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Disturbance size and severity covary in small and mid-size wind disturbances in Pennsylvania northern hardwoods forests

Chris J. Peterson [a,*], Lisa M. Krueger [a,1], Alejandro A. Royo [b], Scott Stark [d], Walter P. Carson [c]

[a] Dept. of Plant Biology, University of Georgia, Athens, GA 30602, United States
[b] USDA Forest Service, Forestry Sciences Laboratory, Irvine, PA 16329, United States
[c] Dept. of Biological Sciences, University of Pittsburgh, Pittsburgh, PA 15260, United States
[d] Dept. of Ecology & Evolutionary Biology, University of Arizona, Tucson, AZ 85721, United States

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ABSTRACT

Do large disturbances differ from small ones in characteristics other than size? The importance of disturbances in forest dynamics is unquestioned, and the size of the disturbed area (size of gap) is the most common way of differentiating disturbances. But few studies have examined other disturbance characteristics to see if small and large disturbances are different. In northern hardwoods forests of northwestern Pennsylvania, a 2003 windstorm event created windthrow gaps ranging in size from 0.1 ha to >100 ha, allowing comparisons across a broad size spectrum, yet with similar species composition, soils, climate, and topography. We selected 17 gaps, ranging in size from 0.05 to 4.0 ha, to compare damage characteristics across a size spectrum. Disturbance severity (both proportion of trees fallen, and proportion of basal area fallen) increased significantly with gap size. Similarity in floristic composition between pre- and post-disturbance stands, decreased with increasing gap size. Larger gaps also caused greater reduction in mean size (diameter) of remaining trees. As expected, larger gaps resulted in greater canopy openness, but canopy openness was significantly influenced by both gap size and severity of canopy disturbance. These findings demonstrate that disturbance size and severity covary in northern hardwood windthrow gaps. Moreover, because of nonrandom impacts across species and size classes, immediate changes in size structure and composition of affected stands were greater in larger gaps. Managers seeking to implement disturbance-based management can use these findings to more closely mimic natural damage effects during harvest operations.

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1. Introduction

Disturbances are one of the fundamental determinants of forest structure, composition, and dynamics (Turner, 2010), and their effects vary with size, severity, frequency, and other disturbance traits (White and Jentsch, 2001). Such complex and multidimensional variation can make it difficult to generalize how disturbance will impact forest regeneration (Webb, 1999). However, if there are predictable correlations among key disturbance attributes, then fewer disturbance characteristics will be required to understand disturbance impacts to forests. An example of a well-established correlation among disturbance characteristics is that large disturbances are less frequent than smaller ones, leading to consideration of 'large infrequent disturbances' as a class (Romme et al., 1998; Turner and Dale, 1998). Seymour et al. (2002) examined disturbance size and frequency across New England and the upper Midwest, and found that some theoretically possible combinations of size and frequency never occurred in nature. However, the relationship of other disturbance characteristics (e.g. severity) with disturbance size is less known. What remains unclear is the degree to which large disturbances differ from small ones, beyond being less frequent. Indeed as Turner et al. (1997) point out, there have been few attempts to rigorously address this question (see also Romme et al., 1998; White and Jentsch, 2001).

Franklin et al. (2000) argued that "from an ecological perspective it is severity of the disturbance that is of greatest interest", and severity lies at the heart of several recent conceptual models of forest dynamics (Frelich and Reich, 1999; Frelich, 2002; Roberts, 2004, 2007). Vegetation response is a function of disturbance severity and only one other key variable (Frelich, 2002), or a function of several components of severity (Roberts 2004, 2007). If size and severity are correlated, then predictive models could use size (usually easier to measure) as a surrogate for severity. Indeed, White and Jentsch (2001) state that researchers have almost universally used gap size as a surrogate for other disturbance charac-

* Corresponding author. Tel.: +1 706 542 3754; fax: +1 706 542 1805.
E-mail address: chris@plantbio.uga.edu (C.J. Peterson).
[1] Address: Dept. of Biological Sciences, University of Tennessee, Martin, TN 38238, United States.

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teristics, but without a strong empirical basis for such substitution. Given this importance, we evaluate the relationship between disturbance patch size and severity for a suite of windstorm gaps in northern hardwood forests of Pennsylvania. We are aware of only one explicit empirical examination of relationships between size and severity of disturbance patches. Turner et al. (1994), studying burned patches formed in the 1988 Yellowstone National Park fires, concluded that indeed, large burned areas are qualitatively different from small ones due to greater burn severity in larger patches.

