Humans as biodiversity engineers

Trait-based approaches to understand human impact on temporal changes in plant communities

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Abstract

Although the current human impact on ecosystems is unprecedented, human activities have been altering ecosystems for millennia. The temporal domain in ecology is understudied but increasingly recognised for its relevance to comprehending natural dynamics and contextualising recent biodiversity change. Understanding how human activities shape plant communities, spatially and temporally, is crucial to anticipate possible undesirable consequences.

Because plants are central to maintaining ecosystem functioning, changes in species composition might alter ecosystem functioning and affect human well-being. However, the links between human impact, species composition and ecosystem functioning are challenging to grasp when solely studying species composition. Trait-based approaches in ecology allow for a greater understanding of relationships between human impact, species composition and ecosystem functioning.

In this thesis, trait-based approaches are applied in novel ways to understand how humans shape plant composition over long time scales. Pollen records are the main source of information on past plant composition. Using the trait-based approach to reconstruct plant functional composition from pollen records, might allow for the extension of the time scales of functional ecology. In **Paper 1** I tested the reliability of using pollen records for reconstructing past plant trait composition. I compared plant trait composition reconstructions based on modern pollen samples with the trait composition of the surrounding vegetation. I found there was high uncertainty in the relationship between vegetation trait composition and pollen-based trait reconstructions. Because of the low sample size in this study, a possible positive relationship between pollen-based reconstructions and vegetation trait composition is not ruled out. However, these results advocate for carefully trait variation within pollen taxa and encourage further testing of the trait-based approach in palaeoecology.

In **Paper 2** I examined how the start of agriculture changed plant functional composition in Europe. To reconstruct plant functional composition from 78 pollen records, I used a novel Bayesian approach to include trait variation within pollen taxa. I demonstrated a four-fold decrease in whole plant size since the beginning of agriculture. Especially in the last 2000 years, a trend towards the acquisitive end of the leaf economic spectrum was shown. Both agriculture and climate may have played a role in this trend. These results indicate that by modifying plant functional composition, early agriculture might have significantly impacted biogeochemical cycles.

In **Paper 3** I tested if life-history traits can explain relatively recent population-level and community-level changes using the global biodiversity database BioTIME. I did not demonstrate a relationship between life-history, human impact and population change. To test how life-history influences community-level changes, I calculated species' contribution to turnover. Life-history traits are important predictors of contribution to turnover, but these effects are conditional on the degree of human use and climate change intensity. Knowing the traits and population changes of species that are strong contributors to turnover, could lead to a better understanding of the processes that drive biodiversity change.

Together, this thesis demonstrates novel ways to use traits for understanding human impacts on plant communities in the temporal domain. It shows that there are challenges in applying traits to understand temporal changes in plant communities, but also that there are new insights to be gained from it.

Keywords: human impact, functional traits, long-term ecological data, palaeoecology, pollen records, life-history, turnover.

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My PhD journey has (mostly) come to an end with this 161-page document. “Time” is a central theme in this thesis and so it has been throughout my PhD. The time during my PhD has felt to pass slowly (primarily in the COVID pandemic) or way too fast (especially at the end!) but has mostly been extremely valuable. I feel incredibly grateful to the people who have made these last 4.5 years so valuable, both academically and personally.

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Contents

1 Introduction

> *When we observe the environment,*
> *we necessarily do so on only a limited range of scales; therefore,*
> *our perception of events provides us with only*
> *a low-dimensional slice through a high-dimensional cake.*
> - Levin (1992)

The scale at which we perceive our environment shapes our understanding of it (Levin, 1992). The processes that shape our environment today, such as climate change and human impact, act on multiple scales (Chave, 2013). However, the observational window of ecology is commonly narrow, especially in the temporal domain (Estes et al., 2018). To understand and predict environmental change, it is essential to observe the environment at multiple scales.

Ecosystems are dynamic and continuously changed by a multitude of factors, both anthropogenic and natural. Although the current anthropogenic impact on ecosystems is unprecedented, people have been shaping ecosystems for millennia (IPBES, 2019). For instance, already 12 000 years ago 95% of temperate woodlands were altered by human societies (Ellis et al., 2021). Human action also played a significant role in the extinction of megafauna at the end of the Pleistocene (Braje & Erlandson, 2013). The onset and global spread of agriculture from about 10 000 years ago transformed ecosystems drastically, driving land cover change and introducing new species intentionally (domesticated animals and crops) and unintentionally (e.g. weeds) (Mazoyer, 2007). Agriculture created more biodiverse and open landscapes (Woodbridge et al., 2020) but also altered natural processes. For instance, agriculture may have increased soil erosion and atmospheric methane as early as 7500 and 4000 years ago, respectively (Fuller et al., 2011; Hoffmann et al., 2013). In recent times, some significant events that increased human impact on ecosystems globally include the European colonial period (1500-1800), the Industrial Revolution (1750) and the Green Revolution (1960-1980) (IPBES, 2019). In the last 50 years, land use change, primarily for agriculture, has had the most significant negative impact on terrestrial ecosystems. Other large drivers of ecosystem change include overexploitation of plants and animals, climate change, pollution and invasive species (IPBES, 2019).

Palaeoecological records and other long-term ecological studies can give insights into the intrinsic variability of ecosystems and can contextualise recent changes (Gillson et al., 2021; Lindenmayer et al., 2012). For instance, palaeoecological records have shown an unprecedented acceleration of rates of vegetation change in the late Holocene (Mottl et al., 2021) and have challenged our notion of "pristine" nature (Levis et al., 2018). However, only an estimated 9% of ecological studies have a duration of more than a decade (Estes et al., 2018). Therefore, palaeoecological records and other long-term ecological data are crucial to increase ecological studies' observational window. We rely on the sustainable and resilient delivery of services by ecosystems, but environmental change threatens the resilient supply of these ecosystem services (Tomimatsu et al., 2013). Environmental change can alter species communities in terms of species richness and abundance (Blowes et al., 2019). Changes in community composition can cascade into changes in ecosystem functioning, as ecosystem functions are mediated by species interactions between each other and their environment (Cardinale et al., 2012). But the links between drivers, species composition and ecosystem functioning are difficult to grasp when solely studying species composition. By replacing species nomenclature with traits, trait-based ecology aspires to a more mechanistic understanding of ecosystem functioning (McGill et al., 2006).

Trait-based approaches are widely embraced in ecology (Hevia et al., 2017; Violle et al., 2014), but their application in palaeoecology is relatively novel (Reitalu & Nogué, 2023). A trait is defined as a measurable characteristic of an organism that can be used comparatively across populations, species or communities (McGill et al., 2006; Volaire et al., 2020). The crucial distinction between a "trait" and a "functional trait" is that a functional trait influences an organism's demographic fitness, thus its fecundity, growth, development and/or survival (McGill et al., 2006; Volaire et al., 2020). Examples of functional traits include plant height, leaf area and seed mass. However, the effect of commonly used functional traits on fitness, and therefore trait "functionality", is highly debated (Streit & Bellwood, 2022; Volaire et al., 2020). The link between functional traits and plant demography is complex and influenced by the environment and evolutionary constraints (Kelly et al., 2021). Life-history traits, which arise from measurements of an individual's survival, development and reproduction might aid in explaining community dynamics (Salguero-Gómez et al., 2018). Examples of life history traits include longevity, number of offspring and generation time. The link between life-history traits and fitness is explicit and fundamentally integrative as it considers environmental and evolutionary constraints (Kelly et al., 2021; Salguero-Gómez et al., 2018).

In contrast with life-history traits, functional traits are relatively easily measured across a large number of species. The availability of data on functional traits in databases such as TRY (Kuppler et al., 2020) and BIEN (BIEN, 2019) has significantly aided the advance of trait-based ecology. Functional traits can quantify important differences between species and communities, such as key dimensions of variation and trade-offs (Bruelheide et al., 2018; Díaz et al., 2016). This makes functional traits useful to identify patterns over broad spatial and temporal scales as well as differences between ecosystems (van der Plas et al., 2020; Volaire et al., 2020).

Understanding how humans shape biodiversity is crucial to anticipate the consequences of human impact in the future. Both trait-based ecology and long-term ecological data can aid prediction in a no-analogue future (Bodegom et al., 2012; Gillson et al., 2021; Lindenmayer et al., 2012). In this thesis, I use the trait-based approach and long-term (palaeo)ecological data to address research questions under the main overarching question:

- **How do you humans alter the trait composition of plants on timescales ranging from decades to millennia?**

The first part of the thesis focuses on the application of the trait-based approach in palaeoecology. It tests the reliability of using pollen records for plant trait reconstruction and applies the approach to understand trait changes following the start of agriculture in Europe.
Paper 1 evaluates how representative pollen records are for reconstructing past plant functional composition. It uses field-collected data from Scotland and Switzerland to test different factors that might affect the relationship between pollen-based trait reconstructions and current-day vegetation.
Paper 2 examines how the start of agriculture changed plant functional composition in Europe. It uses 78 pollen records from across Europe to reconstruct plant functional composition and estimate the impact of climate and the start of agriculture.

The second part of the thesis uses long-term ecological data and life-history traits to understand relatively recent plant community composition changes worldwide.
Paper 3 uses the BioTIME database (Dornelas et al., 2018) to examine the contribution of life-history traits and human impact to population-level and community-level changes. It tests if life-history traits and human impact can explain population trends. Single species or species groups undergoing large abundance changes could drive compositional change metrics (Di Cecco & Hurlbert, 2022). This paper

also evaluates if recent global plant compositional change can be attributed to species with similar life-history traits.

2 Background

2.1 Trait-based ecology

In this thesis two types of traits are used, functional traits and life-history traits. Whilst arising from two distinct ecological disciplines, functional ecology and population ecology, life-history traits and functional traits are related (Figure 2.1) (Salguero-Gómez et al., 2016).

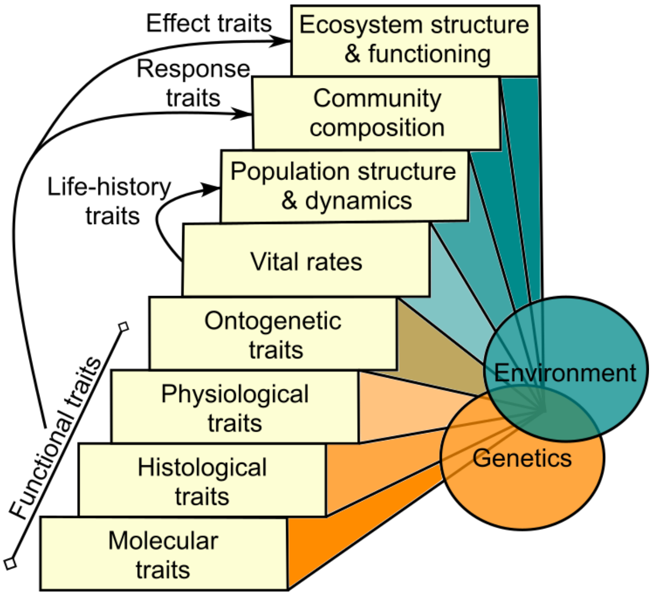

Figure 2.1 Relationship between functional traits, life-history traits, community composition and ecosystem functioning (Salguero-Gómez et al., 2018). The general focus of functional ecology is on physiological (e.g. leaf nitrogen content) and ontogenetic traits (e.g. plant height). Functional traits are used to describe the effect of drivers on community composition (through response traits) and community composition effects on ecosystem functioning (through effect traits). Functional ecology often omits the step from functional traits to vital rates (fitness) and population dynamics, this step can be characterised by life-history traits. Figure adapted from (Salguero-Gómez et al., 2018).

The functional trait is the foundational stone of functional ecology (Volaire et al., 2020). The application of functional traits is two-fold: they can be used both for predicting how communities respond to environmental change (defined as response traits) and how community composition relates to ecosystem functioning (defined as effect traits) (Suding et al., 2008)(Figure 2.1). In this response-effect framework, traits are hypothesized to draw links between drivers, species composition and ecosystem functioning (Hevia et al., 2017). Traits aid the characterization of ecological communities into a set of parameters that are useful understanding community response to changes in biotic and abiotic factors (Funk et al., 2017). The establishment of general relationships between traits and the environment is of great importance for predicting the effect global change on ecosystems. A particular strength of combining functional trait data with time series is that temporal mismatches in traits and environment can be studied, potentially discovering legacies of climate and humans on contemporary ecosystems (Blonder et al., 2018; Gaüzère et al., 2020).

In an analysis of 46 000 plant species, Díaz et al. (2016) showed that species mainly (75%) differ in two dimensions. The first expresses the plant’s size and its leaves and seeds. The other reflects the leaf economic spectrum, which describes trade-offs in leaf investments. On one end of this spectrum, species with thin, nitrogen-rich and fast-growing leaves are positioned, while at the other end conservative species with thick, longer-lived and slow-growing leaves are found (Wright et al., 2004). Soil and climatic factors can account for a great part of the global variety in these two trait spectra;

The variation in size-related traits can be explained by energy and light limitation and the variation in the leaf economic spectrum are mainly explained by climate and soil fertility (Joswig et al., 2022).

Life-history traits relate to organisms' survival, growth and reproduction (Salguero-Gómez et al., 2016). These traits are calculated from matrix population models, which are models that describe the life-cycles of organisms (Caswell, 2000). Remarkably, similar trade-offs in life-history traits are evident for functional traits. The main axis expresses variation in species' pace-of-life, from fast-growing, short-lived species to slow-growing, long-lived species. The second axis classifies species according to their reproductive strategy, from highly reproductive organisms with multiple reproductive events in a life span, to poorly reproductive organisms with only one reproductive episode before death (Salguero-Gómez et al., 2016). The trade-offs in life-history traits are similar to the trade-offs in functional traits, for instance, the pace-of-life of species is related to organism size (Pettorelli et al., 2005; Salguero-Gómez et al., 2018). However, they do not exactly match (Kelly et al., 2021). Therefore, functional traits and life-history traits can be used complementary, but not replaced by one another.

2.2 Functional palaeoecology

Although the reconstructing of past plant trait composition from pollen data is relatively new, the functional characterization of palaeoecological assemblages is not novel (Reitalu & Nogué, 2023). The field of functional palaeoecology is broad and rapidly developing. Past functional ecological approaches in palaeoecology include the classification of pollen data in to plant functional types (Prentice et al., 1996) and life history types (Lacourse, 2009) and the use of Ellenberg values (Birks, 1993). The reconstruction of past trait composition can either involve the direct measurements on palaeoecological remains (e.g. bones of animals, shells of micro-organisms or fossil leaves) or the assignment of modern trait data to proxies from the palaeoecological record (Brown et al., 2023).

Trait-based approaches have also been applied in deep-time and other taxa than plants. For example, testate amoebae can be used to reconstruct past water tables in peatlands (Fournier et al., 2015). Moreover, measurements on the stomata and vein density of macrofossils can aid climate reconstruction of the Cretaceous (Blonder & Enquist, 2014; McElwain, 2018). A distinct challenge in functional palaeoecology, as opposed to modern functional ecology, is keeping track of the taphonomic, chronological and taxonomic uncertainties inherent to palaeoecological datasets (Brown et al., 2023).

Pollen records are the main source of information on past plant composition. Recent pollen-based reconstructions of past plant trait composition have revealed associations between vegetation functional characteristics and past climate change, human impact and fire history (Adeleye et al., 2023; Brussel et al., 2018; van der Sande et al., 2021). Although the trait-based approach in palaeoecology has the potential to provide a greater understanding of long-term changes in ecosystem processes, there are some methodological concerns arising from the properties of pollen data. Firstly, pollen records are of low taxonomic resolution; this makes assigning modern plant trait data challenging, as trait variation within pollen taxa can be substantial (Adeleye et al., 2023). Secondly, pollen counts do not exactly represent past plant abundances and the relevant spatial scale represented by the pollen record is difficult to assess.

Enormous quantities of pollen are produced, transported and mixed by animals, wind and water. As pollen grains sediment and are preserved, most often in lakes and bogs, they can continuously record past vegetation (Birks et al., 2016). The production, dispersal and preservation of pollen influence how representative pollen assemblages are for a given vegetation community (Traverse, 2007).

While small and insect-pollinated herbs (such as Orchidaceae) are rarely represented in the fossil pollen record, tall and wind-pollinated trees (such as *Pinus*) are generally overrepresented in it (Faegri & Iversen, 1989; Meltsov et al., 2011; Traverse, 2007). The pollen of wind-pollinated taxa are also dispersed at greater distances so that the source area could be a couple of orders of magnitude greater than that of insect-pollinated taxa. Landscape openness also affects pollen dispersal, as tree canopies and other objects can intercept pollen dispersal (Abraham et al., 2022). Lastly, pollen preservation can differ depending on the environment and the chemical structure of the pollen's outer layer. For instance, *Populus* pollen do not preserve well because of a low sporopollenin content in the pollen outer layer (Traverse, 2007).

Despite the complex relationship between the pollen record and the surrounding vegetation, pollen records are the most important proxy for past plant composition. Pollen can provide reliable proxies for past species richness (Abraham et al., 2022; Reitalu et al., 2019). However, careful consideration of taxa-specific differences in pollen productivity, dispersal and the relevant spatial scale is needed (Reitalu et al., 2019; Reitalu & Nogué, 2023).

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Paper 1: Testing the reliability of pollen data for reconstructing long-term changes in plant trait composition

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Code and data availability: All code necessary to run this analysis is available in the GitHub repository: https://github.com/Annegreet/PollenTraitValid. All data will be made available upon publication of the paper.

3 Testing the reliability of pollen data for reconstructing long-term changes in plant trait composition

Abstract

Trait-based approaches in palaeoecology can open new opportunities for studying past ecosystem dynamics and functioning. Pollen records are the main proxy for reconstructing past plant community composition, but the relationship with plant trait composition is complex. To test the reliability of pollen data for reconstructing past plant trait composition, we compare plant trait composition reconstructions based on modern pollen samples with the trait composition of the surrounding vegetation. Using a novel Bayesian approach for reconstructing trait composition from pollen data, we incorporated uncertainty related to trait variability within pollen types. With a dataset of 16 sites from the Cairngorms in Scotland, we tested for the influence of known factors that affect the representation of pollen assemblages for vegetation composition, including spatial scale, pollen productivity, plant functional type and pollination mode. Furthermore, we explored whether pollen-based reconstructions reflect trait changes along an elevation gradient with 27 sites in Switzerland. We found a general high uncertainty in the estimated relationship between vegetation trait composition and pollen-based trait reconstructions. This high uncertainty is most likely caused by variation in pollen taxa and taxon-specific differences in pollen productivity and dispersal. Because of the low sample size and high trait variation in pollen types in this study, positive relationships between pollen-based reconstructions and vegetation trait composition may exist. However, we advocate careful consideration of trait variation within pollen taxa and encourage further testing of the trait-based approach in palaeoecology.

3.1 Introduction

Functional traits offer valuable insights into the processes that drive biodiversity change and ecosystem functioning, as they can characterise complex community dynamics (Funk et al., 2017; Hevia et al., 2017). While the functioning of modern ecosystems is often contingent on past human and environmental factors (Blonder et al., 2018; Jõgiste et al., 2017; Levis et al., 2017), the observational duration of trait-based studies is generally at most a couple of decades (Estes et al., 2018). To go beyond this limited time scale of functional ecology, considerable interest in the trait-based approach has arisen in palaeoecology (Adeleye et al., 2023; Sande et al., 2019). By characterising pollen assemblages based on functional traits, insights could be obtained on how drivers of vegetation change shape plant community composition on time scales from centuries to millennia. For instance, van der Sande et al. (2019) found that on a 7000-year time scale, human disturbance supersedes climate change effects on plant trait composition in the Amazon and that human-induced fire favoured tall-growing taxa with large seeds. Furthermore, Reitalu et al. (2015) showed that climate warming after the last glacial maximum in Northeast Europe allowed the spread of tall-growing plants with large seeds and limited vegetative reproduction.

Although palaeoecological studies that have applied a trait-based approach to sedimentary pollen records show promising results, it is a relatively new approach of which the intricacies should be explored more. Little is known about whether pollen records provide a good proxy for past plant trait composition (but see Blaus et al., 2020; Carvalho et al., 2019). A common way of describing the functional composition of a plant community is the community-weighted mean (CWM), which is the average of the species' trait values weighted by their relative abundances (Funk et al., 2017). However, methodological issues arise when calculating the CWM trait values of a pollen assemblage. The relative taxon abundance in a pollen assemblage does not directly represent the taxon abundance in the vegetation because of taxon-specific differences in pollen production and dispersal (Faegri & Iversen, 1989). Pollen of wind-pollinated taxa are produced in larger quantities and are dispersed over greater distances than insect-pollinated taxa (Meltsov et al., 2011). One way of dealing with this biased representation of specific taxa is to separate pollen data into functional groups, such as woody and non-woody taxa (Blaus et al., 2020) or wind and not wind-pollinated taxa (Weng et al., 2006). Alternatively, over- or under-representation can be corrected with taxon-specific pollen productivity estimates. These correction factors down-weight the contribution of dominant taxa in pollen assemblages (Githumbi et al., 2022).

Another challenge in reliably reconstructing past trait composition is to attribute functional trait data to the taxa found in pollen records, as pollen records can rarely be resolved to the species-level resolution (Birks, 2020). Trait variation within pollen taxa can be substantial depending on the trait and the diversity of the taxon (Albert et al., 2010; Prinzing et al., 2008). This might be especially problematic in the case of large, abundant plant families that cannot easily be resolved to a lower taxonomic level, such as the Poaceae family. Furthermore, assigning species to pollen taxa is not straightforward and requires deciding the relevant source species for the pollen types in the record. In this study, we use a Bayesian approach for modelling trait composition from pollen data to incorporate the uncertainty arising from the low taxonomic resolution of pollen records. Our approach allows for the consideration of the full trait distribution of the pollen taxon to the calculation of an abundance weighted mean on the level of the pollen assemblage.

In the present study, we used two newly collected datasets from Scotland and Switzerland to test the pollen-vegetation trait relationship. We address two questions. First, what factors influence the pollen-vegetation trait relationship? Using a field study from the Cairngorms, Scotland, we investigated the effect of spatial scale, plant functional group and correction factors on the representativeness of pollen assemblages for functional trait reconstruction. We expected that the functional composition of wind-pollinated and woody taxa is best represented by the pollen-based reconstructions, especially at a greater spatial scale. Alternative to forming a direct representation of past plant trait composition, pollen-based trait reconstruction might be better suited to study relative changes in trait composition (Sande et al., 2021). Therefore our second question was, can pollen-based trait reconstruction predict changes in trait composition along environmental gradients? We expected pollen to reproduce trait changes along elevational gradients as shown by van der Sande et al. (2021). Using pollen, vegetation and trait data collected along an elevation gradient in Switzerland, we tested if pollen assemblages can predict relative changes in trait composition.

3.2 Method

We collected modern pollen samples, trait and species composition data in Scotland and along an altitudinal gradient in Switzerland. Modern pollen samples collected from moss can be used to compare to contemporary vegetation, acting as modern analogue to palaeoecological pollen records (Davis et al., 2013; Meltsov et al., 2011; Reitalu et al., 2019). Moss tissues act as pollen traps and accumulate pollen on average two years of pollen rain (Pardoe et al., 2010). We then reconstructed the trait composition from the modern pollen samples with the trait composition of the vegetation

3.2.1 Study design Scotland

We collected data from 16 sites in the Cairngorms National Park, Scotland, United Kingdom. Sites were selected to represent four dominant habitats in the area: grassland, heathland, deciduous forest and coniferous forest. Sampling locations were at least 1 km apart, sufficient to prevent pollen source areas from overlapping (Bunting et al., 2013).

Study design mostly followed the protocol of Bunting et al. (2013). This protocol allows for testing the spatial scale represented by a pollen sample that is taken in the centre of three concentric rings. The taxa composition of the pollen sample is then compared with the species composition of the three rings (Appendix S1). The three concentric rings were 10 m, 100 m and 1000 m in radius. We surveyed the inner ring (10 m) and the middle ring (100 m) in the field. In the inner ring, we recorded 17 sub-plots of 0.25 m: one in the centre, 3 in every wind direction at 3, 6 and 10 meters, and one in the NE, NW, SE and SW directions (Figure 3.1). In the middle ring, we selected between 4 and 6 plots of 5 x 5 meter in a stratified random design based on vegetation types identified in the field. Vegetation abundance was estimated using percentage cover. The vegetation cover of the outer ring was estimated using QGIS and land cover maps (QGIS Development Team, 2021; Scottish Government, 2022).

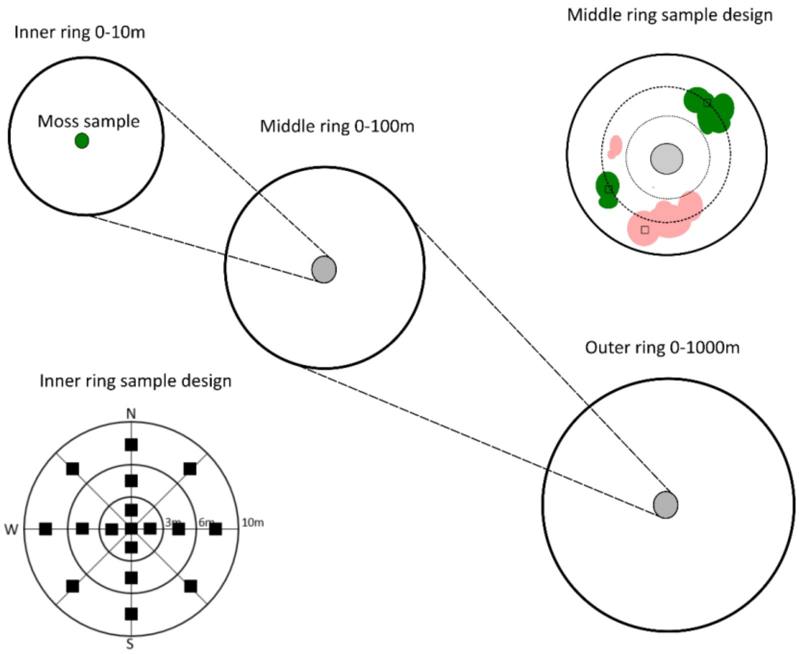

Figure 3.1 Sampling design in Scotland, following the protocol of (Bunting et al., 2013).

