The influence of landscape context on short- and long-term forest change following a severe ice storm

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Abstract

1. When deforestation results in small forest fragments surrounded by a non-forest matrix, forest stands within these fragments experience changes in structure and community composition. They also continue to experience natural disturbances like hurricanes and

ice storms. It is unclear whether the landscape context of forest stands influences plant community response to natural disturbances.

2. Using data from surveys of forested plots in the years immediately following and 19 years after a severe ice storm, we measured changes in woody stem density, species richness, and beta diversity.
3. Plots with greater storm damage had greater gains in stems and species, and greater shifts in community composition. In addition, there were interactions between the degree of storm damage and landscape context. The short-term effects of storm damage were magnified in plots with less forest on the surrounding landscape and farther from the forest edge. In plots with high damage, a return towards pre-storm conditions over the long-term occurred more often in plots farther from the forest edge compared to those close to the edge.
4. Synthesis: Future climate scenarios predict increases in severe weather and accompanying ecosystem disturbance. Our results show that it is important to consider landscape context when assessing the response of forest communities to such disturbances.

Keywords: community composition; deforestation; fragmentation; landscape matrix; recovery; natural disturbance; species richness; succession

1. Introduction

Human dominance of landscapes has resulted in the loss and fragmentation of forests around the world (Lindenmayer and Fischer 2006, Riitters et al. 2016). The conversion from large, contiguous forests to small patches embedded in a matrix of agricultural and urban land results in changes in forest structure, diversity, and species composition that are predictable based on landscape context and plant traits (e.g. Metzger 2000, Dupré and Ehrlen 2002, Kolb and Diekmann 2005, McCune and Vellend 2015). For example, McCune and Vellend (2015) found that, over a four-decade period, forest stands with low amounts of forest in the surrounding landscape were more likely to be colonized by exotic, annual, shade-intolerant species than stands embedded in large areas of forest. In addition to the changes forests undergo as a result of anthropogenic deforestation, they also continue to respond to natural disturbances such as fire, hurricanes, and ice storms. It is important to understand how reduction of forest cover on a landscape influences forest response to natural disturbances to be able to predict how forest ecosystems will change in the future with further forest loss and changes in climate (Laurance and Cochrane 2001, Catterall et al. 2008, Smart et al. 2014). But few studies have attempted to measure these potential interactions, particularly over the timescales necessary to document long-term compositional changes in forest communities.

There is a large literature regarding forest change following natural disturbances. Firstly, disturbances that create gaps in forest canopies often result in greater stem density and increased species richness compared to pre-storm conditions or undisturbed areas (Peterson 2000, von Oheimb et al. 2007, Fisher et al. 2013, Smart et al., 2014). An increase in light and nutrient availability following the loss of larger canopy trees results in increased growth of existing saplings and/or allows colonization by new species (Whitney and Johnson 1984, Canham 1989, Arii and Lechowicz 2007, Xi and Peet 2011). Alternatively, recovery following canopy damage can proceed mainly by root sprouting of residual mature trees, resulting in little or no change in species richness (Chazdon 2003, Dietze and Clark 2008, Plotkin et al. 2013).

Beta diversity, defined as the variability in community composition among sites (Whittaker 1972), can also be altered by natural disturbances (Liebsch et al. 2008, Myers et al. 2015). Severe disturbance can result in lower beta diversity if species that are more susceptible to damage cannot survive the disturbance or adapt to post-disturbance conditions, leaving only a subset of less susceptible species to accumulate in communities (e.g. Heydari et al. 2017). However, beta diversity may increase in cases where dominant species are most affected by the disturbance, leaving more resources available for uptake by a more diverse group of subordinate species (Silva Pedro et al. 2016).

Finally, natural disturbances can affect forest succession. In some cases, large natural disturbances set succession back to an earlier stage by killing larger, late-seral species and therefore favouring younger, pioneer species (Kosugi et al. 2016). In other cases, disturbance accelerates succession, by removing lingering early-seral species that had been slowing the rise to dominance of late-seral species (Abrams and Scott 1989, Rhoads et al. 2002, Zhao et al. 2006, Allen et al. 2012). Clearly, the impact of natural disturbances on forest communities is complex, and depends on the disturbance type, frequency and severity, as well as the composition and successional stage of the forest at the time of the disturbance (Everham and Brokaw 1996, Turner et al. 1998, Tremblay et al. 2005).

Landscape context – by which we mean the amount of forest surrounding a focal forest stand and the proximity of the stand to the nearest forest-matrix edge – could affect forest response to natural disturbance in two ways. First, it can change the frequency of natural disturbances, or the degree of damage they cause. For example, small isolated forest fragments may experience forest fires less frequently due to the inability of fire to spread across non-forested areas (Weir et al. 2000), but they may experience greater damage from hurricanes due to a greater area of forest being closer to forest edges, which are more susceptible to damage from high winds (Schwartz et al. 2017). Second, landscape context could influence the short- and long-term response of forest communities to natural disturbances by affecting the mechanisms by which communities respond to disturbance - specifically, by affecting regeneration (Catterall et al. 2008). The density of seeds and seedlings of matrix-associated generalist, shade-intolerant, and exotic species is predicted to increase in landscapes with smaller areas of forest, and at sites within forest patches that are closer to the forest-matrix boundary (Garwood 1989). Therefore, canopy gaps may be more likely to be colonized by generalist or exotic species in forest stands in landscapes where non-forest habitat predominates, and closer to the boundary between the forest and the agricultural matrix, compared to forest stands in high-forest landscapes or located far from the forest-matrix edge (Kupfer et al. 1997, Catterall et al. 2008, Laurance and Curran 2008, Smart et al. 2014). Canopy gaps may also experience a greater increase in stem density at sites surrounded by less forest and closer to the forest-matrix edge due to this higher density of seeds or seedlings of light-loving, matrix-associated species when compared to sites far from the forest-matrix edge or in landscapes dominated by unbroken forest. This second potential influence of landscape context is more difficult to test, because the response of plant communities to disturbance typically unfolds over decades; therefore, data on species richness and community composition over long timescales are required, ideally both before and after the occurrence of a natural disturbance.

In this study, we use detailed forest surveys conducted immediately following, three years, and nineteen years after a severe ice storm to measure changes in stem density, species richness, and composition over time, and to test for an effect of landscape context on these changes. Ice storms occur when warm fronts moving across cold landscapes cause the formation of thick ice layers on the surface of objects, and they are a relatively frequent disturbance of temperate forests in northeastern North America (Lemon 1961). In early January 1998, an exceptional ice storm hit a large area of Canada and the northeastern United States (Regan 1998). In the region near Ottawa, Canada, where our study takes place, 60-80mm of ice accumulated on tree branches and other surfaces, causing losses of branches and entire trees to breakage (Kerry et al. 1999). Land use in this region is primarily agricultural, with forests confined to patches surrounded by crop fields or pastures. If landscape context has a significant influence on the post-storm response of forests in this area, we predicted that the short- and/or long-term effects of the storm on stem density, species richness, and community composition would be moderated by (1) the amount of forested area in the landscape surrounding each forest stand, or (2) the distance of the measured stand from the nearest forest-matrix edge. Specifically, we tested for interactions between the amount of damage caused by the ice storm and these two landscape context variables in predicting changes in stem density, species richness, and community composition over time. We hypothesized that increases in stem density, species richness, and shifts in composition would be greater with greater ice storm damage, and that this effect would be magnified in stands located in low-forest landscapes, or closer to the forest-matrix edge.

2. Materials and methods

2.1. Study area

We conducted this study in forests near Ottawa, Ontario, Canada (45°25'N 75°41'W), within the Great Lakes-St. Lawrence forest region (Fig. 1; Crins et al. 2009, Ontario Ministry of Natural Resources and Forestry 2018). Forests here are dominated by hardwoods, including sugar maple (*Acer saccharum*), beech (*Fagus grandifolia*), and Eastern hop-hornbeam (*Ostrya virginiana*). On average, 758mm of rain and 224cm of snow fall in the area each year; the annual mean temperature is 6.38°C (Environment and Natural Resources 2017). The topography is gentle, with elevations ranging from 71m to 122m above sea level on flat to nearly flat slopes. The study sites are patches of deciduous or mixed forests located in rural areas, mostly surrounded by crop fields or pastures, except for one site which is situated in a municipal park now surrounded by recent suburban development. All forests in this region have experienced some level of selective harvest for firewood or timber. In 1998, the stands in our study ranged from 16.9cm to 22.4cm in mean diameter at breast height (DBH) of all trees greater than 10cm DBH, with maximum DBH ranging from 17.8cm to 118.5cm.