How might size and severity covary? It is known that the most intense tornadoes (rated EF4 and EF5 on the Enhanced Fujita Scale) have larger damage paths than lower-intensity tornadoes (Brooks, 2004). Suspecting that a similar size–intensity relationship exists for thunderstorm winds, we might predict that larger convection cells in the broader storm system produce greater wind speeds, and therefore we hypothesize that (1) cells causing larger blowdown patches will inflict greater damage (i.e. higher severity). If this hypothesis is true, then several corollaries are suggested. It is known that wind disturbances selectively damage larger trees in a given stand, and that species with weaker wood generally show greater vulnerability to wind damage than their associates (Everham and Brokaw, 1996; Webb, 1999; Peterson, 2004, 2007). Therefore, greater severity of damage should cause greater reduction in (standing) tree size and greater shifts in species composition between the pre- and post-disturbance stand. Note that this expectation is distinct from the probable consequences of disturbances that are not size selective (trees are removed independently of their size, causing little change in size distributions), or from the consequences of disturbances (e.g. floods, surface fires) that preferentially remove smaller size classes (expected consequence is removal of the lower tail of the size distribution). Because of the greater removal of dominant trees by winds, evenness among species should be increased by wind disturbance; therefore we also hypothesized that greater severity of damage should increase diversity. In sum, we hypothesize that larger gaps would have (2) greater reduction in mean tree size; (3) greater change in species composition; and (4) increased species diversity.

For wind disturbances in particular, we know of no published studies that compare characteristics of windthrow gaps across a large range of gap sizes, though numerous studies have examined the 'small' ($\ll$0.5 ha) end of the gap size spectrum (e.g. Runkle, 1981, 1982, 1985; Canham, 1988; Poulson and Platt, 1989; Lertzman, 1992; Royo et al., 2010). In this study, we exploit the existence of numerous recently-created windthrow gaps that span the small-to-medium size range (0.05–4 ha; Evans et al., 2007). Using gaps created at the same time and in the same general area reduced variation in canopy composition, elevation, soil type, and time since disturbance, among other factors, thereby allowing us to hone in on the relationship between gap size, severity, and immediate change in forest vegetation.

In applied contexts, the rise of disturbance-based management (Attiwill, 1994; Perera et al., 2004; Drever et al., 2006) has managers seeking quantitative ranges for natural disturbance characteristics; these natural ranges can provide boundaries for size, severity, shape, etc., of disturbances resulting from human forest interventions. The rationale is that forest species are likely to be adapted to natural disturbance characteristics, and therefore forest plant communities are unlikely to experience severe detrimental impact from the natural events that are typical in a region. Consequently, management actions that fall within the range of natural variability in size, severity, frequency, and other characteristics, should have minimal negative impact on community and ecosystem structure and function, and therefore be more sustainable. While a great deal of research has documented size and frequency of disturbance regimes in temperate forests (Runkle, 1985; Everham and Brokaw, 1996; Webb, 1999), little attention has been directed towards severity. Those studies that employ historical reconstructions (e.g. Lorimer, 1977; Canham and Loucks, 1984; Foster, 1988a), can provide great temporal depth and sometimes extensive spatial coverage, but they seldom evaluate severity.

2. Materials and methods

2.1. Study sites

Previous studies have documented the patterns of damage to northern hardwood forests of Allegheny National Forest in western Pennsylvania, following tornadoes in 1985 (Peterson and Pickett, 1991) and 1994 (Peterson 2000, 2007). In this study, we focus on the 'small' to 'medium' part of the size continuum, by examining 17 canopy gaps created by a severe windstorm that struck northwestern Pennsylvania in July 2003. The storm created >200 gaps within Allegheny National Forest (ANF), ranging in size from 0.1 ha to >40 ha.

The ANF is characterized as having a continental climate, with warm summers and long, cold winters, with an average July temperature of 18.9 °C and an average annual temperature of 7.8 °C. Precipitation averages 1067 mm per year, with 38% falling between June and October (Bjorkbom and Larson, 1977). The majority of ANF, and all of our study sites, are located on the Allegheny Plateau, a rugged highland characterized by broad level plateaus dissected by steep river valleys; elevations range from 305 to 732 m. Soils are mostly sandstones and siltstones, and are rocky and acidic (Table 1). According to soil surveys, all of the sites were considered to have only 'slight' risk of treefall, on the basis of soil characteristics; while fragipans are often present, rooting depth is almost always >50 cm, implying that variation in severity of damage is not likely due to soil differences (Table 1).

The vegetation of the gaps we studied is classified as the Allegheny hardwoods variant of the broader northern hardwoods type. Major dominant tree species are *Acer rubrum*, *Acer saccharum*, *Prunus serotina*, and *Fagus grandifolia*, with somewhat lesser abundances of *Tsuga canadensis*, *Betula alleghaniensis*, *Betula lenta*, and *Fraxinus americana*. Understory vegetation is dominated by *Acer pensylvanicum* and *F. grandifolia* (mostly root sprouts) in the shrub layer, and a variety of mesic forest ferns (e.g. *Dennstaedtia punctilobula* and *Thelypteris noveboracensis*) and forbs (e.g. *Oxalis acetosella*) in the field layer (Royo et al., 2010). Large gaps often have extensive carpets of *Rubus allegheniensis* (Peterson and Pickett, 1995; Peterson and Carson, 1996).