3.2.2 Study design Switzerland

We used pollen, trait and vegetation data from 27 sites that were monitored in the context of the Biodiversity Monitoring Switzerland (BDM). This is a systematic sampling grid for the long-term monitoring of plant and animal species in Switzerland (FOEN, 2022). The sites were sampled across Switzerland and span elevations between 545 m.a.s.l and 2348 m.a.s.l, the elevation gradient is characterised by decreasing mean annual temperature from 10 ◌̊C to 0 ◌̊C and a total annual precipitation between 520 mm and 1904 mm (Appendix S1). Of these sites, 18 were in forests (545-1672 m.a.s.l) and 9 in grassland (716-2348 m.a.s.l). We also used trait and species composition data from an additional 17 sites surveyed in the BDM network, but for which pollen data was unavailable.

The plots were 1.8 m in radius and contained 4 sub-plots. In the centre of this plot, the moss sample was taken. Each sub-plot was a quadrant of 0.16 m^2 with nine points (a 3 x 3 grid), and the percentage cover of the species present at the nine points was estimated (Figure 3.2).

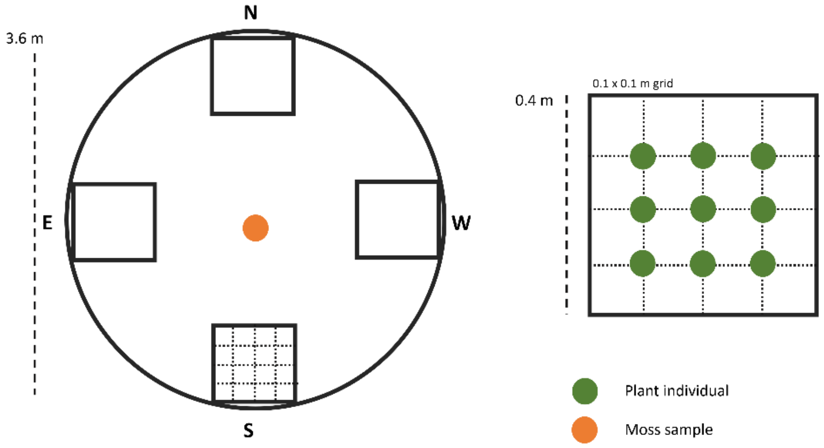

Figure 3.2 Sampling design in Switzerland.

All species names from the Scottish and Swiss data were standardised according to the Leipzig Plant Catalogue using the *lcvplants* and *lcvp* R packages (Freiberg et al., 2020). R version 4.2.2 was used throughout the study (R Core Team, 2022)

3.2.3 Trait data collection

We selected three traits for analysis: specific leaf area (SLA), leaf area (LA) and plant height. These traits reflect different components in the spectrum of plant strategies (Diaz et al., 2016). In Scotland, trait data were collected in the middle ring (100 m). Trait data were collected following standardised protocols (Pérez-Harguindeguy et al., 2016). For determining plant height, 10 flowering individuals were measured in situ at every site, non-flowering individuals were selected if flowering individuals were not available. We collected five leaf samples per species to determine specific leaf area (SLA) and leaf area (LA). Leaves were weighed and scanned with a standard flatbed scanner within 72 hours of collection. The surface area of each leaf was analysed using thresholding and the region of interest function in ImageJ (version 1.53)(Schneider et al., 2012). Samples were dried at 70 °C for 72 hours to constant dry weight before measuring dry weight. In Switzerland, the trait data were collected for species present at the nine points in the 3 x 3 grid, the method for measuring the traits was consistent across Scottish and Swiss sites.

3.2.4 Pollen analysis

Moss samples were treated with 10% KOH, passed through a 100 µm sieve and then put through standard acetolysis (Faegri & Iversen, 1989). Samples were mounted in glycerol and pollen were identified with a light microscope under x400 and x1000 magnification using the key of Faegri & Iversen (1989). At least 600 pollen grains per sample were counted.

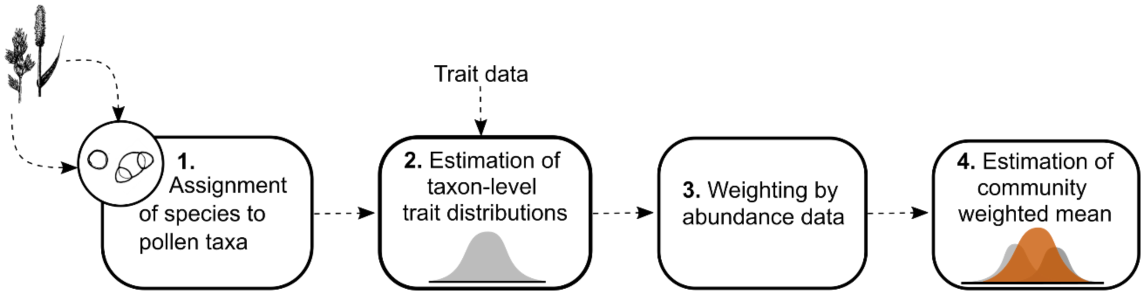

Figure 3.3 Schematic of the estimation of the community weighted mean from the pollen data. The CWM of the vegetation was estimated in the same way, starting at step 2.

3.2.5 Pollen to species translation table

For reconstructing plant trait composition from pollen data, assumptions need to be made about which species contributed to the pollen types found in our records. We created two pollen-to-species translation tables (step 1, Figure 3.3). The first is a table of the species that we found in the field surveys with their pollen-equivalents. The second table considers the case when little to no information is available about the source species of the pollen, as is generally the case of reconstruction from palaeoecological pollen records. This table was constructed as follows; We used the *rgbif* package to download the current distribution of species belonging to each pollen taxon in Scotland and Switzerland from the Global Biodiversity Information Facility database (Chamberlain et al., 2021; GBIF.org, 30 November 2022). Species distribution data were queried using the pollen taxonomic name, i.e. the lowest taxonomic resolution to which the pollen could be identified.

3.2.6 Calculation of community weighted mean

To model the trait composition of the pollen assemblages, we used the pollen-to-species translation table and previously gap-filled trait data from the TRY database (Kattge et al., 2019; Schrodt et al., 2015)(Kattge et al., 2020; Schrodt et al., 2015). The field collected trait data was used to model the trait composition of the vegetation, supplemented by the TRY dataset in case of missing values. We use the community weighted mean (CWM) to characterise plant functional composition, which here is specified as the trait distribution of a taxon, i.e. the species in the vegetation data or the pollen taxon in the pollen data, weighted by its abundance. The CWM was modelled hierarchically. First, the trait distribution on the taxon level was estimated using at least 10 trait observations per taxon. We assume that the trait data of SLA, LA and plant height follows a lognormal likelihood distribution, so that

$$trait_{i|j}^{observed} \sim lognormal(\mu_j, \sigma_j) \tag{1}$$

Where *i* represents each trait observation of a taxon (*j*) from the trait data. μ_j and σ_j are the mean trait value and the standard deviation per taxon, respectively. Vague priors were used for the taxon mean and standard deviation estimation. We then modelled the CWM as a mixture of normal distributions that were weighted by the species abundance or pollen percentage, so that

$$CWM_s \sim \sum^{n} \pi_{j|s} Normal(\mu_j, \sigma_j) \tag{2}$$

Where *n* is the total number of taxa, and π_j the abundance of each pollen taxon or species at a given site *s*. The mean (CWM_{mean}) and the standard deviation (CWM_{sd}) of the pollen data was subsequently used in the further analysis, where CWM_{sd} forms a measure of uncertainty in the estimate of CWM_{mean}. To check the performance of this model, we compared these CWM estimates with CWM calculations from the commonly used FD package (Laliberte & Legendre, 2010; Laliberté, 2014). To test the effect of dominant pollen taxa on the CWM estimates, we removed one taxon at time and re-calculated CWM.

3.2.7 Relationship between pollen and vegetation community weighted mean

To test the relationship between pollen-based reconstructions of CWM and vegetation CWM, we used the data collected in Scotland. We standardised the CWM values and applied a generalised linear model with a student's-t distributed likelihood for pollen CWM (CWM_{mean}^{pol}) and vegetation CWM (CWM_{mean}^{veg}) as the single predictor so that,

$$CWM_{mean}^{pol} \sim t(\beta \quad CWM_{mean}^{veg}, CWM_{sd}^{pol}, df) \tag{3}$$

The slope β is a correlation-like metric defined with a flat prior between -1 and 1, meaning that we consider all values of β equally probable.

$$\beta \sim Uniform(-1,1) \tag{4}$$

We estimated the degrees of freedom (df) of the t-distribution using an exponential prior with a mean (λ) of 30, as the t-distribution becomes approximately normal at values of 30 and above.

$$df \sim Exp(\lambda) \tag{5}$$

Four factors were tested for their influence on the representation of the vegetation by the pollen-based trait reconstructions: The effect of spatial scale, the use of pollen correction estimates, the separation of vegetation and pollen data into plant functional types, and the separation of vegetation and pollen data into pollination modes.

To test the effect of spatial scale on how representative pollen assemblages are for trait composition reconstruction, we compared vegetation CWM and pollen CWM in the rings of 10 m, 100 m and 1000 m in radius.

To test the ability of corrections for pollen productivity to improve pollen-vegetation trait relationships, we compare CWM estimates based on uncorrected pollen data with two common ways of correcting pollen data: the use of pollen productivity estimates (PPEs) and the Hellinger transformation. PPE data came from Githumbi et al. (2022), who recently synthesised PPEs of European plant taxa. We excluded taxa without PPE's, this led to the exclusion of, on average, 2% of the Scottish pollen data (max 10%). PPE's can be markedly different between studies (Bunting & Farrell, 2022) and dispersal models used (Theuerkauf et al., 2013). Therefore we tested the effect of this uncertainty by randomly drawing 100 PPE's from a normal distribution parameterised by the mean and the standard deviation of the PPE values provided by Githumbi et al. (2022). Pollen percentages were also corrected by the Helinger transformation (square root of the relative abundance), as this is a common transformation of pollen data that does not cause the loss of data.

To test the representation of different plant functional groups on the accuracy of pollen-based reconstructions, pollen were allocated to two plant functional groups according to Reitalu et al. (2019), namely woody (trees and shrubs) and non-woody species (grasses, herbs and dwarf shrubs of the Ericaceae family). The classification of Reitalu et al. (2019) was also used to allocate pollen to pollination modes, either wind-pollinated or not wind-pollinated. At some sites, coverage of a particular plant functional type or pollination mode was very low, therefore we excluded sites with less than 5% cover of the plant functional type or pollination mode from the analysis.

3.2.8 Community weighted mean changes with elevation

To test if pollen-based trait reconstructions reflect vegetation trait composition changes of the vegetation along an elevation gradient, we used the data collected in Switzerland. We fitted a generalised linear model with elevation as the single predictor, so that the likelihood of the CWM values is defined as follows,

$$CWM^{mean} \sim t\left(\alpha + \beta Y_{elev}, CWM^{sd}, df\right) \tag{6}$$

Where α and β are the intercept and the slope, respectively, supplied by vague priors. Y_{elev} is the elevation as the linear predictor. This model was applied to both the pollen and the vegetation CWM values. We modelled this relationship for woody and non-woody taxa separately. We again excluded sites with less than 5% cover of the plant functional type from the analysis.

3.3 Results

3.3.1 Relationship between pollen and vegetation community weighted mean

We find a high uncertainty in the estimated relationship between pollen CWM and vegetation CWM, at any scale or correction (Figure 3.4). We find significant relationships between vegetation CWM and pollen CWM for leaf area and plant height, but not for SLA. The choice of pollen-to-species translation table has an effect on the representation of the vegetation CWM by the pollen data. Using the field-based species we find significant relationships between pollen CWM and vegetation CWM for leaf area and plant height. The correction for taphonomic effects does not significantly improve the relationship between pollen CWM and vegetation CWM.

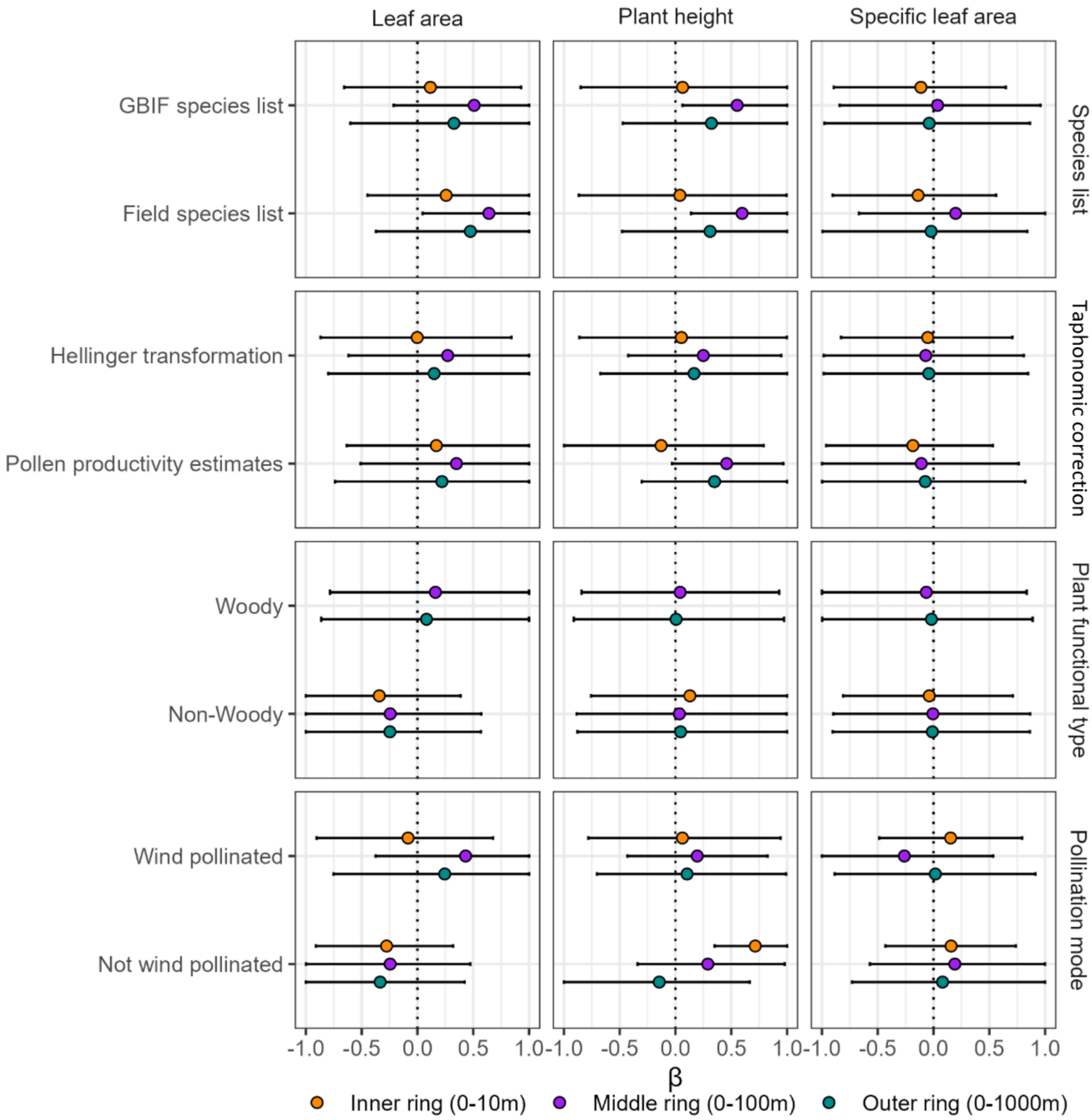

Figure 3.4 Relationship between vegetation CWM and pollen CWM in Scotland for three traits and four treatments. The traits (leaf area, plant height and specific leaf area) are shown in the columns. The four different treatments, described in the text, are shown in the rows. Whisker plots show the mean estimated slope and the 95% credibility interval.

We expected that the trait composition of wind-pollinated and woody vegetation would be better represented by the pollen data than the trait composition of non-woody or not wind-pollinated taxa, especially at a greater spatial scale. However, we only find that the plant height of not wind-pollinated taxa is well represented by the pollen data at the smallest spatial scale (0-10 m).

3.3.2 Trait change along an elevation gradient

We expected the pollen data to reproduce the trends in vegetation trait change along the elevation gradient. We found decreasing plant height, leaf area and SLA with elevation for both woody and non-woody vegetation with increasing elevation (Figure 3.5). Pollen CWM does not accurately reflect the trait changes with elevation that are demonstrated by the vegetation. The leaf area of woody and non-woody plants is underestimated by the pollen data. The steep decrease in plant height of woody taxa along the elevation gradient is not reproduced by the pollen data. The plant height of non-woody taxa is stable in both the vegetation and the pollen data. The SLA of the vegetation decreases along the elevation gradient for both woody and non-woody taxa, but this trend was not observed in the pollen data.

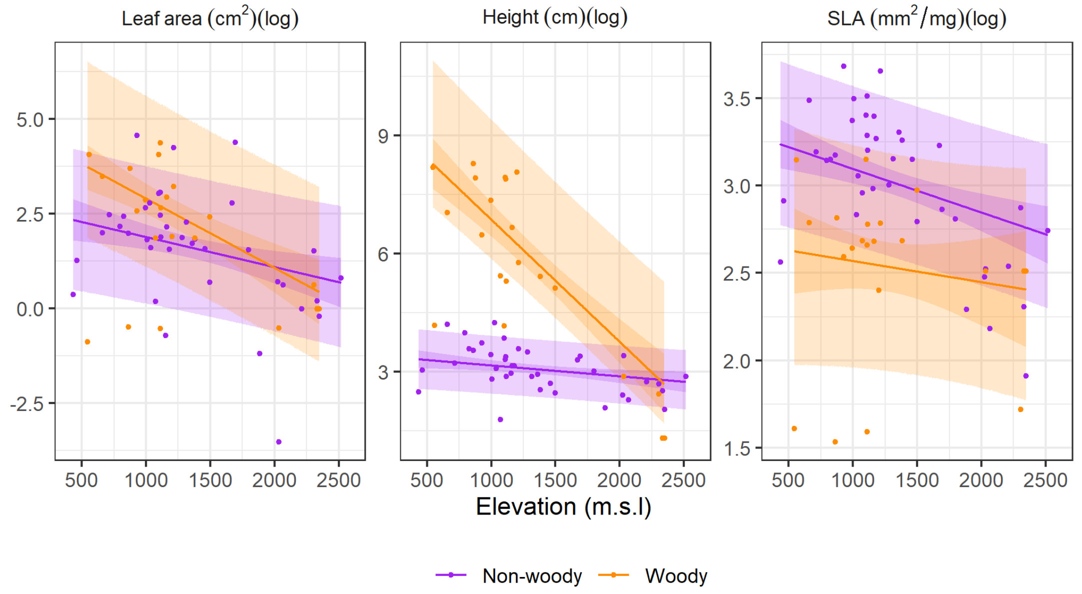

Figure 3.5 Vegetation CWM change with elevation in Switzerland for two plant functional types, woody and non-woody. The darker shaded area shows the 95% credibility interval and the lighter shade area shows the 95% prediction interval.

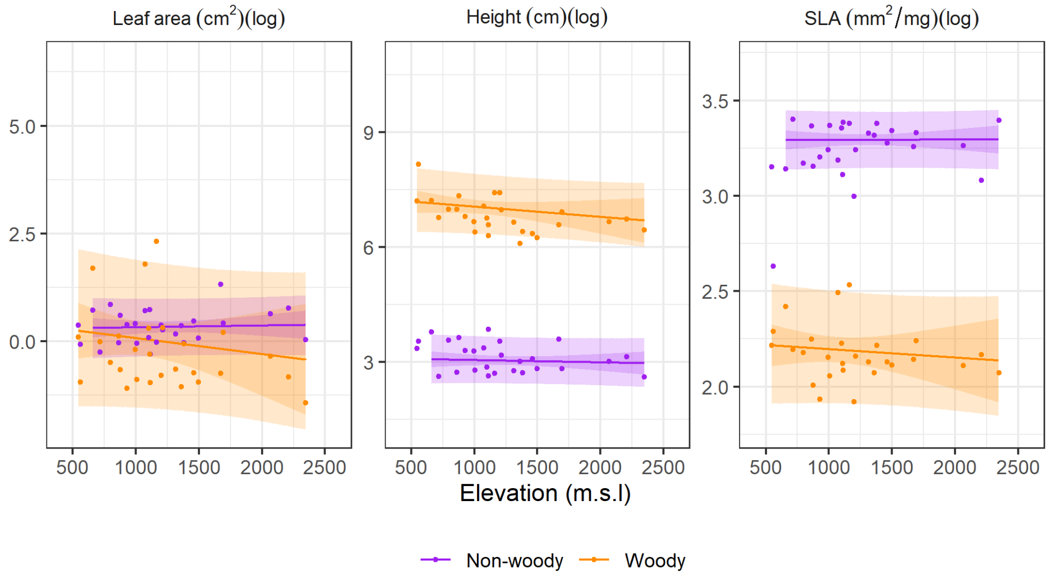

Figure 3.6 Pollen CWM change with elevation in Switzerland for two plant functional types, woody and non-woody. The darker shaded area shows the 95% credibility interval and lighter shade area shows the 95% prediction interval.

3.4 Discussion

The ability to use pollen records for the reconstruction of past plant trait composition would allow for a novel way of interpreting past vegetation changes. However, the relationship between vegetation trait composition and pollen-based trait reconstructions is complex and not well explored (but see Carvalho et al. (2019), Blaus et al. (2020), Brussel and Brewer (2021) and van der Sande et al. (2021)). Here, we find ambiguous relationships between vegetation and pollen CWM. Next to known issues with pollen data, such as the difficulty of assessing the relevant spatial scale and taxon-specific differences in pollen productivity, we find that trait identity and trait variation within pollen taxa is of great importance when reconstructing functional composition from pollen data.

We incorporated the uncertainty arising from the trait variation within pollen taxa in estimating CWM using a Bayesian approach. By using this approach we highlighted that trait variation in pollen taxa could be a primary source of uncertainty in establishing relationships between vegetation and pollen CWM. When correlating CWM estimates based on mean taxon trait values, using a frequentist approach, we find more significant relationships between pollen CWM and vegetation CWM (Appendix S5). The number of species included in a pollen taxon is an important factor influencing the mean and the variation of the trait distribution of pollen taxa (Appendix S4). Reducing the species list to field-observed species improved the relationship between leaf area and plant height of the vegetation and the pollen-based reconstructions (Figure 3.4). Thus, reducing the uncertainty arising from the low taxonomic resolution of pollen data is a prime point of research for the advance of "functional palaeoecology" (Reitalu & Nogué, 2023). The taxonomic resolution of past plant composition reconstructions could, for instance, be improved by combining pollen data with macrofossil data, spectral analyses, ancient DNA or species distribution modelling (Birks & Birks, 2000; Parducci et al., 2017; Svenning et al., 2011; Zimmerman et al., 2016).

Trait variation within pollen taxa depends on the trait and the taxon in consideration. For instance, the plant height variation in *Betula* genus is considerable, while the SLA variation is relatively minor compared to other dominant taxa in the data set (Appendix S4). Our field study in Scotland was performed in a heterogenous environment of mixed vegetation types, making it difficult to distinguish whether particular taxa contribute more to the uncertainty in the trait reconstruction. A mismatch between the field measured trait data and the trait data from TRY can also be a reason for the lack of significant relationships between pollen and vegetation CWM (Appendix S4). The data in TRY is collected in a variety of environments, therefore not necessarily representing the local conditions in Scotland or Switzerland (Siefert et al., 2015).

Here we applied PPEs to correct for taxon-specific differences in pollen production, but it did not improve the relationship between pollen CWM and vegetation CWM (Figure 3.4). Applying PPE's did correct the representation of the vegetation by the pollen data for some taxa (e.g. *Pinus*, *Betula*), although not all (e.g. Ericales) (Appendix S2). PPE estimates can vary across studies because of environmental variation, habitat structure, species composition and data collection method (Bunting & Farrell, 2022). The variation in PPE estimates can affect the pollen abundance of a taxon by up to 10 percent (Appendix S2). A single taxon can have a considerable effect on the reconstructed trait value, but its impact depends on the trait and the abundance of the taxon. For instance, leaf area is generally overestimated by the pollen data. This is possibly due to the abundance of *Betula* in the samples, as removing *Betula* from the samples decreases leaf area more than other taxa (Appendix S6). Similarly, Ericales seems to have a great influence on pollen SLA trait values (Appendix S3 and S6). Therefore, developing PPE's and understanding their properties in different environments is important for improving representation of vegetation by pollen data and consequently reconstructing trait composition from pollen data (Bunting & Farrell, 2022).

