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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

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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^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, understorey 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 understorey 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 understorey 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^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-m^2 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., Bruelheide & 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-m^2 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 ^{o}C and mean monthly July temperature of 16.5 - 17.5 ^{o}C (Goudie & Burden 1994). The region is densely populated (401 persons per km^2 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-m^2 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:

$\beta 3 * \beta 4$: 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:

$$cSLA_j = sum (SLA_{ij} \ x \ (cov_{ij}))/sum(cov_{ij}), \qquad 1)$$

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 *ΣDi* community heterogeneity metric using the 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 ΣDi 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 ΣDi indicated how much of the explanatory power of ΣDi 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, β2). Increased woody basal area was associated with decreased species richness (Table 1, β4) 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, β6).

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 β2). 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 (ΣDi) 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 ΣDi 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-m^2 increase in woody basal area per 200 m^2, 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, βs7* βs6). 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 *Chryosplenium 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 $200m^2$ 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-Grerup & 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 200m^2. 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 (Bruelheide & Luginbühl 2009).

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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

Figure S1 Phytosociological composition of the study plots in the baseline year of 1971.

Figure S2 Distributions of measured variables in storm (1) and non-storm (0) sites.

Table S1 Percentage of the variation in response variables explained by hypothesized predictor variables.

Table S2 Path analysis of change in cover-weighted Specific Leaf Area (cSLA).

Figure S4 Path analysis diagram for change in cover-weighted SLA between 1971 and 2002.

Table S3 Significance tests of change in understorey community heterogeneity (ΣDi).

Text S1 Notes on variation partitioning.

Text S2 OpenBUGS code.

Text S3 Notes on construction of the path analysis in OpenBUGS.

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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[(richness 2002 + 1)/ (richness 1971 + 1)]

Description	**Parameters**	**Mean**	**St dev**	**Monte Carlo SE**	**2.5%tile**	**median**	**97.5%tile**	**Bayes *P* value**
Regression coefficients								
Species richness change given difference in survey date	β1	0.001572	0.001418	0.00002	-0.00112	0.001536	0.004463	0.1280
Species richness change given storm exposure	**β2**	0.2791	0.1003	0.00137	0.07788	0.2795	0.4765	**0.0045**
Species richness change given within-site beta diversity in 1971	**β8**	-0.1862	0.05196	0.00048	-0.2914	-0.1856	-0.08451	**0.0003**
Woody basal area change given storm exposure	β3	0.06268	0.07264	0.00088	-0.08131	0.06193	0.2063	0.1859
pH change given storm exposure	β9	-0.23	0.2228	0.00481	-0.6668	-0.231	0.2155	0.1130
pH change given woody basal area change	β5	-0.1243	0.1025	0.00059	-0.3224	-0.1253	0.07724	0.1446
pH change given mean soil pH across survey years	**β7**	0.2971	0.06795	0.00283	0.1648	0.2972	0.4309	**0**
Species richness change given woody basal area change	**β4**	-0.4076	0.07978	0.00064	-0.5644	-0.4075	-0.2523	**0**
Species richness change given pH change	**β6**	0.1094	0.04278	0.00030	0.02605	0.1093	0.1937	**0.0062**
Path coefficients								

Storm effect on richness change via pH change via Basal area change	βs3* βs5*βs6	-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	βs3* βs4	-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	**βs7* βs6**	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 south east England (Kirby 2006). 'Dir' indicates increased or decreased frequency between surveys where binomial *P*<=0.05.

Species	**No storm**					**Storm**				
	1971	**2002**	**Change**	**Bin *P***	**Dir**	**1971**	**2002**	**Change**	**Bin *P***	**Dir**
Solidago virgaurea(I)	0	5	5	0.063		23	2	-21	0.000	down
Oxalis acetosella (I)	42	23	-19	0.025	down	33	14	-19	0.008	down
Deschampsia flexuosa	27	2	-25	0.000	down	21	6	-15	0.006	down
Sanicula europaea (I)	4	2	-2	0.688		17	3	-14	0.003	down
Rubus idaeus	14	4	-10	0.031	down	14	4	-10	0.031	down
Ranunculus acris	5	1	-4	0.219		7	0	-7	0.016	down
Hypericum pulchrum (I)	5	2	-3	0.453		0	6	6	0.031	up
Chrysosplenium oppositifolium(I)	5	5	0	1.000		0	6	6	0.031	up
Carex binervis	0	0	0			0	6	6	0.031	up
Carex pilulifera	3	1	-2	0.625		0	7	7	0.016	up
Luzula campestris/multiflora	4	2	-2	0.688		0	7	7	0.016	up
Cirsium vulgare	1	2	1	1.000		0	7	7	0.016	up
Hypericum tetrapterum	0	0	0			0	7	7	0.016	up
Senecio jacobaea	0	4	4	0.125		0	8	8	0.008	up
Betula pubescens	5	10	5	0.302		2	10	8	0.039	up
Carex remota (I)	2	15	13	0.002	up	3	12	9	0.035	up
Galium saxatile	5	0	-5	0.063		0	9	9	0.004	up
Anthriscus sylvestris	1	4	3	0.375		1	10	9	0.012	up
Anthoxanthum odoratum	5	3	-2	0.727		2	11	9	0.022	up
Teucrium scorodonia	0	0	0			0	9	9	0.004	up
Prunus avium	5	21	16	0.002	up	0	10	10	0.002	up
Ranunculus repens	7	20	13	0.019	up	5	15	10	0.041	up
Arum maculatum	8	25	17	0.005	up	12	23	11	0.090	
Salix caprea	4	5	1	1.000		1	12	11	0.003	up

