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Comparing modern and presettlement forest dynamics of a subboreal wilderness: Does spruce budworm enhance fire risk?

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Abstract. Insect disturbance is often thought to increase fire risk through enhanced fuel loadings, particularly in coniferous forest ecosystems. Yet insect disturbances also affect successional pathways and landscape structure that interact with fire disturbances (and vice-versa) over longer time scales. We applied a landscape succession and disturbance model (LANDIS-II) to evaluate the relative strength of interactions between spruce budworm (*Choristoneura fumiferana*) outbreaks and fire disturbances in the Boundary Waters Canoe Area (BWCA) in northern Minnesota (USA). Disturbance interactions were evaluated for two different scenarios: presettlement forests and fire regimes vs. contemporary forests and fire regimes. Forest composition under the contemporary scenario trended toward mixtures of deciduous species (primarily *Betula papyrifera* and *Populus* spp.) and shade-tolerant conifers (*Picea mariana*, *Abies balsamea*, *Thuja occidentalis*), with disturbances dominated by a combination of budworm defoliation and high-severity fires. The presettlement scenario retained comparatively more "big pines" (i.e., *Pinus strobus*, *P. resinosa*) and tamarack (*L. laricina*), and experienced less budworm disturbance and a comparatively less-severe fire regime. Spruce budworm disturbance decreased area burned and fire severity under both scenarios when averaged across the entire 300-year simulations. Contrary to past research, area burned and fire severity during outbreak decades were each similar to that observed in non-outbreak decades. Our analyses suggest budworm disturbances within forests of the BWCA have a comparatively weak effect on long-term forest composition due to a combination of characteristics. These include strict host specificity, fine-scaled patchiness created by defoliation damage, and advance regeneration of its primary host, balsam fir (*A. balsamea*) that allows its host to persist despite repeated disturbances. Understanding the nature of the three-way interaction between budworm, fire, and composition has important ramifications for both fire mitigation strategies and ecosystem restoration initiatives. We conclude that budworm disturbance can partially mitigate long-term future fire risk by periodically reducing live ladder fuel within the mixed forest types of the BWCA but will do little to reverse the compositional trends caused in part by reduced fire rotations.

Key words: Abies balsamea; *disturbance ecology; insect–fire interactions; LANDIS-II; Laurentian mixed forest; Minnesota; spruce budworm; succession.*

Introduction

Insect disturbance is often presumed to increase fire risk by enhancing fuel loads and opening the canopy, which can dry out the understory (McCullough et al. 1998, Parker et al. 2006). In dry coniferous forests of North America, fire suppression may contribute to enhanced insect activity by a combination of increased forest connectivity, altered age structure (Raffa et al. 2008), and proliferation of fire-sensitive, shade-tolerant tree species vulnerable to insects (Swetnam and Lynch 1993, Parker et al. 2006). Insect disturbance is often viewed as a symptom of stressed forest conditions related to altered fire regimes (Hessburg et al. 1999), and a key factor leading to catastrophic fire risk within contemporary forests (McCullough et al. 1998, Parker et al. 2006). However, recent research is challenging the idea that insect disturbance leads to enhanced fire activity and severity, on the grounds that changes to fuel architecture in response to insect disturbance are often nonlinear due to the combined effects of increased dead fuel and thinned canopy fuels (Romme et al. 2006, Jenkins et al. 2008, Lynch and Moorcroft 2008, Simard et al. 2008). Long-term consequences of insect disturbance for fire risk are even less understood, since insect disturbance influences successional pathways affecting future forest conditions that have subsequent repercussions for future fire and insect disturbance (Kulakowski et al. 2003, Jasinski and Payette 2005, Bouchard et al. 2006).

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Reciprocal interactions between fire, insects, and vegetation change have particular relevance for the mixed Laurentian forests of northeastern Minnesota, USA. Prior to Euro-American settlement, much of this region was occupied by vast pine forests subject to relatively frequent fire. The combination of exploitative logging at the end of the 19th century and strict fire suppression policies following World War II have dramatically changed the character of these forests to a mixture of remnant pine, aspen, and spruce–fir forests (Ahlgren and Ahlgren 1984). The relative importance of insect disturbance is thought to have increased in response to these changes. For example, fire suppression has encouraged the prolific regeneration of balsam fir (*Abies balsamea*), the primary host species for spruce budworm (*Choristoneura fumiferana*, Clemens) (Heinselman 1996). Spatially shifting spruce budworm outbreaks within northeastern Minnesota have caused widespread mortality of balsam fir and to a lesser extent white spruce (*Picea glauca*) for the past six decades (Williams and Birdsey 2003). Fleming et al. (2002) found the incidence of large fires to increase during a limited window of time following budworm defoliation in boreal Ontario, where the length of this window increased from the comparatively wet forests of eastern Ontario to the drier forests of western Ontario in the vicinity of Minnesota. Budworm-induced mortality creates dead ladder fuels composed of broken tops and branches that can transmit a slow-burning surface fire into a fast-burning crown fire (Stocks 1987). Yet live fir and spruce, with their low-branching architecture and flammable foliage, may also act as live ladder fuels within mixed conifer forests and as canopy fuels within older spruce–fir forests. Consequences of reciprocal interactions between spruce budworm disturbance, forest composition, fuel dynamics, and fire disturbance on long-term fire risk are therefore not well understood (Fig. 1).

To increase our understanding of these reciprocal interactions, we asked the following questions in the context of the Boundary Waters Canoe Area (BWCA) wilderness in northeastern Minnesota, USA: (1) What are the consequences of spruce budworm disturbance on forest vegetation and fire risk for the BWCA? (2) What was the historic importance of spruce budworm prior to Euro-American settlement in terms of forest composition and the fire regime? The fire and vegetation history of the BWCA are among the best studied in the world (Heinselman 1973, Frelich and Reich 1995, Heinselman 1996, Frelich 2002). By comparison, insect disturbance history for the BWCA, and its repercussions for vegetation change, is far less understood.

We simulated reciprocal interactions among fire, budworm, and vegetation within the 430 000-ha BWCA using the landscape disturbance and succession model, LANDIS-II (Scheller et al. 2007*b*). Specifically, we simulated forest and fire dynamics both with and without budworm disturbances for two different scenarios representing (1) contemporary forests and fire regimes and (2) presettlement forests and fire regimes. We evaluated the response of vegetation (composition, age structure, and landscape pattern), fire disturbance (area and severity), and spruce budworm disturbance (area and severity) to these different scenarios. Results from our study provide an objective assessment of the relative role of spruce budworm in influencing both historical and contemporary forest composition and fire regimes, as well as its relevance to ecosystem management efforts within the BWCA.

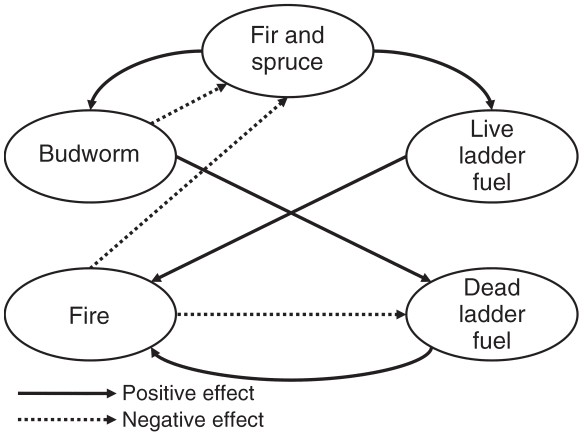

FIG. 1. Hypothesized interactions between fire and budworm disturbance as mediated by forest composition.

METHODS

Study area and background

The BWCA is a protected wilderness area situated at the transition zone between boreal and northern temperate forest biomes (Pastor and Mladenoff 1992) in Minnesota (Fig. 2). The climate is humid continental, with long cold winters and generally continuous snow cover from late November to mid-April and short warm summers (Heinselman 1996). Undulating and glacially carved terrain is underlain by Canadian Shield bedrock, with soils formed primarily from glacial till. Upland soil moisture is strongly influenced by variable depth to bedrock, and the landscape is embedded with abundant lakes and wetlands (Heinselman 1996). Major forest types include: jack pine and black spruce on coarse shallow soils; balsam fir and paper birch on deeper loams; red maple, aspen, birch, and fir on moist but not wet sites; red pine on shallow rocky soils; and birch and white pine along lakes and streams (Frelich 2002; see Table 1 for scientific names). Wetland forests are also common and include forested peatlands in different combinations of black spruce, tamarack, and white cedar, and rich wetland forests dominated by black ash or white cedar (Minnesota Department of Natural Resources 2003).

