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Citation

Published Version
doi:10.1111/1365-2745.12291

Permanent link
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Accessibility
Quantifying the impact of an extreme climate event on species diversity in fragmented temperate forests: the effect of the October 1987 storm on British broadleaved woodlands

Smart, SM\textsuperscript{1*}, Ellison, AM\textsuperscript{2}, Bunce, RGH\textsuperscript{3}, Marrs, RH\textsuperscript{4}, Kirby, KJ\textsuperscript{5}, Kimberley, A\textsuperscript{1}, Scott, WA\textsuperscript{1} and Foster, DR\textsuperscript{2}

1 NERC Centre for Ecology & Hydrology, Library Avenue, Bailrigg, Lancaster LA1 4AP UK
2 Harvard Forest, Harvard University, 324 North Main St, Petersham, MA 01366, USA
3 Estonian University of Life Sciences, Freidrich Reinhold Kreutzwaldi 1, 51014 Tartu, Estonia
4 Ecology and Ocean Sciences, Nicholson Building, University of Liverpool, L69 3GP UK
5 Department of Plant Sciences, South Parks Road, Oxford, OX1 3RB, UK

*Correspondence author. E-mail: ssma@ceh.ac.uk

SUMMARY

1. We report the impact of an extreme weather event, the October 1987 severe storm, on fragmented woodlands in southern Britain. We analysed ecological changes between 1971 and 2002 in 143 200-m\textsuperscript{2} plots in 10 woodland sites exposed to the storm with an ecologically equivalent sample of 150 plots in 16 non-exposed sites. In both years, understory species-richness, species composition, soil pH and woody basal area of the tree and shrub canopy were measured.

2. We tested the hypothesis that the storm had deflected sites from the wider national trajectory of an increase in woody basal area and reduced understory species-richness associated with ageing canopies and declining woodland management. We also expected storm disturbance to amplify the background trend of increasing soil pH, a UK-wide response to reduced atmospheric sulphur deposition. Path analysis was used to quantify indirect effects of storm exposure on understory species richness via changes in woody basal area and soil pH.

3. By 2002, storm exposure was estimated to have increased mean species richness per 200 m\textsuperscript{2} by 32%. Woody basal area changes were highly variable and did not significantly differ with storm exposure.
4. Increasing soil pH was associated with a 7% increase in richness. There was no evidence that soil pH increased more as a function of storm exposure. Changes in species richness and basal area were negatively correlated: a 3.4% decrease in richness occurred for every 0.1-m² increase in woody basal area per plot.

5. Despite all sites substantially exceeding the empirical critical load for nitrogen deposition, there was no evidence that in the 15 years since the storm, disturbance had triggered a eutrophication effect associated with dominance of gaps by nitrophilous species.

6. Synthesis: Although the impacts of the 1987 storm were spatially variable in terms of impacts on woody basal area, the storm had a positive effect on understorey species richness. There was no evidence that disturbance had increased dominance of gaps by invasive species. This could change if recovery from acidification results in a soil pH regime associated with greater macronutrient availability.

Key-words: Bayesian Structural Equation Modelling, biodiversity, extreme weather, global change, land-use, mixed models, path analysis, plant traits, resilience
INTRODUCTION

Ecosystems embedded in densely populated landscapes are increasingly exposed to novel combinations of stressors, including pollutant deposition, land-use and climatic change (Foster et al. 1997; Verheyen et al. 2012). Predicting the impacts of these changes on biodiversity and ecosystem function requires quantification of the responses of ecosystems to these anthropogenic press disturbance regimes and how they interact with pulse disturbances such as extreme weather impacts, to generate potentially novel outcomes (Smith et al. 2009).

Important insights can come from analysis of natural perturbations that have operated in combination with other factors (e.g., Bruehlheide & Luginbühl 2009; Romme et al. 2011). This depends on the serendipitous availability of data before and after the event in control and impacted areas and where like-with-like contrasts can be constructed (Flinn & Vellend 2005). In Britain, an ideal example is provided by the October 1987 storm. Its impact on broadleaved woodland ecosystems was partially captured by a detailed national ecological survey of 16 200-m² plots in each of 103 woodlands carried out in 1971 and repeated in 2002 (Kirby et al. 2005a; Corney et al. 2006). Ten of the 103 woodlands were exposed to the October 1987 storm (Fig. 1). The availability of a regional series of sites not exposed to the storm allowed the selection of reference woodlands for comparison. We focus on the response of the understorey because in temperate forests this is where most of the plant diversity is concentrated (Flinn & Vellend 2005). The biodiversity of the understorey in ancient woodlands also is of high conservation value and is often different from secondary woodlands of more recent origins (Peterken & Game 1984; Motzkin et al. 1999; Kimberley et al. 2014).

The 1987 storm event was typified by wind speeds thought only to be likely every 200 years and locally gusting to 160 kph (Burt & Mansfield 1988). An estimated 15 million trees
were blown down across southeast England. Damage was locally severe; however wind speeds and the extent of damage to trees were variable within the storm-track, resulting from context dependent interactions between topography, tree species, form, age, substrate and variation in wind strength (Whitbread 1991; Hopkins 1994; Harmer 2012). The variation in impact and the difficulty in explaining its source within the storm-track was summarized by Peterken (1996) “.. storm damage generally appeared to be random and patchy at all scales. Some districts were devastated, whilst others within the storm-track were virtually untouched. Some very exposed stands escaped with little more than superficial branch-break. It was rarely possible to find a reason why one tree within a wood fell while its neighbors survived.”

Previous analysis of all 103 woodland sites showed a widespread suppressive effect of increased shading on understorey plant species density as woodland canopies aged following intensive timber removal across many British forests during and just after the end of World War II (Kirby et al. 2005a). This pattern was associated with a mean loss of eight species per plot across the national sample (Kirby et al. 2005a).

Analysis also showed a national increase in woodland soil pH (from a mean of 4.98 to 5.31 between the 1971 and 2002 surveys (Kirby et al. 2005a) consistent with recovery of soils following reductions in atmospheric sulphur deposition since the early 1970s (Kirby et al. 2005a; Kirk et al. 2006). Soil pH increased less where woody basal area had increased the most, a pattern consistent with the build up of soil organic matter with shading and succession and a proportionally greater input from higher C:N tree leaf litter and woody debris.