2.2. Data collection

In 1997, Contreras (2002) identified 29 non-overlapping 1km^2 landscapes with forest cover of each landscape ranging from 7% to 95% of the total area. He chose 10 sampling plot locations within each landscape, both forested and non-forested. Each plot measured 12.5m by 25m. During the summer of 1998, after the ice storm, surveyors attempted to re-locate the plots with varying amounts of success. Surveyors in 1998 marked the plots with flagging and metal tags.

Each summer, from 1998 to 2001, researchers surveyed these plots using the same protocol as the 1997 surveys (Brommit et al. 2004, Charbonneau and Fahrig 2004, Darwin et al. 2004). Because we could only be certain of high plot relocation accuracy from 1998 onwards, we used the 1998 survey as the baseline for measuring change over time. Although the ice storm caused significant canopy loss, most individuals were still standing and therefore measured in 1998. Therefore we consider the 1998 data a valid baseline for measuring the changes that followed the ice storm.

In 1998, surveyors measured the percent crown loss due to the ice storm for all trees in each plot (Darwin et al. 2004). They then calculated the plot damage index (pdi) as the percent crown loss multiplied by the basal area of each tree, summed across all individuals and divided by the total basal area of all trees in the plot, according to the following equation:

$$Plot\ Damage\ Index\ (pdi) = \frac{\Sigma[\pi r^2(\%\ crown\ loss)]}{100\ \times\ [\Sigma \pi r^2]}$$

where r is the radius of each tree at breast height (1.3m).

In the summer of 2017, we used GPS coordinates and field notes to re-locate and re-survey a subset of the forest plots established in 1998. We re-surveyed only plots within 40km of downtown Ottawa that had not been clear cut between 2001 and 2017, and where we could obtain permission from landowners. We surveyed a total of 69 plots in 17 landscapes (Fig 1). At 44 of these plots, fragments of tags or flagging indicated we were definitively at the site of the previous re-surveys. For the others, we used the GPS coordinates from 2001 (5-10m accuracy).

In accordance with the earlier surveys, we delineated a 12.5m by 25m rectangular plot within which we identified to species and counted all trees of at least 10cm diameter at breast height (DBH). Within this larger plot, we delineated a 6.25m by 12.5m shrub-sapling plot in which we identified and counted all shrubs and saplings less than 10cm DBH and at least one metre in height. We standardized plant species names following Reznicek et al. (2011). To ensure consistency throughout years, we lumped some species to genus level where accuracy of previous surveys was in doubt.

Using aerial photos from 1999 (City of Ottawa 2018) and 2015 (DigitalGlobe 2010, 2015a, 2015b, 2016), we digitized the forests within which our plots were located in ArcMap version 10.6 (ESRI 2011). Forests were easily distinguished from cropland and urban land, and also from shrubland, which is rare in the region. We measured the total amount of forest (area in hectares) surrounding each plot within 200m, 500m, and 1000m of the plot in each year. We chose these distances based on previous research in which landscape context within 500m was correlated with plant community metrics (McCune et al. 2017, McCune and Vellend 2015), but recognizing that the strongest effects might occur at larger or smaller distances (Jackson and Fahrig 2015). We also measured the distance of each plot from the nearest forest edge (i.e. the forest-matrix boundary; Fig. 1B). We measured these landscape context factors in two years because there have been significant changes in forest cover in the study area since 1998, mostly in the form of deforestation. Based on our experience in the field, the most recent forest cover estimates which we based on satellite imagery ranging from 2010-2015 were accurate for our sites in 2017.

2.3. Analyses

2.3.1. Region-wide responses

We first tested for changes across all plots over time. To test for changes in woody stem density and species richness, we used a linear mixed effects model for each response variable, with plot within landscape as a random effect. To determine whether there were any significant differences between years in (1) stem density and (2) species richness, we compared a model with ‘year’ as a predictor to one with only the random effect using a likelihood ratio test. We used a post-hoc test with adjusted p-values using Bonferroni correction to analyze pairwise differences between years. To determine changes in beta diversity in the years following the ice storm, we used non-metric multidimensional scaling (NMDS) ordination based on Bray-Curtis dissimilarities to visualize the range of woody plant community composition occupied by all the plots in each year (Bray and Curtis 1957, McCune and Grace 2002). We then used a test of difference in multivariate dispersions (PERMDISP; Anderson et al. 2006) with pairwise comparisons between years to determine whether beta diversity changed significantly between years. We ran the ordination and the PERMDISP analysis on the matrix of pairwise dissimilarities of plots based on the Bray-Curtis dissimilarity metric calculated on square-root transformed stem counts for each species in each plot. Canopy and understory layers have been found to have differing responses to disturbance (e.g. Bače et al. 2017), so we tested three subsets of data: trees only (≥10cm DBH), shrubs and saplings only (<10cm DBH and >1m tall), and an overall community assessment which combined both subsets. Surveyors did not count all the tree stems in 2000; therefore we omitted that year.

To determine which species became more frequent and/or abundant on the landscape 3 years and 19 years after the storm we used an indicator species analysis (ISA). ISA computes an ‘indicator value' for each species based on its relative abundance and relative frequency in different experimental groups and uses permutation to test for significance (Dufrêne and Legendre 1997). While ISA is most often used to determine which species are indicators of specific habitat types or experimental treatments (McCune and Grace 2002), it can be used in the same way to determine which species are indicators of different points in time (e.g. McCune and Vellend 2013). We hypothesized that shade-intolerant species would increase following the ice storm as they took advantage of canopy gaps, and then decline again as gaps closed and shade-tolerant species recovered. We determined the shade tolerance of each species based on Niinemets and Valladares (2006).

2.3.2. Plot-level responses

We then tested for effects of ice storm damage, landscape context (i.e. forest amount and distance to nearest forest-matrix edge), and interactions between ice storm damage and each of the two landscape context variables on plot-level changes in stem density, species richness, and species composition. We carried out these tests on all size classes (trees and shrubs/saplings), and on the shrub/sapling size class alone. As the results for these two sets were qualitatively nearly identical, for simplicity we report only the results for the total community. We first plotted stem density and species richness over time for each plot. We also plotted the Bray-Curtis dissimilarity of each plot in 1999, 2001, and 2017 compared to the same plot itself in 1998 to track plot-level shifts in species composition over time, based on the square-root transformed stem counts for all woody species.

We defined the change in stem density, the change in species richness, and the Bray-Curtis dissimilarity of each plot in 2001 compared to 1998 as the short-term change following the ice storm, and the changes in 2017 compared to 1998 as the long-term change. This resulted in 6 response variables (Table 1). We then built a model for each response variable with predictors ice storm damage (pdi), amount of forest, distance to the nearest forest edge, and interactions between pdi and each of the two landscape context variables. In addition, we included covariates that might also influence the response (Table 1). For change in stem density and species richness, we included starting stem density (number of stems in 1998) or starting species richness, respectively, because starting conditions could influence the likelihood that a plot experiences increases or decreases in the number of stems or species. We also included an index of plot wetness, which we calculated as the average wetness coefficient of all woody species in the plot in 2017, weighted by their abundances. We compiled the wetness coefficient for each species from the Michigan Floristic Quality Assessment System (Reznicek et al. 2014) and available online (Reznicek et al. 2011). Wetness coefficients range from 5 to -5, where species with a score of 5 are obligate upland species, and those rated -5 are obligate wetland species (Oldham et al. 1995). Forest response to disturbance can vary in xeric versus mesic sites (Whitney and Johnson 1984). For change in species composition, we included as covariates the starting species richness, and starting species composition, based on the score of each site in 1998 on the NMDS axis with the greatest variation. We did not include wetness index in these models due to a very strong correlation between starting composition and wetness index (see below). We also included average DBH as a covariate for changes in species composition, because shifts in species composition in response to natural disturbances can vary in stands of different ages (Peterson 2000).

Before building each model, we examined the correlations between all explanatory variables. Due to high correlations between forest amount measured within different distances of the plots, we used only the 1000m measurement because it provided the greatest explanatory power in a comparison of univariate models. For the long-term response, we used the forest amount and distance to edge calculated for 2015, while for the short-term response, we used the forest amount and distance to edge calculated for 1999. No two explanatory variables in the final candidate models had a correlation coefficient greater than 0.53 (Table A1, Supporting Information).

