

Ecological importance of intermediate windstorms rivals large, infrequent disturbances in the northern Great Lakes

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Abstract. Exogenous disturbances are critical agents of change in temperate forests capable of damaging trees and influencing forest structure, composition, demography, and ecosystem processes. Forest disturbances of intermediate magnitude and intensity receive relatively sparse attention, particularly at landscape scales, despite influencing most forests at least once per generation. Contextualizing the spatial extent and heterogeneity of such damage is of paramount importance to increasing our understanding of forested ecosystems. We investigated patterns of intermediate wind disturbance across a forested landscape in the northern Great Lakes, USA. A vegetation change tracker (VCT) algorithm was utilized for processing near-biennial Landsat data stacks (1984–2009) spanning forests sustaining damage from four recent windstorms. VCT predominantly maps stand-clearing disturbance and regrowth patterns, which were used to identify forest boundaries, young stands, and disturbance patterns across space and time. To map wind damage severity, we compared satellite-derived normalized difference vegetation index (NDVI) values calculated from pre- and post-storm Landsat imagery. A geographic information system (GIS) was used to derive wind damage predictor variables from VCT, digital terrain, soils/landform, land cover, and storm tracking data. Hierarchical and random forests regressions were applied to rank the relative importance of predictor variables in influencing wind damage.

A conservative estimate of aggregate damage from the intermediate windstorms (extrapolated to ~150,000 ha, ~25,500 severe) rivaled individual large, infrequent disturbances in the region. Damage patterns were relatively congruent among storms and became more spatially heterogeneous with increasing disturbance intensity. Proximity to forest-nonforest edge, stand age, and soils/landform were consistently important damage predictors. The spatial extent and distribution of the first two damage predictors are extremely sensitive to anthropogenic modifications of forested landscapes, the most important disturbance agent in the northern Great Lakes. This provides circumstantial evidence suggesting anthropogenic activities are augmenting and/or diminishing the ecological effects of the natural wind disturbance regime. Natural disturbances of intermediate size and intensity are significant agents of change in this region, and likely in other regions, deserving more attention from ecologists and biogeographers.

Key words: blowdown; hierarchical partitioning; landscape ecology; mixed northern hardwoods; northern Wisconsin; random forests; remote sensing; Upper Peninsula of Michigan; vegetation change tracker.

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INTRODUCTION

Temperate forest ecosystems are inherently dynamic, continually responding to exogenous disturbances at a range of spatial and temporal scales (Foster et al. 1998, Boose et al. 2004, Woods 2004, Millward et al. 2010; Flatley et al., *in press*) and seldom achieving equilibrium (Foster 1988). Ecologists and biogeographers have studied disturbances since the early 20th century, but our appreciation and understanding of disturbances has increased dramatically over the last several decades (cf. White and Jentsch 2001). The convenience of examining weak to strong disturbances in plot-scale studies has led to numerous analyses and improved explanations of these phenomena (e.g., Downs 1938, Curtis 1943, Woods and Shanks 1959, Young and Hubbell 1991, Bellingham et al. 1995). An enhanced comprehension of landscape-scale disturbances coincides with the rapid development of landscape ecology and the growing appreciation for the influences large, infrequent disturbances (LIDs) exert on species composition, structure, demography, and ecosystem processes (Foster et al. 1998, Turner et al. 1998, Turner 2005). Fires (Schulte and Mladenoff 2005), hurricanes (Boose et al. 1994), and blowdowns (Canham and Loucks 1984, Foster and Boose 1992, Rich et al. 2007) have garnered widespread attention, but ice storms, floods, volcanic eruptions, tornados, and insects are stimulating increased interest (cf. Foster et al. 1998, Bebi et al. 2003, Stueve et al. 2007).

In forest ecosystems, LIDs typically damage trees across several tens to hundreds of thousands of hectares or more, inflicting widespread catastrophic damage approaching or exceeding 70% canopy loss (Canham and Loucks 1984, Foster and Boose 1992, Hanson and Lorimer 2007). However, LIDs may also damage a significantly smaller area of trees depending on the location and characteristics of specific disturbances, necessitating explicit descriptions of disturbance size, intensity, and recurrence interval applicable for disparate regions and disturbance types (Foster et al. 1998). Resultant damage patterns are commonly spatially heterogeneous, closely dependent upon interactions between the disturbance event and abiotic and biotic landscape features, triggering the patchy

development of new stands that may require decades or centuries to return to pre-disturbance conditions (Foster et al. 1998, Turner et al. 1998, Boose et al. 2004, Schulte and Mladenoff 2005). The significance and practicality of studying LIDs and their associated ecological ramifications are undeniable (Foster et al. 1998, Turner 2005). However, the recurrence interval of LIDs occasionally greatly exceeds the lifespan of tree species occupying a landscape of interest (cf. Bormann and Buell 1964, Frelich and Lorimer 1991b, cf. Boose et al. 2001, Woods 2004, Schulte and Mladenoff 2005). Hence, one might surmise that more frequently occurring intermediate disturbances also play a pivotal role in shaping complex mosaics of trees on forested landscapes (Woods 2004, Busby et al. 2009). In fact, intermediate disturbances may damage extensive areas, foster the development of landscape heterogeneity, and exert a strong influence on species composition, structure, demography, and ecosystem processes (Frelich and Lorimer 1991a, Dyer and Baird 1997, Boose et al. 2001, White and Jentsch 2001, Woods 2004, Hanson and Lorimer 2007). Compared to LIDs, damage from intermediate disturbances tends to be patchier, less catastrophic, and usually occurs over tens of thousands of hectares or less. Damage typically removes 30–60% of the canopy, but patchy areas of catastrophic damage (>70% canopy loss) are common (Dyer and Baird 1997, Hanson and Lorimer 2007, Fraver et al. 2009). Criteria for identifying intermediate disturbances are inevitably subjective, but the critical elements appear to be an event markedly less severe (in terms of storm intensity and area impacted) and more frequent than rare benchmark LIDs, yet strong enough to inflict patchy catastrophic damage and not considered a gap disturbance.

An intricate mosaic of uneven-aged conifers, hardwoods, and conifer-hardwood mixes dominate forests throughout the northern Great Lakes region of the United States (Fig. 1). Disturbance is the principle driver of landscape changes in forest structure and function in this region, where weak topographic and climatic gradients exhibit only moderate influence (Canham and Loucks 1984, Woods 2004, Schulte and Mladenoff 2005, Hanson and Lorimer 2007). Historically, fire and wind were the most important natural disturbance agents. Wildfire suppression has