These large-scale changes in soils, land-use, and atmospheric deposition in British woodlands define the ecological context against which we test our primary hypothesis: that the October 1987 storm changed sites in the storm-track away from the national trajectories of
canopy growth and reduction in understorey species-richness. Since we were interested in how
storm exposure impacted species richness and species and trait composition via changes in soil
and canopy, a path analysis was constructed and tested (Fig. 2).

We also tested whether the interaction between storm disturbance, the chronic effects of
long term increases in nitrogen deposition and the reduction in acidifying sulphur deposition
since the early 1970s in Britain and other parts of Europe (RoTAP 2012) had driven changes in
understorey species composition and whether this had tended to homogenize the flora between
storm-impacted sites. For example, had gap creation within the storm track triggered a
eutrophication effect leading to dominance by rapidly growing generalist species with high
specific leaf areas (SLA), including non-natives (Gilliam 2006; Verheyen et al. 2012). This
follows from the novelty of patch conditions and forest context following the 1987 storm relative
to the landscape of pre-industrial Britain. Small forests surrounded by intensive land-use make it
more likely that gaps will be colonised by edge species favoured by exposure to macronutrient
surpluses and more suited to modern land-use in addition to residual vegetation typical of older
forest (Smart et al. 2005; Smart et al. 2006a,b; Kimberley et al. 2013). Nitrogen limitation in the
understorey is also likely to have been alleviated by atmospheric deposition, although its impact
on the vegetation will depend upon the pH of the substrate and phosphorus availability (Stevens
et al. 2011; Verstraeten et al. 2013). Enrichment impacts on the understorey were analysed by
quantifying and interpreting differences in the species composition of the understorey in 1971
versus 2002 between storm exposed plots and those outside the storm-track and by quantifying
changes in cover-weighted SLA given the positive association between this trait and more
productive soils (Kimberley et al. 2014; Laughlin 2011).
Our hypotheses find support from within three conceptual frameworks. Together they describe the outcomes of natural disturbance factors interacting with global change drivers to impact understorey species composition in fragmented forests embedded in the often intensively farmed landscapes of the temperate zone. The model of Roberts (2004) considers the response of the woodland understorey as a function of the severity of disturbance to soil, canopy and herbaceous vegetation. The partitioning of effects among these three ecosystem compartments aligns well with the driving variables and their postulated linkage via regression equations in our path model (Fig 2). The storm event is the key exogenous disturbance whose impacts we hypothesise to be propagated through to change in understorey species richness and composition. The principal effect of the storm is expected to be via canopy damage leading to a reduction in woody basal area (Fig 2, β3 and β4) but direct residual effects are also possible where for example canopy removal or damage to individuals is not detectable via basal area change (Fig 2, β2). Soil disturbance and its effect on the understorey is considered in terms of the relationships between changing soil pH between surveys and change in species richness or cover-weighted Specific Leaf Area (Fig 2, β6). Soil pH change is then modelled as a function of background variation in pH (Fig 2, β7), the impact of storm disturbance (Fig 2, β9) and change in woody basal area (Fig 2, β3 and β5).

The Roberts (2004) model provides a foundation for understanding the impact of natural disturbance agents within human-dominated landscapes but does not explicitly consider global change drivers. Their impacts on the woodland ecosystem are considered in terms of the Hierarchical Response Framework (HRF) of Smith et al. (2009). The critical insight here is that ecosystems experience pulsed changes in resources within natural limits to which the biota is adapted and where local ecosystem feedbacks can exert control over these changes in resource
availability. Anthropogenic activity introduces press rather than pulse regimes involving directional, chronic changes in resource availability from land-use, population growth and atmospheric pollutants (Smith et al. 2009). Local ecosystem feedbacks cannot moderate these changes in resource availability because the origins of these resource inputs are geographically distant from the impacted ecosystem. The consequence is biotic change which maybe rapid and stepwise when triggered by interaction with a pulse of disturbance. In forest ecosystems for example, storm events remove the canopy temporarily reducing the influence of the dominant plant species on ecosystem processes. In our sample of woodlands, understorey development in post-storm gaps could reflect an interaction with high cumulative N deposition and recently reduced deposition of acidifying pollutants. We speculate that a small number of generalist winners more typical of the surrounding farmed landscape could have increased in abundance at the expense of forest specialist ‘losers’ and that non-random filtering has occurred preferentially on storm-exposed sites as a result of the alleviation of light and nutrient limitation. This conjecture includes aspects of the biodiversity and biogeochemistry hypotheses in Smith et al. (2009). If the same pattern is seen across sites then this would also be consistent with the notion of biotic homogenisation (McKinney & Lockwood, 1999; Baeten et al. 2012).

Lastly, we test hypotheses that concern the influence of the background species pool and within-site beta diversity on change in local species richness. Sites with greater beta diversity and a larger species pool might be expected to provide a greater pool of potential colonists for exploiting the mosaic of abiotic conditions resulting from storm disturbance thus leading to higher richness in individual plots post-storm. In non-storm sites, higher beta diversity in 1971 could result in a larger reduction in mean richness per plot if shading and lack of management filters the understorey favouring a smaller number of residual shade tolerators. Thus the
relationship between beta diversity and changing species richness in plots is likely to be dependent on storm disturbance and the extent to which within-site heterogeneity correlates with species pool size. For example, in European forests changes in beta diversity tend to have been driven more by reduction in species pool size rather than turnover of existing forest species or the spread of immigrants into more locations within each site (Baeten et al. 2012; 2014). We therefore included within–site beta diversity in 1971 in our path model (Fig. 2, β8) and also tested whether change in beta diversity had occurred between surveys, whether directions of change differed depending on storm exposure and whether the influence of beta diversity was largely due to differences in site species pool size.

MATERIALS AND METHODS

Study region

We analysed data from 26 woodlands all located in southern England between 48m and 198m above sea level (Fig. 1). Regional climate is temperate maritime (Peel et al. 2007) with annual precipitation of 600 - 800 mm, a mean January temperature of 3 - 4.5 °C and mean monthly July temperature of 16.5 - 17.5 °C (Goudie & Burden 1994). The region is densely populated (401 persons per km² in England in 2012 - [www.ons.gov.uk]) and has seen widespread intensification of agriculture since the end of World War II, including drainage and improvement of land, mechanization of agriculture, and increases in agricultural productivity (North 2000; Chamberlain et al. 2000). However, the study area also has the highest proportional cover of broadleaved woodland in the British Isles (Morton et al. 2011). Woodland sites within the storm track were selected as those coinciding with wind speeds above 144 kph in the peak gust wind
footprint defined by the RMS Europe Windstorm Model for the October 1987 storm (Risk Management Solutions 2007).

