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Vegetation community changes in European woodlands amid a changing climate: a palaeoecological modelling perspective.

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Climate has an important role in shaping the composition and structure of woodlands. There is considerable uncertainty regarding how woodlands will respond to climate change over the next hundred years. To better understand likely responses to contemporary climate change, this paper analyses taxonomic richness, evenness and community similarity in palaeoecological data from 31 European woodlands during an abrupt cooling and warming event c. 8,200 years ago. Repeated measures ANOVAs demonstrated there was no significant overall difference in richness or community evenness over time. A single significant pairwise contrast was found (richness decreased as climate warmed) but was short-lived, indicating that high-level effects were temporary. However, analysis of species turnover measured using community similarity revealed substantial changes (only 24% of species remained at some sites after climatic change), indicating that the actual species within that community had altered. General(ised) Linear Models showed variation in the direction and magnitude of community change was not related to the broadscale biogeographical variables of latitude, longitude or altitude. Our research has several important implications for practitioners involved in community ecology research and woodland management. Although site-level richness is largely unaffected, we caution that there will be considerable species turnover in woodlands as the climate warms. As species turnover at individual sites will have a negligible effect if driven by localised random processes, we recommend practitioners to consider long-term gamma diversity wherever possible. This shifts focus towards landscape-scale approaches that span generations rather than the typical 3-5-year span of funding, management plans and political cycles.

Keywords: 8.2 ka event; climate change; ecological stability; community similarity; diversity; species turnover

Introduction

The influence of humans on Earth's vegetation and climate is becoming increasingly profound. Mean global terrestrial air temperatures have increased by 0.8°C since 1900 (Hansen et al. 2006), while the twelve hottest years since records began in 1880 have all occurred since 2000 (NASA/GISS 2021). Climate change projections for Europe suggest a 4 - 5°C temperature increase in Mediterranean and Boreal zones, with an increase of 3°C likely in Central Europe and 2°C in the UK and Ireland over the next 80 years (Christensen et al. 2007).

Although higher annual temperatures (driven by an increase in atmospheric CO_2) can increase tree growth rates and promote establishment of woodlands (Broadmeadow 2002; Anderson et al. 2006), shifting climatic envelopes and increasing frequency of extreme weather events associated with climate change can strongly influence woodland plant communities (Broadmeadow et al. 2009; Ray et al. 2010; Cavers and Cottrell 2015; Hoegh-Guldberg et al. 2018). The effects can be especially profound at latitudinal extremes and high altitude, where the vegetation is vulnerable to environmental disturbance (Breshears et al. 2008).

It is often assumed that the overall impacts of a warming climate on woodland biodiversity will be substantial and, in many cases, negative (Hooper et al. 2012; Pimm et al. 2014, McGill et al. 2015). However, the impacts of contemporary climate change can be surprisingly challenging to identify in established woodlands, particularly as long-lived arboreal species may be relatively tolerant of wide variations in annual weather conditions. This tolerance is evidenced by ancient trees, some of which established 600 years ago (in the case of the Tortworth Chestnut in Gloucestershire) and survived the cold winters of the Little Ice Age (17th Century) and are currently surviving the recent increase in hot summers.

Woodlands, particularly ancient woodlands and ancient semi-natural woodlands, provide an exceptionally valuable habitat for wildlife (Goldberg et al. 2007; Rotherham 2011) as well as providing a multitude of ecosystem services (Quine et al. 2011; Bullock et al. 2014). Maintaining rich and diverse woodlands is, therefore, important in conservation contexts, with many practitioners increasingly moving from single-species initiatives to landscape-scale approaches that focus on entire ecological communities (Lawton et al. 2010; Jones 2011; Donaldson et al. 2017). This often involves considering changes in the richness (number of species), evenness (uniformity of species within the community) and species assemblages. Underpinning research often focuses on understanding spatial patterns or temporal change, including responses to weather and climate, over the short-term (Rull 2012). It is important that where community and successional processes span centuries, as is common in woodland communities in response to climate, that longer timescales are used to analyse change so that impacts are fully understood (Willis and Birks 2006; Rull and Vegas-Vilarrúbia 2011). Thus, present day ecological patterns are often best understood, and likely future predictions most robust, when consideration of long-term change is undertaken using palaeoecological evidence (Davies and Bunting 2010; Rull 2010; Chambers et al. 2017).

Palaeoecological studies quantifying long-term change throughout the Holocene epoch (last c. 11,700 years) demonstrate that, following the termination of the last ice advances, the climate has been relatively stable (Joannin et al. 2012). Climax vegetation communities became established across Europe during the Early Holocene period, following ecological successional processes that occurred without anthropogenic interference, which resulted in a relatively open mosaic wood-pasture landscape (Vera 2000; Whitehouse and Smith 2004; 2010). An abrupt climate event occurred 8,200 calendar years ago (known as the 8.2 ka event: Figure 1) broadly characterised by a sudden cooling and warming event culminating in a 1 – 3 ^{o}C air temperature change over the Northern Hemisphere (Matero et al. 2017) (although there is evidence from oceanic records that the pattern might be rather more complex than this: Wiersma and Jongma (2010)). The 8.2 ka event occurred at a time when the vegetation responses would have been largely uninfluenced by anthropogenic activity (Olsson et al. 2010; Collins et al. 2012). It was widely observed across Europe and although sample resolution and dating accuracy can complicate precise temporal relationships, the event is regarded as synchronous across the continent (Alley et al. 1997). However, there were differences in the climate changes across Europe, with cooler conditions identified in the north compared with cooler and drier conditions in the south (Alley and Ágústsdóttir 2005; Prasad et al. 2009). Seasonality was also affected with cooler drier winters and longer cooler summers (Prasad et al. 2009). This event, particularly the warming trajectory, provides a unique opportunity to assess the vegetation impacts of past climate changes, which are similar in magnitude to changes forecast over the next 80 years, to further understand the likely responses of woodland vegetation communities to contemporary climate change.