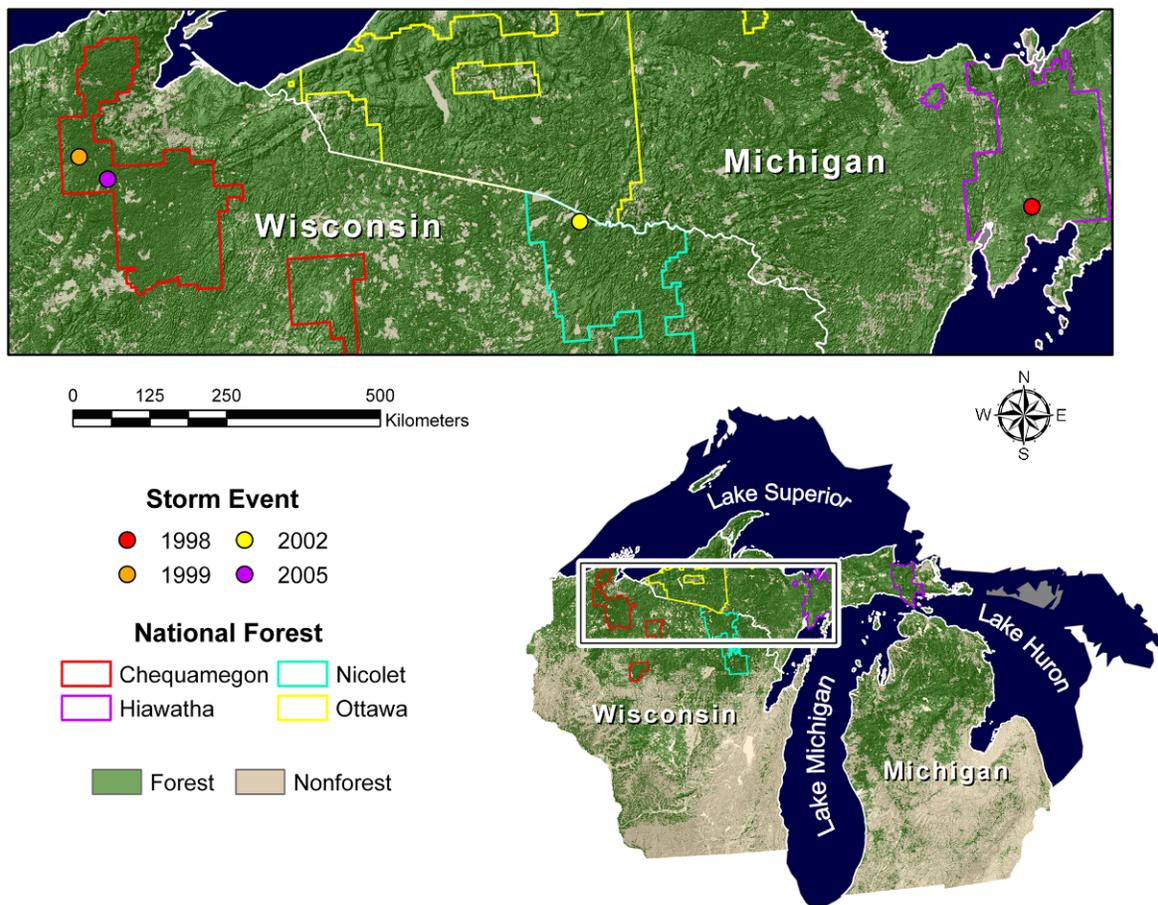


Fig. 1. Point locations of study sites influenced by the four windstorms. Note the 2005 Wisconsin storm site is in relatively close proximity (~ 70 km) to the 1999 Wisconsin storm site. However, only a relatively confined area of $\sim 5,000$ ha was significantly impacted by the 2005 Wisconsin storm and damage overlapping with the 1999 Wisconsin storm was not observed on the satellite imagery.

diminished the influence of fire, leaving wind as the predominant natural agent of forest disturbance in this region (Schulte and Mladenoff 2005). Estimates of return intervals for catastrophic wind disturbance from LIDs are variable, ranging from ~ 450 years in a few instances upwards to 1000 years or much more in other cases (Whitney 1986, cf. Woods 2004, Schulte and Mladenoff 2005). These return intervals easily exceed the approximately 150–350 years lifespan of many dominant tree species in the region (Frelich and Lorimer 1991b). Benchmark catastrophic wind disturbances include the Flambeau Forest blowdown in northern Wisconsin during July of 1977 and the Boundary Waters blowdown in northern Minnesota during July of 1999. The first caused 344,000 ha of damage (7% cata-

strophic) with estimated wind speeds approaching 253 km/h; the second caused 190,000 ha of damage (30% catastrophic) with estimated wind speeds approaching 185 km/h (cf. Canham and Loucks 1984, cf. Schulte and Mladenoff 2005). Conversely, intermediate wind disturbances usually influence portions of all stands in this region at least once during the expected lifespan of dominant tree species (Frelich and Lorimer 1991b). These comparatively frequent, but much smaller and less intense wind disturbances, likely are crucial for maintaining a mosaic of uneven aged forest stands in the region.

Interactions between storm intensity and tree susceptibility, both of which may vary greatly over small distances, affect the severity and extent of forest damage (Boose et al. 1994, Nelson

et al. 2009). The physical mechanisms controlling forest susceptibility to wind damage are generally well known and mostly relate to wind exposure, species type, the tensile strength of wood, tree health, rooting stability, and the meteorological characteristics of the storm, among others (Foster 1988, Webb 1989, Brokaw and Walker 1991, Matlack et al. 1993, Boose et al. 1994, Everham and Brokaw 1996, Peterson 2004, Schulte and Mladenoff 2005, Laurance et al. 2006, Busby et al. 2008). Despite this robust understanding of wind damage in forests, ecologists and biogeographers do not fully understand the expression of damage at multiple spatial scales with storms of varying intensities, magnitudes, and recurrence intervals (Woods 2004, Busby et al. 2009). There is an adequate and gradually expanding quantity of plot- and landscape-scale studies investigating catastrophic wind damage. Field techniques assessing tree and/or stand properties are commonly exploited for the former (cf. Everham and Brokaw 1996) and public land survey data and/or hybrid GIS modeling/field techniques for the latter (e.g., Whitney 1986, Foster and Boose 1992, Schulte et al. 2005). Alternatively, spatially explicit remote sensing and GIS modeling are used in some landscape-scale studies (Boose et al. 1994, Nelson et al. 2009). Fewer studies examine plot-scale intermediate disturbances (but see Frelich and Lorimer 1991a, Dyer and Baird 1997, Woods 2004, Hanson and Lorimer 2007, Busby et al. 2009) and there is a dearth of spatially explicit landscape-scale studies.

We designed this research to address the aforementioned literature gap and investigate the following specific questions: (1) How does aggregate forest damage from intermediate windstorms compare to damage from individual LIDs? (2) What factors are most important in influencing the spatial patterning of damage? (3) How consistent are the most important factors at influencing forest damage between multiple windstorms across space and time?

METHODS

Study area

We evaluated spatial patterns of forest damage sustained from four windstorms of intermediate magnitude and intensity associated with unusu-

ally strong thunderstorms (at least 80 km/h sustained winds with gusts near 115 km/h or more) in northern Wisconsin and the Upper Peninsula of Michigan, USA (Figs. 1, 2, 3, and Table 1). We restricted the analyses to four because selection criteria necessitated choosing windstorms from the late 1990s to 2000s on United States Department of Agriculture (USDA) Forest Service national forest lands (national forests) with extensive historical records. This strategy allowed assessments of pre-storm forest conditions via remote sensing, the identification of potentially confounding disturbances, and reliable demarcations of storm impact perimeters. The study area is located in the northern Great Lakes region of North America, which consists of a humid continental climate and is designated a Laurentian Mixed Forests Province (Bailey et al. 1994). The mixed forest province is a transitional zone between the boreal forests to the north and the broadleaf deciduous forests to the south and southeast. It includes mixtures of coniferous (e.g., *Abies balsamea*, *Picea glauca*, *Pinus banksiana*, *Pinus resinosa*, and *Pinus strobus*) and deciduous (e.g., *Acer rubrum*, *Betula papyrifera*, *Populus tremuloides*, *Quercus ellipsoidalis*, and *Quercus rubra*) species in many locations along with interspersed patches consisting of almost exclusively coniferous or deciduous trees. The landscape exhibits gentle topographic relief varying only slightly over distances of hundreds of meters, stippled with an eclectic mix of surficial geology features associated with a series of glacial advances and retreats between 1.8 million and 11,000 years ago.

The geography of this region favors the development of intense convective thunderstorms during the growing season that sometimes generate damaging wind downbursts. Benchmark catastrophic blowdowns usually result from the development of a series of multiple downbursts in derecho formations (Peterson 2004). Tornadoes and gales associated with intense low pressure also cause wind damage, but non-tornadic winds associated with thunderstorms inflict the most damage to forests (Peterson 2004). The contemporary landscape of the area is also partly a product of extensive logging and development (Radeloff et al. 2005, Perry et al. 2008, Pugh et al. 2009).



Fig. 2. Photograph of a *P. tremuloides* (quaking aspen) stand damaged by the 1999 Wisconsin storm in Chequamegon National Forest (photo by Steven Katovich, USDA Forest Service, Bugwood.org).

Disturbance and forest mapping strategy

Generating spatially explicit maps of continually shifting forest boundaries across space and time is necessary for understanding intermediate wind disturbance patterns in forests at landscape scales. Recent technological advancements make this possible for the first time. The *North American Forest Dynamics* (NAFD) project (Goward et al. 2008) introduced novel remote sensing methods capable of exploiting biennial or near-biennial stacks of Landsat satellite imagery to generate the necessary data (Huang et al. 2010). At the heart of the data processing, the vegetation change tracker (VCT) algorithm currently utilizes Landsat 4–5 Thematic Mapper (TM) and Landsat 7 Enhanced Thematic Mapper Plus (ETM+) data from 1984–present and uniquely considers the spectral responses of all pixels in the Landsat stacks (Huang et al. 2010). VCT tracks changes in the values of Landsat pixels (30-m resolution) every two years (for ~25 years) and identifies anomalies that are indicative of disturbance,

recovery, persisting forest, persisting nonforest, or persisting water. Areas of persisting forest tend to be relatively stable over time, but disturbance and subsequent recovery (e.g., temporary reduction in canopy cover from harvest activity or stand-clearing tornadic windthrow) or lack of recovery (e.g., permanent change in land use from housing development) generate unique changes in the response signal. This allows for the generation of historical maps outlining dynamically changing forest boundaries and stand ages (Fig. 4). VCT facilitates efficient and broad-scale mapping of changes due to human activity and natural disturbance, and allows for subsequent importation into a GIS environment. We exploited output products from VCT to characterize pre-storm stand conditions and derive some of the predictor variables (see *Deriving the Predictor Variables* below). We did not use VCT to map wind damage severity because the algorithm is most sensitive to stand-clearing disturbances and is less sensitive to



Fig. 3. Photograph of an older *P. resinosa* (red pine) and *P. strobus* (eastern white pine) stand damaged by the 1999 Wisconsin storm in Chequamegon National Forest (photo by Steven Katovich, USDA Forest Service, Bugwood.org).