The floristic affinities of the sample reflected the soils of southeastern England: base poor brown earths and podzols (Rodwell 1991). Forty percent of plots were referable to the W10 *Quercus robur* – *Pteridium aquilinum* – *Rubus fruticosus* woodland and 20% to the W16 *Quercus* spp – *Betula* spp – *Deschampsia flexuosa* woodland. The major woodland community type of calcareous to neutral soils in south east England, the W8 *Fraxinus excelsior* – *Acer campestre* – *Mercurialis perennis* woodland, was represented by 11% of plots (see Fig. S1 in Supporting Information). Canopy dominants comprised *Quercus robur* (in 77% of plots), *Corylus avellana* (62%), *Fraxinus excelsior* (61%), *Betula pubescens* & *pendula* (48%), *Acer pseudoplatanus* (39%) and *Fagus sylvatica* (38%). Nomenclature for plants follows Stace (1997).

**Survey design and data collection**

Full details of the sampling design and sampling methods were published by Kirby *et al.* (2005a,b) and Corney *et al.* (2006). In summary, the Great Britain (GB) Woodland Survey was based on sites representing woodland types as determined from an earlier multivariate classification of 2453 British woodlands (Ratcliffe 1977; Bunce 1982). Woodland sites were visited in 1971 and again in 2002. Indicators of woodland management and surrounding land-use were recorded at site level and from 16 random 200-m² square plots located in each woodland. Cover and presence of all vascular and selected non-vascular plants were also recorded in each plot. Individual trees and shrubs were identified and counted and the diameter at 1.3 m above-ground (DBH) was measured for stems > 1 cm diameter. Understorey species richness comprises
the count of vascular plants, common bryophytes and species of trees and shrubs but only where these were present as seedlings or saplings (individuals <1.3m in height and <1cm DBH). Fresh soil pH was measured in deionized water on a homogenized 15cm topsoil sample taken from each plot. A Quality Assurance (QA) survey of a subset of the sites was carried out in 2002 (Kirby et al. 2005b). QA procedures were also applied to the soils analysis including a partial re-analysis of the stored 1971 samples (see Kirby et al. 2005a,b for details). The repeat visit in 2002, as far as possible, recorded all data from the same plot based on 1:10,000 site maps prepared at the time of the first survey. A quantitative analysis of plot relocation error was carried out by comparing mean similarity coefficients between temporal pairs of plots assumed to have been recorded in the same locations in 1971 and 2002 versus similarity coefficients for randomized pairings of plots within the same site. Results are reported in Kirby et al. (2005b) and showed that, on average, attempts to re-find the 1971 plot resulted in greater similarity between temporal pairs than randomized pairs.

Datasets

Data from the 1971 survey of the 10 sites situated inside the October 1987 storm-track were matched with a dataset of plots from 1971 in sites outside the storm-track (Fig. 1). The floristic composition of the storm sites was used to stratify non-storm exposed sites. These plots were then randomly sampled to identify a dataset that was floristically equivalent to the storm-exposed sites and for which plots and sites had equivalent average levels of pre-storm soil pH, understorey species richness, mean woody basal area and mean cover-weighted SLA (Fig. S2). This selection process yielded 150 plots in 16 non-storm exposed sites and 143 plots in the 10 sites inside the storm-track.
All sites were exposed to roughly equivalent levels of other potential driving variables, including changes in atmospheric deposition of sulphur and nitrogen compounds, and intensive land-use surrounding each woodland in 1971 (Fig. S2). All storm-exposed and non-storm sites showed substantial reductions in modeled S deposition between 1970 and 2000 (Fig. S2). Deposition of N at all sites was substantially above the empirical critical load (10-20 kg N ha\(^{-1}\) yr\(^{-1}\): Tipping et al. 2013), whether inside the storm track or not (Fig. S2), but storm-track sites were exposed to lower modeled N deposition in 2000.

Path analysis
The path model specified in Fig. 2 was implemented in OpenBUGS version 3.2.1 (http://www.openbugs.info/w/) (Grace et al. 2012). The separate regression models that made up the path model were initially run within SAS (Little et al. 2000). This was done to derive parameter estimates against which to help check the outputs from the OpenBUGS model. The hierarchical structure of the data was specified by implementing a random-intercepts model in OpenBUGS on all covariates that were measured on plots within sites (Kéry 2010).

To produce standardized regression coefficients and path coefficients, one version of the path model was run with all covariates centred and standardized to zero mean and unit variance – see Supplementary Material. A second path analysis was run to generate regression coefficients and residual variances for variation partitioning (Gajewski et al. 2006; Shipley 2000). In the latter, covariates were neither centred nor standardized. The regression coefficients in the latter model also were used to interpret the estimated effect of a unit change in hypothesized explanatory variables on proportional change in understorey species-richness between 1971 and
2002. Since species-richness change between surveys was transformed to ln[(richness 2002 + 1)/
richness 1971 + 1)], the regression coefficients involving species richness were back-
transformed by exponentiating them in order to derive an estimate of the effect of the
explanatory variable on the proportional change in species richness from 1971 to 2002. For
example if the average richness in 1971 were twice the 2002 value then the raw ratio would be
0.5 and the parameter estimate approximately -0.69. Storm impact was coded as 1 (storm) and 0
(no-storm) in the data.

Two Monte Carlo Markov chains were initialized for each path analysis with varying
starting values. Convergence of all posterior distributions was monitored with trace plots and by
the Gelman-Rubin statistic (Kéry 2010). After a 20,000 iteration burn-in, a subsequent 20,000
iterations were summarized to describe posterior distributions for all parameters of interest.