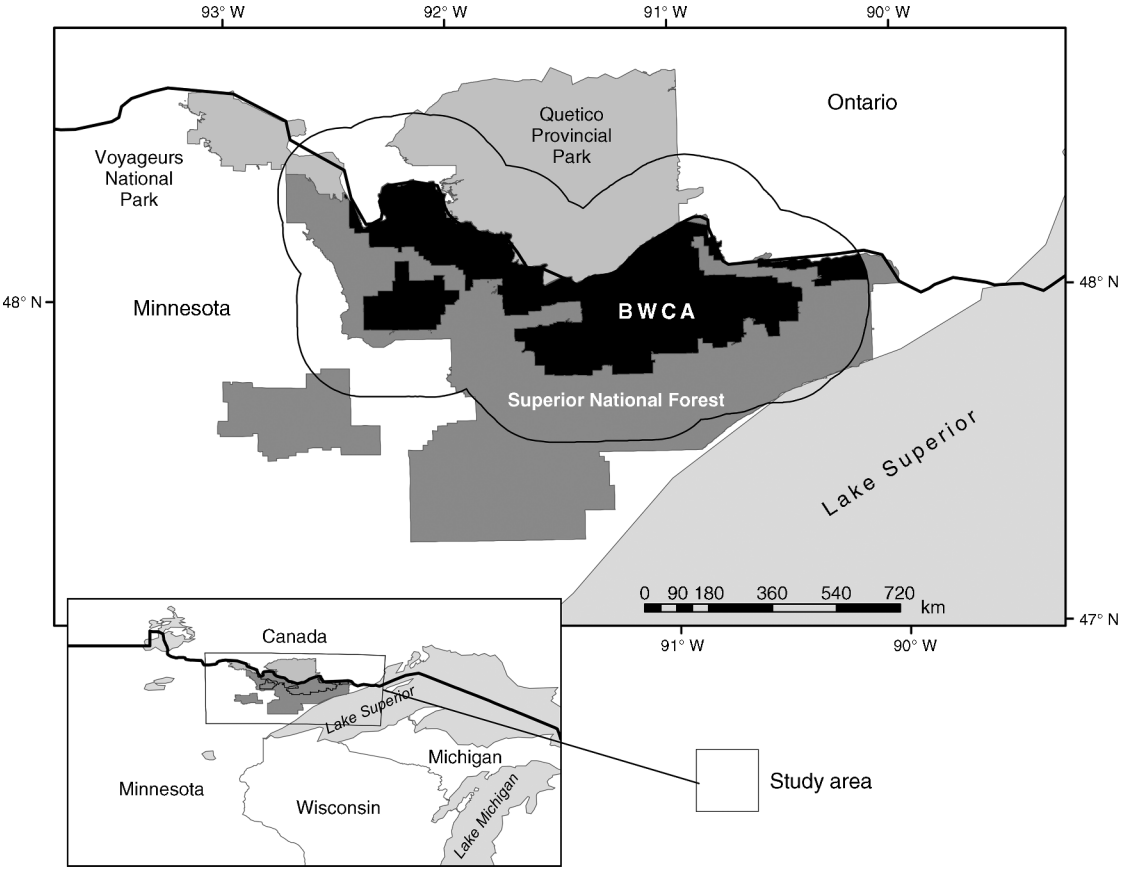

FIG. 2. The study area simulated included both the Boundary Waters Canoe Area (BWCA; Minnesota, USA) and a 22-km buffer to minimize edge effects; results are reported only for the BWCA, represented in black.

Fire disturbance history of the BWCA has been well characterized by Heinselman (1973) and the importance of fire in shaping forest communities in the region is well recognized (Baker 1989, Frelich and Reich 1995, Frelich 2002, Scheller et al. 2005). While the presettlement fire regime was dominated by crown fires, surface fires were still common and important for maintaining red and white pine (Frelich and Reich 1995, Heinselman 1996).

TABLE 1. Tree species life history attributes (Burns and Honkala 1990, Heinselman 1996).

Common name	Scientific name	Longevity (yr)	Maturity (yr)	Tolerance		Seed dispersal (m)		Postfire regeneration
				Shade	Fire	Effective	Maximum	
Balsam fir	*Abies balsamea*	150	20	5	1	30	160	
Tamarack	*Larix laricina*	175	35	1	1	50	200	
White spruce	*Picea glauca*	225	40	3	2	30	200	
Black spruce	*Picea mariana*	200	22	3	3	80	200	semi-serotiny
Jack pine	*Pinus banksiana*	175	17	1	2	20	100	serotiny
Red pine	*Pinus resinosa*	300	20	2	4	12	275	
White pine	*Pinus strobus*	325	25	3	3	60	210	
White cedar	*Thuja occidentalis*	300	35	5	1	45	60	
Red maple	*Acer rubrum*	125	10	3	1	100	200	vegetative
Paper birch	*Betula papyrifera*	165	25	2	2	200	5000	vegetative
Black ash	*Fraxinus nigra*	150	35	2	1	100	200	vegetative
Trembling aspen	*Populus tremuloides*	140	25	1	2	500	5000	vegetative
Pin oak	*Quercus ellipsoides*	200	35	2	4	30	3000	vegetative

Notes: Longevity is life expectancy in absence of disturbance; maturity is age to sexual maturity. Tolerance is rank-ordered (1 = highly intolerant, 5 = highly tolerant). For seed dispersal distance parameters, effective distance captures 95% of dispersal distance; maximum is the maximum possible dispersal distance. For regeneration, serotiny refers to opening of cones following fire and has priority over other regeneration types if it occurs. Black spruce is assumed semi-serotinous with 10% probability (see Appendix A), jack pine is 100% serotinous. Vegetative reproduction (stump sprouting) has priority over seed reproduction and occurs with 50% probability (maple, birch, ash) or 100% probability (aspen, oak).

Active fire suppression in the region began around 1911 and continues to the present. Current fire rotations are estimated at about 400 years. We added a 22-km buffer around the BWCA to minimize edge effects affecting fire and other spatial processes associated with the BWCA boundary (Fig. 2). Results are reported only for the area within the BWCA boundary.

Despite the current wilderness designation of the BWCA, approximately half of the area was significantly affected by timber harvesting activities (Heinselman 1996). The first wave of harvesting occurred between 1895 and 1930 and focused on large-diameter white and red pines. Later, pulpwood harvest focused on jack pine, spruce, and aspen, and occurred sporadically between 1935 and 1978. No harvesting has occurred since then. Wind throw also affects the structure and composition of forests in the region (Frelich 2002).

Eastern spruce budworm periodically disturbs fir and spruce forests across the boreal forest of North America. Major spruce budworm outbreaks in the BWCA occurred around 1920, 1960, and 1990 (Robert et al., *in press*). Balsam fir is most susceptible to spruce budworm disturbance, followed by white spruce and then black spruce (Hennigar et al. 2008). Mature host trees older than 50 years are also more susceptible to damage than young trees (MacLean 1980). Mixed stands containing deciduous tree species often sustain less damage to fir and spruce than pure stands of host species (Su et al. 1996, Cappuccino et al. 1998). Forests with high mortality from recent budworm damage burn with high intensity, particularly in spring before the leaf-out of deciduous shrubs (Stocks 1987).

Model description

LANDIS-II (Scheller et al. 2007*b*) is a process-based model that simulates broad-scale ($>10^5$ ha) landscape dynamics, including succession, disturbance, seed dispersal, forest management, and climate change effects (Mladenoff 2004). Landscapes are represented as a grid of interacting cells with user-defined cell size, in this case 1 ha. Individual cells have homogeneous light environments, and are aggregated into land types with homogeneous climate and soils. Forest composition at the cell level is represented as age cohorts of individual tree species that interact via a suite of vital attributes (i.e., shade tolerance, fire tolerance, seed dispersal, ability to sprout vegetatively, and longevity) to produce nondeterministic successional pathways sensitive to disturbance type and severity. LANDIS-II consists of a core collection of libraries and a collection of optional extensions that represent the ecological processes of interest (Scheller et al. 2007*b*).

We used the extension Age-list Succession (v 2.0; Mladenoff and He 1999, Scheller and Domingo 2008) to simulate the presence or absence of tree species cohorts based on land-type-specific probabilistic establishment, spatially explicit seed dispersal (Ward et al. 2005), and published tree species life history attributes (Burns and Honkala 1990, Heinselman 1996) (Table 1). We applied the Dynamic Fire and Fuel System extensions (v1.0; Sturtevant et al. 2009) to simulate interactions among fire, vegetation, insect disturbance, weather, and landscape structure. The fuel extension translates species cohort information into fuel classes used by the fire extension to estimate fire spread rates and estimate fire effects. We applied a duration-based approach to simulate the fire regime, where frequency and size distribution from fire records are used to calibrate a duration distribution for fire events (Didion et al. 2007, Yang et al. 2008). The resulting fire regime is sensitive to simulated changes in landscape fuel composition and configuration (Sturtevant et al. 2009). Fire events are initiated probabilistically (Yang et al. 2004), and fire weather characterized by the Canadian Forest Fire Weather Index System (Van Wagner 1987) is randomly selected from daily weather records stratified by season (i.e., spring leaf-off, summer leaf-on, and fall leaf-off). Fuel-specific fire spread rates vary locally as a function of wind direction and topography using equations from the Canadian Forest Fire Behavior Prediction (FBP) System, where surface vs. crown fire behaviors are integrated into the empirical rates of fire spread (Forestry Canada Fire Danger Group 1992). Crown fraction burned (i.e., the proportion of live canopy fuel burned) for each cell within a burned area is estimated as a function of the local rate of fire spread and the fuel type for the site (Forestry Canada Fire Danger Group 1992). Estimated crown fraction burned is then used to assign each burned site to one of five burn severity classes ranging from low (surface fire, 1) to high (crown fire, 5) (Sturtevant et al. 2009). Cohort mortality is a combined function of age (youngest most susceptible) and tree species fire tolerance (He and Mladenoff 1999).

Spruce budworm disturbance was simulated using the Biological Disturbance Agent extension (v1.0; Sturtevant et al. 2004), with minor adjustments to better capture host-specific impacts published for spruce budworm (see *Model parameterization*). Insect outbreaks occur at intervals specified by a mean and standard deviation estimated from historic records. When an outbreak occurs, a "site vulnerability" value (range 0–1) is calculated for all forested sites as the average value of the oldest cohort of each tree species as a food resource for the insect, based on empirical host preference parameters. Site-level resources may be averaged with nearby sites to modify site vulnerability based on surrounding context. Site vulnerability translates into a probability of disturbance, and if disturbed, site vulnerability defines the ability of the disturbance to kill host cohorts (severity) based on host susceptibility. Killed cohorts are translated by the dynamic fuel extension into percent dead fir and spruce that affects ignition probability and fire spread rates (Stocks 1987, Forestry Canada Fire Danger Group 1992, Sturtevant et al. 2009).

