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ORIGINAL PAPER

Applying palaeoecological analogues to contemporary challenges: community-level effects of canopy gaps caused by systematic decline of a prevalent tree species

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Abstract Temperate woodland vegetation is initially determined by spatiotemporal and historical factors, mediated by complex biotic interactions. However, catastrophic events such as disease outbreaks (e.g., sweet chestnut blight, ash dieback), infestations of insect pests, and human-accelerated climate change can create canopy gaps due to systematic decline in, or loss of, tree species that was once an important part of the canopy. Resultant cascade effects have the potential to alter the composition of woodland ecosystems quickly and radically, but inherent lag times make primary research into these effects challenging. Here, we explore change in woodland vegetation at 10 sites in response to canopy opening using the Elm Decline, a rapid loss of *Ulmus* in woodlands across northwestern Europe ~ 5800 years ago that coexisted alongside other stressors such as increasing human activity, as a palaeoecological analogue. For arboreal taxa, community evenness significantly decreased, within-site turnover significantly increased, and richness remained unchanged. Changes in arboreal taxa were highly site-specific but there was a substantial decline in woody climbing taxa, especially *Hedera* (ivy), across the majority of sites. For shrub taxa, richness significantly increased but evenness and turnover remained consistent. Interestingly, however, there was a significant increase in abundance of shrubs at 70% of sites, including *Calluna* (heather), *Ilex* (holly) and *Corylus* (hazel), suggesting structural change. Surprisingly, there was no change in richness, evenness or turnover for herb taxa, possibly because change was highly variable spatially. However, there was a marked uptick in the disturbance indicator *Plantago* (plantain). Overall, these findings suggest that woodlands with sustained reduction in, or loss of, a tree species that once formed an important part of the canopy has profound, but often spatially idiosyncratic, impacts on vegetation diversity (richness), composition (evenness), stability (turnover), and on abundance of specific taxa, especially within the shrub layer. Use of this palaeoecological analogue, which was itself complicated by cooccurring changes in human activity, provides a valuable empirical insight into possible cascade effects of similar change in canopy opening in contemporary settings, including Ash Dieback.

Keywords Canopy opening · Community composition · Palaeoecological analogue · Disturbance · Cascade effects

Introduction

Woodland vegetation community composition is initially determined by spatiotemporal factors such as location, connectivity, origin, and age (Peterken 1996; Brudvig and Damschen 2011; Palo et al. 2013; Rackham 2015; Swallow et al. 2020; Uroy et al. 2023). However, because woodlands are complex and dynamic habitats that support multiple co-occurring species, interspecific interactions also modify vegetation composition (Goodenough and Hart 2023; Kermavnar et al. 2023). Such interactions then influence other taxonomic guilds including birds (Hinsley et al. 2009; Hewson et al. 2011), mammals (Holland and Bennett 2007) and invertebrates (Jukes et al. 2001; Tudor et al. 2004). Changes in vegetation assemblage and/or structure can, therefore, have cascade effects throughout the ecosystem (Amar et al.

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2006; Gregory et al. 2007; Fox et al. 2015; Homburg et al. 2019; Blumgart et al. 2022; Bowler et al. 2023; Scopes et al. 2023).

Protecting and managing woodlands is important to conserve biodiversity and ecological distinctiveness, as well as to maintain ecosystem services such as carbon sequestration and hydrological regulation (Lorenz and Lal 2010; Bullock et al. 2014; Revell et al. 2021). However, challenges such as climate change, outbreaks of pests or disease, and high levels of herbivory can threaten woodland composition and the ecosystem services they provide (Fuller 2001; Rackham 2008; Gimona et al. 2012; Davies et al. 2017; Freer-Smith and Webber 2017; Green et al. 2021; Yu et al. 2021; Tew et al. 2024). This is especially true when one specific tree species has higher susceptibility to a particular threat than other co-occurring species. Loss of, or severe decline in, any tree species that forms an important part of the canopy can have cascade effects throughout the ecosystem. For example, canopy gaps due to loss of *Abies alba* (silver fir) can cause understorey homogenization and loss of herb diversity (Nagel et al. 2019). In that case, community-level effects were evident within 30 years and were thus discernible via field studies. However, the lag times usually inherent in ecological systems between measurable cause and quantifiable effect often exceed field study timescales (Goodenough and Webb 2022). Moreover, due to woodland complexity and the presence of local modifiers of vegetation, it is often difficult to predict how canopy opening resulting from loss of a tree species will affect the overall ecosystem (Kermavnar et al. 2023).

Throughout Europe, the fungal pathogen *Hymenoscyphus fraxineus* is causing severe and widespread Ash Dieback (Mitchell et al. 2014; Needham et al. 2016; Enderle et al. 2019). Indeed, decline in *Fraxinus* (ash) is already impacting woodlands (Enderle et al. 2019), with predictions that *Fraxinus*-dominated woodlands will undergo further substantial community change especially where functional diversity is low (Loo 2009; Patacca et al. 2023). Whilst numerous studies have investigated the cause, distribution, and management of Ash Dieback (e.g. Mitchell et al. 2014; Needham et al. 2016; Enderle et al. 2019), and some research has examined ecological correlates of disease magnitude (Erfmeier et al. 2019), studying community-level effects is challenging. To date, because of challenges imposed by lag time in primary ecological studies, such research is largely predictive, being based on likely differential effects of canopy opening on field-layer taxa (Hinsley & Pocock 2014; Mitchell et al. 2014; Needham et al. 2016; Hultberg et al. 2020).

Lack of research on cascade effects of canopy gaps resulting from systematic decline in a specific tree species is not restricted to ash woodland, nor to disease as a cause of change. Other examples include decline in: (1) *Acer platanoides* (Norway maple) in Massachusetts due to non-native wood-boring pests (Francis and Elmes 2017); (2) *Quercus* (oak) due to unregulated herbivory in Appalachia (Fajvan and Wood 1996); (3) *Fagus* due to drought in central Europe (Mette et al. 2013); and (4) *Abies* and *Thuja* (cedar) due to elevated summer temperatures in North America (Iverson and Prasad 2001). There is also potential for increasingly extreme weather to create significant canopy gaps in woodland of any composition, especially those with over-mature trees (Forestry Commission 2022). In such instances, lag times mean that understanding community-level effects is necessarily based on qualitative predictions, quantitative modelling, or GIS-based forecasting.

A different approach to overcoming lag time challenges when studying ecological cascade effects is to “learn from the past” (Goodenough and Webb 2022). In palaeoecological research, sub-fossilised pollen is used to analyse vegetation histories, and, ergo, changing community ecology (e.g. Chambers et al. 2007; Barak et al. 2016; Manzano et al. 2020). Richer and Gearey (2018) and Webb and Goodenough (2021) extended this framework to use palaeoecological analogues to predict vegetation responses to contemporary environmental change. Although there are several well-studied tree declines in the palaeoecological record—including *Tsuga canadensis* (Eastern hemlock) decline in the USA ~ 5000–6000 years ago (Calcote 2003) and *Tilia* (lime) across the United Kingdom around ~ 2500–3000 years ago (Grant et al. 2011)—the most pronounced tree decline in northwestern Europe was the dramatic loss of *Ulmus* (Elm) ~ 5800 years ago. This well-studied, abrupt, and often permanent Elm Decline is reported frequently in palaeoecological records in Britain, Ireland and Scandinavia, and occasionally in parts of mainland Europe (Andersen and Rasmussen 1993; Digerfeldt 1997; Gandouin et al. 2009; Jamrichová et al. 2017; Kearney and Gearey 2024; Kaiser et al. 2023). However, although this phenomenon is well studied, research has focused on documenting spatiotemporal trends (e.g. Parker et al. 2002; Giesecke et al. 2017; Kearney and Gearey 2024), with little research exploring community-level ecological consequences.