Table 1. Characteristics of the four windstorms.

Descriptor	Four intermediate windstorms of interest			
	1998	1999	2002	2005
Month and day	May 17	July 31	July 21	September 13
State	Michigan	Wisconsin	Wisconsin and Michigan	Wisconsin
County	Delta	Bayfield	Forest and Iron	Bayfield
Top estimated sustained wind speed (km/h)	111	112	80	84
Top estimated wind gust (km/h)	130+	160+	115+	115+

partial canopy disturbances.

To construct Landsat data stacks spanning the areas impacted by the four windstorms, we acquired ~25 years of near-biennial level one terrain-corrected Landsat TM imagery (except for one ETM+) from the United States Geological Survey (USGS) for each of three Landsat scenes (Tables 2–4). We selected mostly cloudless and high quality imagery from the growing season (defined as the middle of June to the middle of September), but selectively excluded some June

and September imagery when phenological conditions during a specific year deviated from normal long-term observations (e.g., during an abnormally cool growing season or unseasonable frosts). VCT also requires digital land cover and elevation data for successful operation. Hence, we obtained the 2001 National Land Cover Database (NLCD) at a spatial resolution of 30 m from the Multi-Resolution Land Characteristics Consortium (Homer et al. 2004) and a digital elevation model (DEM) of 30 m spatial resolution

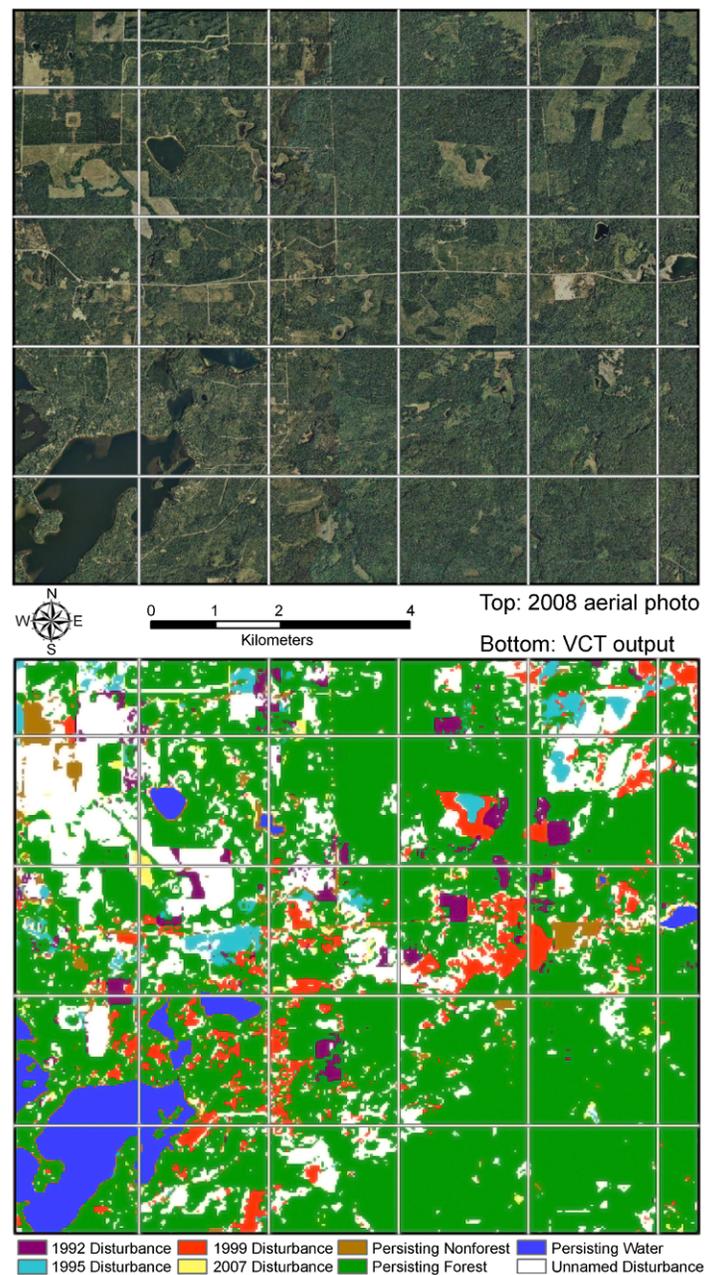


Fig. 4. VCT compared to a 2008 1-m resolution aerial photograph from the National Agricultural Imagery Program. VCT is predominantly sensitive to stand-clearing catastrophic disturbances. Thus, we determined it was reasonable to use the last year of disturbance as an indicator of stand age.

from the USGS generated by version 2 of the shuttle radar topography mission (SRTM). We processed all data with techniques similar to those described by Huang et al. (2010) and Thomas et al. (2011).

Mapping, verifying, and quantifying wind damage

To enhance the detection of wind disturbance patterns, we used normalized difference vegetation index (NDVI) values derived from carefully selected pre- and post-windstorm Landsat imag-

Table 2. Landsat imagery selection information for p23r28.

Acquisition year	Acquisition date	Satellite sensor	Comments
1984	July 18	Thematic Mapper	
1987	June 9	Thematic Mapper	Warm spring temperatures
1988	July 29	Thematic Mapper	
1989	September 2	Thematic Mapper	
1992	July 24	Thematic Mapper	
1994	August 15	Thematic Mapper	
1996	July 3	Thematic Mapper	Included in VCT processing
1996	August 4	Thematic Mapper	Only used for pre-storm NDVI
1998	August 10	Thematic Mapper	Post-storm NDVI
1999	June 26	Thematic Mapper	Warm spring temperatures
2000	September 8	Thematic Mapper	Normal fall and no early freeze
2002	July 20	Thematic Mapper	
2003	June 21	Thematic Mapper	No late spring frosts or extreme cold
2006	July 15	Thematic Mapper	
2007	August 3	Thematic Mapper	
2009	September 9	Thematic Mapper	Very warm fall temperatures

Table 3. Landsat imagery selection information for p24r28.

Acquisition year	Acquisition day	Satellite sensor	Comments
1985	August 13	Thematic Mapper	
1986	August 16	Thematic Mapper	
1987	September 4	Thematic Mapper	Warm fall temperatures
1990	June 24	Thematic Mapper	Mostly normal spring temperatures
1991	August 18	Thematic Mapper	
1994	September 7	Thematic Mapper	Mostly normal fall temperatures
1995	June 22	Thematic Mapper	Warm and dry spring
1997	July 29	Thematic Mapper	
1999	July 27	Thematic Mapper	
2001	September 2	Enhanced Thematic Mapper	Only used for pre-storm NDVI
2002	July 11	Thematic Mapper	Post-storm NDVI
2003	September 16	Thematic Mapper	Warm fall temperatures
2004	September 18	Thematic Mapper	Warm fall temperatures
2007	June 23	Thematic Mapper	Warm spring temperatures

Table 4. Landsat imagery selection information for p26r28.

Acquisition year	Acquisition day	Satellite sensor	Comments
1985	September 12	Thematic Mapper	Mostly normal fall temperatures
1987	June 14	Thematic Mapper	Early spring with record early ice-out
1989	July 21	Thematic Mapper	
1992	August 14	Thematic Mapper	
1993	August 1	Thematic Mapper	
1995	September 8	Thematic Mapper	No hard frost until late September
1998	June 28	Thematic Mapper	Pre-storm NDVI, normal spring
1999	July 25	Thematic Mapper	Only used for post-storm NDVI
1999	September 3	Thematic Mapper	
2001	August 7	Thematic Mapper	
2003	July 12	Thematic Mapper	
2005	July 17	Thematic Mapper	Included in VCT processing
2005	August 2	Thematic Mapper	Only used for pre-storm NDVI
2006	August 21	Thematic Mapper	Only used for post-storm NDVI
2007	July 7	Thematic Mapper	
2009	June 26	Thematic Mapper	Mostly normal spring temperatures

ery (near anniversary dates, within the growing season, no more than two years prior to the disturbance, and no later than one year after) (Tables 2–4). We preferred precise (± 1 week) anniversary dates within one year of the respective windstorm, but cloud cover and questionable image quality prevented us from achieving this goal for the 1998 Michigan storm (p23r28 in Table 2). NDVI (Rouse et al. 1973, Tucker 1979) is a ratio between red and near-infrared spectral reflectance that is extremely sensitive to the health or vigor of vegetation and is effective for examining landscape-scale disturbance patterns in temperate forests (e.g., Stueve et al. 2007, Millward et al. 2010). In forested landscapes, comparatively high NDVI values are indicative of a healthy and intact canopy with little damage. Comparatively low post-storm NDVI values signify damage to forest canopy. Subtracting the pre-storm NDVI from the post-storm NDVI results in an image where, ostensibly, all negative NDVI difference values represent varying degrees of wind damage and those near zero signify no wind damage. For example, catastrophic/severe damage evident in Figs. 2 and 3 corresponds to the low NDVI difference values (near -20) in the upper right panel of Fig. A2 (Appendix A).

