composition and biomass has been validated in several systems, its ability to reproduce the observed fine-scale spatial structure - within species and between species - has not been evaluated, limiting confidence for gap-based management and spacing prescriptions. Most prior validations of SORTIE-ND have focused on non-spatial attributes such as species composition, biomass, and basal area (e.g., Beaudet et al., 2011; Bose et al., 2015; Maleki et al., 2020). Our study therefore complements this work by evaluating the model's capacity to reproduce fine-scale spatial patterns, which is a central feature of neighbourhood-based individual-tree models.

Here we test whether SORTIE-ND can recover the observed fine-scale spatial structure of 1-ha forest plots in a boreal mixedwoods. Using a post-fire chronosequence, we initialize simulations to match the species composition and size structure of younger stands (based on time since last fire), run the simulations for a sufficient time to match the age of the older stands, then compare the spatial structure of the simulated stands to the observed older stands. Spatial structure is quantified with inhomogeneous L-functions for univariate (within-species) and bivariate (between-species) patterns to isolate interaction signals from intensity gradients (Law et al., 2009; Baddeley et al., 2005, 2015). Thus, we aim to understand whether SORTIE-ND can reproduce within and between species spatial structure.

2. Methodology

2.1. Study site

We worked in the Lake Duparquet Research and Teaching Forest (LDRTF) station, northwestern Québec, Canada, within the balsam fir (*Abies balsamea*)–white birch (*Betula papyrifera*) bioclimatic domain (Ministère des Forêts, de la Faune et des Parcs, 2021). The LDRTF spans ~8000 ha (Fig. 1) and has a cold continental climate (mean annual temperature ~1 °C; mean annual precipitation ~985 mm, ~30 % during the growing season). Forests are mixed stands of boreal conifers - balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), and eastern white cedar (*Thuja occidentalis*) - and shade-intolerant hardwoods - trembling aspen (*Populus tremuloides*) and white birch (*Betula papyrifera*) (Bergeron, 2000). Early successional stands are typically dominated by aspen and birch, whereas fir and white cedar increase in later stages. Wildfires and insect outbreaks are the dominant natural disturbances; a major spruce budworm (*Choristoneura fumiferana*) outbreak occurred from 1972 to 1987 (Bergeron et al., 1995; Morin and Laprise, 1993, 2001).

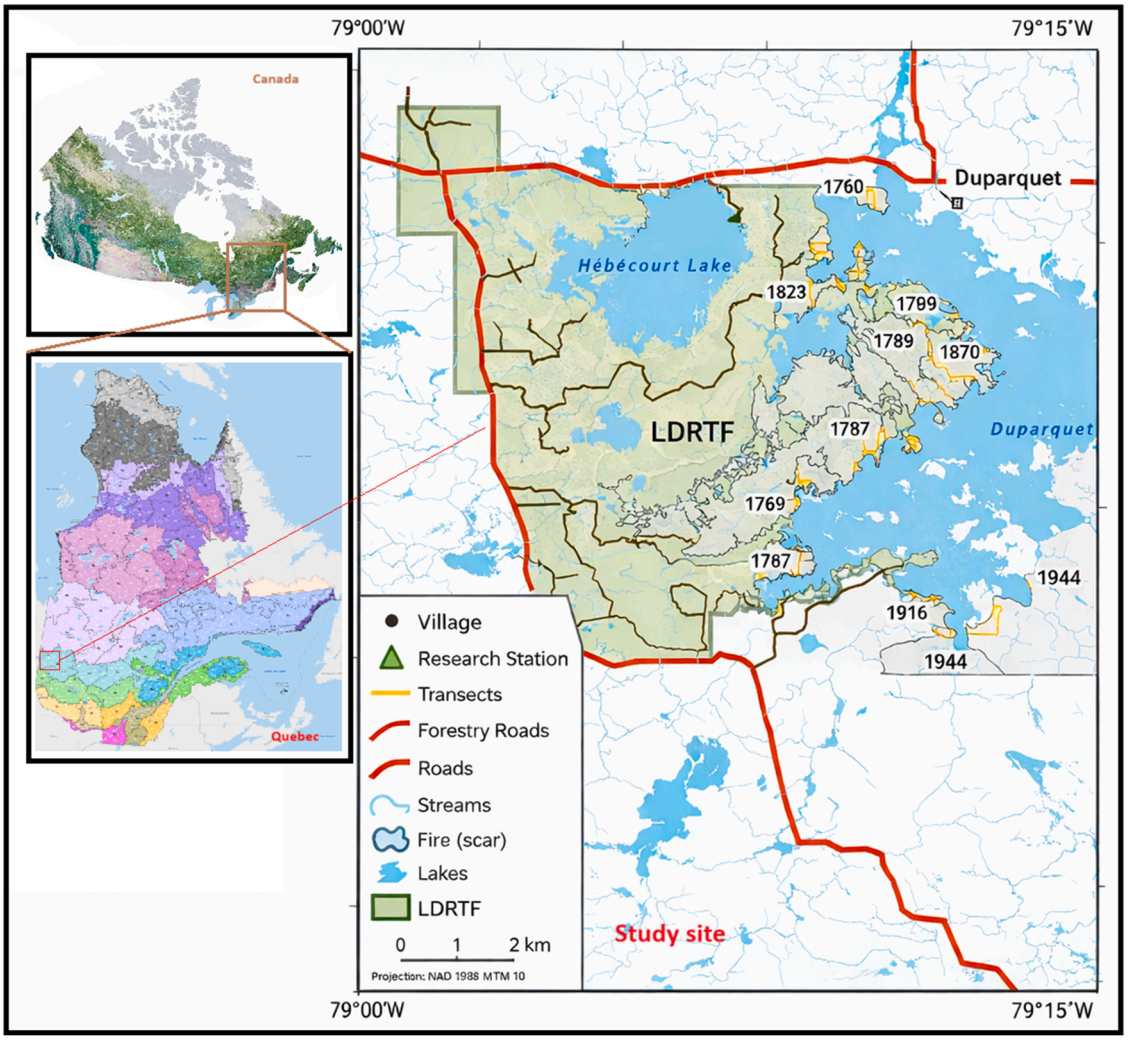

Fig. 1. Lake Duparquet Research and Teaching Forest station.