Here, we explore change in woodland vegetation communities in response to canopy opening, using the Elm Decline as a palaeoecological analogue. Because change in community ecology is inherently site-specific, even when due to the same stimulus, we take a multi-site approach to establish broad trends in response to canopy gaps at ten woodland sites from northwest Europe. We establish temporal trends in richness, evenness and within-site turnover, as well as exploring responses of individual taxa to synthesize general patterns. We hope that a better understanding of woodland community change in response to loss of an important arboreal species will provide useful insights into how woodlands might adapt to current and future tree-loss events, such as those predicted due to diseases, pests, and climatic change.

Methods

Data acquisition and manipulation

Overview

There were many sites that could have been suitable for inclusion in this study, but locating these in an ad-hoc way would inherently have been biased based on incomplete and subjective pre-existing knowledge of authors or sites, whether the original paper specifically mentioned the Elm Decline, and the date of the publication, and whether the paper was available and searchable electronically. Moreover, the existence of a suitable paper did not axiomatically mean that the underpinning data were available for analysis within our research, nor that those data would have a suitable level resolution in dating. Therefore, to ensure that methods were transparent and objective, as well as being effective in the identification of sites that had available data, we followed the precepts of PRISMA (Page et al. 2021) to develop a clear workflow for site selection that would be repeatable.

Identification of potential sites and basic screening

The Neotoma database (Williams et al. 2018) was mined to identify sites across the British Isles—England, Wales, Scotland, Northern Ireland and the Republic of Ireland—with palynological data available in raw format as grain counts. Using this platform, potential sites were identified that met the screening criteria that there was: (1) an associated peer-reviewed published output; (2) at least two radiocarbon dates between 8000 and 4000 calendar Years Before Present (YBP); and (3) $\geq 2\%$ *Ulmus* in the time-sediment horizon equating to 6500 YBP. The requirement for two radiocarbon dates was predicated on the need for a robust age-depth model to calculate sedimentation rates using IntCal20—the latest calibration curve for terrestrial sites in the Northern Hemisphere (Reimer et al. 2020)—to enable interpolated dates to model time (1000 years) post-dating the Elm decline. The *Ulmus* criterion was based on 2% being the minimum pre-decline *Ulmus* percentage observed in a previous study of 25 woodland sites in Ireland affected by the Elm Decline (Kearney and Gearey 2024). Applying the *Ulmus* threshold at 6500 YBP was based on that same study finding that, although the Elm Decline was not spatially synchronous, it always occurred relatively soon after 6500 YBP. The fourth and final criterion was to ensure that each potential site was likely to be woodland with a relatively closed canopy, such that sites with $< 28\%$ arboreal pollen were excluded. This threshold was selected based on minimum values of arboreal pollen found at woodland sites in contemporary studies of pollen deposition being 28–29%, (Bunting 2002; Tinsley and Smith 1974 respectively). Over 100 sites were initially identified. Once each had been screened, 24 sites were carried through for more detailed assessment.

Detailed assessment of screened sites

For the 24 sites identified meeting the four above screening criteria, palynological data were extracted. Because different taxa produce pollen at different rates, there is a disconnect between vegetation assemblage and pollen abundance. Raw pollen counts thus needed to be corrected using taxon-specific Relative Pollen Productivity Estimates (RPPEs) to enable robust analysis of change in vegetation unbiased by differential pollen production (Andersen 1970; Parsons and Prentice 1981; Jackson 1994; Prentice and Webb 1986). To ensure RPPEs were as accurate as possible, the majority of the correction values were taken from Wieczorek and Herzschuh (2020), which collated data from different regions (e.g. Broström et al. 2008; Li et al. 2017). This removed much of the bias in variability inherent in RPPE values usually generated by single-site datasets. For taxa not listed by Wieczorek and Herzschuh (2020), RPPE values were taken from single-site studies (Bradshaw 1981; Bunting and Farrell 2022), or based upon RPPE values from similar taxa (Andersen 1970; Bradshaw 1981; Out and Verhoeven 2014). To apply RPPE corrections at each site, raw pollen data were converted to percentages for each time-sediment horizon, and these values were divided by the relevant taxon-specific RPPE value. RPPE-corrected values were used in analysis of within-turnover and change in individual taxa. Following the protocol of Kearney and Gearey (2024), the presence of a potential Elm Decline—a sustained reduction in *Ulmus*—at each site was examined by visually inspecting RPPE-corrected *Ulmus* abundance in each time-sediment horizon. Where no Elm Decline was evident, the site was immediately excluded ($n = 14$), with the remaining sites ($n = 10$) being taken through to a final verification step.

Verification

Where there was visual evidence for Elm Decline ($n = 10$), the period during which *Ulmus* underwent sustained reduction was identified, together with pre-decline and post-decline periods described below and shown visually in Fig. 1; a minimum of two time-sediment horizons was necessary in each period:

- "Pre-decline": the period before sustained *Ulmus* decline, during which *Ulmus* abundance was stable at relatively high values or fluctuating within a relatively narrow

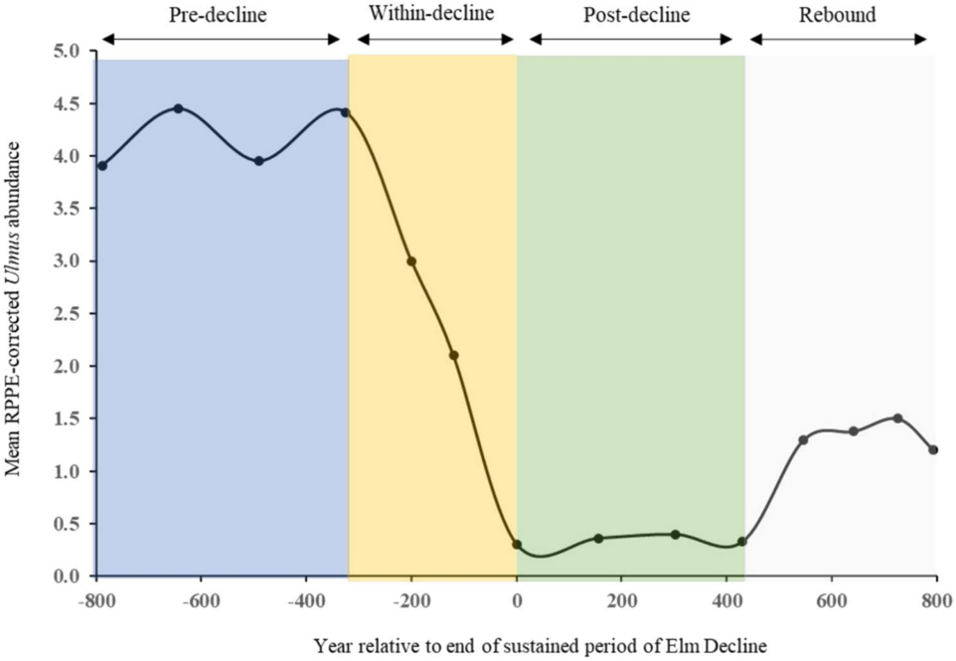


Fig. 1 Schematic of the Elm Decline time periods (colours link to those used on Figs. 3 and 4 for ease of reference)

range of high values, with no overall temporal change; maximum duration 1000 years dependent on sediment deposition and sampling rates.

