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ECOSYSTEMS

Ice Storm Damage Greater Along the Terrestrial-Aquatic Interface in Forested Landscapes

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ABSTRACT

Ice storms are an important and recurring ecological disturbance in many temperate forest ecosystems. In 1998, a severe ice storm damaged over ten million hectares of forest across northern New York State, eastern Canada, and New England impacting ecosystem processes across the landscape. This study investigated the spatial arrangement of forest damage at the terrestrial-aquatic interface, an ecological edge of importance to aquatic habitat and nutrient cycling. Vegetation indices, derived from satellite imagery and field-based data, were used to measure forest canopy damage across a 2045 km^2 region in northern New York State affected by the 1998 storm. We investigated the forest damage gradient in the riparian zone of 13 stream segments of varying size (92.5 km total length) and 13 lakes (37.4 km of shoreline). Large streams (-fourth and fifth order), occurring in forests that received modest ice damage ($<15\%$ disturbance coverage), exhibited significantly more damage in the riparian zone within 25 m of the water than in adjacent forest sections; F(3,12) = 7.3 $P = 0.005$. In similar moderately damaged forests, lake shorelines were significantly more damaged than interior forests; F(3,9) = 6.4 $P = 0.013$. Analysis of transitions in damage intensity revealed that canopy disturbance followed a decreasing trend (up to 3.5 times less) with movement inland from the terrestrial-aquatic interface. The observed predisposition of forest to disturbance along this ecosystem interface emphasizes the role of the physical landscape in concentrating the movement of wood from the forest canopy to locations proximate to water bodies, thus reinforcing findings that ice storms are drivers of ecological processes that are spatially concentrated.

Key words: ice storm; ecological disturbance; forest; terrestrial-aquatic interface; streams; lakes; littoral zone; remote sensing; transition analysis; Adirondacks.

INTRODUCTION

Ice storms, fires, and hurricanes are disturbances that occur across broad spatial extents and influence ecosystem processes with varying intensity and temporal regularity. These disturbances produce a mosaic of varying damage severities that frequently modify ecosystem function (Cadenasso and others 2003; Laurance and others 2001). Ice

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storms annually impact an area of U.S. forest about one-third of that disturbed by fire (Dale and others 2001; Lautenschlager and Nielsen 1999); they are a particularly important recurring disturbance in forests of the northeastern United States and eastern Canada (Bragg and others 2003; Melancon and Lechowicz 1987; Smith 2000). Variability in ice accumulation and wind regimes produce substantial spatial heterogeneity in forest damage intensity (Dupigny-Giroux and others 2003; Millward and Kraft 2004), which frequently causes abrupt changes in forest ecosystems and associated watersheds, including tree mortality, movement of wood from the canopy to forest floor, and increased nutrient export (Houlton and others 2003; Kraft and Warren 2003; Rebertus and others 1997).

The influence of wood from streamside forests upon key stream ecosystem processes has been recognized for many years (Bilby and Likens 1980; Harmon and Chen 1991; Keller and Swanson 1979), and there is an increasing recognition that lakes embedded within a forested landscape are similarly influenced by long-term wood inputs from trees within the shoreline riparian forest (Francis and Schindler 2006; Guyette and others 2002; Marburg and others 2009). Material from the terrestrial environment (for example, litter fall, woody debris) that enters aquatic ecosystems provides habitat structure for aquatic organisms, contributes to the stream food web, and influences both biogeochemical and hydrological processes (Gurnell and others 2005; Wallace and others 1997; Warren and others 2007). Large wood can affect the flow of organic matter from terrestrial ecosystems into surface waters and the transport of organic materials within aquatic ecosystems (Latterell and Naiman 2007; Marburg and others 2006). In addition, the light environment along small streams is influenced by forest gap dynamics that are tightly correlated with forest stand development processes and fine-scale canopy disturbances (Runkle 1982; Van Pelt and Franklin 2000; Keeton and others 2007). In larger rivers, wood can retain plant propagules (seeds, plant fragments) and offers protection from erosion, abrasion, and in some cases drought and herbivory (Abbe and Montgomery 1996; Doyle 1990; Latterell and others 2006; Palmer and others 2000). In lakes, near-shore wood along shorelines provides structural complexity and can contribute to the retention of organic material in the littoral zone (Francis and others 2007).

Several lines of evidence led us to evaluate whether ice storm damage is disproportionally large along the terrestrial-aquatic interface in forests of the northeastern U.S., thereby mediating the flow of wood from the forest canopy to adjacent lakes and streams. First, the frequency and extent of ice storm disturbances in this region is relatively large by comparison with other forest disturbances, such as fire (Letty and others 2004). In addition, ice storm disturbances have heterogeneous impacts upon forests and are likely susceptible to local environmental influences (Millward and Kraft 2004). Finally, the aforementioned importance of wood inputs to streams and lakes—in conjunction with evidence that an ice storm can increase wood deposition to streams (Kraft and others 2002)—provided incentive to try to understand landscape factors that influence locations where this wood deposition is most likely to occur.