To ensure we were evaluating wind damage, we perused extensive records available for national forests in the northern Great Lakes. We selected windstorms not associated with other potentially confounding major disturbances and masked known forest harvests and development (with VCT and GIS inventory layers from local foresters) between the NDVI image acquisition dates. We also utilized USDA Forest Service Forest Inventory and Analysis (FIA) plot data and post-storm damage assessments from local foresters (at the stand-level) to perform validations of 242 points. Information gleaned from FIA plots and stand-level damage assessments indicate increasingly negative NDVI difference values correspond with progressively more severe forest damage and that stable or slightly positive values correspond with no damage (Appendix A: Figs. A1 and A2). We assumed that NDVI difference values predominantly represent varying degrees of wind damage from the four windstorms, or lack thereof, although there may be some background noise stemming

from local disturbances, as is indicated by outliers.

Additionally, we utilized the uppermost NDVI difference value in the interquartile range for the “light” validation category as the maximum limiting threshold for estimating the area of forest damage attributable to each windstorm (Fig. A2). We assumed all NDVI difference values below this threshold denoted wind damage. We performed similar procedures targeting the “severe” validation category for making estimates of severe wind damage (Fig. A2). Estimates were only performed inside the defined perimeter of storm impact areas in national forests, as determined by Forest Service land records, National Climatic Data Center (NCDC) storm archives, radar archives (when available), field damage reports, and discussions with local foresters. We therefore suspect area estimates of regional damage are quite low because of confirmations of widespread damage outside the boundaries thus established. Our estimates should be treated as minimum areas for wind disturbance resulting from the four windstorms in national forests.

Deriving the predictor variables

We searched the existing literature on plot- and landscape-scale wind disturbance research to identify a suite of potential predictor variables for forest susceptibility to wind damage. Our selections were constrained to site-level factors including elevation, slope aspect, slope angle, soils/landform type, forest types, stand age, proximity to forest-nonforest edge, windward forest-nonforest edge, proximity to forest-water edge, windward forest-water edge, and proximity to storm path (e.g., Brokaw and Walker 1991, Foster and Boose 1992, Schulte and Mladenoff 2005, Busby et al. 2008). The first three predictors are standard DEM-based derivations acquired from the processed SRTM data (considering all eight surrounding pixels for slope aspect and slope angle). We acquired soils/landform type from the Natural Resources Conservation Service’s SSURGO database (Soil Survey Staff 2010). We obtained forest types from the 30-m NLCD 2001 database, which differentiates between coniferous, deciduous, and coniferous-deciduous mixed forest types. Other tree-specific factors would have been interesting to examine and

likely exerted some influence on damage patterns, but we did not include any of these predictors because of challenges with modeling them over expansive landscapes.

We used VCT categorical disturbance outputs and GIS layers from local foresters (denoting year of harvest) to determine stand age by calculating the number of years between the most recent pre-storm stand-clearing disturbance and windstorm of interest. All forests originating before the 1980s remain aggregated for this predictor variable because the Landsat data stacks span the last ~25 years and only sparse GIS data are available prior to the 1990s, but subsequent years have temporally explicit stand ages available. Despite this lack of comprehensive coverage, we chose to include the stand age data in our analyses because susceptibility to damage from wind changes rapidly with stand age (Evans et al. 2007) and most stands existing prior to the 1980s are 50+ years old in areas of persisting forest that are rarely harvested. Hence, we would expect a strong relationship between stand age and wind damage. We derived proximity to forest-non-forest edge by calculating Euclidean distance from the outside perimeter of all forested areas existing prior to the respective windstorm of interest, as determined by VCT (including edges for recently harvested stands less than five years old). Therefore, pixels on forest edge receive a value of zero and pixels inside forest edge sequentially increase in distance until reaching the center of the patch of interest. We also calculated Euclidean direction for these data and used a cosine transformation to produce a linear variable corresponding with the prevailing wind direction for each windstorm. For example, northwest winds are sometimes associated with thunderstorms in the area and the derived linear direction variable would be “northwestness” with northwest being 1 and southeast -1 . To avoid overlapping influences with forest-lake edge and determine whether bodies of water are unique contributors to wind damage, we designated areas of water as forest when deriving distance and direction from forest edge. Subsequently, we removed the water mask and implemented similar Euclidean distance procedures to calculate distance and direction from bodies of water larger than 100 ha that were delineated by VCT. To determine proximity to

storm path, we collected coordinates for the movements of all four windstorms from NCDC reports, field damage assessments, and radar archives. We used this information to create a storm path polyline in a GIS and calculated Euclidean distance expanding out from both sides.

Sampling design and statistical analyses

We devised a stratified random sampling strategy inside the perimeter of the areas impacted by each respective windstorm. The generation of at least 260 points per storm ensured a minimum allotment of 20 points per independent variable (Hirzel and Guisan 2002) after data transformations. We increased the sample size proportionately with the storm impact area to mitigate potential scaling discrepancies and facilitate impartial comparisons, beginning with the 2005 WI storm (the smallest windstorm by area). We restricted the distribution of the sampled points to pre-storm forested areas identified by the VCT and maintained a proportional allotment of points spanning the full range of NDVI difference values (i.e., evenly distributed by damage thresholds in Fig. A2). We also prevented the sampling of points within 30 m of forest boundaries to avoid potential false positives for wind damage associated with shifting edge shadows, subtle georectification errors, and/or pixels only partially overlapping forest edge. Enhanced wind damage associated with forest edge may infiltrate the interior forest well beyond 100 m (cf. Laurance et al. 2006). Therefore, excluding data within a 30-m buffer of forest boundaries should not greatly detract from the ecological significance of modeling and including distance to forest edge in the statistical analyses.

We implemented a statistical modeling strategy to test the null hypothesis that wind damage sustained by forests is random. We chose regression in the hierarchical partitioning framework (“all.regs” and “hier.part” functions with the 2010 hier.part package in R 2.10.0) because it is capable of handling correlated independent variables and provides reliable rankings of predictor importance statistically based on the rejection or acceptance of a null hypothesis (Mac Nally 1996, 2002). However, hierarchical regressions introduce potential rounding errors when

considering more than nine variables, may underestimate the significance of uncorrelated variables, and cannot consider more than thirteen variables. We identified twelve potentially important predictor variables when including spatial autocorrelation (modeled as discussed by Stueve et al., *in press*). Consequently, we first applied random forests regressions ('randomForest' and 'rf_import' functions with the 2010 randomForest package in R 2.10.0) and interpreted the mean decrease in accuracy rankings to identify which three variables to exclude from the hierarchical regressions (Breiman 2001). The random forests machine-learning approach readily handles a large number of correlated predictor variables and nonlinear data with abnormal distributions (Breiman 2001). Before applying hierarchical partitioning, we normalized the nine remaining independent variables with data transformations and removed outliers to reduce skewness and kurtosis to less than one; satisfying the more stringent data distribution requirements of hierarchical regressions (i.e., mostly linear relationships and normal distributions). In each case, we experimented with several different data transformations and selected the most effective one for final transformations. After applying the hierarchical regressions, we determined statistical significance by calculating Z-scores with the 'rand.hp' function available with the 2010 hier.part package in R 2.10.0 (Mac Nally 2002). In an effort to lend more credence to the relative rankings gleaned from hierarchical partitioning, we applied random forests to the final nine variables with expectations of discovering similar results.