2.2. Field methods

Aerial reconnaissance of the ANF shortly after the July 2003 storm showed >200 gaps, which were manually drawn onto a map (Evans et al., 2007). We randomly selected gaps within several size categories to choose our 17 study sites. Gaps were sampled during July and August 2004. To characterize gap size, we measured two perpendicular axes, and used these to define the length of dimensions for the appropriate geometric shape (oval, circle, half-circle) for calculating area (in m^2) of the gap (Table 1).

Within each disturbed area, we established several parallel transects across the gap, on which damage survey points were distributed in a stratified random manner. For the 13 larger gaps, we sampled 16 damage survey points whereas the four smallest gaps had 7–13 survey points, because of space limitations. The damage survey points nearest the disturbed area edge were a minimum of 7.5 m from the intact forest; all others were further into the disturbed area. All trees (>10 cm dbh) within 7.5 m of a damage survey point were tallied for species, size (diameter at 1.4 m, or

Table 1
Characteristics of 17 disturbed areas investigated in Allegheny National Forest, PA. Trees sampled and basal area are for the samples only, not for the entire gaps. "Down" includes trees trunk broken or uprooted. All gaps were formed by the July 2003 storm.

Site	Area (ha)	Shape	# Trees sampled	Basal area (m^2)	% Trees down	% B.A. down	Openness (min–max)	Rooting depth (cm)	Soil windthrow hazard	Soil type
Q2	0.05	Oval	30	3.11	26.7	38.5	No data	>100	Slight	Sandy loam
S049	0.05	Square	62	3.63	29.0	35.7	10.7–14.8	41–69	Slight	Loam, clay loam
T12	0.1	Oval	91	6.73	31.9	50.1	14.2–30.1	>100	Slight	Channery sandy loam
T27	0.1	Oval	81	6.39	49.4	59.8	10.7–19.3	41–69	Slight	Loam, clay loam
T01	0.1	Oval	69	6.86	17.4	32.5	9.8–22.1	~74	Slight	Silt loam, channery silt loam
W904	0.2	Circle	101	9.39	53.5	59.9	12.4–34.5	~74	Slight	Silt loam, channery silt loam
73A	0.2	Oval	46	5.72	26.1	24.5	11.0–23.0	51–76	Slight	Silt loam
PS4B	0.3	Oval	176	14.62	69.3	69.5	13.0–39.2	41–69	Slight	Loam, clay loam
73	0.5	Square	80	9.38	47.5	46.7	7.5–21.6	51–76	Slight	Silt loam
T19	0.5	Oval	87	9.20	50.6	55.6	8.4–30.3	51–91	Slight	Silt loam, clay loam
107	0.8	Half oval	111	8.90	53.6	73.7	12.0–49.9	>100	Slight	Channery silt loam
PS4	1.0	Half oval	207	11.97	62.3	70.7	9.1–38.1	~74	Slight	Silt loam, channery silt loam
W850	1.1	Oval	166	10.97	38.6	55.3	13.4–37.3	~74	Slight	Silt loam, channery silt loam
T45	2.1	Oval	100	10.13	48.0	66.6	17.4–46.6	>100	Slight	Channery sandy loam
KEFSB	2.6	Oval	181	14.46	60.8	60.8	16.0–54.0	51–76	Slight	Silt loam
T61	3.1	Oval	91	11.16	38.5	44.0	No data	>100	Slight	Channery sandy loam
KEFNB	4.0	Oval	116	13.09	75.9	86.9	18.2–57.7	41–69	Slight	Channery loam

dbh), status (live or dead), and type of damage (intact, branches broken, bent, leaning, canopy broken, trunk snapped, or uprooted). All saplings (>2 m tall but <10 cm dbh) within 5 m of a damage survey point were similarly tallied and classified. Above each damage survey point, we took a hemispherical canopy photo from a height of 1.5 m. We used a Nikon Coolpix 885 digital camera mounted on a tripod, with a bubble level. Digital photos were examined using Gap Light Analyzer software, to quantify the amount of openness.

Although there is no generally agreed-upon metric of damage severity for forest gaps, many researchers use the proportion of trees removed from the canopy. This metric could prove a poor indicator of actual change to the community when there are large size differences among trees; in these situations, basal area fallen probably provides a better index of damage. We used both measures – proportion of stems and proportion of basal area – to characterize severity of disturbance in our gaps. For purposes of characterizing change in resource availability, we do not recommend use of proportion of trees living vs. dead, as many *fallen* trees can remain alive for years (Walker, 1991, 1995; Cooper-Ellis et al., 1999), thus yielding an underestimate of overall canopy disturbance.

We examined the relationship between gap size and response variables using Pearson correlations. We log-transformed size to approximate a normal distribution; in all correlation results described below, 'size' refers to the log-transformed values, untransformed sizes are shown in graphs with a logarithmic *x*-axis. Characteristics of the gaps considered were: the two measures of damage severity, change in floristic composition (measured as similarity), change in standing tree sizes, type of treefall (broken vs. uprooted), and the size-treefall risk relationship.