An ice storm's influence within a specific forest is dependent upon the accumulated ice load, wind exposure and duration, as well as stand and individual tree characteristics. Tree species vary in their resistance to ice storm damage, with conifers usually reported to experience less damage than broadleaf deciduous trees (Boyce and others 2003; Hopkin and others 2003; Millward and Kraft 2004). Tree growth form (physiognomy)—such as the presence of broad crowns and fine branching—can influence an individual tree's resistance to ice storm damage (Proulx and Greene 2001; Smith and others 2001; Smolnik and others 2006). Trees growing on the periphery of the forest often have large, imbalanced crowns with longer and lower branches on the open side, by contrast with the dominance of trees with smaller crowns and fewer lower limbs in interior forest stands. Direct exposure to precipitation may also cause trees along a forest edge to accumulate more ice adjacent to the canopy opening (Seischab and others 1993).

Broad-extent evaluations of the influence of physical landscape characteristics on ecological disturbances have been undertaken for hurricanes (Boose and others 2001; Foster and Boose 1992), fires (Mildrexler and others 2007; Rollins and others 2002), and ice storms (Dupigny-Giroux and others 2003; Millward and Kraft 2004; Stueve and others 2007). Although several studies (Millward and Kraft 2004; Pasher and King 2006) have investigated the aggregation of damage and its spatial arrangement across an affected landscape, no previous work has evaluated the potential role of the terrestrial-aquatic interface as an influence upon the extent of forest damage, thereby subsequently influencing key ecological processes that occur at these locations. The overall goal of our study was to focus upon the terrestrial-aquatic interface as a geographic location for the concentration of forest damage and subsequent movement of wood from the canopy into aquatic systems. Specifically, we evaluated the following questions: (1) Was forest damage greater closer to streams and lake shorelines compared with interior forest? and (2) Did the probability of site-specific damage intensity change with the transition from forest edge (location at stream edge or lake shoreline) to interior forest?

MATERIALS AND METHODS

Site Description

The study area encompassed the high peaks region of the Adirondack Park in northern New York State (Figure 1). Topography in this region is complex with an elevation range spanning 25–1650 m above sea level (Millward and Kraft 2004). Most forests within the park were first logged prior to 1900. Broadleaf deciduous and coniferous forests represent 53 and 23%, respectively, of the park, and the remaining land cover comprises agriculture, built areas, and water (Vogelmann and others 2001). Broadleaf deciduous forest is dominated by maple (*Acer spp*.), aspen (*Populus spp*.), American beech (*Fagus grandifolia*), and birch (*Betula spp*.); coniferous forest is dominated by red spruce (*Picea rubens*), balsam fir (*Abies balsamea*), eastern hemlock (*Tsuga canadensis*), and white pine (*Pinus strobus*) (Keeton and others 2007; Manion and others 2001). In a survey of riparian forest communities adjacent to 15 streams of the central and western Adirondack Mountains, the proportion of conifers in the riparian zone ranged from 4 to 72% (mean = 35%; median = 34%) (Warren and others 2009). Typical geomorphic features in Adirondack watersheds include thin soils, steep slopes, and glacial till covering igneous and metamorphic bedrock. Water features in the park include over 3,000 lakes and greater than 48,000 km of mountain streams and brooks that combine to form a network of 1,600 km of Adirondack rivers (Adirondack Park Agency 2003).

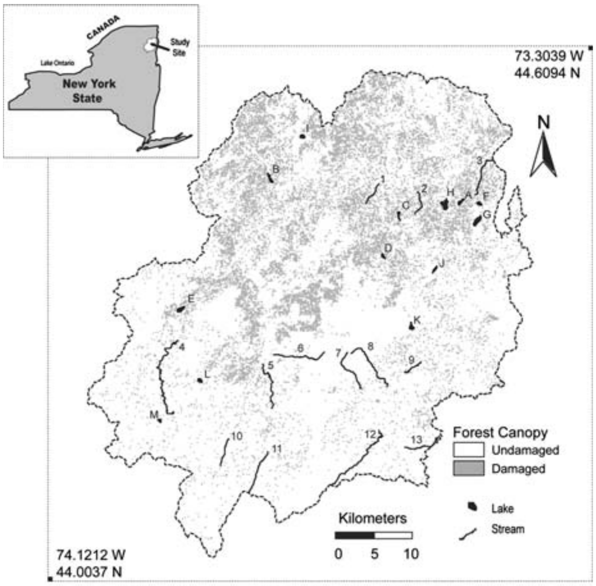


Figure 1. Location of study area in the Adirondack Mountains of northeastern New York State. *Shaded areas* represent forest damaged by the 1998 ice storm. *Number* and *alphabetic schemes* correspond, respectively, to streams and lakes investigated (see Table 1 for full descriptions).