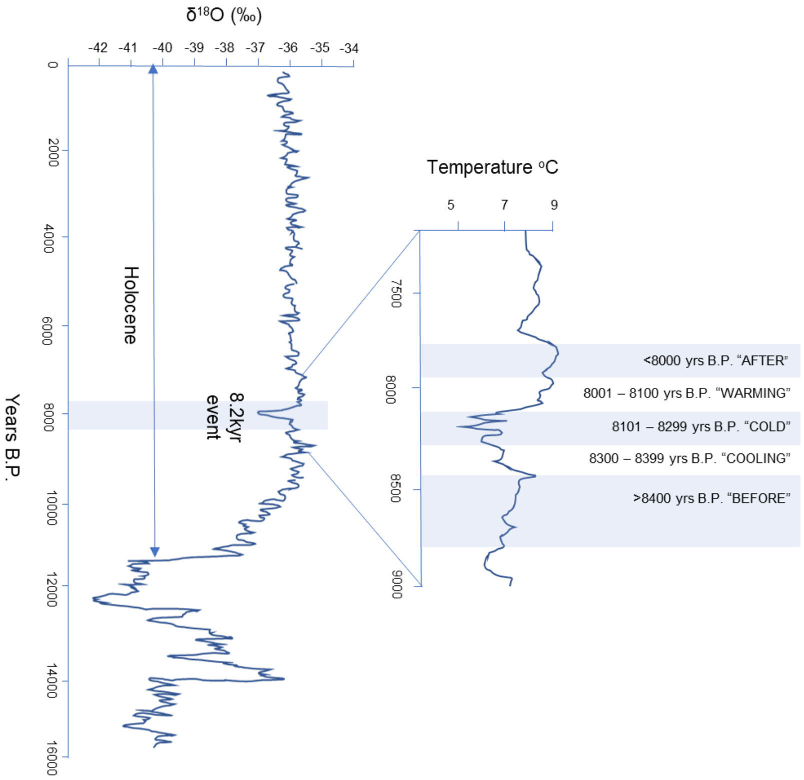


Figure 1. Left: Holocene 50-year moving average oxygen isotope curve (after: Kobashi et al. 2007) from GISP2 Greenland ice core commonly used to infer temperature in the Northern Hemisphere. Note the relative stability during the Holocene and the abrupt 8.2 ka event. Right: The pollen inferred annual mean temperature record in Europe (after: Veski et al. 2004) including time periods used in this study.

This paper will explore change in woodland vegetation communities using palaeoecological data as a proxy for vegetation change during the 8.2 ka event. We utilise 31 wooded sites from 13 countries across Europe with robustly-dated palynological (pollen and spore) records to establish temporal trends in richness, evenness and community similarity over time. We consider both the overall vegetation community and the herbaceous and shrub sub-community, which might be more sensitive to climate change and better able to adapt quickly (shorter-lived, r-strategist species = shorter lag time). We hope that better understanding of widescale changes in vegetation in response to past climatic change will provide useful insights into how woodlands are likely to respond to current and future periods of climatic change.