2.2. Sampling protocol

We used inventories conducted between 1990 and 2019 across the LDRTF, focusing on two datasets (Maleki et al., 2021b):

LDRTF-TRANSECT: 596 square plots (256 m^2; 16 m × 16 m) spaced at 50 m intervals along transects that sample different successional stages regenerated after eight fires (1760, 1797, 1823, 1847, 1870, 1916, 1944, 1964). In each plot, all trees with DBH ≥ 5 cm were identified (species), status recorded (live/dead) and measured. These plots were sampled in 1991 and re-sampled in 2009 and were used to develop the SORTIE-ND parameter file for the LDRTF.
LDRTF-HECTARE: Six permanent 1-ha plots established in stands representing fire years 1760, 1823, 1847, 1870, 1916, and 1944. Sites were selected to be representative of the average compositions observed in the transects. All living and dead trees (standing and down) with DBH ≥ 5 cm were measured, identified to species, and mapped in X–Y coordinates. Stand-level compositional changes were validated dendrochronologically (Bergeron and Charron, 1994; Bergeron and Dubue, 1988).

A summary of transect stand ages and basal areas at the 1991 measurement is provided in Table 1.

2.3. SORTIE-ND simulation

We used SORTIE-ND, an individual-based, spatially explicit model of stand dynamics (Murphy, 2011; Pacala et al., 1996; Busing and Mailly, 2004). The model represents trees as points with size and state variables whose growth, mortality, and recruitment are functions of local neighbourhood conditions (e.g., light competition) and dispersal. Process sub-models include tree allometry, light availability, growth, mortality, and recruitment (Bose et al., 2015). For the LDRTF, a parameter file has been developed and refined (Poulin and Messier, 2008; Bose et al., 2015), improving model behaviour for major species of the Eastern Canadian mixed boreal forest: balsam fir (*A. balsamea*), trembling aspen (*P. tremuloides*), jack pine (*Pinus banksiana*), white birch (*B. papyrifera*), white spruce (*P. glauca*), eastern white cedar (*T. occidentalis*), and mountain maple (*Acer spicatum*).

Initialization and run settings. Simulations were run on 100 m × 100 m plots (matching the hectare plot extent) with a 1-year time step. All parameters followed Maleki et al., 2020. For each run, initial tree lists were created from the LDRTF-TRANSECT species-by-DBH composition (density of stems by species and DBH class) for a given fire cohort, with stems positioned at random within the plot for the baseline design. This upscaling from 16 × 16 m transect plots to the 1-ha simulation extent removes any fine-scale spatial structure present in the initial conditions. This was necessary to generate several independent initializations per fire cohort. Randomizing tree positions at the hectare scale removes any inherited fine-scale structure from the initial datasets. This makes our validation intentionally conservative: SORTIE-ND must generate spatial structure de novo through its neighbourhood processes. Any observed mismatch therefore reflects missing or simplified mechanisms in the model rather than initial-state artefacts.

Chronosequence pairing and duration (T): For each comparison, we simulated T years, where T equals the difference in time-since-fire between an "initial" transect cohort and a "final" hectare plot to which it was compared (Table 2). Hectare plots from fire years 1823, 1847, and 1870 served as final stands because they represent mixed successional stages with diverse species assemblages. Transect cohorts from 1847, 1870, and 1916 provided initial conditions. We excluded the 1760 cohort (cedar-dominated) and the most recent cohorts (1944, 1964) where conifers were nearly absent.

2.4. Spatial pattern analysis

We focused on the four most abundant species across cohorts - *Abies balsamea, Populus tremuloides, Betula papyrifera*, and *Picea glauca* - to ensure adequate sample sizes (Table 3). To obtain stable estimates, we required ≥ 100 adult trees of a species in a hectare plot to include it in analysis. For each simulated–observed comparison, we retained only simulations with at least as many individuals as the corresponding hectare for the focal species (or species pair). This is necessary in order to match the number of trees for spatial pattern analyses, as described further below.

We quantified spatial structure with the inhomogeneous L-function, the square-root transform of the inhomogeneous K-function, for both univariate (within-species) and bivariate (cross-type) patterns (Ripley, 1981; Law et al., 2009; Baddeley et al., 2005, 2015). Inhomogeneous forms standardize by local density (estimated with a Gaussian kernel), thereby separating small-scale interaction signals from large-scale

Table 2
Matrix of simulation timesteps for different combination of initial and final stand age.

	Observation for model verification	Hectare Fire Years	1823	1847	1870
Observation for model initialization		Stand age at measure year (2011)	188	164	141
Transect Fire years	Stand age at measure year (1991)				
1847	144		T = 44		
1870	121		T = 67	T = 43	
1916	75		T = 113	T = 89	T = 66

Table 1
Spatial distribution of sampling plots in the Lake Duparquet Research and Teaching Forest (LDRTF) station.

Fire year	Stand age (years)	Number of transects	Plot counts	Mean basal area (m^2ha^{-1}) of standing live trees				
				ABA	BPA	PGL	PTR	TOC
1823	168	5	66	4.32	3.88	2.46	8.03	0.53
1847	144	4	74	6.84	4.62	5.40	11.88	0.77
1870	121	6	64	3.46	5.86	4.46	12.78	0.02
1916	75	3	52	4.54	7.63	1.99	16.74	0.97
1944	47	4	71	3.81	9.34	0.81	11.57	0.22

Abbreviations:
ABA= *Abies balsamea*.
BPA= *Betula papyrifera*.
PGL= *Picea glauca*.
PTR= *Populus tremuloides*.
TOC= *Thuja occidentalis*.

Table 3
Number of trees (DBH ≥ 5 cm) per stand across fire years.

Fire Year	ABA	BPA	PGL	PTR
1870	72	115	226	243
1847	298	43	127	162
1823	194	22	61	208

density gradients. We used a Gaussian kernel with σ = 10 m for intensity estimation and analysed distances up to 10 m, which corresponds to the neighbourhood scale at which we expect competitive effects in mixed forests, and matches the neighbourhood radius used to calculate crowding effects in our SORTIE-ND parameterization (Canham et al., 2004).

This choice of spatial scales also supports the use of the inhomogeneous L-function in our analysis**.** By focusing on distances up to 10 m, we restrict the comparison to the neighbourhood scale at which competitive interactions operate in SORTIE-ND. At the same time, the Gaussian kernel used for intensity estimation (σ = 10 m) captures broader density gradients operating at scales larger than the interaction radius. This combination ensures that the inhomogeneous L-function isolates fine-scale interaction patterns while appropriately accounting for larger-scale variation in tree density. As a result, the method enables a valid comparison of fine-scale spatial structure between simulated and observed stands, even when their broader-scale intensity patterns differ.

The use of an inhomogeneous L-function also resolves any apparent inconsistency between complete spatial randomness (CSR) initialization and subsequent analysis. CSR removes only pre-existing fine-scale structure from the initial conditions, while the inhomogeneous estimator adjusts for larger-scale intensity gradients that develop during simulations. Thus, fine-scale neighbourhood interactions can still be validly compared between observed and simulated stands.