In 1998 a severe ice storm occurred across northern New York, eastern Canada and northern New England (hereafter 'the 1998 storm'). Disturbance caused by the 1998 storm was extensive and comparable to damage resulting from powerful hurricanes (Hooper and others 2001). Freezing rain and drizzle were reported by Environment Canada (1998) to have had a combined accumulation of 80 h during the storm's 7-day duration from January 4th to 10th (45–60 h is the annual average freezing precipitation for St. Lawrence Valley). Heavily impacted areas in the vicinity of our study area received in excess of 100 mm of freezing rain and ice pellets (DeGaetano 2000; Environment Canada 1998). Winds consistently blew from the northeast and ranged between 7 and 24 km/h with gusts up to 35 km/h (DeGaetano 2000).

Data Selection and Preparation

Satellite data from the Landsat Thematic Mapper (TM) sensor were processed to provide visible and near-infrared electromagnetic radiation intensity values for a lattice of pixels (25 by 25 m) in the northeastern Adirondacks covering a region totaling 2045 km^2 (Landsat TM Track 14/Frame 29; 8/21/90 & 8/27/98). Selection of these satellite data was necessitated by criteria including: pre- and post-storm dates, forest phenological similarity (that is, data acquired during anniversary weeks in August), minimal cloud cover, and suitable atmospheric visibility (that is, minimal humidity or atmospheric particulate). In situ measurements of forest canopy damage were incorporated into a change detection model (Millward and Kraft 2004) using extensive ground verification data provided from a study by Manion and others (2001). We used the percent breakage statistic derived by Rubin and Manion (2001) to model canopy damage. A subset of 23 plots within the 2045 km^2

region were selected from those randomly sampled by Manion and others (2001) for canopy damage modeling and verification (see Millward and Kraft 2004). We calculated the Normalized Difference Vegetation Index (NDVI), a measure of vegetation presence and vigor (Pettorelli and others 2005), using a standardized ratio of estimated atmospherically corrected surface reflectance values for each of the satellite images.

Forest Change Analysis

Forest canopy change resulting from ice damage was evaluated using image differencing of NDVI values calculated for the 1998 and 1990 satellite imagery. For purposes of this study, we confirmed that the 1998 ice storm represented the only major weather event during the 1990s that significantly influenced forest canopy integrity across a broad geographic extent within the northeastern Adirondack Park. We reviewed logging records held by the Adirondack Park Agency to confirm that only minor amounts of tree removal had occurred in the study area between acquisition of the 1990 and 1998 satellite images. Atmospheric normalization of these data satisfied the assumption that a zero mean for stable NDVI values in the difference image reflected no forest canopy change. Therefore, negative values in the resultant NDVI difference image were forest locations that experienced varying degrees of forest canopy alteration.

To distinguish 'true' forest damage from natural processes affecting vegetative vigor and density, we created a general linear model (GLM) using damage measurements from 16 forest plots, randomly selected from the pool of 23 (see Millward and Kraft 2004). In each of these 1-ha field plots, a measurement of canopy breakage was estimated. Forest canopy damage was quantified throughout the study area by classifying the NDVI difference according to the equation for the GLM. To avoid misclassification of damage, we excluded NDVI difference values that corresponded to less than ten percent canopy damage because damage of this low magnitude could not be conclusively attributed to the ice storm (Irland 1998; Manion and others 2001). The upper boundary (NDVI difference value) was determined by the maximum value of forest damage in the observed data (64%). Damage intensity measurements (per pixel) were collapsed into ordinal classes (no damage: <10%; moderate: 10–40%; high: >40%).

Selection and Classification of Aquatic Features

Thirteen stream segments and thirteen lakes were identified for investigation within the 2045 km^2 study region (Figure 1, Table 1). We first compiled a list of all lakes and streams in the region from the United States Geological Survey (USGS) spatial database provided by the Adirondack Park Agency, then generated a 500-m zone of influence around each feature and analyzed this area for the presence of built structures using high spatial resolution aerial photos. All water bodies with clear anthropogenic activity within their vicinity (that is, evidence of multiple buildings and/or shoreline clearance) were removed from the list of potential study sites. Lakes that were smaller than 10 ha were considered to have too little shoreline for adequate analysis, therefore, were removed from consideration. We randomly selected 13 water bodies in each category from the remaining streams and lakes for analysis.

No suitable streams of a high order within a region of high forest damage coverage were available within the study area, likely because greater coverage of damaged forests was concentrated in an elevational band higher than where such streams usually occur (Millward and Kraft 2004). Further, no streams of suitable length for analysis were available within areas of moderately damaged forest. Previous research (Millward and Kraft 2004) used a semivariogram analysis to determine that ice damaged forest was spatially aggregated across the study region, and that high-intensity damage sites occurred in patches with an area of influence approximating 150 m. Consequently, the proportion of damaged forest pixels was calculated for a 150-m zone from the water's edge into the interior forest, and this metric was used as a measure of the general intensity of ice storm damage within the area associated with a particular water body (that is, stream or lake). A forest location was considered to have experienced ice storm damage if an associated pixel was determined to have experienced greater than ten percent canopy breakage (that is, a 10% change in NDVI intensity, which corresponded to both moderate and high-intensity damage classifications for individual pixels) (Millward and Kraft 2004).