Digitalis purpurea	4	10	6	0.180		7	19	12	0.029	up
Prunus laurocerasus	3	2	-1	1.000		2	14	12	0.004	up
Cardamine hirsuta/flexuosa	6	7	1	1.000		1	13	12	0.002	up
Lysimachia nemorum (I)	8	10	2	0.815		11	25	14	0.029	up
Athyrium filix-femina	12	13	1	1.000		3	17	14	0.003	up
Holcus mollis	30	22	-8	0.332		16	32	16	0.029	up
Juncus effusus	22	15	-7	0.324		13	30	17	0.014	up
Glechoma hederacea	28	26	-2	0.892		17	34	17	0.024	up
Acer pseudoplatanus	73	80	7	0.628		35	55	20	0.045	up
Dryopteris dilatata	62	64	2	0.929		30	51	21	0.026	up
Carpinus betulus	0	2	2	0.500		20	42	22	0.007	up
Galium aparine	19	40	21	0.009	up	7	31	24	0.000	up
Anemone nemorosa (I)	11	20	9	0.150		3	33	30	0.000	up
Hyacinthoides non-scripta (I)	50	54	4	0.769		52	82	30	0.012	up
Poa nemoralis/trivialis	42	51	9	0.407		35	67	32	0.002	up
Luzula pilosa (I)	46	13	-33	0.000	down	21	13	-8	0.229	
Chamerion angustifolium	34	7	-27	0.000	down	16	9	-7	0.230	
Potentilla sterilis	20	6	-14	0.009	down	13	6	-7	0.167	
Ligustrum vulgare	16	5	-11	0.027	down	8	2	-6	0.109	
Hieracium 'indeterminate'	11	0	-11	0.001	down	3	0	-3	0.250	
Ribes nigrum (I)	10	1	-9	0.012	down	5	2	-3	0.453	
Abies sp.	0	6	6	0.031	up	2	0	-2	0.500	
Epilobium montanum	19	2	-17	0.000	down	14	13	-1	1.000	
Polypodium vulgare sens.lat. (I)	6	0	-6	0.031	down	0	0	0		
Ranunculus ficaria	0	9	9	0.004	up	0	2	2	0.500	
Arrhenatherum elatius	7	0	-7	0.016	down	3	5	2	0.727	
Pinus nigra	0	6	6	0.031	up	0	2	2	0.500	
Cirsium arvense	1	8	7	0.039	up	5	7	2	0.774	
Brachypodium sylvaticum	20	42	22	0.007	up	9	14	5	0.405	
Geranium robertianum	13	31	18	0.010	up	9	15	6	0.307	

Stachys sylvatica	1	8	7	0.039	up	13	19	6	0.377
Arctium agg.	13	2	-11	0.007	down	5	12	7	0.143
Ilex aquifolium	66	107	41	0.002	up	72	90	18	0.181

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.

