

# Windstorm damage and forest recovery: accelerated succession, stand structure, and spatial pattern over 25 years in two Minnesota forests

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Received: 19 April 2012 / Accepted: 19 October 2012 / Published online: 27 October 2012  
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**Abstract** We evaluated 25 years of change in wind-impacted oak and pine-dominated sites in the Cedar Creek Ecosystem Science Reserve, Minnesota, USA. We address the question: how did the storm alter stand architecture and spatial pattern and how did this affect recovery and recruitment? We mapped and marked all stems greater than 1 cm in diameter in a 0.25 ha oak-dominated plot and a 0.30 ha pine-dominated plot. After the initial sampling in 1983, plots were resurveyed four times in the 25 years following the windstorm. We used ordination and diameter distributions to describe compositional and structural characteristics of the sites. The stands are compositionally converging after the windstorm with both moving towards a late-successional forest type dominated by shade-tolerant tree species. The architecture in both sites is similar through time; sites have transitioned from bimodal diameter distributions to

reverse-J distributions. We used Ripley's  $K$  point pattern analysis to assess spatial patterns of tree mortality and recruitment within each site. In the pine site, surviving trees were significantly clumped, but mortality and recruitment patterns did not significantly differ from random. In the oak site, the storm did not substantially alter the spatial pattern of surviving trees, but subsequent recruitment was significantly associated with trees killed by the storm at scales within 6–8 m and significantly dissociated with surviving trees at scales greater than 1 m. The dynamics of accelerated succession observed here are mediated by the damage and mortality initially sustained and its corresponding effects on spatial patterns of surviving and recruiting trees.

**Keywords** Cedar creek ecosystem science reserve · Forest architecture · Forest succession · Spatial point pattern · Windstorm

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## Introduction

Wind disturbance is an important modifier of forest structure, spatial pattern, and successional processes in many forest systems (Everham and Brokaw 1996). Patterns of wind-induced damage and mortality may vary according to tree species, tree size, tree density, soil properties, landscape position, wind intensity, and wind exposure (Canham et al. 2001; Arévalo et al.

2000; Frelich 2002; Rich et al. 2007; Everham and Brokaw 1996). Given the potential variability of wind-related damage, differential tree mortality from a windstorm may alter the successional process by pushing forest composition back to an earlier or towards a later-successional state, modifying the rate of species change, or altering a forest's successional trajectory (Frelich 2002; Xi et al. 2008). Necessarily, differential mortality and damage from windstorms alters the architectural characteristics of stands and the spatial pattern of trees in wind-damaged forests (Xi et al. 2008; Hanson and Lorimer 2007; Foster and Boose 1992). Understanding tree spatial pattern provides the necessary context for understanding aspects of canopy replacement (Busing 1996; Horn 1974; Woods 1979), regeneration (Condit et al. 1992; Norton 1991), persistent changes in forest dynamics after disturbance (Alekseev and Zherebtsov 1995; Vacek and Lepš 1996), and spatial relationships between tree species (Duncan 1991; He et al. 1997). Consequently, understanding the structural and biological dynamics associated with spatial pattern facilitates a better understanding of the interactions between tree species and disturbance and how that affects the process of forest succession. This understanding will ultimately serve the management of natural forest areas (Moeur 1993).

The frequency of wind-related damage and mortality in forests is expected to increase as damaging winds associated with hurricanes, tornados, and other types of storms are expected to increase with global climate change (Overpeck et al. 1990). This scenario is also likely for forests of central North America which regularly experience catastrophic windstorms (Frelich 2002). In this study, we revisit two forest stands in Minnesota, one oak-dominated, the other pine-dominated, which have been periodically monitored since a windstorm impacted the area in 1983 (Arévalo et al. 2000).

Arévalo et al. (2000) initially reported on the site and determined that damage differed between sites, with the pine site being more heavily impacted than the oak site in terms of mortality and overall damage. The differential damage and mortality were related to the abundance of species in each site and their corresponding probabilities of mortality and damage. They also determined that the two sites were becoming compositionally similar in the years following the storm despite initial compositional dissimilarity, and

the likelihood that the two sites were initially in different successional states. Additionally, they concluded that both sites were experiencing accelerated succession, where rather than push the forest back to an earlier compositional state, the windstorm provided opportunity for later-successional tree species to rapidly increase in both sites.

In this study, we report continued compositional changes in both sites following additional monitoring. Additionally, we investigate the immediate and lasting effects of the windstorm on tree spatial pattern and stand architecture. Here we address the question: how did the initial damage alter the stand architecture and spatial pattern and how did this affect the subsequent recovery and recruitment? We hypothesize that changes in stand architecture were largely mediated by initial damage levels and species-specific responses. Additionally, we hypothesize that spatial patterns of wind-induced mortality will largely be random, but that subsequent recruitment will be spatially non-random with respect to overstory mortality. We investigate these patterns in order to better understand how forest architectural changes and patterns of tree mortality and recruitment interact and affect succession in each site.