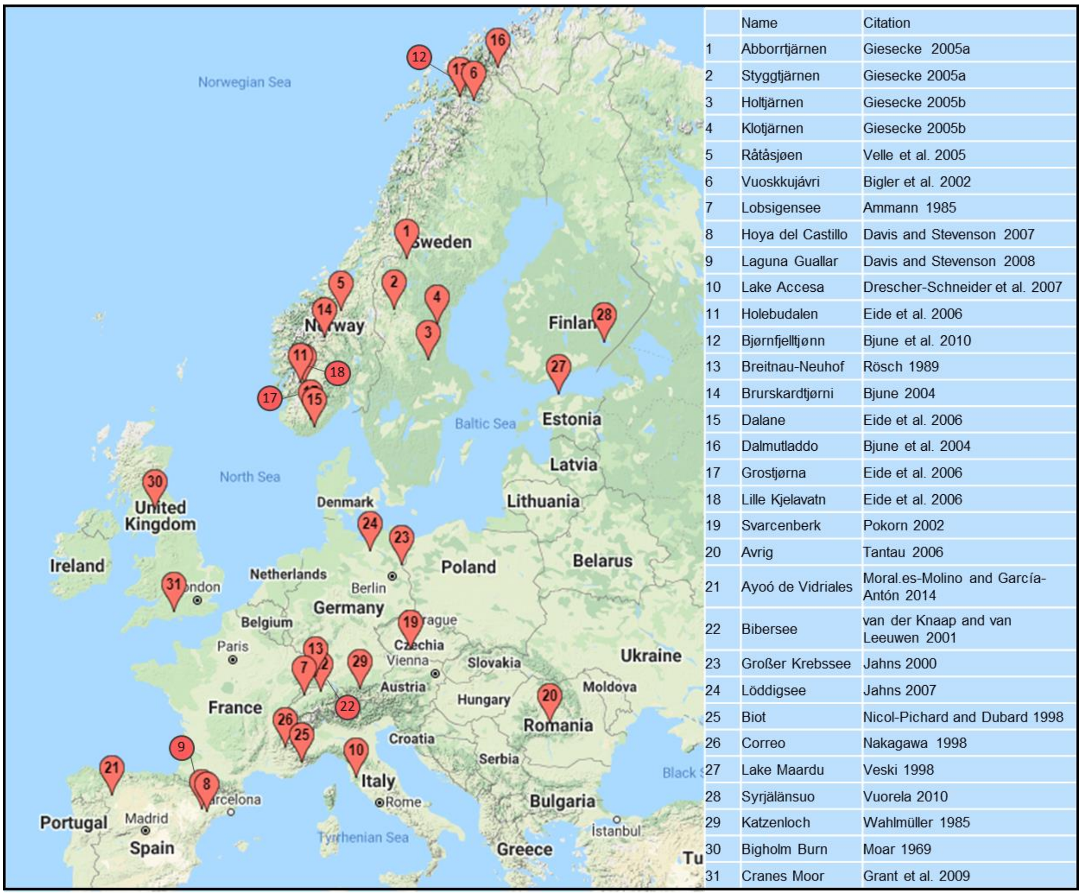
Method

Data acquisition

Initially, the European Pollen Database (EPD) (Fyfe et al. 2009) was mined to extract every site from across Europe that spanned the 8.2 ka event and that was associated with a published output in a peer-reviewed journal. This gave 73 possible sites from 19 countries: this meant that this study adopted a comprehensive approach rather than selecting or choosing particular sites. A rigorous quality control process was then undertaken and only those sites that were considered to be woodland, high-resolution, and robustly-dated, were retained. After this screening step, full palynological data were extracted from the EPD for 31 lacustrine sites across 13 countries (latitude: 41° to 69° N; longitude: 6° W to 28° E; altitude:

5 m to 1309 m; Figure 2). Each site had multiple radiocarbon dates underpinning a robust age-depth model to calculate sedimentation rates at that specific site. This information was used to select the appropriate time-sediment horizons, and thus the appropriate palynological assemblages. The age-depth models generated by the original authors at the time of publication were used without subsequent recalibration using IntCal20 (the latest calibration curve for terrestrial sites in the Northern Hemisphere) because, as Stuiver et al. (1998) and Reimer (2020) conclude, recalibration in the early Holocene has a negligible effect on the dates generated. Sites with radiocarbon dates taken from bulk samples spanning multiple horizons (i.e. where the sample resolution of radiocarbon dating did not match the sample resolution of palynological analysis) were rejected.

All 31 retained sites had palynological data predating the 8.2 ka event (hereafter termed ‘Before’: >8400 calibrated years before present), at the peak of the event (‘Cold’: 8101-8299 cal. BP), and postdating the event (‘After’: <8000 cal. BP); palynological data were also available for the (shorter) transitional periods for some sites (‘Cooling’: 8300-8399 cal. BP, n = 22; ‘Warming’: 8001-8100 cal. BP, n = 23).



	Name	Citation
1	Abborrtjärnen	Giesecke 2005a
2	Styggtjärnen	Giesecke 2005a
3	Holtjärnen	Giesecke 2005b
4	Klotjärnen	Giesecke 2005b
5	Råtåsjøen	Velle et al. 2005
6	Vuoskkujávri	Bigler et al. 2002
7	Lobsigensee	Ammann 1985
8	Hoya del Castillo	Davis and Stevenson 2007
9	Laguna Guallar	Davis and Stevenson 2008
10	Lake Accesa	Drescher-Schneider et al. 2007
11	Holebudalen	Eide et al. 2006
12	Bjørnfjelltjønn	Bjune et al. 2010
13	Breitnau-Neuhof	Rösch 1989
14	Brurskardtjørni	Bjune 2004
15	Dalane	Eide et al. 2006
16	Dalmutladdo	Bjune et al. 2004
17	Grostjørna	Eide et al. 2006
18	Lille Kjelavatn	Eide et al. 2006
19	Svarcenberk	Pokorn 2002
20	Avrig	Tantau 2006
21	Ayoó de Vidriales	Moral.es-Molino and García-Antón 2014
22	Bibersee	van der Knaap and van Leeuwen 2001
23	Großer Krebssee	Jahns 2000
24	Löddigsee	Jahns 2007
25	Biot	Nicol-Pichard and Dubard 1998
26	Correo	Nakagawa 1998
27	Lake Maardu	Veski 1998
28	Syrjälänsuo	Vuorela 2010
29	Katzenloch	Wahlmüller 1985
30	Bigholm Burn	Moar 1969
31	Cranes Moor	Grant et al. 2009

Figure 2. European sites selected and included in this study. All palynological data were collated from the European Pollen Database (Fyfe et al. 2009). Original publications for each site are referenced within this figure.

To ensure that we focused exclusively on sites that, at the time of the 8.2 ka event, were vegetated with closed-canopy woodland and thus likely supporting a mature woodland community (Joannin et al. 2012), we only included sites that had ≥ 51% arboreal pollen in each sample horizon (min = 57.1%; max = 98.8%). The rationale was that 51% arboreal pollen was the average for sites supporting ‘relatively open canopy’ in woodlands in West Yorkshire, UK (Tinsley and Smith 1974; Bunting 2002) while 50% was reported as the indicative value of woodland presence at or near upland sites (Birks 1988).