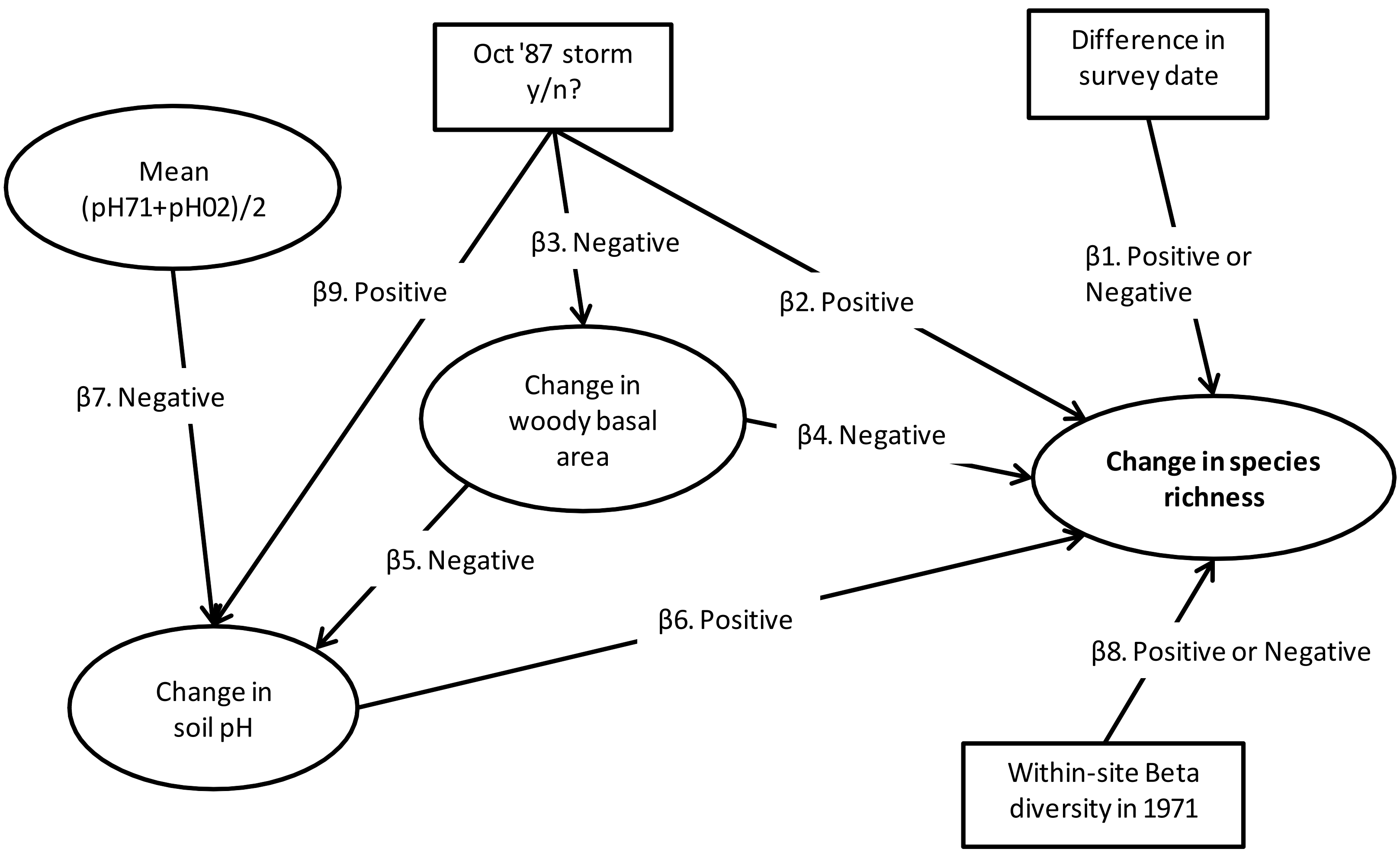


Fig 3: Results of analysis of October 1987 storm impacts on changes in woodland attributes between 1971 and 2002 in England. Squares indicate site-level covariates. Ovals indicate plot-level covariates. Thick arrows indicate significant paths. Dashed arrows indicate a negative regression relationship. Numbers are regression coefficients based on uncentred and unstandardized data. Understorey species-richness change was analysed as ln ((richness 2002 + 1)/ (richness 1971 + 1)).

