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ABSTRACT

The persistence of landscape-scale disturbance legacies in forested ecosystems depends in part on the nature and strength of feedback among disturbances, their effects, and subsequent recovery processes such as tree regeneration and canopy closure. We investigated factors affecting forest recovery rates over a 25-year time period in a large (6 million ha) landscape where geopolitical boundaries have resulted in important land management legacies (managed forests of Minnesota, USA; managed forests of Ontario, Canada; and a large unmanaged wilderness). Stand-replacing disturbance regimes were quantified across management zones, both inside and outside a central ecoregion, using a time series of classified land cover data constructed at 5-year intervals between 1975 and 2000. The temporally variable disturbance regime of the wilderness was characterized by fine-scaled canopy disturbances punctuated by less frequent large disturbance events (i.e., fire and blow down). The comparably consistent disturbance regimes of the managed forests of Minnesota and Ontario differed primarily in the size distribution of disturbances – principally clearcut harvesting. Using logistic regression we found that a combination of time since disturbance, mapped disturbance attributes, climate, and differences among management zones affected pixel-scale probabilities of forest recovery that reflect recovery rates. We conclude that the magnitude of divergence in landscape disturbance legacies of this region will be additionally reinforced by regional variations in the human and natural disturbance regimes and their interactions with forest recovery processes. Our analyses compliment traditional plot-scale studies that investigate post-disturbance recovery by (a) examining vegetation trends across a wide range of variability and (b) quantifying the cumulative effects of disturbances as they affect recovery rates over a broad spatial extent. Our findings therefore have implications for sustainable forestry, ecosystem-based management, and landscape disturbance and succession modeling.

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1. Introduction

Spatial legacies of forest disturbances can persist from decades to millennia (Foster et al., 2002). Such legacies may include persistent spatial structure (Schoennagel et al., 2008), forest age distributions (James et al., 2007; Fenton et al., 2009), compositional patterns (Bouchard et al., 2006; Rhemtulla et al., 2009), and ecosystem characteristics such as nitrogen retention and carbon balance (Houlton et al., 2003; Pan et al., 2011). Legacies can result from a single broad-scale event that abruptly changes the character of the system (Foster et al., 1998; Schoennagel et al., 2008), or from the cumulative effects of many smaller-scale disturbances that entrain system dynamics – such as patch structure – over time (Spies et al., 1994). Understanding the processes that affect the persistence of such legacies over time is critical for ecosystem-based management (Grumbine, 1994) and the development of strategies to help mitigate or adapt to novel disturbance regimes (Buma and Wessman, 2011).

The persistence of spatial structure in forested landscapes affected by stand-replacing disturbance (i.e., a landscape-scale disturbance legacy) is determined by the processes of forest recovery and succession. Here we define forest recovery to mean the canopy closure of the young replacement trees following a disturbance event that removed the overstory trees (Swanson et al.,

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2011). Under this definition, forest recovery rates define the window of time over which disturbance-caused fragmentation persists and has the capacity to influence future disturbances and ecosystem services, such as wildlife habitat (Turner et al., 2001). In many systems forest recovery can be delayed due to either poor tree recruitment (Foster, 1983; Simard, 2009), competition with established understory vegetation (Royo and Carson, 2006; Gilliam, 2007), or both (Lavoie and Sirois, 1998). Such delays have long-term consequences for landscape age structure, with implications for sustainable forestry (Doyon et al., 2011), carbon storage (Pan et al., 2011), insect outbreaks (Robert et al., 2012), and wildlife habitat (Manolis et al., 2002; King et al., 2009; Landriault et al., 2012).

While processes affecting forest recovery, such as site productivity, seedbed conditions, proximity to seed source, and ability to reproduce vegetatively have been well-studied at fine spatial scales (Greene et al., 1999), it is not clear how these processes scale-up to affect forest recovery rates at broader landscape scales. Plot-scale studies are, by necessity, limited to a subset of conditions affecting variation in recovery patterns that may be context-dependent (e.g., Foster and King, 1986). Spatially continuous data sets derived from remote sensing provide opportunities to evaluate post-disturbance vegetation trends across a much wider range of variability than could be achieved through plot-scale analysis alone. Several studies have used such data to study both forest disturbance and recovery rates within tropical forest systems (Chazdon, 2003; Crk et al., 2009). In contrast, land cover change studies from temperate and boreal biomes focus primarily on disturbance patterns (Turner et al., 1996; Cushman and Wallin, 2000; Cohen et al., 2002). The few landscape-scale studies that investigated forest recovery confirm that recovery patterns vary depending on the type of disturbance and the spatial context under which the disturbance occurred (Schroeder and Perera, 2002; Schroeder et al., 2007). We are not aware of any empirical temperate or boreal studies that explicitly examine the interactions among disturbances and recovery patterns.

We examined forest recovery within a 25-year time series of land cover maps at five year intervals within a large (~6 million ha) landscape at the international boundary between Minnesota (USA) and Ontario (Canada) (Fig. 1). The landscape is centered on the Border Lakes Ecoregion (BLE; 2 million ha), where political boundaries separate divergent forest disturbance histories: a central conservation zone (natural disturbance only), a fine-grained forest management zone characterized by small cut blocks in Minnesota, and a coarse-grained forest management zone characterized by large cut blocks in Ontario (Shinneman et al., 2010; James et al., 2011). Comparison of recovery rates across such divergent land management histories within the same ecoregion minimizes confounding effects of variation in biophysical covariates to focus on interactions between disturbance regimes and forest recovery patterns. For context, managed lands within a 50 km buffer surrounding the BLE were separately analyzed to determine relative consistency in disturbance regimes, composition, and recovery patterns inside and outside the focal ecoregion.

Stand-replacing disturbance regimes were quantified across the differently managed zones, both inside the BLE and within a 50 km buffer surrounding the BLE (Fig. 1), in terms of disturbance rates, patch size distributions, and vegetation pre- and post-disturbance using a time series of classified land cover data constructed at 5-year intervals between 1975 and 2000. We compared multiple logistic regression models that predicted pixel-scale annual forest recovery probabilities (i.e., probability of a disturbed pixel recovering to forest each year). *A priori* models were evaluated in two steps to address two related questions. First, what combination of time-dependence and measurable disturbance attributes best predicts the rate of forest recovery? Second, to what extent, if any, do climate variables or unmeasured differences among management and ecoregion zones improve predictions from step 1? The most plausible models emerging from step 2 provide insights into how disturbance in the different forest zones affects forest recovery rates, the extent to which the study design controlled for biophysical drivers, and the degree to which spatial covariates can help predict future forest recovery patterns.

2. Methods

2.1. Study area

The Border Lakes Ecoregion (BLE) crosses the international border between Ontario (Canada) and Minnesota (USA) and lies within the transition zone between the Great Lakes-St. Lawrence mixedwood and boreal forest regions (Fig. 1). Geology of the BLE is dominated by Precambrian bedrock that was scoured by past glacial activity, leaving a thin layer of silty to sandy glacial till and areas of bare bedrock, and is typified by a high density of lakes and wetlands (Superior Mixed Forest Ecoregional Planning Team, 2002). Forest types are best described as "near boreal" (Heinselman,

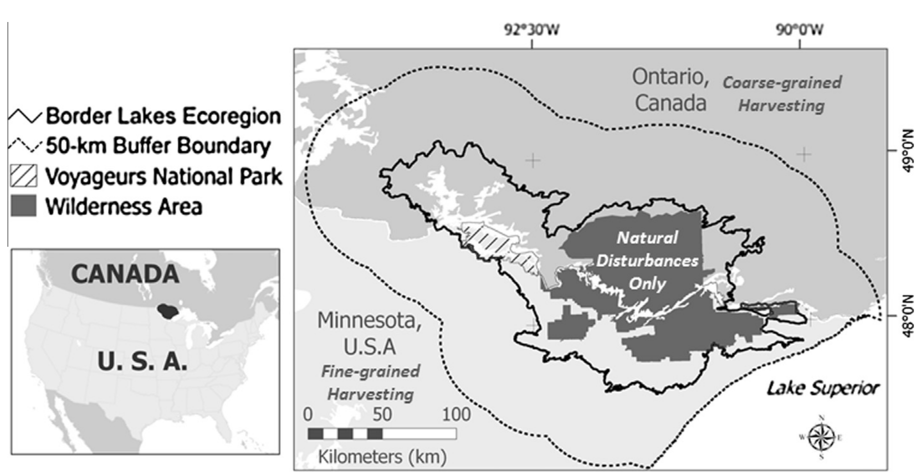

Fig. 1. Study area. The focus area is the Border Lakes Ecoregion that contains three zones: Minnesota managed forests, Ontario managed forests, and wilderness. A 50-km buffer surrounding that ecoregion contains additional managed lands in Ontario and Minnesota, for a total of five zones analyzed. The area within Voyageurs National Park is dominated by water, and therefore not included within our analysis.

1973) with a high proportion of boreal tree species (i.e., *Pinus banksiana*, *Picea mariana*, *Picea glauca*, *Abies balsamea*, *Populus tremuloides*, *Betula papyrifera*, *Larix larcinia*), as well as tree species near the northern limit of their range (e.g., *Pinus strobus*, *Pinus resinosa*, *Acer rubrum*). Included in the BLE are mixed-ownership timber-managed (referred to hereafter as "managed") forests in Minnesota that include the Superior National Forest and Kabetogama State Forest, as well as managed forest in Ontario (Shinneman et al., 2010). Forest harvest patterns diverged sharply between Minnesota and Ontario approximately 50 years ago, coinciding with mechanized clear-cutting operations (primarily for pulpwood) on both sides of the border. In particular, clearcuts within managed Canadian forests were comparatively larger in size than managed American forests to the south (James et al., 2011). Between these managed regions lies an approximately 1 million-ha wilderness and recreation area that includes Quetico Provincial Park in Ontario and the Boundary Waters Canoe Area Wilderness in Minnesota where no timber harvest has occurred since the early 1970s. Other disturbances occurring within the study area include wildfires and blow down – including the very large "Independence Day" blow down event that occurred within the wilderness area on July 4, 1999 (Frelich, 2002).