RESULTS

Extent of windstorm damage

Aggregate forest damage (light, moderate, and severe) sustained in national forests from all four windstorms was about 50,000 ha (approximately 17% or 8,500 ha of which was severe damage). The 1998 Michigan, 1999 Wisconsin, 2002 Wisconsin and Michigan, and 2005 Wisconsin storms respectively accounted for approximately 14,000 ha, 11,000 ha, 20,000 ha, and 5,000 ha of damage (corresponding to about 24%, 30%, 6%, and 12% of severe damage). The proportion of severe damage also displayed a positive relationship

with disturbance intensity; the highest percent severe damage occurred during the 1999 Wisconsin storm (~160 km/h wind gusts) and the lowest was in the 2002 Wisconsin and Michigan storm (~115 km/h wind gusts) (Table 1). These estimates are constrained to damage within the boundaries of national forests. Additional extensive windstorm damage was reported beyond these boundaries, but delineating a storm impact perimeter outside national forests was problematic.

Significance and relative importance of damage predictor variables

In terms of the hierarchical regression models, we rejected the null hypothesis for all four windstorms, which indicates forest damage sustained from the windstorms was not random (Fig. 5). The cumulative percent independent variance explained was 34%, or more, for each of the four windstorms (45% for 1998 Michigan, 71% for 1999 Wisconsin, 34% for 2002 Wisconsin and Michigan, and 37% for 2005 Wisconsin windstorms), exhibiting a strong positive relationship with storm intensity (Fig. 5 and Table 1). The model for the 1999 Wisconsin storm (~160 km/h wind gusts) had the highest explanatory power and the 2002 Wisconsin and Michigan storm (~115 km/h wind gusts) had the lowest. The hierarchical regressions also generally corresponded well with the random forests approach, except for a few subtle discrepancies, lending additional credence to the validity of our analyses (Fig. 5). Proximity to forest edge, stand age, and soil type/landform were consistently important predictors of wind damage significant at the 99% confidence level. Conversely, predictor variables related to forest-lake edge, topography, wind pitch, distance to storm path, and forest type were marginally important or not statistically significant (Fig. 5).

Patterns of forest damage

The spatial patterning of forest damage is distinct and relatively consistent between windstorms (Fig. 6 and Appendix B: Fig. B1). Locations near forest-nonforest edge, within mature stands, and on landforms with comparatively shallow-moist and deep-moist soils are most susceptible to wind damage. However, deep soils generally displayed the most damage.

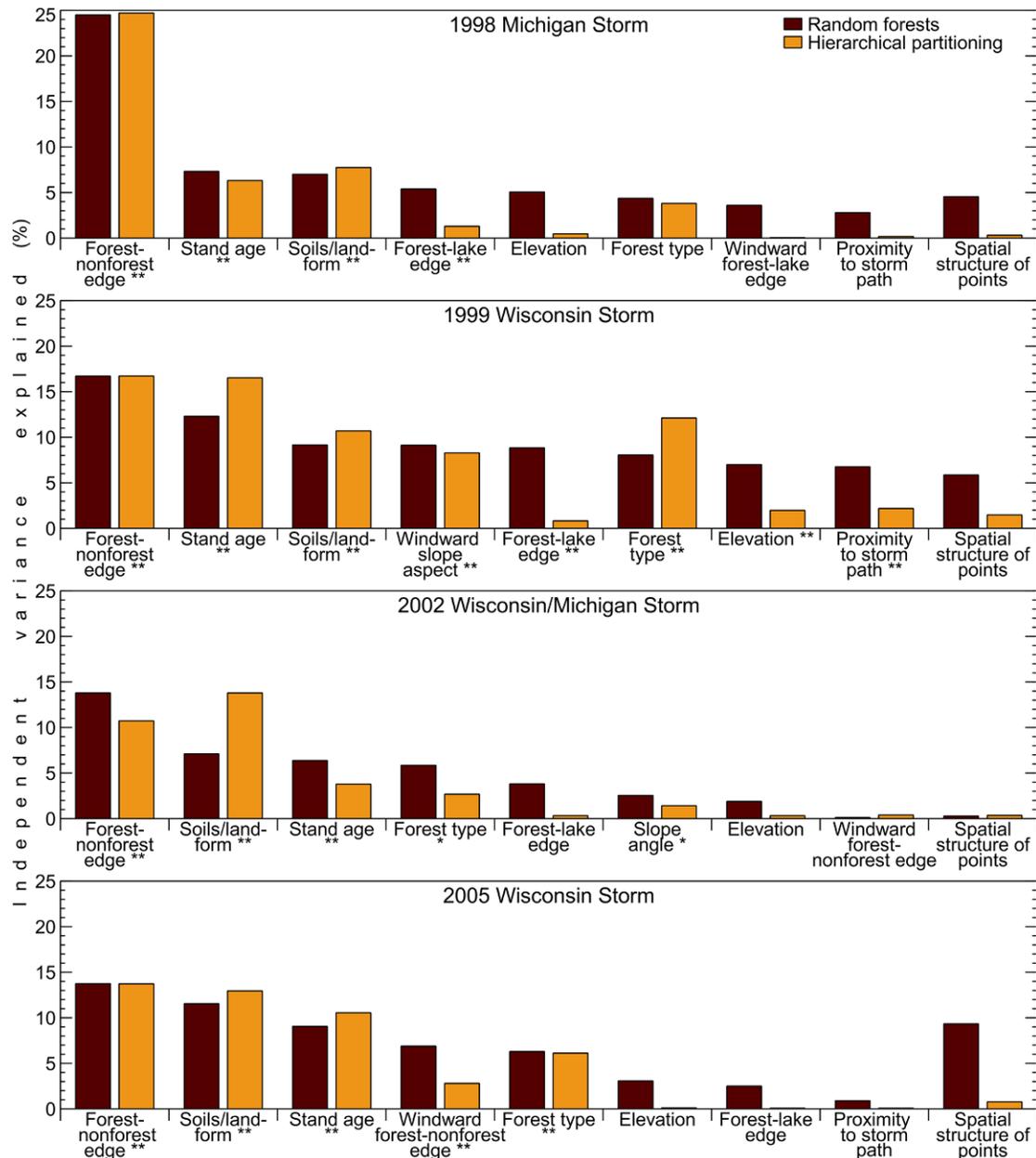


Fig. 5. Relative importance of the predictor variables in influencing wind damage patterns as determined by random forests (standardized output) and hierarchical partitioning regressions.

Other instances where wind damage was enhanced include locations near forest-lake edge, in deciduous forest, on windward forest-lake edges, on windward slope aspects, at moderately high elevations, and near the storm path (Appendix B: Figs. B2 and B3). However, these trends are not universally important between all four wind-

storms.

DISCUSSION

The spatiotemporal aggregate of forest damage sustained from the four intermediate windstorms is of considerable size and certainly rivals