We modelled change in stem density and change in species richness using linear models. Because the Bray-Curtis dissimilarity metric takes values between 0 and 1 (McCune and Grace 2002), we used generalized linear models (GLM) with a beta distribution and a logit link to model changes in community composition. We standardized all response variables prior to building GLMs by subtracting the mean and dividing by the standard deviation. For the linear models we used the ‘arm’ package in R to standardize by centering and dividing by twice the standard deviation. We checked for spatial autocorrelation in the residuals of all models using spline correlograms. Because we found no evidence of spatial autocorrelation, we treated plots in the same 1km^2 landscape as independent (Dormann et al. 2007). For each response variable, we built a model with all our candidate predictors. We then identified the minimum adequate model using backwards stepwise selection and AIC. If a predictor or an interaction was not included in the minimum adequate model, we considered the predictor not to be significantly related to the response and we did not consider it further. After we had fit the minimum adequate model for each response variable, we performed marginal fitting of terms (‘drop1’ test) by dropping each of the terms from the minimum adequate model to determine which predictors and interactions had a significant effect on the response variable once all other variables in the minimum model were accounted for. We visualized the relationships between each predictor in the minimum model and the response variable using partial residual plots. These plots show the conditional effect of each predictor on the response variable by holding all other predictors constant at their median. That is, the y-axis value for each data point is adjusted to remove the fitted effect of the other predictors in the model (Breheny and Burchett 2017).

We conducted all analyses using R version 3.3.3 (R Core Team 2017). We used the package ‘multcomp’ to perform post-hoc tests (Hothorn et al. 2008), and the ‘vegan’ package for ordinations and the PERMDISP analysis (Oksanen et al. 2017). We ran the indicator species analysis using the ‘labdsv’ package, with 10,000 permutations (Roberts 2016). We used the ‘nlme’ package to fit linear models (Pinheiro et al. 2017), and packages ‘betareg’ and ‘glmmTMB’ to fit GLMs (Cribari-Neto and Zeileis 2010, Brooks et al. 2017). We used the packages ‘arm’ to standardize predictor variables (Gelman and Su 2018), ‘MASS’ for stepwise model selection and marginal fitting of terms (Venables and Ripley 2002), ‘ncf’ for spatial correlograms (Bjornstad 2018), and ‘visreg’ to create partial residual plots (Breheny and Burchett 2017).

3. Results

3.1. Region-wide responses

Stem density varied between years for trees, shrubs/saplings, and all woody stems combined (See Table A2, A3, Supporting Information). The greatest change was in the shrub/sapling layer, where stem density increased considerably after the storm, and then declined to levels similar to 1999 by 2017 (Fig. 2A). Species richness also changed significantly between years, primarily in the shrub/sapling layer (Table A4, A5, Supporting Information). Shrub/sapling species richness increased significantly by 1999 and has remained significantly higher than 1998 levels (Fig 2B). There were no significant changes in beta diversity across all plots for any subset (Table A6, Fig. A1, Supporting Information).

There were no significant indicator species for trees: no tree species was significantly more frequent and/or abundant in 2001 or in 2017 compared to 1998 (Table A7, Supporting Information). In the shrub/sapling layer, choke cherry (*Prunus virginiana*), beaked hazelnut (*Corylus cornuta*), ash (*Fraxinus americana/pennsylvanica*) and nannyberry (*Viburnum lentago*) were indicators of 2001 compared to 1998. Saplings of the shade tolerant tree sugar maple (*Acer saccharum*) and the moderately shade tolerant shrub bristly gooseberry (*Ribes cynosbati*) were also indicators of 2001 (Table A7). By 2017, chokecherry, hazelnut, and sugar maple were still more frequent and abundant in the shrub/sapling layer than they had been in 1998, but nannyberry and gooseberry were no longer indicators. However, the shade tolerant blue beech (*Carpinus caroliniana*) and alternate leaved dogwood (*Cornus alternifolia*) were more frequent and abundant in the 2017 shrub/sapling layer compared to 1998 (Table A7).

3.2. Plot-level responses

Plot-level trajectories in stem density, species richness, and species composition were highly variable across plots, and even between plots located in the same 1km^2 landscape (Fig. A2, A3, Supporting Information; Fig. 3). While stem density tended to peak two years after the ice storm, and then decline towards 1998 levels, changes in species richness and composition were more variable, and did not tend to return towards 1998 levels.

3.2.1 Short-term changes in stem density and species richness

The degree of canopy loss (pdi) was a significant predictor of changes in stem density and species richness from 1998 to 2001, with more heavily damaged plots gaining more stems and species (Table 2, Fig. 4A). Landscape context was also a significant predictor of short-term changes in stem density and species richness, with plots having more forest in the surrounding landscape tending to gain fewer stems and species (Table 2, Fig. 4B). Models for short-term change in stem density and species richness did not include interactions between the amount of ice storm damage and landscape context.

3.2.2 Long-term changes in stem density and species richness

By 2017, the difference in stem density compared to 1998 was negatively related to ice storm damage, with more damaged plots having gained fewer stems, all else being equal (Table 2). The number of stems gained between 1998 and 2017 declined with greater amounts of forest within 1000m of the plot, and with a higher starting density. The change in species richness between 1998 and 2017 was no longer predictable based on ice storm damage once other predictors were taken into account, but was strongly related to starting species richness, with plots having lower species richness in 1998 tending to gain more species by 2017 (Table 2, Fig. 5D). The models for long-term change in stem density and species richness both included an interaction between plot damage and distance to the forest edge: plots farther from the forest-matrix edge showed a negative relationship between ice storm damage and long-term gain in stems and species (Table 2, Fig. 5E).

3.3.3 Changes in community composition

The models of short- and long-term change in community composition both included interactions between ice storm damage and landscape context (Table 2, Fig. 6, Fig. 7). In the short-term, there was a positive relationship between greater damage and a larger shift in species composition, particularly in plots surrounded by lower amounts of forest and in plots farther from the forest edge (Fig. 6). Changes in species composition in the short-term were smaller in plots with lower species richness in 1998, and plots surrounded by higher amounts of forest within 1000m (Fig. 6).

Over the long-term, changes in composition were smaller in plots with greater ice storm damage, and in plots surrounded by greater amounts of forest (Fig. 7). Plots with starting composition on the lower end of the main ordination axis tended to shift less in composition over the long term – these plots are drier sites dominated by sugar maple. The minimum adequate model for long-term shifts in composition included an interaction between plot damage and distance to the forest edge (Fig. 7E; Table 2). Plots that sustained high levels of damage in the ice storm were more similar in composition to their 1998 composition if they were farther from the forest edge (Fig. 7E).

4. Discussion

Our results confirm the relatively well-known effects of both natural disturbance and landscape context on forest communities. More importantly, we found interactions between these two drivers of change. This supports our prediction that landscape context can moderate plant community response to a natural disturbance and emphasizes the importance of landscape context when assessing plant community response to natural disturbance in fragmented landscapes (Laurance and Cochrane 2002, Chazdon 2003, Catterall et al. 2008, Smart et al. 2014).

4.1 Effects of storm damage

Across all plots, the density of shrubs and saplings increased dramatically by 2001, as documented by Darwin et al. (2004). By 2017, 19 years after the storm, average stem density of shrubs and saplings had declined nearly to original levels. This peak and subsequent decline in the density of shrubs and saplings is a common finding in studies of forests after natural disturbances, although the timing of the peak varies between regions (White et al. 1985, Tremblay et al. 2005, Zhao et al. 2006, Heartsill Scalley et al. 2010, Kosugi et al. 2016).

Short-term increases in total stem density were greater with greater storm damage (Table 2). Greater canopy damage likely resulted in increased resource availability to understory seedlings and small shrubs and saplings, facilitating their growth (e.g. Peterson and Pickett 1995). However, the difference in stem density between 2017 and 1998 was *negatively* correlated with ice storm damage, all else being equal. It is possible that intense sprouting of damaged canopy trees in heavily damaged sites (Brommit et al. 2004) actually resulted in faster canopy closure in those sites and therefore less opportunity for sustained stem recruitment over the long-run.