Wind-pollinated taxa and woody taxa are generally best represented by pollen assemblages, but also after separating the data into these groups, we still find highly uncertain relationships (Figure 3.4) (Blaus et al., 2020; Meltsov et al., 2011). The only significant relationship between pollen CWM and vegetation CWM was found for the plant height of not wind-pollinated taxa in the inner ring. This might be because the pollen source of not wind-pollinated taxa is small and plant height variation in not wind-pollinated taxa might be lower than in wind-pollinated taxa (Eriksson et al., 2002; Moles et al., 2009).

Pollen-based trait reconstructions have been shown to reflect trait-composition changes along environmental gradients such as elevation (van der Sande et al., 2020) and climate (Barboni et al., 2004). Here we find that leaf area, SLA and plant height of the vegetation decrease with increasing elevation. As elevation increases, environmental filtering favours species that are adapted to colder conditions, these species are generally short and have small, tough leaves (Junker & Larue-Kontić, 2018; Kraft et al., 2015). Contrary to expectations, the pollen assemblages do not reproduce the changes in vegetation CWM. All trait values stay relatively stable with increasing elevation. This might be caused by the upward transport of pollen from the valley, which can cause the homogenisation of pollen assemblages (Cañellas-Boltà et al., 2009). Furthermore, the vegetation data in Switzerland was collected in small plots, which might not reflect the pollen source area well.

We make two recommendation for the reconstruction of trait composition from pollen data. First, correct for taphonomic effects, many of the confounding variables in this study are related to the inherent to the production and dispersal properties of pollen. Improving quantitative reconstructions of past plant compositions will also aid the reconstruction of past plant functional composition. Further studies should also test pollen-trait relationships in other ecosystem types and at greater spatial scales. Second, future pollen-based functional composition reconstructions should consider the trait variation within pollen taxa more carefully. This can be done by Bayesian methods as done here or Monte Carlo simulation such as done in Brussel and Brewer (2021). Despite showing little evidence for pollen being a reliable proxy for past trait composition, we do not discourage the use of it. Our sample size was low and positive relationships between pollen CWM and vegetation CWM were not refuted by this analysis. We do advocate for caution of the use of pollen for reconstruction of past plant trait composition and encourage further testing of the validity of this proxy.

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Appendix S1: Site characteristics

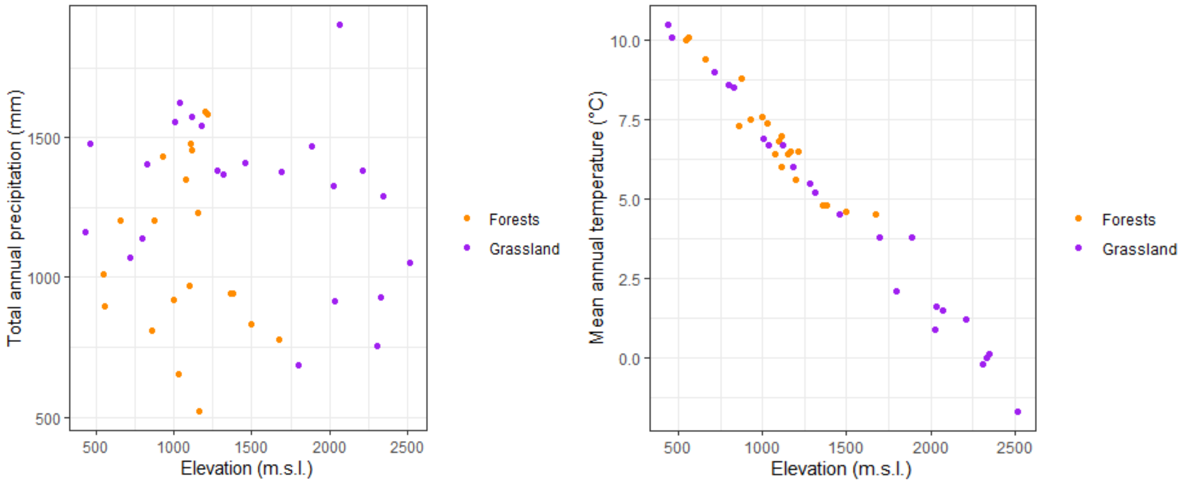

Figure S1.1 Annual mean temperature and precipitation for the sites sampled in Switzerland.

Appendix S2: Representation of the vegetation by the pollen data

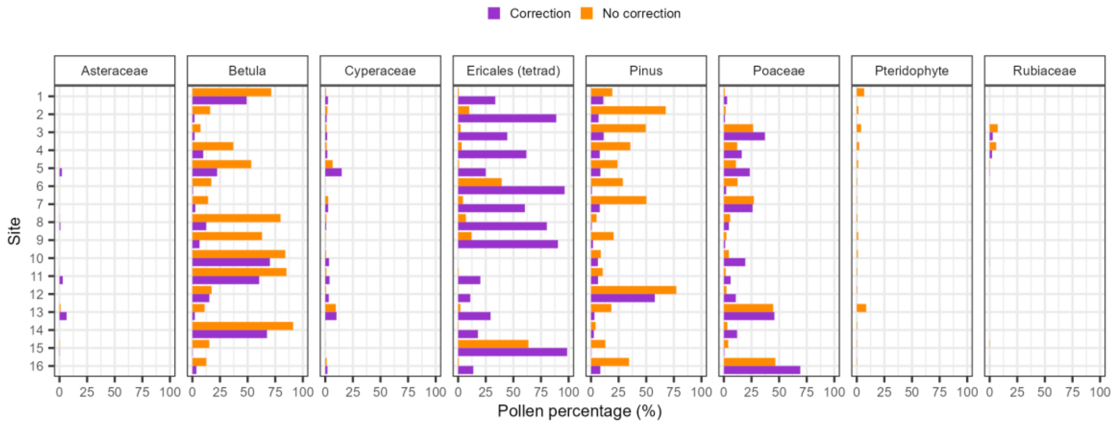

Figure S2.1 Pollen percentages of the most abundant pollen taxa (>5%) at the 16 sites surveyed in Scotland. Different colours indicate if pollen were corrected by pollen productivity estimates.

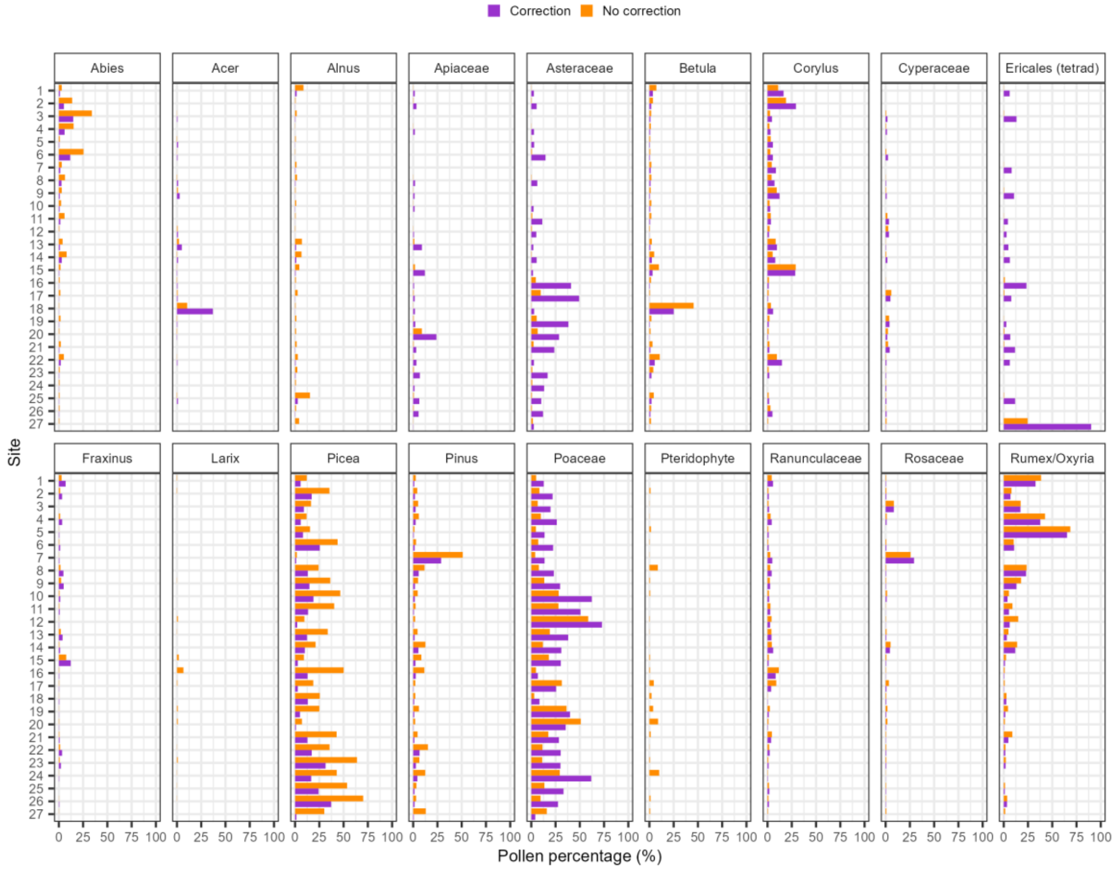

Figure S2.2 Pollen percentages of the most abundant pollen taxa (>5%) at the 27 sites surveyed in Switzerland. Different colours indicate if pollen were corrected by pollen productivity estimates.

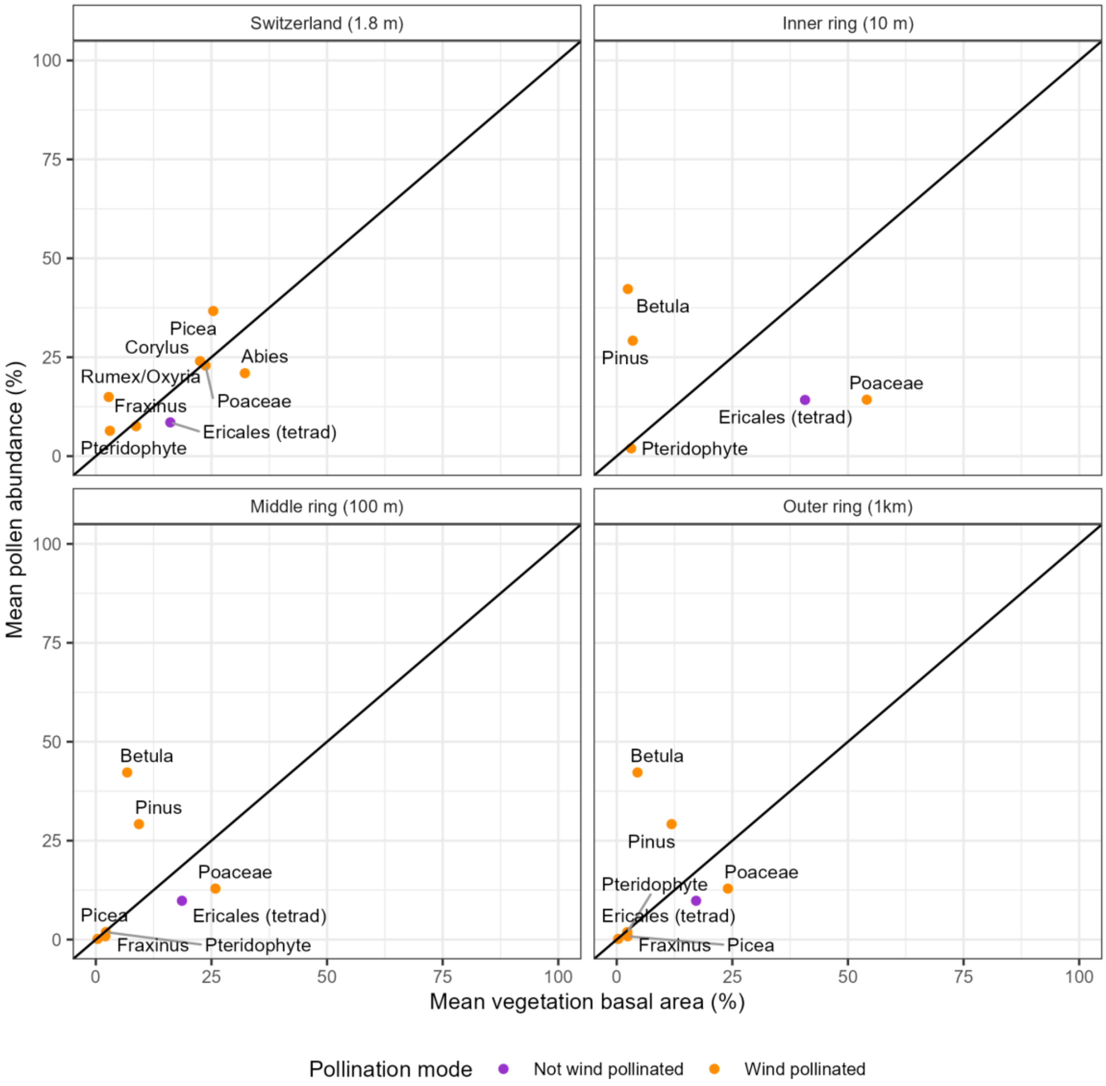

Figure S2.3 Vegetation abundance (%) compared pollen abundance (%) of the most abundant pollen taxa (>5%). Black diagonal line marks perfect representation of the vegetation by the pollen data. Colour of the points indicate the pollination mode of the taxon, either wind or non-wind pollinated.

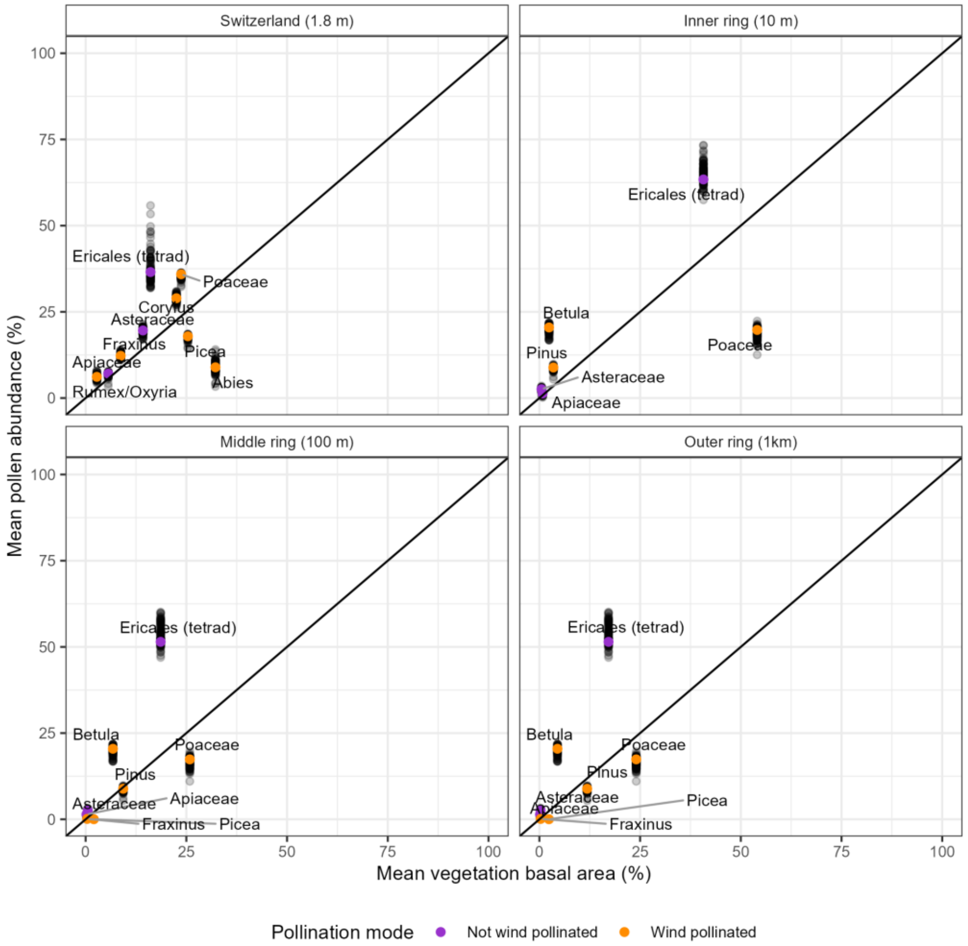

Figure S2.4 Vegetation abundance (%) compared with adjusted pollen abundance (%) of the most abundant pollen taxa (>5%). Black diagonal line marks perfect representation of the vegetation by the pollen data. Grey dots show the effect of uncertainty around pollen productivity estimates. Colour of the points indicate the pollination mode of the taxon, either wind or non-wind pollinated.

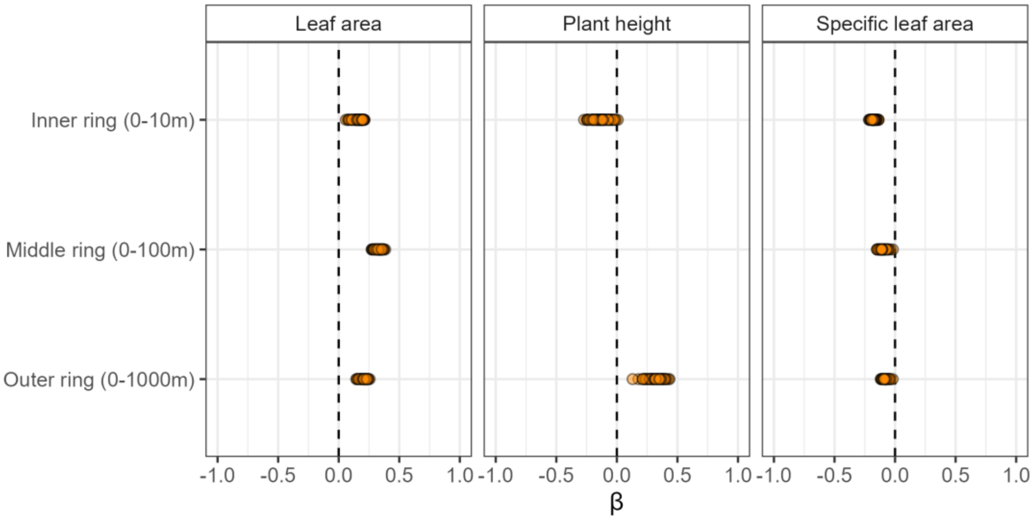

Figure S2.5 Effect of the uncertainty in pollen productivity estimates on the mean estimates of slope between pollen CWM and vegetation CWM.

Appendix S3: Scatter plots pollen and vegetation CWM trait values

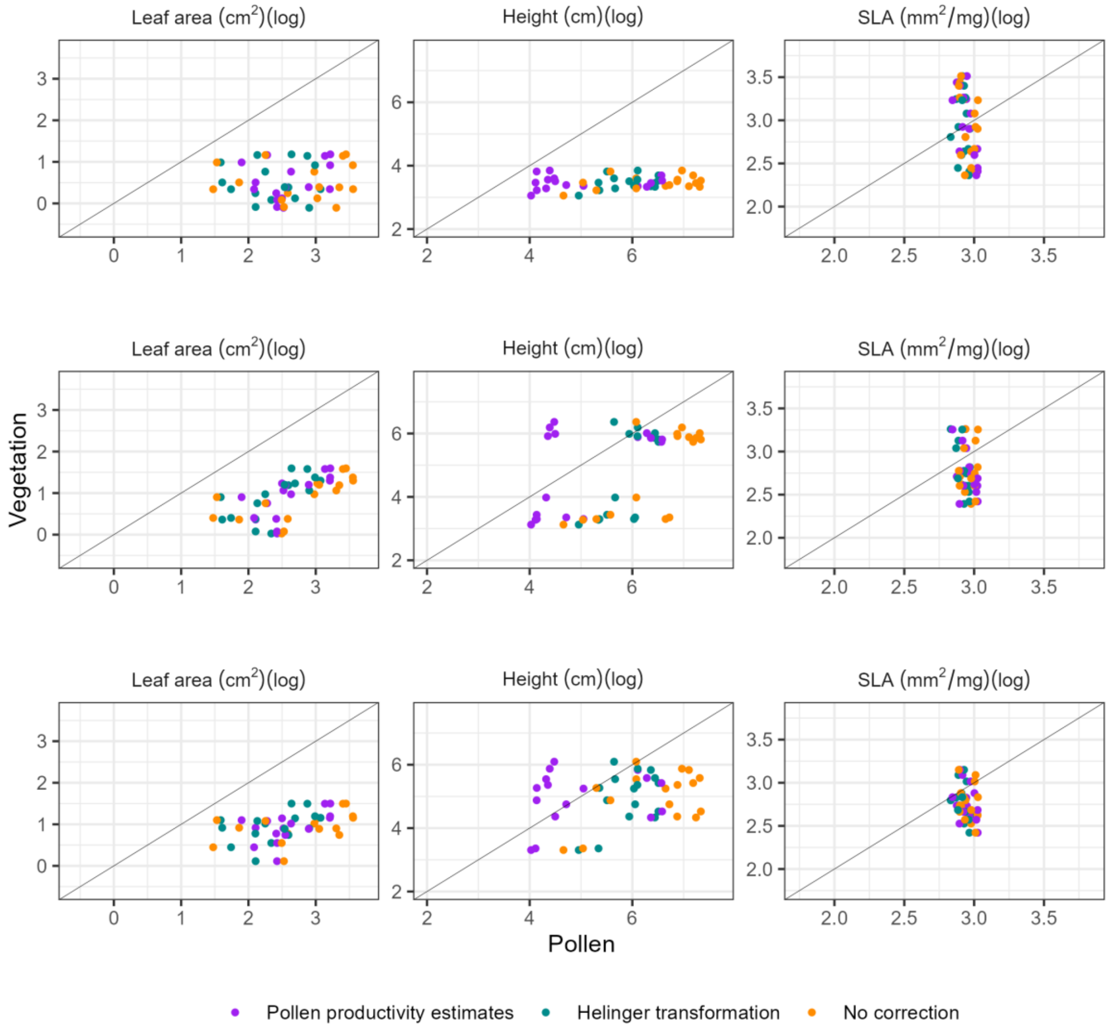

Figure S3.1 Pollen-based reconstructions of CWM trait values compared with vegetation CWM trait values. Colours indicate the kind of correction of the pollen data.

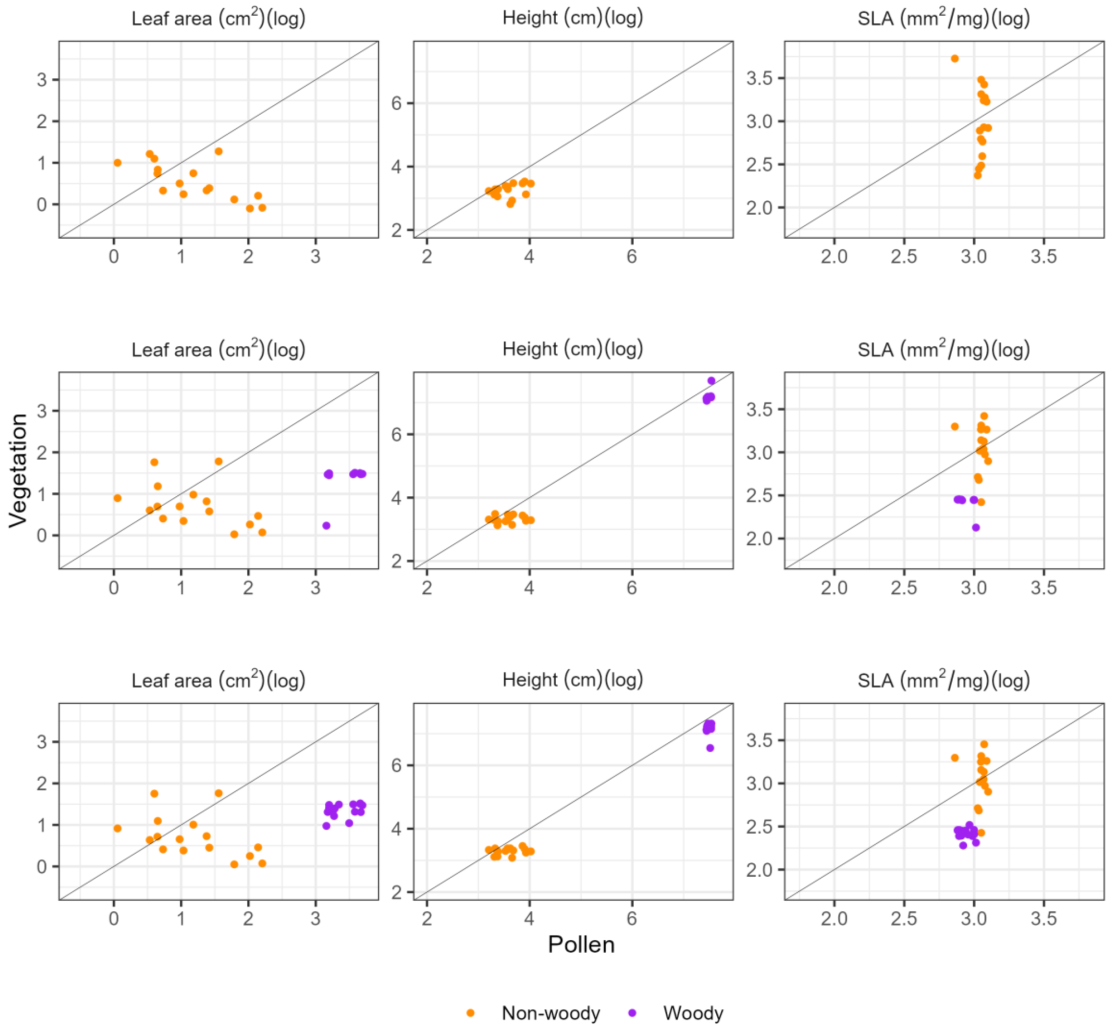

Figure S3.2 Pollen-based reconstructions of CWM compared with vegetation CWM values. Colours indicate the plant functional type of the taxa.