Palynological data were extracted for the time periods of interest using the taxonomic level given by the original author(s). As the taxonomic level to which pollen and spores could be identified varied for different taxa, and at different sites, the overall dataset contained family-level, genus-level and species-level data. This was not problematic because all analysis related vegetation from one time-sediment horizon to other time-sediment horizons at the same site. Thus, while this study involved multiple sites, change was always quantified site-specifically and the multiple change estimates from each site were further analysed or averaged (see later) rather than raw data from multiple sites being analysed together to produce one overarching vegetation change estimate. Palynological counts for individual sites varied from 229 – 2,478 per time period in different studies (mean = 769) but all data analysis used relative or proportional data to account for site-level variation. The total sample size across all time periods and all sites was 105,323 individual data points. Where the original authors included data on bryophytes and ferns, these were excluded, as were data on other non-vascular micro-remains (algae and fungal hyphae), which had not been recorded consistently between studies.

Data manipulation

From the palynological data, three metrics were calculated. Taxonomic richness was calculated for each site for each time period as a simple sum of the taxa found. Community evenness, the extent to which the relative abundance of each taxon was similar (uniform distribution) or dissimilar (skewed distribution with some taxa dominating and other taxa being rare), was also calculated for each time period. As noted by Legendre and Legendre (1998) and Peros and Gajewsk (2008), evenness is an important metric in community ecology, but one that remains under-utilized in palaeoecological research. There are numerous evenness indices but here Shannon’s Evenness (E_H) was adopted as this has been used previously for palynological data by Hellman et al. (2009). This was calculated using Shannon's Diversity Index (H) (equation 1) and dividing this value by the natural logarithm (*ln*) of the taxonomic richness (equation 2):

Equation 1: $\mathrm{H} = -\sum_{i=1}^{s} pi \ln pi$

Equation 2: $\mathrm{E_H} = \frac{\mathrm{H}}{lnS}$

Where S is the total number of species (taxa) in the community and *pi* is the proportion of species *i* (Shannon 1948). The resultant metric runs between 0 and 1, with 1 indicating complete evenness (i.e. all taxa uniformly abundant).

The third metric was Jaccard's Co-efficient of Community Similarity (CC_j), which is a pairwise value used to summarise the overlap in the actual species within a community between two different sites or, as here, between two different time periods at the same site. This was calculated using equation 3.

Equation 3: $\mathrm{CC_j} = \frac{\mathrm{c}}{\mathrm{S}}$

Where c is the number of species common to both communities and S is the total number of species found in both communities. The index runs between 0 and 1, with 1 indicating a complete overlap in species. CCj was calculated pairwise to compare community similarity between the time periods: (1) After *versus* Before; (2) After *versus* Cold; (3) Cold *versus* Before. These time periods were chosen because palynological data were available for each of these periods at all sites. This approach has been used previously to assess homogenization of fish communities over time (Rahel 2000).

In all cases, to allow lag effects in the vegetation community to be assessed (i.e. that a change in climatic conditions might take some time to be reflected, especially for arboreal taxa), metrics were calculated both for the overall vegetation community and the herbaceous and shrub sub-community.

Data analysis

To establish whether there were significant differences in taxonomic richness and evenness between the different time periods, a repeated measures ANOVA framework was used. This meant that differences were calculated based on a per-site basis to allow for repeated sampling of the same site (and thus avoid pseudoreplication in analyses). This also accounted for the fact that sites involved different researchers, different sample sizes, and data reported at different taxonomic levels. Four repeated measures ANOVAs were calculated: (1) richness for overall community; (2) richness for herbaceous and shrub sub-community; (3) evenness for overall community; and (4) evenness for herbaceous and shrub sub-community. The Greenhouse–Geisser method was used to compensate for a lack of sphericity in all analyses. Post-hoc testing was used for pairwise comparisons with a Bonferroni correction applied to allow for multiple comparisons.

To understand any relationship between species turnover, as measured by CCj, and species richness, we graphically compared CCj between time periods with richness. Then, to identify whether temporal change in richness and evenness between time periods was related to the spatial variables of latitude, longitude and altitude, General Linear Models were used. Change over time was calculated for both richness and evenness metrics for: (1) After *versus* Before; (2) After *versus* Cold; and (3) Cold *versus* Before. This was undertaken for the overall community and the herbaceous and shrub sub-community, which gave 12 new dependent variables, six describing change in richness and six describing change in evenness. In all cases, change was a simple calculation of the later time period relative to the earlier time period, such that the resultant figure encompassed both the direction of change (positive for an increase, negative for a decrease) and the magnitude of change (deviation from zero). Although each change variable was the mathematical difference between two count variables (richness) or the mathematical difference between two proportional variables (evenness), each of the 12 new variables conformed to a normal distribution, centred on zero, and were thus deemed suitable for analysis within a simple linear framework: residuals were also assessed and found to be homoscedastic and normally distributed in all cases.

To establish whether temporal change in CCj between time periods was related to the spatial variables of latitude, longitude and altitude, as well as the latitude*altitude interaction term, Generalised Linear Models were performed with a binomial distribution and a logit link function to allow for the fact that CCj values were effectively proportional data. Six analyses were undertaken in total to model firstly the overall community and secondly the herbaceous and shrub sub-community for: (1) After *versus* Before; (2) After *versus* Cold; and (3) Cold *versus* Before.

Results

For all sites combined, there were 48 arboreal taxa including coniferous trees (e.g. *Abies*, *Picea*, *Pinus*) and deciduous trees (e.g. *Acer, Alnus*, *Betula*, *Fagus, Ilex, Quercus, Salix*). There were also 183 non-arboreal (herbaceous and shrub) taxa spanning flowering plants (including *Artemisia, Calluna, Filipendula, Potentilla, Plantago*, and *Rumex*), grasses and cereals (Poaceae, Cerealia), rushes (*Juncus*), sedges (*Carex*), reeds (*Phragmites australis*), and horsetails (*Equisetum*). In total, the combined dataset comprised 231 taxa.