Unlike stem density, average species richness did not return to pre-storm levels by 2017. Two things may have contributed to this pattern. First, it may take longer than the 19 years in our study for species richness to return to pre-storm conditions (eg. Metzger et al. 2009, Kosugi et al. 2016, Liu et al. 2017). For example, in a 60-year study of two forests in Japan following a typhoon, Kosugi et al. (2016) found that species richness peaked 37 years after the storm, before declining gradually. Alternatively, the ice storm may have allowed colonization by new species that are able to establish permanently. In contrast to our prediction, species that increased significantly in abundance or frequency included both shade-tolerant and intolerant species. Sheil (2001) found that over a 54-year observation of five plots that experienced canopy loss, an increase in the number of shade-tolerant species resulted in an increase in species richness that was sustained over time. Canopy damage can allow shade-intolerant species to grow and/or colonize, but it can also provide more light for shade-tolerant, sub-canopy species which allows them to grow into the shrub/sapling size class, and hence be measured (e.g. Batista and Platt 2003, Zhao et al. 2006).

Greater canopy damage was correlated with a larger short-term increase in species richness. Many studies have found that natural disturbances increase forest diversity (e.g. Heartsill Scalley et al. 2010, Fischer et al. 2013, Kosugi et al. 2016). By 2017, canopy damage was no longer a significant predictor of the change in species richness since the storm, once other predictors were accounted for. Some of the species that were able to grow/colonize following the storm have likely not been able to survive as the canopy has closed.

The species composition of forests across our study area as a whole was not changed by the ice storm: there was no evidence of biotic homogenization and no shift in composition across all 69 forest plots. However, compositional change at the plot level has been considerable. Although some plots are returning towards the composition of pre-storm communities, most plots are not (Fig 3). Heartsill Scalley et al. (2010) similarly found that differences in community composition initiated by a hurricane in a Puerto Rican forest were still evident 15 years later. However, Plotkin et al. (2013) found that community composition had returned nearly to the starting point by 5-10 years after a simulated hurricane. The forest communities in our study area are dynamic at the local scale, yet in aggregate they are steady, aligning with the 'shifting mosaic steady state' theory of Bormann and Likens (1979), except applied to species composition rather than biomass. Historical ecologists have cautioned that local-scale trajectories cannot be extrapolated from regional patterns (e.g. Swetnam et al. 1999). The reverse is also true: local-scale change in species composition in response to a large disturbance cannot be extrapolated to infer change in species composition at a regional scale.

At the plot level, short-term shifts in community composition were greater with greater canopy damage. Zhao et al. (2006) found the same effect in hurricane damaged forests in South Carolina. Interestingly, we found long-term shifts in composition tended to be smaller with greater canopy loss. We speculate that heavily damaged plots may have been shifted back to an earlier seral stage by the ice storm, and after 19 years have returned towards their starting composition, whereas less damaged plots have proceeded along ‘natural’ successional pathways away from their starting composition.

4.2 Effects of landscape context

Landscape context affected post-storm changes in stem density. Plots surrounded by more forest gained fewer stems in the short- and long-term, independent of the degree of storm damage. Forest stands in small forest fragments surrounded by open, agricultural land likely have a greater number of shade-intolerant, edge- or open-habitat adapted species as seedlings and/or in the seedbank – due to a greater abundance of such species in low-forest landscapes – which quickly take advantage of canopy gaps leading to a greater increase in stem density (Kupfer et al. 1997, Catterall et al. 2008, Laurance and Curran 2008, Smart et al. 2014).

As with stem density, short-term gain in species richness was greater in plots with smaller amounts of forest in the surrounding landscape. This pattern is consistent with the prediction that a greater number of edge- or open-habitat adapted species are found in the understory and/or the seedbank of forest plots with more open land in the surrounding landscape, in addition to shade-tolerant forest species, leading to a greater diversity of species able to colonize (Kupfer et al. 1997). While we lack data on seedling and seedbank composition, the abundance-weighted mean shade tolerance of species in the shrub/sapling layer in 1998 was significantly positively associated with forest amount within 1000m, supporting our prediction of a greater availability of propagules of matrix-associated shade-intolerant species in low-forest landscapes (see Supporting Information, Table A8).

Landscape context affected both short- and long-term compositional change. Plots in landscapes with less forest became less similar to their starting composition over time compared to plots embedded in more extensively forested landscapes. This is consistent with our prediction that plots in landscapes with less forest were more susceptible to colonization by new shade-intolerant, disturbance-tolerant species associated with the open habitats of the non-forest matrix, which is an ongoing process (e.g. McCune and Vellend 2015). While the distance to the forest edge was also a predictor in models of both short- and long-term shifts in species composition, it was not significant once accounting for other predictors in the minimum models, but was important as a moderator of the effects of storm damage (see below).

The long-term change in composition was also affected by starting composition, with plots in drier forests dominated by sugar maple showing smaller shifts in composition (Fig. 7D). This matches the results of Whitney and Johnson (1984) who found that xeric sites showed the least compositional change after an ice storm in Virginia. They suggested this was because xeric sites have similar species in both the canopy and understory. Indeed, in our dataset the compositional similarity between the tree layer and the shrub-sapling layer within the same plot was greater for drier plots (See Supporting Information, Figure A4).

4.3 Interactions between storm damage and landscape context

The models for four out of six response variables included interactions between the amount of canopy loss from the ice storm and one or both measures of landscape context. In particular, these interactions had a strong influence on short-term shifts in community composition, even after other important predictors had been accounted for.

The positive correlation between canopy damage and short-term shifts in composition was steeper in plots with low amounts of surrounding forest. This result is consistent with the idea that forest stands in small forest fragments surrounded by a lot of open, agricultural lands experience greater propagule pressure from disturbance-tolerant, open-habitat species (Kupfer et al. 1997, Chazdon 2003, Catterall et al. 2008, Smart et al. 2014, McCune and Vellend 2015). When a disturbance damages the canopy, these stands see even greater shifts in composition due to a greater likelihood of these open-habitat species colonizing and/or maturing from seedlings into the shrub/sapling layers. In contrast to our hypothesis, the positive relationship between storm damage and compositional shifts was actually steeper in plots most distant from the forest edge, rather than closer to it. We found this surprising at first, as we expected plots closer to edges would tend to be colonized by more shade-intolerant, edge-loving species. However, because plots close to the forest edge already had a significant component of shade-intolerant, edge-loving species, an increase in such species due to storm damage would not cause as great a shift in composition as for plots far from the forest edge, where such species were not already present, or were present only as suppressed seedlings.

Models of long-term changes in stem density, species richness, and community composition all included interactions between the amount of storm damage and distance to the forest-matrix edge. Among plots with the greatest amounts of storm damage, those far from the forest edge had the lowest long-term gains in stems and species, and the smallest shifts in species composition compared to 1998 levels. It seems that the long-term establishment of matrix-associated species whose colonization was facilitated by natural disturbance is less likely to occur in stands farther away from the matrix.

4.4 Conclusion

The variation explained by the models ranged from 16% to 30%. We acknowledge that, in addition to the predictors in our models, other unmeasured factors such as anthropogenic disturbances (e.g. selective logging) or natural disturbances (e.g. grazing, disease) likely affected the responses. Nevertheless, our study illustrates that human disturbance in the form of forest fragmentation via deforestation can influence how forest stands respond to natural disturbances. The impacts of the reduced forest area and increased proximity to non-forested matrix on remaining forest communities are not just direct, but also indirect. Stands located in landscapes with little forest, but relatively far from the forest edge experienced the greatest changes in community composition with storm damage. However, over the long term, heavily damaged stands far from the forest edge were more likely to return towards pre-storm conditions. If climate change continues along its projected trajectory, severe winter ice storms are predicted to become more frequent in eastern Ontario and the northeastern United States (Klima and Morgan 2015). This may lead to a permanent shift in composition throughout forest fragments, even in sites far from forest edges.

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Authors' contributions

L.F. and T.A.C. designed the original sampling methodology; T.A.C. collected data prior to 2000; J.L.M. conceived the study; J.I.L. and J.L.M. collected the data from 2017, analyzed the dataset, and led the writing of the manuscript; all authors contributed critically to the drafts and gave final approval for publication.

Data accessibility

We intend to archive our data on the Dryad Digital Repository.