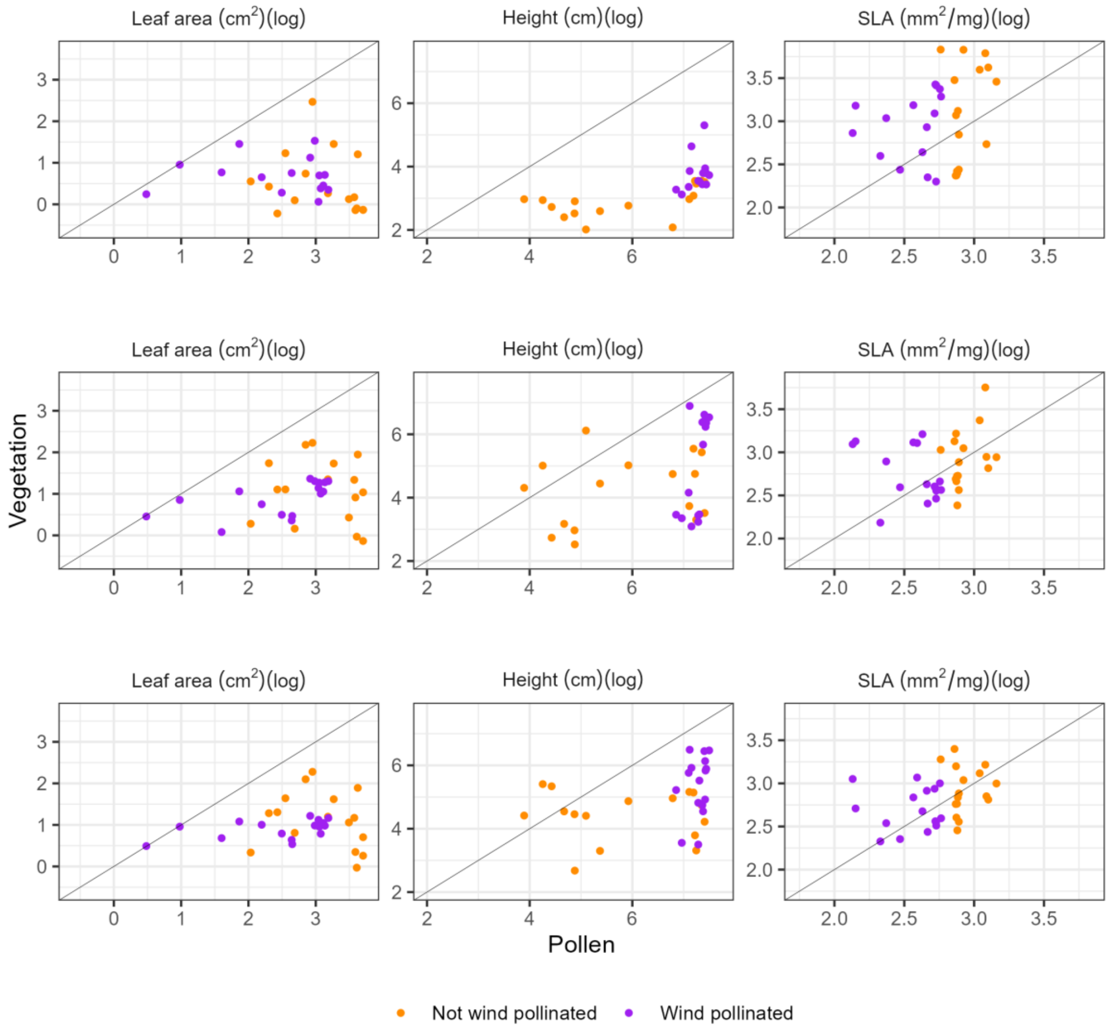

Figure S3.3 Pollen-based reconstructions of CWM compared with vegetation CWM values. Colours indicate the pollination mode of the taxa.

Appendix S4: Trait values of the pollen taxa

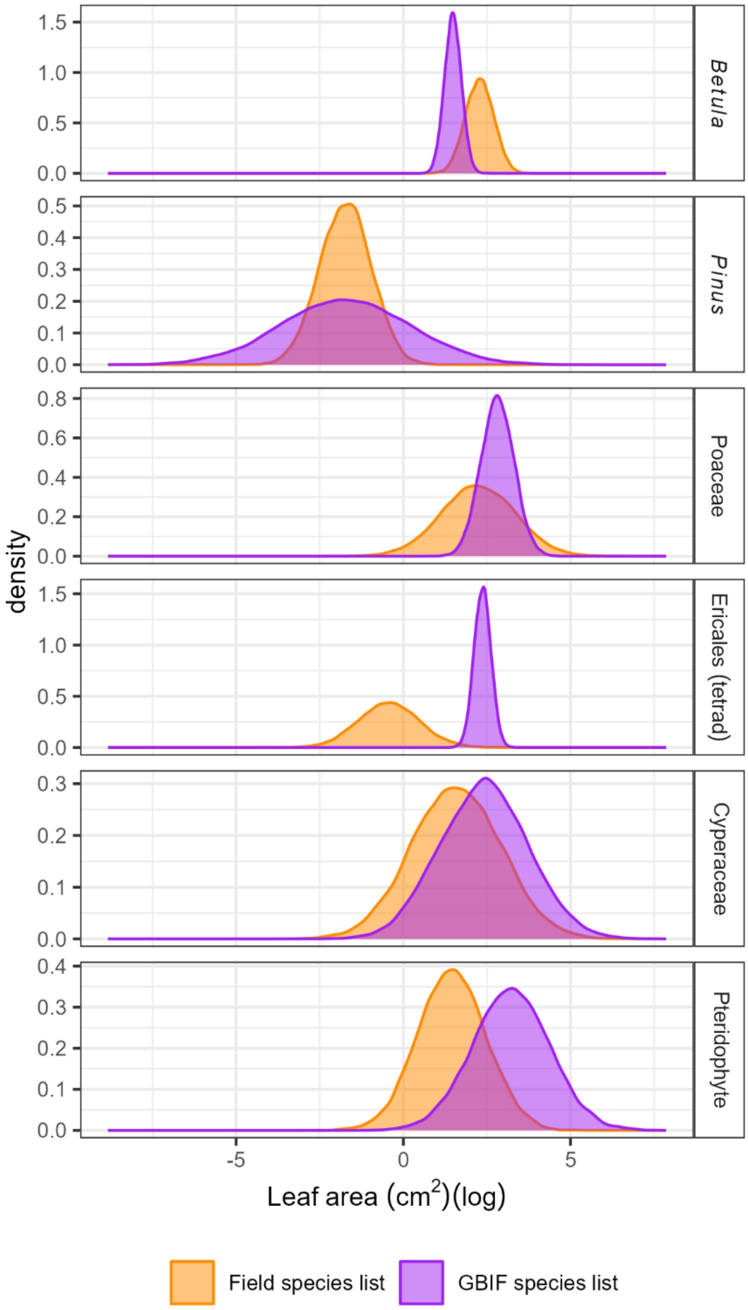

Figure S4.1 Leaf area trait values of the most abundant taxa in Scotland (>5%). Bars display the trait data from the gap-filled TRY data, black lines indicated the modelled distribution.

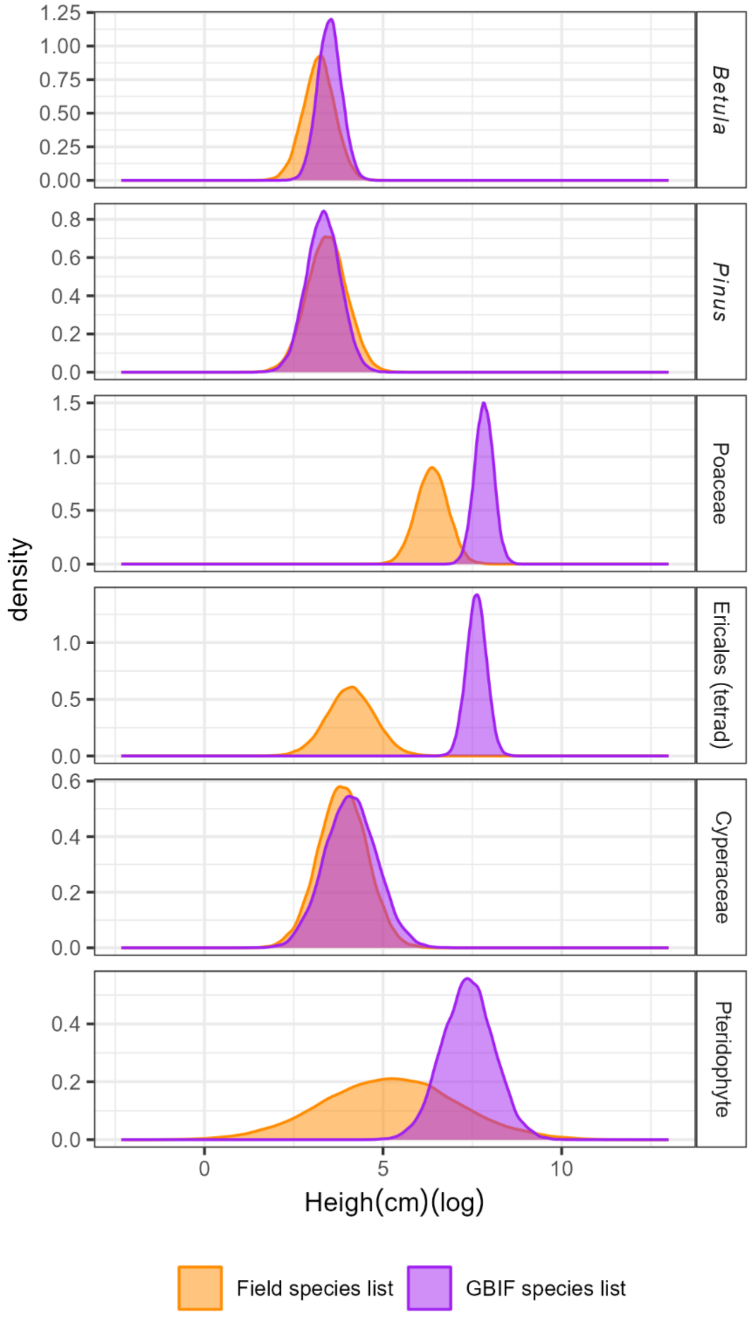

Figure S4.2 Specific leaf area trait values of the most abundant taxa in Scotland (>5%). Bars display the trait data from the gap-filled TRY data, black lines indicated the modelled distribution.

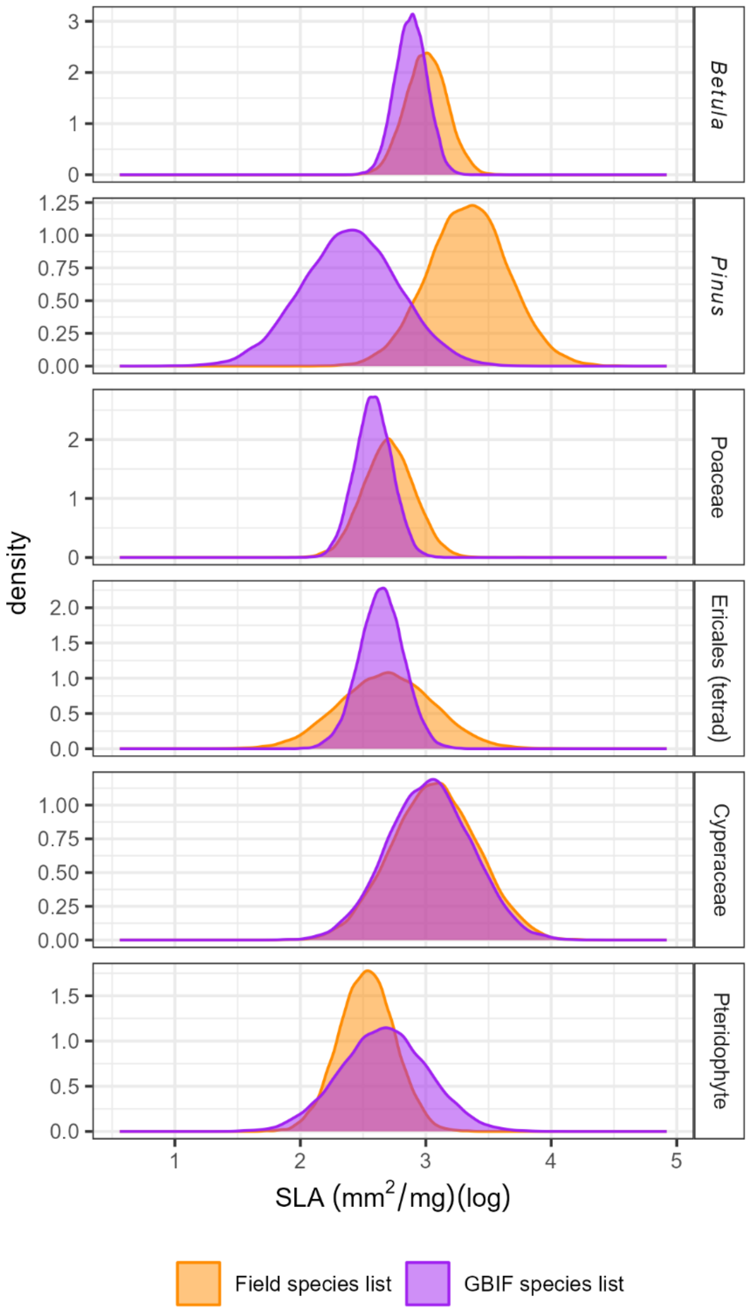

Figure S4.3 Plant height trait values of the most abundant taxa in Scotland (>5%). Bars display the trait data from the gap-filled TRY data, black lines indicated the modelled distribution.

Table S4.1 Number of trait observations and species by taxon in the gap-filled trait data using the GBIF translation table.

Pollen taxon	Number of species	Number of trait observations
Abies	15	978
Acer	21	1872
Alnus	6	559
Apiaceae	88	4222
Asteraceae	347	13799
Betula	9	1532
Corylus	3	368
Cyperaceae	155	6077
Ericales (tetrad)	42	4049
Fraxinus	7	716
Geraniaceae	32	1466
Larix	2	446
Picea	11	3111
Pinus	16	9871
Plantago	11	1101
Poaceae	270	16157
Populus	8	548
Pteridophyte	58	1002
Quercus	18	5906
Ranunculaceae	93	3425
Rosaceae	263	9423
Rumex/Oxyria	28	1621

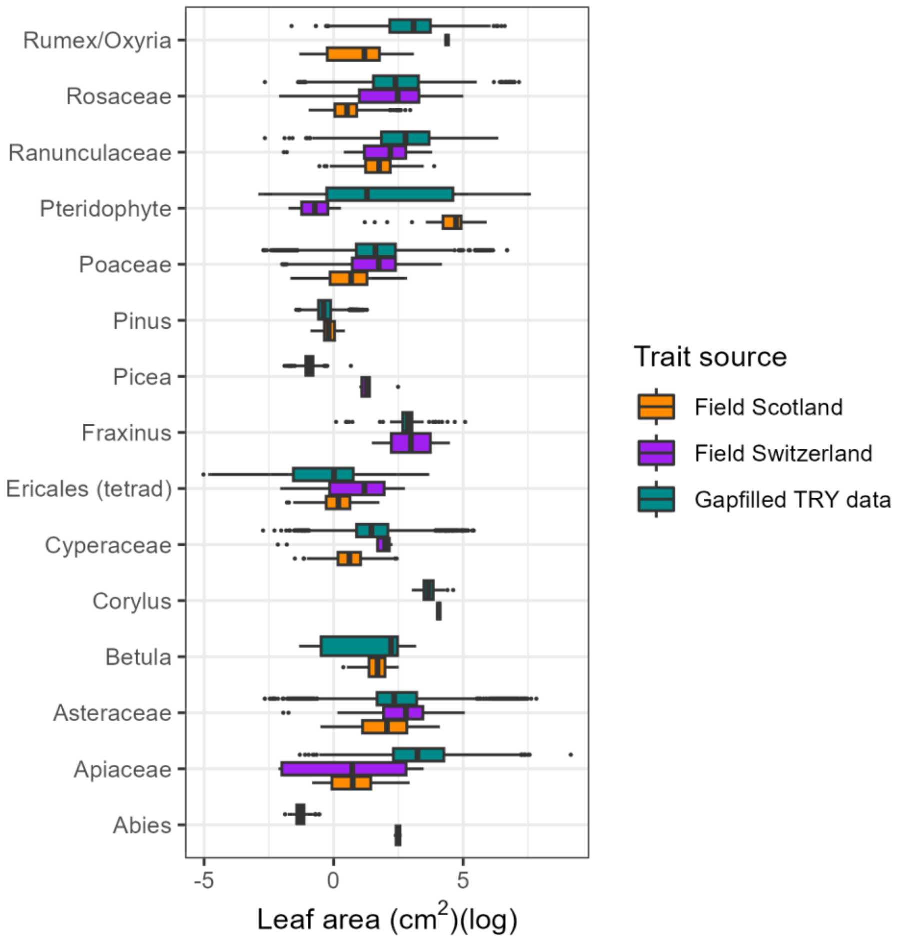

Figure S4.4 Comparison between the trait data collected in the field with the gap-filled trait data obtained from TRY.

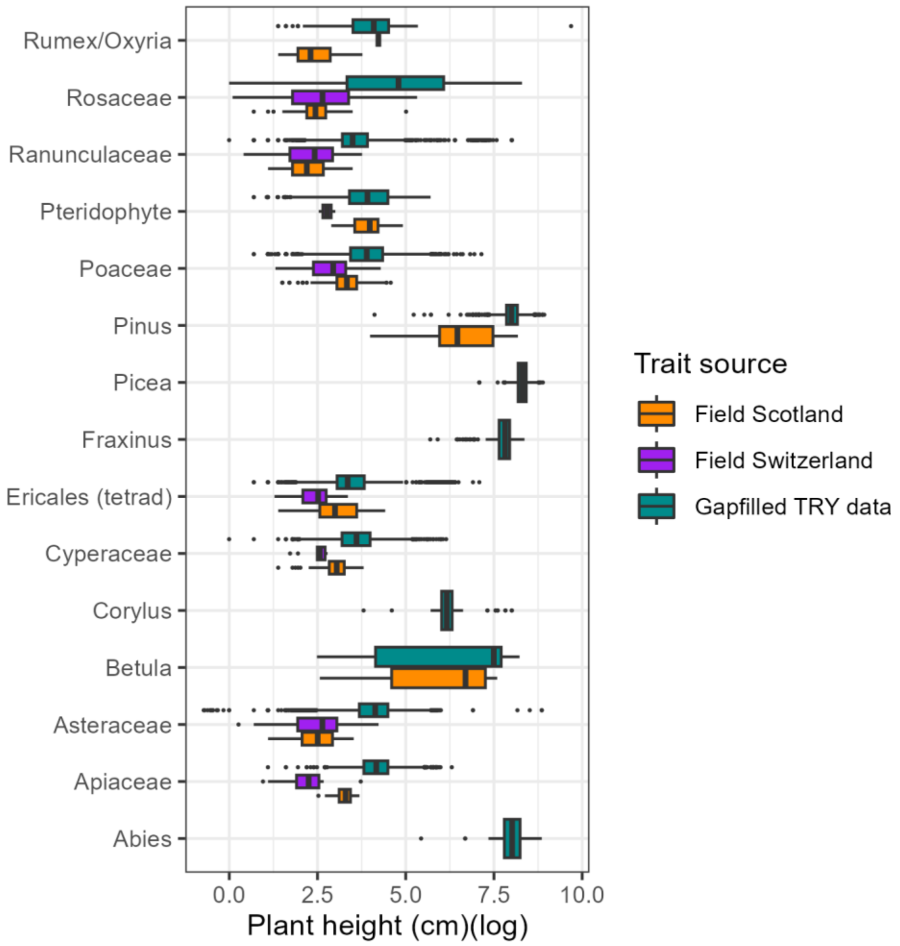

Figure S4.5 Comparison between the trait data collected in the field with the gap-filled trait data obtained from TRY.

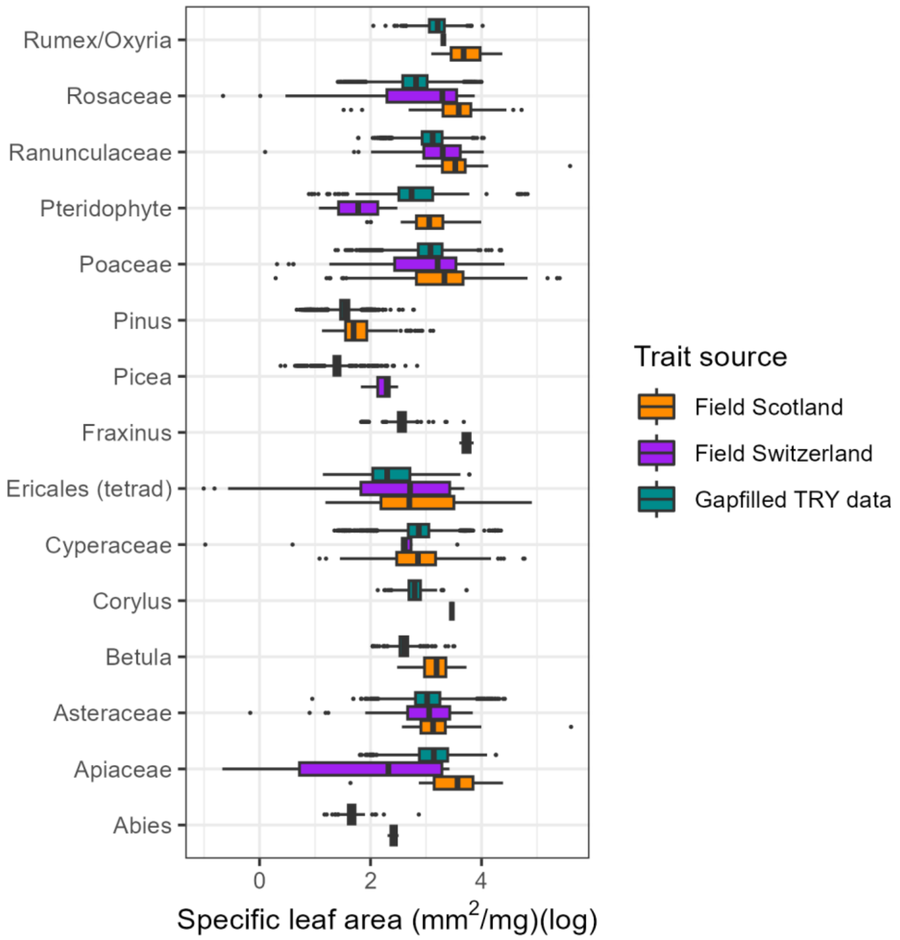

Figure S4.6 Comparison between the trait data collected in the field with the gap-filled trait data obtained from TRY.

Appendix S5 Correlation CWM values without considering trait variation within pollen taxa

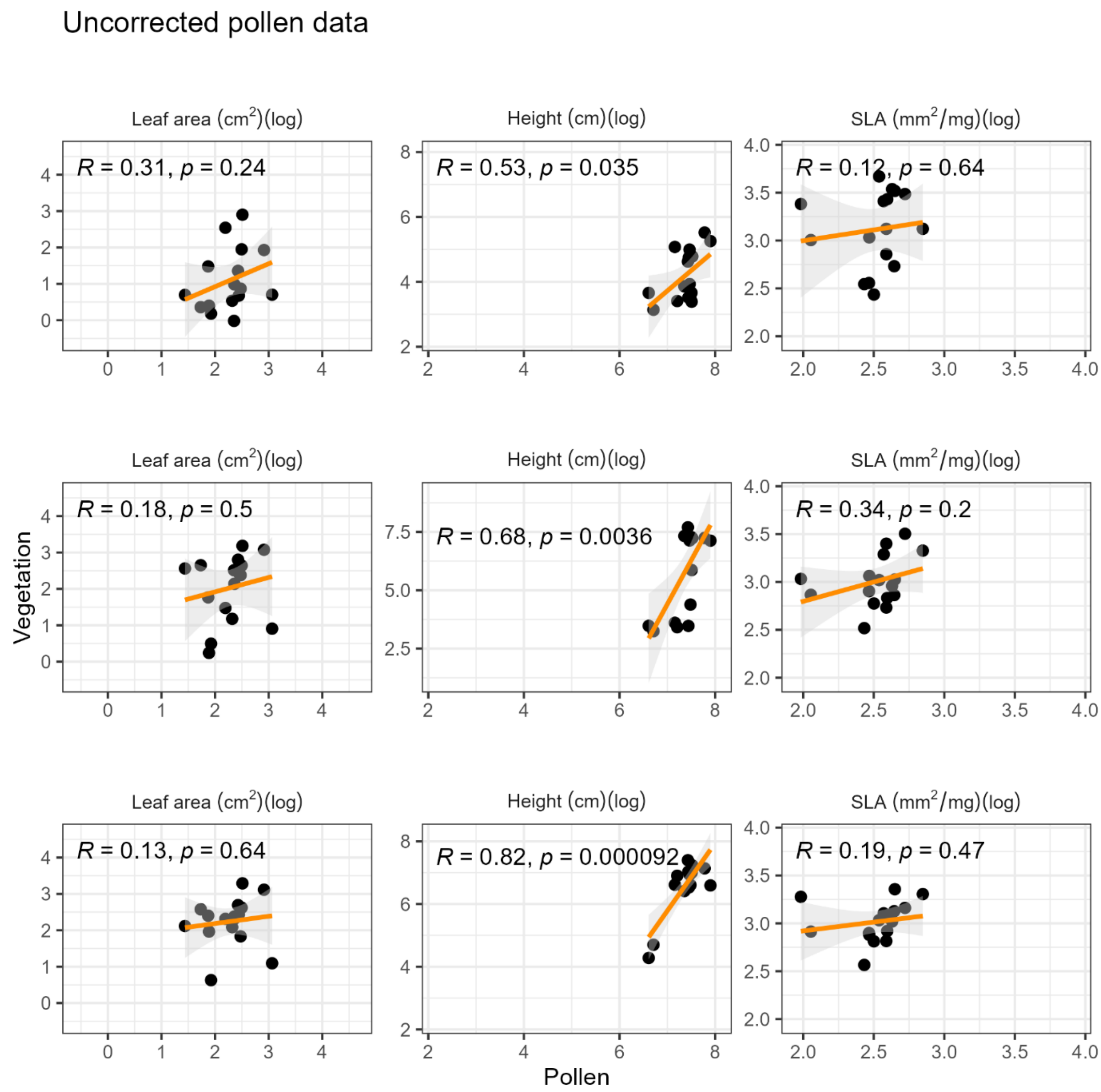

Figure S5.1 Correlation between the CWM of pollen and vegetation CWM when not considering variation within pollen taxa.