Although simulations were initialized under CSR, this does not conflict with our use of the inhomogeneous estimator. The σ = 10 m kernel bandwidth is larger than the 0–10 m interaction scale, allowing fine-scale patterns to be compared even when broader-scale intensity gradients differ. Thus, the statistical properties of the inhomogeneous estimator remain valid under our initialization design.

With these considerations in place, we next outline the statistical functions used to evalute spatial structure. We quantified spatial structure using Ripley's K(r), which is the cumulative expected number of neighbors within distance of an arbitrary individual, scaled by intensity; under CSR with constant density λ, the theoretical $K(r)=\pi r^2$ (Ripley 1981). We then used the variance-stabilized transformation $L(r) = K(r)/\pi$, which is especially convenient because CSR corresponds to a straight line $L(r) = r$; departures of L(r) - r above or below zero indicate clustering or inhibition, respectively (Ripley 1981). Because tree density varies across each plot, we employed the inhomogeneous versions $K_{inhom}(r)$ and $L_{inhom}(r)$, which reweight by the spatially varying intensity to separate small-scale interaction signals from larger-scale density gradients (Baddeley et al., 2005; Law et al., 2009; Baddeley et al., 2015). To ensure comparability, we matched the number of individuals by randomly subsampling simulated trees when more trees of that species were present in the simulation than in the observed hectare; we verified via additional calculations that this subsampling does not bias L(r) under homogeneity and kept the same procedure for inhomogeneous summaries to maintain a common workflow. We report whether the observed L(r) lies within the envelope across distances as an indicator of agreement. Simulation envelopes represent the minimum and maximum values of the inhomogeneous L-function at each distance r across all simulation runs. These envelopes describe the full range of spatial pattern variation produced by SORTIE-ND for each species–stand comparison and are used descriptively to assess whether the observed pattern falls within the variability generated by the model. All point-pattern analyses were performed in R (v4.0.2) with the spatstat family of packages (Baddeley and Turner, 2005).

3. Results

Species densities differed among hectare plots across fire years (Table 3). Trembling aspen (*Populus tremuloides*) was most abundant in the 1870 and 1823 hectares, whereas balsam fir (*Abies balsamea*) dominated the 1847 hectare. To ensure stable point-pattern estimates, we analysed only species with ≥ 100 adult trees per hectare. Consequently, balsam fir was excluded from the 1870 hectare, white spruce (*Picea glauca*) from the 1823 hectare, and paper birch (*Betula papyrifera*) from the 1823 and 1847 hectares.

Figs. 2–4 compare observed and simulated spatial patterns using L-functions. In each panel, the dashed line denotes complete spatial randomness (CSR). Values above/below CSR indicate clustering/repulsion at a given distance. Model–data agreement is interpreted when the observed curve lies within the simulation envelope.

3.1. Univariate (within-species) patterns

Balsam fir: Observed fir patterns showed short-distance repulsion (deficit of same-species neighbours at small r) in the 1823 and 1847 hectares, with neutral to weak aggregation at larger distances (Figs. 2–4). Simulations reproduced the short-distance inhibition for both comparisons. A modest deviation occurred for the 1847 hectare at intermediate distances when initialized from the 1870 and 1916 transects, whereas simulations based on multiple cohorts aligned more closely with the 1823 hectare.

Aspen: The 1823 hectare exhibited an approximately neutral pattern, whereas the 1847 hectare showed repulsion at intermediate distances (~5–10 m) (Figs. 2, 4). Simulations initialized from the 1870 and 1847 transects matched the neutral pattern for 1823 up to ~10 m. In contrast, simulations for the 1847 hectare (initialized from 1870) were closer to neutral than the observed repulsion, indicating a discrepancy at intermediate distances. We did not include 1916-initialized runs for aspen due to insufficient adult stems to meet the inclusion threshold.

White spruce: Observed spruce patterns were broadly neutral in both 1847 and 1870 hectares, with a slight aggregation at ~5–7 m (Figs. 3 and 4). Simulations captured the overall neutrality but did not consistently reproduce the modest peak at 5–7 m.

Paper birch: In the 1870 hectare, birch showed clustering at short distances (0–5 m) and neutrality beyond. Simulations initialized from 1916 produced a largely random pattern, failing to reproduce the observed short-range clustering (Fig. 4).

3.2. Bivariate (between-species) patterns

Across the 1823-ha window, the cross-type L function indicated clustering between balsam fir and trembling aspen, and the simulations reproduced this pattern (Figs. 2, 4). In the 1847-ha window, observations showed aggregation between balsam fir and spruce at most distances except near the origin, but this joint pattern was not reproduced by the simulations (Fig. 3). By contrast, trembling aspen and spruce exhibited largely neutral cross-type patterns, and simulations were broadly consistent with neutrality (Figs. 3, and 4).

4. Discussion

Overall, SORTIE-ND reproduced short-distance inhibition in balsam fir and the near-neutral pattern of aspen in the older hectare, partially captured the broadly neutral pattern of white spruce but missed a modest aggregation at ~5–7 m, and did not reproduce the short-range clustering of paper birch. For species pairs, agreement was strongest for fir–aspen (clustering reproduced) and weakest for pairs involving spruce (fir–spruce aggregation not reproduced; aspen–spruce largely neutral and matched). These outcomes indicate that the model captures neighbourhood processes for dominant species where interactions are primarily light-mediated but underperforms where vegetative