TABLE 2. Comparison of contemporary and presettlement scenarios.

Variable	Contemporary scenario Value	Contemporary scenario Source data	Presettlement scenario Value	Presettlement scenario Source data
Fire regime		†		‡
Mean fire size (ha)	333		12 019	
Fire rotation (yr)	426		122	
Initial forest condition		§		¶
Balsam fir	27		22	
Red maple	4		2	
Paper birch	32		35	
Black ash	2		2	
Tamarack	5		21	
White spruce	19		17	
Black spruce	45		24	
Jack pine	33		26	
Red pine	6		10	
White pine	9		15	
Aspen species	34		18	
Pin oak	0		0	
White cedar	3		8	
Forest age		#		||
Mean (yr)	96		122	
SD (yr)	59		122	
Skewness	0.4		2.0	

Notes: Values for initial forest condition are the percentages of tree species within the Boundary Waters Canoe Area (BWCA), Minnesota, USA. Presence within the contemporary scenario was defined by >10% of basal area within a Forest Inventory and Analysis (FIA) plot. In the presettlement scenario, values are the average percentages of species within the BWCA based on three replicate initial conditions generated by LANDIS-II (See Appendix A).

† Shinneman et al. (2010).

‡ Heinselman (1973).

§ FIA plots assigned to satellite-derived forest community types (Wolter et al. 1995); host tree species defined by Wolter et al. (2008).

¶ Initialized using General Land Office Survey bearing tree plots (Almendinger 1997) stratified by biophysical units (Cleland et al. 2005); replicate initial conditions generated by the model in a three-stage process (see Appendix A).

Time series of land cover (Wolter and White 2002, Pastor et al. 2005).

|| Derived by the model based on the application of the presettlement fire regime.

A 10-year time step was used for all extensions, where the order of simulation within a time step was wind disturbance, fire disturbance, budworm disturbance, and succession. We selected this order because wind and fire disturbances occur on fast time scales (i.e., minutes to days or weeks), budworm disturbance occurs at intermediate time scales where mortality is a consequence of multiple years of defoliation (MacLean 1980), and succession takes place over decades. Further, the observed window of enhanced fire incidence occurs between 6 and 16 years following defoliation in the vicinity of the BWCAW (Fleming et al. 2002). Hence simulated fires respond to budworm disturbance in the decade following an outbreak, approximating the "window of opportunity" estimated by Fleming et al. (2002).

Study design and scenarios

Our simulation experiment focused on two key differences between presettlement and contemporary forests (forest composition and fire regimes) for which there was robust empirical data from presettlement forests (Heinselman 1973, Almendinger 1997). The contemporary scenario was initiated with conditions representing the BWCA in the year 2000. The presettlement scenario approximated forest dynamics that might have occurred in the absence of Euro-American settlement. Several simplifying assumptions were applied: (1) weather and climate were assumed identical between contemporary and presettlement scenarios; (2) the wind disturbance regime was held constant across all scenarios; and (3) the spruce budworm disturbance regime, defined by its return interval (mean and standard deviation) and its spatial synchrony (i.e., the spatial extent over which the outbreak occurs during a given decade) was held constant across all insect disturbance scenarios. Critical differences between scenarios are summarized in Table 2.

Model parameterization

Land types and species establishment.—Land types were delineated by combining available soil surveys with a biophysical classification (Table 3). We assigned soil water-holding capacity and monthly climate statistics to each land type using soil attributes and interpolated weather data, respectively (Table 3). Species probability of establishment (P_{est}) represents the probability of cohort recruitment of a species given adequate light (He et al. 1999). P_{est} values were calculated as a function of species climatic and edaphic tolerances as applied to the climate and soil conditions for each upland land type (Gustafson et al. 2010) (Table 4). Species establishment within forested wetland types were estimated differently, by calibrating species P_{est} parameters to maintain steady-state observed frequencies of species occurrence within each forest lowland type under presettlement conditions (Table 4). Detailed methods used to define land types and estimate P_{est} parameters are provided in Appendix A.

Initial conditions.—The contemporary scenario was initialized with forest species and age cohorts representative of year A.D. 2000, using a combination of forest inventory and analysis (FIA) plot data and satellite image classifications that included a detailed map of spruce budworm host species (balsam fir and spruce species; Wolter et al. 2008) (Tables 2 and 3). Presettlement vegetation was initialized to be representative of A.D. 1868, corresponding with the end of the "presettlement period of good record" (i.e., 1727–1868) defined by Heinselman (1973). We approximated presettlement conditions in a two-stage process using bearing tree records from the General Land Office (GLO) survey falling within the Northern Superior Uplands ecological section. First, 7360 section corner GLO plots were stratified by community type (i.e., fire dependent,

TABLE 3. Spatial data sets used to parameterize the contemporary and presettlement scenarios.

Spatial data set	Description	Use	Reference
Satellite-derived land cover			
Vegetation classification	detailed (Anderson level III) vegetation classification applied to multitemporal and multi-season Landsat Thematic Mapper (TM) data circa 1992	initial conditions (contemporary)	Wolter et al. (1995)
Land cover classification	land cover classification (Anderson level II) applied to a time series of Landsat TM (dates: 1984, 1990, 1995, 2000)	land type designation for non-forest cover types; forest age (contemporary)	Wolter and White (2002), Pastor et al. (2005)
Fir and spruce abundance	relative basal area of balsam fir and spruce species mapped using partial least squared regression applied to multitemporal Landsat TM (circa 2002).	spruce budworm host species initial conditions (contemporary)	Wolter et al. (2008)
Abiotic environment			
Climate	interpolated monthly climate variables (maximum temperature, minimum temperature, precipitation) mapped at 1 km resolution (1970–2000)	tree species probability of establishment (P_{EST})	McKenney et al. (2006)
Biophysical units	fine-scaled land classification based on soils, landform, and presettlement fire history and vegetation from GLO (Minnesota only)	land types; presettlement initial conditions	Cleland et al. (2005)
STATSGO2	U.S. General Soil Map of general soil association units (Minnesota only)	land types; soil attributes	Soil Survey Staff (2002)
Ontario Land Inventory (OLI)	landscape units mapped at 1:250 000 using aerial photography and soil surveys (Ontario only)	land type stratification; soil attributes	Elkie et al. (2000)
Forest plots			
FIA	FIA plots from Minnesota ($n = 7242$)	initial tree species composition (contemporary)	Smith (2002)
GLO	General Land Office survey points documenting bearing trees ($n = 7359$)	initial tree species composition (presettlement)	Almendinger (1997)
Fire history	historical reconstruction of fire events based on fire scars	limited forest age data; presettlement fire regime	Heinselman (1973)
Modern fire records	combined fire records from Minnesota Department of Natural Resources, U.S. Forest Service, and Ontario Ministry of Natural Resources (1960–2005)	contemporary fire regime	Shinneman et al. (2010)

forested wetland, etc.) and seral stages based on their composition. The plots were probabilistically assigned to biophysical units and a preliminary forest age map representing the best available disturbance history information, though incomplete, for 1868. We then applied a constant presettlement fire regime for three separate replicate LANDIS-II simulations lasting 750 years, at which point forest composition approximated equilibrium. The resulting time since fire disturbance maps were used as replicate age maps representing realistic landscape patterns of forest age. Stratified GLO plots were then reassigned to these age maps (i.e., stage 2) to ensure that presettlement forest composition was preserved. The resulting maps represent spatially realistic replicate approximations of forest composition and age structure circa 1868. See Appendix A for more detail on these initial conditions methodology.

Disturbance regimes.—The dynamic fuel extension classified sites into standard fuel types from the Canadian FBP based on the species age list for a given site and whether the site was recently disturbed (Table 5). We parameterized relative fuel-specific ignition rates based on fire occurrence patterns observed elsewhere in the boreal forest (Krawchuk et al. 2006) (Table 5). The contemporary fire regime was parameterized using recent fire records that reflect patterns of human-caused ignitions and fire suppression practices (Shinneman et al. 2010) (Table 3). The presettlement fire regime within the BWCA was parameterized using fire records from 1727 to 1868 (Heinselman 1973). Fire regimes for the adjacent buffer were stratified by biophysical unit and parameterized based on GLO records (Cleland et al. 2005). Daily weather records (1971–2006) from a nearby weather station (Atikokan, Ontario, Canada; 48.7° N, 91.6° W) were used to generate a database of daily fire weather indices that drive fire behavior of individual fire events (Sturtevant et al. 2009). Dates with fire weather index of less than 10 were assumed unable to carry a fire and discarded from the database (Simard 1973). Lognormal mean and standard deviations of fire durations were then calibrated to reproduce the contemporary and presettlement fire size distributions.

TABLE 4. Species probability of establishment parameters (P_{est}).