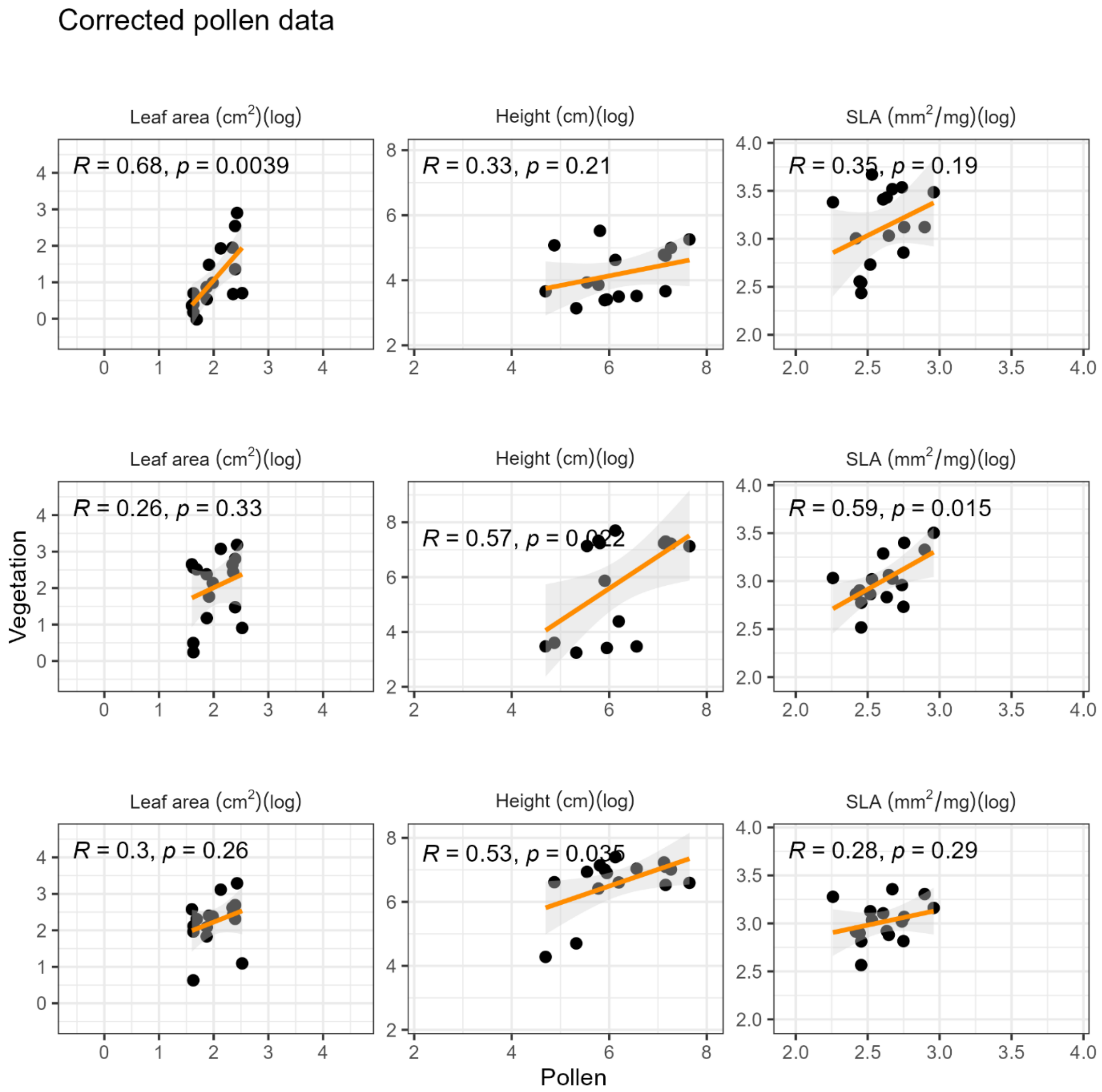

Figure S5.2 Correlation between the CWM of pollen and vegetation CWM when not considering variation within pollen taxa. Pollen data here is corrected with pollen productivity estimates.

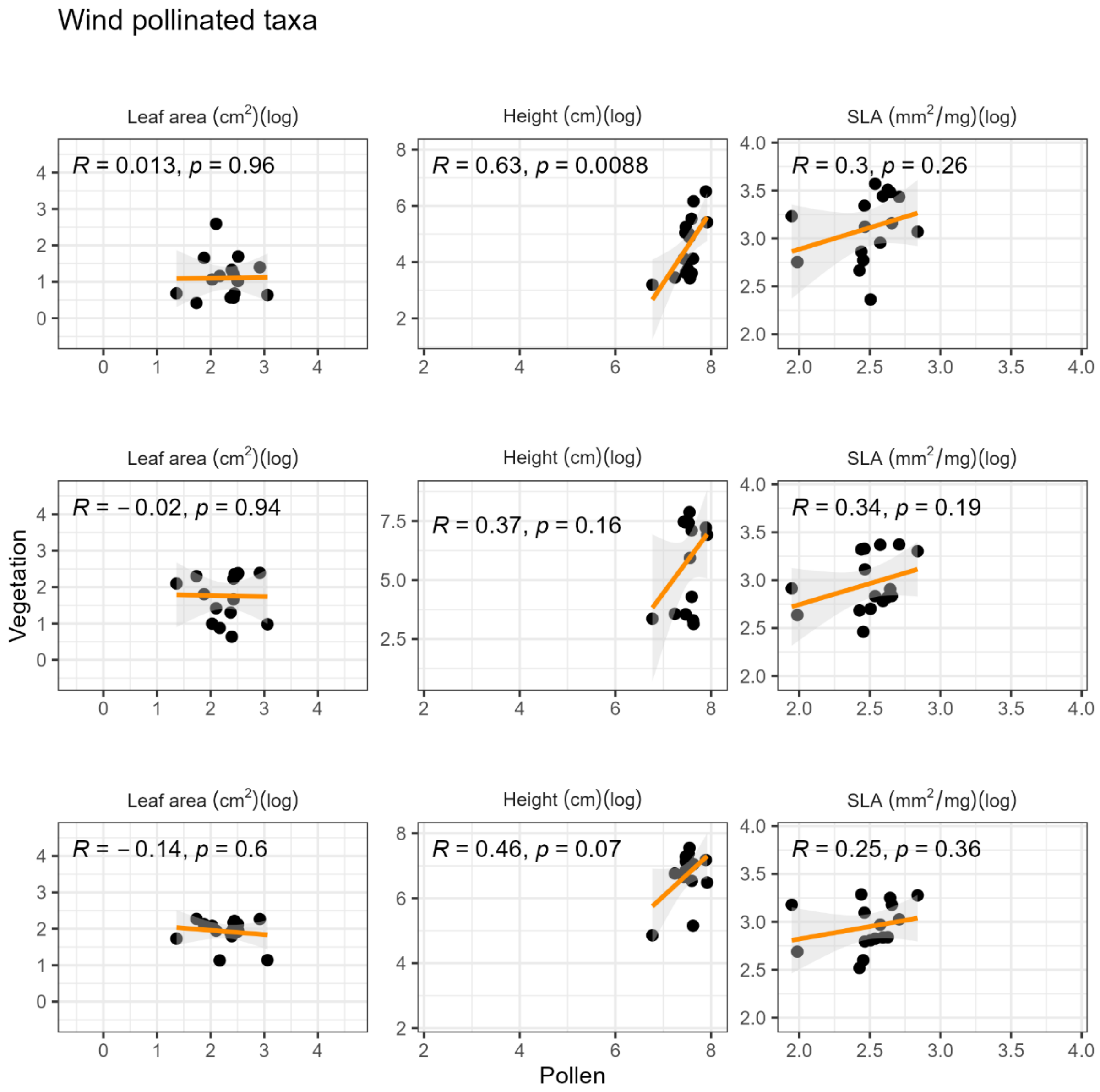

Figure S5.3 Correlation between the CWM of pollen and vegetation CWM when not considering variation within pollen taxa. Wind-pollinated taxa only.

Non-woody taxa

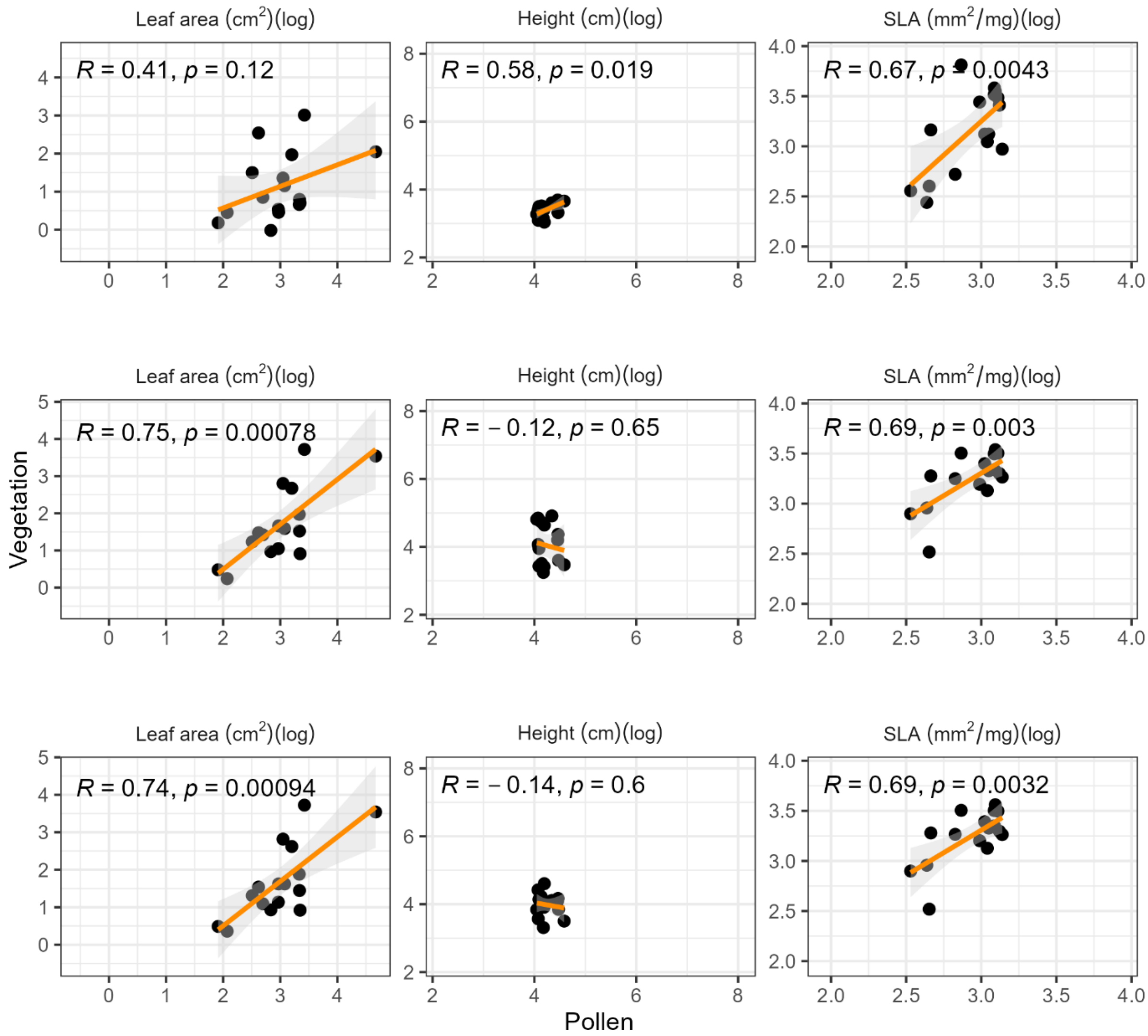

Figure S5.4 Correlation between the CWM of pollen and vegetation CWM when not considering variation within pollen taxa. Only non-woody taxa.

Woody taxa

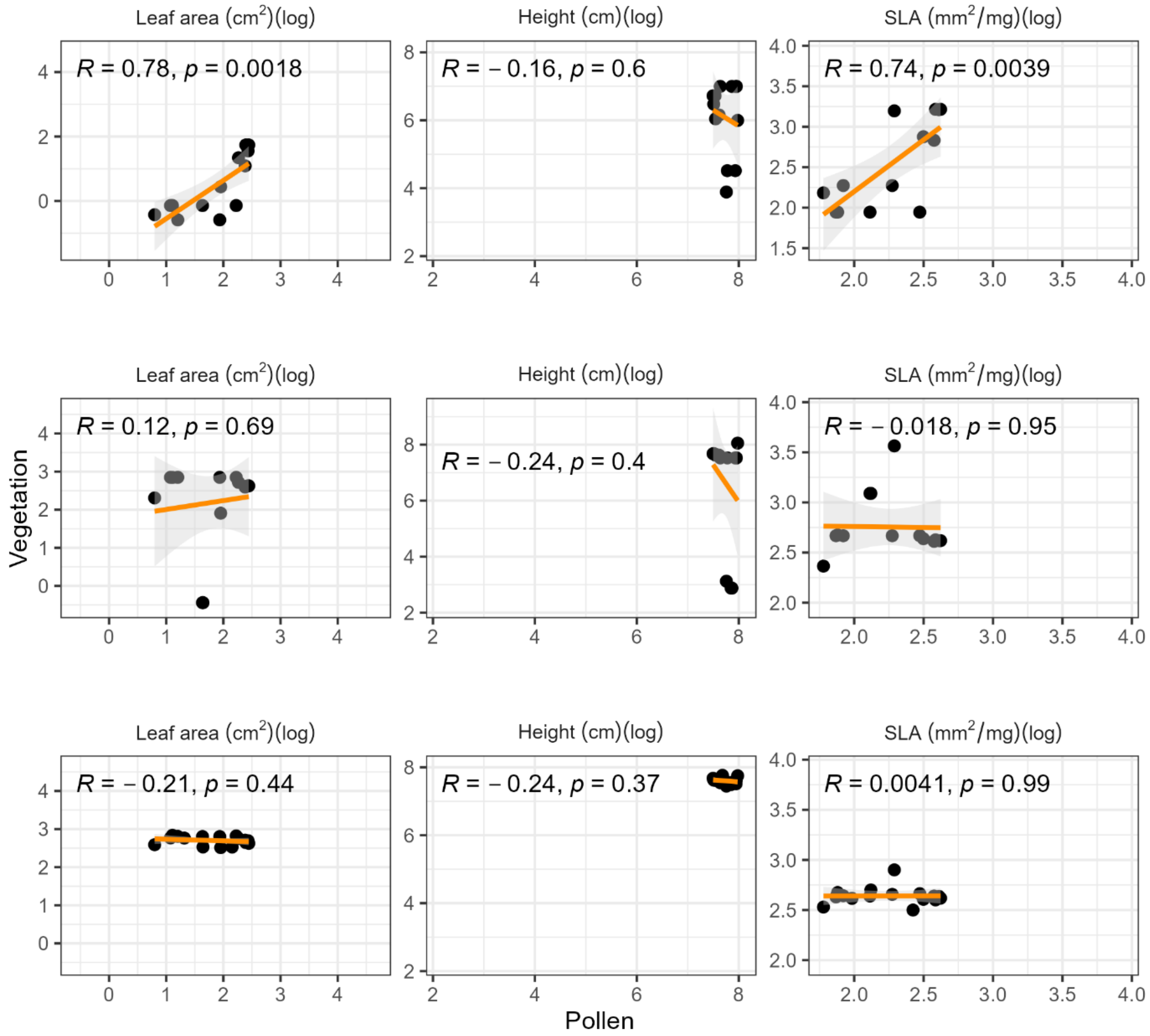

Figure S5.5 Correlation between the CWM of pollen and vegetation CWM when not considering variation within pollen taxa. Only woody taxa.

Appendix S6: Effect of removal of taxa on CWM trait values in the middle ring

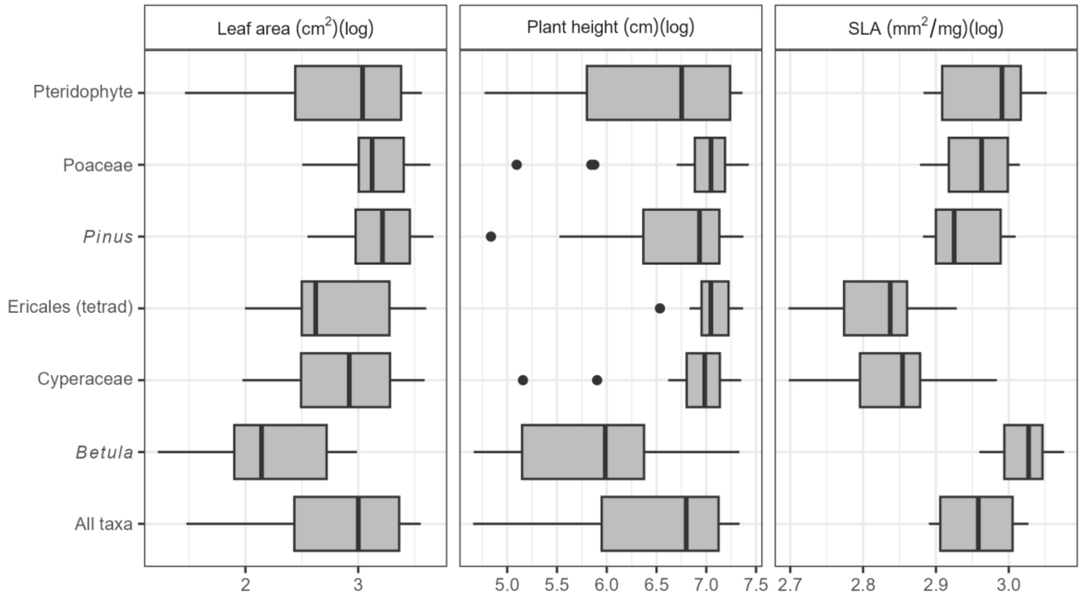

Figure S6.1 Effect of removal of taxa in the pollen data, every boxplot represents the distribution of CWM values in the Scottish data when removing one of six most dominant pollen taxa.

Paper 2: Pollen-based reconstruction reveals the impact of the onset of agriculture on plant functional trait composition

The following chapter has been published in Ecology Letters:

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Author contributions: AV designed the study supervised by MJS, SM and FS. AV conducted the analysis with help of FS. AD provided data. AV wrote the manuscript and all authors contributed substantially.

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Code and data availability: R-scripts and the datasets necessary to run the analysis are available in OSF repository (doi: 10.17605/OSF.IO/JK5BF).

4 Pollen-based reconstruction reveals the impact of the onset of agriculture on plant functional trait composition

Abstract

The onset of agriculture improved the capacity of ecosystems to produce food, but inadvertently altered other vital ecosystem functions. Plant traits play a central role in determining ecosystem properties, therefore we investigated how the onset of agriculture in Europe changed plant trait composition using 78 pollen records. Using a novel Bayesian approach for reconstructing plant trait composition from pollen records, we provide a robust method that can account for trait variability within pollen types. We estimate an overall fourfold decrease in plant size through agriculture and associated decreases in leaf and seed size. We show an increase in niche space towards the resource-acquisitive end of the leaf economic spectrum. Decreases in leaf phosphorus might have been caused by nutrient depletion through grazing and burning. Our results show that agriculture, from its start, has likely been gradually impacting biogeochemical cycles through altered vegetation composition.

4.1 Introduction

Recent studies have demonstrated that humans began to alter the world's ecosystems earlier and to a greater extent than previously thought (Ellis et al., 2021; Mottl et al., 2021; Stephens et al., 2019). Agriculture is considered to be the dominant activity through which humans have induced change in ecosystems. In northwestern Europe, forest clearance, burning and land management for agriculture increased openness, heterogeneity and biodiversity of landscapes from 5500 (Central Swiss Alps) and 6000 years ago (British Isles) (Colombaroli et al., 2013; Woodbridge et al., 2020). Agriculture also alters ecological processes. For instance, agriculture may increase erosion and loss of soil organic carbon with such impacts noted as early as 7500 years ago (Hoffmann et al., 2013; Houben, 2008; Notebaert et al., 2009). Plants are central to many ecosystem processes and their variable forms and functions mean that they influence these processes in different ways, including decomposition (Cornwell et al., 2008), carbon storage (De Deyn et al., 2008) and erosion control (Zuazo & Pleguezuelo, 2009). Yet little is known about how agriculture changes plant functional composition on timescales of centuries to millennia.

The onset of agriculture may alter plant functional composition in multiple ways. Firstly, the intentional removal of woody species to create agricultural land may have changed plant functional composition. In pre-agricultural Europe, closed forest most likely dominated fertile upland areas, although open vegetation, maintained by large herbivores and fire, was common on floodplains and infertile soils (Svenning, 2002). Disturbances by agriculture create opportunities for fast-growing species which disperse rapidly. Especially In the early stages of agriculture, fallowing would have created a heterogeneous agricultural landscape, with areas in use and in various stages of succession (Mazoyer & Roudart, 2007). Secondly, agriculture can change plant functional composition through the deliberate introduction of species and associated spread of weeds. Crop plants have been selected over millennia for traits that make them more suitable for human consumption and production, such as higher net photosynthesis rates, higher leaf nitrogen content and higher seed production (Roucou et al., 2018). Weed species typically have high growth rates and produce a high number of seeds (Navas, 2012). Finally, agricultural practices can alter plant community functional composition by changing biotic and abiotic factors (Laliberte & Tylianakis, 2012). Even Europe's earliest farmers implemented intensive land management practices, such as livestock manuring and water management (Bogaard et al., 2013).

Whilst land use appears to have strongly controlled northwestern European vegetation composition since the mid-Holocene, climate was a main driver of vegetation change throughout the Holocene as well (Marquer et al., 2017). 12 000 years ago, mean annual temperature on the Northern Hemisphere was about 2 ˚C lower than the temperature in the 19th century (Kaufman et al., 2020). The increase in temperature at the beginning of the Holocene led to the expansion of mixed deciduous forest, while boreal forest and tundra and steppe vegetation shifted northwards (Roberts, 1998). Maximum forest cover in Europe was reached between 8000 and 6000 BP (i.e. years before 1950) (Roberts et al., 2018). The replacement of tundra and steppe vegetation by forest consequently changed plant functional composition by increasing plant height and other size-related traits such as leaf size and seed mass (Moles et al., 2009). Further changes in size-related traits may have occurred through succession within the woodland primarily driven by light competition (Douma et al., 2012). Furthermore, as temperature and water availability are main constraints on the primary productivity of terrestrial ecosystems, rising temperatures in the early Holocene could also have facilitated more competitive species that typically have large leaves and high leaf nutrient concentration (Wright et al., 2017).

The large number of palynological records produced over the last century are invaluable archives of temporal vegetation dynamics. Pollen records have been used to study local or regional history and compiled to reconstruct continental scale vegetation patterns using landscape reconstruction algorithms (see for instance Roberts et al., 2018). Many pollen records are now available in open repositories, most prominently via the Neotoma database (Williams et al., 2018). This allows meta-analyses which can consider site-specific factors like bioclimatic zones and timings of different land-use activities. Classifying pollen according to their functional characteristics or ecological attributes allows comparisons and generalizations across taxa and biomes. In palaeoecology, the classification of pollen types into plant functional types is commonplace, the simplest division being made between arboreal and non-arboreal pollen (Birks, 2020). More refined plant functional types have been used in vegetation reconstruction by biomisation (Davis et al. 2015) and climate reconstructions using the modern analogue technique (Mauri et al. 2015). However, because plant functional types are relatively coarse categorizations, the range in trait values can be larger within types than between them (Wright et al., 2005). Furthermore, functional types may not capture key plant characteristics that govern relationships between environmental and ecosystem change (Funk et al., 2017; Thomas et al., 2019). In ecology and biogeography, the use of plant traits has become popular in the past two decades, aided by the upsurge in the availability of data on plant traits (Kattge et al., 2020). Functional traits can provide a better understanding of community assembly as well as ecosystem functioning (Hevia et al., 2017). Here we specifically use the term “functional trait” for traits that influence an organism’s fecundity, growth, development or survival and that have been previously defined as representing key dimensions of variation both at the species and the community level (Bruelheide et al., 2018; Diaz et al., 2016; Volaire et al., 2020).