Based on these evaluations of damaged pixels, water bodies were classified according to the spatial coverage of ice storm damage within the adjacent forest (low: <15% of pixels categorized as having been damaged by the ice storm; moderate: 15–30% of pixels damaged; high: >30% of pixels

Table 1. Physical Characteristics and Classifications of Streams and Lakes

Map ID	Stream	Damage class	Average damage (%)	Order	Order class	Catchment area (km^2)	Area (ha)	Length (km)	Elevation (m)
1	Green St. Br.	High	33.6	2,3	Low	5.8–12.3	–	3.5	293–150
2	Gay Br.	High	43.1	2,3	Low	0.3–4.6	–	3.6	550–139
3	Little Trout Br.	High	42.7	2,3	Low	0.6–8.2	–	6.6	341–30
4	West Ausable	Low	8.4	4,5	High	54.1–144	–	16.3	647–506
5	East Ausable	Low	10.8	5	High	102.8–209.9	–	8.2	293–270
6	Gulf Br.	Low	6.2	2,3	Low	1.9–15.0	–	7.8	842–317
7	Jackson Br.	Low	9.8	2,3	Low	0.9–9.3	–	6.7	818–249
8	Barton Br.	Low	11.5	2,3	Low	0.6–9.3	–	8.8	723–172
9	Main Boquet	Low	11.6	5	High	204.5–210	–	3.5	166–159
10	Ore Bed Br.	Low	3.1	2	Low	0.8–5.4	–	3.9	1134–686
11	Gill Br.	Low	1.8	2,3	Low	0.3–7.7	–	6.2	993–424
12	East Boquet	Low	8.8	4	High	50.7–91.2	–	12.3	334–207
13	Cold Br.	Low	8.0	4	High	52.8–58.8	–	6.1	466–314
	Lake								
A	Keenan	High	44.4	–	–	–	18.3	2.8	350
B	Newberry	High	46.9	–	–	–	21.1	3.9	353
C	Trout	High	45.3	–	–	–	13.9	3.2	260
D	Lawson	High	38.9	–	–	–	10.6	2.0	203
E	Connery	High	39.9	–	–	–	32.7	2.9	257
F	Hadley	Moderate	26.2	–	–	–	15.4	1.8	186
G	Highland Forge	Moderate	25.9	–	–	–	50.1	3.9	177
H	Butternut	Moderate	30.7	–	–	–	65.0	4.9	346
I	Slush	Moderate	24.1	–	–	–	16.5	2.9	223
J	Frances	Low	9.9	–	–	–	12.2	2.6	506
K	Big	Low	12.5	–	–	–	21.3	3.4	189
L	Round	Low	15.1	–	–	–	19.1	1.7	635
M	Heart	Low	10.6	–	–	–	10.4	1.4	660

Average damage was calculated as the proportion of pixels classified as damaged within 150 m of the length of each lake or stream shoreline evaluated. The upper boundary (NDVI difference value) was determined by the maximum value of forest damage in the observed data (64%). Canopy damage measurements were collapsed into ordinal classes (no damage = 0–10%, moderate = 10–40%, intense = 40–64%) using natural breaks in the average damage (%) data.

damaged). Given the well-established relationship between catchment area and stream bankfull width (Dunne and Leopold 1978), catchment area was calculated for each of the stream segments as a method of estimating relative differences in forest canopy opening (bankfull width) created by the stream. We designated streams as 'large' or 'small' based on Strahler (1957) stream order as calculated from USGS 1:24,000 maps. Large streams were high-order; 4th or 5th order with greater than 50 km^2 watershed area. Small streams were 2nd and 3rd order with watershed areas less than 15 km^2 (Table 1).

Damage at the Terrestrial-Aquatic Interface

To compare ice damage between forest at the terrestrial-aquatic boundary and interior forest, we evaluated the canopy in four 25-m wide zones that extended 100 m inland from each stream and lake. A general linear mixed model (GLMM) procedure (Fahrmeir and Tutz 2001) was used to compare differences in canopy damage as a function of distance from the terrestrial-aquatic edge. A GLMM offers the flexibility to model the mean of a response variable with the inclusion of a random effects predictor, similar to constructing a randomized block design to reduce error variance when using ANOVA. This approach was selected because of its ability to account for site-specific differences in forest damage among stream segments and lake riparian zones. Each 25-m riparian zone section was considered to be a fixed-effect categorical variable; stream and lake sites were treated as a random effects categorical variable.