We divided the BLE into three management zones – Wilderness, Minnesota managed, and Ontario managed (Fig. 1). The use of the BLE controls for biophysical factors affecting forest recovery because it is internally similar in terms of climate, soils, land forms, and forest composition. Given the scale of the BLE, climatic gradients across its land area are nonetheless expected. Step 2 in our analysis (see Section 2.4) was included to account for such gradients. In addition, we included a 50-km buffer area surrounding the BLE to create two additional managed zones, one each for Ontario and Minnesota, for a total of five analysis zones encompassing 6 million ha. Zones outside the BLE represent a more diverse range of edaphic, topographic, and climatic conditions ranging from the steep and climatically moderated north shore of Lake Superior to the flat Southern Agassiz Peatlands dominated by lowland conifer forests to the west (Superior Mixed Forest Ecoregional Planning Team, 2002). Hence the comparison of management zones within the BLE focuses on the effects of forest management on spatial legacies (i.e., disturbance patch structure and forest recovery rates) while controlling for biophysical covariates. The comparison of similarly managed zones inside and outside the BLE focuses on the effects of biophysical differences while controlling for land management practices. Because the wilderness falls almost exclusively within the BLE, we did not divide wilderness into separate spatial zones. The Voyageurs National Park also falls within the extent of our study area, but was excluded from our analysis because its area is dominated by islands and water (Fig. 1).

2.2. Mapped land cover and forest disturbances

Land cover and forest disturbances were mapped at five-year intervals from 1975 to 2000 using a combination of Landsat MSS, TM and ETM+ datasets (Wolter et al., 2012a). Landsat MSS data were resampled to 28.5 m resolution using a nearest neighbor transformation to duplicate the spatial resolution of the Landsat TM and ETM+ sensor data. Landsat MSS, TM, and ETM+ data were all transformed to top of atmosphere reflectance using their respective sets of calibration coefficients according to Price (1987), Thome et al. (2004). The original 1990 "base classification," from which change classes prior to 1990 and after 1990 were determined, was a near-species level forest cover classification (Wolter and White, 2002) derived using a layered multi-temporal classification process (Lozano-Garcia and Hoffer, 1985). Spatially-explicit Phase II forest inventory data (Minnesota Department of Natural Resources) and 1:40,000 color infrared aerial photographs (May and September 1991) served as ground truth and validation data, with an overall accuracy of 75% (Kappa = 74%) (Wolter and White, 2002). This near-species level classification was then recoded to Anderson level II classes (Anderson et al., 1976): water, emergent vegetation, sphagnum bog, "grass" (a combination of grasses & forbs), brush, conifer regeneration, hardwood regeneration, and conifer, mixed, and hardwood forest types. Upland and lowland vegetation classes (e.g., upland conifer vs. lowland conifer) were further differentiated using available wetland inventories (Wilen, 1990; Wulder et al., 2003). Final overall accuracy and forest class accuracy in the simplified 1990 base classification increased to 89% and 79% (Kappa = 87% and 77%), respectively (Wolter et al., 2012a, Appendix A).

Vegetation change between time periods (e.g., 1985 and 1990) was quantified using the normalized difference moisture stress index (NDMSI; see Hunt and Rock, 1989; Wilson and Sader, 2002; Wolter and White, 2002) applied to leaf-on imagery from the respective time periods. Pixels that showed differences in this index >1.5 standard deviations (+/−) between time periods were designated as changed pixels; all others were considered unchanged. Change analysis between dates involving MSS (1975–1980) or MSS and TM (1980–1985) imagery used differences in visible red reflectance between image dates because the MSS sensor did not have a shortwave infrared band required to calculate NDMSI (Desclée et al., 2007). Pixels identified as changed were classified using an iterative, self-organizing, maximum likelihood classifier into one of the 17 cover classes. Leaf-off winter Landsat images were used to identify conifers below hardwood overstory to more accurately discern the hardwood, conifer, and mixed-wood forest classes (Wolter et al., 2008). Pixels mapped as a forest type at one time step, but classified as a transitional cover type (i.e., grass, brush or regenerating forest) in the next time step, were assumed to be disturbed during the time interval between classification dates. Finally, large natural disturbances (i.e., fire and blow down $\geqslant$ 100 ha) were identified using their unique spectral signatures observed within the entire Landsat archive (1972–2000), where selected pixels were reclassified to distinguish these large disturbance types from all other disturbances (Wolter et al., 2012b).

2.3. Forest disturbance regimes

Patches of disturbed forest were defined using an eight-neighbor rule to enhance connectivity of forest openings in a landscape dominated by forest, applied to forest disturbance maps for each of the five-year time periods using Fragstats (v3.3, McGarigal et al., 2002). Patches were assigned to one of the five zones within the differently managed areas of the BLE (Fig. 1) and patches that overlapped zone boundaries were assigned to the zone containing the majority of the patch area, where ties between zones were decided randomly. In spite of our efforts to convert imagery to common spatial and radiometric resolutions, examination of the 1985 forest disturbance map indicated that some of the mapped disturbances between 1980 and 1985 were an artifact of the change in Landsat sensors (i.e., MSS to TM/ETM+). This is the result of uncorrectable differences in resolving power between these sensors (MSS and TM/ETM) – resulting in fine-grained "changes" in forest cover between 1980 and 1985 (Moore and Bauer, 1990). We reduced the influence of this artifact by defining the minimum forest disturbance patch size as 4 ha for all dates (Appendix A).

The proportion of forest land area disturbed and disturbance patch size distributions were estimated for each zone and time period combination. Patch size distributions were area-weighted, where the frequency of a given size observation was multiplied by the number of disturbed cells within the patch (Turner et al., 2001). We evaluated differences among area-weighted disturbance patch size distributions using zone and time period as fixed effects within a generalized linear mixed model (PROC GLIMMIX; SAS version 9.2). We used a lognormal distribution and identity link function, with post hoc comparisons contrasted using Tukey's comparisons and significance assessed at $\alpha = 0.05$. We further examined ecosystem (i.e., upland or lowland) and compositional (i.e., hardwood, conifer, or mixed) bias of forest disturbances by comparing disturbance rates in each of the six ecosystem and composition combinations against their landscape proportional abundance by time period and zone.

2.4. Forest recovery

We tabulated the transitional cover type following forest disturbance over time to estimate type-specific recovery rates at the scale of the study landscape. We then estimated forest recovery probabilities using logistic regression within the program MARK (White and Burnham, 1999) and its companion package for R (v2.12.1, R Development Core Team, 2010), RMark (v1.9.9, Laake and Rexstad, 2012). We considered each disturbed pixel to be a marked individual and tracked its condition (transitional or forest) through "recaptures" at each 5-year interval available from the imagery. Because we could track each pixel throughout the time series, we set the recapture probability to 1. The program estimates the "survival" probability of disturbed cells, which was converted to recovery probability (i.e., $P_{\text{recovery}} = 1 - P_{\text{disturbed survival}}$). Due to the large number of pixels in the landscape, we performed the analysis on a one-percent subset ($n = 91{,}144$ disturbed pixels) randomly selected from the full dataset of nearly 10 million disturbed pixels across the time series.

We developed four sets of *a priori* candidate models for evaluation based on hypothesized relationships between the predictor variables and forest recovery probability (Table 1, Appendix B). Within a model set, plausible models were selected using Akaike's Information Criterion adjusted for sample size and overdispersion ($QAIC_C$, Burnham and Anderson, 2002). Candidate models were ranked according to $QAIC_C$ values, and model weights (w_i) were calculated to provide the weight of evidence for each model. We evaluated the sensitivity of candidate model weight of evidence to variability in $\hat{c}$ (overdispersion) using integer values of $\hat{c}$ ranging from 1 to 4 (Bartzen et al., 2010). A $\hat{c}$ value of 1 is equivalent to assuming no overdispersion, and overdispersion factors are typically not larger than 4 if the model structure is correct (Burnham and Anderson, 2002). Alternative models with $w_i \geqslant 0.05$ (across any of the 4 levels of $\hat{c}$) were considered plausible and retained as candidates for model set combinations. Step 1 of our analyses addressed our first question by selecting the most plausible models based on disturbance attributes and time dependence variables (Table 1, Appendix B). Step 2 of our analyses addressed our second question by combining plausible Step 1 models with Climate and Management/Ecoregion Zones variables (Table 1, Appendix B). Climate variables for Step 2 were defined by three orthogonal axes from a principal component analysis of spatially interpolated monthly climate normals averaged across the time period corresponding with the study (1976–2000; McKenney et al., 2006) (Appendix B). The first component (PC1) was negatively correlated with summer temperature and positively correlated with precipitation during leaf-off periods, generally increasing from west to east. The second component (PC2) was negatively correlated with winter temperature and corresponded with increasing latitude. The third component (PC3) was negatively correlated with late summer precipitation and positively correlated with summer and fall minimum temperatures, and corresponded primarily with the moderated climate along the Lake Superior shoreline.

We evaluated the goodness-of-fit for the final models resulting from Step 2 using the deviance chi-square test and the Hosmer–Lemeshow test (Lemeshow and Hosmer, 1982). We used the rescaled R^2 (Nagelkerke, 1991) to compare fitted model deviance to null model (intercept-only) deviance as an additional relative mea-

Table 1
Candidate model summary and independent variable predictions for probability of forest recovery (Appendix B).