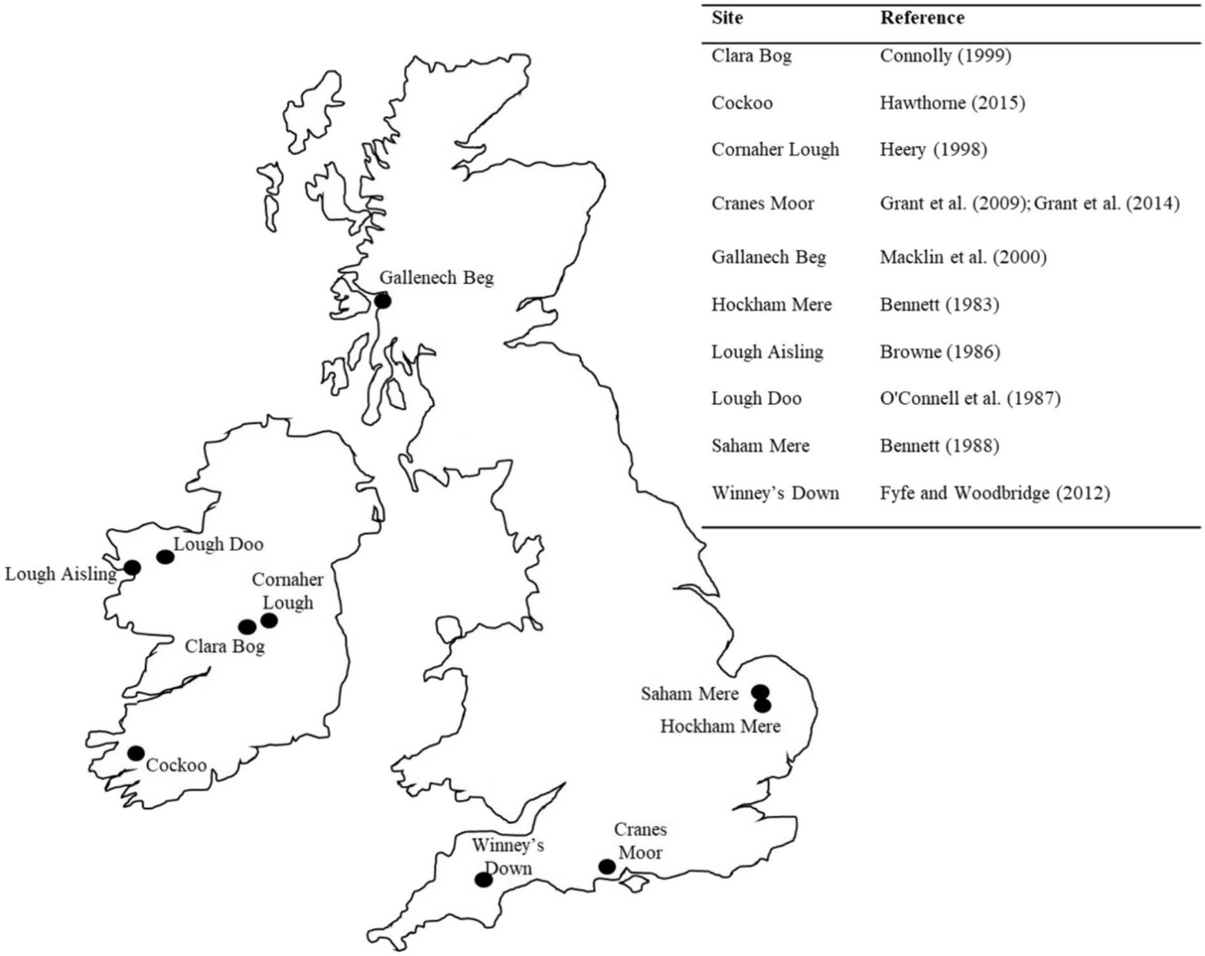
- "Within-decline": the period between the start of sustained *Ulmus* decline and the lowest value of *Ulmus* recorded; duration entirely data-driven and thus site dependent.
- "Post-decline": the period after sustained *Ulmus* decline, during which *Ulmus* was stable at low values or fluctuating within a relatively narrow range of low values with no overall temporal change; maximum duration 1000 years dependent on sediment deposition, sampling rates, and whether *Ulmus* rebounded.
- "Rebound": rebound of *Ulmus* from sustained low post-decline values; not always present.

Throughout this study, we are using change in the abundance of *Ulmus* during and after the Elm Decline as a proxy for woodland structural changes and canopy opening, which cannot be quantified directly. The 1000-year maximum window post-decline was selected as being an ecologically relevant timespan during which any vegetative change relating to the canopy changes caused by the Elm Decline, which might be affected by lag times, should be evident. It should be noted that while the process of (and criteria for) designating time periods was standardised, *Ulmus* abundance was site specific, as was duration and the number of time-sediment horizons. To confirm the presence of the Elm Decline at all potential study sites, a one-way ANOVA with Tukey post-hoc testing was run to ensure *Ulmus* abundance post-decline was statistically significantly lower than pre-decline. All sites passed the verification step; the final sample size was 10 sites (latitude: 50.622 N to 56.384 N; longitude: − 9.588 W to 0.833 E) that had significant Elm Decline (and as per Fig. 2).

Taxonomic richness

As the taxonomic level to which pollen can be identified based on morphological characteristics varies for different taxa, each site contained a combination of family-level, genus-level and species-level data. This inconsistency was not problematic because analysis of vegetation change was always undertaken at site level, or nested within site, and although taxonomic resolution differed *between* sites it was temporally consistent *within* each site. This meant that identified temporal patterns were not an artefact of changing taxonomic resolution over time and rendered taxonomic smoothing unnecessary. Each taxon was classified into one of three categories: (1) arboreal–woody species with the potential to form an overarching canopy; (2) shrub–woody species that *typically* occur in the scrub stratum within a woodland ecosystem; (3) herb–all non-woody vascular species from the field and herb layers of a woodland ecosystem including forbs, grasses, sedges, and rushes.

In contemporary ecological studies, taxonomic richness is usually a simple count of the number of taxa present. However, in palynological data variability occurs in the number of pollen grains counted by different researchers at different sites, as well as between time-sediment horizons in the same stratified sequence. This can present problems as taxonomic richness is fundamentally, and non-linearly,



Site	Reference
Clara Bog	Connolly (1999)
Cockoo	Hawthorne (2015)
Cornaher Lough	Heery (1998)
Cranes Moor	Grant et al. (2009); Grant et al. (2014)
Gallanech Beg	Macklin et al. (2000)
Hockham Mere	Bennett (1983)
Lough Aisling	Browne (1986)
Lough Doo	O'Connell et al. (1987)
Saham Mere	Bennett (1988)
Winney's Down	Fyfe and Woodbridge (2012)

Fig. 2 Location of the ten sites used in this study with data sources

dependent on the number of grains counted (Birks and Line 1992; Birks 2007). To avoid differences in sample effort biasing analysis, rarefaction was used to create a corrected taxonomic richness metric using PAST v4.12 (Hammer and Harper 2001; Hammer 2022); this approach has been used extensively within palaeoecological research (e.g. Li 2018; Robles-López et al. 2018; Pardoe 2021). Rarefied richness values were calculated for each time-sediment horizon at each site using the grain count for the lowest sample size at that site; this process was undertaken for the overall community and then separately for arboreal, shrub, and herb taxa. All analysis of taxonomic richness thus used (rarefied) pollen counts rather than RPPE-corrected values.

Taxonomic evenness

As noted by Legendre and Legendre (1998) and Peros and Gajewski (2008), taxonomic evenness—the extent to which relative abundance of each taxon is similar (uniform distribution) or dissimilar (skewed distribution)—is an important ecological metric that remains relatively underutilized in palaeoecological research. Here, we calculated Shannon's Evenness (E_H) for each time-sediment horizon. This involved quantifying Shannon's Diversity Index (H) with rarefaction applied using PAST v4.12. This ensured computed H values were calibrated relative to the lowest sample size at that site, in the same way that taxonomic richness had been corrected. Then, to get rarefied evenness for each time-sediment horizon, we undertook an extra manual step to divide the (rarefied) H value for each horizon by the natural logarithm of the (rarefied) taxonomic richness value for the same horizon to get (rarefied) E_H values. This metric was bounded between 0 and 1, with 1 indicating complete evenness (all taxa being uniformly abundant). In all cases, rarefied E_H values were calculated for the overall community and then separately for arboreal, shrub, and herb taxa. All analysis of evenness thus used the (rarefied) pollen counts rather than RPPE-corrected values.

Within-site turnover

While pollen data, after rarefaction, were appropriate for calculations of taxonomic richness and taxonomic evenness, consideration of within-site turnover necessitated use of RPPE-corrected values. This ensured analysis was reflective of vegetative change rather than change in the pollen profile. Of the many methods available for quantifying the similarity between two communities, we selected Bray–Curtis (Bray and Curtis 1957). This is highly effective for empirical ecological data as it is based on relative abundance rather than just presence/absence (e.g. Jaccard; Sørensen) and is robust in relation to outliers (Shaw 2003). Bray–Curtis similarity was computed in PAST v4.12 for each time-sediment horizon at each site relative to the previous time-sediment horizon within the stratified sequence. Bray–Curtis distance, which is more intuitive for considering turnover (i.e. dissimilarity), was then manually calculated. As per richness and evenness, turnover was calculated for the overall community and then separately for arboreal taxa, shrub taxa, and herb taxa.