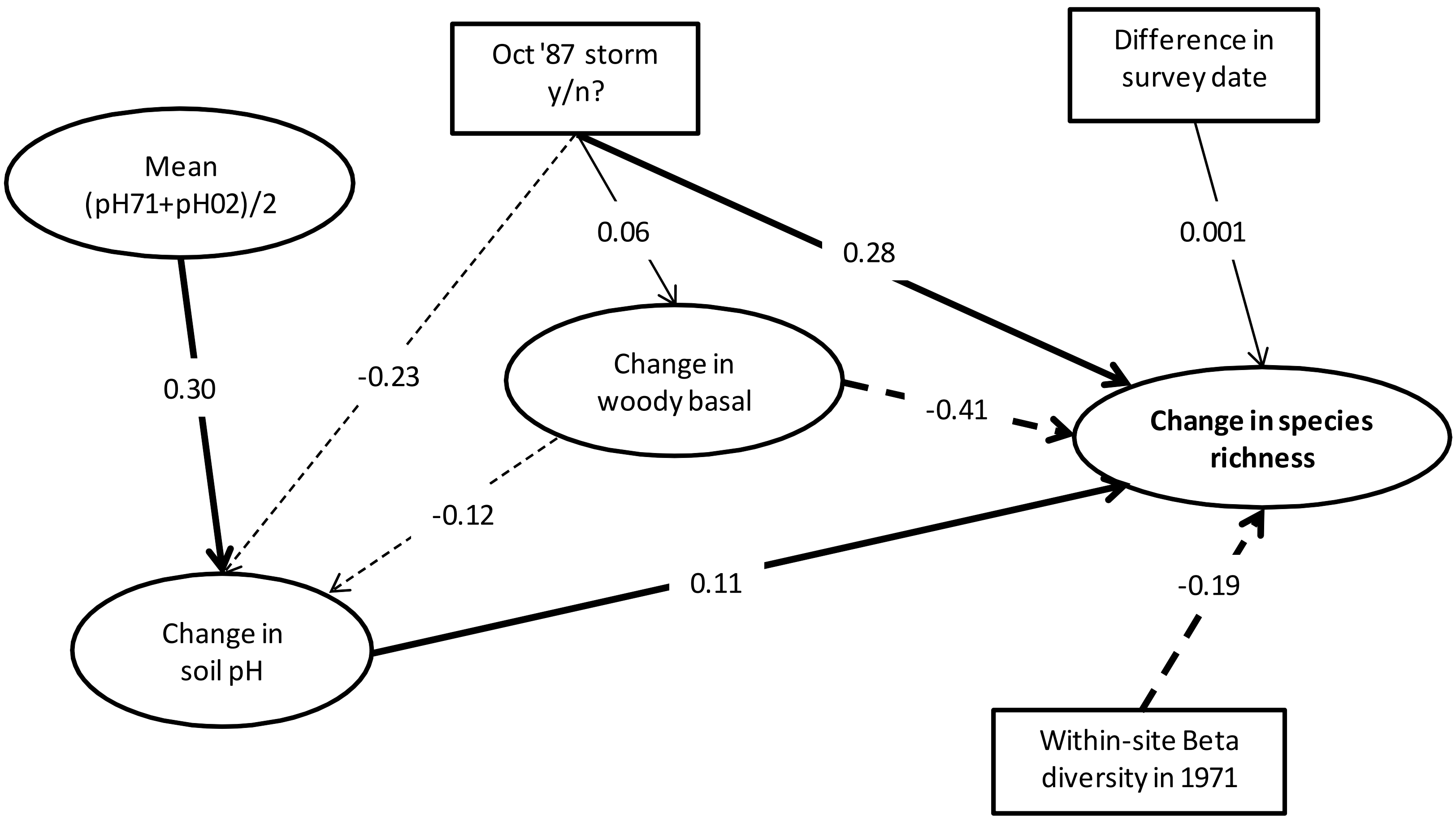


Fig 5: Percentage variation explained given hypothesized relationships. Only variables hypothesized to be causally influenced by another variable are on the vertical axis. Therefore, since between-plot changes in species richness were expected to be impacted by all variables its variance was decomposed into the largest number of factors. The height of each bar indicates the total amount of variation in each variable that was explained.