Recently, the trait-based approach has been applied in several palaeoecological studies to investigate, among other things, the effects of climate and fire on community trait composition (Blaus et al., 2020; Brussel et al., 2018; Carvalho et al., 2019; Reitalu et al., 2015; van der Sande et al., 2019). However, reliable reconstructions of past trait composition are hindered by the general low taxonomic resolution of the palynological record, which can rarely be resolved to the species level (Birks, 2020).

As trait data are usually collected at the species level, ascribing trait values to taxa in the pollen record is not straightforward. Trait variation within species, let alone genera or families, can comprise a substantial part of the total trait variation in communities (Siefert et al., 2015). Because of the low taxonomic resolution of pollen data, previous attempts to reconstruct functional diversity from pollen data using mean trait values to represent a whole taxon might have introduced a large amount of uncertainty (Blaus et al., 2020; Carvalho et al., 2019; van der Sande et al., 2019). Here we offer a new approach to reconstruct functional composition from pollen records. We use Bayesian modelling to consider the full trait distribution within each pollen taxon and account for the consequences of low pollen taxonomic resolution in community-level trait reconstruction (Bjorkman et al., 2018; Funk et al., 2017).

By reconstructing plant trait composition in multiple pollen records from a variety of different northwestern European locations, we aim to determine trends in plant trait composition within landscapes undergoing the transition to agriculture. We also assess the relative importance of climate versus agriculture in driving these trends. More specifically, we aim to 1) determine whether functional composition exhibits spatial and/or temporal patterns throughout the Holocene in northwestern Europe, 2) examine whether agriculture triggered a change in functional composition, and 3) assess the additional role of climate in driving functional composition. We analyse 78 northwestern European pollen records with agricultural histories, spanning the time period from 10 000 BP to the present. Our results provide a first assessment of the changes that the early establishment of agriculture induced in plant trait composition at macroecological scales, which is fundamental to understanding ecological processes of community assembly under human modification.

4.2 Methods

4.2.1 Selection of study sites

To identify relevant studies, we conducted a structured search in Web of Science using search terms related to agriculture, the time period and the spatial coverage (full list of search terms is presented in Appendix S1 in Supporting Information). 210 publications were retrieved after filtering for relevance. To be included, agriculture had to be identified as one of the drivers of vegetation change in the article, the studies also had to cover more than 500 years and include a dated pollen record. Both arable and pastoral agriculture was considered in the search. We only included studies from which we could retrieve raw pollen data, which left us with 78 sites. The *Neotoma* R package was used to retrieve 74 pollen records from the Neotoma database, in particular its constituent databases the European Pollen Database and the Alpine Pollen Database (Fyfe et al., 2009; Goring et al., 2015; Williams et al., 2018). Pollen records for an additional four sites were supplied by a study author (Davies, 1999). We recorded site characteristics and the start and type of agriculture as defined by the authors of the original studies. An overview of the sites is presented in Appendix S2.

4.2.2 Preparation of the pollen data

To overcome inconsistencies in pollen nomenclature that exist between laboratories, the pollen nomenclature was harmonised based on the nomenclature of Mottl et al. (2021) and the European Pollen Database (Flantua et al., 2021; Giesecke et al., 2019).

Pollen counts do not precisely represent species abundance because of taxon-specific differences in pollen productivity and dispersal (Dawson et al., 2016; Seppä, 2013). To correct for this, pollen counts were divided by pollen productivity estimates, which are correction factors obtained from comparison between modern vegetation and pollen surface sediment samples (Bunting et al., 2013). Only taxa with pollen productivity estimates (PPEs) were selected for further analyses (Wieczorek & Herzschuh, 2020, table 3 & 4) (Appendix S3). On average, this resulted in the exclusion of 2.7% of the total pollen count.

To standardize the radiocarbon dating calibration method across cores, we constructed new chronologies for all records using the *Bchron* R package and the chronological information published in Neotoma (Haslett & Parnell, 2008).

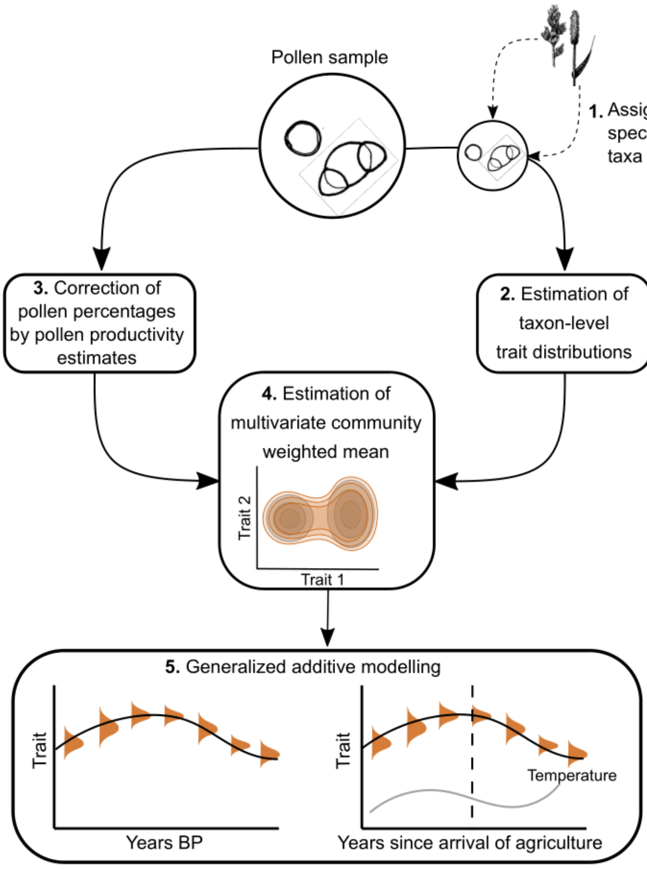

Figure 4.1 Diagram representing the structure of analysis. 1) Species were assigned to pollen types using the current geographical distribution of the pollen taxon in the GBIF database. 2) Trait distribution at the taxon level was estimated using gap-filled data trait data from the TRY database. 3) Pollen percentages were corrected by pollen productivity estimates. 4) Trait distribution at the community level was estimated by weighting the taxon estimates by the corrected pollen percentages 5) Community trait values were modelled using generalized additive models.

4.2.3 Attributing species to pollen taxa

Trait data is usually collected at the species level, thus to infer trait values at the pollen taxonomic level, we needed to make assumptions about the species belonging to each pollen taxon in our data set (Figure 4.1). For this purpose, we made a conversion table for pollen taxon to species from the current distribution of terrestrial species in each pollen taxon in our entire study area. Species distribution data for every pollen taxon in our study area was downloaded from the Global Biodiversity Information Facility database the *rgbif* R package using the pollen taxonomic name and study area's country names as search criteria (Chamberlain et al., 2021; GBIF, 2019). Possible duplicates and incorrectly geo-referenced observations were cleared from the species distribution data using the *coordinatecleaner* R package, which flags occurrence records to databases of common spatial errors in biological collection data, such as country and province centroids or the location of biodiversity research institutions (Zizka et al., 2019). To improve matching of species names to the trait data, the *taxonstand* R package was used to standardize the species nomenclature according to 'The Plant List' (Cayuela et al., 2012; The Plant List, 2013). To filter out (semi)-aquatic species, we used Ellenberg indicator values for moisture which were downloaded from the TRY database (Ellenberg & Leuschner, 2010; Kattge et al., 2020). Species for which the Ellenberg values were unknown (68%) were retained in the dataset. The resulting conversion table was used for every site in the dataset, and thus included all species found in the geographic range of this study.

4.2.4 Selection of traits

Ten traits were selected for the analysis: plant height, specific leaf area (SLA), leaf area, leaf nitrogen, leaf phosphorus, leaf carbon, leaf dry matter content (LDMC), seed length, seed mass and seed count. These traits represent key axes of trait variation in plants, as well as main plant strategies that we expect to be affected by the onset of agriculture (Diaz et al., 2016; Grime, 1988; Pierce et al., 2017). Plant height was included because the size of plants and their parts reflect a key dimension of variation in plants (Diaz et al., 2016). The trade-off between SLA and leaf nutrients on the one hand and LDMC on the other is well established and relates to the resource acquisition strategy of species, referred to as the leaf economic spectrum (Wright et al.). Finally, we included seed traits to represent ruderal species which might benefit from increased disturbance by agriculture. These species are characterised by large leaves with high nutrient content, combined with small and numerous seeds (Grime, 1998; Pierce et al., 2017; Westoby et al., 2002).

We used trait data from the TRY database (Kattge et al., 2020), which is currently the largest global database of plant functional traits. This trait data was previously gap-filled using Hierarchical Bayesian Probabilistic Matrix Factorization (HBPMF), an approach specifically developed for plant functional trait imputation (Schrodt et al., 2015). All analyses were done using log-transformed trait values to approach normally distributed data.

4.2.5 Calculating community weighted mean values

We used a novel Bayesian modelling approach for reconstructing plant trait composition from pollen records. Using the gapfilled trait data of the species that were assigned to the pollen taxa, we first modelled the trait distributions at the pollen taxonomic level. Traits are inherently correlated because organisms have to balance their allocation to survival, growth and reproduction with the availability of resources (Diaz et al., 2016). To allow correlation between traits, we modelled the trait distribution of pollen taxa using a Multivariate Normal distribution for the likelihood, so that

$$trait_{i|j}^{observed} \sim Normal_k(\boldsymbol{\mu}_j, \boldsymbol{\Sigma}_j) \tag{1}$$

where *i* represents a trait observation from pollen taxon *j* from the gap-filled trait data, and *k* the number of dimensions of the multivariate distribution, corresponding to ten traits in this analysis. $\boldsymbol{\mu}_j$ is a vector of mean trait values of length *k*. $\boldsymbol{\Sigma}_j$ is a covariance matrix of *k* by *k*. Vague priors were used for the taxon mean and standard deviation estimation, so the posterior is strongly informed by the data. The trait data were Z-score standardized before modelling.

We then modelled the trait distribution of a community (community weighted mean, CWM) by weighting the taxon trait distributions of each pollen taxon by the corrected pollen percentages at site *s* and moment in time *y*, so that

$$CWM_{s,t} \sim \sum \ \pi_j Normal_k\,(\boldsymbol{\mu}_j, \boldsymbol{\Sigma}_j) \tag{2}$$

where n is the total number of taxa and π_j the abundance of pollen taxon at a given site s and moment in time t. We carried through the mean (CWM^{mean}) and the standard deviation (CWM^{sd}) of the modelled distribution in the subsequent analyses to account for inherent uncertainties in estimations of the mean weighted trait value.

All Bayesian models were run in JAGS (v4.3.0), a program for Bayesian analysis using Markov Chain Monte Carlo simulation (MCMC). The *runjags* R package provided an interface for running JAGS in R (Denwood, 2016). The performance of the MCMC random walk, i.e. the chain, to sufficiently represent the posterior was reviewed by checking effective sample size and chain convergence using the *coda* R package (Plummer, 2004; Plummer et al., 2006). The JAGS code for all models can be found in Appendix S4. We also performed the analysis using a univariate Beta for LDMC and log-Normal likelihood distribution for the other traits (Appendix S5).

4.2.6 Principal component analysis

To explore variation in the community trait values of all 10 traits, a principal component analysis (PCA) was performed on the mean estimates of CWM (CWM^{mean}) using the *prcomp* function in R. To investigate spatial and temporal differences in multivariate trait composition, we plotted the sample scores of the first and second principal component for six clusters that were based on the proximity of sites to each other. We ran generalized additive models (GAMs) with a smooth for time and random effect of site for the first two principal components and the six clusters using the *mgcv* package. To test the sensitivity of the analysis to the inclusion of plant height, as a trait that is obviously affected by agriculture, we recalculated CWM^{mean} without plant height, and performed the PCA on these values (Appendix S6).

4.2.7 Trait composition change over time

To examine trends in individual trait values over time, we used Bayesian GAMs. In this analysis, both the estimates of CWM^{mean} and CWM^{sd} were used. The JAGS code for the GAM was generated using the *jagam* function of the *mgcv* R package and adjusted to include the estimates of CWM^{sd} and a random effect of site (α_s) (Wood, 2016; Wood, 2017).

$$CWM_{s,t}^{mean} \sim Normal\big(\beta_0 + f(time) + \alpha_s, CWM_{s,t}^{sd}\big) \tag{3}$$

where *f(time)* is the smoothing function for time before present. To show the dispersion of the reconstructed trait values and give some insight in to species compositional changes, we plotted the reconstructed community trait values as points together with the modelled trends and coloured them by the proportion of trees. JAGS code for the GAMs can be found in Appendix S4. Model fit was evaluated by simulating datasets from the posterior as done in Simpson (2018) and Wood (2016). Robustness of the trends to the choice of sites was tested by running the GAMs while leaving one site out at the time. Effect of uncertainty in the radiocarbon dating was evaluated by running the GAMs using 50 randomly sample age distributions from the posterior of the *Bchron* age models. These simulations can be found in Appendix S7.

4.2.8 Effects of agriculture and climate on trait composition

We assessed relationships between the arrival of agriculture and changes in CWM by fitting another GAM with a smoothing function for the time since the arrival of agriculture *(f(agriculture))*. Where possible, the start of agriculture at each site was retrieved from the associated publication and was thus based on the original author's expert knowledge of the pollen record, other palaeoecological records, and archaeological findings, depending on the study. When this information was not clearly defined in the publication, the EUROEVOL and the ArchaeoGLOBE databases were used to distinguish the before and after agriculture time period in the records. The EUROEVOL dataset consists of radiocarbon dated archaeological findings from Neolithic Europe and the ArchaeoGLOBE holds consensus data on the extent of agriculture in that region (Manning et al., 2016; Stephens et al., 2019). Eighteen sites were removed from the dataset for this analysis as they already had agriculture present before the start of the pollen record. To account for climatic change through time, we included a smoothing function for temperature in the model *(f(temperature))*. Mean annual temperature simulations were obtained from CHELSA-TraCE21k(Karger et al., 2020) (Appendix S8). CHELSA-TraCE21k is a downscaling algorithm of the TraCE21k palaeoclimate simulations that can generate global temperature estimates at a temporal resolution of 100 years and 30 arcsec spatial resolution for the last 21 000 years. Site was included as a random effect (α_s).

$$CWM_{s,t}^{mean} \sim Normal\big(\beta_0 + f(agriculture) + f(temperature) + \alpha_s, CWM_{s,t}^{sd}\big) \qquad (4)$$

To show the dispersion of the reconstructed trait values and give some insight in to species compositional changes, we plotted the reconstructed community trait values as points together with the modelled trends and coloured them by the proportion of crop species. R version 4.0.5 was used throughout this study (R Core Team, 2021).

4.3 Results

4.3.1 Site characteristics and pollen taxa

The start of agriculture at the sites ranged between 7000 BP and 750 BP. Arable farming was identified in the majority of sites (69/78). Tree cultivation was performed in 15 sites, mainly in the south of the study area. In four of the 78 sites, primarily in upland areas, pastoralism was the sole type of farming identified. Other important drivers of vegetation change as identified in the original publications were climate (40/78), fire (anthropogenic and natural; 34/78) and woodland clearance for iron smelting (14/78).

Forty-seven pollen taxa were included in the analysis and a pollen-type-species conversion table was made for all of them. In total, the trait data for 2357 species were included in the analysis. An overview of the number of species included in a pollen taxon and the number of trait observations can be found in Appendix S3.

4.3.2 Spatial and temporal differences in multiple traits

The first two components of the PCA account for 75.8% of the total variation CWM^{mean} (Figure 4.2, Table 4.1). The first principal component (47.5%) mainly represents the variation in plant size and their organs, with the strongest contribution of leaf area, seed size and plant height. The second principal component (28.3%) expresses variation in traits of the leaf economic spectrum, where communities of high specific leaf area and high leaf nutrients are found on one end of the spectrum and communities of high leaf carbon and LDMC at the opposite end. Seed count is the strongest contributor to the third component (10%) (Appendix S6). The strongest positive correlation was found between size-related traits, such as seed mass and seed length (*r* = 0.96, 95% credibility interval; [0.957, 0.961]) and seed mass and leaf area (*r* = 0.88 [0.87, 0.89]). Correlation was also high between leaf traits, such as leaf phosphorus and leaf area (*r* = 0.75 [0.74, 0.76]). Leaf carbon and specific leaf area were negatively correlated (*r* = -0.71 [-0.72, -0.7]) (Appendix S9).

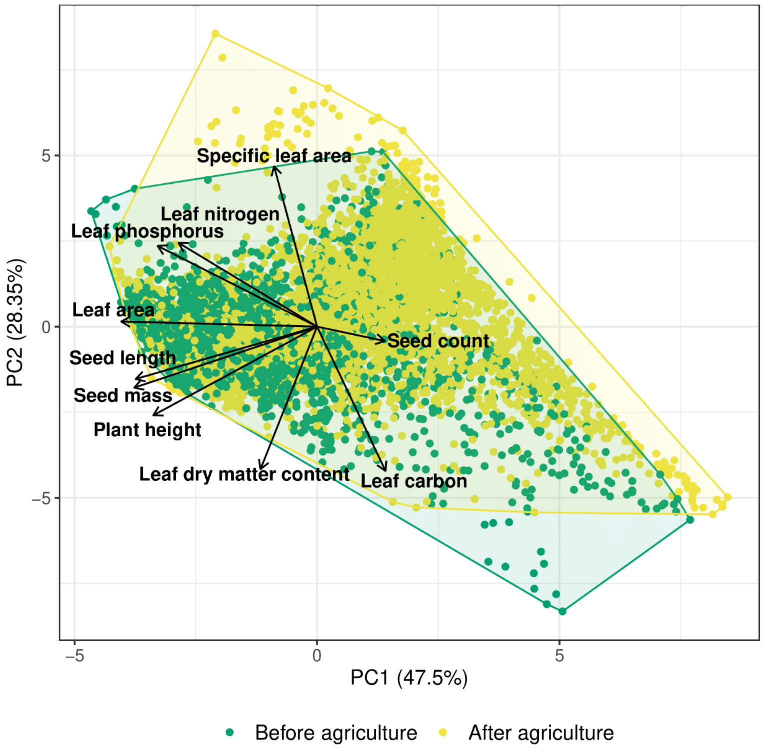

Figure 4.2 Principal component analysis of community level trait values. Every coloured point represents the reconstructed community trait value. The colour indicates whether the observation is from before or after agriculture. Table 4.1 presents the loadings of the traits on the principal components.

Table 4.1 Loadings of traits on the principal components.

Trait	**PC1**	**PC2**	**PC3**
Leaf area	-0.449	0.017	0.034
Seed mass	-0.419	-0.198	0.037
Seed length	-0.416	-0.17	0.001
Plant height	-0.375	-0.288	-0.103
Leaf phosphorus	-0.365	0.262	0.173
Leaf nitrogen	-0.317	0.272	0.064
LDMC	-0.13	-0.463	0.311
Specific leaf area	-0.098	0.52	0.107
Seed count	0.155	-0.047	0.914
Leaf carbon	0.157	-0.468	-0.097
Proportion of variance explained (%)	47.5	28.3	10

The lowest scores on the first principal component are found in the early Holocene (10 000 - 6 000 BP). Trends in the first principal component are similar and increasing across the study area, indicating a general decrease in community whole plant size. The trend in the second principal component changes from about 4 000 BP in the most Southern sites and 2 000 BP in the rest of the study area, meaning communities become higher in SLA and lower in leaf carbon (Figure 4.3).

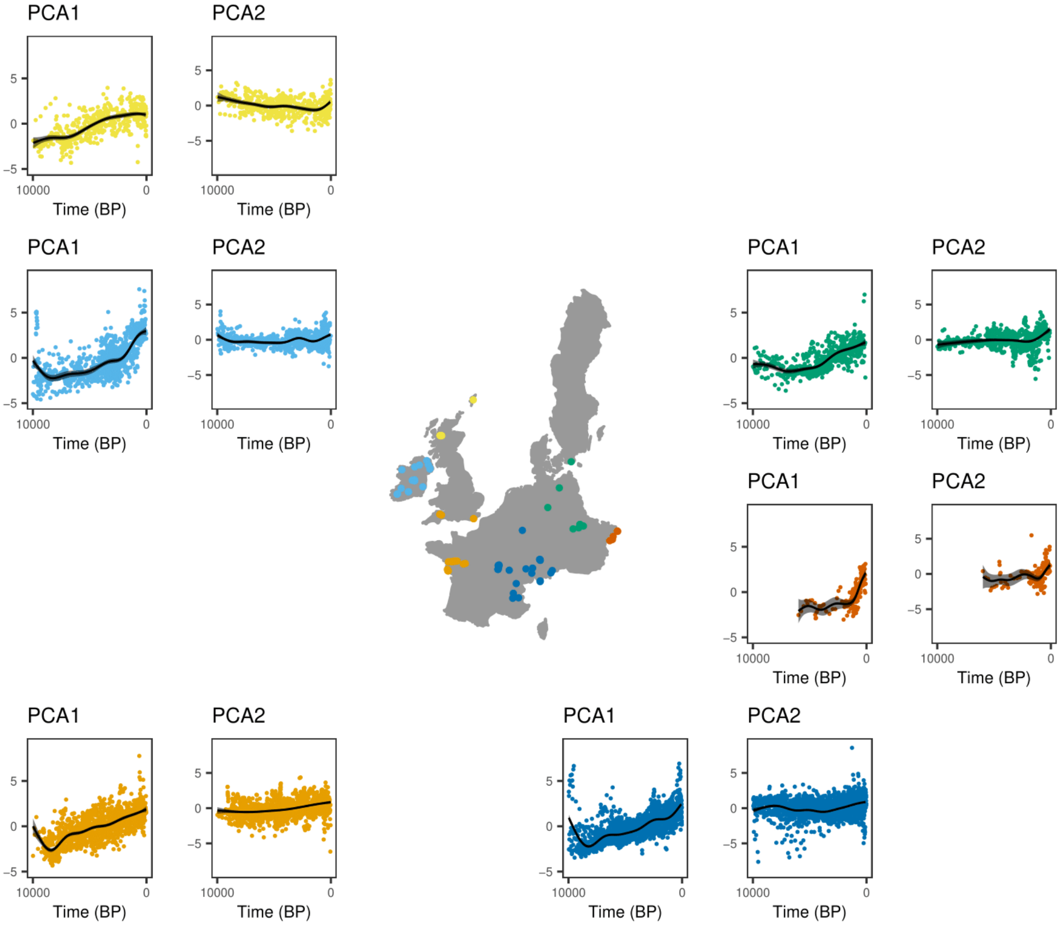

Figure 4.3 Trends in the first and second principal component over time for six clusters of proximate sites (see Table 4.1 and Figure 4.2). The first principal component comprises the variation in plant, leaf and seed size while the second principal component expresses variation in traits of the leaf economic spectrum.

4.3.3 Changes in individual traits over time

Community plant height, leaf area, seed size increased in the first half of the Holocene and decreased from about 7500 BP (Figure 4.4). Community plant height was on average highest at 7700 BP with 4.3 m [3.5, 5.3], and lowest at the present with 0.76 m [0.6, 1.0]. Leaf phosphorus and LDMC decrease significantly over time. LDMC decreases from 0.33 g/g [0.31, 0.34] to 0.30 g/g [0.29, 0.31]. SLA, leaf carbon, leaf nitrogen and seed number remain stable over time.