## Methods

### Study area

The study was conducted at two permanently marked plots in the Cedar Creek Ecosystem Science Reserve, one of the U.S. National Science Foundation's Long Term Ecological Research (LTER) sites, located in Anoka and Isanti Counties, Minnesota. The plots were established after a windstorm damaged the forests in July 1983 (Arévalo et al. 2000). The plots were placed in two different forest sites: an oak site dominated by *Quercus borealis* and a pine site dominated by *Pinus strobus*. The plots are less than 1 km apart and have similar sandy soils and level topography.

### Field methods

We mapped and permanently marked all tree stems in a 50 × 50 m plot in the oak site and a 50 × 60 m plot in the pine site. In both plots diameter at breast height

(DBH, 1.4 m from ground level), species,  $x$ - $y$  coordinates, mortality, and damage categories were recorded for all living and dead stems greater than 1 cm in diameter. Trees with multiple stems were tagged and measured separately if the stems branched below 1.4 m. The first sampling was conducted in July 1983, 2 weeks after the windstorm. Trees killed by the storm were marked during the first sampling and used to reconstruct the pre-storm forest structure. The plots were resurveyed in 1990, 1993, 1997, 2004, and 2008 for all variables mentioned above.

### Data analysis

Following Arévalo et al. (2000), we applied detrended correspondence analysis (DCA; Hill and Gauch 1980), a type of indirect gradient analysis, using CANOCO v.4.5 (ter Braak and Šmilauer 2002) to explain species compositional change and determine successional trajectory in the two sites following continued monitoring. We used tree species basal area from each sampling period for our ordination.

To assess changes in forest architecture, we evaluated trends in diameter distributions through time. For these analyses, we excluded stems that were less than 2.5 cm in DBH. Additionally, we used principal components analysis (PCA; ter Braak 1983), a type of direct gradient analysis, to explain the architectures of the two forest communities through time. We based on this PCA on frequency of 10 cm DBH classes for all trees in each site. The use of PCA as a tool to describe stand architecture is a somewhat novel application of this method that, to our knowledge, has not been applied elsewhere. This technique may be a useful tool, particularly in evaluating differences in forest architecture between sites and through time.

Lastly, we evaluated the spatial point pattern of trees in each site using Ripley's  $K$  statistic (Ripley 1981). Ripley's  $K$  is an accumulative function, where  $K(r)$  is the expected number of points in a circle of radius  $r$  centered at an uncounted arbitrary point, divided by the intensity,  $\lambda$ , of the pattern. To facilitate interpretation, a commonly applied square root transformation of  $K(r)$ , the  $L$ -function, was applied (Ripley 1981). Here, we calculated the univariate  $K$ -function ( $K_{11}(r)$ ) and bivariate  $K$ -function ( $K_{12}(r)$ ) using the software Programita (Wiegand and Moloney 2004). In the univariate tests, we tested null hypotheses of complete spatial randomness for all living stems in

each sampling period. In the bivariate analyzes, we tested null hypotheses of spatial randomness of windstorm-induced mortality in both sites, and spatial randomness of tree recruitment after the storm in both sites. To evaluate windstorm-induced mortality, we tested a null hypothesis of random labeling where the occurrence of live trees and dead trees are random with respect to each other. To evaluate post storm recruitment, we tested a null hypothesis of spatial independence of recruiting trees from trees that survived or died after the windstorm. This hypothesis was evaluated for each monitoring event following the storm. To evaluate these hypotheses, we constructed 95 % confidence envelopes using a Monte Carlo simulation to determine whether the points were significantly clumped or dispersed at scales up to 12 m. Positive departures from randomness indicate a significant clumping of the pattern, while negative departures indicate a significant repulsion of the pattern.

### Results

Ordination of tree basal area revealed a pattern of continued compositional convergence between the two sites (Fig. 1). This pattern is consistent with that initially described by Arévalo et al. (2000). In the case of DCA, axes may be interpreted in units of beta diversity (units of species standard deviations; Hill and Gauch 1980), and thus give a sense of the magnitude of the compositional difference between sites and compositional change through time. The first axis of the DCA reveals a gradient separating the two sites (Fig. 1). The pine forest is following a path through ordination space towards the oak forest, becoming compositionally similar to the oak site (Fig. 1). Presently, both sites remain distinct in their composition and relative abundance of individual species. However, if both sites continue along this track they will at some point in the future be relatively indistinguishable. Overall, compositional change appears to be occurring more rapidly in the pine site than in the oak site. Additionally, it appears that succession has proceeded in both sites, with both forests moving towards shade tolerant, later-successional species at the top of the panel and away from shade-intolerant, early successional species at the bottom of the panel (Fig. 1). The initial effect of the disturbance on species composition is the same