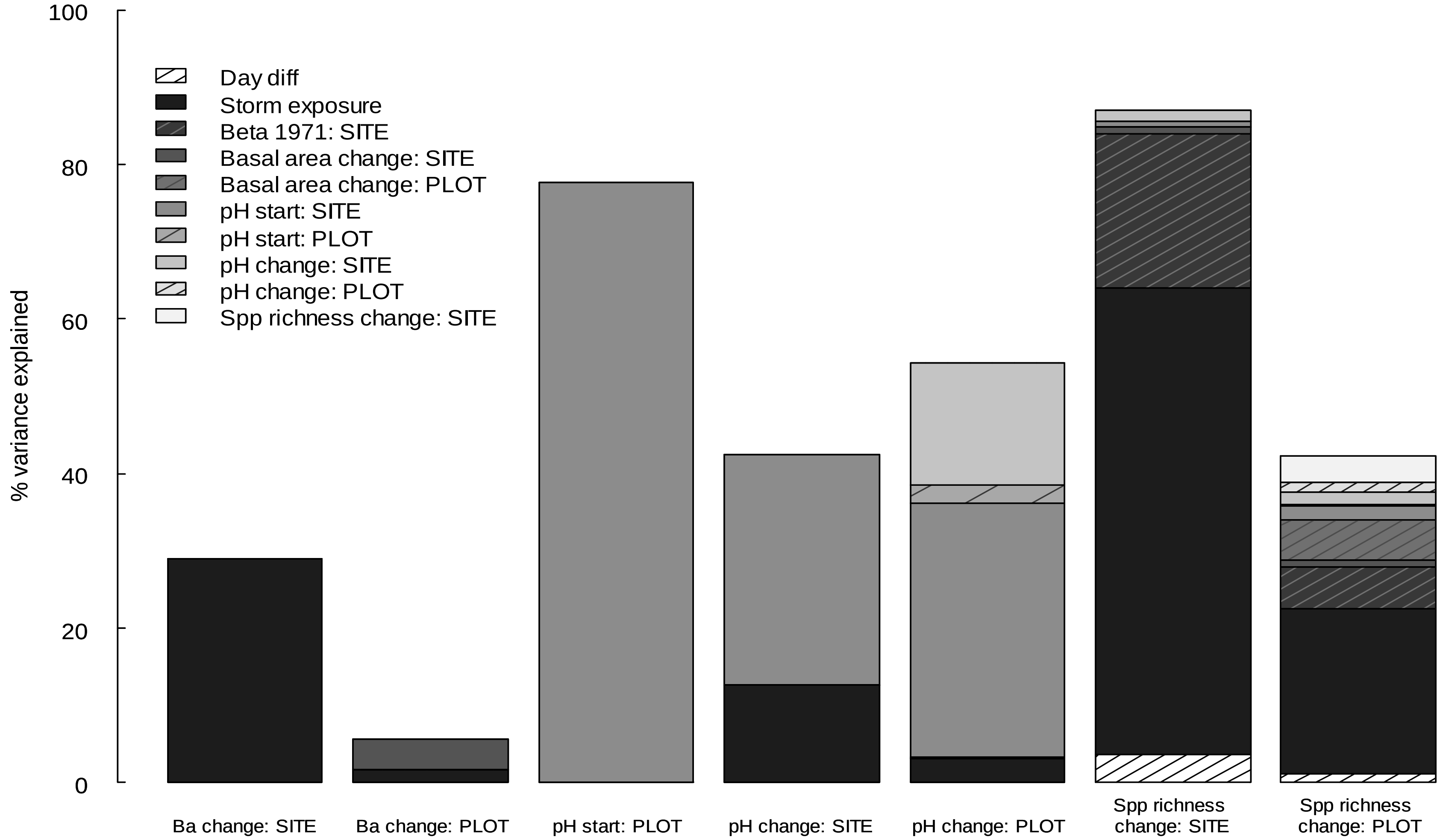


Fig 6: Change in soil pH between 1971 and 2002 versus mean pH in the two survey years. Mean pH is plotted on the axis to avoid regression to the mean artefacts where sampling error results in extreme values switching back to near average values thus causing a strong negative slope. Random sampling of heterogenous soils within plots results in individually large changes in pH. N=293 plots across 26 woodland sites in SE England.