Data analysis

To get an overall understanding of implications of canopy opening due to the effects of the Elm Decline on vegetation communities, we calculated Kruskal–Wallis tests for rarefied taxonomic richness, rarefied taxonomic evenness and within-site turnover, for the overall community and also separately for arboreal, shrub and herb taxa (n = 12 tests). In all cases, the grouping variable was time period (pre-decline, within-decline, and post-decline); rebound was excluded from this analysis as this was not present at all sites. We created graphs to visualise trends, which were supported by Mann–Whitney tests as non-parametric post-hoc analyses to follow Kruskal–Wallis and allow significant pairwise differences to be identified. These analyses were conducted in IBM SPSS v29.

Then, to analyse vegetation change in relation to canopy gaps due to the Elm Decline in more detail, a Generalised Linear Model (GLM) framework was used. Rarefied richness in each time-sediment horizon at each site was entered as the dependent variable and two palynological measures were added as covariate predictors: (1) *Ulmus* abundance at each time-sediment horizon using RPPE-corrected data; and (2) short-term change in *Ulmus* for each time-sediment horizon compared to the previous horizon (change direction indicated by negative or positive values; change magnitude indicated by deflection from zero). To allow site-specific differences in effects of the Elm Decline to be quantified, a nested framework was used with each palynological variable nested within Site ID. Four richness models were run to analyze, separately, overall community, arboreal taxa, shrub taxa, and herb taxa. This analytical framework was used also to analyze change in evenness using rarefied E_H values and for within-site turnover using Bray–Curtis distance. For all 12 models, GLMs used a gamma distribution with log link function, which consistently returned lower delta Akaike Information Criterion scores than scale models.

Finally, to understand the responses of specific taxa to the structural changes in the woodlands caused by the Elm Decline, we undertook SIMPER analysis for each site in Past v4.12. This used Bray–Curtis scores on RPPE-corrected data to allow identification of the most influential taxa driving the dissimilarity. As this analysis was pairwise, we undertook comparisons firstly for post-decline versus pre-decline and secondly for rebound versus post-decline. Together, this allowed consideration of which taxa differed after *Ulmus* had decreased post-decline relative to initial conditions and recovery.

Results

Evidence for Elm decline

There was conclusive evidence for the Elm Decline at our study sites. On average there was a 79% decrease in *Ulmus* abundance in ecological communities post-decline relative to pre-decline at the same site (minimum = 67% decline; maximum = 94% decline). This decline was statistically significant at all sites (one-way ANOVAs $P < 0.05$ in all cases; tests not shown). Follow-up Tukey post-hoc pairwise comparisons showed that *Ulmus* abundance was significantly lower after the Elm Decline relative to before the Elm Decline at all sites (Fig. 3a–j), with eight out of ten sites also showing at least one additional significant pairwise difference (Fig. 3a, b, d, f–j). This provided good evidence for structural changes in the woodland, including canopy opening.

Although *Ulmus* decline was observed at all sites, there were notable differences in pre-decline values from RPPE-corrected *Ulmus* abundance being as high as ~ 18% (e.g. Clara Bog and Gallanech Beg; Fig. 3a, d) to as low as ~ 2% (Lough Aisling and Winney's Down; Fig. 3f, j). Notwithstanding these initial differences, *Ulmus* abundance dropped to zero or very close to zero for at least one time-sediment horizon post-decline at all sites, although it was notable that *Ulmus* was not lost completely for > 1 horizon at any site. When averaging across all sites, *Ulmus* abundance using RPPE-corrected values were: pre-decline = 7.71%, within-decline = 4.33% and post-decline = 2.13%. When figures were recalculated just for sites that had a recovery phase (Fig. 3h–j) values were: pre-decline = 5.76%, within-decline = 1.99%; post-decline = 1.09%; rebound = 2.02%. This compared with sites where *Ulmus* did not

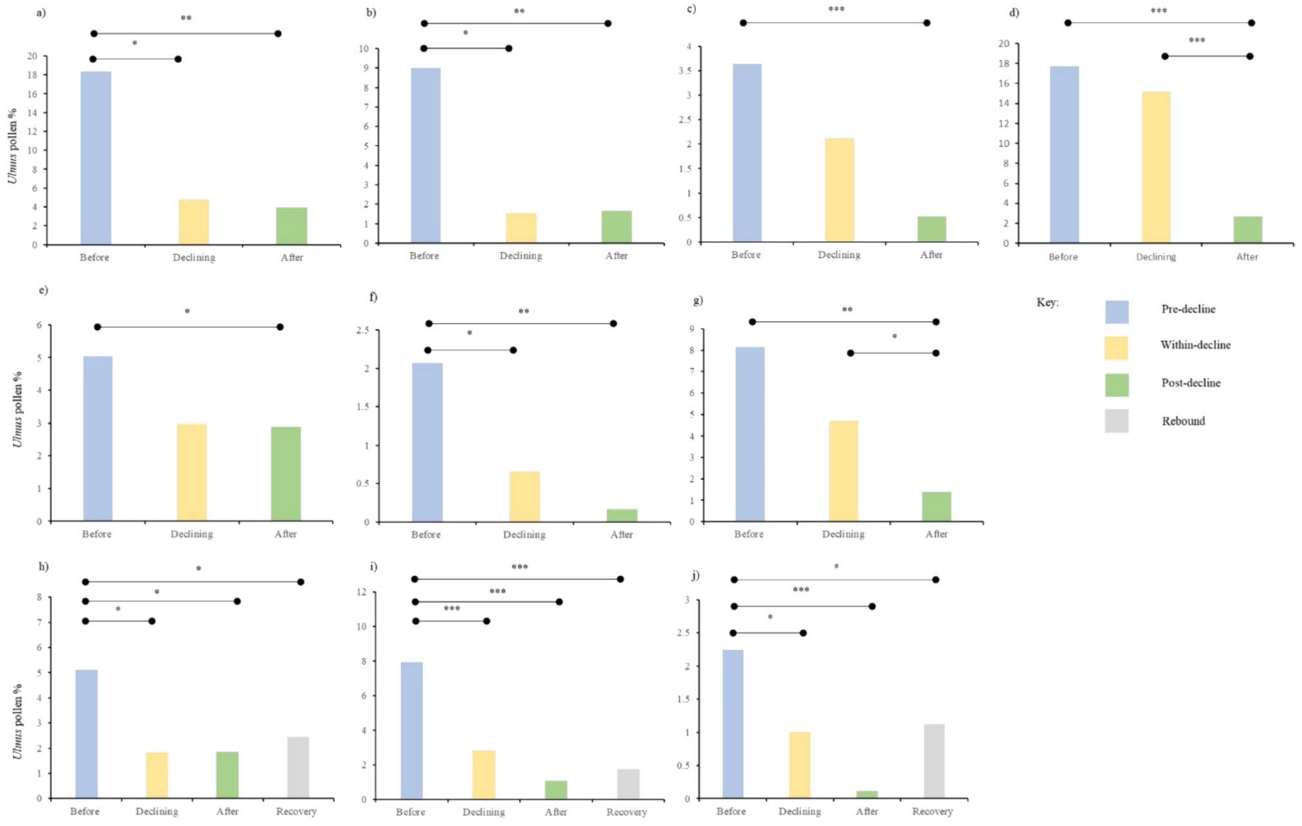


Fig. 3 Mean *Ulmus abundance* (RPPE-corrected values) before the Elm Decline (blue), within the decline (yellow), after the decline(green) and, where relevant, during rebound (grey). Sites listed: **a** Clara Bog; **b** Cornaher Lough; **c** Cranes Moor; **d** Gallanech Beg; **e** Hockham Mere; **f** Lough Aisling; **g** Lough Doo; **h** Cockoo; **i** Saham Mere; and **j** Winney's Down. One-way ANOVAs with Tukey post-hoc testing show statistical differences between communities. Asterisks indicates a significant difference $* < 0.05$; $** < 0.01$; $*** < 0.001$

rebound (Fig. 3a–g) thus: pre-decline = 8.33%, within-decline = 5.33%; post-decline = 2.35%. This suggested that sites with a higher initial *Ulmus* abundance declined to low *Ulmus* levels (~2%) post-decline that then remained fairly consistent, whereas sites with lower pre-decline *Ulmus* abundance originally decreased even further but subsequently rebounded to a similar *Ulmus* abundance (~2%).