There was no significant overall difference in vegetation richness or evenness over time, either for the overall vegetation community or for the herbaceous and shrub sub-community (repeated measures ANOVA results: Table 1). However, post-hoc testing revealed some significant pairwise comparisons between specific time periods. There was a statistically significant decrease in overall richness as the climate warmed between the peak of the 8.2 ka event (Cold mean = 25 taxa; Warming mean = 22 taxa; P = 0.015; Fig 3a), which was driven by this pattern occurring in the herbaceous and shrub sub-community (Cold mean = 15 taxa; Warming mean = 12 taxa; P = 0.010; Fig 3b). For evenness, there was variability between time periods, especially for the herbaceous and shrub sub-community (Fig 3d), but there were no significant pairwise comparisons.

Table 1: Repeated measures ANOVA results for taxonomic richness and community evenness comparing five different time phases relative to the 8.2 ka climate event (Before, Cooling, Cold, Warming, After) at 31 sites across Europe [F = Fisher (the ANOVA test statistic), d.f. = degrees of freedom, p = probability].

	Richness			Evenness		
	F	d.f.	P	F	d.f.	P
Overall vegetation community	0.789	1.848	0.455	1.551	2.424	0.223
Herbaceous/shrub sub-community	1.012	1.790	0.369	1.391	1.740	0.265

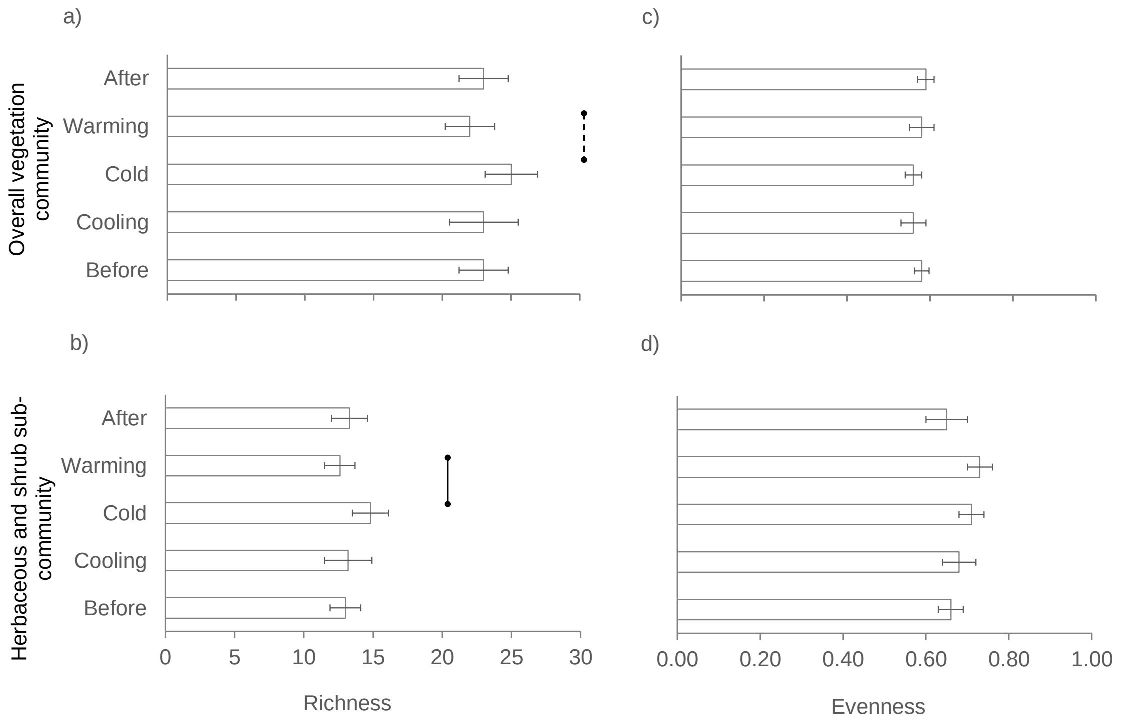


Figure 3: Vegetation community richness and evenness based on analysis of palynological data from different time periods for: (a-b) overall community; and (c-d) herbaceous and shrub sub-community. Significant contrasts (post-hoc testing with Bonferroni correction after repeated measured ANOVA) are shown, with dashed line indicating P < 0.05 and solid line indicating P < 0.01.

Although the repeated measures ANOVA indicated that there were no overall significant changes in community richness and evenness, and only minimal short-term changes between Cold and Warming time periods for richness, these analyses do not allow for changes in actual vegetation assemblages due to species turnover. Jaccard’s analysis demonstrated that there were substantial changes in communities at the same site over time. When assessing the overall vegetation community, the similarity before the 8.2 ka event and the peak of that event (Before *versus* Cold) ranged between 0.44 and 0.72 (mean = 0.60), while the similarity after the 8.2 ka event compared to the peak of that event (After *versus* Cold) ranged between 0.40 and 0.76 (mean = 0.60) (Figure 4). A similar but more extreme pattern was seen when comparing the herbaceous and shrub sub-community alone to assess turnover in field and herb layers rather than the overall vegetation community: mean similarity dropped to 0.24 for both Before *versus* Cold and After *versus* Cold (Figure 4).