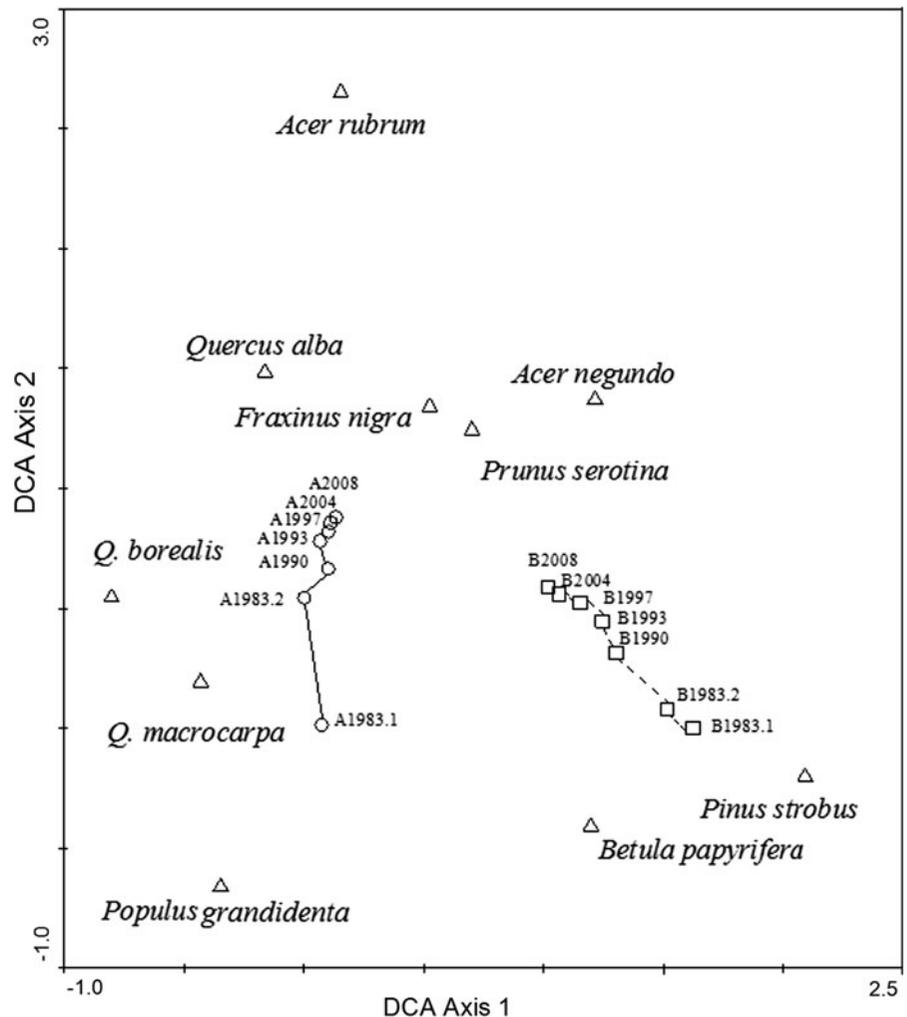
direction as that followed by both forest sites through time.

In both forests, pre-storm diameter distributions appeared weakly bimodal (Fig. 2a, b), but after the storm and through time they have become reverse-J distributions (Fig. 2a, b). In both sites, larger size classes experienced higher mortality from the storm and numerous trees recruited post-disturbance (Arévalo et al. 2000). Recruitment after the storm allowed smaller size classes to dominate the distribution (Fig. 2a, b). Though distribution shapes are similar, tree density in the oak forest was consistently higher than the pine forest throughout the study period (Fig. 2a, b).

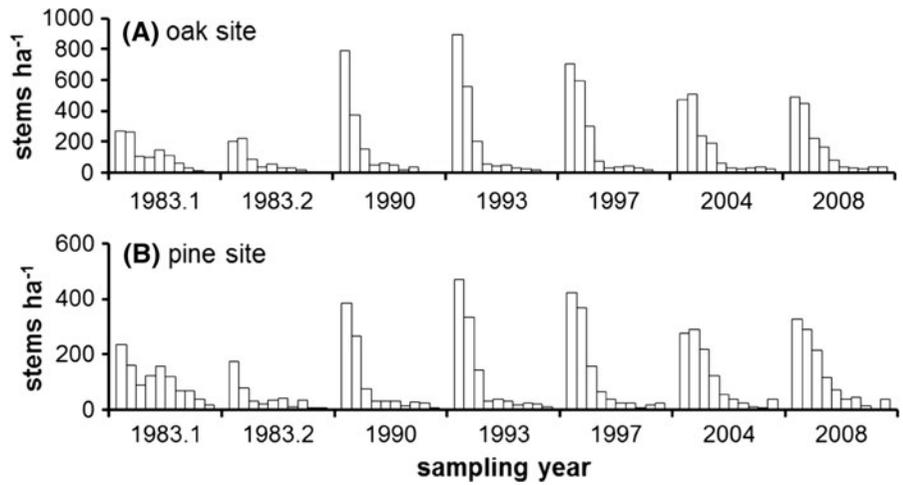
In both sites, the windstorm appears to have induced a similar structural trajectory (Fig. 3). In Fig. 3, PCA axis 1 represents a gradient of tree size,