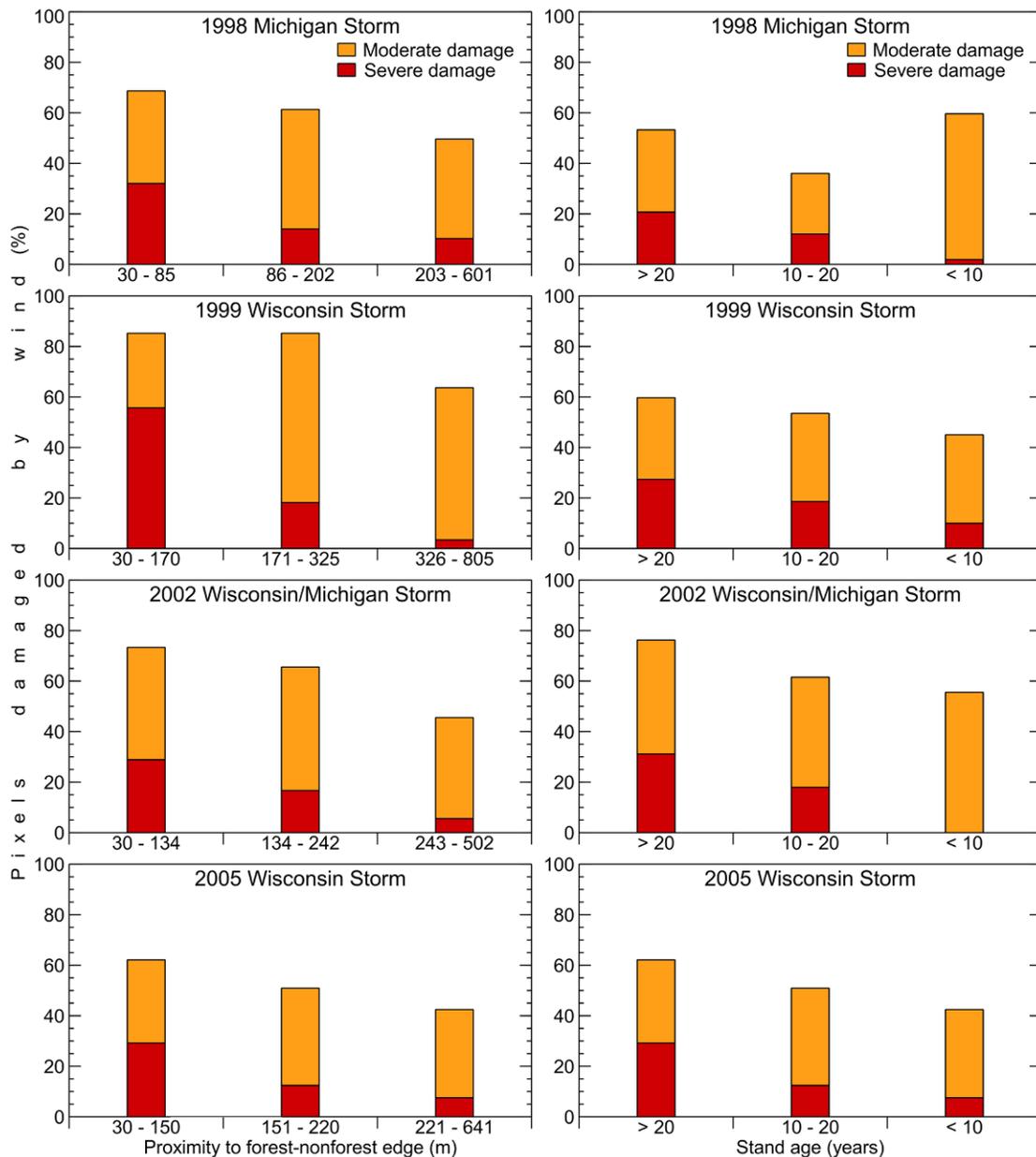


Fig. 6. Wind damage trends for two of the three most important predictor variables. The y-axis represents percent of pixels damaged in the respective category for each predictor. We derived values from the stratified random points utilized for the statistical analyses in each storm and classified damage based off the upper quartile thresholds for the moderate and severe categories in the NDVI validation data (Fig. A2).

individual LIDs in the region. Due to Landsat data constraints and challenges associated with validation, we only examined windstorms between 1998 and 2005 in suitable national forests (representing only ~10% of all forested lands in

the northern Great Lakes). But, an extremely conservative extrapolation (i.e., assuming identical forest damage occurs every 50 years within or beyond national forests) encompassing the lowest estimated lifespan of existing dominant tree

species (150 years) suggests at least 150,000 ha (50,000 ha \times 3) are similarly damaged (25,500 ha severe) within a typical canopy generation. This approximation approaches the spatial extent of damage for individual benchmark LIDs in the region, both in terms of total area of forest damaged and the extent of severe damage (Canham and Loucks 1984, Schulte and Mladenoff 2005). The extrapolation is also probably low because of the restricted area considered in the analyses, conservative NDVI thresholds, and support in the literature for similar or more frequently occurring intermediate disturbances spanning large spatial extents in the Great Lakes (Frelich and Lorimer 1991*b*, Schulte and Mladenoff 2005) and other forested regions (Foster 1988, Bellingham et al. 1995, Boose et al. 2001, Boose et al. 2004).

More importantly, the relatively consistent rankings of wind damage predictors across space and time suggest the damage effects from individual windstorms of intermediate size and intensity are ecologically significant in aggregate. This trend contradicts some previous research that suggests damage patterns from storms of any intensity may be quite variable (Busby et al. 2009). Two factors provide a plausible explanation for this discrepancy. First, logic suggests identical land use, geologic, and disturbance history throughout the Great Lakes region likely engendered similar interactions between windstorms, forests, and the surrounding landscape. Second, modeling the most important predictor variables (particularly proximity to forest edge) and potential correlations with wind damage at broad scales has been problematic in the past, especially in landscapes where the area of forest edge shifts rapidly. When only considering moderately important predictor variables, the seemingly identical trends abate (Fig. 5). For example, close linkages between topography and wind damage are evident in the 1999 Wisconsin storm and become inconsequential in the other three storms. Therefore, with the proper context, our results echo previous research. Indeed, it appears that evidence supporting identical relative rankings of the most important wind damage predictors across space and time is an important finding. Yet, we caution that these relatively consistent trends may be subject to change if there are local shifts in land manage-

ment practices and/or the natural disturbance regime (Boose et al. 2001). Additionally, there may be inconsistencies beyond the boundaries of national forests.

Spatial patterns of wind damage becoming more pronounced with increased disturbance intensity (both in terms of statistical importance and total area of severe and predictable damage) supports the hypothesis that moderately intense disturbances generate the most distinct spatially heterogeneous damage patterns compared to weak or intense events (Turner 2005). However, the exceptionally high explanatory power of the 1999 storm may have been bolstered by a weaker windstorm influencing the area during the same summer. We also discovered many intuitive damage patterns identical to those reported in the Great Lakes (Frelich and Lorimer 1991*a*, Peterson 2004, Schulte and Mladenoff 2005) and other regions (Foster 1988, Foster and Boose 1992, Laurance et al. 2006). Increased wind exposure and decreased flexibility of trees likely accentuates wind damage in older stands. VCT also allowed us to consider two unique landscape-scale predictors of wind damage associated with proximity to, and direction from, forest-nonforest edge. The negligible importance of direction of wind exposure and dominant importance of proximity to forest-nonforest edge is likely a consequence of increased turbulence as wind enters (Irvine et al. 1997) and exits (Gash 1986) forested areas in addition to asymmetrical tree growth near forest edges (Brisson 2001). Locally, windward forest-nonforest edges may be more susceptible, but overall, simple forest-nonforest edge was the most significant. The penetration of enhanced wind damage to 100 m from forest edge, and beyond, corroborates reports from previous plot-scale research in South America (Laurance et al. 1998, Laurance et al. 2006). In some cases, interactions between wind and the surface of large water bodies may exacerbate damage (i.e., beyond the standard forest-nonforest edge effect) near forest-lake edge generally, and on windward sides of lakes. The relatively strong wood of many conifers apparently made them less susceptible to damage than ubiquitous early-succession deciduous trees (Webb 1989). As expected, topography was marginally important in this relatively flat landscape (Schulte and Mladenoff 2005), but

windward slope aspects and moderately high elevations experienced disproportionately high levels of damages in some cases. We attribute these patterns to increased wind exposure associated with topographic position.

Observations of heavy windthrow in comparatively moist soils is consistent with previous research and likely a consequence of diminished root anchoring capabilities, but observations of increased windthrow on deep (>1.5 m), well-drained soils appear to contradict the literature. A review by Schaetzl et al. (1989) finds uprooting of trees to be more likely on soils inhibiting the growth of deep roots, whether by a hardpan, stoniness, water table, or other factors. Schaetzl et al. (1989) also differentiate between *uprooting* and *bole snapping*. Hubert (1918) is among the first to identify uprooting as more likely in shallow-rooted trees and bole snapping among those trees with deep roots. Naka (1984) suggests trees species vary in their likelihood of uprooting versus snapping: conifers commonly uproot and hardwoods tend to break. Bole breaks also occur more frequently among trees possessing large or tall crowns, large height-diameter ratios, or disease-weakened structural characteristics (Stathers et al. 1994). We currently are unable to effectively separate these components of windthrow in the satellite imagery, but our results suggest impacts of species- and tree-specific factors in windthrow are worthy of further investigation.

Our findings also have important implications concerning the magnitude of interactions between natural and anthropogenic disturbances. The potential for linkages and feedbacks between these types of disturbances is well established (cf. Busby et al. 2008). Yet interestingly, the spatial extents of two of the most important predictors of wind damage in our study, proximity to forest-nonforest edge and stand age, are highly susceptible to the principal disturbance agent in the region—anthropogenic activities associated with forest harvest and development activities (Schulte and Mladenoff 2005). This suggests the magnitude of the link between anthropogenic and natural disturbances in the northern Great Lakes is quite strong. Human activities can drastically alter the age of forest stands and the degree of fragmentation (Radeloff et al. 2005), potentially creating feedback loops that may

enhance or diminish the effects of wind disturbance. Forested landscapes are becoming increasingly homogeneous and fragmented throughout the northern Great Lakes region (Radeloff et al. 2005, Schulte et al. 2007) and other regions across the globe (Riitters et al. 2000). If increased disturbance frequency associated with forest edge and older stands can preferentially modify species composition, structure, demography, and ecosystem processes, then anthropogenically induced increases in forest edge and stand age (via selectively protecting reserves of old stands) may be accentuating the effects of wind disturbance. Disproportionately large areas of young stands associated with forest harvest recovery may also be diminishing the influence of wind disturbance. However, the supporting evidence presented here for such assertions remains circumstantial.