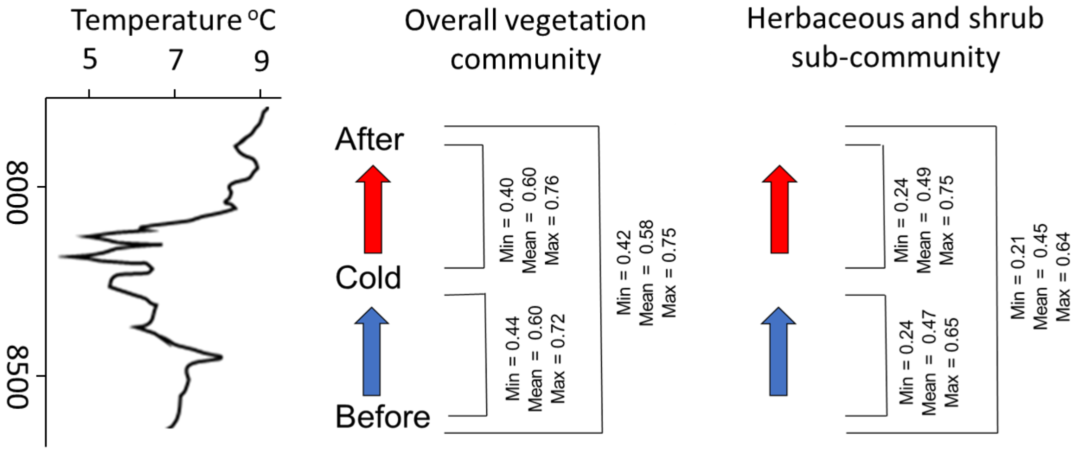


Figure 4: Jaccard’s Coefficient of Community Similarity (CCj) contrasts to quantify change in vegetation communities due to species turnover at each site (0 = no taxa in common; 1 = all taxa in common). Blue arrows signify cooling; red arrows signify warming. Left: The annual mean temperature curve for the same time periods (after: Veski et al. 2004).

There was no relationship between CCj in different time periods and species richness in the earlier time period, suggesting that resilience to climate change in the extent of species turnover was not influenced by species richness (Figure 5). There was also no clustering of sites in geographical regions, suggesting a lack of broadscale spatial patterns.

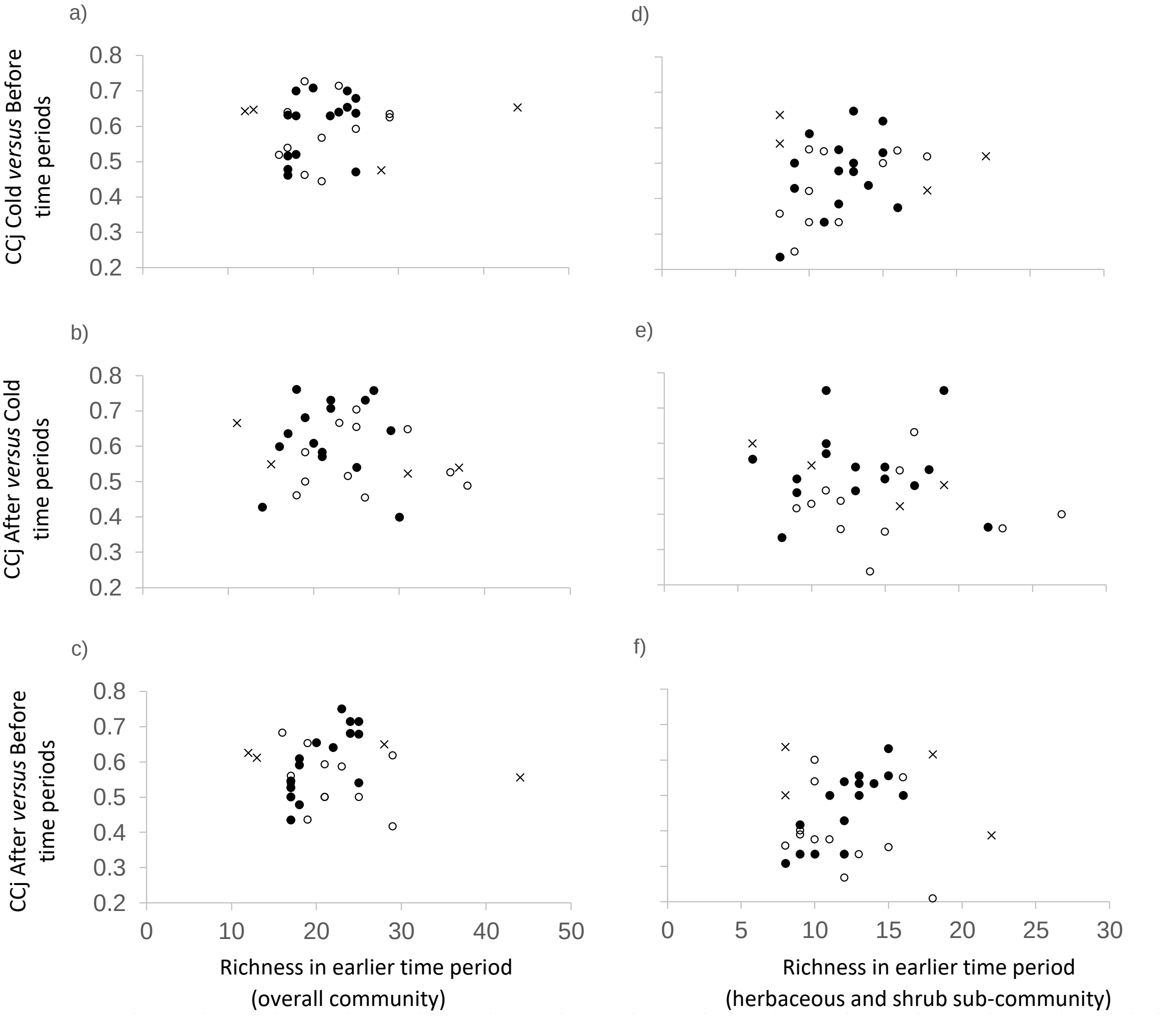


Figure 5: CCj at each site in different time periods relative to species richness at that site in the earlier time period for: (a-c) overall vegetation community; and (d-f) herbaceous and shrub sub-community alone. Sites in Scandinavia are shown using black circles; sites in mainland Europe and the UK are shown using open circles; sites in the Mediterranean are shown using crosses. There is considerable variation but no overall correlation; there is no obvious clustering based on geographical location.