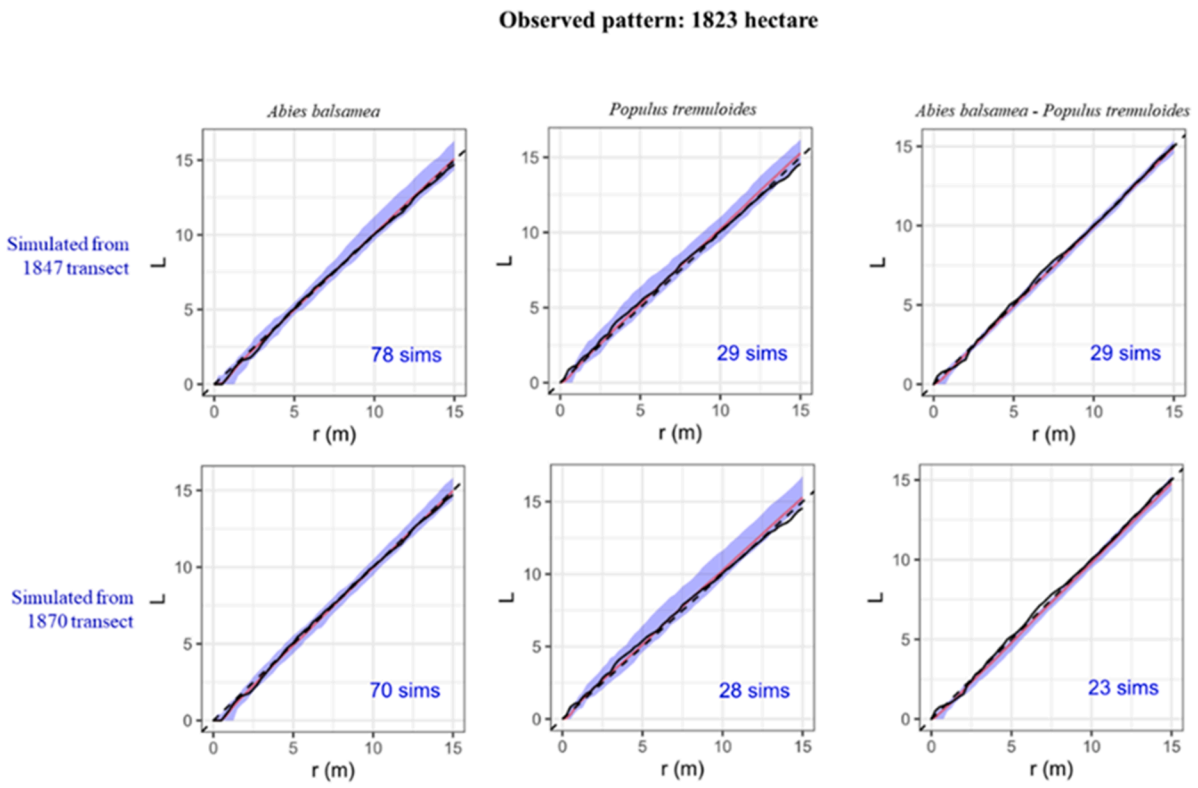

Fig. 2. Comparison between the inhomogeneous L function for the observed fire year 1823 and the homogenous L function for the simulated fire years 1847 and 1870. The black solid line is the observed pattern in the hectare plot; the red line is the mean of the simulations from SORTIEND and the blue shaded area is the range of values across all simulation runs. The black dashed line represents a neutral pattern (complete spatial randomness).

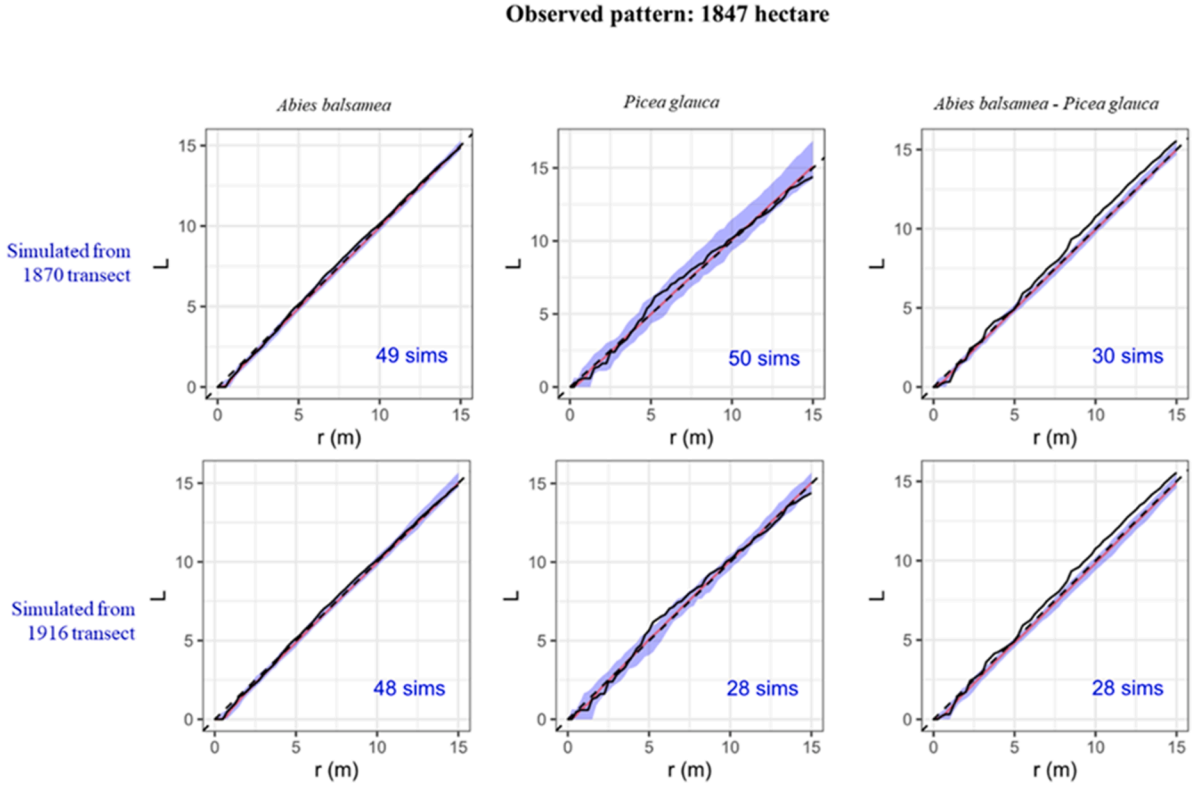

Fig. 3. Comparison between the inhomogeneous L function for the observed fire year 1847and the homogenous L function for the simulated fire years 1870 and 1916. The black solid line is the observed pattern in the hectare plot; the red line is the mean of the simulations from SORTIEND and the blue shaded area is the range of values across all simulation runs. The black dashed line represents a neutral pattern (complete spatial randomness).