Independent Variables	Description	Predictions[a]
Disturbance attributes		
Transitional type (TT)[b]	Fire, Grass, Brush, Regeneration	F < G < B < R
Ecosystem Type (ET)	Lowland, Upland	L < U
Prior Forest Type (PFT)[c]	Hardwood, Mixed, Conifer	H > M > C
Distance to Nearest Edge (LOGDIST)	Log10 distance (m) (continuous)	–
Alternative Candidate Models	Null + individual (4) + additive (10) + multiplicative (8) = 23	
Time dependence		
Year of Transition ($YEAR_T$)	Year transition was detected	?
Year of Disturbance ($YEAR_D$)	Year disturbance was detected	?
Time Since Disturbance (AGE)	Age classes defining time since disturbance	+
Sensor Artifact (ARTIFACT)	Time periods[d] potentially affected by the change in Landsat sensor	?
Alternative Candidate Models	Null + individual (3) × ARTIFACT combinations (7) = 22	
Climate[e]	Principle components (continuous) defining climatic variation	
PC1	West to east, increasing summer temp, decreasing leaf-off precip	?
PC2	South to north, decreasing winter temp	–
PC3	Increasing proximity to Lake Superior, decreasing late summer precip, increasing summery & fall min temp	+
Alternative Candidate Models	Null + complete additive (1) = 2	
Management zones		
Management type	Managed, Wilderness	?
Regional Management	Minnesota Managed (MN), Ontario Managed (ON), Wilderness (Wild)	?
Regional Management × Ecoregion[f]	MN inside BLE (MN_BLE), MN outside BLE, (MN_Buff), ON inside BLE (ON_BLE), ON outside BLE (ON_Buff), Wilderness (Wild)	?
Alternative Candidate Models	Null + individual (3) = 4	

[a] Direction of association (+, −) with a continuous variable, or rank order of ordinal variable (e.g., $x < y$). Question mark (?) means no *a priori* prediction (i.e., exploratory).
[b] Transitional cover type immediately following disturbance.
[c] Forest type immediately before disturbance.
[d] 1980–1985 transition = t_1; 1980–1990 transition = t_2; 1985–1990 transition = t_3 (Appendix A).
[e] Climate component descriptions describe underlying correlations.
[f] Border Lakes Ecoregion (BLE).

sure of model improvement. To evaluate the relative influence of the different covariates, we calculated predicted recovery probabilities using the mean values (continuous) or proportional distribution (categorical) for each covariate to generate effect displays (Fox, 2003), which graphically depict the response values across a range of values for a single covariate while all others are held constant.

3. Results

3.1. Forest disturbance regimes

Rates of disturbance were generally higher within managed forests relative to wilderness, but similar between the managed zones of Minnesota and Ontario (Fig. 2a). We attribute the apparent increase in area disturbed during the 1985 time step to change in resolution between Landsat MSS and Landsat TM sensors. Restricting forest disturbances to those patches greater than 4 ha reduced this artifact but did not eliminate it (Appendix A). Also, disturbance rates in Minnesota managed areas were reduced more by the minimum patch size restriction than the other zones, likely because some harvest blocks were smaller than this threshold within this zone. Nonetheless, all subsequent results are reported using a minimum patch size of 4 ha. With the exception of the 1990 time step, the area of disturbed forest increased through time within wilderness (Fig. 2b). Disturbance rates within managed areas of Ontario also increased over time, though the increase was most apparent outside the BLE. Disturbance rates in Minnesota managed areas remained comparatively stable until a notable decrease in disturbances in the last time step (Fig. 2b).

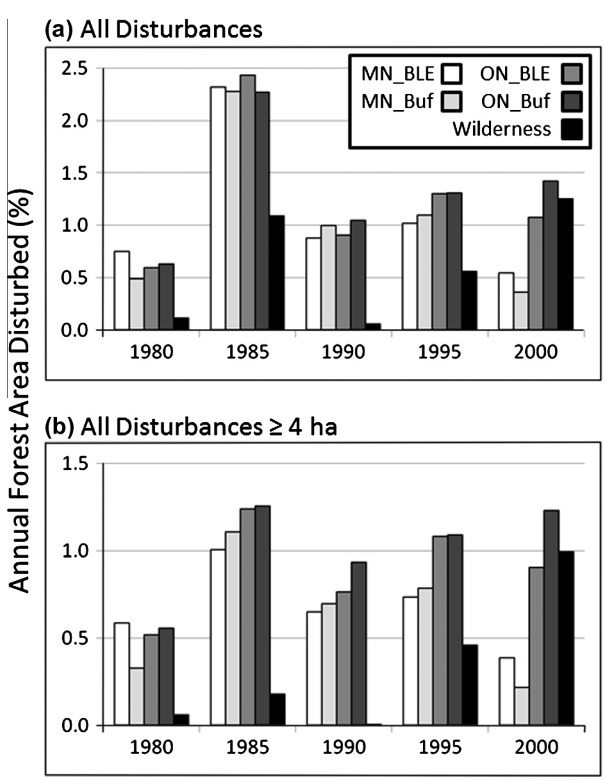

Fig. 2. Annual percent of total forest area disturbed by zone and time step. (a) No minimum disturbance patch size, and (b) Minimum disturbance patch size of 4 ha. The year label represents the 5-year period ending with the year indicated. Zones are identified by the following abbreviations: managed areas of Minnesota (MN), managed areas of Ontario (ON), Wilderness, managed areas inside the Border Lakes Ecoregion (BLE), and managed areas in the surrounding 50-km buffer (Buf).

The majority of canopy-replacing forest disturbances converted forests to grass (i.e., graminoid and herbaceous), followed by brush and then regenerating tree cover (Fig. 3). The area affected by large natural disturbances (fire and blow down) varied between less than one percent and 18% of the total disturbed area in time steps 1990 and 2000 respectively (Fig. 3a), but accounted for 75% of the disturbed forests in the wilderness over the 25-year period (Fig. 3b). Tree regeneration was more common immediately following disturbances in Minnesota than in other management zones (Fig. 3b).

Forest disturbances in managed areas of Minnesota indicated positive transition bias toward both upland conifer and upland hardwood cover types and a negative bias against lowland conifer (Fig. 4). Forest disturbances in managed areas of Ontario were biased toward upland conifer but against upland hardwood, with no apparent bias observed for lowland conifer. Wilderness disturbances varied strongly with respect to type bias through time. Disturbances for the 1985 time step suggest bias toward disturbance of upland hardwood was common across all zones, suggesting the artifact due to change in sensor may have itself had a compositional bias. Compositional biases for all zones indicated a trend towards neutral by the final time step (Fig. 4).

Zone had the strongest effect on area-weighted patch sizes ($F_{4,31605} = 1537$, $p < 0.0001$) followed by disturbance year ($F_{4,31605} = 240$, $p < 0.0001$) and a significant interaction term ($F_{16,31605} = 145$, $p < 0.0001$). Area-weighted disturbance patch distributions were the most consistent through time in Minnesota managed zones, and least consistent through time within wilderness, where the wilderness zone included both the smallest and largest mean area-weighted patch sizes in different time steps (Fig. 5). Mean area-weighted patch size distributions in managed zones of Minnesota were an order of magnitude smaller than those observed in managed zones of Ontario early in the time series, but Ontario patch sizes declined through time to approach the size distributions for managed areas of Minnesota. Area-weighted patch size distributions were very similar across the ecoregion boundaries after accounting for the differently managed zones (Fig. 5).

3.2. Forest recovery

The transitional type following forest disturbance generally followed a logical pattern from grass to brush to regeneration to forest through time, while large burns had the longest recovery time (Table 2). Land cover transitions indicated that a substantial amount of disturbed forests remained as transitional cover 16–20 years post-disturbance, particularly when the forest was disturbed by large burns or reduced to a grass (i.e., herbaceous) state. Six candidate Step 1 models received weights > 0.05 across all values of $\hat{c}$, each with similar goodness-of-fit statistics (i.e., rescaled R^2). All of these plausible models included each of the individual disturbance attribute variables, AGE, and ARTIFACT variables representing change-detection artifacts introduced by the change in sensor from MSS to TM that affected 1980–1985 and 1985–1990 transitions (Table 3). The only differences among plausible Step 1 models were the number of interactions with the LOGDIST variable (ranging from zero to 2 interactions) and whether the 1980–1990 transition was retained as an ARTIFACT variable (Table 3).

Plausible final models (i.e., model weights > 0.05) resulting from Step 2 were three different Step 1 candidates combined with both Climate and the five-category Zone variable (i.e., all management and ecoregion combinations) (Table 4). As with Step 1, differences between these models were limited to the number of ARTIFACT transitions retained and the number of interactions with the LOGDIST variable (Table 4). Regarding model goodness-of-fit, all plausible models from both steps had p-values < 0.001 for the deviance chi-square and the Hosmer–Lemeshow tests. Choice of

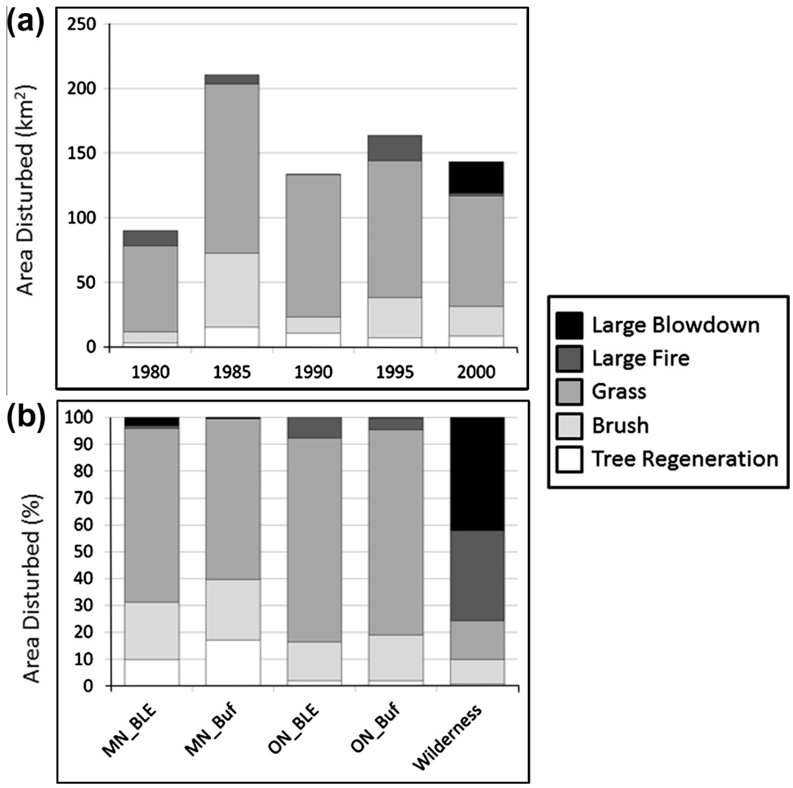

Fig. 3. The transitional type resulting from forest disturbances by (a) time step (total area) and (b) zone (percent area). The year label represents the 5-year period ending with the year indicated. Zones are identified by the following abbreviations: managed areas of Minnesota (MN), managed areas of Ontario (ON), Wilderness, managed areas inside the Border Lakes Ecoregion (BLE), and managed areas in the surrounding 50-km buffer (Buf). Note that an extreme wind event (Independence Day Blowdown) contributed the vast majority of wind-disturbed area within Wilderness.