Common name	Upland forest land types			Lowland forest land types†		
	Minimum	Maximum	Mean‡	Acid bog	Peatland	Rich wetland
Balsam fir	0.19	0.61	0.38	0	0.56	1.00
Tamarack	0.50	0.95	0.73	1.00	1.00	1.00
White spruce	0.48	0.62	0.55	0	0	1.00
Black spruce	0.54	0.95	0.79	1.00	0.03	0.01
Jack pine	0.25	0.80	0.61	0	0	0
Red pine	0.03	0.57	0.18	0	0	0
White pine	0.01	0.34	0.09	0	0	0.03
White cedar	0.07	0.48	0.23	0	1.00	1.00
Red maple	0.00	0.07	0.01	0	0	0.31
Paper birch	0.37	0.62	0.45	0	0.002	0.04
Black ash	0.00	0.45	0.18	0	0	1.00
Trembling aspen	0.26	0.61	0.49	0	0	0.01
Pin oak	0.00	0.05	0.00	0	0	0

† Calibrated to achieve steady-state dynamics under presettlement forest conditions.
‡ Area-weighted mean P_{est} across all upland forest land types in the BWCA.

Calibrations were performed for the approximate length of time represented by each respective fire record (i.e., 20 years and 150 years for contemporary and presettlement scenarios, respectively).

Wind disturbance was simulated using the Base Wind extension v1.3 (Scheller et al. 2007*a*). Wind disturbance was calibrated identically for all scenarios to have a 500-year rotation for blowdowns (severity class $\geq$3), and mean and maximum size of blowdown events of 93 and 3600 ha, respectively (Scheller et al. 2005). Since harvest practices occurring outside the BWCA boundary can influence forest composition and age structure in the buffer zone, and may in turn affect neighborhood processes (i.e., seed sources, fire spread, etc.) inside the BWCA, we simulated harvest activities in areas of the buffer zone currently open to timber management using the Harvest extension (v1.2; Gustafson et al. 2000). The harvest regime (i.e., rates, treatment sizes, specific prescriptions, etc.) was parameterized from Shinneman et al. (2010).

Budworm outbreak characteristics (return interval and spatial synchrony) were parameterized using tree-ring reconstructions of outbreaks within the study area over the last century (Robert et al., *in press*) (Table 6). Tree species host preferences for spruce budworm and resulting vulnerability to budworm defoliation were parameterized using the "rules of thumb" offered by MacLean (2004) based on extensive research in eastern Canada (MacLean and Ostaff 1989, Taylor and MacLean 2005, Hennigar et al. 2008), and synthesis of budworm impact studies from across Canada and including Minnesota (MacLean 1980). These parameters

TABLE 5. Fuel types and associated parameters.

FBP fuel type	Description	Ignition probability	Spread rate (m/min)	
			MinROS	MaxROS
C1†	tamarack/cedar	0.1	0.2	13.0
C2	spruce–fir	0.8	4.0	56.2
C3	old jack pine	0.6	0.8	55.9
C4	young jack pine	0.4	4.8	57.4
C5	white and red pine	0.4	0.2	21.8
D1	deciduous	0.0	0.2	13.0
M1/M2‡	mixed conifer–deciduous	Variable	0.2	46.3
M3/M4§	dead fir and spruce	1.0	0.6	127.2
D1	open (no species)	0.0	0.2	13.0
C2	young jack pine–spruce–fir	0.4	4.0	56.2
C2	old jack pine–spruce–fir	0.6	4.0	56.2
O1a	wetland	0.0	0.3	107.6
O1b	upland grass	1.0	0.3	139.7

Notes: Minimum rate of spread (MinROS) was calculated using weather record with the lowest fire weather index (FWI; 10). Maximum rate of spread (MaxROS) was calculated using the record with the highest FWI (59). FBP is the Canadian Forest Fire Behavior Prediction System.

† Fuel parameters (spread) equal to D1, but treated as conifer fuel type.

‡ M1/M2 fuels have weighted averages for probability and ROS dependent on the mixture of deciduous and conifer fuels. MinROS assumes the minimum proportion of conifer and leaf-on (M1) condition for deciduous component, and MaxROS assumes the maximum proportion of conifer and leaf-off (M2) condition for deciduous component.

§ M3/M4 fuels have ROS dependent on the proportion of dead fir. MinROS assumes 10% dead fir, and MaxROS assumes 100% dead fir.

TABLE 6. Spruce budworm disturbance parameters.

Species	Age 0–10 yr		Age 20–40 yr		Age 50+ yr	
	Value	Susceptibility	Value	Susceptibility	Value	Susceptibility
Balsam fir	0.25	0.0	0.5	0.5	1.0	1.0
White spruce	0.25	0.0	0.5	0.15	1.0	0.42
Black spruce	0.25	0.0	0.5	0	1.0	0
Deciduous species	0	0	0	0	0	0
Nonhost conifers	ignored	0	ignored	0	ignored	0

Notes: Value is the relative host value as a food resource for spruce budworm. Deciduous species decrease resource food value (Su et al. 1996), and nonhost conifers are ignored. Susceptbility is the probability of mortality if a disturbance occurs (Maclean 2004). The outbreak return interval (the interval between outbreak events [Robert et al., *in press*]) is 33.5 ± 10.6 yr (mean ± SD). Outbreaks are assumed to occur synchronously across the entire landscape (Robert et al., *in press*) and have a neighborhood radius of 150 m (this defines number of adjacent cells used to estimate host resource value).

were consistent with studies from northern Minnesota, with the exception that black spruce is not killed by budworm disturbance in Minnesota (Batzer 1969, Campbell and Albers 1985) (Table 6). Neighborhood influence on site vulnerability was limited to adjacent cells, consistent with studies from New Brunswick (Su et al. 1996, but see Cappuccino et al. 1998). Modifications to the biological disturbance agent extension included more precise host preference and susceptibility parameters (Table 6) and modification of mortality rules to emulate cell-scale gaps in budworm host (Kneeshaw and Bergeron 1998), but sparing 10-year-old balsam fir cohorts as advance regeneration (Morin 1994, Frelich 2002) (Appendix A).

Statistical analyses

The four scenarios were analyzed as a two-way factorial experiment with two levels (two time periods with and without spruce budworm). Each treatment combination was simulated for 300 years. We applied a power analysis (Proc GLMPOWER, SAS v9.1; SAS Institute, Cary, North Carolina, USA) using the variance from three initial replicates, target treatment effect $\alpha = 0.05$, and the acceptable type II error rate $\beta = 0.05$, to determine that 12 replicates was appropriate for the experiment (Gustafson et al. 2010). In our case, variation among replicates reflects stochasticity within the model relative to the magnitude of the response, rather than actual variation in nature. Contemporary scenarios used the same initial condition for all replicates, whereas presettlement scenarios used three replicate initial conditions.

Vegetation response to the main effects was quantified as the percent occupancy by each tree species and landscape metrics of forest seral stages at simulation years 0, 150, and 300. Seral stages independent of forest types corresponded with growth stages defined for fire-dependent communities in the region (Minnesota Department of Natural Resources 2003): 1–60 yr (early seral), 61–120 yr (mid seral), 121–180 yr (late seral), and >180 yr (old-growth). Landscape metrics applied to seral stage included percent cover, mean patch size, and the aggregation index (He et al. 2000). Nonmetric multidimensional scaling (NMS; Mather 1976, Kenkel and Orloci 1986) was applied using within PC-ORD (Version 6; McCune and Mefford 2011) to summarize forest composition and landscape pattern metrics and to compare landscape composition and structure among scenarios. We applied a general relativization to the data columns (i.e., variables) of landscape metrics to standardize the analysis with respect to their different units. The Sørenson distance measure was used to construct both ordinations. Dimensionality was selected based on a Monte Carlo test, using 50 runs with the actual data set and 250 runs with randomized data, with a maximum of six possible axes (McCune and Grace 2002). Varimax rotation was applied to maximize the loadings of individual variables on the dimensions of the reduced ordination space.

We evaluated the response of budworm host types to main effects by rank-ordering the following eight forest types (derived from species dominance) according to their relative value as budworm host and by averaging their landscape abundance over the last five simulation decades: non-host deciduous, non-host conifer, mixed host/deciduous, mixed host/non-host conifer, black spruce, spruce–fir, and primary host (balsam fir and white spruce). We used the same method to output landscape abundance of fuel types rank-ordered according to relative ignition probability. Finally, the three landscape metrics applied to seral stage were also applied to balsam fir age cohorts susceptible to budworm disturbance (>10 years old).

Fire disturbance responses to the main effects were quantified by estimating the mean fire return interval based on the cumulative area burned during the simulations and mean fire severity weighted by the area burned. For spruce budworm scenarios, we contrasted spruce budworm disturbance (area and severity) between contemporary and presettlement scenarios. Shapiro-Wilks test and visual examination of stem and leaf plots (UNIVARIATE procedure) indicated response variables were normally distributed. Treatment effects on each response variable were estimated using the

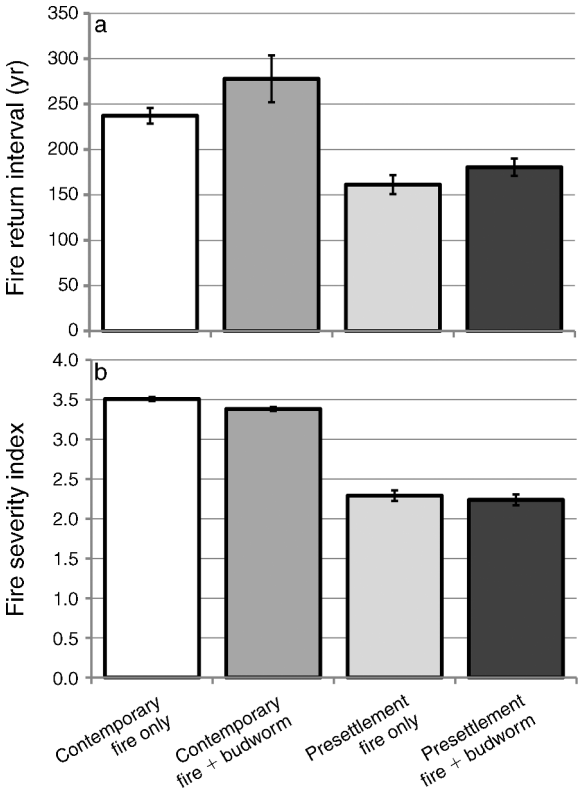

FIG. 3. (a) Fire return interval (least-squares mean) and (b) fire severity index (mean; fire severity classes range from low [surface fire, 1] to high [crown fire, 5]) by scenario by treatment. Values for each response variable were estimated using fires from the entire 300-year simulation period, averaged across 12 replicates. Error bars represent 95% confidence intervals.