For one lake or stream within forest of a particular damage level, we calculated the proportion of shoreline-inland transitions in which changes were observed in forest damage magnitude between pixels located within the riparian zone adjacent to a lake or stream (0–25 m) and the next zone inland (25–50 m). Each ‘transition’ was calculated by comparing the damage in a shoreline pixel to its companion inland pixel (Rook’s case); therefore, nine possible transitions could occur between three possible damage classes found along the lake or stream shoreline and three potential damage classes in adjacent inland pixels (that is, a 3 × 3 matrix of transitions). We categorized streams by both size and damage class; lakes were classified by damage class alone. From each stream class (small/low damage, small/high damage, and large/low damage) we randomly selected one stream for our transition analysis; the same was done for lakes using damage class.

RESULTS

The cumulative length of streams investigated in our analyses was 92.5 km, and the total terrestrial-aquatic boundary analyzed was twice this length because both stream banks were considered (Table 1). We analyzed 13.7 km of small streams surrounded by forests with high levels of ice storm damage (mean level of forest damage: 39.6%) (Table 1), and 32.4 km of small streams surrounded by forests with low levels of ice storm damage (mean level of forest damage: 6.5% forest damage) (Table 1). Large streams in areas of low forest damage totaled 46.4 km in length, and the mean level of ice storm canopy damage was 9.5% (Table 1). The cumulative perimeter of the 13 evaluated lake shorelines was 37.4 km (Table 1). The high damage lakes averaged 42.9% damage coverage in the surrounding forest. A total of 14.8 km of high damage shoreline were assessed. Lakes within forests that experienced moderate-damage coverage included a total of 13.5 km of shoreline and averaged 26.7% areal canopy damage. Lakes within forests that experienced low-damage coverage had a total of 9.1 km of shoreline and averaged 12.0% areal canopy damage.

A statistically significant difference in the proportion of canopy damage was found between adjacent riparian zones extending inland from high-order streams surrounded by forests with low-damage coverage. Specifically, in forests with low damage, a significantly greater proportion of tree damage was observed within 25 m of large streams than at locations further from the water (Figure 2; $F(3,12) = 7.3$ $P = 0.005$). In these large streams the significant difference in damage within the riparian area occurred between the first zone evaluated (0–25 m inland from the streamside) and all other zones (25–50, 50–75, and 75–100 m). A statistically significant difference in proportion of canopy damage between adjacent 25-m zones was also found in lakes located in areas with low amounts of forest damage (Figure 2; $F(3,9) = 6.4$ $P = 0.013$). In this case, the significant difference occurred between the first (0–25 m inland) and the fourth zone (75–100 m) evaluated. No significant differences in canopy damage ($\alpha = 0.05$) were found for the other stream or lake classifications (Figure 2).

Transitions in damage intensity were analyzed among 310 pixel pairs along Cold Brook, a large stream positioned within a forest that experienced low-damage coverage. For moderately and highly damaged pixels adjacent to the stream, 64 and 35%, respectively, were observed to pair with an undamaged pixel one zone inland (Figure 3). Using the transition diagram and number of pixels in each damage intensity class, we determined: (1) 17% of streamside pixels of higher damage intensity were adjacent to pixels of a lower damage intensity one zone inland from the stream edge; (2) 6% of streamside pixels of lower damage intensity were adjacent to inland pixels of a higher damage intensity; and (3) that remaining pixels (78%) retained the same damage intensity classification with transition one zone inland. The majority of transitions in this latter category—in which the ice storm damage category remained the same in adjacent forest locations—encompassed forest areas that were undamaged by the ice storm.

The small stream within a forest that experienced low-damage coverage exhibited damage intensity transitions that were very similar to those found for the high-order stream surrounded by forests with low amounts of ice storm damage (Figure 3). For example, 73 and 39% of the moderately and highly damaged streamside pixels adjacent to Barton Brook were adjacent to an undamaged pixel 25 m inland. In this stream we found that: (1) 21% of the streamside pixels of higher damage intensity were adjacent to pixels of a lower damage intensity one zone inland from the stream edge; (2) 6% of the streamside pixels of lower damage intensity were adjacent to inland pixels of a higher damage intensity; and (3) 73% of the remaining adjacent pixels maintained the same ice storm damage class with transition one zone inland. Similar to the high-order stream evaluated in a forest with generally low amounts of ice storm damage, the majority of transitions in this latter category were also undamaged.

For small streams within forests that experienced high amounts of canopy damage (376 pixel pairs along Little Trout Brook), we found that 32 and