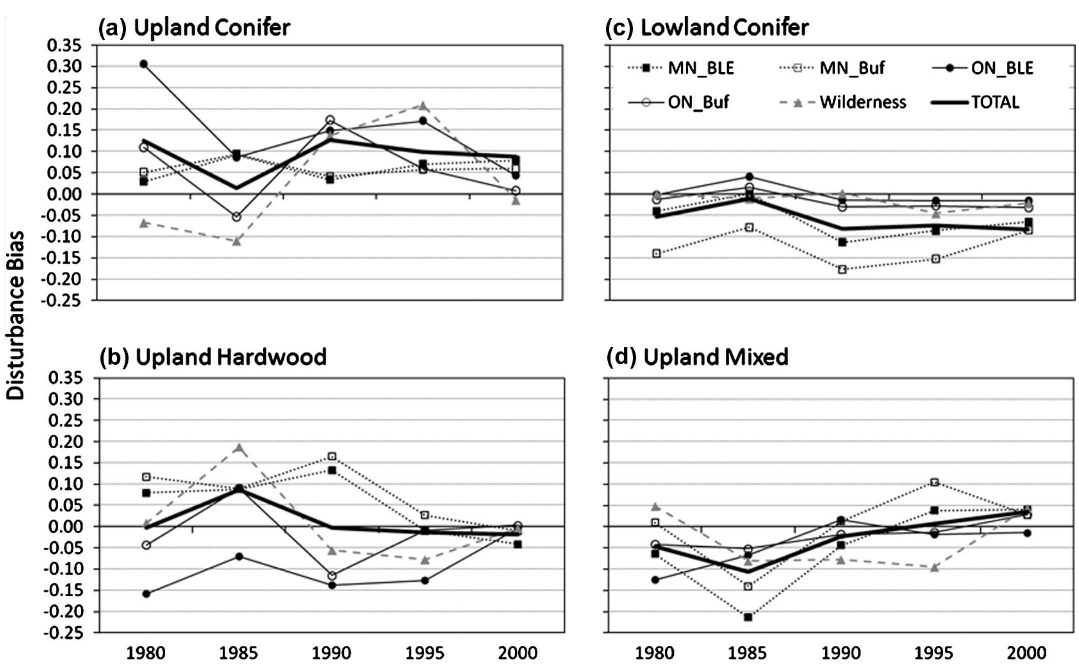

Fig. 4. Disturbance of a given forest type proportional to its relative abundance within the total study area and the different zones of analysis (i.e., bias). Positive values indicate forest types that were disturbed more frequently than their proportional representation on the landscape ("biased towards"), and negative values indicate forest types disturbed less frequently than their proportional representation on the landscape ("biased against"). Zones are identified by the following abbreviations: managed areas of Minnesota (MN), managed areas of Ontario (ON), Wilderness, managed areas inside the Border Lakes Ecoregion (BLE), and managed areas in the surrounding 50-km buffer (Buf). TOTAL represents the entire study area.

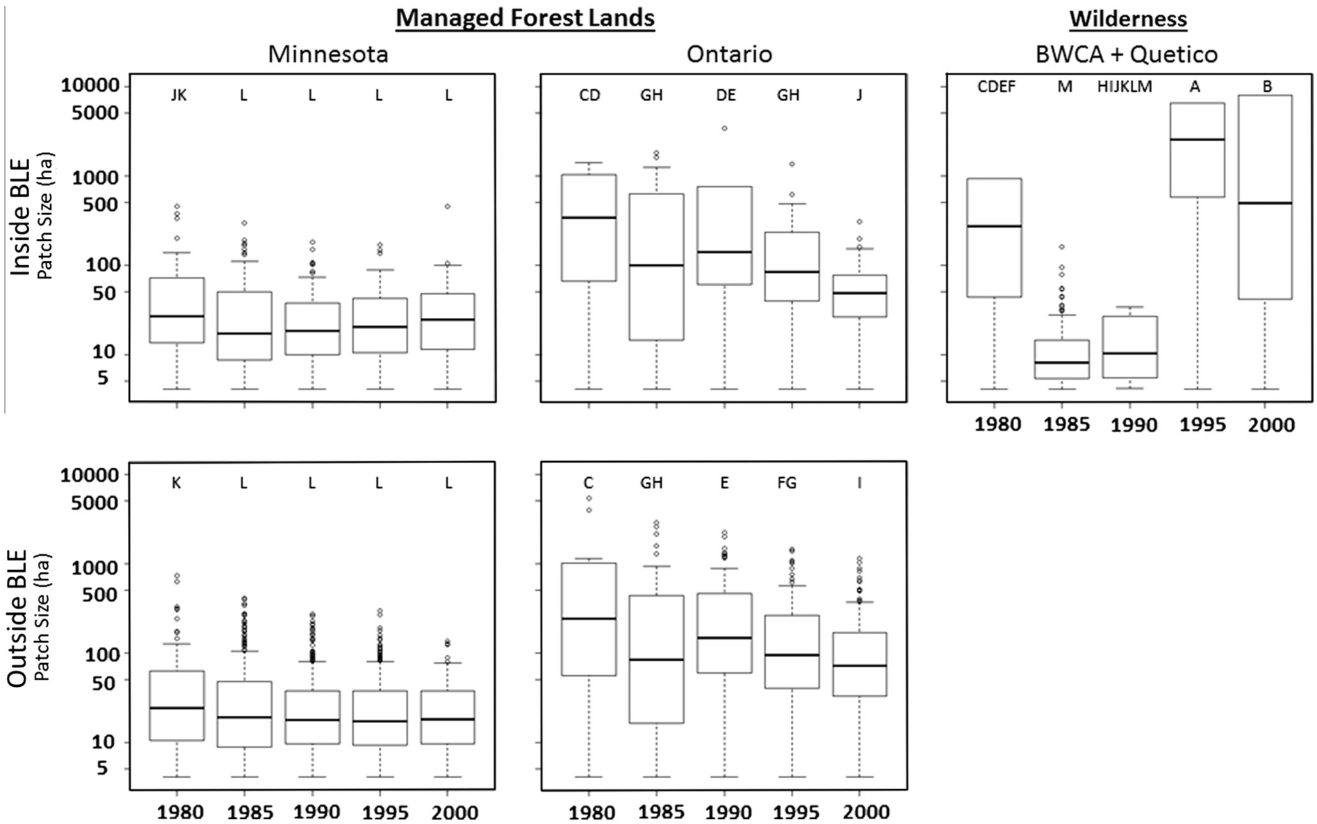

Fig. 5. Box and whisker plots of area-weighted forest disturbance patch sizes, stratified by analysis zone and time period. The year label represents the 5-year period ending with the year indicated. Heavy lines represent median values, the box is defined by upper and lower quartiles, and the ends of the whiskers contain the range of values with extreme values identified as circles. Letter symbols reflect statistically different ($\alpha = 0.05$) groupings based on Tukey's post hoc comparisons.

Table 2
Land cover transitions (%) following forest disturbance, separated by initial disturbed land cover type, at 5-year intervals.

Initial type	Years since	Changed to type (%)			
	Disturbance	Grass	Brush	Regeneration	Forest
Fire	1–5	72	26	1	0
	6–10	58	26	14	1
	11–15	48	26	22	3
	16–20	61	16	16	6
Grass	1–5	79	9	7	3
	6–10	57	21	17	4
	11–15	47	20	25	7
	16–20	29	20	28	20
Brush	1–5	4	86	6	4
	6–10	5	77	10	8
	11–15	5	74	9	11
	16–20	8	26	13	52
Tree regeneration	1–5	0	0	90	10
	6–10	1	0	87	11
	11–15	2	0	78	19
	16–20	4	3	3	89

the most plausible model based on weight was somewhat sensitive to the value of $\hat{c}$, where models with fewer parameters were given higher weight at higher values of $\hat{c}$. The rescaled R^2 values improved moderately in Step 2 from Step 1, but among the final most plausible models there was little difference in rescaled R^2 values.

The relative influences of different covariates were demonstrated by plotting the mean annual recovery probability for each level of each covariate using the means from all other covariates (i.e., effect displays; Fig. 6). Forest recovery probability was substantially higher during the 1980–1985 transition (t_1) relative to all other 1–5 year old transitions, supporting our assertion that the change in resolution between Landsat MSS and Landsat TM sensors resulted in false transitions at forest/nonforest boundaries (i.e., rapid "recovery" where no change had actually occurred). By contrast the 1985–1990 forest recovery probability (t_3) was much closer to the recovery probability for all other 1–5 year-old disturbances, and the 1980–1990 transition was not retained as a separate factor in the model. These results suggest the model appropriately accounted for the primary artifact introduced by the change in Landsat sensor, and that this artifact did not carry over substantially to subsequent time steps.

The forest recovery analysis estimated the annual probability of a disturbed pixel changing to forest. These annual probabilities, when applied across space and time, determine the rate of forest recovery. Hereafter, when referring to recovery rates, we have inferred relative rates based on the relative annual recovery probabilities. Forest recovery rate increased with time since disturbance (AGE), and the transitional type (TT) following the disturbance strongly affected forest recovery rate, with burned cells the slowest to recover to forest, and tree regeneration the fastest to recover to forest within any given 5-year time step. These results are logically consistent with the process of forest recovery, and simply quantify time-dependence and the role of rapid recolonization (including regeneration enhancement methods such as planting and coppice management), respectively, on recovery rates. Also consistent with our predictions, disturbed lowland forests had a lower rate of recovery than disturbed upland forests, and the recovery rate decreased with distance to edge. While disturbances affecting hardwood types had a somewhat higher rate of

Table 3
Most plausible models selected from Step1 and associated statistics.