Effects of Elm decline on vegetation community metrics

Across all sites and all time-sediment horizons, rarefied taxonomic richness calculated using pollen counts was lowest for shrub taxa (mean = 3.06 taxa), intermediate for arboreal taxa (mean = 6.98), and highest for herb taxa (mean = 7.71). Rarefied evenness calculated on pollen counts differed substantially between taxa, being highly uneven within the shrub sub-community (mean $E_H = 0.30$), while the arboreal and herb communities were considerably more even (mean $E_H = 0.73$ and 0.78, respectively). Within-site turnover calculated using Bray–Curtis dissimilarity on RPPE-corrected values was, on average, lowest for arboreal taxa (mean = 0.18), intermediate for shrub taxa (mean = 0.33) and highest for herb taxa (mean = 0.44).

When testing for any impact of the canopy opening associated with the Elm Decline on richness, evenness and within-site turnover using Kruskal–Wallis and Mann–Whitney tests, several patterns emerged. For each taxonomic group, richness values were approximately equal pre-decline and within-decline (Fig. 4a–d). Visually, richness in the overall community and the arboreal sub-community decreased by ~ 50% post-decline in comparison to pre-decline levels (Fig. 4a, b). The opposing trend was found for shrub and herb taxa, where richness increased by ~ 100% post-decline relative to pre-decline (Fig. 4c, d). High levels of within- and between-site variation meant that the only statistically significant pattern was for shrub richness (Table 1; Fig. 4c). For evenness, a significant pattern was found for the arboreal sub-community due to a significant decrease in evenness post-decline relative to pre-decline levels (Table 1; Fig. 4f). This significant pattern contrasted with fairly uniform evenness temporally for the overall community (Fig. 4e) and for shrub and herb taxa (Fig. 4g–h). For

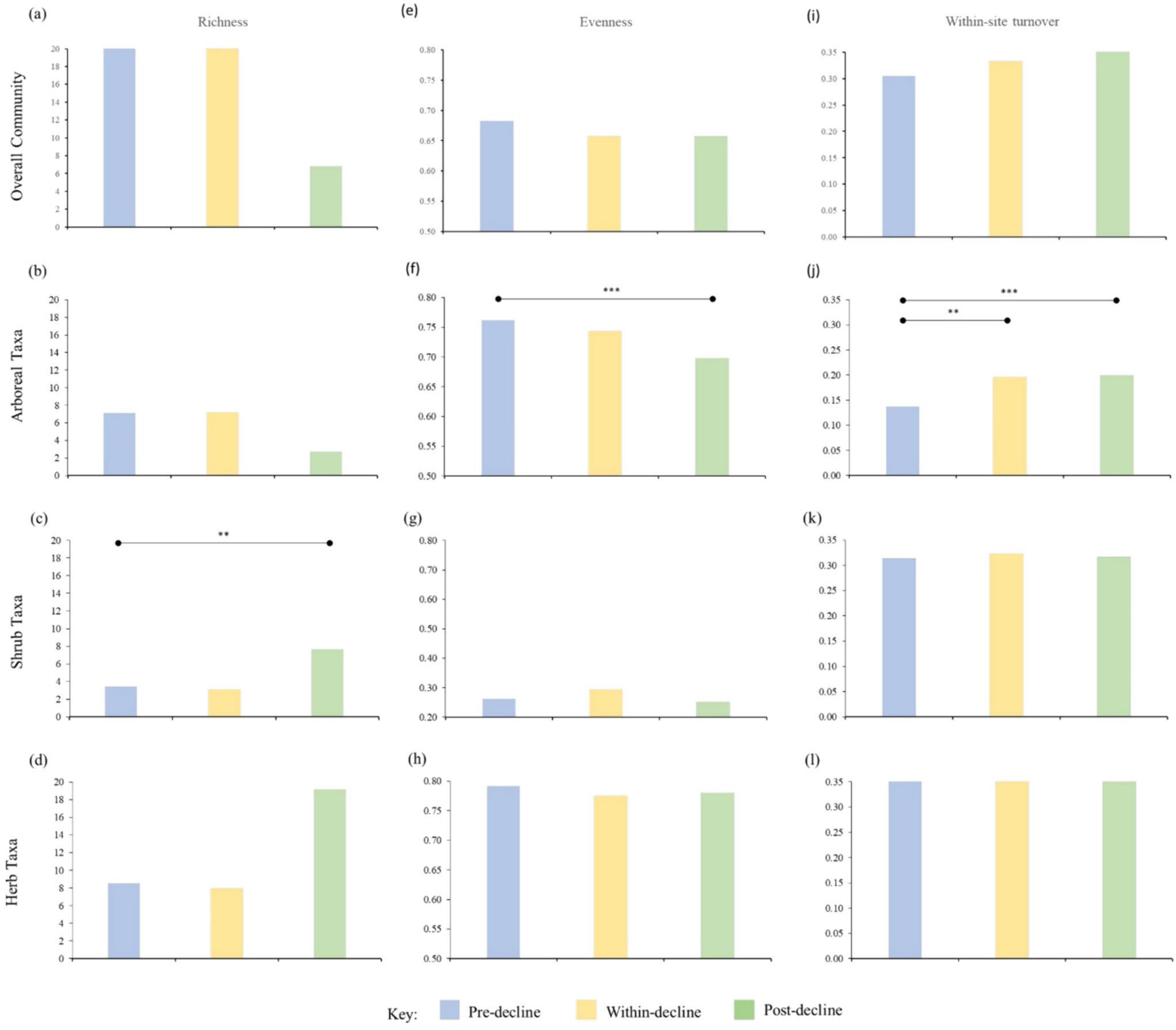


Fig. 4 Mean values across all sites pre-decline, within-decline and post-decline for: **a – d** rarefied taxonomic richness (number of taxa); **e – h** rarefied taxonomic evenness (0 – 1 index); and **i – l** within-site turnover (0 – 1 index) calculated on RPPE-corrected data. Asterisks indicate a significant difference via Mann–Whitney pairwise tests $* < 0.05$; $** < 0.01$; $*** < 0.001$

Table 1 Kruskal–Wallis tests for temporal change in rarefied richness and rarefied evenness (pollen counts) and within-site turnover (RPPE-corrected values)

Taxa	Richness		Evenness		Within-site turnover	
	H	P	H	P	H	P
Overall community	2.940	0.230	1.595	0.450	3.191	0.203
Arboreal taxa	3.207	0.201	11.677	**0.003**	15.395	**< 0.001**
Shrub taxa	7.314	**0.026**	0.315	0.854	1.536	0.464
Herb taxa	2.036	0.361	0.681	0.712	0.777	0.678

Tests conducted in relation to Elm Decline period (pre-decline, within-decline, post-decline); df = 2 in all cases. Mann–Whitney tests, undertaken as non-parametric post-hoc analyses, are shown in Fig. 4

Bold in table 1 highlights values that are statistically significant turnover, significant patterns were found for arboreal taxa due to turnover being lower pre-decline and higher post-decline (Table 1; Fig. 4j). There was little change for other taxonomic groupings (Fig. 4i, k – l).