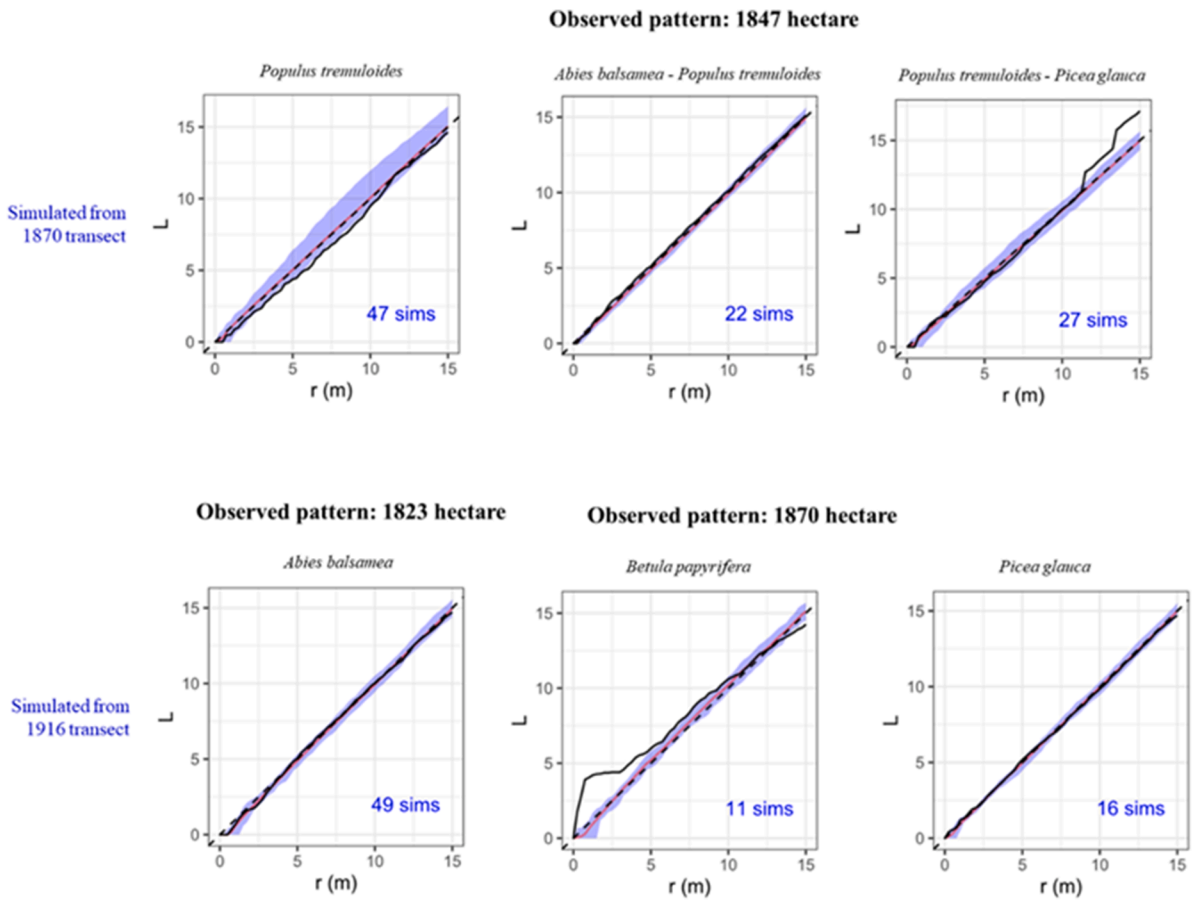

Fig. 4. Comparison between the inhomogeneous L function for the observed fire years 1823,1847, 1870 and the homogenous L function for the simulated fire years 1870 and 1916. The black solid line is the observed pattern in the hectare plot; the red line is the mean of the simulations from SORTIE-ND and the blue shaded area is the range of values across all simulation runs. The black dashed line represents a neutral pattern (complete spatial randomness).

regeneration or microsite/substrate dependence drive fine-scale structure. It is important to note that SORTIE-ND has been previously validated for non-spatial stand attributes such as composition, density, and basal area in boreal and mixedwood forests (Ameztegui et al., 2017; Beaudet et al., 2011; Bose et al., 2015; Gray and He, 2009; Maleki et al., 2021a). Our goal here was therefore not to repeat those analyses, but to evaluate fine-scale spatial structure, which has received considerably less attention despite being a defining feature of individual-based forest models. This spatial validation complements existing non-spatial assessments and highlights model processes that require refinement. Together, these considerations clarify the specific contribution of our study: evaluating whether SORTIE-ND can regenerate observed fine-scale structure under realistic but structurally simplified initial conditions.

Although several species–stand combinations exhibited patterns close to CSR, the inhomogeneous L-function allowed us to detect cases where the observed curve fell outside the simulation envelope. These deviations identify situations where key processes in SORTIE-ND are missing (e.g., clonal propagation, substrate-mediated recruitment). Therefore, similarity or disagreement between observed and simulated L-functions provides meaningful diagnostic information on model adequacy and limitations, making this approach suitable for fine-scale spatial validation. Importantly, when the observed L(r) curve lies outside the simulation envelope, this indicates that SORTIE-ND lacks one or more neighbourhood processes needed to reproduce the observed spatial pattern. This provides a direct and interpretable link between L-function similarity and model adequacy.

A further methodological limitation arises from the use of small (16 × 16 m) transect plots to construct initial stand conditions. Randomizing tree positions at the hectare scale removes any pre-fire spatial legacy, meaning that SORTIE-ND must generate fine-scale patterns de novo. This design choice was intentional: it provides a stringent evaluation of the model's capacity to reproduce observed spatial structure, but it also implies that discrepancies may reflect missing processes or initial structural features that were not reconstructed.

4.1. Balsam fir

Balsam fir (shade-tolerant) showed short-distance repulsion in both 1823 and 1847 hectares, consistent with strong intraspecific competition/self-thinning at neighbourhood scales and recruitment linked to small canopy openings. Empirical neighbourhood analyses studies show that light-mediated growth/mortality submodels can generate these patterns, aligning with our reproduced short-distance inhibition ($r \lesssim 5$ m) (Canham et al., 2004; Papaik and Canham, 2006). This supports the model's use for gap-based prescriptions where fir is abundant. Given fir's susceptibility to spruce budworm, realistic fine-scale dispersion is relevant for anticipating vulnerability clusters and optimizing spacing or small-gap interventions.

4.2. Trembling aspen

Aspen was near-neutral in the older hectare (1823) but showed repulsion at ~5–10 m in the younger hectare (1847). Simulations matched the neutral pattern in the older stand but tended towards neutrality in the younger stand, underestimating the intermediate-distance repulsion. A likely reason is the absence of explicit vegetative propagation (root suckering) in SORTIE-ND. Aspen's clonal root

suckering and occasional stump sprouting readily generate patch–gap mosaics and spacing among genets that vary with disturbance history and age structure; omitting explicit clonal modules and initializing individuals at random can therefore dampen emergent repulsion (Frey et al., 2003; Namroud et al., 2005; Jean et al., 2019).

4.3. White spruce

Observed spruce patterns were broadly neutral with a small aggregation peak (~5–7 m) in both 1847 and 1870 hectares; simulations captured overall neutrality but missed the peak. White spruce recruitment is microsite-sensitive across the eastern boreal, with elevated establishment on rotten logs, disturbed mineral soil, and moist mounds (Simard et al., 1998; Gagné et al., 2019).. Thus, without an explicit substrate/moisture layer, the model cannot concentrate recruits on favourable patches, which would attenuate or erase the mid-scale clustering seen in observations. Our ≥100-adult inclusion rule may also bias evaluation toward abundant cohorts, under-representing strongly substrate-limited cases.