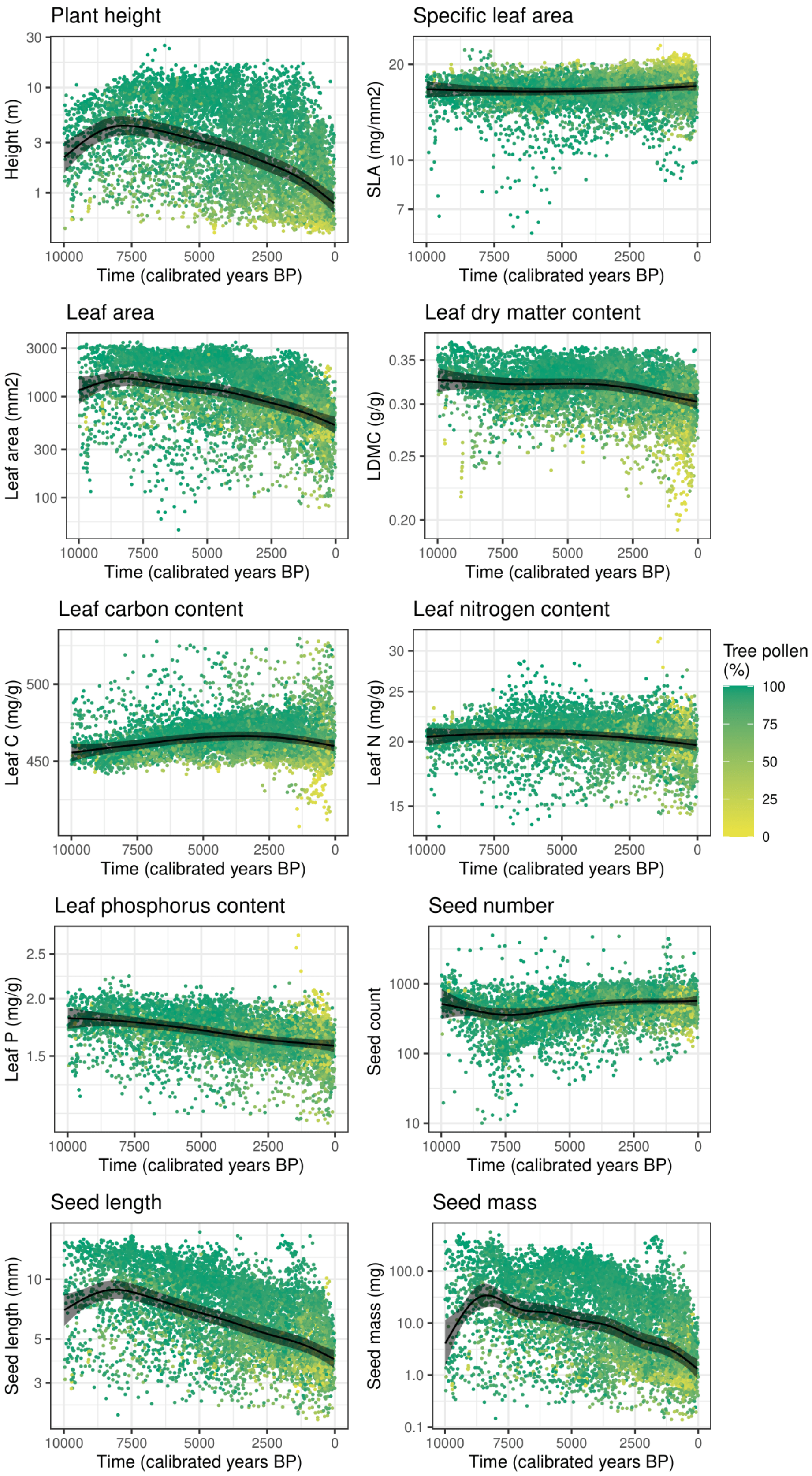

Figure 4.4 Smooth lines represent the generalized additive model (GAM) of the relationship of CWM of 10 traits with time (calibrated years before present), for all 78 sites. 95% Credibility interval is indicated by the shaded area. The reconstructed trait values are plotted and colored by the corrected proportion of tree pollen at that time point.

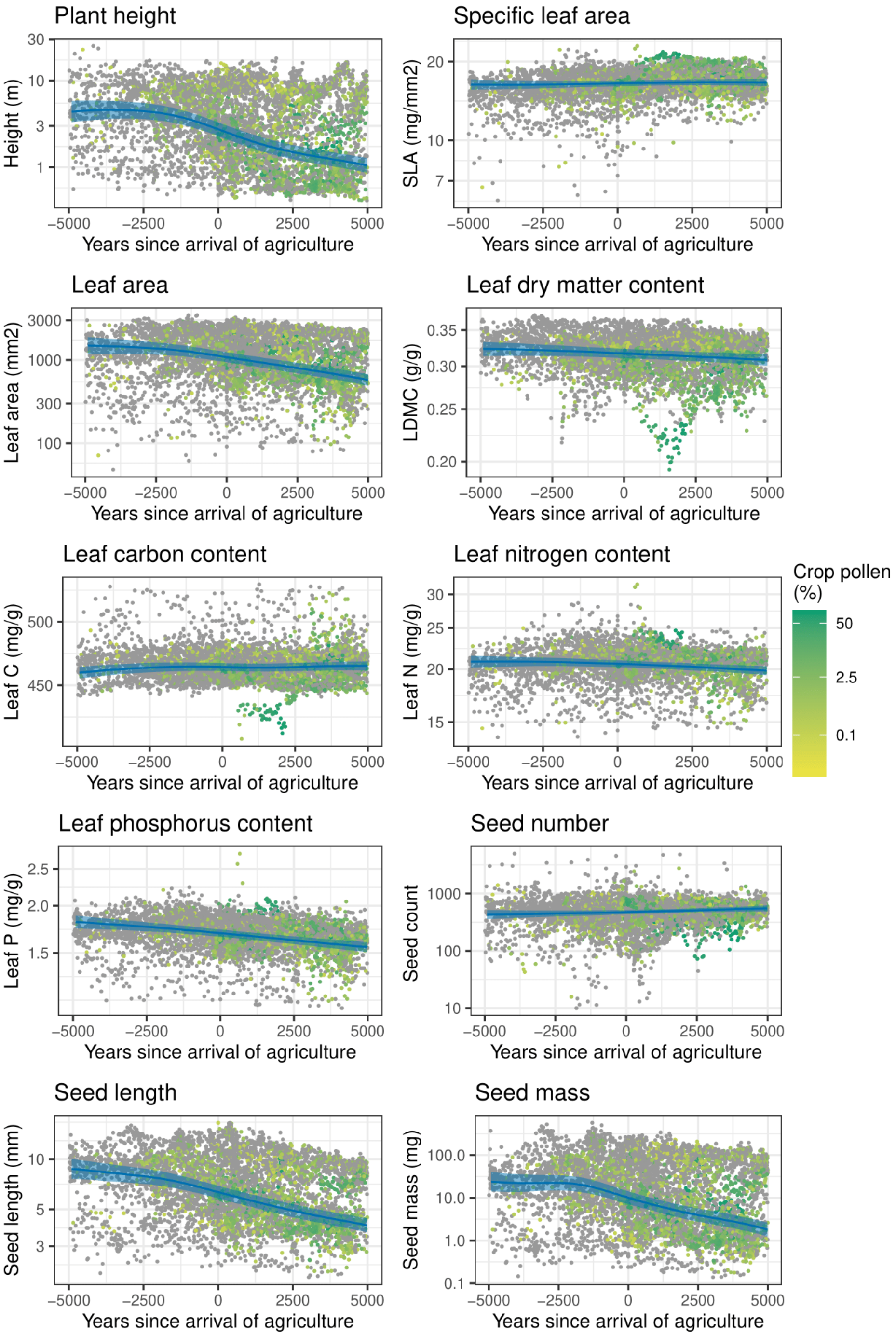

Figure 4.5 Partial component plots of the relationship between the 10 traits and years since arrival of agriculture. 18 sites were removed in this analysis, because agriculture was already present before the start of the records. 95% Credibility interval is indicated by the shaded area. The reconstructed trait values are plotted and colored by the corrected proportion of crop pollen (log transformed) at that time point.

4.3.4 Effects of agriculture and climate on trait composition

Plant height and seed size decrease around the onset of agriculture and onwards (Figure 4.5), whereas climate had little effect on these traits in the time period investigated in this study (Figure 4.6). Seed mass changes from 23.8 mg [14.0, 40.4] 5 000 years before the arrival of agriculture to 9.5 mg [6.7, 13.4] at the start of agriculture, and to 1.8 mg [1.2, 2.6] 5000 years after the arrival of agriculture. Leaf traits were influenced by climate, with increases in SLA, leaf area and leaf nutrients corresponding with increasing temperature. Leaf area and leaf phosphorus decrease with agriculture, leaf phosphorus from 1.69 mg/g [1.65, 1.73] at the start of agriculture to 1.55 mg/g [1.51, 1.60] at the present. No relationship between the arrival of agriculture and SLA, leaf carbon, leaf nitrogen and LDMC could be detected.

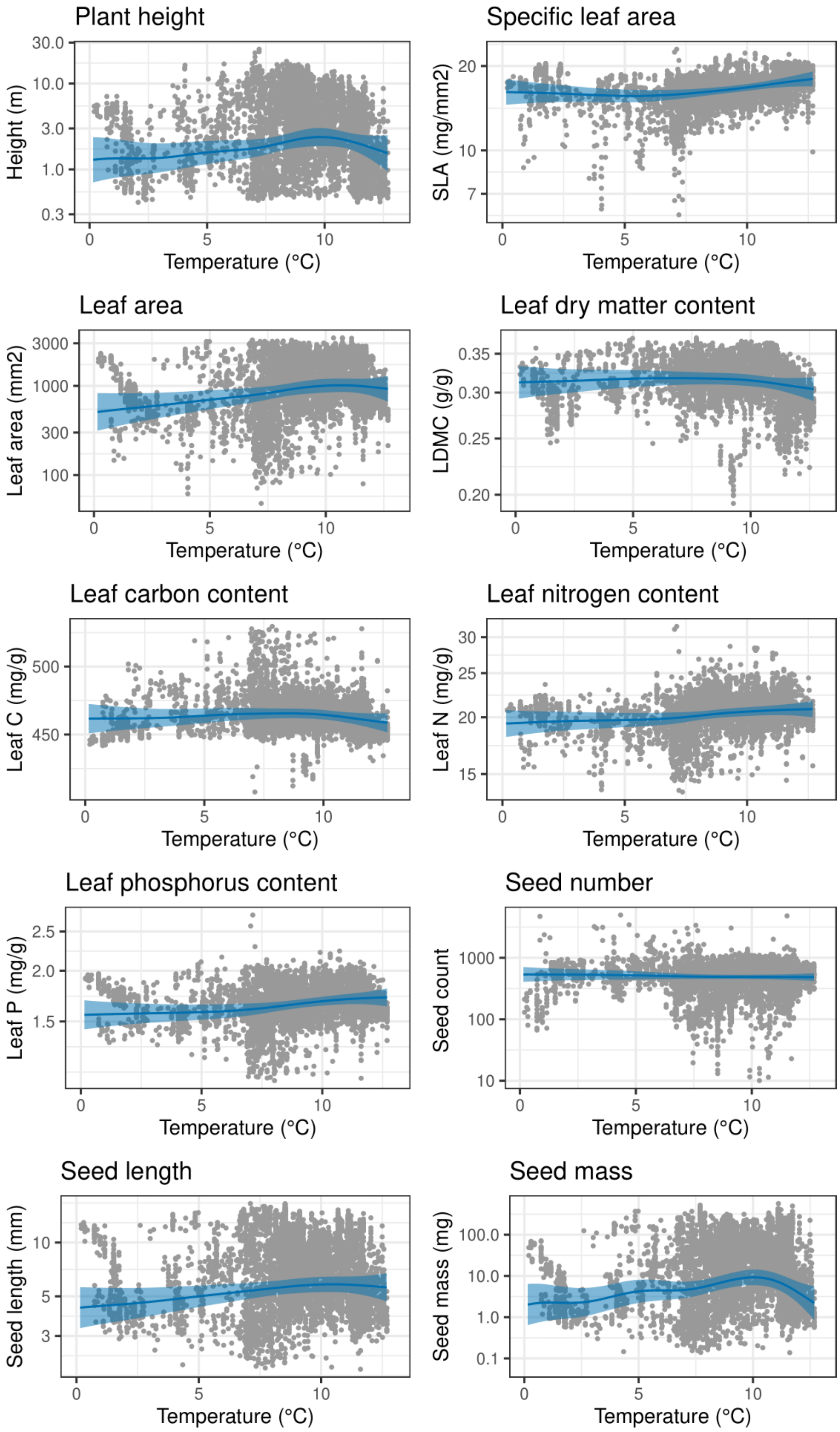

Figure 4.6 Partial component plots of the relationship between the 10 traits and temperature. 18 sites were removed in this analysis, because agriculture was already present before the start of the records. 95% Credibility interval is indicated by the shaded area.

4.4 Discussion

By combining functional trait and pollen data we have identified changes in functional composition of northwestern European sites after the onset of agriculture. These results are especially important for the understanding human impacts on carbon and nitrogen cycles. We find a general decrease in whole plant size alongside a shift in trait space related to the leaf economic spectrum after the onset of agriculture. The changes in the leaf economic spectrum emerge from a gain of communities with a resource-acquisitive strategy and a loss of communities with a resource-conservative strategy (Figure 4.2). Both agriculture and climate play a role in explaining the changes in plant community trait composition, but the contribution of these factors varies with the different traits (Figure 4.4, Figure 4.5 and Figure 4.6). Plant height and seed size appear to be especially influenced by agriculture and little by climate, whereas leaf traits appear to be influenced by both agriculture and climate.

4.4.1 Decrease in whole plant size is triggered by the onset of agriculture

The trend in the first principal component demonstrates a common decrease in the size of whole plants, seeds and leaves across the study area (Table 4.1, Figure 4.2 and Figure 4.3). This decrease is likely solely attributable to the onset of agriculture as we found little effect of climate on seed size or plant height (Figure 4.6). A decrease in plant height is the most intuitive change due to the opening of forest for agriculture, shown in many previous studies (Rey et al., 2019; Roberts et al., 2018). Here we find an overall four fold reduction in plant height in our study area since the start of agriculture (Figure 4.5). Plant height is the most important predictor of vegetation carbon storage (Conti & Diaz, 2013), thus quantification of the effect of the onset of agriculture on plant height is central to the understanding of human impact on the carbon cycle. Although decreasing plant height with agriculture is not terribly surprising, the fact that we can identify and quantify this trend demonstrates that pollen-based functional reconstructions can provide reliable insights, even though some pollen types vary widely in plant height (Appendix S10).

We hypothesized that opening up of ecosystems for new agricultural land by fire or deforestation, provides an advantage to species that are fast growing and rapidly dispersed. These species are characterized by low seed size and high seed count to facilitate effective dispersal (Pierce et al., 2017). Although our results show a reduction in seed size with the arrival of agriculture, seed count remains stable over time (Figure 4.5). We thus find only limited support for this hypothesis. The decrease in seed mass and length with the arrival of agriculture is most likely also due removal of forests, as plant height and seed size are highly correlated (Diaz et al., 2016).

4.4.2 Communities became more resource-acquisitive

We show a trend towards the acquisitive end of the leaf economic spectrum, especially in the last 2000 years (Figure 4.3 and Figure 4.4). This is likely both driven by agriculture and climate (Figure 4.5 and Figure 4.6). With increasing temperature at the beginning of the Holocene, limits on primary productivity were released, giving a competitive advantage to species with traits that support rapid growth and efficient use of available resources (Wright et al., 2017).

We expected that due to the onset of agriculture, communities would become more resource-acquisitive because of the deliberate manipulation of soil fertility and the characteristics of crop and early successional species (Roucou et al., 2018). The gain in resource-acquisitive species could have consequences for ecosystem functioning (Lavorel & Grigulis, 2012; Reich, 2014). Acquisitive communities have highly digestible litter and a high availability of nutrients leading to rapid decomposition rates and low litter accumulation (Cornwell et al., 2008). Although some communities after agriculture occupy trait space outside the range found before agriculture, there is a significant overall decrease in leaf phosphorus and leaf area (Figure 4.5). We think that this seemingly contradictory result is due to differences in the trajectories of agriculture among locations. Crop species as well as other agricultural indicator species (e.g. *Rumex*, *Plantago*) are high in leaf phosphorus content (Appendix S10). However, the depletion of nutrients by grazing, burning and removal of trees favoured the establishment of heathland, especially in Scotland and Ireland, which is low in leaf phosphorus and leaf area (Hjelle et al., 2010; Trondman et al., 2015; Webb, 1998).

4.4.3 Uncertainties and future directions

Our Bayesian modelling approach for functional composition reconstruction allowed us to account for the uncertainty introduced by the low taxonomic resolution of the pollen records. The method can furthermore be expanded to other traits and can be used for the quantification of functional diversity, which is likely to be an important contributor to ecosystem functioning alongside the dominance of trait values (Garnier et al., 2015). Palaeoecological studies provide a rich array of proxies on past ecosystem functioning, including erosion control and nutrient retention (Bennike et al., 2021; Jeffers et al., 2015). Combining these proxies and functional composition reconstructions could open a new avenue for research into the relationships between plant composition and ecosystem functioning, and the legacies of human presence. While we were able to incorporate the uncertainty caused by the low taxonomic resolution of pollen data, a limitation of this study is that we have not been able to evaluate the effect of trait dispersion within pollen taxa on the community-level trait reconstruction. Further work will be needed to examine this effect. Better ways of making conversion tables to assign species to pollen taxa could reduce the amount of uncertainty in the reconstructions. For this more information on past species distributions is necessary, for instance from macrofossil records (Birks & Birks, 2000), ancient DNA from lake sediments (Parducci et al., 2017) and species distribution modelling (Svenning et al., 2011). It is also important to reflect that this landscape scale analysis may have masked finer-scale trends and that we have not been able to study the effect of differences in agricultural method and intensity between sites. Lack of independent data regarding the variable agricultural trajectories at sites made us unable to study these factors. Furthermore, here we included mean annual temperature as the only climate proxy, while other climatic factors as well as soil differences could also be important in explaining plant trait composition (Joswig et al., 2022). However, the approach we developed for reconstruction of plant functional composition can easily be applied in more nuanced analyses. These kinds of analyses will be significantly aided when more pollen records and other palaeoecological proxies are published in public databases.

The palaeoecological record provides a unique long-term perspective into the legacies of human impact and can, by applying concepts from ecology and biogeography, provide us with valuable insights on the maintenance of ecosystem functioning in a domesticated world. This analysis is the first empirical demonstration of common changes in the plant functional trait composition of landscapes in the transition to agriculture. Our results show that early agricultural might had significant impacts on biogeochemical cycles through modifying vegetation composition, and we show that these impacts can be demonstrated early on.

4.5 References

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Appendix S1: Search terms

Search terms for the structured search in Web of Science

TS= (agricultur* OR cultivat* OR farm* OR agrarian OR agro*)

AND

TS = (Holocene OR prehistor* OR pal*eo* OR Neolithic OR Mesolithic OR "Bronze Age" OR "Iron Age" OR Roman OR "middle ages" OR Medieval OR BP OR AD OR BC OR millen*)

AND

TS = (Europe* OR Netherlands OR Dutch OR Belgium OR Belgian OR German* OR "United Kingdom" OR "Great Britain" OR British OR Ireland OR Irish OR "British Isles" OR France OR French OR Switzerland OR Swiss OR Austria* OR Sweden OR Swedish OR Denmark OR Danish OR "Czech Republic" OR Czech* OR Scandinavia)

Appendix S2: Site characteristics and references

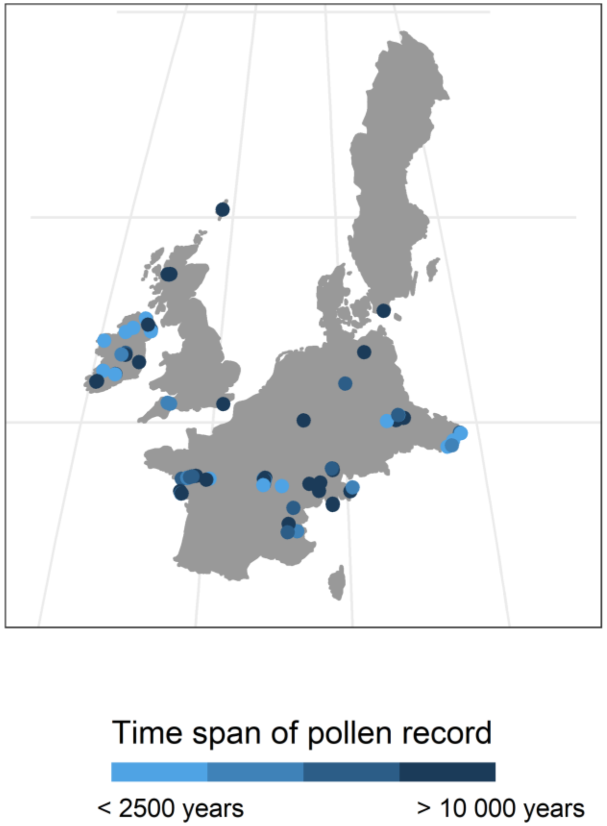

Figure S2.1 Location of the 78 pollen records that were used in this study. Sites are colored by the time span of the pollen record.

Table S2.1 Site characteristics and references

Site name	Elevation (m a.s.l.)	Site type	Size	Citation
Ancenis	5	Marsh	-	Cyprien, A.L. 2001. Chronologie de l'interaction de l'homme et du milieu dans l'espace central et aval de la Loire (Ouest de la France). Doctoral dissertation. Université de Nantes, Nantes, France. Cyprien, A.L., L. Visset, and N. Carcaud. 2004. Evolution of vegetation landscapes during the Holocene in the central and downstream Loire basin (Western France). Vegetation History and Archaeobotany 13(3):181-196. Pastore, R.T. 1987. Fishermen, furriers, and Beothuks: the economy of extinction. Man in the Northeast 33:47-62.
Ballinderry	80	Lake	1.3 ha	OCarroll, E. 2012. Quantifying woodland resource usage in the Irish midlands using archaeological and palaeoecological techniques. Doctoral dissertation. University of Dublin, Trinity College, Dublin, Ireland.
Ballynahatty bog	36	Lake	0.2 ha	Plunkett, G., F. Carroll, B. Hartwell, N.J. Whitehouse, and P.J. Reimer. 2008. Vegetation history at the multi-period prehistoric complex at Ballynahatty, Co. Down, Northern Ireland. Journal of Archaeological Science 35:181-190.
Bjärsjöholmssjön	50	Ancient lake	-	Göransson, H. 1991. Vegetation and man around Lake Bjärsjöholmssjön during prehistoric time. Lundqua Report 31. Berglund, B.E., M.J. Gaillard-Lemdahl, and H. Göransson. 1991. The Bjäresjö area. Pages 167-174 in B.E. Berglund, editor. The cultural landscape during 6000 years in southern Sweden - the Ystad project. Ecological Bulletins 41.
Borheen Lough	476	Lake	2.45 ha	Hawthorne, D., & Mitchell, F. J. (2016). Identifying past fire regimes throughout the Holocene in Ireland using new and established methods of charcoal analysis. Quaternary Science Reviews, 137, 45-53.
Brede Bridge	2	Floodplain mire	-	Waller, M.P. 1993. Flandrian vegetational history of south-eastern England. Stratigraphy of the Brede valley and pollen data from Brede Bridge. New Phytologist 126:369-392.
Camban		Peat basin	-	Davies A (1999) High spatial resolution Holocene vegetation and land-use history in west Glen Affric and Kintail. University of Stirling

Site name	Elevation (m a.s.l.)	Site type	Size	Citation
Carquefou	11	Bog	-	Cyprien, A.L. 2001. Chronologie de l'interaction de l'homme et du milieu dans l'espace central et aval de la Loire (Ouest de la France).. Doctoral dissertation. Université de Nantes, Nantes, France. Cyprien, A.L., and L. Visset. 2001. Paleoenvironmental study of the Carquefou site (Massif Armoricain, France) from the end of the Sub-boreal. Vegetation History and Archaeobotany 10(3):139-149. Visset, L., A.L. Cyprien, A. Ouguerram, D. Barbier, and J. Bernard. 2004. Les indices polliniques d'anthropisation précoce dans l'Ouest de la France: le cas de Cerealia, Fagopyrum et Juglans. Annales Littéraires, Série Environnement, Société et Archéologie 777(7):69-79.
Carrach Mor		Peat basin	-	Davies A (1999) High spatial resolution Holocene vegetation and land-use history in west Glen Affric and Kintail. University of Stirling
Champ Gazon	585	Blanket mire	-	Jouffroy-Bapicot, I. 2010. Evolution de la végétation du massif du Morvan (Bourgogne - France) depuis la dernière glaciation à partir de l'analyse pollinique. Variations climatiques et impact des activités anthropiques.. Doctoral dissertation. Université de Franche-Comté, Besançon, France. Jouffroy-Bapicot, I., B. Vannière, E. Gauthier, H. Richard, F. Monna, and C. Petit. 2013. 7000 years of vegetation history and land-use changes in the Morvan Mountains (France): A regional synthesis. The Holocene 23(12):1888-1902.
Changeon	28	Riverine	-	Cyprien, A.L. 2001. Chronologie de l'interaction de l'homme et du milieu dans l'espace central et aval de la Loire (Ouest de la France). Doctoral dissertation. Université de Nantes, Nantes, France. Cyprien, A.L., L. Visset, and N. Carcaud. 2004. Evolution of vegetation landscapes during the Holocene in the central and downstream Loire basin (Western France). Vegetation History and Archaeobotany 13(3):181-196.
Clara Bog	59	Raised bog	-	Connolly, A. 1999. The Paleoecology of Clara Bog, Co. Offaly. Doctoral dissertation. Trinity College, University of Dublin, Dublin, Leinster, Ireland.
Claraghmore	78	Raised bog	51 ha	Plunkett, G. 2009. Land-use patterns and cultural change in the Middle to Late Bronze Age Ireland: inferences from pollen records. Vegetation History Archaeobotany 18:273-295.
Cordemais	5	Marsh	-	Cyprien, A.L. 2001. Chronologie de l'interaction de l'homme et du milieu dans l'espace central et aval de la Loire (Ouest de la France). Doctoral dissertation. Université de Nantes, Nantes, France. Visset, L., A.L. Cyprien, A. Ouguerram, D. Barbier, and J. Bernard. 2004. Les indices polliniques d'anthropisation précoce dans l'Ouest de la France: le cas de Cerealia, Fagopyrum et Juglans. Annales Littéraires, Série Environnement, Société et Archéologie 777(7):69-79.