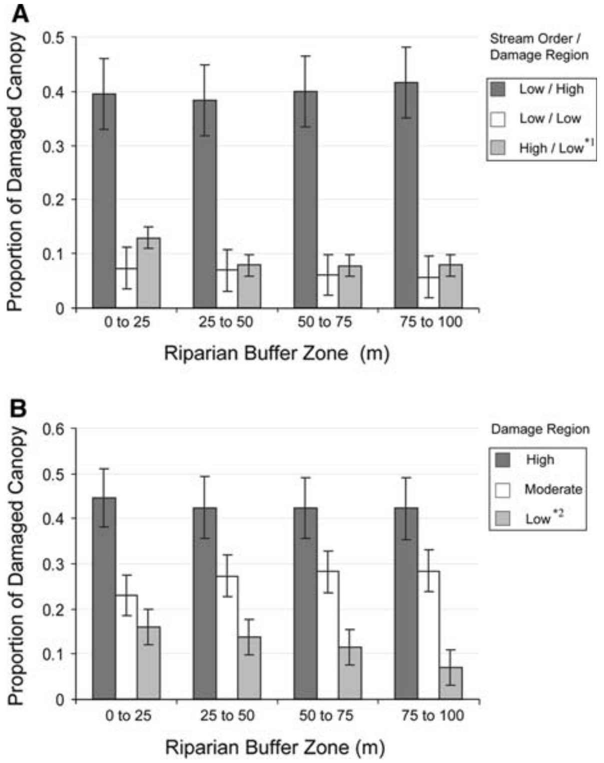


Figure 2. Proportion of damaged forest canopy as a function of **A** distance from stream edge and **B** lake shoreline. Streams are classified according to order and areal coverage of proximate forest damage; the lake classification reflects only areal coverage of proximate forest damage (see Table 1). Error bars represent 95% confidence intervals. *1 Significant difference overall in the percent canopy damage with distance inland from stream edge investigated; F(3,12) = 7.3 *P* = 0.005. *2 Significant difference overall in the percent canopy damage with distance inland from lake shoreline investigated; F(3,9) = 6.4 *P* = 0.013.

30% of moderately and highly damaged pixels adjoining the stream were located adjacent to undamaged forest 25 m inland (Figure 3). Overall, we found that twice as many streamside locations exhibited a decrease in ice storm damage in an inland direction (30% of pixels decreased in damage intensity; 14% increased). Overall, Little Trout Brook was found to have 56% of its pixels retain the same intensity value with movement on zone inland from the shoreline, three quarters of which were in the undamaged class.

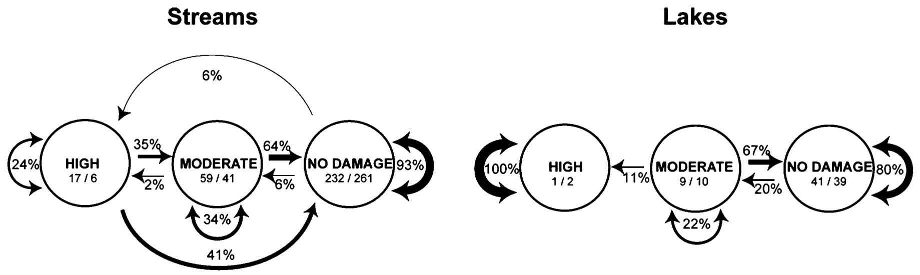
Transitions were calculated for 52 pixel pairs along the shoreline of Round Pond, a lake positioned within a forest that experienced low-damage coverage. For moderately damaged pixels adjacent to the lake, 67% were located next to an undamaged pixel one zone inland; the one highly damaged shoreline pixel was located adjacent to an inland pixel with the same damage intensity. Overall, we found that: (1) 12% of the shoreline pixels with high or moderate damage were adjacent to pixels of a lower damage intensity one zone inland from the lake edge; (2) 18% of the shoreline pixels of lower damage intensity were adjacent to inland pixels of a higher damage intensity (89% of these were transitions from no to moderate damage intensity); and (3) 71% of the shoreline pixels had the same intensity of ice storm damage as the adjacent pixel one zone inland (the majority remained undamaged).

Slush Pond, a lake surrounded by forest that experienced moderate damage was evaluated using 62 pixel pairs along its shoreline. For moderately and highly damaged shoreline pixels, 40 and 56% were paired with an undamaged pixel one zone inland (Figure 3). This analysis showed that 23% of the shoreline pixels of higher damage intensity were adjacent to pixels of a lower damage intensity one zone inland from the lake edge, and that 8% of the shoreline pixels of lower damage intensity were adjacent to inland pixels with greater ice storm damage. As with other streams and lakes, most (69%) shoreline and inland locations showed the same intensity of ice storm damage.

The largest lake evaluated (97 pixel pairs along the shoreline of Newberry Pond, which was located in an area of high coverage of ice storm damage) did not exhibit the same trends observed adjacent to lakes in locations with lower coverage of ice storm damage. Only 21 and 16% of the moderately and highly damaged pixels, respectively, adjacent to the lake shoreline were paired with an undamaged pixel one zone inland (Figure 3). Overall, we found that 27% of the pixels along the lake shoreline were located adjacent to an inland pixel with lower levels of damage, and 26% were located adjacent to a pixel with greater damage. By contrast with the other lakes, only about half (47%) of the paired streamside/inland locations included damage levels of the same intensity.