Testing hypothesised paths

All response variables could be approximated by normal error distributions. Thus, path
coefficients were calculated by sampling from the posterior distributions of the products of
standardized regression coefficients (Grace 2006). The following path coefficients were
specified to test particular hypotheses as follows:

\[ \beta_3 \times \beta_4: \] Exposure to the 1987 storm was associated with increased species-richness or reduced
loss of richness via the effect of reduced woody basal area and hence greater light availability at
ground level (Kirby 1988). Thus the storm was expected to have deflected the wider national
trend for canopies to age and close (Kirby et al. 2005a).
β3* β5*β6: Storm-driven reductions in woody basal area increased species-richness by driving increased soil pH in forest gaps. Mechanisms include reduced input of lower pH, higher C:N leaf litter and woody debris compared to sites not exposed to the storm (van Oijen et al. 2005) and increased input of higher pH litter from early successional trees, shrubs and gap-phase herbs (Sydes & Grime 1981; Nordén 1994; Cooper-Ellis et al. 1999; Borschenius et al. 2004), or increasing pH via soil disturbance (Guo et al. 2004; Strandberg et al. 2005; van Oijen et al. 2005).

β7* β6: Given that lower pH soils have been more susceptible to historical acidification impacts in the UK, these soils should show a greater recovery than higher pH soils (Norton et al. 2012; Kirk et al. 2006). Since changes in species richness are expected to respond positively to increased pH, lower pH soils should have increased most in species richness because of changes in soil pH (Borschenius et al. 2004; De Keersmaeker et al. 2004). However, if increased soil pH covaries with, or results from, eutrophication, then this could drive understorey dominance and reduced richness (Kirby 1998; Erjnaes et al. 2003; Brewer et al. 2012). The mean of the soil pH in 1971 and 2002 was used as the predictor to circumvent any regression to the mean artefact associated with plot relocation error (Kirk et al. 2006).

All direct and indirect effects were also tested taking into account that, on average, woodland sites were surveyed 38 days earlier in 2002 than in 1971 and closer to the height of the growing season (Fig 2, β.1) We therefore expected to detect more species in each plot in 2002 than in 1971.
Variance partitioning

In path analysis, covariates can be response variables as well as explanatory variables. The covariate at the terminal node of the path diagram – in this case change in species richness – was subject to explanation by the largest number of preceding explanatory variables, some of which are conditional on intermediate variables. This results in variation in species-richness change being broken down into the largest number of variance components. Other covariates in the path diagram are explained by progressively fewer effects, whilst exogenous variables such as storm exposure and difference in date of site survey are not subject to explanation by any preceding variables (Fig. 2). Variance explained was also decomposed to the site and plot level since predictors such as storm exposure and within-site beta diversity in 1971, were only measured at the site scale while others were measured within plots and so can potentially explain between plot and between site variation.

Changes in species composition

A binomial test (Zar 1984) was used to calculate the cumulative probability of the observed number of presences of each species in either 1971 or 2002, assuming a 50% chance of occurring in either year. The results convey inequality in the distribution of records between years in the sample plots as a basis for interpreting whether there appears to have been an increased chance of recording species associated with nutrient enrichment in 2002 in the storm-impacted plots versus the non-storm plots.
The impact of enrichment on changes in understorey species composition also was quantified by analysis of differences in cover-weighted SLA between years and within storm versus non-storm sites. Cover-weighted SLA was calculated as follows:

\[ cSLA_j = \frac{\sum (SLA_{ij} \times (cov_{ij}))}{\sum (cov_{ij})} \quad \text{1) } \]

where \((cov_{ij})\) was the square root transformed percentage cover value for species \(i\) in each sample plot \(j\). All calculations of \(cSLA\) used a single published value per species. SLA values were taken from Grime et al. (1995), Kleyer et al. (2008) and Wright et al. (2004). All vascular plant species had SLA values. \(cSLA\) was also analysed in another version of the path analysis model in Fig. 2 and subjected to the same hypothesized drivers of change to determine whether there was any relationship with soil pH change, woody basal area change, site beta diversity and the direct effect of storm exposure.

**Beta diversity change and effects on species richness**

Beta diversity within each site in each year of survey and change between surveys was calculated based on the \(\Sigma Di\) community heterogeneity metric using the \(rDev\) function in R provided by Baeten et al. (2014). This metric sums the binomial deviances associated with variation in species frequency across plots in a site. Deviance is greatest for species occupying 50% of plots and so the metric attains lower values as species increase in commonness or rarity. Because we were only interested in impacts on the understorey, the metric was calculated after excluding records for all canopy trees and shrubs.
Beta diversity values for the understorey across each site in 1971 were entered into the path model as predictors of change in plot-level species richness (Fig 2). The regression was re-run with the $\Sigma Di$ metric standardized by species pool size to remove the effect of differences in site species richness. We simply divided each site value of the metric by the size of the site pool. Comparing the residual variation between a regression model based on standardized versus unstandardized values of $\Sigma Di$ indicated how much of the explanatory power of $\Sigma Di$ was due to differences in site richness rather than between-plot frequency.

**RESULTS**

*Species richness*

Plots inside the storm-track had a lower loss of understorey species richness or increased in richness (Figs. 3, 4a and Table 1, $\beta_2$). Increased woody basal area was associated with decreased species richness (Table 1, $\beta_4$) and increasing soil pH was associated with increased species richness, yet change in woody basal area and soil pH did not differ significantly between storm and non-storm sites (Figs. 3, 4b, 4d and Table 1, $\beta_6$).

Interpretation of the regression coefficients based on path analysis of uncentred and unstandardised data (Table 1) indicated that storm exposure resulted in an estimated mean 32% increase in species-richness by 2002; estimates ranged from 8% to 61% (Table 1, 95% credible interval on $\beta_2$). A 3.4% reduction in species richness was estimated to occur for every 0.1 m$^2$ increase in woody basal area and a 12% increase in species richness was estimated to occur for every one pH unit increase (Table 1). Species richness on average increased by 2% for every 10 days earlier plots were sampled in 2002 relative to 1971.
In total, 39% of the observed between-plot variation and 87% of the between-site variation in species-richness was explained by the path model (Fig. 5 and Table 1). The best predictors at the site level were within-site beta diversity of the ground flora across each site in 1971 (20%) and storm exposure (60%). Collinearity between difference in survey date and 1971 beta diversity was observed; when both predictors were included in the path model the variation explained by difference in survey date dropped from 16% to 3.6%. Change in mean soil pH across sites explained 2% of the mean change in species richness. Despite the expectedly influential role of woody basal area change as a driver of gap creation and changing light regime, only 0.8% of mean change in species richness among sites and 5.2% of change in species richness among plots within sites, was explained by mean woody basal area change (Fig. 5). Species-richness change among plots within sites was highly variable and weakly correlated with the variation in mean species-richness change across sites. Consequently only 3.5% of the between-plot variation in species-richness change was explained by between-site variation in species-richness change (Fig. 5).