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Tables

Table 1: candidate predictor variables used to model each response variable

response	**candidate predictors**	**predictor type**
change in stem density *(short-term = stem density 2001 –density 1998; long-term = density 2017-density 1998)*	ice storm damage (pdi)	disturbance
	total forest area within 1000m	landscape context
	distance to nearest forest edge	landscape context
	pdi x forest area	disturbance x landscape context
	pdi x distance to edge	disturbance x landscape context
	stem density 1998	covariate
	wetness index	covariate
change in species richness (SR) *(short-term = SR 2001 –SR 1998; long-term = SR 2017 –SR 1998)*	ice storm damage (pdi)	disturbance
	total forest area within 1000m	landscape context
	distance to nearest forest edge	landscape context
	pdi x forest area	disturbance x landscape context
	pdi x distance to edge	disturbance x landscape context
	species richness 1998	covariate
	wetness index	covariate
change in community composition *(short-term = Bray-Curtis dissimilarity, 2001 vs. 1998; long-term = Bray-Curtis dissimilarity, 2017 vs. 1998)*	ice storm damage (pdi)	disturbance
	total forest area within 1000m	landscape context
	distance to nearest forest edge	landscape context
	pdi x forest area	disturbance x landscape context
	pdi x distance to edge	disturbance x landscape context
	starting composition	covariate
	average DBH 1998	covariate
	species richness 1998	covariate

Table 2: Model parameters for predictors included in the minimum adequate model obtained for each response v

drop1 tests. Estimates are standardized partial regression coefficients.

Response	**Predictor**	**Estimate**	**SE**	**p (dr**
short-term change in stem density	*pdi*	*30.96*	*12.67*	*0.017*
	forest amount	*-31.78*	*13.12*	*0.018*
	wetness index	19.01	12.11	0.121
long-term change in stem density	*pdi*	*-34.12*	*15.04*	*0.027*
	forest amount	-25.65	14.92	0.091
	distance to edge	-8.01	13.91	0.566
	stem density 1998	*-61.46*	*13.95*	*<0.00*
	pdi x distance to edge	*-51.10*	*34.74*	0.146
short-term change in species richness	*pdi*	*2.21*	*0.62*	*<0.00*
	forest amount	*-1.33*	*0.62*	*0.034*
long-term change in species richness	pdi	-0.50	0.73	0.498
	forest amount	-1.07	0.75	0.161
	distance to edge	0.01	0.72	0.990
	species richness 1998	*-2.18*	*0.67*	*0.002*
	pdi x distance to edge	-2.87	1.72	0.101
short-term change in community composition	*pdi*	*0.22*	*0.11*	*0.050*
	forest amount	-0.21	0.11	0.068
	distance to edge	0.07	0.10	0.459
	average DBH 1998	0.16	0.09	0.089
	species richness 1998	*0.24*	*0.10*	*0.016*
	pdi x forest amount	*-0.30*	*0.10*	*0.005*
	pdi x distance to edge	*0.28*	*0.12*	*0.019*
long-term change in community composition	pdi	-0.20	0.10	0.052
	forest amount	*-0.22*	*0.11*	*0.048*
	distance to edge	-0.00	0.10	0.973
	starting composition	0.19	0.10	0.054
	pdi x distance to edge	-0.17	0.12	0.141

* predictors that explain a significant amount of variation in the response once all other predictors in the models ($p<0.05$ in drop1 tests) are italicized

† adjusted R^2 for linear models, pseudo-R^2 for models of change in community composition

Figures

Figure 1. (A) Map outlining the boundaries of the study region. Forests within greater city limits in 2015 (green shading), agricultural land use (yellow), urban development (grey), and black squares showing the locations of the 17 landscapes. (B) One 1km^2 landscape showing study plots (black circles). Dotted lines illustrate the distance to the nearest forest edge for two plots, with one (i) having a smaller distance than the other (ii). (C) The location of the study area (red shading) within the province of Ontario (white), and in relation to the surrounding areas in Canada (hatched) and the United States (grey).

Figure 2**.** Comparison of average (A) density and (B) species richness of the shrub/sapling layer in each year. Error bars are ± 2 SE. Letters above the error bars indicate significant differences between years.

Figure 3. The trajectory over time of the Bray-Curtis dissimilarity of each plot compared to its starting composition in 1998. Dissimilarity values closer to zero indicate greater similarity in composition. Plots are grouped according to the 1km^2 landscape in which they are located. Landscapes are ordered from top left to bottom right based on increasing average area of forest within 1000m of each plot in 1999. damage = a factorial representation of plot damage index (pdi) where dotted lines indicate plots with pdi lower than the median and solid lines indicate plots with pdi higher than the median.

Figure 4. Partial residual plots based on the minimum adequate model for the change in species richness from 1998 to 2001 (see Table 2). Note that for each panel, all other variables in the model are held at the median. ** indicates p<0.05 in drop1 test, * indicates 0.1>p>0.05 in drop1 test.

Figure 5. Partial residual plots based on the minimum adequate model for the change in species richness from 1998 to 2017 (see Table 2). Note that for each panel, all other variables in the model are held at the median. Panel E illustrates the interaction between plot damage index and distance to forest edge – the continuous variable distance to forest edge has been divided into 3 categories by taking cross-sections at the 10th, 50th, and 90th percentiles. Confidence bands are omitted for clarity. ** indicates p<0.05 in drop1 test, * indicates 0.1>p>0.05 in drop1 test.

Figure 6. Partial residual plots based on the minimum adequate model for the change in community composition from 1998 to 2001 (see Table 2). Note that for each panel, all other variables in the model are held at the median. Panels F and G illustrate the interactions between plot damage index and forest amount, and plot damage index and distance to nearest forest edge, respectively – the continuous variables distance to forest edge and forest amount have been divided into 3 categories by taking cross-sections at the 10th, 50th, and 90th percentiles. Confidence bands are omitted for clarity. ** indicates p<0.05 in drop1 test, * indicates 0.1>p>0.05 in drop1 test.

Figure 7. Partial residual plots based on the minimum adequate model for the change in community composition from 1998 to 2017 (see Table 2). Note that for each panel, all other variables in the model are held at the median. Panel E illustrates the interaction between plot damage index and distance to the nearest edge – the continuous variable distance to forest edge has been divided into 3 categories by taking cross-sections at the 10th, 50th, and 90th percentiles. Confidence bands are omitted for clarity. ** indicates $p<0.05$ in drop1 test, * indicates $0.1>p>0.05$ in drop1 test.