Alternative model[a]	Num param	AICc	Weight ($\hat{c} = 1$)	Weight ($\hat{c} = 2$)	Weight ($\hat{c} = 3$)	Weight ($\hat{c} = 4$)	Rescaled R^2
TT + ET + PFT + LOGDIST + TT:LOGDIST + PFT:LOGDIST + AGE + t_1 + t_3	18	30183.06	0.62	0.34	0.21	0.14	0.257
TT + ET + PFT + LOGDIST + TT:LOGDIST + PFT:LOGDIST + AGE + t_1 + t_2 + t_3	19	30185.04	0.23	0.13	0.08	0.05	0.257
TT + ET + PFT + LOGDIST + TT:LOGDIST + AGE + t_1 + t_3	16	30186.62	0.11	0.38	0.45	0.39	0.256
PTT + ET + PFT + LOGDIST + TT:LOGDIST + AGE + t_1 + t_2 + t_3	17	30188.61	0.04	0.14	0.17	0.14	0.256
TT + ET + PFT + LOGDIST + AGE + t_1 + t_3	13	30210.96	0.00	0.00	0.06	0.18	0.256
TT + ET + PFT + LOGDIST + AGE + t_1 + t_2 + t_3	14	30212.85	0.00	0.00	0.02	0.07	0.256

[a] TT = transitional type; ET = ecosystem type, PFT = previous forest type; LOGDIST = log distance from edge; AGE = time since disturbance; ARTIFACT: t_1 = 1980–1985 transition; t_2 = 1980–1990 transition; t_3 = 1985–1990 transition (Appendix A). See Table 1 for variable definitions.

Table 4
Most plausible models selected from Step 2 (final) and associated statistics.

Alternative model[a]	Parameters	AICc	Weight ($\hat{c} = 1$)	Weight ($\hat{c} = 2$)	Weight ($\hat{c} = 3$)	Weight ($\hat{c} = 4$)	Rescaled R^2
TT + ET + PFT + LOGDIST + TT:LOGDIST + PFT:LOGDIST + AGE + t_1 + t_3 + PC1 + PC2 + PC3 + ZONE_5	25	29120.18	0.72	0.59	0.44	0.34	0.288
TT + ET + PFT + LOGDIST + TT:LOGDIST + PFT:LOGDIST + AGE + t_1 + t_2 + t_3 + PC1 + PC2 + PC3 + ZONE_5	26	29122.18	0.27	0.22	0.16	0.13	0.288
TT + ET + PFT + LOGDIST + TT:LOGDIST + AGE + t_1 + t_3 + PC1 + PC2 + PC3 + ZONE_5	23	29128.62	0.01	0.19	0.40	0.53	0.287

[a] TT = transitional type; ET = ecosystem type, PFT = previous forest type; LOGDIST = log distance from edge; AGE = time since disturbance; t_1, t_2, and t_3 = potential sensor artifacts; PC1, PC2, and PC3 = principle components of climate; ZONE_5 = management × ecoregion zones. See Table 1 for definitions.

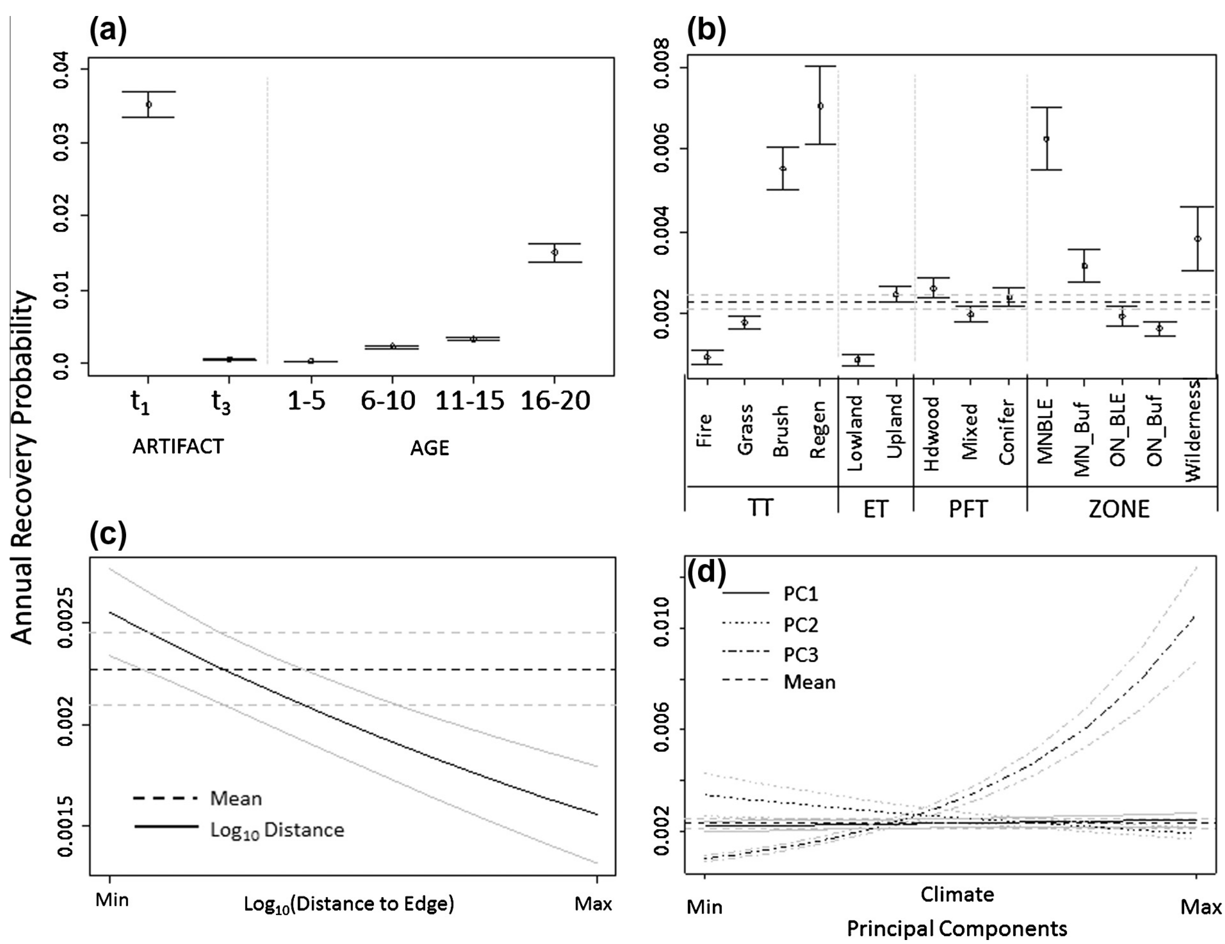

Fig. 6. Effects displays produced by the most plausible model predicting the annual recovery probability for forest disturbances (Table 4). Plot (a) depicts the effects of the temporal model components, including the 2 unique transitions impacted by the Landsat sensor artifact, and the 4 AGE classes, on the annual probability of recovery using the mean value for all other model components. Plotted values indicate the mean with 95% confidence intervals. Plots (b), (c), and (d) depict the influence of each non-temporal model component on the annual probability of recovery for the 6–10 year AGE class. All other AGE classes showed similar patterns among the non-temporal components. Horizontal dashed lines in plots (b), (c) and (d) represent the same mean recovery probability as the 6-10 AGE class in plot (a) for reference. The Min and Max range values for plots (c) and (d) represent the minimum and maximum values for the corresponding variable in the analysis data set.

recovery than those affecting conifer types, disturbances affecting mixed forests had the lowest rate of recovery. Effect displays indicated that climate component 1 (longitude) had virtually no influence on recovery rate, climate component 2 (latitude) had a mild negative influence on recovery rate, and climate component 3 (lake moderation) had a strong positive effect on recovery rate. Examination of Zone effects suggested that forest recovery was slowest in Ontario managed zones, and fastest within the portion of the Minnesota managed area within the BLE.

4. Discussion

Understanding sources of variability contributing to patterns of vegetation recovery is essential to inform not only ecosystem-based management, but also sustainable forest planning efforts within systems commonly impacted by natural disturbances. Past studies examined characteristics of forest management patterns in northern Minnesota (Wolter and White, 2002; Pastor et al., 2005) and the implications of divergent land management histories on compositional legacies in the BLE (Shinneman et al., 2010; James et al., 2011). Our study builds on this research by formally characterizing the disturbance regimes across management zones and examining the consequences of those disturbance regimes on forest recovery rates that ultimately define future spatial legacies.

4.1. Disturbance regimes

Disturbance patterns documented within the large contiguous wilderness in this study are consistent with past studies that suggest frequent but fine-scaled disturbances, punctuated by large but infrequent fire and wind events (Heinselman, 1973; Frelich, 2002). Fine-scaled disturbances that created canopy openings meeting the minimum size criteria (i.e., 4 ha) include small fire and wind events, mortality caused by spruce budworm (*Choristoneura fumiferana*) defoliation (Frelich, 2002), and aspen decline associated with drought, fungal diseases, and defoliation stress (Frey et al., 2004). The widespread blow down disturbance during the 1995–2000 period was caused by a single event in 1999 (i.e., Independence Day Blowdown). Such extreme events, while rare, have occurred elsewhere in the Great Lakes region in the last few decades (Frelich, 2002). Fires are actively suppressed by land management agencies across the entire study region, though some lightning-caused fires have been permitted to burn under observation within wilderness areas, and suppression activities within such areas are limited by road access (Shinneman et al., 2010). More recently (i.e., since 2000) three wildfire events in excess of 10,000 ha have burned within the wilderness area. Given such wide temporal variability of these disturbances, 25 years is insufficient to fully characterize the natural disturbance regime. Nonetheless observed disturbance patterns in the wilderness serve as a useful control for comparison with disturbance patterns within the managed regions of the BLE.