We examined the relationship between tree size (dbh) and treefall risk in a coarse sense by grouping trees into three broad size categories (10–29.9 cm dbh, 30–49.9 cm dbh, and 50–69.9 cm dbh; the few trees >70 cm dbh were excluded from this classification) and calculating proportions of trees standing vs. fallen. To further explore how probability of treefall varied among tree sizes, we performed logistic regressions with dbh as the predictor and tree fate (standing vs. fallen) as the binary response variable. One useful result from logistic regression analysis is the odds ratio, which quantifies the increase in the odds of the 'event' (in this case, treefalls) happening, for one unit change (in this case, 1 cm of diameter increase) in the predictor variable. The odds ratio thus allows a quantitative comparison among species in how their risk of falling changes with size in these wind disturbance gaps.

If disturbance removes species from the stand in proportion to their (predisturbance) abundances, then pre- and post-disturbance samples of the same site should have very high similarity; conversely, lack of similarity indicates the amount of immediate compositional change caused by the wind disturbance. We calculated pre- vs. post-disturbance floristic composition using only standing trees, with the Bray–Curtis index of similarity: $S = 1 - [\Sigma(x_i - y_i)/\Sigma(x_i + y_i)]$, where x_i and y_i are the abundances of species i in two different samples. To further explore how gap size influenced species composition, we performed a nonmetric multidimensional scaling ordination in PC-Ord 4.01, using pre- and post-disturbance standing tree data from the 17 gaps. The difference in ordination space between the pre-disturbance and post-disturbance points indicates the extent of compositional change. For our purposes, we arbitrarily chose a 2-axis final solution in the NMS; used the Sorensen distance measure; a random starting configuration; step length of 0.20; stability criterion of 0.005 standard deviations change between iterations; and a maximum of 50 iterations.

We tested for independent ability of gap size and gap disturbance severity to predict canopy openness using forward stepwise multiple regression; openness was the response variable, and independent variables were gap size and gap severity based on stems or basal area. All statistical tests were performed using Sigma-Stat 3 (Systat Software, Inc.).

3. Results

The sampled gaps formed in 2003 ranged in size from <0.1 ha to 4.0 ha (Table 1); most were best characterized as oval or half-oval in shape. Damage within the gaps differed substantially, whether measured as percent of trees down (17–75%), or as percent of basal area down (24–87%; Table 1). This difference in severity of damage among gaps cannot be attributed to differences among gaps in tree size or floristic composition. In several cases, it was possible to test for differences in proportion of trees fallen, within size categories of single species; this eliminates interspecific and size effects. For

trees in the 10–29.9 cm dbh category, gaps differed significantly in proportion of trees fallen for *A. rubrum* ($p < .025$, 7 gaps), *A. saccharum* ($p < .001$, 10 gaps), *B. alleghaniensis* ($p < .001$, 4 gaps), and *F. grandifolia* ($p < .001$, 8 gaps). For trees in the 30–49.9 cm dbh category, fewer species were sufficiently abundant for testing among many gaps, but three were nevertheless significantly different among gaps: *A. rubrum* ($p < .001$, 6 gaps), and *P. serotina* ($p < .01$, 9 gaps). Thus, even within a particular species and size class, gaps differed in severity of damage.

Across gaps, there were consistent species and size effects on tree damage. In 15 of the 17 gaps, the proportion of trees fallen increased from the smallest to the largest size categories (in our three-size-category analysis). In many gaps, there was a significant logistic regression relationship between tree dbh and probability of treefall (see below). The ranking of species' relative vulnerability to damage was roughly consistent among gaps. In four gaps there were sufficient *A. rubrum* and *A. saccharum* for statistical comparisons within the 10–29.9 cm dbh size category; in all four gaps, the *A. saccharum* were more windfirm than *A. rubrum*, and in three of the four this difference was statistically significant ($p > 0.1$ in KEF NB, $p < .05$ in KEF SB, PS4, and Well850). In three gaps it was possible to compare *B. alleghaniensis* and *B. lenta* to other species in the 10–29.9 cm size range (cf. Canham et al. (2001) observation that birches were less damaged than other species). In two of the three gaps fewer birches were fallen than other species of similar size: 8.7% of *B. lenta* vs. 60.0% of *A. rubrum*, and 10.3% of *B. alleghaniensis* vs. 27.7% of *A. saccharum* and 58.3% of *A. rubrum* in another gap. In three gaps in which *P. serotina* was abundant in the 10–29.9 cm dbh size class, it was among the most heavily damaged species (64.3%, 83.3%, and 74.1% fallen, in gaps KEF SB, PS4, and PS4B, respectively). Nevertheless, these interspecific differences in windfirmness did not cause the differences in damage severity among gaps: there was no correlation between the level of damage and proportion of trees that were windfirm (*A. saccharum*, *B. alleghaniensis*, and *B. lenta*, Pearson $r = -.142$, $p = .56$, $n = 17$.