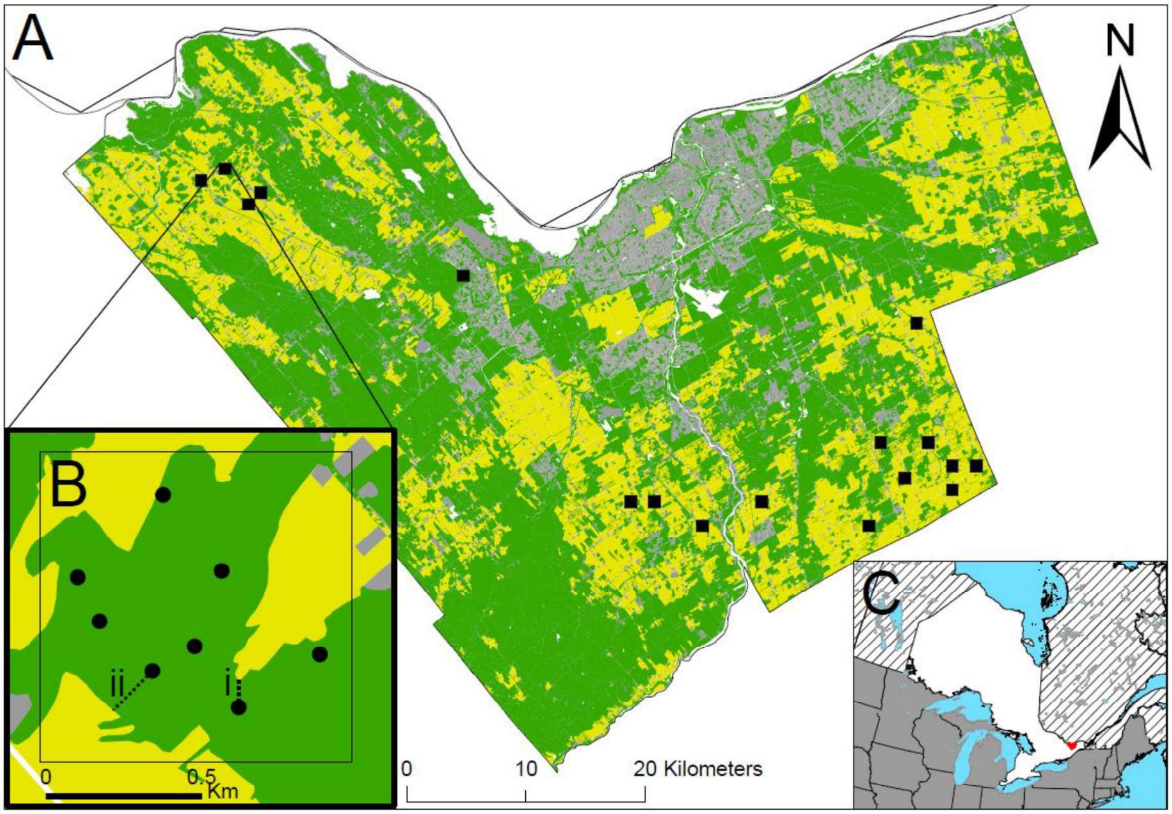
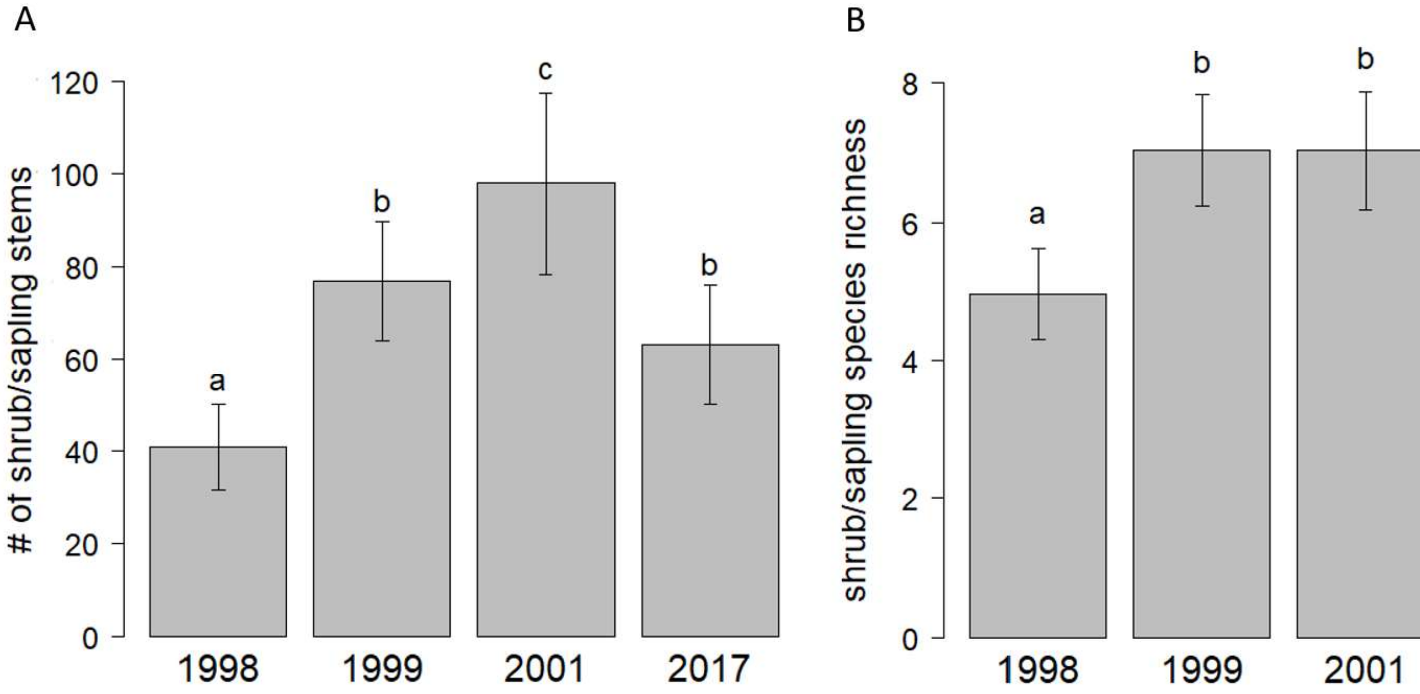


Figure 1.


A
# of shrub/sapling stems
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60
80
100
120
a
b
c
b
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1999
2001
2017
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shrub/sapling species richness
0
2
4
6
8
a
b
b
1998
1999
2001

Figure 2.

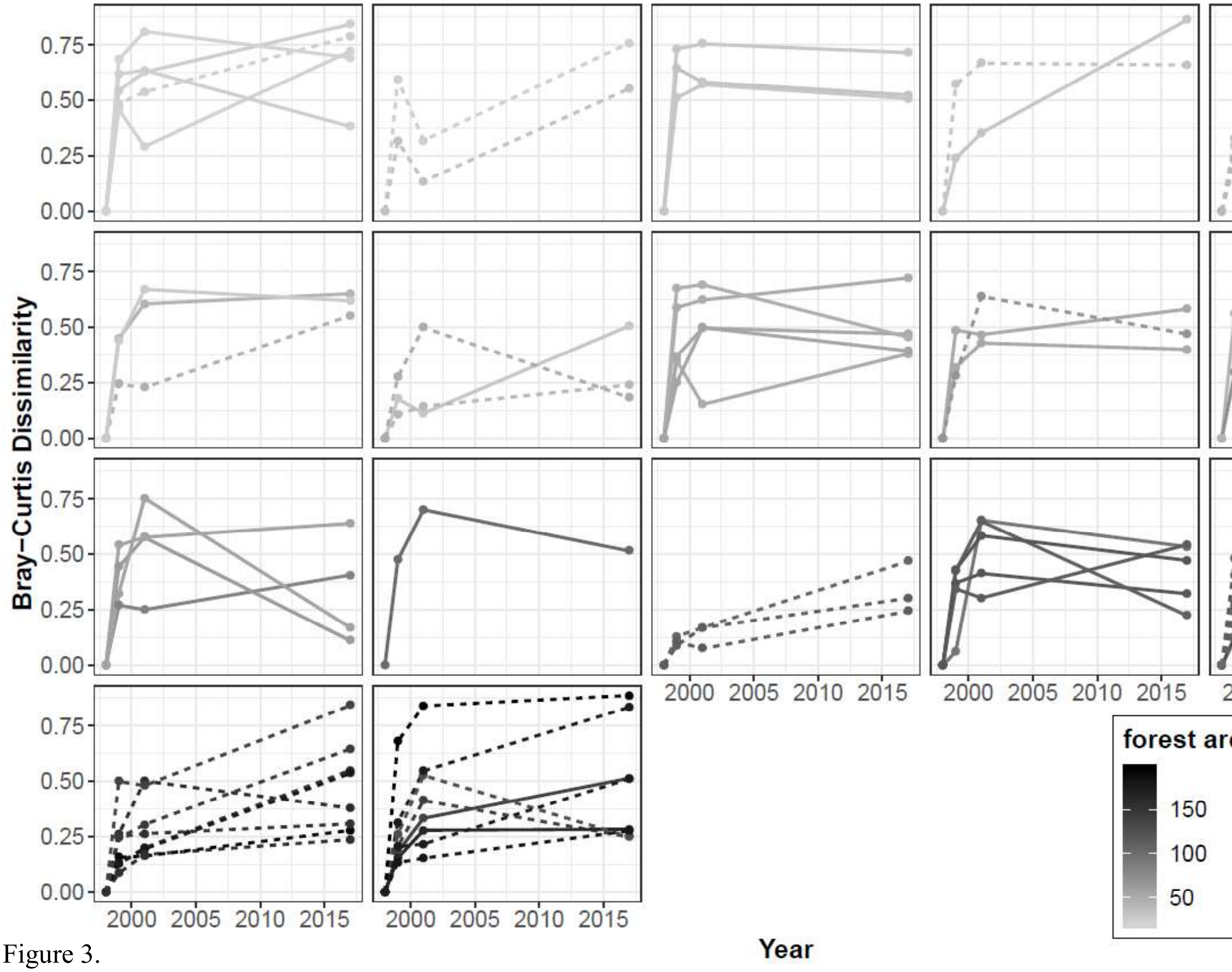
Bray–Curtis Dissimilarity
0.00
0.25
0.50
0.75
2000
2005
2010
2015
Year
forest are
150
100
50

Figure 3.