Within-site beta diversity ($\Sigma Di$) in 1971 was a stronger predictor of change in species richness, explaining 20% of the mean change in richness among sites (Fig 5). The relationship was negative indicating that higher beta diversity in 1971 was associated with a greater loss of species richness over time or smaller gains in richness for sites that increased in species richness. The interaction with storm exposure was not significant. When standardized $\Sigma Di$ values were regressed against species richness change, variance explained dropped to 4% so that the majority of the explanatory power of the beta diversity measure was due to differences in the size of the species pool between sites and not turnover of species between plots.
Soil pH

Soil pH increased between 1971 and 2002 across all sites (Fig. 4b), changes that were significantly correlated with an increase in understorey species richness (Table 1, β6). Contrary to expectation soil pH was more likely to increase significantly in plots with a higher initial pH (Table 1, β7). Mean site-level soil pH explained 30% of the between-site change in soil pH but mean plot-level soil pH explained only 2.4% of the plot-level change in soil pH (Fig. 5).

Variation in mean site pH was able to explain 78% of the variation between plots indicating that most of the variation was between sites with much less between plots within sites. Change in woody basal area at plot level only explained 0.2% of the change in soil pH at plot level. Explanatory power at site level was an order of magnitude less. Soil pH change did not significantly differ between storm and non-storm sites (Table 1, β9).

Woody basal area

There was no evidence of a difference in basal area change between plots inside or outside the storm-track (Fig 4d). However, storm exposure explained 29% of the variation in mean woody basal area change among sites (Fig. 5). An average 1.2% decrease in soil pH was estimated to occur with every 0.1-m² increase in woody basal area per 200 m², but this estimate ranged between a 3.2% decrease and a 0.7% increase and was therefore not significant (Table 1, 95% credible interval on β5).

Indirect effects

Mean soil pH in 1971 and 2002 had a significant positive effect on change in species richness via soil pH change (Table 1, β6), however the effect size, as measured by the path coefficient, was
very small (Table 1, $\beta_s7* \beta_s6$). No other significant indirect relationships were detected where storm exposure impacted species-richness change via impacts on mediating variables (Table 1, path coefficients).

Changes in species composition

Five species were more frequent by 2002 in both storm and non-storm sites of which two, *Ranunculus repens* and *Galium aparine*, are widespread generalist species extremely common in lowland Britain. Thirty-three species were more frequent in storm-impacted sites by 2002 but were not significantly different in frequency in non-storm sites (Table 2). These included the alien shrub *Prunus laurocerasus* and the widespread weeds *Senecio jacobaea* and *Cirsium vulgare*. However, the majority of species that increased in frequency in storm sites but not in non-storm sites were more typical of base-poor, low productivity substrates, such as *Carex binervis*, *C.pilulifera*, *Juncus effusus*, *Holcus mollis*, *Digitalis purpurea* and *Teucrium scorodonia* (Table 2). Five of the species that increased only on storm sites are considered ancient woodland specialists in south eastern England; *Anenome nemorosa*, *Hyacinthoides non-scripta*, *Lysimachia nemorum*, *Hypericum pulchrum* and *Chrysosplenium oppositifolium* (Table 2). Moreover, all increasing generalist species that would be favoured by nutrient enrichment were still much less frequent in 2002 than typical woodland species (Table 2).

Cover-weighted SLA did not change significantly between surveys either in storm-impacted or non-storm sites (Fig. 4c) and was not significantly explained by any of the path model relationships – Supplementary Material. Thus, fifteen years after the storm, differences in species frequency and plant trait contribution between storm and non-storm plots showed no evidence of a widespread shift toward assemblages that would indicate eutrophic conditions.
Changes in understorey beta diversity

Eighteen of the 26 sites showed significant changes in beta diversity between 1971 and 2002. On storm exposed sites the only significant changes were increases, while on non-storm sites five decreased and seven increased - see Supplementary Material.

DISCUSSION

The effects of the October 87 storm on understorey species richness

By 2002 exposure to the 1987 storm had significantly offset the reduction in species richness associated with non-impacted sites and typical of the long-term trend in woodlands across Britain (Fig. 4a). Among the range of predictors tested, storm exposure had the strongest effect on the change in mean species richness across woodland sites; it had 40 times the explanatory power of mean soil pH change and 75 times the explanatory power of mean woody basal area change. Despite this apparently strong effect, both woody basal area change and the species-richness response were highly variable across plots and forest sites. Contrary to expectation storm exposure explained only 29% of the change in mean woody basal area across sites, which in turn explained a miniscule 0.8% of mean site-level species richness change. Yet storm exposure directly and uniquely explained 60% of the change in mean site-level species richness. The mechanism whereby storm exposure impacted species richness but independently of change in woody basal area must comprise a range of other disturbance effects. These include gap creation by blowdown of trees with stems outside plots but whose canopies shaded plots. Also moderate damage to trees could have resulted in additional light penetration at ground level but where trees continued to grow. If not killed, most of the broadleaved canopy species can re-sprout and re-leaf quickly. Thus change in basal area may not be strongly correlated with post-
disturbance changes in canopy cover that alter light availability and impact species richness
(Clinton & Baker 2000; Brewer et al. 2012; Barker-Plotkin et al. 2013). Whilst all 10 sites were
exposed to the storm, the extent of disturbance reported by surveyors varied from none to
widespread (Kirby et al. 2005b). For example, many fallen trees were reported as still alive and
vigorously regrowing in 2002. Indeed a recent assessment indicated that the majority of timber
was not damaged. In the two counties completely within the storm track 24% of standing timber
volume was blown down in East Sussex and 18% in Kent (Harmer 2012). However, the apparent
absence of significant change in woody basal area in the storm-impacted sites seems at odds with
the likely effects of such exposure. A possible explanation is that the interval of 15 years
between the storm and the 2002 survey was sufficient for regrowth to have achieved woody
basal area values similar to those in the first survey in 1971. Previous analysis has shown that
substantially younger cohorts of stems were present across the survey sites in 1971 than in 2002
(Kirby et al. 2005a). Such an explanation assumes that widespread reduction in basal area of an
equivalent magnitude to the storm must have occurred around the mid-1950s. This could reflect
the culmination of severe post-WWII timber extraction but in the absence of historical
management information for the sites involved this is a matter for speculation and further
enquiry.