Gap size and proportion of stems down were positively correlated ($r = .499$, $p < .05$); as were gap size and proportion of basal area down ($r = .494$, $p < .05$, Fig. 1). The proportional reduction in size of standing trees (pre-disturbance vs. post-disturbance) was positively correlated with gap size ($r = .562$, $p = .012$, Fig. 2). Bray–Curtis similarity (pre- vs. post) was negatively correlated with gap size ($r = -.521$, $p < .05$, Fig. 3). In multidimensional representation of composition (not diversity), changes in plot positions (e.g. from pre-disturbance position to post-disturbance position in the ordination) indicate changes in composition. Notably,

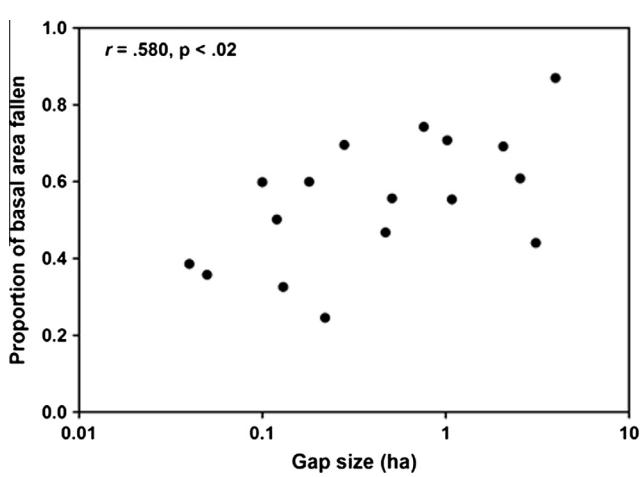

Fig. 1. Relationship between disturbed area ("gap") size (in ha) and proportion of basal area fallen, for 17 wind-disturbed gaps in northwestern Pennsylvania.

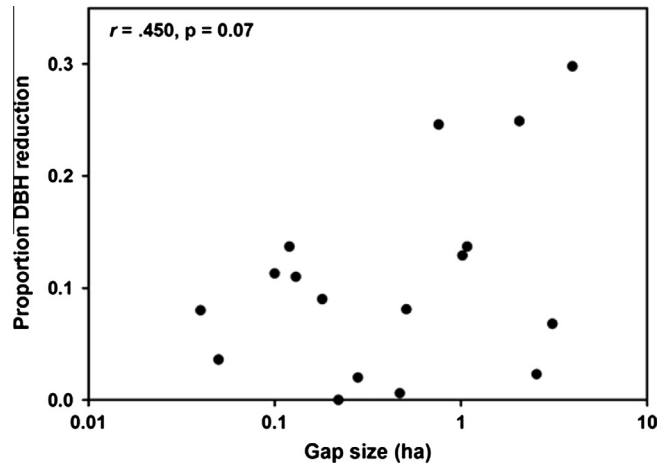

Fig. 2. Relationship between disturbed area ("gap") size (in ha) and proportional reduction in trunk diameter (at 1.4 m) of standing trees; pre-disturbance vs. post-disturbance, for 17 wind-disturbed gaps in northwestern Pennsylvania.

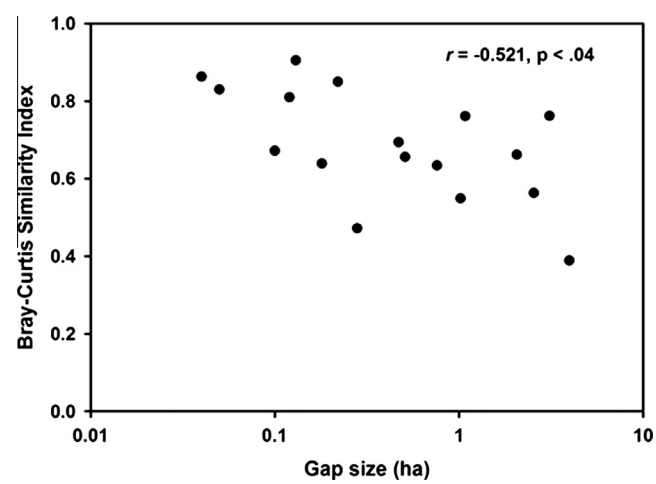

Fig. 3. Relationship between disturbed area ("gap") size (in ha) and floristic similarity, pre-disturbance vs. post-disturbance, for 17 wind-disturbed gaps in northwestern Pennsylvania.