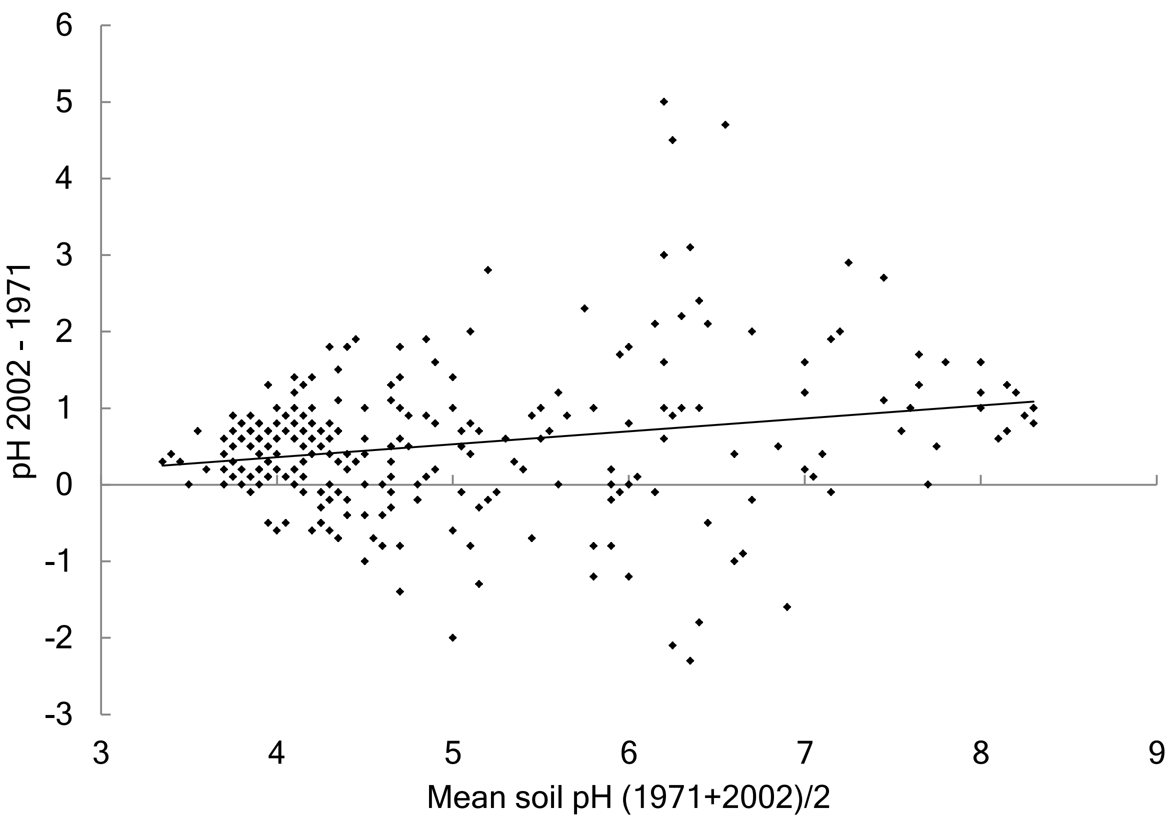
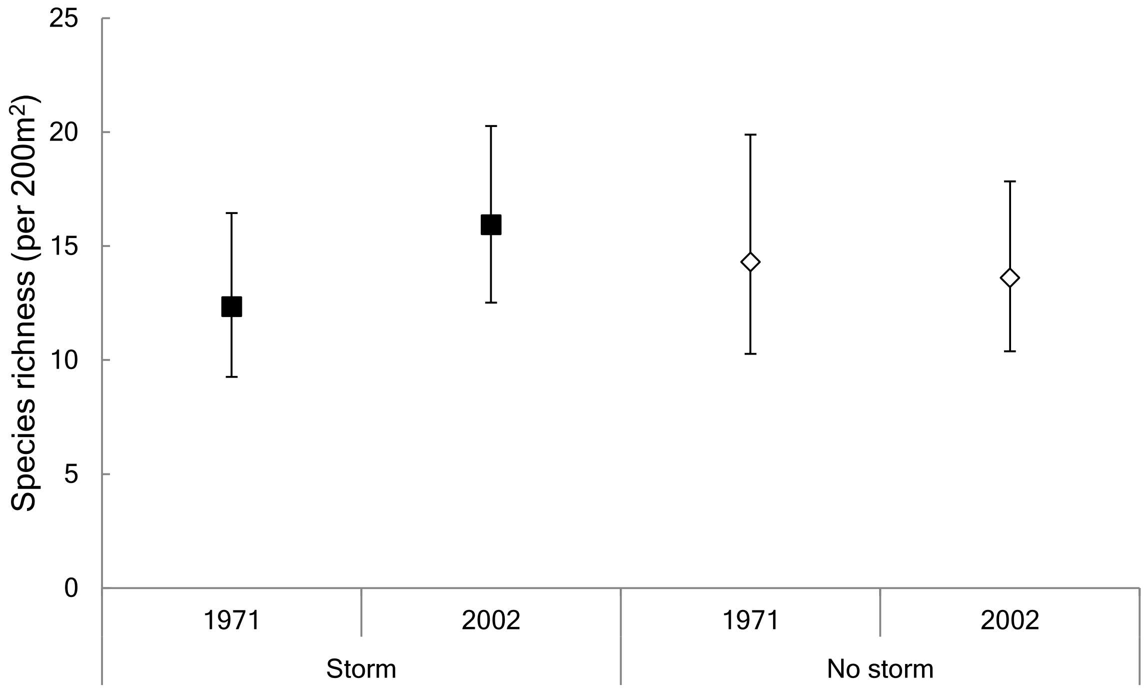
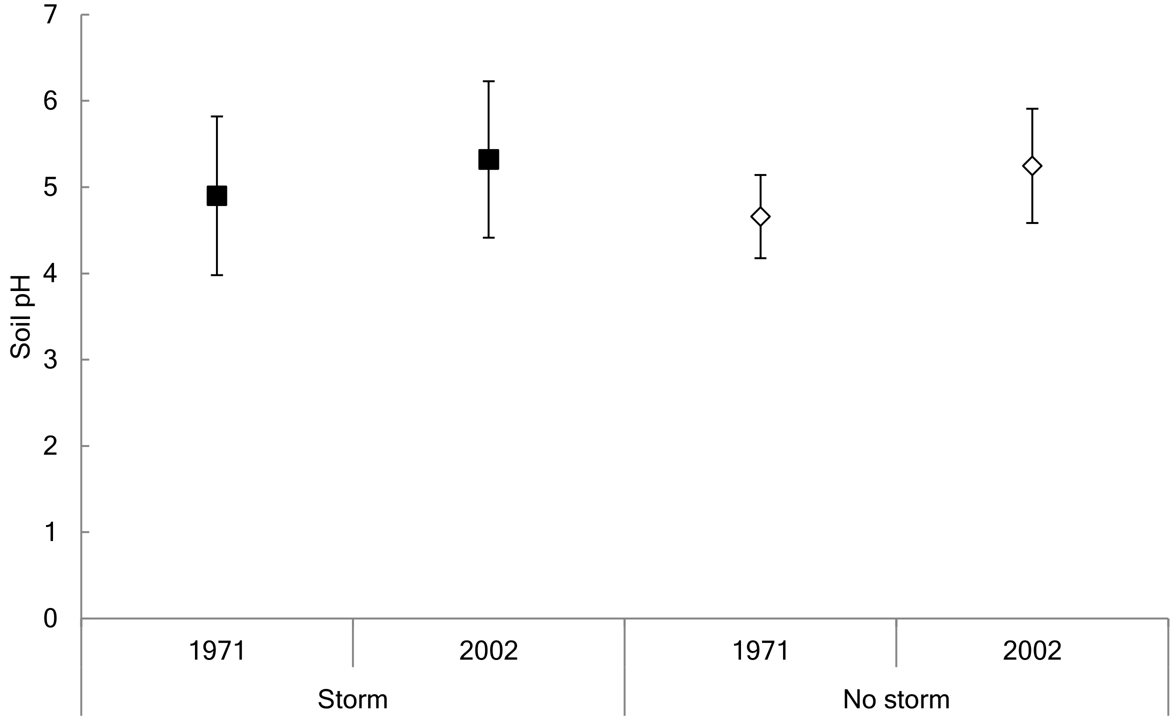