4.4. Paper birch

Birch exhibited short-range clustering (0–5 m) in the 1870 hectare but simulations from 1916 initial conditions were near-random, failing to reproduce clustering. Birch regeneration often involves stump sprouts or local seed rain near recent gaps (Sperling et al., 2025); the model's lack of stump sprouting/vegetative modules and the random initial placement likely reduce small-scale aggregation. In addition, fewer suitable simulations (lower adult counts) reduce power to detect clustering in envelopes.

4.5. Species pairs

The simulations reproduced the observed clustering of balsam fir and trembling aspen (~1823 ha), consistent with complementary resource use and spatial coexistence as represented in the light/competition submodels (Coates et al., 2003; Canham et al., 2004). In contrast, the observed aggregation of balsam fir and spruce (~1847 ha) was not reproduced, likely because key microsite heterogeneity (e.g., cool/moist patches, coarse woody debris) is absent from the model environment. For trembling aspen and spruce, both observations and simulations were largely neutral, aligning with expectations of weak direct competition (Senecal et al., 2004) given their divergent regeneration niches and growth rates.

Several factors likely explain the model–data mismatches observed here. First, some processes are unrepresented or simplified: vegetative propagation (root suckering, stump sprouting) in aspen and birch is absent, microsite/substrate and moisture heterogeneity that strongly governs white spruce recruitment is not mapped, and episodic mortality and herbivory (e.g., insect outbreaks) are omitted. Incorporating explicit clonal recruitment rules, adding spatial substrate/moisture layers, and allowing stochastic disturbance pulses are established pathways to capture event-driven spatial change in individual-based models (Coates et al., 2003; Thorpe et al., 2010). Second, initialization and analysis choices can dampen fine-scale signals: random spatial initialization removes empirical small-scale structure; robustness checks for bandwidth (σ) and r-range are recommended by point-pattern method guides (Asselin et al., 2001; Turner and Gardner, 2015; Ben-Said 2021). Finally, our validation is internal to one region; stronger generality claims would come from cross-cohort or cross-region train–test splits, as recommended in comparative neighbourhood-modeling studies (Papaik and Canham, 2006).

For fir and aspen, SORTIE-ND reproduced key fine-scale structures relevant to gap-based silviculture and spacing decisions (e.g., anticipating self-thinning in fir and neutral/weakly repulsive aspen neighbourhoods). For spruce, prescriptions that depend on microsite-driven aggregation should be treated cautiously unless substrate/moisture layers are integrated. For birch, planners should not rely on current model settings to predict clumped regeneration following disturbance; explicit vegetative modules are needed. Overall, the model is useful for scenario testing in mixedwoods when its process coverage matches the focal species and when structural uncertainty (distance-specific fit) is communicated. Therefore, the continued development of new modeling approaches in forest sciences is essential to better understand changes on ecosystem structure, functioning, and resilience (Hof et al., 2021). These models are key tools in forest management, specially under rapidly changing environmental conditions (Girona et al., 2023).

5. Conclusion

Fine-scale spatial structure encodes the strength and scale of intra- and interspecific interactions in boreal mixedwoods and is therefore directly relevant to gap-based silviculture and spacing decisions. Because fine-scale spatial structure underpins neighbourhood competition and regeneration dynamics, validating this component is essential for credible scenario analysis. Using a post-fire chronosequence and point-pattern statistics, we found that SORTIE-ND reproduces short-distance inhibition in balsam fir and the near-neutral pattern of trembling aspen in older stands, partially captures the broadly neutral pattern of white spruce but misses a modest aggregation at ~5–7 m, and fails to reproduce the short-range clustering observed for paper birch. For species pairs, agreement was strongest for fir–aspen (clustering reproduced) and weakest for fir–spruce (aggregation not reproduced), while aspen–spruce was largely neutral in both observations and simulations.

These results support using SORTIE-ND to explore stand-to-landscape scenarios where neighbourhood light competition dominates (e.g., fir and older aspen). However, predictive confidence is lower where fine-scale structure depends on vegetative regeneration (aspen, birch) or microsite/substrate and moisture heterogeneity (spruce). Practically, managers can rely on the model to assess spacing and small-gap treatments for fir and mixed fir–aspen stands, but should treat projections for spruce aggregation and birch clumping with caution unless additional processes are represented.

Key limitations include the absence of explicit clonal propagation and stump sprouting, lack of substrate/moisture layers to steer spruce recruitment, omission of episodic mortality and herbivory, random spatial initialization of younger stands, and internal validation within a single forest region. Priorities for improvement are to incorporate these processes, test robustness to bandwidth and distance choices, and conduct cross-cohort/ cross-region train–test evaluations. With these enhancements, SORTIE-ND would provide more reliable fine-scale spatial forecasts under changing disturbance and climate regimes, strengthening its utility for mixedwood management. Together, our results demonstrate both the potential and the current boundaries of SORTIE-ND for fine-scale spatial prediction in boreal mixedwoods.

CRediT authorship contribution statement

Animesh Ghose: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Philippe Marchand:** Supervision, Project administration, Funding acquisition, Data curation, Conceptualization. **Kobra Maleki:** Writing – review & editing, Validation, Methodology. **Miguel Montoro Girona:** Writing – review & editing, Visualization, Validation.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Animesh Ghose reports financial support was provided by Mitacs Inc. If there are other authors, they declare that they have no known

competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgement

We would like to extend our gratitude to Mitacs acceleration award for supporting this research project. Besides we would like to extend our thanks to Lake Duparquet Research and Teaching Forest (LDRTF) station for sharing the forest inventory data.

Data availability

The authors do not have permission to share data.

References

Ameztegui, A., Cabon, A., De Cáceres, M., Coll, L., 2017. Managing stand density to enhance the adaptability of Scots pine stands to climate change: A modelling approach. Ecol. Model. 356, 141–150. https://doi.org/10.1016/j.ecolmodel.2017.04.006.

Ameztegui, A., Coll, L., Benavides, R., Valladares, F., Paquette, A., 2012. Understory light predictions in mixed conifer mountain forests: role of aspect-induced variation in crown geometry and openness. For. Ecol. Manag. 276, 52–61.

Ameztegui, A., Coll, L., Messier, C., 2015. Modelling the effect of climate-induced changes in recruitment and juvenile growth on mixed-forest dynamics: The case of montane–subalpine Pyrenean ecotones. Ecol. Model. 313, 84–93.