LIDs receive considerable attention in the literature and leave indelible signatures on landscapes during one spectacular, rare event, but more frequently occurring intermediate disturbances likely play an equally important role in engineering the spatial mosaic of forests on northern Great Lakes landscapes, and probably other regions. This hypothesis is identical to classic concepts in fluvial and aeolian geomorphology that contend much of the “work” performed on landscapes can be attributed to moderately intense and comparatively frequent events (Wolman and Miller 1960). We assert intermediate disturbances deserve careful consideration from ecologists and biogeographers in the future.

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APPENDIX A

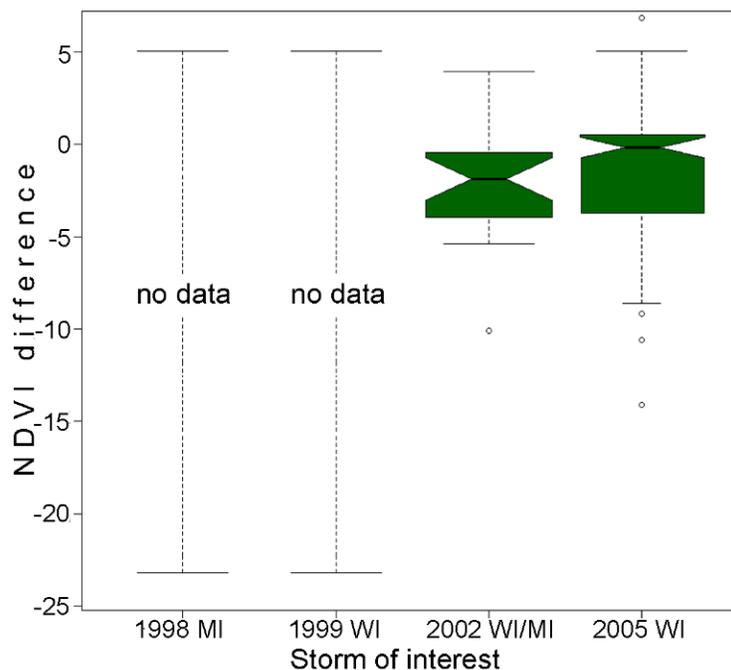


Fig. A1. Box and whiskers plots display the distributions of rescaled NDVI difference values extracted from the coordinates of 100 undamaged FIA field plots near the areas impacted by two windstorms (50 plots each). We used a single 30×30 m pixel for determining the NDVI difference values. The subtle overlap of notches for “2002 WI and MI” and “2005 WI” indicates similar median values. We strictly used FIA field plots for validating undamaged forest because the spatially heterogeneous damage patterns from the storms only damaged a few FIA plots. As expected, the vast majority of values hover near or slightly above zero.

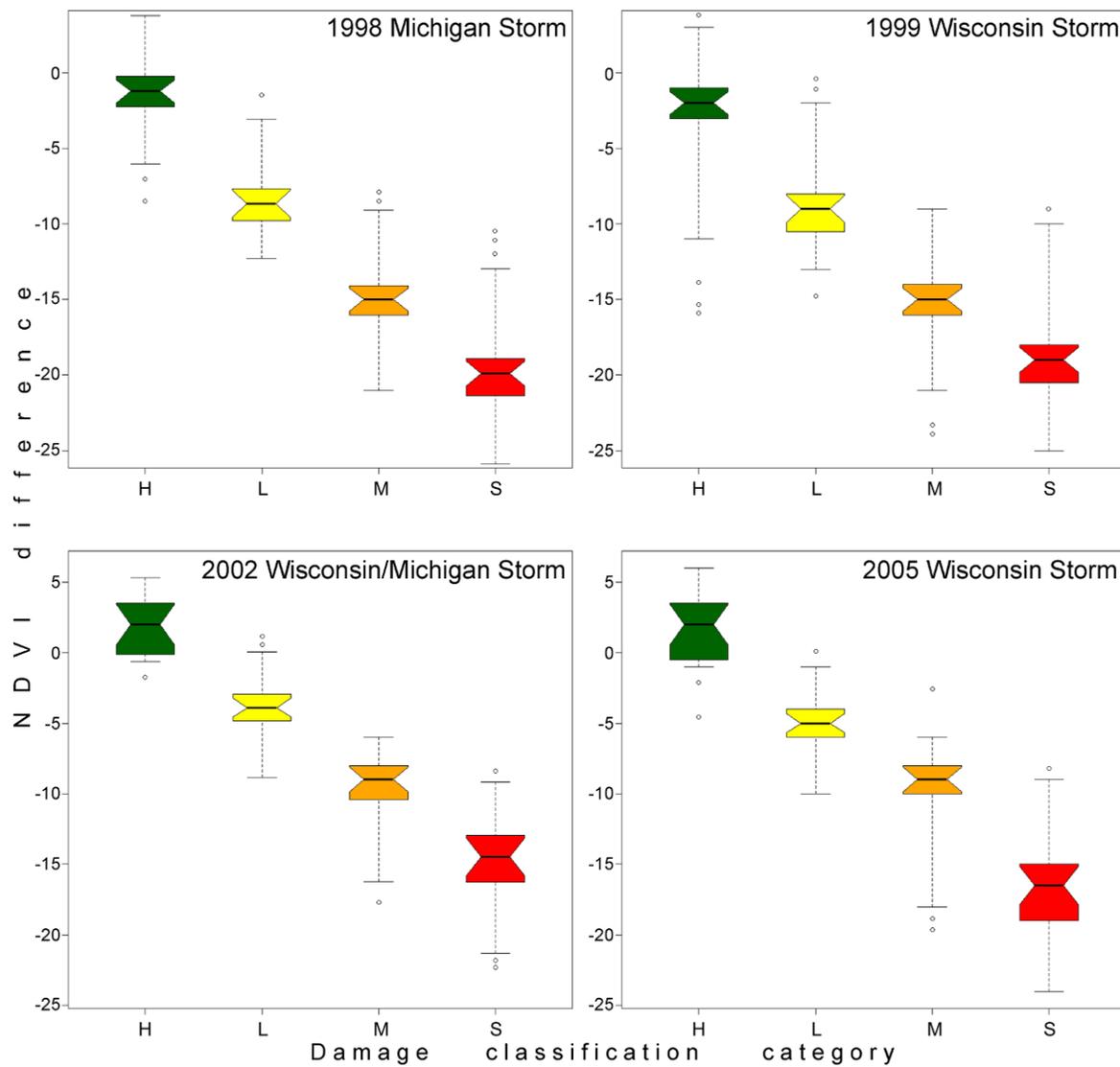


Fig. A2. Validations of forest damage associated with each windstorm. Box and whiskers plots display the distributions of rescaled NDVI difference values extracted from a random sample of 12 points collected from each of four stands with wind damage, or lack thereof, verified from the field. “H” corresponds to a healthy and undamaged stand, “L” to a lightly damaged stand, “M” to a moderately damaged stand, and “S” to a severely or catastrophically damaged stand. We used field reports from local foresters and immediate post-storm aerial surveillance to identify stand damage and a single 30×30 m pixel for determining the NDVI difference values. The absence of overlapping notches in the boxes indicates the median values are different. As expected, increasingly negative values correspond with the most heavily damaged stands.