Fig 4: Means +/-95% confidence intervals for: a) Understorey species-richness, b) soil pH, c) cover-weighted Specific Leaf Area (cSLA), d) woody basal area (m^2) per $200m^2$ plot, and e) beta diversity of the understorey in each site (*ΣDi*). Data from 293 woodland plots within 26 woodland sites in 1971, recorded again in 2002. 10 sites were exposed to the October 1987 storm.

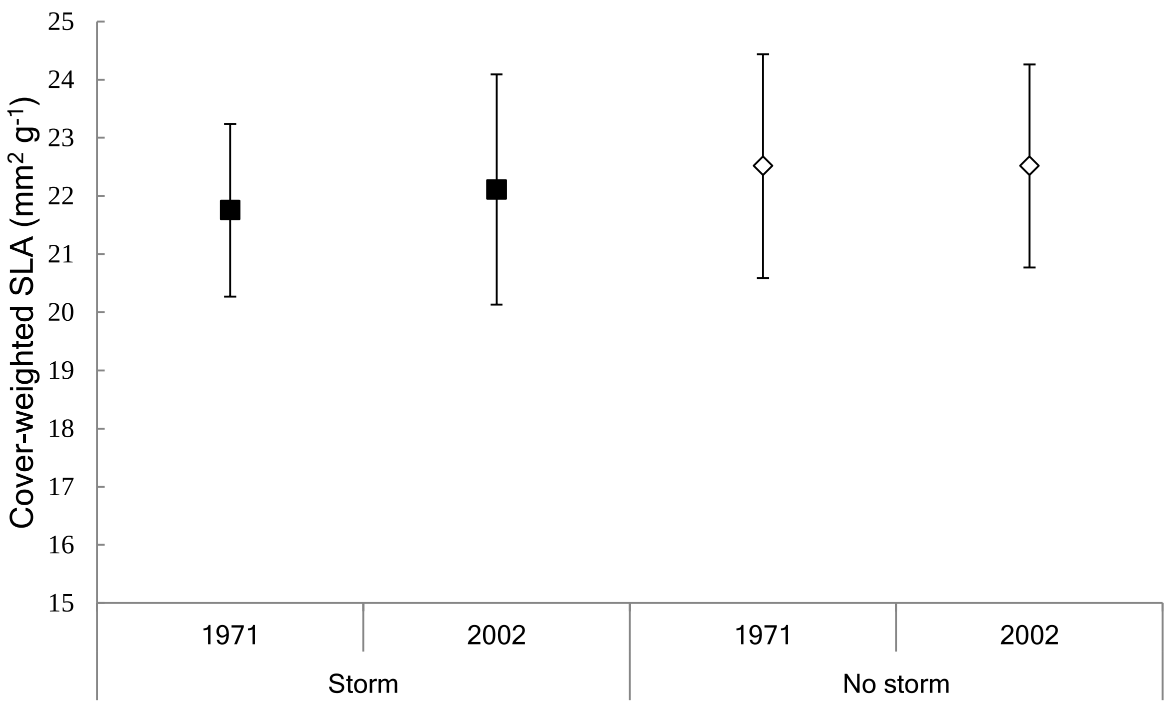
a)