where years with smaller-sized trees predominating are orientated towards the right side of the panel and years predominated by larger-sized trees are oriented towards the left side of the panel. PCA axis 2 represents a gradient of forest development, with the highly disturbed forest appearing at the bottom of the panel and the recovering/pre-storm forest appearing at the top of the panel, illustrating structural change since the storm. After the storm, both forests went through a period of high regeneration, where smaller size classes were more important (Fig. 3). Until the most recent samplings (2004 and 2008), the pine forest appears to have an overall slower rate of recovery than the oak forest (Fig. 3). This is likely because the pine forest was more severely damaged by the windstorm and the oak forest had more prolific stump-sprouting (Arévalo et al. 2000). The scores from the most recent

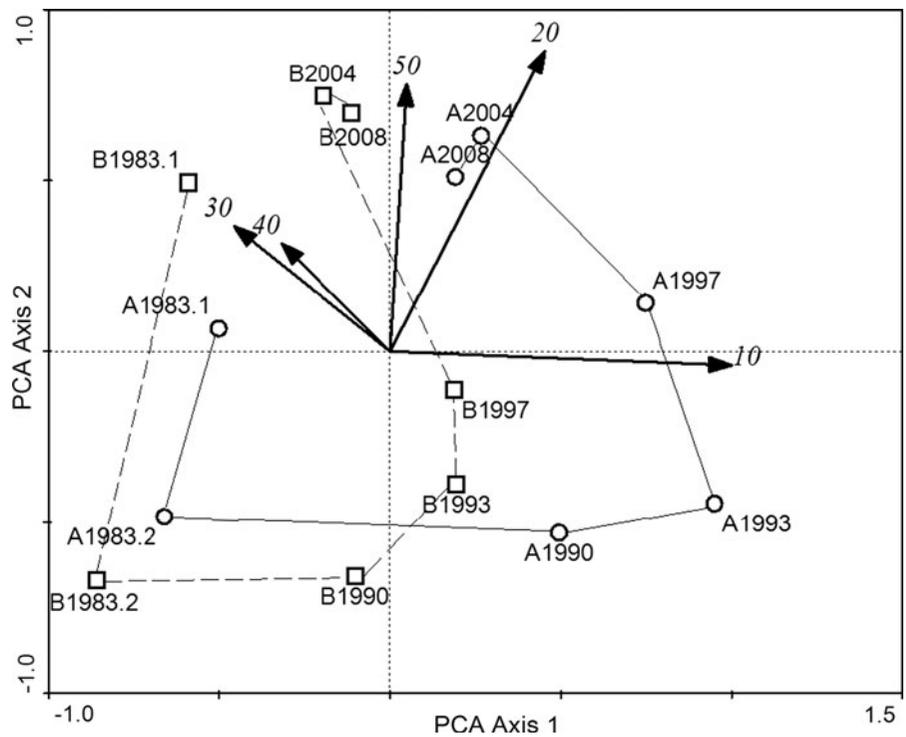
**Fig. 1** DCA biplot of species scores and site scores for the first and second axis based on basal area of trees (eigenvalues were 0.700 and 0.125). The site scores are represented by circles or squares depending on site. The “A” prefix for each point indicates the oak-dominated site; the “B” prefix indicates the pine-dominated site. 1983.1 indicates before the storm; 1983.2 indicates after the storm. The *solid line* indicates the path of the oak-dominated site through ordination space, the *dashed line* indicates the path of the pine-dominated site through ordination space. Species scores (*triangle symbols*) for the most abundant species are shown above



**Fig. 2** Diameter distributions for **a** oak forest and **b** pine forest during each sampling year. Each *bar* represents a 5 cm DBH class interval, the leftmost bar represents <5 cm, and the rightmost bar represents >45 cm. 1983.1 indicates before the windstorm, 1983.2 indicates after the storm