Since storm salvage operations were also apparent in the aftermath of the storm, it is
unclear how these may have altered woody basal area and impacted the structure and species
composition of gaps (cf. Cooper-Ellis et al. 1999; Brewer et al. 2012; Barker-Plotkin et al.
2013). During the 2002 resurvey, land owners often reported how destructive the storm had
been, but also indicated that it had been the stimulus for interventions, including clearing out
fallen timber and dead wood and then restocking. However, surveyors’ reports indicated how the
apparent effects of post-storm tidying varied greatly; in some places these effects were linked to further suppression of understorey species-richness following dense restocking, whilst in others they were associated with greater light penetration and herbaceous regrowth and the removal of dead wood (also see Whitbread 1991).

The severity of canopy damage and the dynamics of recovery depends on a range of other scale-dependent factors, including legacy effects of management, slope, tree species and age, ground wetness, nutrient availability, litter inputs and plant traits (Foster & Boose 1992; Whitbread & Montgomery 1994; Peterson & Pickett 1995; Cooper-Ellis et al. 1999; Clinton & Baker 2000). Even if canopy gaps are created, the subsequent timing and direction of change in species richness depends upon propagule availability from nearby populations and the persistence of vegetative material in and around gaps (Whitney & Foster 1988; Vellend 2003; Roberts 2004). Post-storm salvage operations as well as these other factors will have undoubtedly contributed to the large amounts of residual variance not explainable by the few predictors applied in the analysis. However, despite the chaotic nature of the storm’s impact at multiple scales, our cross-site study explained 87% of the change in mean species richness at site-level and provides a novel estimate that exposure of woodland plots to the storm increased understorey species-richness per 200m² by an average of 32% of their starting values in the following 15 years.

Changes in species diversity; was there evidence of a eutrophication effect?

In four of the storm-exposed sites, surveyors reported locally vigorous colonization of canopy gaps by species whose consolidation was associated with low species-richness. Colonising dominants included the non-native, invasive shrubs *Prunus laurocerasus* and *Rhododendron* spp,
the native rhizomatous fern *Pteridium aquilinum* and dense juvenile stems of the native tree *Betula pubescens*. Rapid gap colonization by a small number of dominants is consistent with other observations on storm-affected sites (Parker 1994; Cole & Weltzin 2005). However, the identity of the species that were more frequent on storm-exposed sites by 2002 did not indicate a widespread increase in nitrophilous species. Whilst a small number of such species were more frequent by 2002, a larger number of woodland specialists and species more typical of low productivity substrates had increased even more. Moreover, cover-weighted SLA did not change significantly indicating no average increase in abundance of species favoured by more enriched conditions. These changes are also consistent with the average increase in plot species richness in storm-exposed sites rather than suppression of species richness by a small number of dominants.

The lack of a eutrophication effect could be attributable to a number of factors. Fifteen years might be too short a time for the expression of a cross-site pattern of competitive suppression in the understorey. However, on storm-exposed sites total atmospheric N deposition ranged from an estimated 31 to 43 kg ha\(^{-1}\) yr\(^{-1}\), well in excess of the current European empirical critical load for nitrogen. Significant species compositional change in the herbaceous understorey has been found elsewhere following addition of lower N loads than this over shorter time intervals (reviewed in Gilliam 2006). Yet, in other experiments and observational studies, changes in dominance and diversity either have been much slower or have not been observed and appear to depend upon the soil chemistry of the study system and the presence of responsive species at the start (De Schrijver *et al*. 2011; Verstraeten *et al*. 2013). It is therefore possible that eutrophication effects have yet to influence understorey dominance hierarchies and may only do so dependent on the biogeochemical susceptibility of different locations.
An additional constraint is soil pH and its influence on macro-nutrient availability (Schaffers 2002; Falkengren-Gjerde & Diekmann, 2003). The non-significant path from storm exposure to soil pH change via woody basal area change means that changes in soil pH were independent of both factors even though significant soil pH change did occur between 1971 and 2002 (Fig. 4b). The overall increase in soil pH is therefore consistent with recovery from acidification following reduced atmospheric sulphur deposition since the mid-1970s (Norton et al. 2012; Kirk et al. 2006) but there is no evidence that this background change in pH was amplified on storm-exposed sites. As more woodlands recover from acidification, those moving into a pH window of between ≈5.5 and 7.0, (Schaffers 2002; Stevens et al. 2011), are expected to show increasing dominance by nitrophiles unless continued lack of disturbance and increased shading prevents such light-demanding species from becoming abundant (De Keersmaeker et al. 2004; Verheyen et al. 2012; Baeten et al. 2009).

A significant positive relationship also was found between soil pH change and species-richness change between 1971 and 2002. A positive spatial relationship between soil pH and species richness is consistent with other datasets for temperate forests (Borschenius et al. 2004; De Keersmaeker et al. 2004; Corney et al. 2006) but it is interesting to find such a clear coupling between species-richness change and soil pH change over time. This suggests a responsive woodland species pool and a signal detectable despite apparent storm-driven changes in species richness within the same dataset. The mean soil pH changed from 4.7 to 5.3 in the 30 years, a change estimated to have driven an average increase of 7% of the 1971 starting species-richness or an addition of 1 species per plot given that the mean richness in 1971 was 14 per 200m². This change moved the average woodland to just below the threshold where macro-nutrient availability confers susceptibility to dominance by nitrophilous species in the understorey and
reduced species richness (Stevens et al. 2011). Moreover, higher pH soils tended to have shown
the greatest increase in pH between 1971 and 2002 (Fig. 6). Soil and vegetation responses to
changing pollutant deposition differ depending upon the biogeochemical starting point and
whether the starting pH was previously reduced by historical acidification (Verstraeten et al.
2013; Baeten et al. 2009). Where pollutant deposition drives pH down to below about 4.2-4.3
species richness typically declines. Mechanisms include toxicity of aluminium and H+ and the
loss of species unable to effectively utilise NH4+ (Stevens et al. 2011; Stevens et al. 2009).
Within the sample of 293 woodland plots, 20 plots moved into the pH>=5.5 window while 54
remained below a pH of 4.2 and 75 moved from below pH 4.2 to between 4.2 and 5.5. These
movements between critical pH windows should predict increases or decreases in diversity
reflecting recovery from acidification and then the onset of eutrophication. However, we do not
know whether these pH changes are a consequence of pollutant deposition driving down pH
earlier in the 20th century with recovery since the late 1970s. Analysis along crossed gradients of
sulphur and nitrogen deposition history and soil pH is not possible for the small sample of paired
storm and non-storm woodlands because all sites saw reduced acidification and all were subject
to high N loads (Fig. S2). With no gradient of effects along which to analyse change no signal
can be attributed (Smart et al. 2012). Analysis of the full set of 103 sites offers a chance of
further characterizing the effects of pollutant deposition on soil pH and understorey diversity but
in the absence of storm disturbance effects.