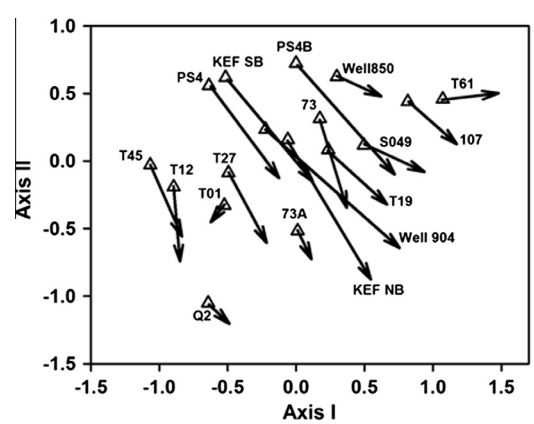

Fig. 4. Nonmetric multidimensional scaling ordination of pre-disturbance and post-disturbance floristic composition in 17 wind-disturbed gaps in northwestern Pennsylvania. Arrows connect pre-disturbance composition (indicated by open triangles) to post-disturbance composition (indicated by tip of arrow). Composition based on standing trees >10 cm dbh.

change in position in NMS ordination space was not significantly correlated with gap size ($r = .339$, $p = .183$, Fig. 4), but was significantly correlated with both proportion of stems down ($r = .845$,

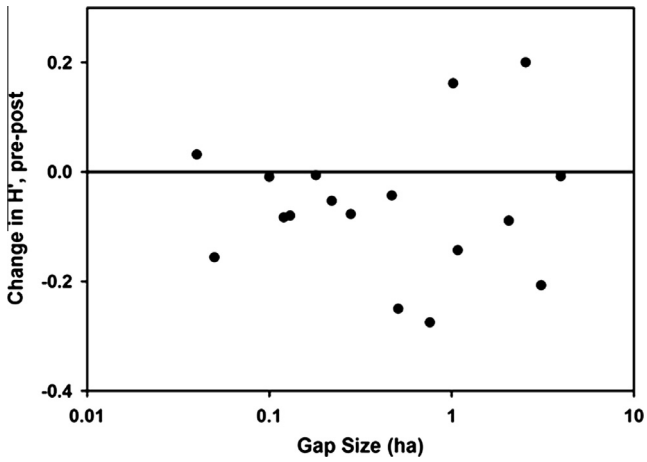

Fig. 5. Pre-disturbance to post-disturbance change in Shannon diversity (H′) of trees >10 cm dbh, for 17 wind-disturbed gaps in northwestern Pennsylvania.

$p < .001$) and proportion of basal area down ($r = .711$, $p < .002$). In our NMS ordination, final instability was 0.0033, and final stress was 19.001%; this rather high level of stress suggests that we cannot have high confidence in particular details of the ordination results. The amount of change in Shannon diversity showed no relationship to gap size ($r = .126$, $p > 0.5$, Fig. 5). Finally, the uproot:trunk breakage ratio was not significantly related to gap size ($r = -.096$, $p > 0.1$).

The multiple regression examined variation in canopy openness in relation to gap size and gap severity (proportion of canopy trees or canopy basal area down); the openness value for each gap was the average across plots within that gap. Gap size entered the model first, as it explained the larger proportion of variation in canopy openness ($n = 15$, $R^2 = .667$, $p = .008$; Fig. 6a). However, canopy damage severity measured by basal area also contributed significantly to the regression (delta $R^2 = .132$, $p = .016$, Fig. 6b). Thus, if severity is considered as proportion of basal area removed from the canopy, it significantly improves predictability of canopy openness beyond size alone. In this multiple regression, proportion of canopy trees down did not enter the model, although this predictor alone was significantly correlated with openness.

To determine if there was evidence for nonlinear relationships between canopy openness and gap size, we performed a polynomial regression using openness vs. gap size. There was no significant higher-order term in the polynomial regression, so we conclude that a linear model adequately characterizes this relationship.

Logistic regressions found significant relationships between probability of treefall and trunk diameter in 9 of the 17 gaps formed in 2003. In all logistic regressions, the risk of treefall increased with trunk diameter (Fig. 7a and b). The effect of changes in tree size on risk of treefall can be expressed as the odds ratio, which describes the increase in odds of treefall for a 1-unit increase in the predictor variable; thus in these examples, for a 1-cm increase in trunk diameter. The odds ratios ranged from 1.024 at