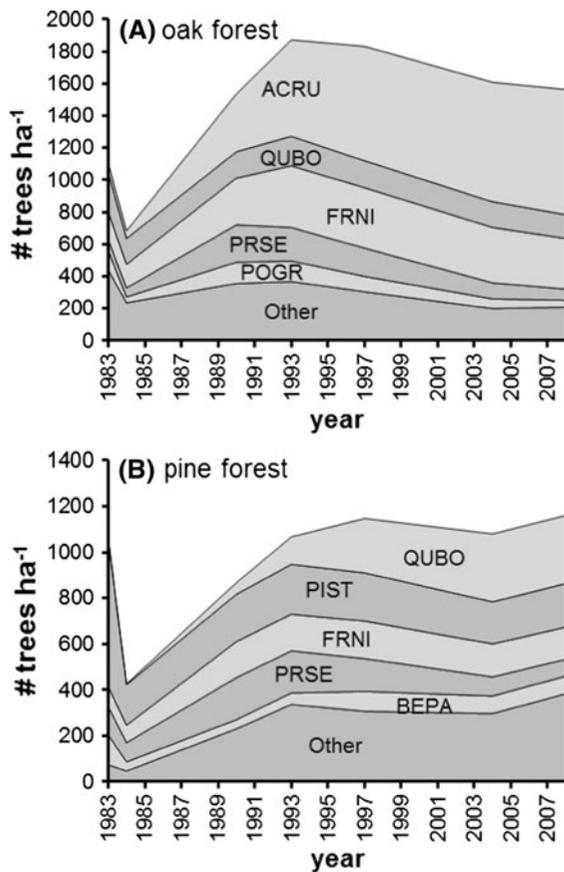


**Fig. 3** PCA biplot of DBH classes based on their frequencies in the oak and pine forest over 1983–2008. The eigenvalues for the first and second axes were 0.868 and 0.092. 10, 20, 30, 40, and 50 represent DBH classes of 2.5–10, 10–20, 20–30, 30–40, and 40–50 cm, respectively. Symbols and site descriptors are the same as Fig. 1



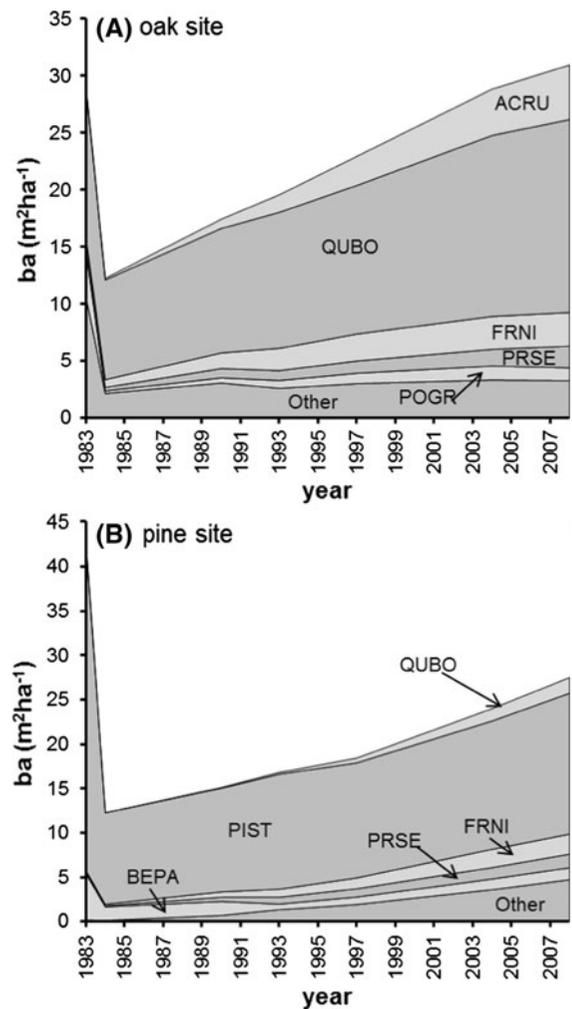
monitoring years (2004 and 2008) are much closer to each other for both the oak and pine site than those from preceding years (Fig. 3), suggesting that the architecture in each site is stabilizing. Additionally, these recent scores have returned to that portion of the ordination closest to those representing the pre-storm state (Fig. 3), suggesting that the stands have partly recovered their pre-storm architecture.

The windstorm reduced overall tree density in both forests (Fig. 4a, b) which allowed for increased recruitment of trees through time. While the oak site appears to be thinning after peaking in tree density during the early 1990s (Fig. 4a), the pine forest appears to be relatively stable in tree density (Fig. 4b). Both sites continue to increase in basal area (Fig. 5a, b), though the oak forest basal area has now exceeded



**Fig. 4** Density of tree species through time. *ACRU*, *Acer rubrum*; *BEPA*, *Betula papyrifera*; *FRNI*, *Fraxinus nigra*; *PIST*, *Pinus strobus*; *POGR*, *Populus grandidentata*; *PRSE*, *Prunus serotina*; *QUBO*, *Quercus borealis*. The “other” category encompasses all other tree species present at the site. Excluding the “other” category, species are arranged top to bottom in order of increasing shade intolerance (following Burns and Honkala 1990)