While natural disturbances still occur within managed forests, the regularity in both disturbance rates and patch size distributions relative to those observed in the wilderness is indicative of a human-dominated disturbance regime (Schroeder et al., 2011). Clearcutting is by far the dominant harvest method within managed forests of the study area (OMNR, 2001; D'Amato et al., 2009; Shinneman et al., 2010). Estimates of average clearcut sizes from other studies in northern Minnesota vary between 15 ha (White and Host, 2008) and 29 ha (D'Amato et al., 2009) depending on the source of the data and the minimum patch size defining clearcuts (2.5 and 5 ha, respectively). Mean area-weighted patch sizes estimated in this study for Minnesota ranged between 19 and 35 ha, and Minnesota patch size distributions were the most consistent of any zone examined (Fig. 5). White and Host (2008) show that this consistency in clearcut size distribution reaches back to the 1900–1940 era when pulpwood logging operations began (Heinselman, 1996). By contrast, mean area-weighted patch sizes for managed forests of Ontario ranged between a high of over 250 ha in the 1980 period to a low of approximately 45–75 ha (depending on ecoregion zone) by 2000, with a clear linear decline evident on a log scale over time (Fig. 5). This decline in patch size corresponds with a change in harvest pattern from contiguous harvest blocks to aggregated but smaller clearcuts separated by residual forest buffers. More recent harvest guidelines for Ontario recommend harvest patterns that emulate natural fire regimes of the boreal forest, with 80–90% of cut sizes ranging between 10 and 260 ha, and the remainder larger than 260 ha (OMNR, 2001). Trends over the last decade in Minnesota indicate an increasing emphasis on patch cuts and partial harvest (D'Amato et al., 2009). Such trends indicate that landscape disturbance legacies in the region will diverge further in the future.

Assuming the Boundary Waters Canoe Area Wilderness is representative of the larger BLE, presettlement fire disturbance rates have been estimated at approximately 0.8% per year based on reconstruction studies (Heinselman, 1973). Available evidence suggests severe wind disturbance was historically less common than fire in this region (Frelich, 2002). Disturbance rates around this presettlement fire disturbance rate, with an average of about 0.5% of the land area disturbed per year. Disturbance rates within the Minnesota and Ontario managed lands of the BLE averaged 0.7% and 0.9% per year (not including the 1980–1985 period affected by the Landsat sensor artifact) – close to the presettlement burn rate. Minnesota patch sizes were most similar to (but still larger than) the background disturbances within wilderness, while Ontario patch sizes were most similar to (but still smaller than) the large natural disturbance events (Fig. 5).

Bias in forest types disturbed within wilderness varied widely through time (Fig. 4) and should be related to the type of disturbance that dominated a given period. For example, forest type bias was not evident in 2000 when wilderness disturbance was dominated by a relatively indiscriminant blow down disturbance event (Frelich, 2002). By contrast, disturbances were biased toward conifer types in 1990 and 1995, corresponding with a peak in budworm defoliation (Robert et al., 2012) and large wildfires (Fig. 3), respectively. Bias in forest types observed in Minnesota and Ontario indicate active selection of conifer stands for harvest, while hardwood stands were also selected for in Minnesota and were selected against in Ontario early in the time series. By the end of the time series, disturbances were neutral regarding hardwood types within both managed areas (Fig. 4). Given that the type of forest disturbed affects its recovery rate (see Section 4.2), these biases in disturbance rates have implications for differential recovery patterns across the differently managed zones.

4.2. Forest recovery

Spatial variation in recovery rates determines the persistence of temporary forest openings across the differently managed zones of the BLE study landscape, and by extension the pattern of forest structure across the landscape. Forest recovery probabilities modeled through our forest cover change analyses represent the cumulative action of both human activities and ecological processes, many of which are not directly measureable at landscape scales. Ecological factors and processes include juvenile tree survival, capacity to reproduce vegetatively, seed source (i.e., aerial seed banks, proximity to reproducing trees), seedbed substrate, biophysical conditions (i.e., soil, drainage, climate), and competition with other life forms. Humans further modify recovery patterns through planting, seed bed preparation, silvicultural techniques (e.g., coppicing, seed tree retention), and vegetation control. The influence of these processes and management techniques are generally well understood at local scales, but their net cumulative effect on landscape to regional-scale forest recovery are rarely measured.

Those disturbed sites classified as tree regeneration and brush in the first five years post-disturbance are unlikely to represent natural regeneration from seed, as seedling establishment takes place over an approximate five-year period (Greene et al., 1999) and require additional time to produce sufficient leaf area to affect spectral reflectance (Coppin and Bauer, 1994). Instead sites with more advanced vegetative states shortly following disturbance likely indicate vigorous vegetative reproduction, plantations, or possibly areas with high post-disturbance survival of advance tree regeneration. Study area-wide conversion of disturbed forests classified initially as tree regeneration and brush back to forest was estimated at 89% and 52%, respectively, as compared with only 20% conversion rate from a grass/herbaceous state and 6% conversion rate from large fires 16–20 years post-disturbance (Table 2). These advanced vegetation states were more common within the managed forest zones – particularly Minnesota – relative to the wilderness (Fig. 3). In fact, one of the critical legal conditions of the 1978 Boundary Canoe Area Wilderness Act was the dedication of funds for silvicultural treatments – including planting – outside the wilderness area to offset the loss of timber resources within the newly designated wilderness (Proescholdt, 1995).

Studies of aspen recovery by suckering suggest approximately 2-m growth in height in the first five years following disturbance, with crown closure within the first ten years (Palik and Pregitzer, 1993; Bergeron, 2000). Similar crown-closure rates have been observed within disturbed stands dominated by birch (Bergeron, 2000). We expect most areas classified as conifer tree regeneration in the first five years following disturbance was attributed to plantations, with white spruce, red pine, and jack pine as the most common plantation species, and where crown closure is anticipated between 10 and 15 years post-disturbance depending on planting density (B. Palik, US Forest Service, personal communication). Tree regeneration and to some extent brush transitional types were more prevalent immediately following forest disturbances in managed forests of Minnesota relative to other zones (Fig. 3). Regeneration methods reported for Minnesota in the 1990s indicate that while methods differ somewhat across land ownerships, conifer seedlings were planted on approximately 20% of the harvested areas while regeneration of the remainder is primarily by vegetative reproduction (D'Amato et al., 2009). Shinneman et al. (2010) estimated that approximately 48% of clearcut area is planted with conifer seedlings within the BLE in Ontario. Compositionally, hardwood forests are more prevalent further south and conifers are more prevalent further north, with differences greatest between Minnesota and Ontario outside the central ecoregion. Hence differences in regeneration methods may be attributed in part to compositional differences between zones, while relative differences in the prevalence of advanced transitional types following disturbance across zones may be attributed in part to more rapid initial vegetative growth of coppiced hardwoods relative to planted coniferous seedlings.

Disturbances with low impact to the forest floor, such as winter harvesting during snow cover and natural openings created by insects and wind damage can release the understory to allow more rapid canopy closure by shade tolerant conifers such as spruce, fir, and cedar (Greene et al., 2002; Brassard and Chen, 2006; Belle-Isle and Kneeshaw, 2007; D'Amato et al., 2011). Our finding that the recovery rate within wilderness – after accounting for the slow recovery following large fire – was similar to managed forests of Minnesota and high relative to managed forests of Ontario may be attributed in part to natural understory release there (Frelich, 2002; D'Amato et al., 2011). It is unknown the extent to which advance regeneration was protected within managed zones of the BLE, but the protection of advance regeneration has increased in practice more generally in Canada starting in the 1990s (Greene et al., 2002). We found no support for time dependence models that would indicate a change in recovery rate due to changes in silvicultural methods over time. In principle our approach should be capable of detecting such an effect, but additional dates may have been necessary to capture the trend if in fact it existed within the study area. Combining the observations of slow comparative recovery following fire, the prevalence of conifer planting and coppice management in the region, and disturbance regimes more dominated by wind and insect disturbance, it is likely that contemporary forests in the border lakes region are recovering faster than would be expected under a presettlement, fire-dominated disturbance regime.

As expected, lowland forests recovered more slowly than upland forest. Lowland conifer forests were most abundant within the Minnesota managed forests, comprising 10% and 20% of the forested land area inside and outside the BLE, respectively, compared with less than 5% of the forested land area in the other three zones. Selection against lowland conifer was also most evident for disturbances within Minnesota managed forests (Fig. 4). Schroeder and Perera (2002) found that large-scale disturbance in boreal forests with high interspersion of lowland and upland forests introduced spatial diversity in recovery rates for a given disturbance event. This process is expected to be less important within managed forests of Minnesota where disturbance patches are characteristically small.

The negative relationship between the log-distance to the nearest forest edge and forest recovery probability is consistent with a seed source influence of forest recovery rates. Studies across a broad range of forest systems document similar neighborhood effects on forest recovery (Chazdon, 2003; Belle-Isle and Kneeshaw, 2007; Schoennagel et al., 2008). Greene et al. (1999, p. 831) conclude there is a "narrow window of opportunity for invasion of clearcuts and burns" within the boreal forest, because seedbed quality degrades rapidly 5–7 years post-disturbance. Indeed the grass/herbaceous state was persistent in this system, particularly following large fire (Table 2). Given the striking differences in patch size distributions among differently managed zones of the BLE, this process has clear implications for the relative persistence of disturbance legacies among zones. The most plausible models also indicated important interactions between nearest forest edge and the transition type following disturbance as well as the composition of the forest disturbed. Both vegetative reproduction (restricted to hardwood types), and planting (restricted to conifer types) should override the need for local seed source, as will the protection of the understory during canopy removal (Foster and King, 1986).

While climatic effects on recovery were not a focus of this study, we recognized climate was nonetheless likely to affect recovery at the scale of investigation, and this prediction was supported by our analyses. Effects plots indicated that climate had a strong influence on forest recovery rate, with the most influential climate component (PC3) correlated with the modified climate near Lake Superior (Fig. 6). This area of modified climate is where northern hardwood systems reach their most northern distribution (Wolter et al., 1995). However we caution that one climate component (PC2) was strongly related to latitude, and therefore confounded with management zone. Forest composition also changed from more hardwood dominated in the south to more conifer dominated in the north. Separate examination of effects plots without the zone variable suggested that PC2 had a stronger influence on forest recovery than did PC3, where forest recovery was negatively correlated with PC2 (i.e., negatively correlated with latitude). None of the models indicated that PC1 (i.e., climatic factors correlated with longitude) had strong influence. While our exploratory analyses suggested that forest recovery was faster within more moderated climates relative to the climate more typical of true boreal forest, correlations among independent variables (climate, management zone, and prior forest type) did not allow us to fully tease apart the relative contributions of these factors as they affected recovery probabilities.