The 12 General Linear Models undertaken to identify whether temporal changes in richness and evenness between time periods were related to spatial parameters (latitude, longitude, and altitude) were all non-significant (model P ≥ 0.133; individual spatial variables P ≥ 0.129) and the amount of variance explained by all models was negligible (adjusted $r^2 \leq 0.094$). The six Generalised Linear Models undertaken to relate changes in vegetation community similarity (CCj) between time periods in relation to the spatial variables of latitude, longitude and altitude, as well as the latitude*altitude interaction term were also all non-significant (model P ≥ 0.277; individual spatial variables P ≥ 0.117) and again the amount of variance explained was negligible (adjusted $r^2 \leq 0.065$). This suggested that while there were site-specific differences in the effect of climatic change on vegetation, this change was not consistently or predictively related to site location at sub-continental scale as also indicated by Figure 5.

The underpinning dataset with richness, evenness, and CCj for all sites is available on an open-access repository via http://eprints.glos.ac.uk/id/eprint/10077.

Discussion

This paper considers temporal change in vegetation over the 8.2 ka event across Europe at a time when climate changed independently of anthropogenic stressors (Olsson et al. 2010; Collins et al. 2012). We conclude that, overall, there was no significant difference in woodland plant community richness and evenness over a rapid cooling and warming event, demonstrating a surprising resilience to changing climate in these metrics of woodland diversity. Even where there were significant pairwise contrasts found in richness as the climate warmed (a significant decrease between Cold and Warming time periods) these were short-lived, indicating effects were temporary rather than permanent. At this high level, therefore, the frequent assumption that impacts of a warming climate on woodland biodiversity will be substantial and, in many cases, negative (Hooper et al. 2012; Pimm et al. 2014, McGill et al. 2015) is not supported.

This high-level resilience is likely partly due to the long-lived nature of arboreal species relative to the time over which change occurred, coupled with the wide tolerance ranges of many *K*-strategist species within mature climax ecosystems (Rull and Vegas-Vilarrúbia 2011; Chaideftou et al. 2012). However, quantifying community similarity using the CCj metric revealed substantial changes between time periods. This indicates that while the number of species (richness) and the relative abundance of different species within the community (evenness) might not have changed, the actual species within that community had altered. There was an overall mean similarity of 0.59 (59%) across all sites and all time periods when considering the overall vegetation community, which dropped as low as 0.40 (40%) at some sites. When the herbaceous and shrub sub-community was analysed alone, the overall mean similarity was 0.47 (47%) with values as low as 0.21 (21%) being seen at some sites. In other words, species turnover was always considerable, and, in some cases profound especially within the herbaceous and shrub sub-community. This suggests that resilience to climate change was considerably lower when considering species turnover rather than simple diversity metrics, a process discussed by Ewel and Bigelow (1996) as climate-induced ecological recombination. It should also be noted that the level of turnover identified here might be underestimated given that much of the palaeoecological data were restricted to genus or family level (because of the challenges in identifying fossilised pollen to species level), and thus some of the more subtle vegetation changes might not have been detectable.

Interestingly, there was no link between CCj scores and initial species richness. This is contrary to the diversity-stability concept, which states that higher richness is associated with higher ecological resilience and stability. This has been a central tenet of community ecology since this was originally postulated by Darwin (1859) and extended by MacArthur (1955) and McNaughton (1977). There is considerable experimental evidence for such a link, at least over short timescales, in communities experiencing climate stress or climate change (e.g. Frank and McNaughton 1991; Tilman et al. 1996). However, this pattern is neither universal nor inevitable (Ives and Carpenter 2007). For example, Vogel et al. (2012) demonstrated that a positive relationship between richness and stability in grassland communities during climate perturbations only occurred in ecosystems that were highly managed, not those that were dominated by natural processes and interactions, while Isbell et al. (2015) suggest that species richness may be more important for stability under moderate rather than extreme environmental change. Moreover, there is increasing evidence that the link between richness and community-level stability is fundamentally influenced by the actual species present, such that the degree of stability in a community depends idiosyncratically on community composition and biotic interactions (Lawton 1994; De Boeck et al. 2017), and thus ecological history (Peterson et al. 1998). This also links to the concept of functional diversity: even a species-poor community might be highly resilient to species turnover and ecological tipping point thresholds if each species has a different functional role, such that all ecosystem links are fully operational, albeit with little redundancy (Ives et al. 2000; Cadotte et al. 2011). This has been demonstrated empirically for Argentinian plant communities (Fonseca and Granade 2001) and simple plant communities compared to tropical rainforests in Costa Rica (Ewel et al. 1991).