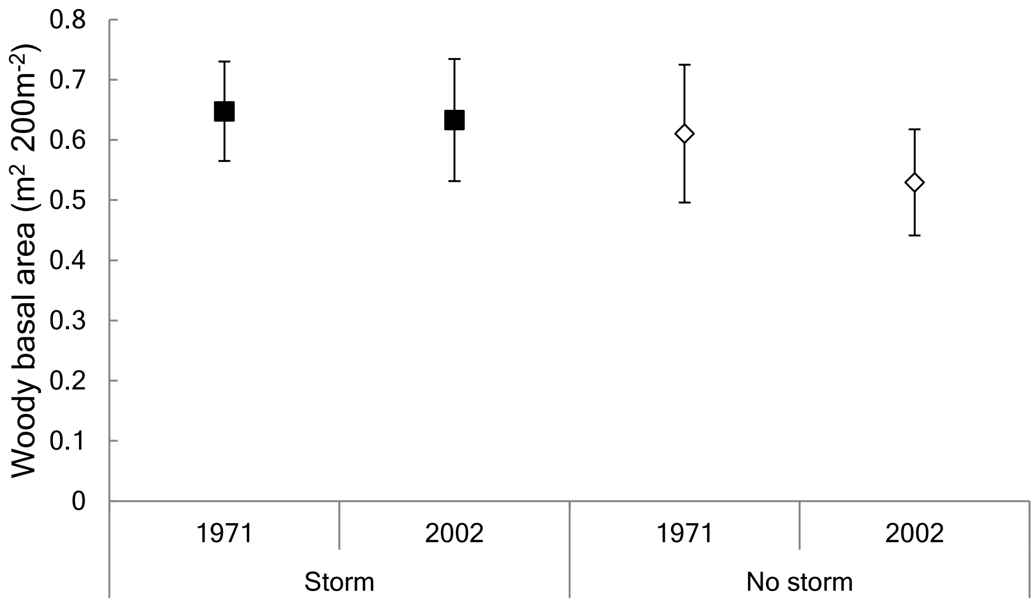
b)


7
6
5
4
3
2
1
0
Soil pH
1971
2002
1971
2002
Storm
No storm

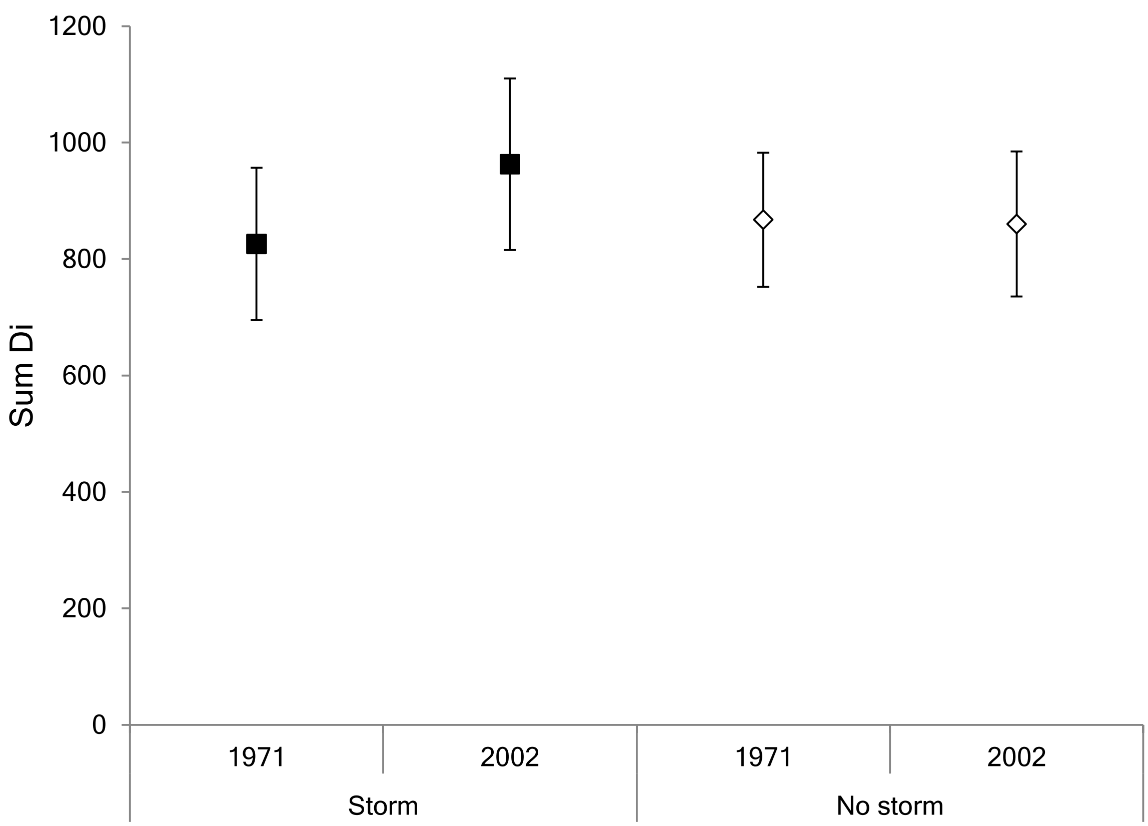
c)


25
24
23
22
21
20
19
18
17
16
15
Cover-weighted SLA (mm² g⁻¹)
1971
2002
1971
2002
Storm
No storm

d)


0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Woody basal area (m2 200m-2)
1971
2002
1971
2002
Storm
No storm

e)


1200
1000
800
600
400
200
0
Sum Di
1971
2002
1971
2002
Storm
No storm