Did the understorey species composition become more homogenous?

Different mechanisms could result in homogenization of the woodland understorey depending
upon exposure to the storm. On storm-disturbed sites homogenization would result where
regenerating understoreys were dominated by a small number of widespread generalists associated with the wider farmed landscapes of lowland Britain, at the expense of a larger pool of typical woodland species. On non-storm exposed sites, suppression of the understorey by continued shading and lack of management would lead to greater homogeneity if the same smaller pool of shade-tolerant plant species persists across sites. The latter scenario appears broadly typical of recent changes in many European forests (Baeten et al. 2014). Our results clearly indicated increased differentiation and heterogeneity of the understorey on storm-exposed sites with no evidence of the release of suppressive nitrophiles. On non-storm sites, within-site beta diversity increased or decreased in roughly equal measure. However, analysis of the wider site series has shown a marked loss of species richness within British broadleaved woodlands with a species-compositional shift toward a more shade-tolerant flora (Kirby et al. 2005a).

Ongoing lack of disturbance is not necessarily a counsel of despair since shaded undisturbed woods may be poor in plant species per unit area but richer in groups of invertebrates, fungi and bryophytes that prefer dead wood, low light, humidity and shade (Townsend 2006; Hambler & Speight 1995). However, these specialist taxa may also be increasingly rare given the fragmentation of woodlands and the negative effects of pollutant deposition.

Developing the conceptual framework of forest responses to global change

A combination of the three conceptual frameworks provided a useful basis for hypothesis generation and testing. Roberts (2004) provides a convenient separation of disturbance effects along three axes that align well with the effect of storm disturbance as a natural pulsed changed in resource availability on soil, understorey and canopy. Roberts (2004) however does not explicitly predict ecosystem dynamics in response to global change drivers. The HRF does so
and in particular makes predictions about the outcome of interactions between natural pulsed
disturbances and externally sourced chronic changes in resources whose scale means that
resource supplies cannot be modified by local ecosystem feedbacks. Finally, the biotic
homogenisation framework has been widely applied to woodland change (Wiegmann & Waller,
2006; Baeten et al. 2012) and increasingly valuable insights are likely to arise from focussing on
how plant traits that are known to drive feedbacks on ecosystem functioning become more
widely represented as global change drivers non-randomly select winning versus losing taxa
from the local and regional species pools (Suding et al. 2008). The likelihood that new colonists
will include widespread generalists typical of human-modified landscapes is increased where
woodland patches are smaller and less buffered by existing older woodland (Kimberley et al.
2014). These spatial effects probably need to be more explicitly factored in when extending the
Roberts (2004) framework to fragmented, small woodlands typical in northern Europe and in
other parts of the temperate zone.

Synthesis

In summary, analysis of this unique dataset has shown that storm events can drive a reversal in
the direction of change in plant species richness resulting from at least 40 years of reduced
canopy disturbance. Direct storm impacts on the understorey were detectable, but quantifying the
links between storm exposure, different types and severities of canopy damage and the impact of
these on soil and understorey vegetation will likely require a wider range of measurements.

Many temperate woodlands are now embedded in intensively managed landscapes and
subject to legacy effects of elevated atmospheric nitrogen deposition but reduced sulphur
deposition. Hence the future consequence of disturbance, whether from storm events or
reinstated management, could be the development of very different herbaceous understoreys
dominated by rapidly growing species more typical of nutrient rich conditions. More frequent
recording at the impacted and unimpacted woodland sites would be highly desirable to determine
the ongoing course of post-disturbance trajectories and the extent to which these help us
understand the resilience of temperate woodlands to the interacting effects of future stressors
(Bruehlheide & Luginbühl 2009).

Acknowledgements
SMS thanks the NERC Centre for Ecology & Hydrology, Mark Bailey, Alan Jenkins, Terry Parr
and colleagues in the Land Use Group for supporting a sabbatical leave at the Harvard Forest
funded by the Charles Bullard fellowship scheme during which this work was initiated. Work by
AME and DRF on this project was supported by the Harvard Forest LTER site, through NSF
grants 0620443 and 12-37491. Comments from the journal editors Lauren Sandhu, Frank Gilliam
and David Gibson, and two anonymous referees greatly improved the original manuscript.
Andrew Titman is thanked for statistical advice. The woodland resurvey was funded by DEFRA,
Natural England, Forestry Commission and the Woodland Trust.

Data accessibility
The woodland survey database is freely available via the following DOI:
- doi.org/10.5285/fb1e474d-456b-42a9-9a10-a02c35af10d2
- doi.org/10.5285/d6409d40-58fe-4fa7-b7c8-71a105b965b4
- doi.org/10.5285/2d023ce9-6dbe-4b4f-a0cd-34768e1455ae
- doi.org/10.5285/4d93f9ac-68e3-49cf-8a41-4d02a7ead81a

SUPPORTING INFORMATION
1 Figure S1 Phytosociological composition of the study plots in the baseline year of 1971.
2 Figure S2 Distributions of measured variables in storm (1) and non-storm (0) sites.
3 Table S1 Percentage of the variation in response variables explained by hypothesized predictor variables.
4 Table S2 Path analysis of change in cover-weighted Specific Leaf Area (cSLA).
5 Figure S4 Path analysis diagram for change in cover-weighted SLA between 1971 and 2002.
6 Table S3 Significance tests of change in understorey community heterogeneity ($\Sigma D_i$).
7 Text S1 Notes on variation partitioning.
8 Text S2 OpenBUGS code.
9 Text S3 Notes on construction of the path analysis in OpenBUGS.
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Hall, UK.

regions*. Cambridge University Press, UK.