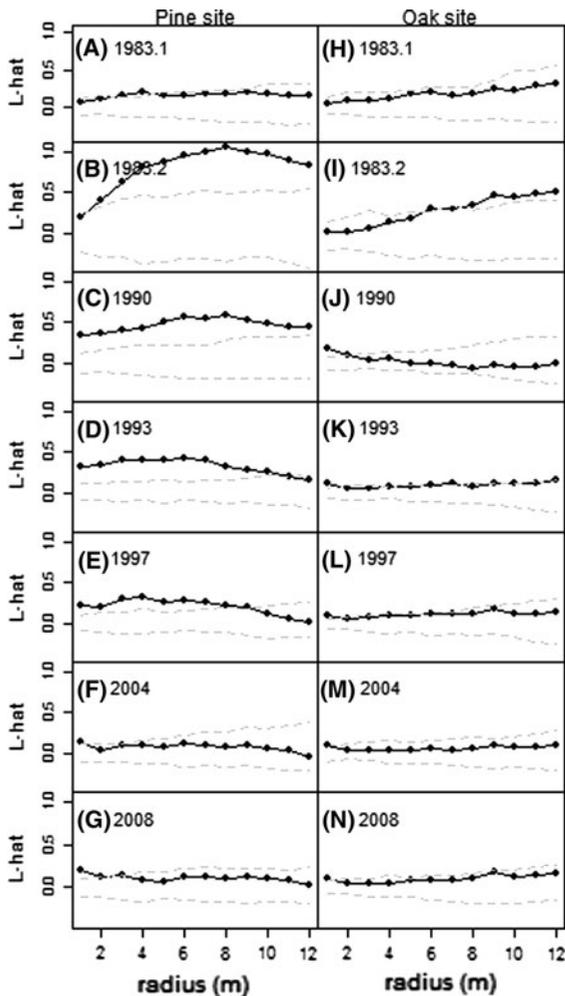
pre-storm levels (Fig. 5A). *Q. borealis* is continuing to contribute the most basal area following the storm in the oak forest (Fig. 5a). The same can be said of *P. strobus* in the pine forest (Fig. 5b). These two species, however, no longer represent the most common tree in their stands as sapling recruitment for those species in their respective sites has been low. Later-successional species such as *A. rubrum* (Fig. 4a) in the oak site and *Q. borealis* in the pine site have increased substantially following the storm (Fig. 4b). It should be noted that while *Q. borealis* is increasing in the pine site, its overall basal area is still relatively low (Fig. 5b). Online Resource 1 contains tables giving complete account of tree species density and basal area in each site during each monitoring event.



**Fig. 5** Basal area of selected tree species through time. Abbreviations and ordering of species is the same as for Fig. 5

Spatial analysis of the univariate point pattern of live trees in each sampling year revealed patterns of aggregation within 12 m in both sites (Fig. 6). In the pine site, prior to the storm, there was significant clustering within 3–4 m (Fig. 6a). The storm, however, greatly altered the spatial pattern of the site, producing a more clumped distribution (Fig. 6b, c). Through time, the clumped pattern persists but at decreasing spatial scales (Fig. 6d, g). In 2004 and 2008, clumping is only evident at finer scales.

In the oak site, the effect of the storm was not as dramatic (Fig. 6h, n). Prior to the storm, the distribution of trees in the site was not significantly different from random (Fig. 6h). After the storm, the mortality produced a slightly significantly clumped pattern of



**Fig. 6**  $L_{11}$  plotted as a function of radius indicating univariate spatial point pattern of dispersal/aggregation. Subplots **a–g** indicate spatial patterns in the pine site for each sampling year, subplots **h–n** indicate spatial patterns in the oak site for each sampling year. *Solid line* indicates the  $L_{11}$  function. *Dashed lines* indicate the upper and lower limits of the 95 % confidence envelope