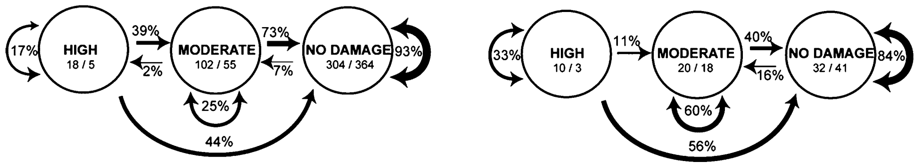
DISCUSSION

Our results showed that greater tree damage occurred along the shoreline of lakes and streams following a large ice storm disturbance, highlighting the role of the physical landscape in concentrating the movement of wood from the forest canopy to locations proximate to water bodies. Although several recent studies of ice storms have used remotely sensed data to evaluate the spatial



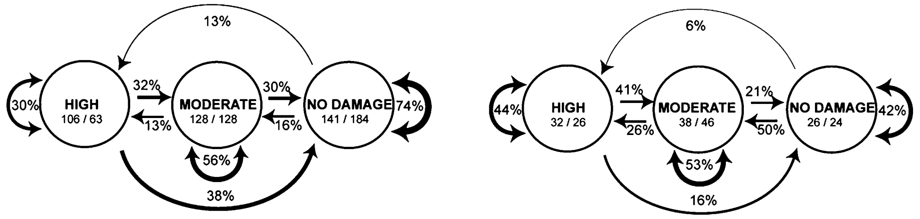
High Order / Low Damage
(Cold Brook)

Low Damage
(Round Pond)



Low Order / Low Damage
(Barton Brook)

Moderate Damage
(Slush Pond)



Low Order / High Damage
(Little Trout Brook)

High Damage
(Newberry Pond)

Figure 3. The proportion of shoreline to inland pixel damage transitions for each of nine categories (that is, a 3 × 3 matrix of transitions from three possible damage classes found along each shoreline and three potential damage classes in adjacent inland pixels) is shown for three study streams and three lakes. For water bodies in which fewer than nine transition arrows are shown (for example, eight transition arrows for Slush Pond), the missing arrow reflects the fact that no such transitions between adjacent pixel damage classes were observed (for example, for Slush Pond, no shoreline pixels categorized as 'no damage' were adjacent to an inland pixel categorized as 'high damage'). Numbers separated by a backward slash within intensity class circles report pixel counts in each riparian zone (0–25 m/25–50 m).

extent of damage intensity (McNeil and others 2008; Pasher and King 2006; Stueve and others 2007), this study provides the first evidence that wood deposition and other consequent effects of an ice storm could be concentrated within a large forested landscape along the shoreline of lakes and streams. Given the key role of wood within both streams and lakes, our analysis suggests that wood inputs across this terrestrial-aquatic boundary result from processes unique to this transition zone and do not simply result from the extension of forest processes, such as tree damage from a disturbance event and subsequent wood deposition on the forest floor. The overall observation that greater forest damage occurred along the riparian boundary highlights the distinct nature of wood dynamics along lake and stream shorelines and illustrates this process as a key component of aquatic ecosystems within forested landscapes.

Key to our ability to interpret observed distribution patterns of tree canopy damage was the use of a transition analysis to evaluate processes occurring along the boundary between forest edges and water bodies (rivers and lakes). This approach was more effective at identifying tree damage adjacent to terrestrial-aquatic boundaries on a finer scale (pixel-by-pixel) than a more traditional statistical analysis (GLMM). The ability of the transition analysis to reveal a 'from-to' spatial trajectory of canopy damage provides useful insight into understanding damage patterns along the terrestrial-aquatic boundary. Although application of a GLMM provided a measure of statistical confidence, this analysis was limited in its ability to distinguish differences between shoreline and inland locations due to averaging the large number of 'transitions' in which no change was found. This transition analysis could be further extended by developing a maximum likelihood procedure to estimate transition probabilities from the available data (Harris and Stocker 1998; White and Burnham 1999). In that type of analysis, each estimate would be determined by finding the parameter value most likely to fit the observed forest damage data.

The GLMM analysis revealed that minimally damaged forest locations ($<15\%$ areal coverage) proximate to lake shorelines were significantly more impacted closer to the terrestrial-aquatic boundary than were those locations farther inland. The same result was found along larger streams (Strahler order 4 or 5; subcatchment >50 km^2). The GLMM analysis showed that streams and lakes within forests with moderate or high levels of ice storm damage were affected more uniformly with distance from the terrestrial-aquatic interface. When transitions in tree canopy damage were evaluated along streams, we observed that less intensely damaged forest patches were located inland from the shoreline. For low-order streams within highly damaged forest, shoreline trees were two times as likely to be damaged as those inland; this difference increased to three times for high-order streams in low damage forest and 3.5 times for low-order streams in low damage forest. A similar analysis along forested lake shorelines revealed that shoreline locations that experienced high damage coverage were equally likely to be adjacent to inland locations that increased or decreased in damage intensity (1:1). By contrast, lake shoreline locations within forests that received a moderate amount of storm damage were almost three times as likely to have greater damage intensity (2.9:1) than locations one zone inland. Damage to trees proximate to the lake shoreline within forest that experienced low storm damage increased 1.5 times in severity with one transition inland.