There were notable differences between community metrics during rebound (closing or partial closing of canopy) relative to other periods of the Elm Decline, as detailed in Table 2. Most significant findings related to within-site turnover, which was significantly higher during rebound compared to pre-decline for arboreal taxa (mean = 0.29 vs 0.21) and shrub taxa (mean = 0.42 vs 0.25). A significant counter pattern was observed for herb taxa, with turnover being lower during rebound relative to pre-decline (mean = 0.41 vs 0.70). Turnover was also significantly higher during rebound than post-decline for shrub taxa (mean 0.42 vs 0.33). The only other significant pairwise comparison was a significant increase in evenness for arboreal taxa during rebound relative to pre-decline (mean = 0.78 vs 0.72).

Site-specific trends

All nested GLMs undertaken to better understand the influence of (RPPE-corrected) *Ulmus* abundance and short-term change in *Ulmus* abundance on community richness, evenness and within-site turnover were significant, with the single exception of turnover for shrub taxa (Table 3). *Ulmus* abundance was a significant term in each of the 11 significant models, while short-term *Ulmus* change (i.e. relative difference in *Ulmus* compared to the previous time-sediment horizon) was significant in only five models. In the five models where both *Ulmus* predictors were significant, the *Ulmus* abundance was notably stronger as a predictor. This suggests that the overall amount of *Ulmus*, which was driven by long-term change, was the main driver in community metrics, rather than short-term changes between time-sediment horizons.

One of the major strengths of the nested analytical framework was the finding that the same analysis resulted in markedly different patterns at different sites (Table 3). To understand this complex picture, we investigated the relative number of sites where change in *Ulmus* abundance and/or short-term *Ulmus* change was positively or negatively associated with the dependent variable, as well as the mean positive and mean negative gradients as a measure of effect size. Together, this information captured both the trend prevalence and trend strength. In most models, the ratio between whether a significant factor was positively or negatively related to the dependent variable was approximately even (no more unbalanced than 60% of sites in one direction versus 40% of sites in the opposing direction) and effect sizes were also approximately equal., However, there were some clear trends: (1) evenness of arboreal taxa was significantly higher when *Ulmus* was more abundant at nine out of ten sites, and the average effect size was considerably larger than found at the single site with the opposing trend; (2) within-site turnover in the overall community was significantly lower when *Ulmus* was more abundant at seven of ten sites; (3) within-site turnover in arboreal taxa was significantly lower when *Ulmus* was more abundant and significantly higher when recent *Ulmus* change was negative (i.e. when *Ulmus* was declining over the short-term) at the majority of sites, with larger effect sizes than for opposing trends. For richness of shrubs, it was also noted that although there was little difference in the ratio of sites with positive and negative trends, at the six sites where higher *Ulmus* abundance was associated with greater richness there was a much larger effect size than found at the four sites where lower *Ulmus* abundance was associated with greater richness.

SIMPER analysis (Table 4) showed substantial dissimilarity in post-decline communities compared to pre-decline (mean dissimilarity = 44.32; minimum = 30.47; maximum = 57.01). Unsurprisingly, the taxa driving dissimilarity were largely site-specific, but there were some general trends. Abundance of shrub taxa increased at seven of the ten sites (*Calluna* at four sites; *Ilex* at three sites; and *Corylus* at two sites). Woody climbing taxa (*Hedera* and *Lonicera*) changed at eight of ten sites although in the case of *Hedera* these changes were conflicting with

Table 2 Comparison of community-level metrics for sites exhibiting rebound in *Ulmus* based on *P* values from Mann–Whitney tests

Taxa	Richness Rebound versus			Evenness Rebound versus			Within-site turnover Rebound versus		
	Pre-decline	Within-decline	Post-decline	Pre-decline	Within-decline	Post-decline	Pre-decline	Within-decline	Post-decline
Overall community	1.000	0.120	0.151	0.160	0.131	0.224	0.483	0.962	0.792
Arboreal taxa	0.620	0.081	0.854	0.302	0.671	**0.027**[a]	0.536	0.888	**0.035**[b]
Shrub taxa	0.083	0.278	1.000	0.741	0.540	0.796	0.021b	0.258	**0.016**[b]
Herb taxa	0.433	0.081	0.090	0.68	0.203	0.113	0.302	0.637	**0.035**[a]

a, lower during rebound; b, higher during rebound

Table 3 Nested generalised linear models of richness, evenness and within-site turnover against the predictors of *Ulmus* abundance and short-term *Ulmus* change in relation to the previous time-sediment horizon

Model			χ^2	P	Site-specific Patterns	
Richness	Overall	Full Model	155.372	<0.001		
	Community	*Ulmus* abundance	250.864	<0.001	−0.074	0.052
		Ulmus change	46.712	<0.001	−0.068	0.025
	Arboreal	Full model	95.496	<0.001		
	Taxa	*Ulmus* abundance	112.125	<0.001	−0.046	0.033
		Ulmus change	24.579	0.006	−0.048	0.025
	Shrub	Full Model	120.779	<0.001		
	Taxa	*Ulmus* abundance	173.396	<0.001	−0.063	0.241
		Ulmus change	7.970	0.632		
	Herb	Full Model	148.719	<0.001		
	Taxa	*Ulmus* abundance	294.767	<0.001	−0.088	0.112
		Ulmus change	50.990	<0.001	−0.054	0.045
Evenness	Overall	Full Model	99.335	<0.001		
	Community	*Ulmus* abundance	130.770	<0.001	−0.010	0.036
		Ulmus change	6.532	0.769		
	Arboreal	Full Model	73.161	<0.001		
	Taxa	*Ulmus* abundance	81.453	<0.001	−0.007	0.034
		Ulmus change	16.998	0.074		
	Shrub	Full Model	136.861	<0.001		
	Taxa	*Ulmus* abundance	201.279	<0.001	−0.159	0.188
		Ulmus change	16.759	0.080		
	Herb	Full Model	109.672	<0.001		
	Taxa	*Ulmus* abundance	151.966	<0.001	−0.026	0.018
		Ulmus change	25.717	0.004	−0.022	0.034
Within-site	Overall	Full Model	41.296	0.003		
Turnover	Community	*Ulmus* abundance	37.553	<0.001	−0.081	0.053
		Ulmus change	11.424	0.325		
	Arboreal	Full Model	88.569	<0.001		
	Taxa	*Ulmus* abundance	103.989	<0.001	−0.145	0.078
		Ulmus change	22.23	0.014	−0.188	0.075
	Shrub	Full Model	17.023	0.651		
	Taxa	*Ulmus* abundance	14.793	0.140		
		Ulmus change	4.655	0.913		
	Herb	Full Model	43.602	0.002		
	Taxa	*Ulmus* abundance	37.274	<0.001	−0.088	0.075
		Ulmus change	11.851	0.295		

RPPE-corrected values were used for all analyses. The site-specific patterns show the proportion of the ten sites with negative correlations (light grey) versus positive correlations (dark grey), with the mean gradient for each grouping given as a measure of effect size; df = 20 for each full model, split equally between each of the two terms as there were 10 sites in all cases and a nested framework was used

decreases at five sites contrasting with increases at two sites. *Plantago*, a species indicative of disturbance, increased in abundance at seven of the ten sites. SIMPER analysis comparing communities immediately post-decline with the *Ulmus* rebound period revealed that *Hedera* increased (after having decreased throughout the Elm Decline), while *Plantago* abundance continued to increase at all three sites with *Ulmus* rebound.