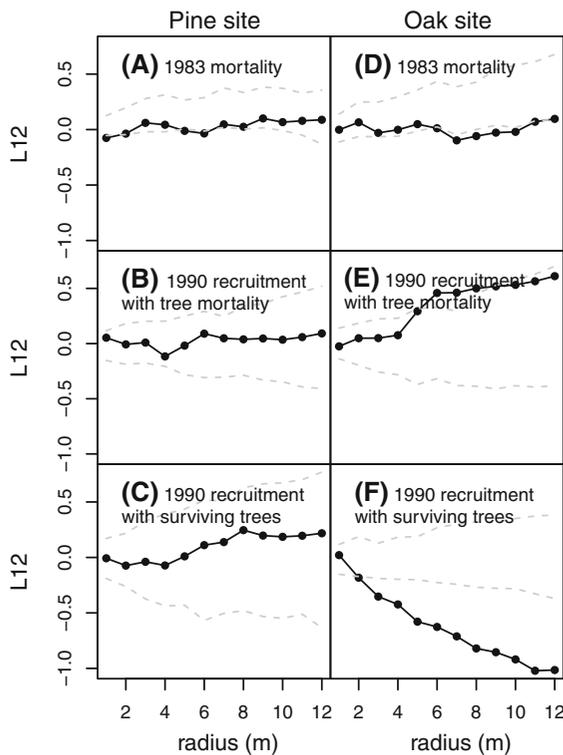
trees within radii of 5–12 m (Fig. 6i). In 1990, there is slightly significant clumping within 1–2 m (Fig. 6j), likely reflective of the high recruitment of individuals in treefall gaps in the site (discussed further in the next paragraph). In 1993, the pattern appears to be a blend of the clustering produced by high recruitment and the initial storm damage (Fig. 6k). From 1997 on, significant clustering is only evident within 1 m (Fig. 6l, n) which likely reflects the sustained, but lower, recruitment in the site. Overall, the windstorm weakly modified the spatial pattern of trees in the oak site.

Spatial analysis of the bivariate pattern in each monitoring year yielded patterns of aggregation and dispersion within radii of 12 m. In the pine site, the storm produced slightly significant patches of mortality at scales within 5–6 m (Fig. 7a), where there were significantly fewer dead trees around live trees than expected. This pattern of mortality, however, did not appear to play a significant role in the pattern of recruitment after the storm as recruits were spatially random with respect to both trees that were killed by the storm (Fig. 7b) and surviving trees (Fig. 7c). The locations of trees in the pine site that recruited after 1990 were not significantly different from random (results not shown).

In the oak site, the spatial pattern of mortality was somewhat patchy as there were slightly significantly fewer dead trees around live trees than expected within scales of 7–10 m scales (Fig. 7d). This patchy mortality apparently affected the recruitment process as trees that recruited by 1990 were positively aggregated with dead trees at scales greater than 5 m (Fig. 7e) and were negatively associated with living trees at scales greater than 1 m (Fig. 7f). In sampling years after 1990, spatial patterns of tree recruitment did not significantly differ from random (results not shown).

### Discussion

The successional trajectories of the pine and oak sites following the windstorm largely follow that described by Curtis (1959) for forests of northern Wisconsin, where shade-tolerant species (i.e., *A. rubrum* in the oak site and *Q. borealis* in the pine site) have replaced trees killed by the storm. Consistent with Arévalo et al. (2000), we found that the mortality from the windstorm has favored a pattern of accelerated succession. Shade-intolerant species suffered high mortality granting shade-tolerant species opportunity to move into the canopy. Accelerated succession is a common outcome of wind disturbance in a variety of forest types, including boreal forests of northern Minnesota (Rich et al. 2007; Dyer and Baird 1997), piedmont forests of North Carolina (Xi et al. 2008), mixed hardwood forests of Texas (Harcombe et al. 2002), forests of the Cascade Mountains in Oregon (Sinton et al. 2000), and Illinois oak forests (Holzmueller et al. 2012). In the absence of fire, windstorms have the potential to accelerate the ongoing “mesophication”



**Fig. 7**  $L_{12}$ -function plotted as a function of radius indicating bivariate spatial pattern of dispersal/aggregation for **a** mortality from the windstorm in the pine site, **b** 1990 recruitment in pine site with respect to trees killed by the storm, **c** 1990 recruitment in the pine site with respect to trees that survived the storm, **d** mortality from the windstorm in the oak site, **e** 1990 recruitment in the oak site with respect to trees killed by the storm, **f** 1990 recruitment in the oak site with respect to trees that survived the storm. *Solid line* indicates  $L_{12}$  function, *dashed lines* indicate upper and lower limits of the 95 % confidence envelope

(Nowacki and Abrams 2008) of North America's eastern forests—where disrupted fire regimes have facilitated the broad-scale succession of shade-tolerant, mesophytic tree species.

The accelerated succession resulting from the increase in shade-intolerant species in both sites is driving the compositional convergence of the two sites. The concept of convergence is implicit in Clements' (1936) idea of a climax community for areas of the same soils and climate. In practice, though, the occurrence of compositional convergence is often difficult to identify given the temporal and spatial constraints of ecological investigation (Lepš and Rejmánek 1991). Consequentially, it is more appropriate to determine the mechanism of a convergence

trend for a particular case, rather than its occurrence (Lepš and Rejmánek 1991).