MIXED procedure in SAS. We evaluated model fit by examining the patterns of residuals with respect to the normality assumption and homogeneity of variance assumption using Levene's test. Where the homogeneity of variance assumption was violated for a given response variable, we selected an appropriate unequal covariance structure (i.e., grouped by one or more treatment effects) (Littell et al. 2006). We also contrasted area burned and mean fire severity during outbreak vs. non-outbreak decades, using the GLIMMIX procedure applied to a gamma distribution with the log link function to accommodate the long right-tailed distributions in each response variable. We applied a heterogeneous autoregressive order 1 covariance structure to account for serial autocorrelation in the temporal sequence of outbreak and non-outbreak periods, respectively, and evaluated the fit using the same methods as above. The relative influence of main effects and their interactions were evaluated based on the direction and magnitude of differences between least-squared treatment means and the uncertainty (i.e., standard error) of those means.

Sensitivity and uncertainty analyses

We conducted a sensitivity analysis by varying key input parameter values by ±10% with 12 replicates and evaluating whether response values varied by more than 10% due to a given parameter change, and whether the changes had meaningful influence over the outcome of the simulation experiment. We evaluated four key input parameters: P_{est}, landscape-wide fire ignition rate, mean spruce budworm outbreak interval, and budworm host value. Species P_{est} and budworm host values were each evaluated as a set (i.e., ±10% across all species). In addition, we evaluated the relative implications of two key assumptions on the outcome of our experiment. First we contrasted our fuel-specific ignition rates (Table 5) with a simpler scenario where all conifer types (including sites disturbed by spruce budworm) had identical ignition rates, all deciduous types had zero ignition rates, and ignition rates within mixed conifer-deciduous types were a linear function of the proportion of conifer content. Ignition parameters were relativized to hold the landscape-wide ignition rate constant between the uncertainty scenario and our main experiment. Second, we contrasted our assumption that young (i.e., 10-year-old) balsam fir cohorts survived budworm disturbance with the alternative assumption that all cohorts of balsam fir were killed if a cell was disturbed.

RESULTS

Disturbance interactions

As expected by our study design, simulated fire return intervals for the presettlement time period (170.9 ± 3.2 [mean ± SE]) were shorter than contemporary fire return intervals (257.5 ± 6.2), but budworm disturbance consistently increased fire return intervals across both time period treatments (229.1 ± 6.3) relative to fire-only scenarios (199.2 ± 3.1 SE) (Fig. 3). Simulated area burned was similar between outbreak and non-outbreak decades for both the presettlement (18 010 ± 1631 ha vs. 18 287 ± 1022 ha, respectively) and contemporary (11 605 ± 655 ha vs. 12 413 ± 742 ha, respectively) time periods. Mean fire severity class (1–5) was higher for the contemporary time period (3.44 ± 0.008), indicating a fire regime dominated by crown-fire dynamics, vs. a mixed fire regime for the presettlement time period (2.26 ± 0.022) (Fig. 3). Budworm disturbance slightly reduced fire severity class when averaged across 300-year simulations (2.81 ± 0.016 vs. 2.90 ± 0.016) (Fig. 3), and slightly increased burn severity class during outbreak decades relative to non-outbreak decades (2.80 ± 0.033 and 2.76 ± 0.024, respectively). While budworm effects on fire severity were most noticeable for the contemporary scenario (e.g., Fig. 3), our results suggest these differences were not very meaningful.

Our sensitivity and uncertainty analyses indicated that the experiment with respect to fire disturbance was insensitive to both minor (i.e., 10%) parameter changes and alternative assumptions evaluated. We observed treatment effects of similar magnitude and direction for both main effects (time period and budworm) in all 10

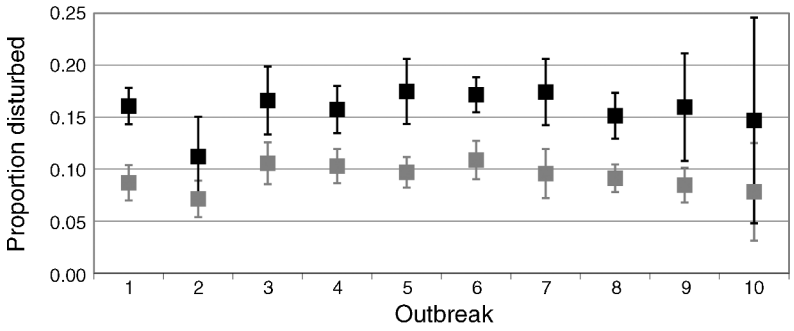

FIG. 4. Proportion of the BWCA disturbed by a time sequence of spruce budworm outbreaks during contemporary (black) and presettlement (gray) scenarios. The *x*-axis represents the sequential order of outbreaks occurring, on average, every 33 years during the 300-year simulations. Error bars represent 95% confidence intervals.

sensitivity and uncertainty experiments. All five sensitivity/uncertainty experiments that included a budworm treatment indicated that budworm disturbance increased fire return intervals for the contemporary scenario, however only one (i.e., reducing tree species P_{est}) indicated budworm had a meaningful effect on fire return intervals for the presettlement scenario. Absolute differences in mean fire return intervals and average fire severity were generally insensitive to the parameter changes and alternative assumptions we evaluated (Appendix B). The largest change in mean fire return interval (MRI) was observed when we increased P_{est} parameters by 10% for the presettlement time period, resulting in a 13% and 15% reduction in MRI for no budworm and budworm treatments, respectively. The same change reduced MRI by only 7% for the contemporary time period treatments. Parameter changes had even less influence on mean fire severity, resulting in less than 3% effect on contemporary fire severity, and less than 4% effect on presettlement fire severity (Appendix B).

Simulated budworm defoliation disturbed almost twice the area during contemporary outbreaks relative to presettlement outbreaks (54 451 ± 1155 ha and 31 941 ± 1155 ha, respectively) (Fig. 4). While average defoliation severity (defoliation severity ranges from light [1] to severe [3]) was higher for contemporary (2.90 ± 0.002) vs. presettlement (2.87 ± 0.006) scenarios, both are very close to the maximum value of 3, indicating high severity at the cell scale. None of the sensitivity or uncertainty analyses changed the outcome of experimental treatments on area disturbed by budworm, and only one sensitivity variable (i.e., decreasing budworm host value by 10%) affected the treatment effect of time period on budworm disturbance severity. Absolute changes in area disturbed by budworm indicated sensitivity to variables different from those observed for fire (Appendix B). When all cohorts of balsam fir were killed within a cell if disturbed by budworm defoliation (as opposed to allowing the 10-year "advance regeneration" to survive), the total area disturbed by budworm was reduced by approximately 23% in both time periods. Notably, this change had virtually no effect on the fire response variables, presumably because live ladder fuels (i.e., balsam fir) compensated for dead ladder fuels (killed fir) (Appendix B). Sensitivity results for budworm disturbance were also not always intuitive. For example, decreasing the interval between outbreaks by 10% (i.e., increasing outbreak frequency) reduced the area disturbed by budworm (15% and 12% reduction for presettlement and contemporary time periods, respectively), but increasing the outbreak interval resulted in no difference (contemporary) or a slight reduction (presettlement time period) of area disturbed by budworm. Likewise, decreasing the tree species host value for budworm resulted in corresponding decrease in area disturbed, but increasing host value had little effect. Sensitivity and uncertainty simulations had virtually no effect on absolute values for average defoliation severity.

Vegetation and succession

The best ordination configuration for landscape species was represented by two axes, yielding a "fair" final stress value of 11.55 (Kruskal 1964). Axis 1 described the majority of variance ($r^2 = 0.74$) and represented compositional differences between presettlement and contemporary time periods (Fig. 5a). There were more red pine, white pine, and tamarack in the presettlement time period, and more shade-tolerant conifers (balsam fir, black spruce, and white cedar) in the contemporary time period. Axis 2 described an additional 16% of the variance, and represented a compositional trend common to both time periods. Wetland hardwood species (black ash and red maple), white spruce, and most shade-intolerant tree species (jack pine, quaking aspen, and paper birch) were negatively associated with axis 2 while white cedar was positively associated with axis 2. The two initial conditions (contemporary and presettlement) were both outliers in the ordination, particularly with respect to axis 2 (Fig. 5a). One additional outlier (a presettlement observation from year 300) was the legacy of an unusually large fire and contained a relatively high proportion of paper birch. This outlier was removed