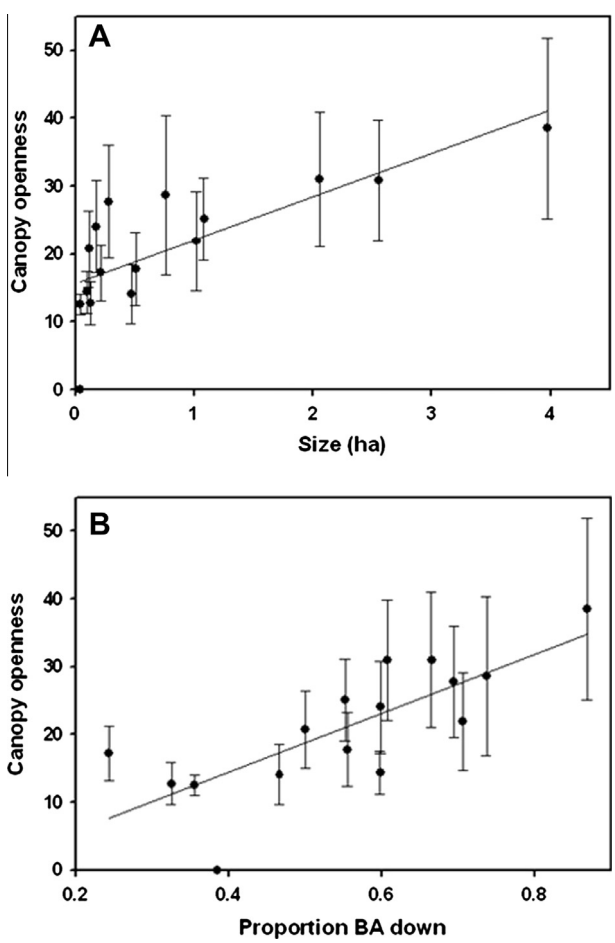

Fig. 6. Relationships between whole-gap canopy openness and (a) disturbed area ("gap") size; and (b) disturbed area ("gap") severity of damage. In (b), severity is based on proportion of basal area fallen.

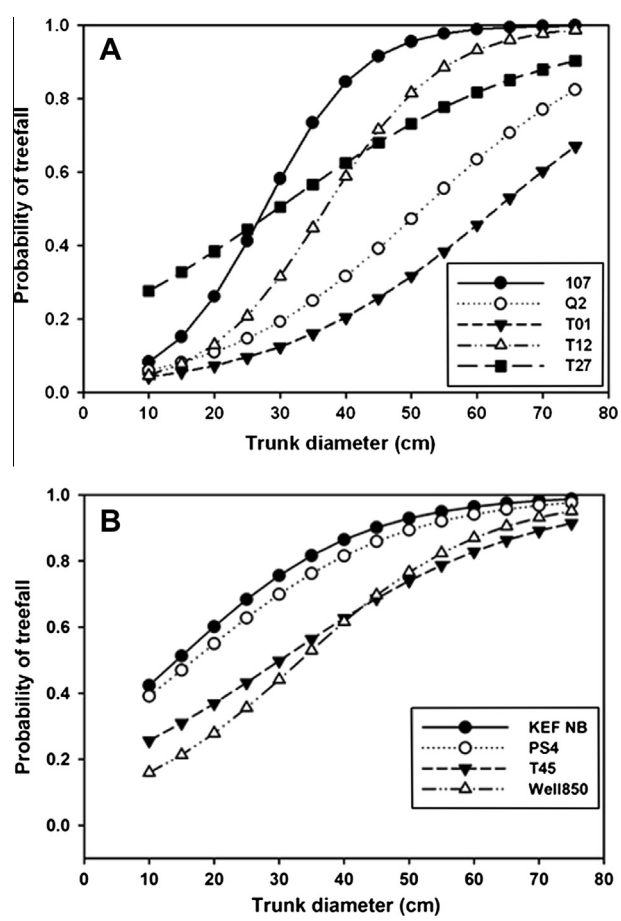

Fig. 7. Predicted probability of treefall as a function of tree size (trunk diameter at 1.4 m, or dbh). Predicted probabilities based on logistic regressions of tree fate (standing or fallen) vs. trunk dbh, by site, with all species pooled. Only trees >10 cm used in regressions. Sites separated into two panels only for clarity.

the W905 site, to 1.147 at the 107 site, these correspond to a 2.4% and 14.7% increase, respectively, in the odds of treefall for 1 cm increases in trunk diameter. Odds ratios showed no correlation with either gap size or severity of damage ($p > 0.1$, $n = 9$) across sites. However, because the probability of treefall at the smallest size (10 cm) differed among sites, the combinations of intercepts and slopes of the logistic regressions yielded substantially different predicted probability of treefall among sites. For example, at 20 cm dbh, the predicted probability of treefall ranged from lows of 0.073 at T01 and 0.110 at Q2, to a high of 0.601 at KEF NB. Similarly, at 60 cm dbh, predicted probability of treefall was least – 0.456 at T01, – and greatest – 0.988 – at 107, respectively.

4. Discussions

Many of our findings reinforce and provide even stronger bases for trends emerging in studies of wind disturbance (e.g. Webb, 1999; Peterson, 2007). As in most other wind disturbance studies, this work found that larger trees are more at risk. Additionally, we found no significant change in the tree size–treefall risk relationship across different-sized gaps, suggesting that this relationship was consistent across gap sizes. We found only one gap out of 17 that suggested a unimodal relationship (cf. Everham and Brokaw, 1996) between tree size and risk of damage; all other gaps supported a monotonic increase (Peterson, 2007). And like a number of other studies, the types of treefall in our study sites did vary with tree size, with uprooting becoming more important in intermediate and large trees, compared to greater trunk breakage among smaller trees (cf. Peterson, 2007). Because larger gaps have greater severity of damage than smaller gaps, this means that larger and more severely-damaged gaps will have greater soil disruption from uprooting.