Previous authors have suggested that the damage caused by an ice storm is intensified by the presence of strong winds (Bruederle and Stearns 1985; Hauer and others 1994; Seischab and others 1993), and Lemon (1961) reported that a moderate accumulation of ice combined with strong winds has the same effect as a heavier deposit with gentle winds. Several studies have shown that wind speed decreases as it moves from an open area deeper into a contiguous forest canopy (Geiger 1965; Irvine and others 1997). Others have found that precipitation can be greater along forest edges compared with the interior (Cadenasso and others 1997; Lindberg and Owens 1993; Weathers and Cadenasso 2001). We speculate that the topographic feature of V-shaped valleys may act to increase the wind susceptibility of forests adjacent to streams during and following an icing event. In such cases, wind is constricted and accelerated along the flanks of hills, through gaps, and along narrow valleys (Bormann and Likens 1979; Roebber and Gyakum 2003; Rosenberg and others 1983).

Coverage of ice damage was greater only along the terrestrial-aquatic interface for high-order streams within forest of low overall damage coverage (GLMM results, Figure 2); transition analysis also showed that similar processes occurred along streams located in forests with low overall damage coverage (Figure 3). This suggests that a wider forest opening along a higher-order stream may predispose forest along the terrestrial-aquatic interface to more areal canopy damage, but that the ratio of decreasing to increasing transition probability for damage intensity appears to have the same trend with movement inland. Therefore, although the overall coverage of forest damage did not increase near the aquatic-terrestrial edge for low-order streams (Figure 2) where damage did occur, the probability of finding damage of similar intensity decreased with movement one zone inland. This finding highlights the sensitivity of the transition analysis, when compared with a GLMM, to evaluate an edge effect.

The pattern of damage decline with distance from the terrestrial-aquatic boundary was different for the investigated lake shorelines than for stream edges. Our results for forests proximate to lake shorelines suggest the presence of a different mechanism that we believe is related to the U-shaped depressions in the landscape where these features are positioned. Although we observed great variability in the proportion of damaged canopy across the four zones investigated for lakes (Figure 2), a significant difference was found between the first zone (0–25 m) and the fourth zone (75–100 m) for lakes within forest that experiences low damage. This could result from the ''bowl-shaped'' topographic setting associated with lakes, which is more likely to allow wind traveling across the water surface to reach further into these riparian forests.

Transition analysis revealed that Round Pond, situated within forest that experienced low-damage coverage, experienced a greater amount (1.5 times) of forest canopy damage inland compared to locations immediately proximate to the shoreline (Figure 3). Trees growing along lake shorelines are 'naturally pruned' by regular exposure to wind and freezing precipitation (William Keeton, University of Vermont, personal communication), which is likely to make them more resilient to ice storm damage below a certain threshold. Where coverage of ice damage was moderate in intensity (Slush Pond), the observed trend in spatial pattern of tree damage was similar to that observed along streams, that is, damage intensity decreased with distance inland from the water's edge. Finally, in forests where the overall coverage of damage was high (Newberry Pond), the probability of site-specific transitions in damage intensity exhibited an equal chance of increase or decrease with movement inland.

Application of transition analysis and transition probability analysis to an ecological boundary question, such as the one addressed here, would benefit from a greater number of replicate lakes and streams. For this project, calculation of transitions for a large area was time-intensive and involved extrapolation from curvilinear vectors (streams and lake shorelines) to raster cells (proximate damaged forest). It would be useful to automate this process in future applications; otherwise researchers may continue to use less computationally intensive approaches, such as GLMM. Our analyses demonstrate that although the GLMM analysis was instructive in identifying aggregate trends in the forest damage zones analyzed, it was limited in its ability to capture important microscale relationships that occur between adjacent pixels.

Natural disturbance and environmental gradients interact in a complex and dynamic manner. Repeated disturbance events in forested ecosystems continually diversify vegetation at the extent of a landscape, creating mosaics of patches with different ages and successional status (Foster and Boose 1992; Mou and Warrillow 2000). Future ecological manifestations of ice damage will likely be influenced by the damage and regeneration history of previously affected locations (Smolnik and others 2006). Given that ice storms are frequent and reoccurring disturbance events in northeastern North America, our observations of greater damage in the riparian zone during ice storms of moderate intensity demonstrate that these events contribute to key ecological processes, such as increasing in wood input to streams and lakes and accelerating succession in riparian forests. Future investigations of landscape-extent ecological disturbances, including ice storms, will be able to take advantage of recently deployed satellite sensors with submeter spatial resolution to further evaluate such processes. These investigations will employ the detail of plot sampling throughout a large contiguous landscape, enabling better characterization of disturbance-related events at ecological boundaries such as those located where intact forests meet the water's edge of lakes and streams.

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