Discussion

Baseline trends

All sites within this study had substantial, sustained and significant Elm Decline; indeed, this was a prerequisite for inclusion in this research, which uses the Elm Decline as a proxy for changing canopy openness. Relative decline in *Ulmus* varied in magnitude between sites (67–94%) and

Table 4 SIMPER analyses of community dissimilarity calculated comparing the vegetation community pre-decline versus post-decline (ten sites) and relative to rebound (three sites)

Comparison and site		*Ulmus* change	Community dissimilarity	SIMPER: Taxa driving community dissimilarity
Pre-decline versus post-decline	Winney's Down	−94%	30.73	*Calluna vulgaris* (−6%); *Plantago lanceolata* (+596%); *Hedera helix* (−16%); Cyperaceae (+49%)
	Saham Mere	−91%	52.33	*Hedera helix* (−67%); *Quercus* (-43%); *Taxus baccata* (+512%); *Tilia cordata* (-82%)
	Lough Aisling	−84%	37.18	*Plantago lanceolata* (gained); *Hedera helix* (+59%); *Ilex* (gained); Poaceae (-17%); *Salix* (+229%)
	Cranes Moor	−82%	38.54	*Calluna vulgaris* (+123%); *Plantago lanceolata* (+82%); *Hedera helix* (−84%); *Myrica gale* (+22%); *Melampyrum* (+476%); *Quercus* (−23%)
	Lough Doo	−80%	38.86	*Ilex aquifolium* (−53%); *Plantago lanceolata* (+276%); *Hedera helix* (+22%); *Calluna vulgaris* (+946%)
	Gallanech Beg	−78%	54.55	*Nymphaea* (+236%); *Lonicera periclymenum* (+24%); *Plantago* (+483%)
	Cornaher Lough	−76%	54.42	*Plantago lanceolata* (−293%); *Ilex* (+389%)
	Hockham Mere	−71%	49.11	*Hedera helix* (−84%); *Corylus* (+67%); *Quercus* (−27%)
	Clara Bog	−69%	57.01	*Plantago* (gained); *Calluna* (+88%); *Hedera helix* (lost)
	Cockoo	−67%	30.47	*Erica* (-39%); *Plantago* (+26%); *Calluna* (+39); *Ilex* (+48%)
Rebound versus post-decline	Cockoo	+38%	62.09	*Plantago* (+177%); *Calluna* (−40%); *Erica* (+19%); Poaceae (−21%); *Ilex* (+1%); *Quercus* (+22%); *Glaucium* (lost); *Salix* (gained); *Hedera* (gained); *Malva* (gained)
	Saham Mere	+148%	42.76	*Plantago* (+562%); *Quercus* (+37%); *Taxus baccata* (-9%); *Hedera helix* (+76%); *Ilex aquifolium* (gained); *Tilia cordata* (+146%); *Corylus* (−16%); Poaceae (+85%)
	Winney's Down	+520%	59.72	*Calluna vulgaris* (−65%); *Plantago lanceolata* (+13%); *Filipendula* (gained); *Hedera helix* (+81%); *Quercus* (−57%); *Juglans* (gained); Ericaceae (gained); Cyperaceae (−50%); *Trifolium* (gained); Poaceae (−52%); *Salix* (+459%); *Alnus* (−70%); *Corylus* (+4%)

This metric is on a scale of 0−100, where higher values indicate higher dissimilarity. All taxa that contributed as much or more to community dissimilarity as Ulmus are named in descending order from the greatest contributor. Note that the contribution rankings depend on the magnitude of the change and the original abundance of that taxon (i.e. the same difference in abundance will have a larger influence for a more abundant taxon than for a less abundant taxon). The direction and magnitude of each taxon difference is illustrated by percentage difference in mean RPPE-corrected values between the communities

there was also notable spatial variation in actual *Ulmus* abundance both pre- and post-decline. The pre-decline abundance of *Ulmus* varied from ~ 2 to 18% between our sites across the British Isles. This roughly accords with ~ 2–22% across the Irish sites studied by Kearney and Gearey (2024), despite our data being RPPE-corrected rather than raw pollen percentages. Post-decline, Kearney and Gearey's sites ranged from "minimal values" to ~ 5%, with 1–2% being typical; this again agrees with our findings despite differences in data. These comparisons are not confounded by site overlap as only one site (Lough Aisling) was common to both studies.

Partial rebound was identified at three study sites (30%): *Ulmus* abundance showed a marked uptick relative to abundance immediately post-decline but remained substantially and significantly lower than pre-decline levels. Similar partial recovery has been seen in other cases where an important tree species has been lost, including *Fraxinus* woodland affected by Ash Dieback (Heinze et al. 2017). This could be driven by natural (and likely heritable) disease resistance, which allows some persistence of the species (Coker et al. 2019), followed by a negative correlation between disease susceptibility and reproductive success facilitating partial recovery as trees with natural immunity have higher reproductive fitness (Semizer-Cuming et al. 2019).

Reduction in a prevalent tree species in woodland will axiomatically change community composition (Needham et al. 2016). Primary research in the USA by Fajvan and Wood (1996) found that loss of mature *Quercus* resulted in increases in subdominant *Acer* species, while high mortality in *Ulmus* due to contemporary Dutch Elm Disease in Sweden led to increases in competitively inferior *Quercus* and *Fagus* (Brunet et al. 2014), which, quite literally, filled the gap. Both these situations accord with the competitor release hypothesis (Crawley 1997). As expected, therefore, there were significant effects of Elm Decline on richness, evenness and within-site turnover in the palaeoecological analogue examined here. Most importantly, the post-decline period was associated with greater unevenness in arboreal taxa and higher rates of arboreal turnover when compared to pre-decline; there was also a substantial and significant increase in shrub richness post-decline relative to pre-decline.

Change in arboreal taxa

Evidence for higher within-site turnover in arboreal taxa both during and post-decline compared to pre-decline is unsurprising. This is driven not only by a decrease in *Ulmus* but also by increases in other arboreal taxa that were, filling the gaps. As such, this metric is essentially recording the magnitude of the ecological response to biotic change at community level, in a similar way to that which has been observed for climate change, both in primary ecological research (Hillebrand et al. 2010; Ulrich et al. 2014; Gibson-Reinemer et al. 2015; James et al. 2017) and when using palaeoecological analogues (Webb and Goodenough 2021). However, change in the arboreal sub-community to become *less* even after decline in a key tree species at first seems counter-intuitive, since this might be expected to rebalance the community and promote greater evenness (Yang et al. 2018). However, this is likely due to canopy gaps at most sites being filled by whatever other arboreal species is/are next most abundant in that community rather than being randomly selected from those present, especially if sub-dominant species are pioneer trees within secondary succession (Fajvan and Wood 1996) or if there is one highly-dominant species where decline in *Ulmus* would likely make the other taxon more dominant as the probability of that species filling the gap would be high. Together, these processes could act to make communities more strongly skewed than previously (Mitchell et al. 2016). This situation has been observed in models of lowland woodland in the UK in relation to simulated Ash Dieback (Needham et al. 2016), and observed in primary studies on loss of dominant trees in the USA and mainland Europe (Fajvan and Wood 1996; Brunet et al. 2014). It was also notable in our data that arboreal richness did not increase, suggesting that gaps were filled by taxa already present in the community, which also supports this explanation. Our findings thus indicate the potential of the palaeoecological record for researching this phenomenon over timespans that exceed those typically possible (and fundable) in primary ecological research, without the assumptions inherent in predictive modelling.

Investigating the effects of *Ulmus* abundance (driven by long-term *Ulmus* decline) and short-term change in *Ulmus* on arboreal taxa in more detail produced some consistent patterns across the majority of sites: (1) evenness was significantly higher when *Ulmus* was more abundant; and (2) turnover was significantly lower when *Ulmus* was more abundant and significantly higher when recent *Ulmus* change was negative. These patterns reinforce the overarching conclusions above and highlight the generality of these findings across most sites. They also suggest that turnover was driven both by long- and short-term change in *Ulmus*, although the former was more important. When considering specific taxa, change in the abundance of *Quercus*, *Taxus*, and *Tilia* was recorded at different sites. Change in *Quercus* and *Taxus* was noted in some of the Irish sites studied by Kearney and Gearey (2024), although that research only documented arboreal taxa that increased contemporaneously with, or immediately after, the Elm Decline rather than change in either direction. This methodological difference, and smaller study area, might explain why there was a more consistent palaeoecological signal in response to canopy changes associated with the Elm Decline in Ireland than the strongly site-specific patterns across the British Isles presented here. Similar idiosyncratic site-specific differences have been found previously when considering the effects of the same broadscale changes, for example, patterns of climate variability 6000–9000 years ago (Seddon et al. 2015) and in response to the abrupt climate perturbation 8200 years ago (Webb and Goodenough 2021). This also agrees with Williams et al. (2011) who found that even when there was widespread directional vegetation change, this was mediated by local biotic and abiotic processes and by stochastic processes such as disturbance events.