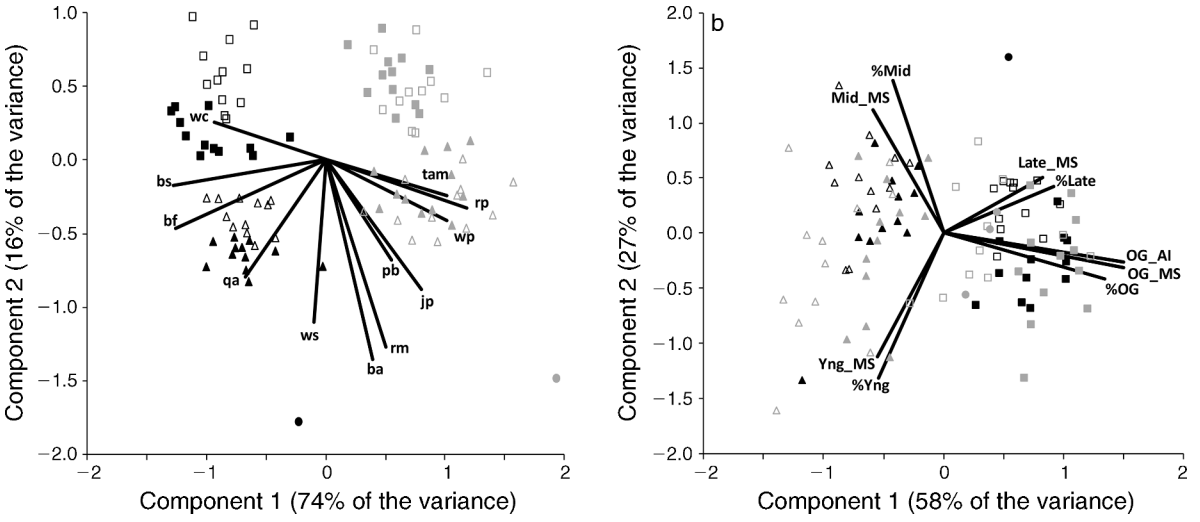

FIG. 5. Nonmetric multidimensional scaling ordination of (a) forest composition and (b) landscape structure of seral stages at simulation years 0 (circles), 150 (triangles), and 300 (squares) for contemporary (black) and presettlement (gray) scenarios. Open symbols represent scenarios without spruce budworm disturbance and solid symbols represent scenarios with spruce budworm disturbance. Vector length represents rank correlations (Kendall's τ) between variables and axes (minimum $\tau = 0.2$). Species abbreviations: bf, balsam fir; ws, white spruce; bs, black spruce; jp, jack pine; rp, red pine; wp, white pine; wc, northern white cedar; tam, tamarack; pb, paper birch; qa, quaking aspen; rm, red maple; ba, black ash. Seral stage abbreviations: Yng, early seral (1–60 yr); Mid, mid seral (61–120 yr); Late, late seral (121–180 yr); OG, old-growth >180 yr. Landscape metric abbreviations: %, percentage of land area; MS, mean patch size; AI, aggregation index.

from both ordinations, while initial conditions were retained for interpretation. Budworm disturbance had a subtle influence on forest composition, which was most obvious for the contemporary scenario, and negatively correlated with axis 2 (Fig. 5a).

The best ordination configuration for landscape seral stage structure was three axes, yielding a "good" final stress value of 7.5. Axis 1 described the majority of the variance ($r^2 = 0.58$) and represented a gradient from younger seral stages to old growth (Fig. 5b). A clear temporal pattern was detected across this axis, with year 150 containing more contiguous young and mid- seral stages than either initial conditions or observations from year 300. We interpret this pattern, observed for both time period treatments, as the break-up of old-growth areas from the initial conditions that reformed by year 300. The addition of budworm disturbance tended to retain comparably larger old-growth areas (Fig. 5b). Axis 2 ($r^2 = 0.27$) represented a gradient from young to mid-aged seral stages. There was a high degree of overlap between the treatments with respect to axis 2, with the presettlement time period scenarios indicating a relatively greater variation along this axis. Axis 3 ($r^2 = 0.12$; not shown) was positively correlated with the aggregation index of mid-seral stages, and primarily separated out the initial conditions for the presettlement scenario.

Examination of tree species trajectories identified a number of compositional similarities between presettlement and contemporary scenarios. Paper birch, black spruce, jack pine, and quaking aspen were abundant throughout both scenarios, with or without spruce budworm disturbance (Fig. 6). White spruce declined across all scenarios, but the decline was stronger when budworm disturbance was applied. In all cases, the decline in white spruce was offset by a concomitant increase in black spruce (Fig. 6). Yet compositional differences between contemporary and presettlement time periods were obvious when classified into forest types rank-ordered according to their value as budworm host (Fig. 7a). Nearly 50% of the landscape was occupied by forest types without budworm host during the presettlement period and fir codominance was rare. Mixed host and nonhost types were dominated by deciduous cover types in the contemporary scenario, and coniferous types for the presettlement scenario. With the exception of jack pine, the rank-order of budworm host quality roughly corresponds with increasing flammability of fuel types in terms of fire probability, spread rates, and fire severity (Fig. 7b).

Balsam fir showed only a slight response to budworm disturbance in terms of landscape abundance, which was inconsistent across contemporary and presettlement scenarios (Fig. 6). However, simulated defoliation disturbance had a strong and consistent influence on the age structure and aggregation of balsam fir. Without budworm disturbance, immature fir (oldest cohort $\leq$30 years old) represented 20% of the sites on average where balsam fir was present, compared to over 50% when budworm disturbance was applied. Balsam fir was also less aggregated when budworm disturbance was applied, with similar aggregation patterns observed for both time periods (Fig. 8). The low aggregation of fir in the initial conditions for the presettlement scenario reflects the

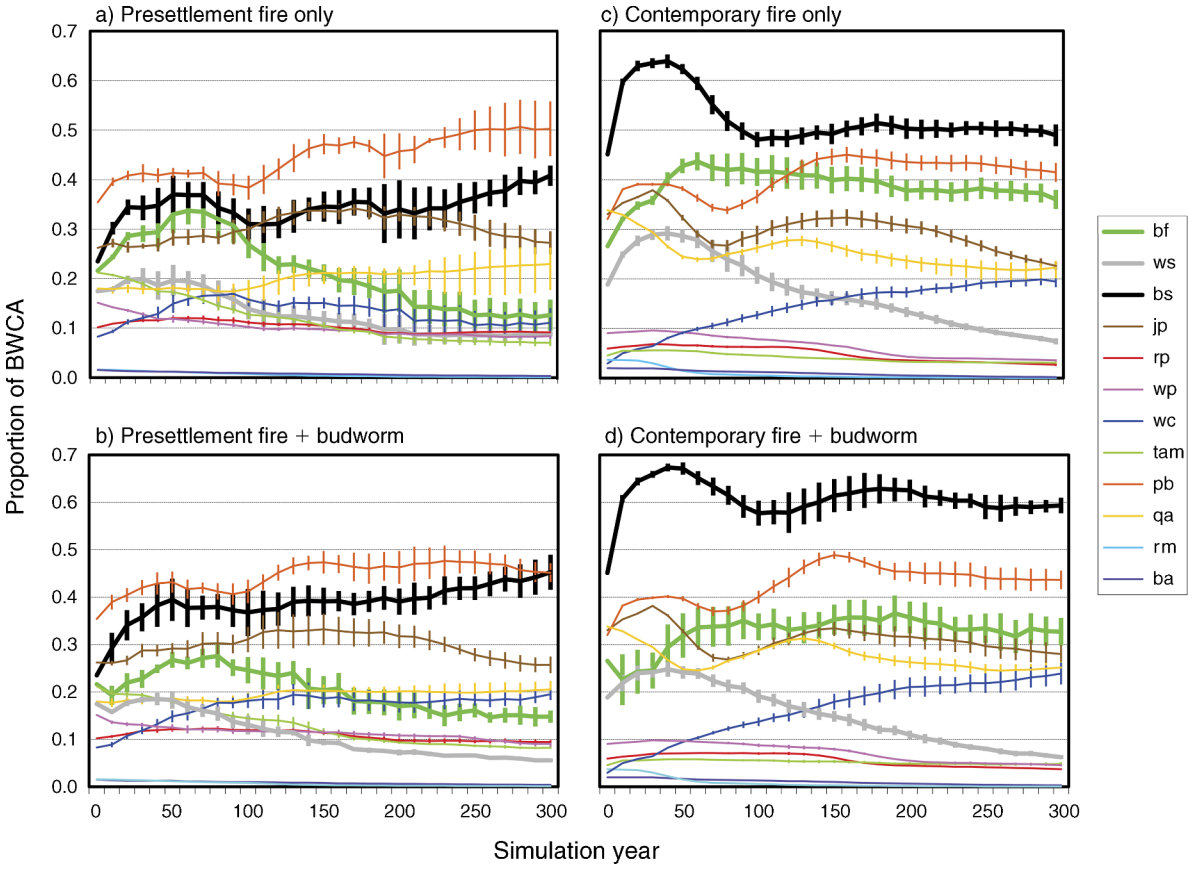

FIG. 6. Tree species presence throughout the simulations for each time period × budworm treatment. Values represent the landscape proportion of the BWCA averaged across the 12 replicates, with error bars representing 95% confidence intervals. Species abbreviations are as in Fig. 5.

initial probabilistic assignment of forest types. By contrast, the aggregation of fir shown for the initial condition of the contemporary scenario was based on tree species-level mapping via remote sensing. This moderate level of mapped fir aggregation was most similar to the simulated patterns of fir when spruce budworm disturbance was applied (Fig. 8). Sensitivity and uncertainty analyses applied to forest types showed that the parameters and assumptions affecting budworm disturbance corresponded strongly with those parameters affecting the relative abundance of balsam fir (Appendix B).