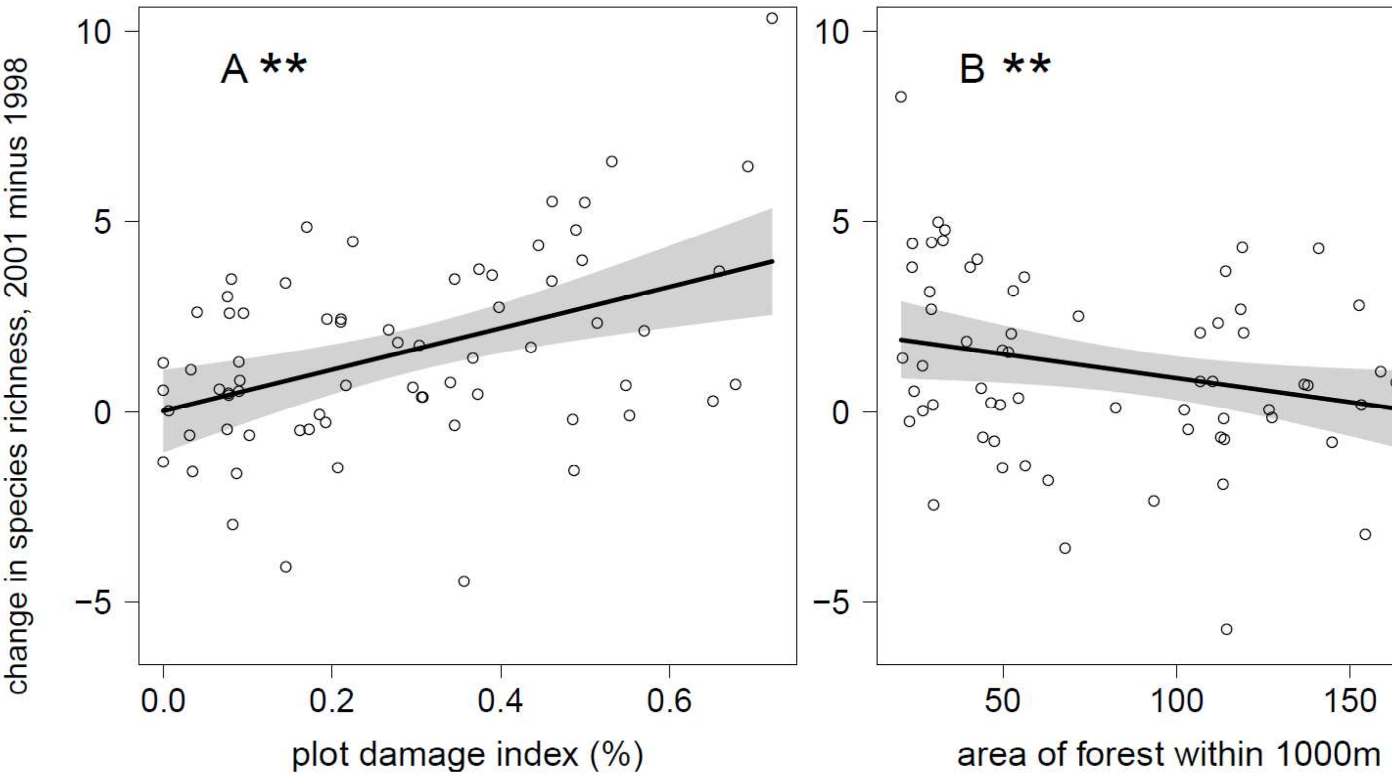
A **
B **
change in species richness, 2001 minus 1998
10
5
0
−5
0.0
0.2
0.4
0.6
plot damage index (%)
50
100
150
area of forest within 1000m

Figure 4

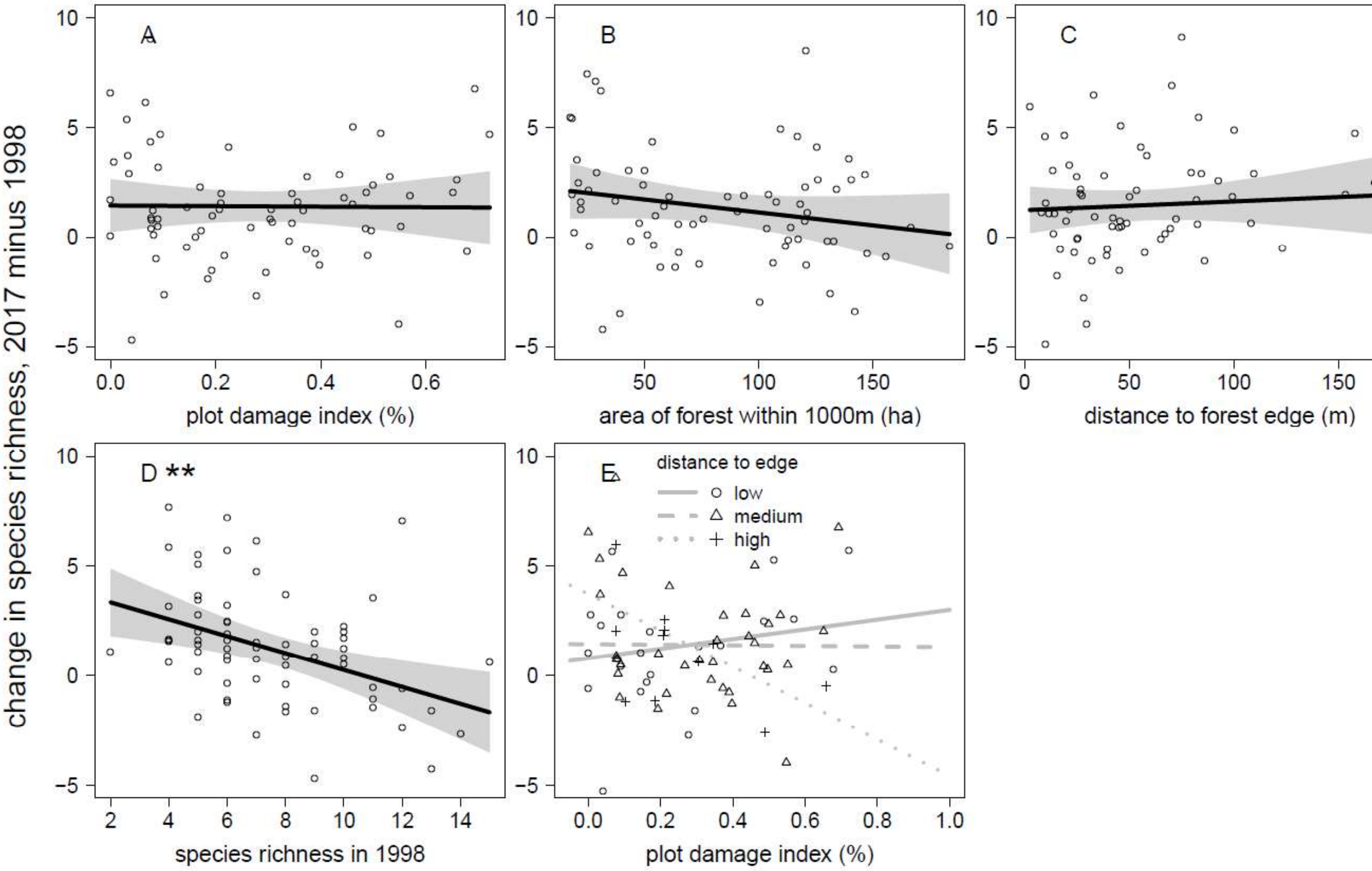
change in species richness, 2017 minus 1998
A
plot damage index (%)
B
area of forest within 1000m (ha)
C
distance to forest edge (m)
D **
species richness in 1998
E
distance to edge
low
medium
high
plot damage index (%)
10
5
0
-5
0.0
0.2
0.4
0.6
50
100
150
0
50
100
150
2
4
6
8
10
12
14
0.0
0.2
0.4
0.6
0.8
1.0