A decrease in the woody climbing taxon *Hedera* was noted at 50% of sites post-decline when compared with abundance of this same species pre-decline, with recovery subsequently noted at two of the three sites showing *Ulmus* rebound. This change is unlikely to be linked directly to loss of *Ulmus* as a host species as *Hedera* has limited host preference, however, as the majority of *Hedera* biomass is on older trees (Castagneri et al. 2013), loss of mature (*Ulmus*) and replacement with younger trees (any species) could have an effect. Alternatively, or in combination, it is possible that loss of *Hedera* post-decline, and subsequent rebound, links to the creation and refilling of canopy gaps. The effect of canopy openness has been noted in modelling of *Hedera* between different woodlands (van Couwenberghe et al. 2011), and is likely driven by *Hedera* preferring deep or intermediate shade (Ellenberg 1991). *Hedera* is also known to decrease at more exposed sites, especially if that increases vulnerability to colder conditions (Metcalfe 2005; Birks 2011).

Change in shrub taxa

The increase in shrub richness and an increase in abundance of important shrub taxa (*Calluna, Ilex* and *Corylus*) at seven of 10 sites with documented Elm Decline in our dataset is interesting since it hints at a likely structural change in woodland habitat in strata other than the canopy. This might result from these species, many of which are woody pioneers within secondary successional processes, increasing in response to greater sunlight and physical space caused by *Ulmus* loss. This was not expected, especially given research by Nagel et al., (2019) in coniferous woodland when the loss of *Abies* from the canopy led to lower shrub richness. However, it does reflect the descriptive palaeoecological findings of Kearney and Gearey (2024) ~ 40% sites were noted to have an increase in shrub species, primarily *Corylus*—it is recognised that, on occasion, *Corylus* can be tall and single-stemmed; classification as a shrub is based likely place in woodland strata at the majority of sites.

If a similar increase in the shrub layer abundance and richness in deciduous woodlands to that seen during the Elm Decline occurs in future scenarios involving canopy gaps as the result of systematic decline in, or loss of, a specific tree species due to non-native pests (Fajvan and Wood 1996; Francis and Elmes 2017), disease (Enderle et al. 2019), and climate change (Iverson & Prasad 2001; Mette et al. 2013), this is likely to alter the composition of faunal guilds in complex ways. For example, an increase in understory would likely change the avian guild, which is strongly determined by habitat (Amar et al. 2006), benefiting some specialist taxa, such as *Luscinia megarhynchos* (nightingale) and *Poecile montanus* (willow tit) (Hewson et al. 2007; Dyda et al. 2009) but decreasing suitability for aerial insectivores such as *Ficedula hypolucea* (pied flycatcher) (Vanhinsbergh et al. 2003). As all three of these species are currently declining rapidly (Amar et al. 2006; Gregory et al. 2007), structural changes in woodlands related to loss of specific tree species would have differential impacts on fauna. This is a level of complexity that has not been fully considered in work, for example, on the impacts of Ash Dieback, which has focused more on changes to *Fraxinus*-associated species and deadwood abundance.

Change in herb taxa

The systematic decline in, or loss of, a specific tree species within woodland will, at least temporarily, create canopy gaps and thus increase sunlight reaching the forest floor. Because this would be to the advantage of light-loving taxa and the disadvantage shade-loving taxa, it was expected that the past Elm Decline—considered in this research as a palaeoecological analogue for tree loss in contemporary settings—would increase turnover in the herb layer. This has been found in primary ecological research (Aszalós et al. 2023) and in predictive work into the likely effects of contemporary Ash Dieback on woodland flora (Needham et al. 2016). It was also expected that such turnover might have altered richness and evenness metrics, although it is noted that turnover can occur in the absence of change in richness and evenness if taxa changes remain balanced (Santini et al. 2017; Webb and Goodenough 2021). Somewhat surprisingly, therefore, we found no significant differences in herb taxa metrics in our study. This might be because the effect of the Elm Decline on herbs, even using relative high-level community metrics of richness, evenness and turnover, was highly site-specific. This is suggested by the split in the number of sites with positive and negative relationships in the influence of *Ulmus* abundance and *Ulmus* change on herb richness, evenness and turnover. Alternatively, the influence of Elm Decline on annual herbs could have been so rapid and short-lived that it is not well reflected in the palaeoecological record. It is also possible that taxonomic resolution played a role if turnover involved species in the same genus (or, in some cases, genera in the same family), which might not be detected given the level to which some taxa can be identified using pollen (Moore et al. 1991; Birks 1993, 2007).

The lack of overall patterns in herb richness, evenness and within-site turnover should not be considered synonymous with there being no effect on herb taxa. Indeed, considering taxa-level changes demonstrates that findings are very site-specific, but there is a general trend in the disturbance-loving *Plantago lanceolata*, which increased at 70% of our study sites and 76% of the sites documented by Kearney and Gearey (2024). It has previously been postulated (e.g., Whitehouse et al. 2014) that the Elm Decline was linked to the contemporaneous onset of Neolithic agriculture rather than disease, with *Plantago* increases at this time being evidence of this. However, Kearney and Gearey (2024) suggested that while the two events might share similar timing, this is correlation rather than causality. For the purposes of our research, the causality of the Elm Decline and subsequent interplay between human activity and natural disturbances in woodland is largely irrelevant in a study of the biotic impacts, especially as contemporary changes in woodland, for example due to Ash Dieback, will be similarly complex due to multiple co-occurring natural and anthropogenic stressors.

Conclusions and relevance to current woodland challenges

In this paper, we have built on the extensive literature on the abrupt, widespread, and often permanent, Elm Decline that occurred throughout much of northwestern Europe ~ 5800 years ago leading to an opening of the tree canopy. Whereas most research to date has focused on spatiotemporal synchrony and causal mechanisms, or has considered the effects of Elm Decline within single-site reconstructions, our aim was to quantify cascade effects of *Ulmus* canopy loss throughout the ecological community. The *raison d'etre* for the research was thus not about past Elm Decline per se, but rather use of this as a palaeoecological analogue through which to consider possible consequences of current and future declines in specific tree species on the wider vegetation community (and thus ecosystem services).

It is important to highlight that because of the rigorous site selection criteria used here, the number of sites that could be included in this study was lower than would be ideal in terms of ensuring general applicability of findings to similar contexts in other parts of the world and should, as with any research on relatively few sites, be considered as indicative rather than definitive. However, the fact that the phytogeography of *Ulmus* is unchanged throughout the last 9500 years (Parker et al. 2002) means that using community responses to change *Ulmus* abundance in the past (at a time of natural and human change) as a proxy for contemporary change (also at a time of natural and human change) is well founded. Moreover, this approach allows consideration of change over much longer time periods than would be possible (or fundable) in primary ecological work and avoids the assumptions and uncertainty implicit in predictive modelling.

The key findings and caveats are outlined below:

1. There were comparatively few generalized findings, even in the relatively high-level community metrics of richness, evenness and within-site turnover. Trends in the abundance of specific taxa contemporaneously with, or immediately after, the Elm Decline were especially spatially idiosyncratic and might change in other locations dependent upon spatiotemporal variables and local conditions.
2. Many, but not all, of the cascade effects in the vegetation community could be linked back to change in ecosystem structure, especially canopy gaps and resultant impacts on understory taxa.
3. Decline in, or loss of, a tree species decreased arboreal evenness rather than increased it, likely because recruitment of arboreal taxa to "fill the gap" was driven by relative abundance of dominant or subdominant taxa.
4. There were substantial and significant decreases in woody climbing taxa, which are not often a focus in primary ecological surveys (Castagneri et al. 2013).
5. Shrub richness and density increased. Mirroring of this finding in the future would have substantial implications on non-vegetative species including invertebrates, birds and mammals, thereby further extending the cascade effects it has been possible to document here. However, high browser density in contemporary ecosystems might reduce scrub invasion (and arboreal regeneration) (Dolman 2010).
6. Vegetation responses in contemporary situations would be complicated by human influence, including silviculture, management and conservation. Indirect effects, such as an increase in non-native species, could also have an effect especially where these species have invasive tendencies or are pioneer species (Needham et al. 2016).

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