Asselin, H., Fortin, M.J., Bergeron, Y., 2001. Spatial distribution of late-successional coniferous species regeneration following disturbance in southwestern Québec boreal forest. For. Ecol. Manag. 140 (1), 29–37.

Attiwill, P.M., 1994. The disturbance of forest ecosystems: the ecological basis for conservative management. For. Ecol. Manag. 63 (2–3), 247–300.

Baddeley, A., Rubak, E., Turner, R., 2015. Spatial point patterns: Methodology and applications with R. CRC Press. https://doi.org/10.1201/b1970.

Baddeley, A., Turner, R., 2005. spatstat: an R package for analyzing spatial point patterns. J. Stat. Softw. 12 (6), 282–290.

Beaudet, M., Harvey, B.D., Messier, C., Coates, K.D., Poulain, J., Kneeshaw, D., Brais, S., Bergeron, Y., 2011. Managing understory light conditions in boreal mixedwoods through variation in the intensity and spatial pattern of harvest: A modelling approach. For. Ecol. Manage. 261 (2011), 84–94.

Ben-Said, M., 2021. Spatial point-pattern analysis as a powerful tool in identifying pattern-process relationships in plant ecology: an updated review. Ecol. Process. 10, 56.

Bergeron, Y., 2000. Species and stand dynamics in the mixed woods of Quebec's Southern Boreal Forest. Ecology 81 (6), 1500–1516.

Bergeron, Y., Charron, D., 1994. Postfire stand dynamics in a southern boreal forest (Québec): a dendroecological approach. Écoscience 1 (2), 173–184.

Bergeron, Y., Dubue, M., 1988. Succession in the southern part of the Canadian boreal forest. Vegetatio 79, 51–63. https://doi.org/10.1007/BF00044848.

Bergeron, Y., Gauthier, S., Kafka, V., Lefort, P., Lesieur, D., 2001. Natural fire frequency for the eastern Canadian boreal forest: consequences for sustainable forestry. Can. J. For. Res. 31 (3), 384–391.

Bergeron, Y., Leduc, A., Morin, H., Joyal, C., 1995. Balsam fir mortality following the last spruce budworm outbreak in northwestern Quebec. Can. J. For. Res. 25, 1375–1384.

Bose, A.K., Harvey, B.D., Coates, K.D., Brais, S., Bergeron, Y., 2015. Modelling stand development after partial harvesting in boreal mixedwoods of eastern Canada. Ecol. Modell. 300, 123–136. https://doi.org/10.1016/j.ecolmodel.2015.01.002.

Brown, M.L., Canham, C.D., Murphy, L., Donovan, T.M., 2018. Timber harvest as the predominant disturbance regime in northeastern U.S. forests: effects of harvest intensification. Ecosphere 9 (3), e02062. https://doi.org/10.1002/ecs2.2062.

Busing, R.T., Mailly, D., 2004. Advances in spatial, individual-based modelling of forest dynamics. J. Veg. Sci. 15 (6), 831–842.

Canham, C.D., LePage, P.T., Coates, K.D., 2004. A neighborhood analysis of canopy tree competition: effects of shading versus crowding. Can. J. For. Res. 34 (4), 778–787.

Carrer, M., Castagneri, D., Popa, I., Pividori, M., Lingua, E., 2018. Tree spatial patterns and stand attributes in temperate forests: the importance of plot size, sampling design, and null model. For. Ecol. Manag. 407, 125–134.

Coates, K.D., Canham, C.D., Beaudet, M., Sachs, D.L., Messier, C., 2003. Use of a spatially explicit individual-tree model (SORTIE/BC) to explore the implications of patchiness in structurally complex forests. For. Ecol. Manag. 186 (1–3), 297–310.

de Römer, A.H., Kneeshaw, D.D., Bergeron, Y., 2007. Small gap dynamics in the southern boreal forest of eastern Canada: do canopy gaps influence stand development? J. Veg. Sci. 18 (6), 815.

Dhar, A., Hawkins, C.D.B., 2011. Regeneration and growth following mountain pine beetle attack: A synthesis of knowledge. J. Ecosyst. Manag. 12 (2), 1–16. http://jem.forrex.org/index.php/jem/article/view/22/84.

Frey, B.R., Lieffers, V.J., Landhäusser, S.M., Comeau, P.G., Greenway, K.J., 2003. An analysis of sucker regeneration of trembling aspen. Can. J. For. Res. 33, 1169–1179.

Gagné, L., Sirois, L., Lavoie, L., 2019. Seed rain and seedling establishment of Picea glauca and Abies balsamea after partial cutting in plantations and natural stands. Forests 10 (3), 221.

Gray, L., He, F., 2009. Spatial point-pattern analysis for detecting density-dependent competition in a boreal chronosequence of Alberta. For. Ecol. Manag. 259 (1), 98–106.

Girona, M.M., Morin, H., Gauthier, S., Bergeron, Y., 2023. Boreal forests in the face of climate change: Sustainable management. Springer Nature.

Hof, A.R., Montoro Girona, M., Fortin, M.J., Tremblay, J.A., 2021. Using landscape simulation models to help balance conflicting goals in changing forests. Front. Ecol. Evol. 9, 795736.

Jean, S.A., Pinno, B.D., Nielsen, S.E., 2019. Trembling aspen root suckering and stump sprouting response to above ground disturbance on a reclaimed boreal oil sands site in Alberta, Canada. New For. 50, 771–784. https://doi.org/10.1007/s11056-018-09698-2.

Kim, S., Bergeron, Y., Raymond, P., Thiffault, N., Girona, M.M., 2025. Natural regeneration 18 years after experimental silvicultural treatments in Canadian boreal forests. For. Ecol. Manag. 585, 122655.

Kneeshaw, D.D., Bergeron, Y., 1998. Canopy gap characteristics and tree replacement in the Southeastern Boreal Forest. Ecology 79 (3), 783–794.

Kneeshaw, D.D., Bergeron, Y., 1999. Spatial and temporal patterns of seedling and sapling recruitment within canopy gaps caused by spruce budworm. Ecoscience 6 (2), 214–222.

Kneeshaw, D.D., Prévost, M., 2007. Natural canopy gap disturbances and their role in maintaining mixed-species forests of central Quebec, Canada. Can. J. For. Res. 37 (9), 1534–1544.

Labrecque-Foy, J.P., Lemay, M.A., Gennaretti, F., Arseneault, D., Montoro Girona, M., 2025. Keeping logs on the past: log driving tells the story of fire regimes in pine forests of eastern Canada. Ecosphere 16 (12), e70473.