Peterken, G.F. & Game, M. (1984) Historical factors affecting the number and distribution of


Table 1: Summary statistics for all model parameters from the Bayesian path analysis of October 1987 storm impacts on British broadleaved woodlands. Posterior distributions of path coefficients (βs) were estimated from analysis of centred and standardized data. See text and Figs. 1 and 2. Significant effects by Bayes P value are emboldened. Species richness change was analysed as $\ln[(\text{richness}\,2002 + 1)/(\text{richness}\,1971 + 1)]$

<table>
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<tr>
<th>Description</th>
<th>Parameters</th>
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<th>St dev</th>
<th>Monte Carlo SE</th>
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<th>median</th>
<th>97.5%tile</th>
<th>Bayes P value</th>
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Path coefficients
| Storm effect on richness change via pH change via Basal area change | $\beta_{s3} \beta_{s5} \beta_{s6}$ | -0.00119 | 0.00221 | 1.83E-05 | -0.00685 | -6.47E-04 | 0.002045 | 0.2549 |
| Storm effect on richness change via basal area change | $\beta_{s3} \beta_{s4}$ | -0.03584 | 0.04174 | 4.59E-04 | -0.1223 | -0.03419 | 0.04349 | 0.1802 |
| Effect of mean pH across survey years on species richness change via pH change | $\beta_{s7} \beta_{s6}$ | 0.05665 | 0.02602 | 2.00E-04 | 0.01182 | 0.05454 | 0.1131 | 0.0058 |

**Residual standard deviations**

| SITE level woody basal area change | 0.09801 | 0.04765 | 0.00145 | 0.008076 | 0.0985 | 0.1933 |
| Random intercepts for (pH 71+02)/2 | 1.148 | 0.1776 | 0.00102 | 0.862 | 1.127 | 1.551 |
| SITE-level pH change | 0.4734 | 0.1066 | 0.00189 | 0.2938 | 0.4633 | 0.7114 |
| SITE-level species richness change | 0.1521 | 0.06665 | 0.00199 | 0.01575 | 0.151 | 0.2884 |
| Difference in date of survey | 39.99 | 5.894 | 0.03106 | 30.4 | 39.3 | 53.44 |
| within-SITE beta diversity in 1971 | 1.032 | 0.1532 | 0.00085 | 0.7842 | 1.014 | 1.382 |
| PLOT-level woody basal area change | 0.4735 | 0.02047 | 0.00017 | 0.4351 | 0.4728 | 0.5157 |
| PLOT-level pH change | 0.803 | 0.03534 | 0.00027 | 0.7377 | 0.8016 | 0.8761 |
| PLOT-level mean pH (71+02)/2 | 0.6154 | 0.02687 | 0.00015 | 0.5654 | 0.6143 | 0.6707 |
| PLOT-level species richness change | 0.6217 | 0.027 | 0.00024 | 0.5717 | 0.6209 | 0.6771 |
Table 2: Differences in species frequency between 1971 and 2002 in paired sample plots (no storm; n=150, storm; n=143). Species are excluded if the cumulative probability of finding the smaller of the two counts, 1971 versus 2002, was >0.05 in both storm and non-storm plots. I = Ancient Woodland Indicators for southeast England (Kirby 2006).

‘Dir’ indicates increased or decreased frequency between surveys where binomial $P<0.05$.

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<th></th>
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Fig 1. The woodlands included in this study showing sites inside and outside the region of south east England associated with the track of the October 1987 storm (grey shaded).
Fig 2: Path diagram depicting hypothesized relationships between ecosystem changes and understorey species-richness change measured in 26 broadleaved woodland sites in lowland Britain in 1971 and again in 2002. Ten of the sites were inside the October 1987 storm track. Expected relationships are indicated by arrows each associated with a numbered regression coefficient linked to hypotheses described in the text. Ellipses indicate covariates recorded at the level of plots within woodland sites. Rectangles indicate effects recorded at the site level only.
Fig 3: Results of analysis of October 1987 storm impacts on changes in woodland attributes between 1971 and 2002 in England. Squares indicate site-level covariates. Ovals indicate plot-level covariates. Thick arrows indicate significant paths. Dashed arrows indicate a negative regression relationship. Numbers are regression coefficients based on uncentred and unstandardized data. Understorey species-richness change was analysed as $\ln \left( \frac{\text{richness}_{2002} + 1}{\text{richness}_{1971} + 1} \right)$. 

- Mean $(\text{pH}_{71} + \text{pH}_{02})/2$
- Change in soil pH
- Change in woody basal
- Change in species richness
- Oct '87 storm y/n?
- Difference in survey date
- Within-site Beta diversity in 1971

Regression coefficients:
- $0.30$
- $-0.23$
- $-0.12$
- $0.06$
- $0.28$
- $0.001$
- $-0.41$
- $0.11$
- $0.06$
- $-0.19$
Fig 5: Percentage variation explained given hypothesized relationships. Only variables hypothesized to be causally influenced by another variable are on the vertical axis. Therefore, since between-plot changes in species richness were expected to be impacted by all variables its variance was decomposed into the largest number of factors. The height of each bar indicates the total amount of variation in each variable that was explained.
Fig 6: Change in soil pH between 1971 and 2002 versus mean pH in the two survey years. Mean pH is plotted on the axis to avoid regression to the mean artefacts where sampling error results in extreme values switching back to near average values thus causing a strong negative slope. Random sampling of heterogenous soils within plots results in individually large changes in pH. N=293 plots across 26 woodland sites in SE England.
Fig 4: Means +/- 95% confidence intervals for: a) Understorey species-richness, b) soil pH, c) cover-weighted Specific Leaf Area (cSLA), d) woody basal area (m$^2$) per 200m$^2$ plot, and e) beta diversity of the understorey in each site ($\Sigma D_i$). Data from 293 woodland plots within 26 woodland sites in 1971, recorded again in 2002. 10 sites were exposed to the October 1987 storm.
d) Woody basal area (m$^2$ 200m$^2$)

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