Figure 5

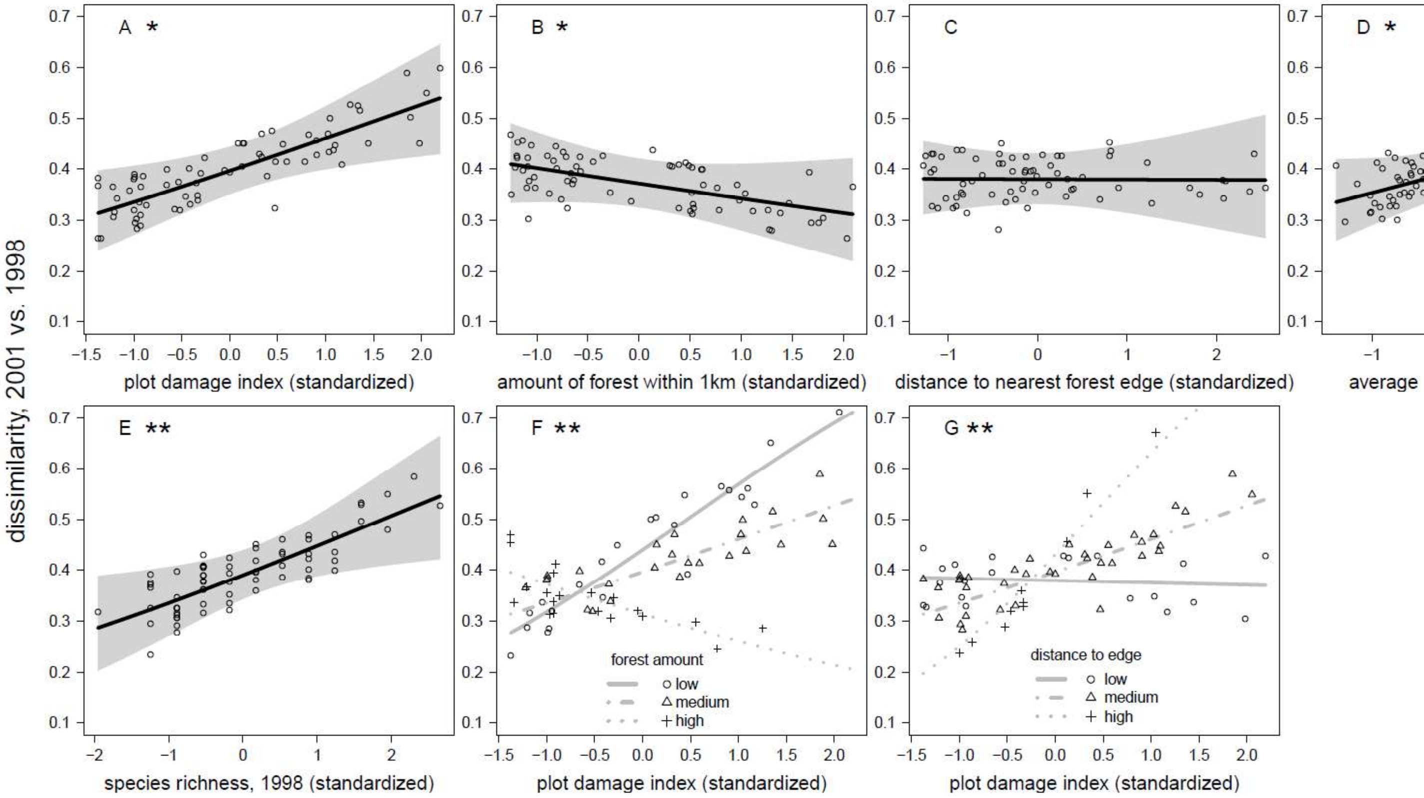
A *
B *
C
D *
E **
F **
G **
dissimilarity, 2001 vs. 1998
plot damage index (standardized)
amount of forest within 1km (standardized)
distance to nearest forest edge (standardized)
average
species richness, 1998 (standardized)
plot damage index (standardized)
plot damage index (standardized)
forest amount
low
medium
high
distance to edge
low
medium
high
0.1
0.2
0.3
0.4
0.5
0.6
0.7
−1.5
−1.0
−0.5
0.0
0.5
1.0
1.5
2.0
−2
−1
0
1
2

Figure 6.

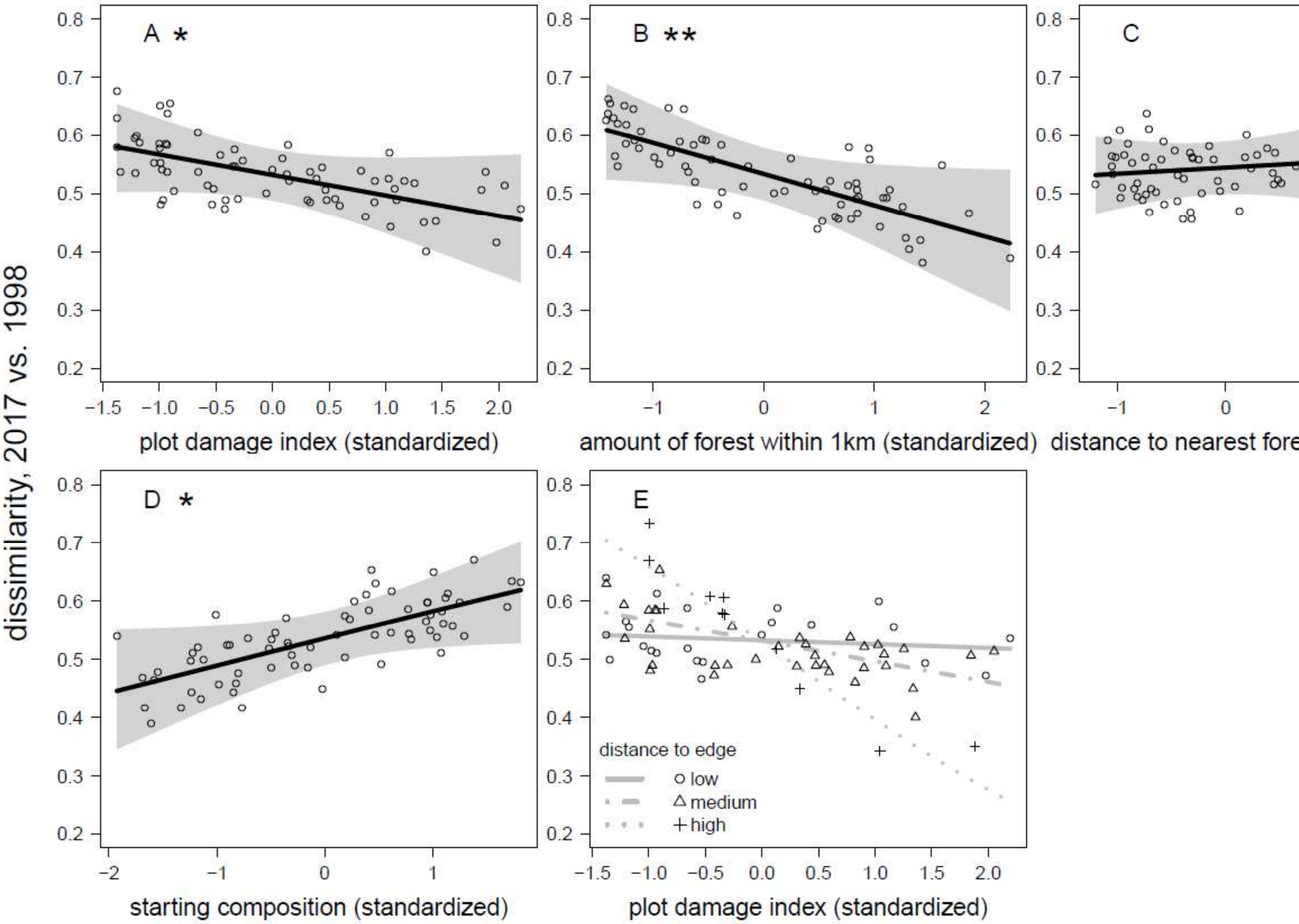
dissimilarity, 2017 vs. 1998
A *
B **
C
D *
E
0.8
0.7
0.6
0.5
0.4
0.3
0.2
−1.5 −1.0 −0.5 0.0 0.5 1.0 1.5 2.0
plot damage index (standardized)
−1 0 1 2
amount of forest within 1km (standardized)
−1 0
distance to nearest fore
−2 −1 0 1
starting composition (standardized)
distance to edge
low
medium
high
−1.5 −1.0 −0.5 0.0 0.5 1.0 1.5 2.0
plot damage index (standardized)

Figure 7