APPENDIX B

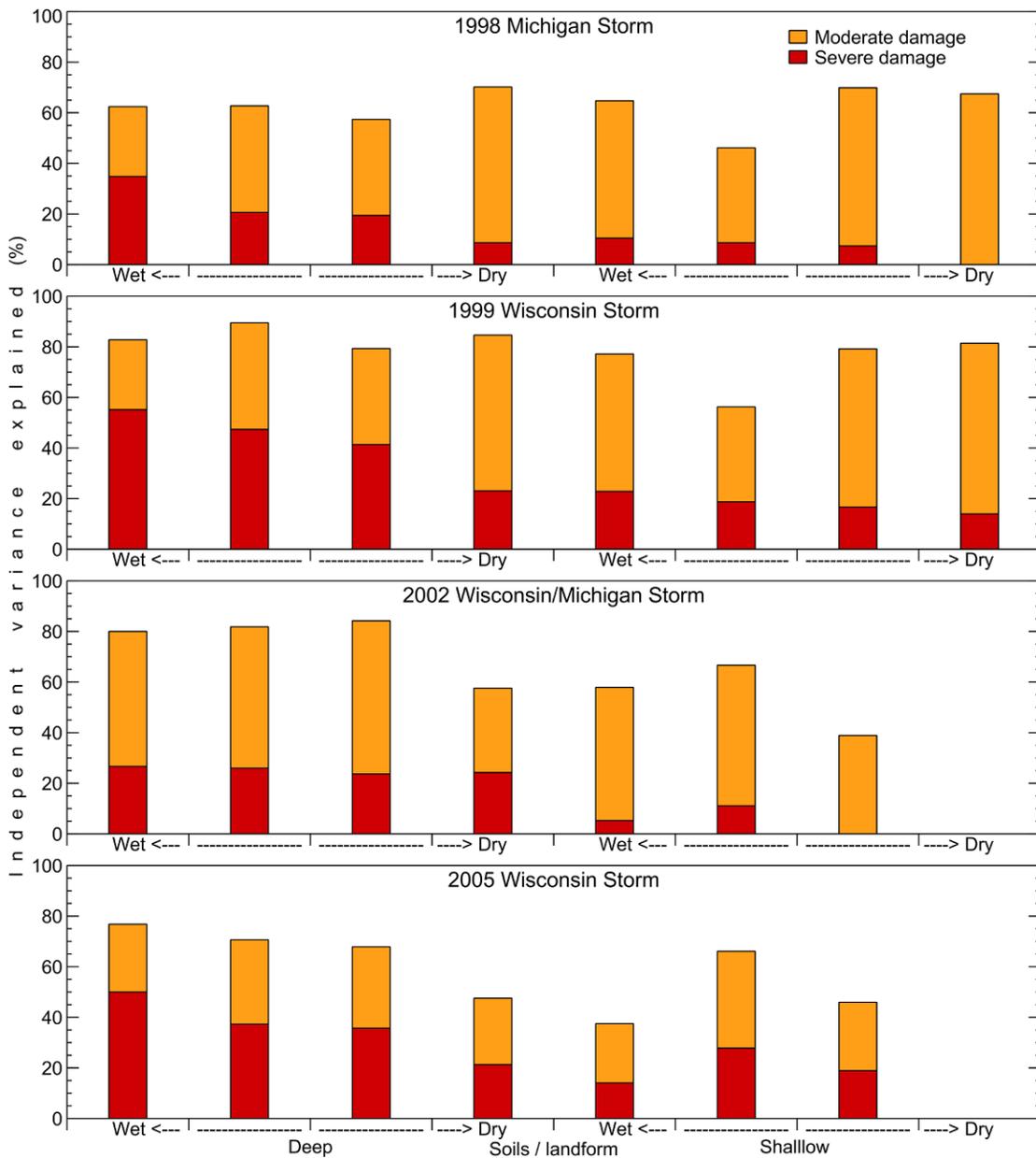


Fig. B1. Wind damage trends for one of the top three most important predictors, following procedures stated in Fig. 6. We generalized detailed soils and landform information gleaned from the NRCS SSURGO database into broad classifications for display purposes. Note the deep and well-drained soils contain a comparatively higher proportion of sand, and areas impacted by the 2002 and 2005 storms contain one less soils/landform description. Deep soils are greater than 1.5 m and shallow soils are mostly between 0.3 and 1.5 m.

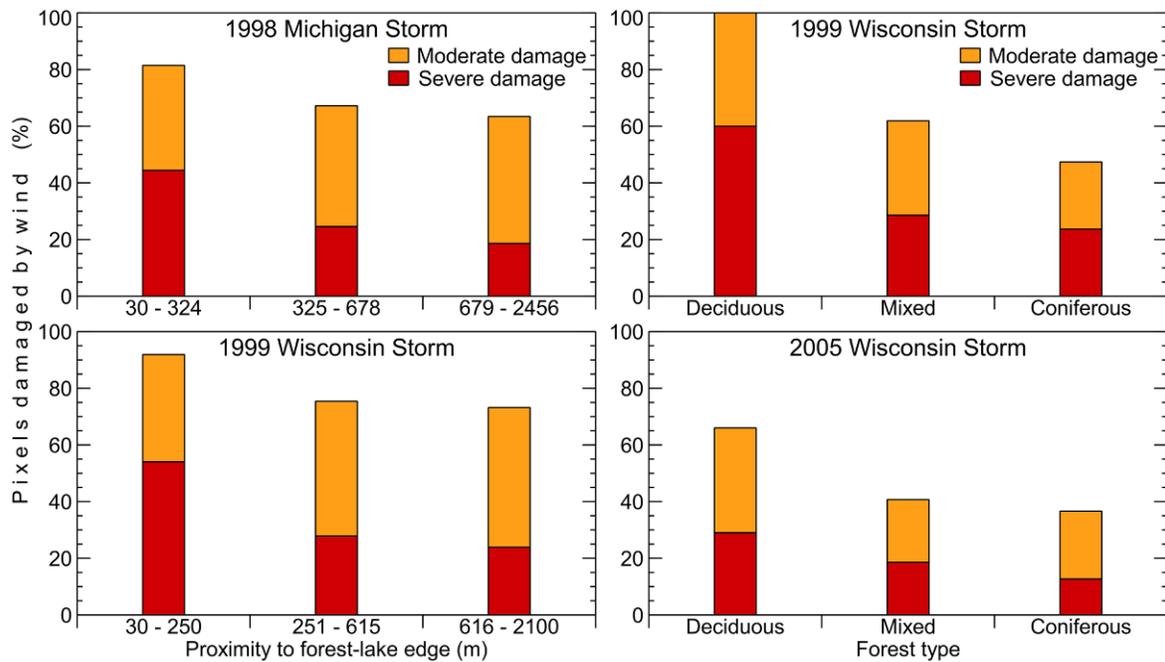


Fig. B2. Wind damage trends for two moderately important predictors, following procedures stated in Fig. 6. The distance ranges in the categories vary slightly because of unique landscape characteristics associated with each storm and efforts to maintain a proportionate number of pixels in each category.

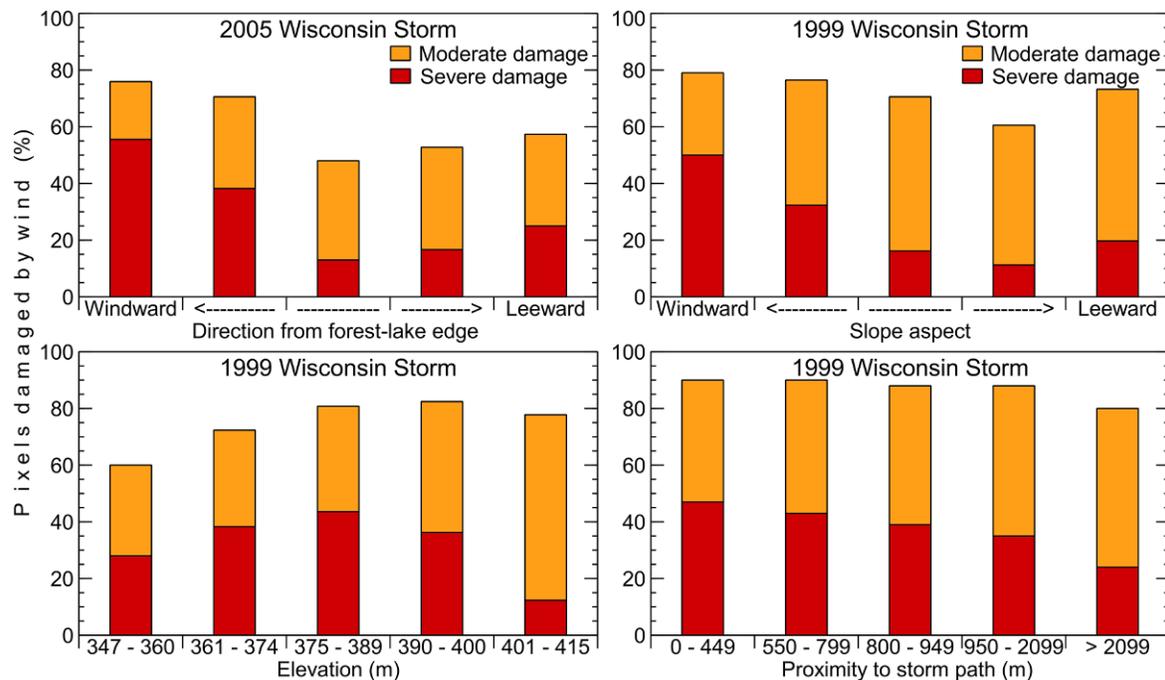


Fig. B3. Wind damage trends for the remaining moderately important predictors, following procedures stated in Fig. 6.