DISCUSSION

Fire–insect interactions

Conventional wisdom has held that tree mortality caused by insect disturbance enhances fire risk (McCullough et al. 1998). Empirical evidence from spruce budworm disturbance supports this viewpoint over short (i.e., year to decade) time scales. Experimental burns in mixed-wood stands similar to those found within the BWCA demonstrated that budworm-caused mortality increased spread rates and facilitated escalation of surface fires to crown fires (Stocks 1987). Fleming et al. (2002) found that the incidence of large fires (>200 ha) in Ontario occurred disproportionately during a limited time window following budworm outbreaks, and that this bias lasted the longest in the western part of the province in the immediate vicinity of the BWCA. Yet Fleming et al. (2002) also observed a decrease in fire incidence immediately beyond this time window. Our results were consistent with this latter result; compositional changes associated with budworm disturbance compensated for immediate fire risks associated with outbreaks, to the extent that long-term fire risk was reduced.

Based on the work of Fleming et al. (2002), we anticipated greater area burned during decades with simulated outbreaks in comparison with non-outbreak decades. Yet the simulated area burned between outbreak and non-outbreak decades were similar for both contemporary and presettlement scenarios. Though balsam fir is widespread across the BWCA, it is rarely dominant (Wolter et al. 2008); hence part of the discrepancy between Fleming's study and ours may be due to the mixed composition relative to true boreal forests further north. A companion simulation study

from central Quebec indicated that budworm did not influence area burned at the century scale, but did not examine outbreak vs. non-outbreak periods with respect to fire (James et al. 2011). While we did observe slightly higher severity of simulated fires during outbreak decades for the contemporary scenario, consistent with the observations of Stocks (1987), this difference was weak and not likely meaningful for either time period scenario. Contemporary fires are predominantly caused by humans and occur more often in spring in Minnesota (Cardille and Ventura 2001). Stands affected by budworm are most flammable in spring prior to the green-up of shrubs that increase the moisture of the forest floor within budworm-disturbed sites, reducing flammability during summer months (Stocks 1987). Presettlement fires, by contrast, were assumed to be predominantly summer fires based on the seasonal timing of lightning strikes in the region (Heinselman 1996). Lynch and Moorcroft (2008) found a decrease in fire frequency following western spruce budworm outbreaks in south-central British Columbia, and speculated that this reduced fire risk may be due to greater moisture on the forest floor within disturbed stands. Western spruce budworm generally causes less mortality in the overstory than eastern spruce budworm (Cooke et al. 2007).

Our results parallel recent investigations of interactions between bark beetle disturbance and fire in western North America. Fire history studies in Colorado, USA, found no evidence to support the traditional beliefs that spruce beetle (*Dendroctonus rufipennis*) disturbance enhanced fire frequency (Bebi et al. 2003) or spread (Kulakowski and Veblen 2007). Kulakowski et al. (2003) found that moderate to severe spruce beetle disturbance reduced the likelihood of burning in a subalpine forest, a result they attributed to enhanced moisture at the forest floor. Under certain circumstances, tree mortality caused by mountain pine beetle (*Dendroctonus ponderosae*) disturbance enhanced the spread of the 1988 fires in Yellowstone National Park (Lynch et al. 2006). Similar to our results, beetle-caused mortality often increases fire severity when burned (Turner et al. 1999, Kulakowski and Veblen 2007). Nonetheless, this response is neither consistently significant nor positive: it depends on the time since beetle disturbance, whether drought coincides with the burn, and how beetle disturbance severity influences vertical and horizontal connectivity of fuels (Knight 1987, Bigler et al. 2005, Derose and Long 2009). Similar to the work of Fleming et al. (2002) and the simulations presented here, these empirical studies find that beetle-caused changes in composition and structure have far more influence on subsequent fire activity than tree mortality per se (Bigler et al. 2005).

In summary, the combination of greater fir abundance during modern times and the shift in the fire season caused by humans does have the potential to enhance fire severity during budworm outbreaks. However we found this response to be weak when averaged across multiple simulated outbreaks within the BWCA. Further, the rank-order of budworm host quality roughly corresponds with increasing flammability of fuel types in terms of fire probability, spread rates, and fire severity (Fig. 7, Table 5). Budworm disturbance therefore reduces long-term fire risk at the landscape scale by decreasing the area and relative dominance of primarily fir and, to a lesser extent, white spruce.

Disturbance–vegetation interactions

The primary host of spruce budworm (balsam fir) has several life history traits that make it a strong competitor, including high shade tolerance, rapid growth response to available light, and wide environmental tolerance (Loehle 1988). These strengths are counteracted by several weaknesses including short longevity and sensitivity to both herbivory and fire (MacLean 1980, Loehle 1988). Disturbance is therefore fundamental to its distribution and relative dominance (Bergeron 2000). Nonetheless, Frelich (2002) downplayed the relative importance of spruce budworm as a factor affecting forest composition in the BWCA, arguing that balsam fir abundance in the area remains stable despite temporal fluctuations in age structure caused by spruce budworm disturbance, because the youngest cohorts generally survive the disturbance. This prediction is consistent with our simulation results; we found budworm had strong influence on the age structure of balsam fir, but far less effect on its landscape abundance. Further, mortality patterns caused by budworm disturbance tend to be patchy at fine spatial scales (Kneeshaw and Bergeron 1998), despite the landscape-to-regional extent of the disturbance (Williams and Birdsey 2003). Such fine-scale heterogeneity in mortality disaggregates balsam fir (Fig. 8), but also places seed-producing and disturbed sites in closer proximity than one might observe following a fire. We suggest it is the combination of advance regeneration and interspersion of seed sources with disturbed sites that maintains balsam fir composition in spite of repeated budworm disturbances. The cumulative response to such budworm–vegetation interactions in our study was a subtle compositional shift for both scenarios (Figs. 5 and 6).

The host-specific nature of insect disturbances can strengthen their dynamic interaction with forest conditions relative to other disturbance types. Indeed, empirical studies of budworm impacts indicate a range of system responses to budworm defoliation disturbance ranging from stand-replacing mortality to gap dynamics, depending on the composition at the time of the outbreak (Ostaff and MacLean 1989, Bergeron et al. 1995, Kneeshaw and Bergeron 1998, Belle-Isle and Kneeshaw 2007). The relative severity of past outbreaks can further influence damage caused by subsequent outbreaks by affecting the landscape abundance of susceptible host (Bouchard et al. 2006). Most of the

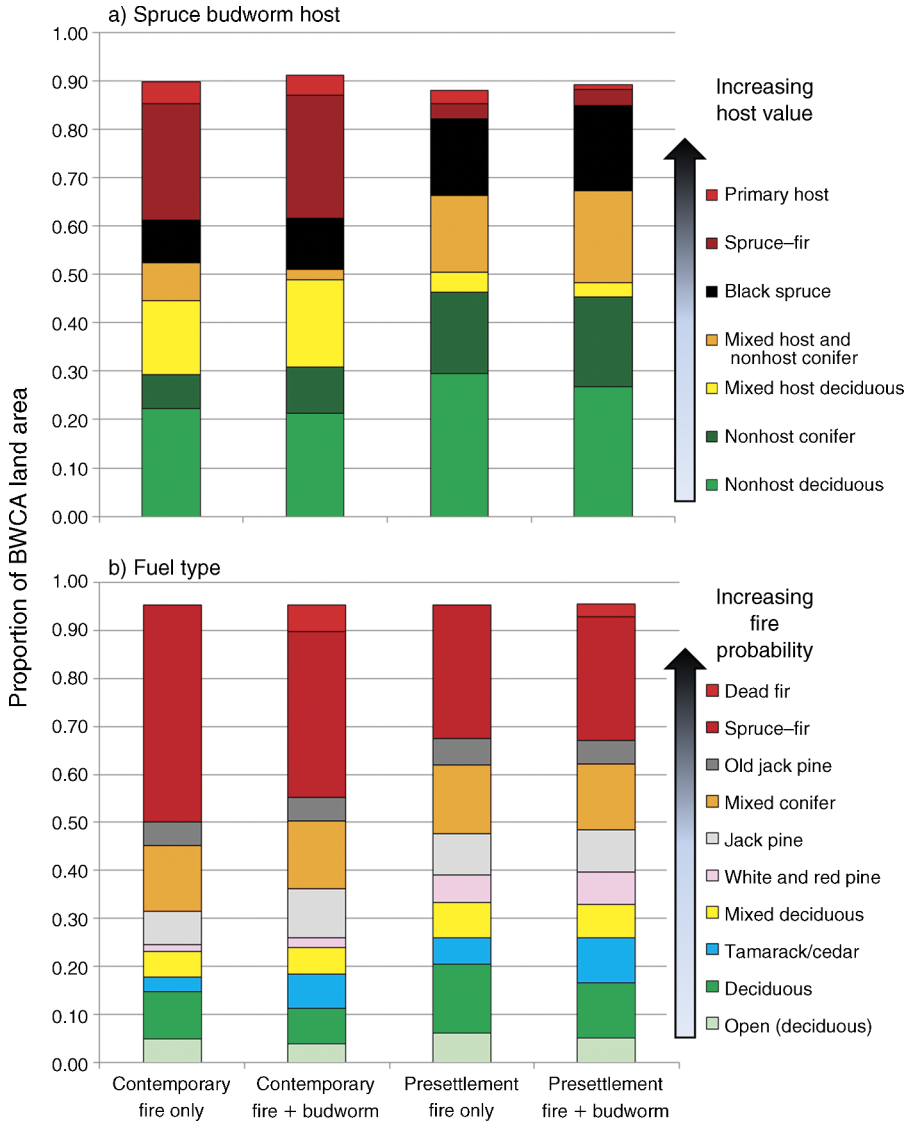

FIG. 7. (a) Forest type classified according to relative value as budworm host contrasted with (b) fuel types rank ordered by relative fire probability across the four experimental treatments. Values represent the landscape proportion of the BWCA averaged across the last five decades of the simulations and the 12 replicates.

variability in budworm damage observed between replicates for a given outbreak (Fig. 4) was due to time since the last outbreak and the fire disturbances in the decades leading to the outbreak, affecting the availability of susceptible fir.