Law, R., Illian, J., Burslem, D.F.R.P., Gratzer, G., Gunatilleke, C.V.S., Gunatilleke, I.A.U.N., 2009. Ecoogical information from satial patterns of plants: insights from point process theory. J. Ecol. 97 (4), 616–628.

Liu, Z., Peng, C., Grandpre, L., Work, T., Huang, C., Kneeshaw, D., 2019. Simulation and analysis of the effect of a spruce budworm outbreak on carbon dynamics in boreal forests of Quebec. Ecosystems 22, 1838–1851.

Maleki, K., Gueye, M.A., Lafleur, B., Leduc, A., Bergeron, Y., 2020. Modelling post-disturbance successional dynamics of the Canadian boreal mixedwoods. Forests 11 (1), 3. https://doi.org/10.3390/f11010003.

Maleki, K., Lafleur, B., Leduc, A., Bergeron, Y., 2021a. Modelling the influence of different harvesting methods on forest dynamics in the boreal mixedwoods of western Quebec, Canada. For. Ecol. Manag. 479. https://doi.org/10.1016/j.foreco.2020.118545.

Maleki, K., Marchand, P., Charron, D., Lafleur, B., Bergeron, Y., 2021b. A 249-year chronosequence of forest plots from eight successive fires in the Eastern Canada boreal mixedwoods. Ecology. https://doi.org/10.1002/ecy.3306.

Ministère des Forêts, de la Faune et des Parcs. 2021. Classification écologique du territoire québécois. (2e éd.)n.d.Gouvernement du Québec. https://mrnf.gouv.qc.ca/documents/forets/inventaire/classification_ecologique_territoire_quebecois.pdf.

Morin, H., Laprise, D., 1993. Chronology of spruce budworm outbreaks near Lake Duparquet, Abitibi region, Quebec. Can. J. For. Res. 23, 1497–1506.

Murphy, L.E., 2011. SORTIE-ND User Manual, Version 6.11.; Institute of Ecosystem Studies. Millbrook, NY, USA.

Namroud, M.-C., Park, A., Tremblay, F., Bergeron, Y., 2005. Clonal and spatial genetic structures of aspen (Populus tremuloides Michx.). Mol. Ecol. 14 (10), 2969–2980.

Pacala, S.W., Canham, C.D., Saponara, J., Jr, J.A.S., Kobe, R.K., Ribbens, E., 1996. Forest models defined by field measurements : estimation, error analysis and dynamics. Ecol. Monogr. 66 (1), 1–43.

Papaik, M.J., Canham, C.D., 2006. Multi-model analysis of tree competition along environmental gradients in southern New England forests. Ecol. Appl. 16 (5), 1880–1892.

Poulin, J., & Messier, C. 2008. Rapport de paramétrisation du modèle de simulation de la dynamique forestière SORTIE-ND pour la forêt boréale et sub-boréale de l'ouest du Québec. Centre d'étude de la forêt (CEF). Available at: http://www.cef-cfr.ca/uploads/CEF/parametrisation.pdf.

Pureswaran, D.S., Grandpré, L.De, Paré, D., Taylor, A., Barrette, M., Morin, H., Régnière, J., Kneeshaw, D.D, 2015. Climate-induced changes in host tree-insect phenology may drive ecological state-shift in boreal forest. Ecology 96, 1840–1891.

Ripley, B.D., 1981. Spatial statistics. John Wiley & Sons. https://doi.org/10.1002/0471725218.

Senecal, D., Kneeshaw, D., Messier, C., 2004. Temporal, spatial, and structural patterns of adult trembling aspen and white spruce mortality in Quebec's boreal forest. Can. J. For. Res. 34 (2), 396–404.

Simard, M.-J., Bergeron, Y., Sirois, L., 1998. Conifer seedling recruitment in a southeastern Canadian boreal forest: the importance of substrate. J. Veg. Sci. 9, 575–582.

Sperling, A.J., Pinno, B.D., Froese, R.E., 2025. Pre-commercial thinning in boreal mixedwoods increases temperature extremes without affecting extreme low soil moisture values. Scand. J. For. Res. 40 (2), 85–94.

Thorpe, H.C., Vanderwel, M.C., Fuller, M.M., Thomas, S.C., Caspersen, J.P., 2010. Modelling stand development after partial harvests: An empirically based, spatially explicit analysis for lowland black spruce. Ecol. Mod. 221, 256–267. https://doi.org/10.1016/j.ecolmodel.2009.10.008.

Turner, M.G., Gardner, R.H., 2015. Introduction to landscape ecology and scale. In: Turner, M.G., Gardner, R.H. (Eds.), Landscape ecology in theory and practice: Pattern and process, 2nd ed. Springer, pp. 1–32 https://doi.org/10.1007/978-1-4939-2794-4_1.

Wiegand, T., Moloney, K.A., 2014. Handbook of spatial point-pattern analysis in ecology. Chapman and Hall/CRC Press, USA.
Yasuda, A., Yoshida, T., Miya, H., Harvey, B.D., 2013. An alternative management regime of selection cutting for sustaining stand structure of mixed forests of northern Japan: a simulation study. J. For. Res. 18 (5), 398–406.
Yataco, A.P., Noor, S., Girona, M.M., Work, T., Despland, E., 2024. Limited differences in insect herbivory on young white spruce growing in small open plantations and under natural canopies in boreal mixed forests. Insects 15 (3), 196.

Further reading

Aakala, T., Kuuluvainen, T., De Grandpré, L., Gauthier, S., 2007. Trees dying standing in the northeastern boreal old-growth forests of Quebec: spatial patterns, rates, and temporal variation. Can. J. For. Res. 50–61.
Canham, C.D., Uriarte, M., 2006. Analysis of neighborhood dynamics of forest ecosystems using likelihood methods and modeling Ecol. Appl 62–73.
Duchesneau, R., Lesage, I., Messier, C., Morin, H., 2001. Effects of light and intraspecific competition on growth and crown morphology of two size classes of understory balsam fir saplings For. Ecol. Manag. 215–225.
Filipescu, C.N., Comeau, P.G., 2007. Aspen competition affects light and white spruce growth across several boreal sites in western Canada. Can. J. For. Res. 1701–1713.
Galipeau, C., Kneeshaw, D., Bergeron, Y., 1997. White spruce and balsam fir colonization of a site in the southeastern boreal forest as observed 68 years after fire Can. J. For. Res. 139–147.
Larson, A.J., Churchill, D., Forest Ecology, 2012. Management Tree spatial patterns in fire-frequent forests of western North America, including mechanisms of pattern formation and implications for designing fuel reduction and restoration treatments For. Ecol. Manag. 74–92.