We also found that species have predictable rankings in windfirmness; as reported elsewhere (Webb, 1999; Canham et al., 2001; Peterson, 2007), *A. saccharum* and *B. lenta* and *B. alleghaniensis* tend to be less damaged for a given size than other species, while *P. serotina* and *A. rubrum* tend to suffer greater damage. These differences in windfirmness appear to be related to rooting pattern and wood strength. We did not find preferential damage to the one common conifer species in our study areas (*T. canadensis*), thus offering little support to reports (e.g. Everham and Brokaw, 1996; Peterson, 2007) of greater vulnerability of conifers relative to hardwoods. The trunks of *T. canadensis* trees taper strongly, an architectural characteristic that may reduce the risk of trunk breakage, and potentially counterbalance the relatively weak wood of this species.

Greater risk to larger trees implies that wind disturbance will select against dominant canopy species. Because most secondary forests differ in the floristic makeup of canopy and understory woody vegetation, this selective damage of the larger trees means that major wind disturbance will shift floristic composition, in addition to reducing the mean size of remaining trees. In our gaps, because the severity of damage increased with gap size, the immediate floristic shift also increased with gap size. This trend is likely to be reinforced by larger and more severe gaps having seedling and sprout regeneration that is more dominated by pioneer species than in smaller/less severe gaps. Consequently, large gaps are likely to have both immediate and long-term changes in composition, with higher likelihood of re-initiating successional sequences (Foster, 1988b; Peterson and Carson, 1996).

In disturbed forest areas (gaps) larger than those created by one or a few trees, some of the canopy trees often survive and remain in the canopy, thereby creating gaps of differing severity of damage (White and Jentsch, 2001; Roberts, 2004). In some systems, disturbance size and severity are thought to be positively correlated (Turner et al., 1994; Frelich, 2002), while it is clear that some other systems experience very large, low-intensity disturbances (e.g. surface fires in tallgrass prairie, Knapp and Seastedt, 1986) and yet others experience disturbances of limited area but very high intensity (landslides, e.g. Myster and Walker, 1997). Our examination of wind-disturbed patches ranging in size from <0.1 to ~4 ha, showed that size and severity were positively correlated, whether severity is based on proportion of stems or proportion of basal area removed from the canopy. We have not found comparable published studies where size and severity have been similarly quantified for a broad range of wind disturbance patch sizes. At the extreme end of the disturbance size spectrum, there does seem to be a correlation between disturbance size and frequency, leading to generalizations about large, infrequent disturbances (e.g. Turner and Dale, 1998). Here we show that, analogous to the size-frequency inverse correlation, size and severity may be positively related. This may provide justification for an inclusive consideration of disturbance 'magnitude' (combining size and severity) in conceptual models of disturbance and recovery, as done in Frelich and Reich (1999).

When researchers attempt to relate disturbance characteristics to regeneration (e.g. Canham, 1988, 1989; Canham et al., 1990; Kobe et al., 1995; Beaudet et al., 2004), a primary intermediary is how the disturbance alters resource availability. Our findings demonstrate that considering both severity as well as size of the disturbed patch will improve prediction of canopy openness, and therefore light availability, an important influence on regeneration. Moreover, because numerous other influences on regeneration are affected by canopy openness (temperature, humidity, decomposition rates, seed dispersal, etc.), the value of considering severity becomes more apparent. We readily acknowledge that light is one among multiple influences on regeneration in forest gaps (e.g. microsites: Peterson et al., 1990; Kuuluvainen and Juntunen, 1998; heterogeneity of conditions; de Chantal et al., 2003), but canopy openness and therefore light availability is commonly one of the most influential factors on regeneration (Hanson and Lorimer, 2007).

Notably, our polynomial regressions did not find any evidence of nonlinearities that would suggest a threshold in the response of openness to canopy gap size, as suggested by Romme et al. (1998). However, we caution that detecting such thresholds may require a large number of samples and low levels of unexplained variation in response variables, and that most studies, including ours, may have inadequate resolution to detect such thresholds (but see Turner et al., 1994). We attribute the continuous response to the purely physical relationship between amount of canopy damage and openness; other response variables that incorporate biotic processes (e.g. seed germination) may be more likely to have critical minimum light or temperature requirements, and therefore exhibit threshold responses to disturbance size or severity (Frelich and Reich, 1999).

5. Conclusions and management implications

Recent calls for managing forests to mimic natural disturbances (Attiwill, 1994, Perrera et al., 2004, Drever et al., 2006) put particular value on the findings reported here. While the size-frequency distribution of windthrow gaps can provide guidance for the sizes of harvested areas in forests, such information is insufficient to suggest whether the intensity of treatment should be similar across all sizes. The findings here imply that in larger gaps, higher levels of damage are typical, with consequent greater reduction in sizes of remaining trees, and greater change in floristic composition. Similarly, harvesting that leaves higher levels of canopy openness in larger harvest areas will parallel effects of natural wind

disturbance. Also, we found no relationship between gap size and immediate change in species diversity (measured as Shannon's H′), suggesting that harvesting prescriptions that aim to mimic natural wind disturbance events should have similar effects on species diversity across a range of gap sizes.

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