In this case, we argue that the convergence trend is better understood in the context of the architectural changes and the spatial patterns of mortality and recruitment in each site. As already mentioned, Arévalo et al. (2000) determined that the pine site was in an earlier successional state and that it experienced a higher level of windstorm damage due to the greater damage and mortality probabilities of its dominant species. As we had hypothesized, this produced a more dramatic change in forest architecture. Additionally, the windstorm greatly altered the overall spatial pattern of trees in the site, resulting in significant clusters of surviving trees at all spatial scales assessed in this study. We had hypothesized that subsequent recruitment would be spatially non-random with respect to mortality. This was not the case in the pine site as the high level of damage produced a recruitment pattern that was not spatially restricted by shading from surviving trees. In this case, shade-tolerant species in the pine site had greater opportunity to establish, explaining the higher level of compositional change observed in the pine site. This is consistent with the idea that the forest gaps resulting from catastrophic events favor an increase in forest species richness, while gaps produced by low level damage or natural senescence serve to maintain or only moderately increase species richness (Arévalo and Fernández-Palacios 1998). At a site in northeastern Minnesota, Bolton and D'Amato (2011) determined creation of canopy gaps alone was insufficient to increase forest diversity. Instead, diversity only increased when there was substantial disturbance to the forest floor (i.e., creation of exposed mineral soil and presence of coarse woody debris) such as that created by the mound and pit topography of wind-thrown forests (Bolton and D'Amato 2011). These conditions are certainly met in the pine site, which experienced high levels of uprooting as a result of the storm (Palmer et al. 2000).

In contrast, the dominant tree species of the oak site, *Q. borealis*, had much lower probabilities of damage and mortality relative to other species in the sites (Arévalo et al. 2000). As a consequence, storm-induced mortality in the site did not greatly alter the architecture or the overall spatial pattern of surviving trees in the site. As hypothesized, this moderate damage and mortality resulted in a spatial pattern of

recruitment that was restricted to gaps produced by the storm, a pattern also observed in moderately disturbed Slovenian forests (Nagel et al. 2006). These gaps allowed opportunity for shade-tolerant species (e.g., *Acer rubrum*) to increase in abundance in the site, but relative to the more heavily damaged pine site, the overall amount of compositional change in the oak site is less. In the oak site, the most wind-impacted trees snapped instead of being uprooted (Palmer et al. 2000), resulted in an overall lower amount of disturbance to the forest understory, which may also help explain the lesser degree of compositional change in the site (Bolton and D'Amato 2011).

Through time forest succession is modified not simply by time since a stand-replacing event, but by a number of factors including edaphic conditions, species' density dependence, and minor disturbance events (Chen and Taylor 2012). This variability may be observed across large geographic areas where multiple forest succession pathways may be identified, depending on finer scale variability in soils and disturbance (Taylor and Chen 2011). Wind, in particular, is an important factor that can increase forest diversity and spur the progression of forest succession (Frelich and Reich 1995; Chen and Taylor 2012). In southern boreal forests, within-stand variation in damage is largely predictable when tree identity and size are taken into account (Peterson 2004). As shown here, such differential susceptibility amongst tree species may result in a varied spatial pattern and intensity of damage due to changes in species abundance across the landscape. Taken into account, this will allow opportunities for better predicting areas most likely to be impacted by wind disturbance events and, given the intensity of the disturbance, the amount of compositional change that might be expected.

Into the future, the rate of compositional change (and by extension, convergence) is likely to slow unless the sites experience some other disturbance event. From monitoring during 2004 and 2008, tree density in both sites is beginning to stabilize or thin as the sites regain their pre-storm architecture. Basal area, though, is continuing to increase in both sites; in the oak site it has now surpassed pre-storm levels but in the pine site, is still roughly two-third of the pre-storm state. Though *A. rubrum* is increasing in the oak forest, *Q. borealis* has maintained a well-stratified diameter distribution in the years following the storm.

The persistent structural diversity of *Q. borealis* may give it a competitive advantage in resource extraction (Yokozawa 1999), which may facilitate its persistence through time. The same may be true in the pine forest where *P. strobus* may maintain a competitive advantage due to its well-stratified diameter distribution in the site. Consequently, the composition of both sites is likely to be primarily characterized by their pre-storm dominants for some time into the future.

## Conclusions

Accelerated succession is an important outcome of windstorm events that may serve to promote compositional convergence in forest stands. The dynamics of this process are mediated, to some extent, by the level of damage and mortality sustained in a particular location and its corresponding effects on spatial patterns of surviving and recruiting trees. The legacy of that initial damage, in this case, affected the spatial patterns and recruitment dynamics in both sites, as well as the rate at which they architecturally recovered.

**Acknowledgments** We thank the staff of the Cedar Creek Ecosystem Science Reserve for the use of their facilities. We thank Jason Joines, Daniel McGlenn, Kiyoshi Sasaki, Fumiko Shirakura, and Shyam Thomas who helped with stand surveys, data preparation, and analysis. Lastly, we thank two anonymous reviewers for their helpful comments on this manuscript.

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