4.3. Management implications

Past research has demonstrated that different disturbance regimes applied cumulatively to different land areas will lead to divergent landscape legacies that can persist over long periods of time (Franklin and Forman, 1987; Spies et al., 1994). The Border Lakes region is a prime example of divergent forest disturbance regimes separated by geopolitical boundaries. Forest recovery rate in this area is comparable to that observed elsewhere in the boreal forest (Schroeder and Perera, 2002; Schroeder et al., 2011) and in temperate forests where growth is environmentally restricted (Schroeder et al., 2007), suggesting divergent legacies will persist in the form of differential landscape structure over time. Our research goes further to suggest the magnitude of the divergence in these landscape disturbance legacies will be underestimated if the disturbance patterns are considered in isolation of the recovery process, because certain attributes that characterize the different disturbance regimes also influence forest recovery rates.

An influential paradigm in sustainable forest management is the emulation of natural disturbances as a model for harvesting practices (Perera et al., 2004). In the case of the Border Lakes region, natural disturbance and recovery patterns within the wilderness area were characterized as fine-scaled disturbances expected to recover quickly, offset by less frequent, coarse-scaled and severe disturbances expected to persist for long periods of time. Managed forests of Minnesota lacked these large-scale and persistent disturbances, whereas managed forests of Ontario were dominated by them. Current harvest trends reported for Minnesota (D'Amato et al., 2009) suggest forestry practices of the future may become increasingly analogous to the background disturbances of the largest reference area for the region. By contrast, current guidelines for Ontario emphasize emulation of catastrophic disturbance– specifically large wildfire (OMNR, 2001). These trends demonstrate the challenge of implementing the emulation paradigm, as each case is a simplification of the more complete disturbance regime embodied by the wilderness reference zone.

While our focus on spatial legacies ignores other important dimensions of the emulation natural disturbance paradigm, including species composition (Moore et al., 1999), age structure (Bergeron, 2000), and biological legacies (i.e., snags, downed woody debris, etc.; Swanson et al., 2011), spatial legacies do have critical implications for sustainable forestry, forest fragmentation, habitat quality, and other ecosystem services. For example, shortening the early successional stage in favor of closed-canopy forests clearly enhances wood supply, and should help mitigate habitat loss and forest fragmentation thought to impact an important subset of boreal songbirds (Schmiegelow and Monkkonen, 2002; Manolis et al., 2002) and other late-successional forest wildlife species (e.g., American marten, *Martes americana*; Landriault et al., 2012). Yet there is also increasing recognition that more persistent early successional stages and greater range of variability in recovery time observed following many natural disturbances can play an important role in the regional biodiversity of predominantly forested areas (Swanson et al., 2011). In addition, Robert et al. (2012) found the legacy of land management in this region influences spatio-temporal dynamics of insect outbreaks, suggesting repercussions for sustainable forestry and regional forest health. Our approach can therefore help inform land managers who must balance a diversity of objectives and values over time and space.

Finally, landscape simulation studies are now routinely applied to evaluate the consequences of disturbance regimes, alternative landscape management strategies, and their interactions on future landscape structure and function (Scheller and Mladenoff, 2007). Forest recovery processes within the underlying models are generally simplified and rarely validated. There is an abundant literature of studies investigating forest recovery processes at traditional plot scales, and the synthesis of these studies can clearly inform parameterization of landscape-scale forest disturbance and succession models (Greene et al., 1999). Yet fine-scaled studies are by necessity a subset of conditions affecting variation in recovery patterns within real landscapes. Spatially continuous data sets derived from remote sensing and other inventory methods therefore provide opportunities to estimate post-disturbance vegetation processes, such as canopy closure, across a much wider range of variability than could be achieved through plot-scale analysis alone. Analyses such as those presented here can therefore serve as important validation of simulated spatial legacies within forested systems examined at broad spatial scales.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2013.10.039.

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APPENDIX 1: Land Cover Change Detection Methods

Wolter et al. (2012a,b) describe the methods for Landsat image selection, processing, land cover classification and change detection at five year intervals over the greater Border Lakes Region. Methods described therein extended previously published work (Wolter and White 2002, Pastor et al. 2005) by simplifying their original classification from 1990 to Anderson-level II, adding earlier dates (i.e., 1975 and 1980 based on Landsat Multi-Spectral Scanner (MSS) imagery and 1985 based on Landsat Thematic Mapper (TM) imagery), and defining methods for accurate change detection between dates with different Landsat sensors. Lowland forest types within the Anderson Level-II classification were further differentiated via intersections with available national-scale wetland inventories (Wilen 1990, Wulder et al. 2003) (Table A1). The 1990 land cover classification served as the “base” year for the time series across the whole region (See Wolter and White 2002). Vegetation change between time periods with Landsat TM or ETM+ imagery (e.g., 1985 and 1990) was defined by differences greater than 1.5 standard deviations in the normalized difference moisture stress index (NDMSI, see Hunt and Rock 1989, Wolter and White 2002, Wilson and Sader 2002) applied to leaf-on imagery from the respective time periods. Pixels identified as changed were classified using an iterative, self-organizing, maximum likelihood classifier into one of 17 cover classes (Table A1). Pixels that did not change from the base year to adjacent time steps adopted pixels values from the base image. Change detection then proceeded stepwise both forward and backward in time from the base image to subsequent adjacent time steps. For change detection between dates involving MSS (1975-1980) or MSS and TM (1980-1985) imagery, 60-m MSS pixels were first rescaled (nearest neighbor) to match the 28.5-m resolution of the 1990 base imagery. Differences in visible red reflectance between image dates were substituted for NDMSI to identify change pixels (Desclée et al. 2007). In the final stage, large-scale (>100 ha) natural disturbances (i.e., fire and blowdown) were identified from the entire Landsat archive (1972-2000) using their unique spectral signatures to distinguish these large disturbance types from all other disturbances. Resulting landcover datasets can be accessed online (Wolter et al. 2012a).

Table A1. Satellite land cover classification used to document forest disturbances across time (Wolter et al. in 2012).

CLASSIFICATION	DESCRIPTION
Water	Surface water including lakes, ponds, rivers, streams, and some wetland areas.
Emergent Vegetation	Wetland areas dominated by wetland emergent species growing above the surface of wet soil or water.
Lowland Grass	Graminoid-dominated low-lying areas with saturated soils.
Lowland Brush	Areas dominated by short woody vegetation over wet or saturated soil.
Sphagnum Bog	Wetlands dominated by *Sphagnum* spp. commonly associated with sparse, small diameter, and stagnant woody vegetation.
Upland Grass	Areas dominated by graminoid vegetation and forbs that do not intersect with any of the wetland inventory moisture modifier data.
Domestic Grass	Areas covered by cultivated or noncultivated herbaceous vegetation dominated by short manicured graminoids and/or forbs.
Upland Brush	Areas dominated by short woody vegetation over relatively dry soil that do not intersect with wetland inventory moisture modifiers.
Conifer Regeneration	Early successional coniferous forest that is spectrally distinct from mature forest classes, brush classes, and early successional hardwood regeneration.
Hardwood Regeneration	Early successional hardwood forest that is spectrally distinct from both forest and nonforest classes.
Lowland Conifer	Forested areas composed primarily of wetland conifer species (e.g., *Picea mariana*, *Larix laricina*, *Thuja occidentalis*) that intersected with wetland inventory moisture modifier data.
Lowland Hardwood	Areas dominated by hardwood tree species commonly associated with wetlands that intersected with wetland inventory moisture modifier data.
Lowland Mixedwood	Forest areas consisting of lowland mixtures of hardwood and conifer species, as specified above, that intersect with wetland inventory moisture modifier data.
Upland Conifer	Forest dominated by upland conifer species that do not overlap with NWI moisture modifier classes.
Upland Hardwood	Forests dominated by upland hardwood species (e.g., *Populus* spp., *Betula papyrifera*, *Acer saccharum*, and *Fraxinus americana*) that are not coincident with wetland inventory moisture modifier
Upland Mixedwood	Forest areas consisting of upland mixtures of hardwood and conifer species, as specified above, that do not intersect with wetland inventory moisture modifier data.
Forest Blow Down	Large (≥100ha) stand-replacing forest disturbance due to extreme wind events.
Forest Fire Burns	Large (≥100ha) stand-replacing forest disturbance due exclusively to wildfire events.
Developed	Lands dominated by residential housing structures, commercial industrial development, and/or copious areas of pavement.

Examination of the 1985 forest disturbance map indicated that some of the mapped disturbances were an artifact of the change in Landsat sensor (i.e., MSS to TM/ETM+) – in particular a difference in image resolution between sensors – resulting in fine-grained “changes” in forest cover between 1980 and 1985. Plotting disturbance area at different minimum patch size thresholds (Figure A1-1) suggested the presence of the artifact was greatly reduced at a minimum patch size of 4 ha, as the 1985 disturbance-minimum patch size relationship began to parallel that of the other dates at this size threshold. Nonetheless, 4 ha represents a balance between minimizing the effect of the artifact while still retaining the vast majority of stand-replacing forest disturbances. We addressed the residual effect of this artifact within the statistical model estimating the probability of forest recovery described in Appendix 2.