Despite decades of academic discourse on the dynamic feedback between spruce budworm population dynamics and forest conditions (Holling 1973, Ludwig et al. 1978, Blais 1983, Royama 1984) there is as of yet no consensus regarding the explicit feedback between forest conditions and budworm population dynamics at landscape scales (Miller and Rusnock 1993, Royama et al. 2005). The only feedback between insect disturbance and forest conditions simulated within our scenarios was the proportion of host as it affects the area disturbed by the budworm. The recent integration of fire behavior models and landscape disturbance and succession models now allow dynamic feedback between forest conditions and fire disturbance (Perera et al. 2003, Sturtevant et al. 2009). Recent investigations of broad-scaled budworm–forest interactions are beginning to lay a foundation upon which analogous dynamic budworm disturbance regimes may be parameterized in the future (Candau and Fleming 2005, Gray 2008; Robert et al., *in press*).

Relative to insect disturbances, fire and its interactions with vegetation within the BWCA have been well studied both empirically (Heinselman 1973, Grigal and Ohmann 1975, Frelich and Reich 1995) and via simulation experiments (Baker 1989, Scheller et al.

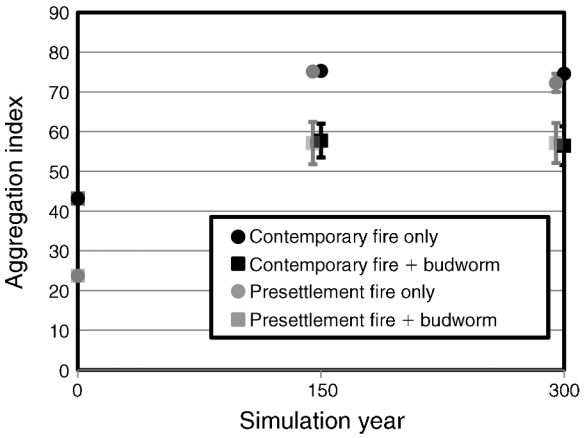

FIG. 8. Aggregation index (AI) applied to balsam fir >10 years old measured at 150-year intervals for contemporary (black) and presettlement (gray) scenarios. Circles represent scenarios without budworm disturbance, and squares represent scenarios with budworm disturbance. Error bars represent 95% confidence intervals.

2005, Shinneman et al. 2010). Our observed trend in the contemporary scenario toward a system with greater dominance of shade-tolerant conifers and mixed forests is broadly consistent with these studies. By explicitly simulating reciprocal feedback between forest vegetation and fire, our study quantified the extent to which such compositional changes are expected to enhance future fire risk. Mean fire rotations decreased to 240 and 275 years for contemporary scenarios without and with budworm, respectively (Fig. 3a), compared with the current fire rotation estimated at 426 years (Table 2). Our results further indicate that fire severity will be higher for future forests relative to the presettlement fire regime (Fig. 3b). Such changes to the fire regime may allow some fire-dependent communities such as jack pine to persist, whereas "big pine" communities dependent on frequent surface fires punctuated by infrequent crown fire may continue to decline over time (Fig. 6) (Palik and Gilmore 2005).

Contrary to our expectations, landscape structure of seral stages did not differ substantially between time period treatments (Fig. 5b). This result is especially curious given that presettlement fires were over an order of magnitude larger than those simulated for the contemporary scenario (Table 2). However the lower severity of presettlement fires allowed some older tree cohorts to survive the disturbance, resulting in residual forests that broke up the connectivity of the simulated burn patterns. Budworm disturbance in these mixed forests is best characterized as a partial disturbance, affecting only the pattern of its host (Fig. 8). By reducing area burned, and retaining old cohorts of nonhost species, budworm disturbance therefore shifted the landscape age structure toward more old-growth forest (Fig. 5b).

Study limitations

Our simulation experiment was simplified to focus on interactions among budworm, fire, and vegetation under conditions for which we had a reasonable empirical basis for comparison among treatments. Several potentially important drivers were therefore excluded from the experiment. Principle among these was climate change both past and future. Other simulation studies have examined the effects of future climate change on vegetation dynamics in this area (Xu et al. 2007, Ravenscroft et al. 2010). Under future warming scenarios both fir and spruce are anticipated to decline in dominance, although the results are sensitive to how these species physiologically respond to enriched CO_2 (Xu et al. 2007). While spruce budworm may exacerbate this decline (Fleming 1996), budworm population dynamics are also influenced by climate and recent analysis suggests a decline in budworm activity along the southern extent of its range (Gray 2008, Régnière et al. 2010). Analogously, the presettlement forests developed under the cooler climate conditions of the Little Ice Age, presumably affecting vegetation, fire, budworm, and their interactions (Bergeron 1998, Weir et al. 2000, Bouchard and Pothier 2008). Future warming effects on precipitation and water budgets remain among the most uncertain in climate model forecasts (IPCC 2007), though most indications are that the BWCA region will become drier (Frelich and Reich 2010). The direction of such changes are critically important for vegetation dynamics on the shallow soils characteristic of the BWCA (Appendix A), and could substantially influence future disturbance interactions (Frelich and Reich 2010).

Explicit feedback between forest conditions and budworm outbreaks in our simulations were limited to defoliator impacts given local and neighborhood forest composition (Table 6). While these relationships are well documented, relative susceptibility of some tree species, particularly black spruce, may be dependent on the amplitude of the budworm population outbreak (Régnière and Nealis 2008). Recent research in the study region suggests that landscape-scale forest conditions may additionally influence the spatial scale (i.e., synchrony), frequency, and intensity of budworm outbreaks (Candau and Fleming 2005; Robert et al., *in press*). Budworm outbreak patterns result from complex, multi-scaled interactions among budworm populations, weather, tree communities, and a complicated food web of predators, parasitoids, hyperparasitoids, and pathogens (Eveleigh et al. 2007), making predictions of outbreak response to future forest conditions problematic (Gray 2008). Nonetheless, both relative tree species susceptibility and spatiotemporal outbreak patterns may change dynamically depending on forest conditions, suggesting potentially stronger feedback processes than those simulated here.

Application of a presettlement fire regime to presettlement vegetation should theoretically lead to stable

forest conditions at the landscape scale. While simulated forest conditions were broadly consistent with our understanding of presettlement forests of the region (Friedman et al. 2001), some observed trends suggested potential discrepancies between actual drivers and simulated processes. For example, tamarack was relatively common as an upland species based on the GLO data, perhaps due to a lack of competition from other species (Gower and Richards 1990). Thus the decline in tamarack (Fig. 6a and b) indicates we may have under-simulated presettlement surface fire history. Indeed, Heinselman's (1973) fire data represent stand-replacing fires, whereas our fires included both surface and crown fire impacts. Decreasing fire rotations to account for surface fire activity may have promoted more tamarack as well as pine. Nutrient-cycling dynamics also influence composition, particularly between conifer and hardwood species (Reich et al. 2001). By ignoring such feedbacks, the balance between conifer and hardwood species may have been affected; this may explain the increasing trend in presettlement birch and aspen (Fig. 6a and b). Forest composition estimated by the GLO data is of course only a short-term indicator of past conditions, and evidence from Baker (1989) suggests that the BWCA landscape is not in equilibrium with its fire regime. Nonetheless, our simulations should not be interpreted as a direct representation of presettlement forest dynamics, nor an actual projection of future forest conditions. Rather our results provide insights into the long-term nature of the insect–budworm–vegetation interaction difficult or impossible to examine using traditional empirical methods alone.

Conclusions

Budworm disturbance has traditionally been viewed as a symptom of past fire suppression policies (Heinselman 1996) and its impacts are clearly visible to a concerned public. Popular perception that such insect disturbances enhance wildfire risk further contributes to the perception of budworm as a "forest health problem" to be solved (Dombeck et al. 2004). Yet evidence of budworm outbreaks in the immediate vicinity of the BWCA has been dated to the early 19th century (Blais 1983), and in other regions spruce budworm outbreaks have affected spruce–fir forests for millennia (Simard et al. 2006). Our study suggests that budworm serves as a natural thinning agent that decreases live ladder fuels by periodically reducing balsam fir content. Returning to the relationships depicted in Fig. 1, the dead ladder fuels contributed by the budworm disturbance have a transient and variable effect on area burned, while the live ladder fuels have a longer-lasting and consistent effect on area burned. The net effect is a reduction of fire risk over long time scales (decades to centuries).

Budworm influence on forest composition is subtle relative to fire, to the extent that budworm disturbance is unlikely to change the direction of compositional change now occurring in the BWCA. Our projected trend, in the absence of climate change, indicates a system dominated by late-successional conifers, more severe fire, and more extensive budworm damage relative to presettlement forests. The combination of changing environment, disturbance regimes, and their interactions with the vegetation of the BWCA presents a formidable challenge to managers seeking to restore forest communities. Similar challenges face land managers across the boreal forest, while analogous challenges face land managers across the globe. Modeling approaches such as this can help tease apart such interactions to provide strategic management guidance in the face of local, regional, and global change.

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Supplemental Material

Appendix A

Expanded model parameterization methods (*Ecological Archives* A022-067-A1).

Appendix B

Sensitivity and uncertainty analysis summary (*Ecological Archives* A022-067-A2).