At the geographical scale of the present study, spatial analysis showed that the direction and magnitude of vegetation change was unrelated to broad-scale spatial variables of latitude, longitude, and altitude for richness, evenness and (despite considerable variation between sites) for community similarity too. This suggests that although woodland communities and ecological processes might differ spatially in predictable ways, including latitudinal diversity gradients (Lamanna et al. 2014), and global patterns in plant traits, morphology and productivity (Madani et al. 2018), there is no predictable biogeographical pattern in vegetation response to climate change. This likely reflects community resilience to change being driven by local factors such as woodland size, geology and soil type, topography and exposure, and local weather patterns (especially precipitation). In particular, it is notable that species richness (and in many cases functional diversity and thus stability) increases with woodland area, as does genetic diversity and thus potentially species' adaptability. Indeed, McCarthy et al. (2005) state that "the mean time to extinction of a single population increases as a power of the habitat area". Moreover, larger woodlands experience less disturbance from adjacent land uses and fewer edge effects caused by greater exposure to extremes of light, temperature fluctuations, and storm damage (Matlack 1994; Swallow and Goodenough 2017). In more connected landscapes, colonisation and recolonisation might be higher because the local pool of species from which to draw is greater (Graae 2000; Honnay et al. 2002). It is also notable that even the broad-scale latitudinal diversity gradient that is so well-known today was much less strong in the past: Silvertown (1985) used palynological evidence to show this trend across Europe was considerably shallower 9,000-8,000 years ago compared to neo-ecological records.

In addition to local abiotic variables affecting the magnitude of vegetation change, variation in local biotic processes might explain part of the variation in vegetation response in the absence of broad-scale geographic patterns. In particular, the age of the woodland at each site will likely have a role, as resilience to change usually increases with woodland maturity (Graae 2000). This is partly driven by plant species having a long history of co-evolution with species in other taxonomic groups, such that ecological interactions, mutualistic relationships, and feedback mechanisms are well-developed (Hubbell and Foster 1986). In particular, the locally spatially-variable role of herbivores has been shown to have a profound effect on plant species turnover (Chase et al. 2000). Linking back to the concept that the degree of community stability depends on species composition (Lawton 1994; De Boeck et al. 2017), the ratio of generalist to specialist species would have a notable effect on the resilience to climate change (Pálinkás 2018). Stochastic processes will also have a variable impact, with chance extirpation of a single species potentially having a minimal effect or triggering substantial cascade effects, especially if keystone species are involved.

Looking forward: predictions, recommendations and caveats

A central aim of this study was to use palaeoecological analysis of woodland vegetation during the 8.2 ka event as a vehicle to improve understanding of likely woodland responses to contemporary climate change. We have deliberately focused on a climate change event of similar magnitude to that predicted over the next 80 years to study vegetation response without this being confounded by anthropogenic processes. This paleoecological approach embraces the framework advocated by Davies and Bunting (2010), Rull (2010), and Chambers et al. (2017). However, it is important to note that the connectivity inherent in the natural wood-pasture mosaic during the 8.2 ka event might have enhanced resilience of woodlands, whereas contemporary climate change is occurring concurrently with other environmental pressures, including habitat loss and fragmentation, impacts of non-native species and pollution. These multiple co-stressors might reduce the resilience of ecological communities to climatic change, and mean that we cannot exclude the possibility that an ecological tipping point (Cairns 2004) might be reached in the future if emissions, and thus climate change trajectory, is not acted upon. This is especially true given that the warming period in the 8.2 ka event was recovery to temperatures experienced before the sudden cooling (i.e. it was returning to the baseline rather than warming from it), and the fact that contemporary climate changes are involving more extreme weather patterns and changes to seasons that were not necessarily seen in the 8.2 ka analogue (Prasad et al, 2009).

Despite these caveats, we predict that if future vegetation responses largely mirror the past changes described here, individual woodland sites are likely to be relatively unaffected in terms of richness and evenness over the next 80 years. It is notable that richness decreases in response to the rapidly changing climate 8,200 years ago were all temporary, before richness recovered. When considering broad scale diversity, this demonstrates the need to resist reacting to short-term change and instead to develop monitoring, management and conservation strategies that span generations rather than the typical 3-5-year span of funding, management plans and political cycles.

We suggest that there will be considerable species turnover in woodlands as the climate warms. This is already being seen to some extent (Guerin et al. 2011; Chaideftou et al. 2012). Our retrospective analysis suggests that, for some sites, this could be profound with magnitude of change being driven not by broad-scale geography but by local abiotic factors, ecological interactions, initial species composition, functional diversity and stochastic processes. Given that, at a landscape scale, species turnover at individual sites will have a negligible effect if turnover is driven by localised and random processes rather than being systematic (Breshears et al. 2008), we recommend that consideration of gamma diversity – rather than alpha or beta diversity – is of paramount importance. This shifts the focus from single-species and single-site conservation to landscape-scale approaches (Lawton et al. 2010; Jones 2011; Donaldson et al. 2017). This also avoids “overmanaging” individual sites with the aim of preventing or buffering natural change, but rather accepts that natural change occurring at multiple sites across the landscape will alter the elements of the landscape mosaic but landscape-level diversity would be less affected. However, extensive and proactive monitoring should be undertaken to identify species that are being systematically lost from multiple sites (Breshears et al. 2008; Guerin et al. 2013). This might include specialist species with narrow tolerance ranges that are more vulnerable to climate change *per se*, or species that less able to compete in climate-induced ecological recombination. Such species need to be prioritised for conservation action at both landscape and individual site scales. This accords with the “management of changing nature” and “innovation in nature” conservation perspectives of Dempsey (2021) and concurrent movement away from paradigms that prioritise species over process, while also realising that *some* single-species initiatives remain valuable.

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