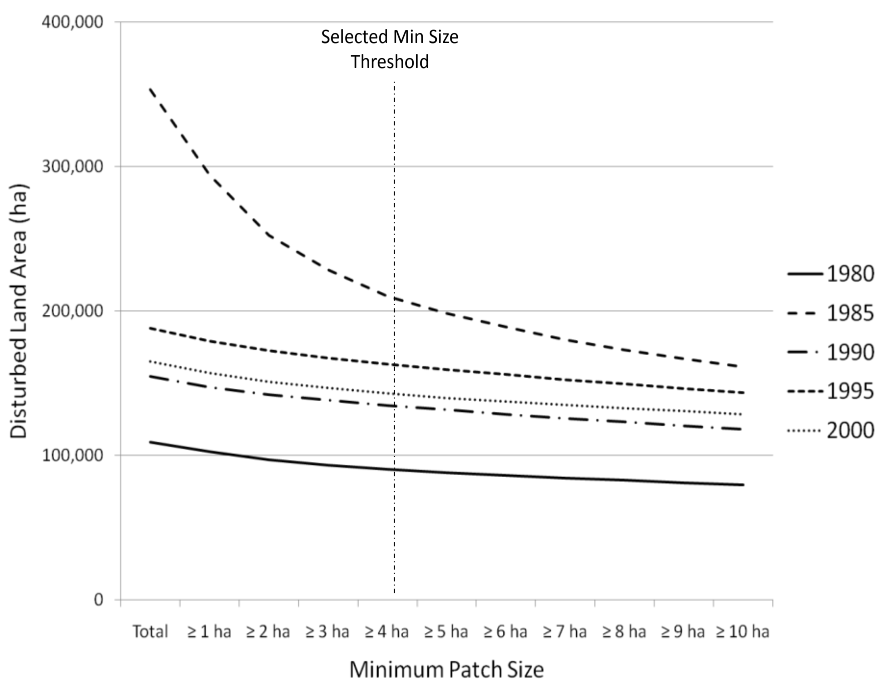

Figure A1-1. The effect of minimum patch size on the calculated total forest area disturbed by 5-year time step.

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APPENDIX 2: Forest Recovery Model Development

We estimated forest recovery probabilities using logistic regression within the program MARK (White and Burnham 1999) and its companion package for R (v2.12.1, R Development Core Team 2010), RMark (v1.9.9, Laake and Rexstad 2012). We considered each disturbed pixel to be a marked individual and tracked its condition (transitional or forest) through "recaptures" at each 5-year interval available from the imagery. The program estimates the "survival" probability of disturbed cells, which was converted to recovery probability (i.e., $P_{recovery} = 1 - P_{disturbed\ survival}$). Hence if the disturbed condition in a particular cell didn't "survive" during a subsequent "recapture", this increases the recovery probability as a function of its associated cell attributes defining the logistic regression model. Due to the large number of pixels in the landscape, we performed the analysis on a one-percent subset (n=91144 disturbed pixels).

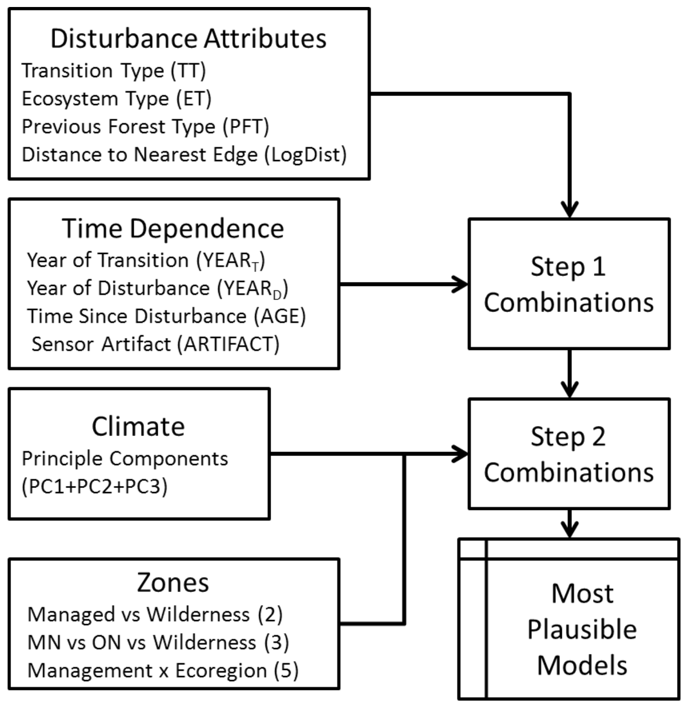

Figure A2-1. Flow chart showing how the different models were combined in two separate steps to determine the most plausible models defining the annual probability of forest recovery.

We developed four sets of *a priori* candidate models for evaluation based on hypothesized relationships between the predictor variables and forest recovery probability, where the combination of model sets were evaluated in two steps to address two related questions (Figure A2-1). First, what combination of time-dependence and measurable disturbance attributes best predicts the probability of forest recovery? Second, to what extent, if any, do climate variables or unmeasured differences among management and ecoregion zones improve predictions from Step 1?

The Time Dependence model set included four *a-priori* models: 1) no time dependence (null model); 2) unique transition probabilities for each year of disturbance ($YEAR_D$); 3) unique transition probabilities for each year of transition ($YEAR_T$); and 4) unique transition probabilities by the time since disturbance (AGE) (Figure A2-2). Previous research suggested the likelihood of transition back to forest after disturbance increases with AGE (Pastor et al. 2005). $YEAR_D$ represents the possibility that internal disturbance properties affecting recovery, such as silvicultural practices or disturbance severity, may have changed over time. $YEAR_T$ represents the possibility that external factors affecting recovery, such as drought or some other climate-related factor, may have changed over time. ARTIFACT models consisted of different time parameter combinations that isolated transitions from 1980 and 1985 disturbances to evaluate whether the change in Landsat sensor (see Mapping Forest Disturbances) might have introduced a bias in transition parameter estimates. All combinations of ARTIFACT models and the four *a priori* models were evaluated to derive the candidate list of Time Dependence models.

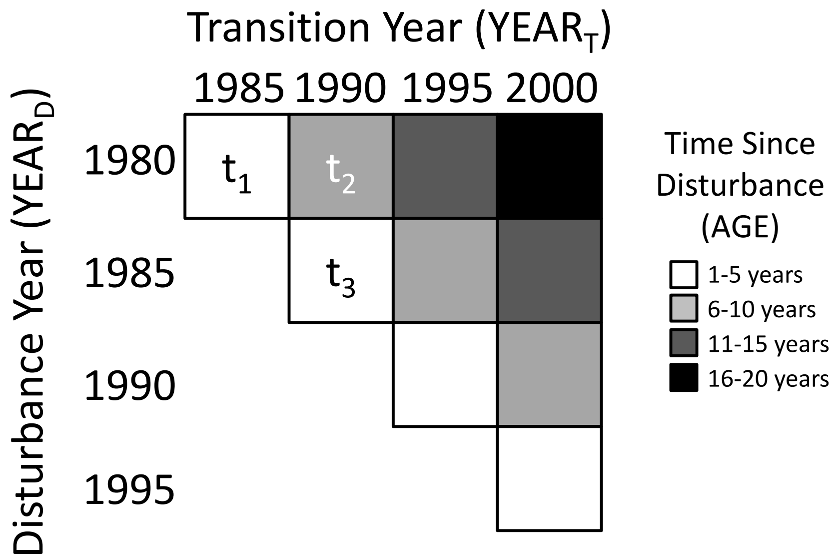

Figure A2-2. Graphic representation of the four factors included within alternative Time Dependence models: disturbance year ($YEAR_D$), transition year ($YEAR_T$), time since disturbance (AGE), and three specific transitions that may have been affected by the change in Landsat sensor (ARTIFACT; t1, t2, and t3).

Disturbance Attribute models were derived from four variables using the following expected relationships. We expected the distance to nearest forest edge would affect the likelihood of establishment by seeding from residual forests, where the influence of seeding would decline rapidly with increasing distance from a seed source (Greene et al. 1999). We therefore used the log (base 10) distance from nearest forest edge (LogDist) to approximate seed source effects. We predicted that lowland forest ecosystem types (ET) would have slower recovery rates than upland forest ecosystems, due to slow tree growth rates on lowlands relative to uplands. We also predicted that the forest type that was disturbed (i.e., previous forest type: PFT) would affect recovery rates. Specifically, disturbed deciduous forests, with their ability to coppice following tree mortality, should have faster recovery rates relative to disturbed conifer forests that must regenerate via seeding. Transitional type (TT) represented the successional state (grass, brush, tree regeneration, burned) indicated by the classification immediately following disturbance. Note that no major blowdown occurred at a time when we could examine its recovery. We expected that changes in TT would be directional. For example, grass should convert to brush or regenerating forest, but not the reverse. TT may also represent differences in disturbance severity (e.g., overstory removal vs. overstory and understory removal) or management practices (e.g., planting). For these reasons, we predicted burned cells would require longer recovery than the vegetated transitional types, and the probability of recovery would be consistent with the above expected directional pattern of vegetation change.

Disturbance Attribute candidate models were defined as all additive combinations of the above four variables, for a total of 14 combinations (Table 2). In addition we included two candidates with multiplicative terms based on hypothesized interactions among covariates. LOGDIST was expected to have the strongest influence on coniferous forest types dependent on regeneration by seeding. Assuming the transition type was related to disturbance severity, TT may also reflect the availability of local seed source that would likewise affect the relevance of distance to forest edge. We assumed that these interaction terms would only be plausible within candidate models that included each of the main covariates from the corresponding interaction term (Table 2). All combinations of candidate models from the Disturbance Attribute and Time Dependence model sets were evaluated for Stage 1, and candidates with model weights ≥ 0.05 across all 4 levels of $\hat{c}$ were retained as plausible candidate models for the next step.

In Stage 2 we evaluated whether climatic variables (Climate), forest management or ecoregion boundaries (Zones) could improve the models estimated in Stage 1 (Figure A2). Using monthly climate data (minimum temperature, maximum temperature, and precipitation) interpolated at 1-km resolution between 1976 and 2000 (McKenney et al. 2006), we calculated average monthly climate statistics for the 25-year time period. Principal components analysis (PCA) was used to reduce these climate data to a small number of orthogonal climate variables. PCA was performed on the correlation matrix using the ‘‘princomp” function in R (R Development Core Team 2010). The broken stick criterion was used to assess significance of ordination axes and significance of loadings within significant axes (Jackson 1993, Peres-Neto et al. 2003), where all significant axes were included in a single climate model. We evaluated three alternatives for the Zone variable. In the first alternative we separated wilderness areas from managed areas (Zones = 2), in the second we separated wilderness, managed areas of Minnesota, and managed areas of Ontario (Zones = 3), and in the third we separate managed areas outside the Border Lakes Ecoregion (BLE) from the managed areas inside the BLE (Zones = 5; note that wilderness was almost completely within the BLE; Fig. 1). Model selection criteria defining plausible models from each model set and step of model development, along with goodness of fit statistics for the final models, are presented in the main text.

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