Site name	Elevation (m a.s.l.)	Site type	Size	Citation
Cuckoo	32	Lake	0.15 ha	Hawthorne, D. 2015. Quantifying fire regimes and their impact on the Irish Landscape. Doctoral dissertation. Trinity College Dublin, Dublin, Leinster, Ireland.
Dallican Water	56	Lake	1 ha	Bennett, K., S. Boreham, M.J. Sharp, and V.R. Switsur. 1992. Holocene history of environment, vegetation and human settlement on Catta Ness, Lunnasting, Shetland. Journal of Ecology 80:241-273. https://www.jstor.org/stable/2261010. [DOI: 10.2307/2261010]
Diheen	554	Lake	0.79 ha	Hawthorne, D., & Mitchell, F. J. (2016). Identifying past fire regimes throughout the Holocene in Ireland using new and established methods of charcoal analysis. Quaternary Science Reviews, 137, 45-53.
Durchenbergried	432	Fen	3 ha	Rösch, M. 1990. Vegetationsgeschichtliche Untersuchungen im Durchenbergried. Pages 9-64 in Siedlungsarchäologie im Alpenvorland II. Forschungen und Berichte zur Vor- und Frühgeschichte in Baden-Württemberg 37. Theiss, Stuttgart. Rösch, M. 1986. Zwei Moore im westlichen Bodenseegebiet als Zeugen prähistorischer Landschaftsveränderung. Telma 16:83-111.
Ecours	4	Riverine	-	Joly, C. 2006. Histoire de la végétation dans l'espace centre-ouest atlantique (France): relations Sociétés/Végétation et évolution du trait de côte depuis le Mésolithique récent-final. Doctoral dissertation. Université de Nantes, Nantes, France. Joly, C., and L. Visset. 2009. Evolution of vegetation landscapes since the Late Mesolithic on the French West Atlantic coast. Review of Palaeobotany and Palynology 154:124-179.
Etang Bouquin	540	Bog	-	Jouffroy-Bapicot, I. 2010. Evolution de la végétation du massif du Morvan (Bourgogne - France) depuis la dernière glaciation à partir de l'analyse pollinique. Variations climatiques et impact des activités anthropiques.. Doctoral dissertation. Université de Franche-Comté, Besançon, France. Jouffroy-Bapicot, I., B. Vannière, E. Gauthier, H. Richard, F. Monna, and C. Petit. 2013. 7000 years of vegetation history and land-use changes in the Morvan Mountains (France): A regional synthesis. The Holocene 23(12):1888-1902.

Site name	Elevation (m a.s.l.)	Site type	Site	Citation
Fangeas	2000	Marsh	60m max.	de Beaulieu, J.L., P. Leveau, C. Miramont, J.M. Palet- Martinez, K. Walsh, M. Court-Picon, F. Ricou, M. Segard, O. Sivan, V. Andrieu-Ponel, M. Badura, G. Bertucchi, C. Bouterin, A. Durand, J.L. Edouard, M. Lavoie, A. Morin, F. Mocci, P. Ponel, A. Pothin, V. Py, B. Talon, S. Tzortzis, R. Bonet, P. Columeau, H. Cortot, and D. Garcia. 2003. Changements environnementaux postglaciaires et action de l'homme dans le bassin du Buëch et en Champsaur (Hautes- Alpes, France). Premier bilan d'une étude pluridisciplinaire. Pages 93-101 in E.P. Collection Environnement, editor. Des Milieux et des Hommes: Fragments d'Histoires Croisées. France. Walsh, K., and F. Mocci. 2003. 9000 ans d'occupation du sol en moyenne et haute montagne: la vallée de Freissinières dans le Parc national des Ecrins (Freissinières, Hautes- Alpes). Archéologie du Midi Médiéval 21:185-198.
Garry Bog	50	Raised bog	155 ha	Plunkett, G. 2009. Land-use patterns and cultural change in the Middle to Late Bronze Age Ireland: inferences from pollen records. Vegetation History Archaeobotany 18:273-295.
Glen West	90	Raised bog	152 ha	Plunkett, G. 2009. Land-use patterns and cultural change in the Middle to Late Bronze Age Ireland: inferences from pollen records. Vegetation History Archaeobotany 18:273-295. Plunkett, G., J.R. Pilcher, F.G. McCormac, and V.A. Hall. 2004. New dates for first millennium BC tephra isochrones in Ireland. The Holocene 14(5):780-786.
Hares Down	255	Valley mire	15 x 200 m	Fyfe, R.M., A.G. Brown, and S.J. Rippon. 2004. Characterising the late prehistoric, "Romano-British" and medieval landscape, and dating the emergence of a regionally distinct agricultural system in South West Britain. Journal of Archaeological Science 31(12):1699-1714.
Holzmaar	425	Volcanic lake	325 m Ø	Brauer, A., T. Litt, J.F.W. Negendank, and B. Zolitschka. 2001. Lateglacial varve chronology and biostratigraphy of lakes Holzmaar and Meerfelder Maar, Germany. Boreas 30:83-88. Litt, T., and M. Stebich. 1999. Bio- and chronostratigraphy of the lateglacial in the Eifel region, Germany. Quaternary International 61:5-16. Litt, T., C. Schölzel, N. Kühl, and A. Brauer. 2009. Vegetation and climate history in the Westeifel Volcanic Field (Germany) during the past 11 000 years based on annually laminated lacustrine maar sediments. Boreas 38:679-690. Litt, T., M. Früchtl, B. Kubitz, and M. Stebich. 1997. Jungquartäre Floren in den Eifelmaaren. Terra Nostra 1997(7):54-62. Notes: Exkursionsführer zur 67. Jahrestagung der Paläontologischen Gesellschaft

Site name	Elevation (m a.s.l.)	Site type	Size	Citation
Horní Lomná	615	Spring fen	0.04 ha	Rybníčková, E., P. Hájková, and K. Rybníček. 2005. The origin and development of spring fen vegetation and ecosystems - palaeogeobotanical results. Pages 29-57 in A. Poulíčková, M. Hájek, and K. Rybníček, editors. Ecology and palaeoecology of spring fens of the West Carpathians. Palacký University Olomouc, Academy of Sciences of the Czech Republic, Masaryk University Brno, Olomouc. Rybníček, K., and E. Rybníčková. 2008. Upper Holocene dry land vegetation in the Moravian–Slovakian borderland (Czech and Slovak Republics). Vegetation History and Archaeobotany 17(6):701–711.
Hornstaad-Hörnle	385	Lake	-	Rösch, M. 1992. Human impact as registered in the pollen record: some results from the western Lake Constance region, Southern Germany. Vegetation History and Archaeobotany 1:101-109. Rösch, M. 1993. Prehistoric land use as recorded in a lake-shore core at Lake Constance. Vegetation History and Archaeobotany 2:213-232. Rösch, M. 1997. Holocene sediment accumulation in the shallow water zone of Lower Lake Constance. Archiv für Hydrobiologie Supplement 107(4):541-562.
Il Fuorn	1805	Peat bog	10 x 10 m	Welten, M. 1982. Pollenanalytische Untersuchungen zur Vegetationsgeschichte des Schweizerischen Nationalparks. Ergebnisse der wissenschaftlichen Untersuchungen im Schweizerischen Nationalpark 16:1-43.
Jaunay	1	Riverine	1	Joly, C. 2006. Histoire de la végétation dans l'espace centre-ouest atlantique (France) : relations Sociétés Végétation et évolution du trait de côte depuis le Mésolithique récent-final.. Doctoral dissertation. Université de Nantes, Nantes, France. Joly, C., and L. Visset. 2009. Evolution of vegetation landscapes since the Late Mesolithic on the French West Atlantic coast. Review of Palaeobotany and Palynology 154:124-179.
Kalven	163	Lake	-	Björck, S., and P. Möller. 1987. Late Weichselian environmental history in southeastern Sweden during the deglaciation of the Scandinavian ice sheet. Quaternary Research 28:1-37. [DOI: https://doi.org/10.1016/0033-5894(87)90030-5]
Kelly's Lough	585	Lake	3	Leira, M., E.E. Cole, and F.J.G. Mitchell. 2007. Peat erosion and atmospheric deposition impacts on an oligotrophic lake in eastern Ireland. Journal of Paleolimnology 38(1):49-71. [DOI: 10.1007/s10933-006-9060-3]

Site name	Elevation (m a.s.l.)	Site type	Size	Citation
Královec	599	Spring fen	0.025 ha	Rybníčková, E., P. Hájková, and K. Rybníček. 2005. The origin and development of spring fen vegetation and ecosystems - palaeogeobotanical results. Pages 29-57 in A. Poulíčková, M. Hájek, and K. Rybníček, editors. Ecology and palaeoecology of spring fens of the West Carpathians. Palacký University Olomouc, Academy of Sciences of the Czech Republic, Masaryk University Brno, Olomouc. Rybníček, K., and E. Rybníčková. 2008. Upper Holocene dry land vegetation in the Moravian–Slovakian borderland (Czech and Slovak Republics). Vegetation History and Archaeobotany 17(6):701–711.
Kubriková	790	Spring fen	0.05 ha	Rybníčková, E., P. Hájková, and K. Rybníček. 2005. The origin and development of spring fen vegetation and ecosystems - palaeogeobotanical results. Pages 29-57 in A. Poulíčková, M. Hájek, and K. Rybníček, editors. Ecology and palaeoecology of spring fens of the West Carpathians. Palacký University Olomouc, Academy of Sciences of the Czech Republic, Masaryk University Brno, Olomouc. Rybníček, K., and E. Rybníčková. 2008. Upper Holocene dry land vegetation in the Moravian–Slovakian borderland (Czech and Slovak Republics). Vegetation History and Archaeobotany 17(6):701–711.
Lac de Praver	1170	Lake	-	Nakagawa, T. 1998. Etudes palynologiques dans les Alpes Françaises centrales et méridionales: histoire de la végétation Tardiglaciaire et Holocène. Doctoral dissertation. Université d'Aix-Marseille, Marseille, France.
Lac du Lauzon	1980	Lake	-	Argant, J., and A. Argant. 2000. Mise en évidence de l'occupation ancienne d'un site d'altitude: analyse pollinique du lac de Lauzon (Drôme). Géologie Alpine 31:61-71.
Lago di Muzzano	337	Lake	22 ha	Gobet, E., W. Tinner, P. Hubschmid, I. Jansen, M. Wehrli, B. Ammann, and L. Wick. 2000. Influence of human impact and bedrock differences on the vegetational history of the Insubrian Southern Alps. Vegetation History and Archaeobotany 9:175-187. Tinner, W., P. Hubschmid, M. Wehrli, B. Ammann, and M. Conedera. 1999. Long-term forest fire ecology and dynamics in southern Switzerland. Journal of Ecology 87(2):273-289. [DOI: 10.1046/j.1365-2745.1999.00346.x]
Lago di Origlio	416	Lake	8 ha	Tinner, W., M. Conedera, B. Ammann, H.W. Gaggeler, S. Gedye, R. Jones, and B. Sagesser. 1998. Pollen and charcoal in lake sediments compared with historically documented forest fires in southern Switzerland since AD 1920. The Holocene 8(1):31-42.

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Site name	Elevation (m a.s.l.)	Site type	Site	Citation
Lake of Annecy	447	Lake	625 ha	Noël, H. 2001. Caractérisation et calibration des flux organiques sédimentaires dérivant du bassin versant et de la production aquatique (Annecy, Le Petit Lac) -Rôles respectifs de l'Homme et du Climat surl'évolution des flux organiques au cours des 6000 dernières années.. Doctoral dissertation. Université d'Orléans, Orléans, France. Dearing, J.A., Y. Hu, P. Doody, P.A. James, and A. Brauer. 2001. Preliminary reconstruction of sediment-source linkages for the past 6000 yrs at the Petit Lac d'Annecy, France, based on mineral magnetic data. Journal of Paleolimnology 25:245-258. Noël, H., E. Garbolino, A. Brauer, E. Lallier-Vergès, J.L. de Beaulieu, and J.R. Disnar. 2001. Human impact and soil erosion during the last 5000 yrs as recorded in lacustrine sedimentary organic matter at Lac d'Annecy, the French Alps. Journal of Paleolimnology 25:229-244.
Le Grand Montarnu	771	Bog	-	Jouffroy-Bapicot, I. 2010. Evolution de la végétation du massif du Morvan (Bourgogne - France) depuis la dernière glaciation à partir de l'analyse pollinique. Variations climatiques et impact des activités anthropiques.. Doctoral dissertation. Université de Franche-Comté, Besançon, France. Jouffroy-Bapicot, I., B. Vannière, E. Gauthier, H. Richard, F. Monna, and C. Petit. 2013. 7000 years of vegetation history and land-use changes in the Morvan Mountains (France): A regional synthesis. The Holocene 23(12):1888-1902.
Le Vernay	595	Bog	-	Jouffroy-Bapicot, I. 2010. Evolution de la végétation du massif du Morvan (Bourgogne - France) depuis la dernière glaciation à partir de l'analyse pollinique. Variations climatiques et impact des activités anthropiques.. Doctoral dissertation. Université de Franche-Comté, Besançon, France. Jouffroy-Bapicot, I., B. Vannière, E. Gauthier, H. Richard, F. Monna, and C. Petit. 2013. 7000 years of vegetation history and land-use changes in the Morvan Mountains (France): A regional synthesis. The Holocene 23(12):1888-1902.
Le Verny des Brûlons	565	Bog	-	Jouffroy-Bapicot, I. 2010. Evolution de la végétation du massif du Morvan (Bourgogne - France) depuis la dernière glaciation à partir de l'analyse pollinique. Variations climatiques et impact des activités anthropiques.. Doctoral dissertation. Université de Franche-Comté, Besançon, France. Jouffroy-Bapicot, I., B. Vannière, E. Gauthier, H. Richard, F. Monna, and C. Petit. 2013. 7000 years of vegetation history and land-use changes in the Morvan Mountains (France): A regional synthesis. The Holocene 23(12):1888-1902.

Site name	Elevation (m a.s.l.)	Site type	Size	Citation
Litzelsee	413	Lake	1.3	Rösch, M., and J. Lechterbeck. 2016. Seven Millennia of human impact as reflected in a high resolution pollen profile from the profundal sediments of Litzelsee, Lake Constance region, Germany. Vegetation History and Archaeobotany 25:339-358.
Lobbs Bog	243	Valley mire	-	Fyfe, R.M., A.G. Brown, and S.J. Rippon. 2004. Characterising the late prehistoric, "Romano-British" and medieval landscape, and dating the emergence of a regionally distinct agricultural system in South West Britain. Journal of Archaeological Science 31(12):1699-1714.
Lobsigensee	514	Lake	8 ha	Ammann, B. 1985. Lobsigensee - Late Glacial and Holocene environments of a lake on the central Swiss plateau. Dissertationes Botanicae 87:127-134.
Löddigsee	43	Lake	150 ha	Jahns, S. 2007. Palynological inverstigations into the Late Pleistocene and Holocene history of vegetation and settlement at the Löddigsee, Mecklenburg, Germany. Vegetation History Archaeobotany 16:157-169.
Logné	4	Bog	120 ha	Barbier, D., and L. Visset. 1997. Logné, a peat bog of European ecological interest in the Massif Armorican, western France: bog development, vegetation and land-use history. Vegetation History and Archaeobotany 6:69-77.
Lough Henney	25	Lake	9.7 ha	Hall, V.A. 1989. A comparative study of the palynology and regional history of some sites in the north of Ireland. Doctoral dissertation. Queen's University, Belfast, Northern Ireland, UK. Hall, V.A. 1991. Detecting redeposited pollen in an Irish lake deposit. Irish Naturalists' Journal 23(10):397-402. https://www.jstor.org/stable/25539592. Hall, V.A., S.J. McVicker, and J.R. Pilcher. 1994. Tephra-linked landscape history around 2310 BC of some sites in Counties Antrim and Down. Proceedings of the Royal Irish Academy, Biology and Environment 94B(3):245-253. https://www.jstor.org/stable/20499942.
Machová	498	Spring fen	0.05 ha	Rybníčková, E., P. Hájková, and K. Rybníček. 2005. The origin and development of spring fen vegetation and ecosystems - palaeogeobotanical results. Pages 29-57 in A. Poulíčková, M. Hájek, and K. Rybníček, editors. Ecology and palaeoecology of spring fens of the West Carpathians. Palacký University Olomouc, Academy of Sciences of the Czech Republic, Masaryk University Brno, Olomouc. Rybníček, K., and E. Rybníčková. 2008. Upper Holocene dry land vegetation in the Moravian–Slovakian borderland (Czech and Slovak Republics). Vegetation History and Archaeobotany 17(6):701–711.

Site name	Elevation (m a.s.l.)	Site type	Size	Citation
Marais de Champtocé	19	Marsh	-	Cyprien, A.L. 2001. Chronologie de l'interaction de l'homme et du milieu dans l'espace central et aval de la Loire (Ouest de la France). Doctoral dissertation. Université de Nantes, Nantes, France. Cyprien, A.L., L. Visset, and N. Carcaud. 2004. Evolution of vegetation landscapes during the Holocene in the central and downstream Loire basin (Western France). Vegetation History and Archaeobotany 13(3):181-196. Visset, L., A.L. Cyprien, A. Ouguerram, D. Barbier, and J. Bernard. 2004. Les indices polliniques d'anthropisation précoce dans l'Ouest de la France: le cas de Cerealia, Fagopyrum et Juglans. Annales Littéraires, Série Environnement, Société et Archéologie 777(7):69-79.
Marais de Méron	6	Marsh	-	Cyprien, A.L. 2001. Chronologie de l'interaction de l'homme et du milieu dans l'espace central et aval de la Loire (Ouest de la France). Doctoral dissertation. Université de Nantes, Nantes, France. Cyprien, A.L., L. Visset, and N. Carcaud. 2004. Evolution of vegetation landscapes during the Holocene in the central and downstream Loire basin (Western France). Vegetation History and Archaeobotany 13(3):181-196.
Marais de Munet	28	Marsh	-	Cyprien, A.L. 2001. Chronologie de l'interaction de l'homme et du milieu dans l'espace central et aval de la Loire (Ouest de la France). Doctoral dissertation. Université de Nantes, Nantes, France. Cyprien, A.L., N. Carcaud, and L. Visset. 2001. Etude paléoenvironnementale du Marais de Distré (Saumurois): géoarchéologie d'une zone himide depuis le Préboréal. Quaternaire 12(1-2):89-101.
Marais des Bourbes	4	Peat bog	-	Joly, C. 2006. Histoire de la végétation dans l'espace centre-ouest atlantique (France): relations Sociétés Végétation et évolution du trait de côte depuis le Mésolithique récent-final.. Doctoral dissertation. Université de Nantes, Nantes, France. Joly, C. 2004. Histoire végétale d'une tourbière littorale: le Marais des Bourbes (Olonne-sur-Mer, Vendée). [History of vegataion in a coastal peat bog: the Marais des Bourbes (Olonne-sur-Mer, Vendée, France)]. Annales de Paléontologie, 90:187-207. Joly, C., and L. Visset. 2009. Evolution of vegetation landscapes since the Late Mesolithic on the French West Atlantic coast. Review of Palaeobotany and Palynology 154:124-179.
Middle North Coombe	122	Spring mire	30 m	Fyfe, R.M., A.G. Brown, and S.J. Rippon. 2004. Characterising the late prehistoric, "Romano-British" and medieval landscape, and dating the emergence of a regionally distinct agricultural system in South West Britain. Journal of Archaeological Science 31(12):1699-1714.
Mongan Bog	40	Raised bog	150 ha	Parkes, H.M., and F.J.G. Mitchell. 2000. Vegetation history at Clonmacnoise, Co. Offaly. Biology and Environment: Proceedings of the Royal Irish Academy 100B(1):35-40.

Site name	Elevation (m a.s.l.)	Site type	Size	Citation
Montbé	562	Bog	-	Jouffroy-Bapicot, I. 2010. Evolution de la végétation du massif du Morvan (Bourgogne - France) depuis la dernière glaciation à partir de l'analyse pollinique. Variations climatiques et impact des activités anthropiques. Doctoral dissertation. Université de Franche-Comté, Besançon, France. Jouffroy-Bapicot, I., B. Vannière, E. Gauthier, H. Richard, F. Monna, and C. Petit. 2013. 7000 years of vegetation history and land-use changes in the Morvan Mountains (France): A regional synthesis. The Holocene 23(12):1888-1902.
Morvich		Peat basin	-	Davies A (1999) High spatial resolution Holocene vegetation and land-use history in west Glen Affric and Kintail. University of Stirling
Moyreen	120	Bog	21	Plunkett, G. 2009. Land-use patterns and cultural change in the Middle to Late Bronze Age Ireland: inferences from pollen records. Vegetation History Archaeobotany 18:273-295.
Nataloup	515	Bog	-	Jouffroy-Bapicot, I. 2010. Evolution de la végétation du massif du Morvan (Bourgogne - France) depuis la dernière glaciation à partir de l'analyse pollinique. Variations climatiques et impact des activités anthropiques. Doctoral dissertation. Université de Franche-Comté, Besançon, France. Jouffroy-Bapicot, I., B. Vannière, E. Gauthier, H. Richard, F. Monna, and C. Petit. 2013. 7000 years of vegetation history and land-use changes in the Morvan Mountains (France): A regional synthesis. The Holocene 23(12):1888-1902.
Oudon	17	Marsh	-	Cyprien, A.L. 2001. Chronologie de l'interaction de l'homme et du milieu dans l'espace central et aval de la Loire (Ouest de la France). Doctoral dissertation. Université de Nantes, Nantes, France. Cyprien, A.L., L. Visset, and N. Carcaud. 2004. Evolution of vegetation landscapes during the Holocene in the central and downstream Loire basin (Western France). Vegetation History and Archaeobotany 13(3):181-196.
Owenduff	150	Bog	6000 ha	Plunkett, G. 2009. Land-use patterns and cultural change in the Middle to Late Bronze Age Ireland: inferences from pollen records. Vegetation History Archaeobotany 18:273-295.
Paleochenal de Neublans	184	Riverine	-	Gauthier, E. 2001. Evolution de l'impact de l'homme sur la végétation du massif jurassien au cours des quatre derniers millénaires. Nouvelles données palynologiques. Doctoral dissertation. Université de Franche-Comté, Besançon, France.
Palü Lunga ob Ramosch	1903	Spring mire	10 x 10 m	Welten, M. 1982. Pollenanalytische Untersuchungen zur Vegetationsgeschichte des Schweizerischen Nationalparks. Ergebnisse der wissenschaftlichen Untersuchungen im Schweizerischen Nationalpark 16:1-43.

Site name	Elevation (m a.s.l.)	Site type	Size	Citation
Pannel Bridge	3	Former fen	-	Waller, M.P. 1987. The Flandrian vegetational history and environmental development of the Brede and Panel Valleys East Sussex. Ph.D. Dissertation. Polytechnic of North London, London, England, United Kingdom.. Doctoral dissertation. Polytechnic of North London, London, United Kingdom. Waller, M.P. 1993. Flandrian vegetational history of south- eastern England. Pollen data from Pannel Bridge, East Sussex. New Phytologist 124(2):345-369.
Port des Lamberts	710	Bog	-	Jouffroy-Bapicot, I. 2010. Evolution de la végétation du massif du Morvan (Bourgogne - France) depuis la dernière glaciation à partir de l'analyse pollinique. Variations climatiques et impact des activités anthropiques.. Doctoral dissertation. Université de Franche-Comté, Besançon, France. Jouffroy-Bapicot, I., B. Vannière, E. Gauthier, H. Richard, F. Monna, and C. Petit. 2013. 7000 years of vegetation history and land-use changes in the Morvan Mountains (France): A regional synthesis. The Holocene 23(12):1888-1902. Monna, F., C. Petit, J.P. Guillaumet, I. Jouffroy-Bapicot, C. Blanchot, J. Dominik, R. Losno, H. Richard, J. Levèque, and C. Chateau. 2004. History and Environmental Impact of Mining Activity in Celtic Aeduan Territory Recorded in a Peat Bog (Morvan, France). Research 38(3):665-673.
Rynholec	478	Marsh	-	Pokorný, P. 2005. Role of man in the development of Holocene vegetation in Central Bohemia. Preslia 77(1):113-128.
Sägistalsee	1940	Lake	7.3 ha	Van der Knaap, W.O., J.F.N. van Leeuwen, A. Fankhauser, and B. Ammann. 2000. Palynostratigraphy of the last centuries in Switzerland based on 23 lake and mire deposits: chronostratigraphic pollen markers, regional patterns, and local histories. Review of Palaeoecology and Palynology 108(6):85-142. [DOI: 10.1191/0959683605hl852ft]
Sheheree Bog	61	Bog	1.96 ha	Mitchell, F.J.G., and T. Cooney. 2004. Vegetation history in the Killarney valley. Pages 481-493 in W. O'Brien, editor. Ross Island: mining metal and society in early Ireland (Bronze age studies, 6).
Silberhohl	180	Peatland	150 m	Chen, S.-H. 1988. Neue Untersuchungen über die spät- und postglaziale Vegetationsgeschichte im Gebiet zwischen Harz und Leine (BRD). Flora 181:147-177.
Sluggan Moss	52	Bog	600 ha	Smith, A.G., and I.C. Goddard. 1991. A 12500 years record of vegetational history at Sluggan Bog, County Antrim, Northern Ireland (incorporating a pollen zone scheme for the non-specalist). New Phytologist 118:167-187. https://www.jstor.org/stable/2557698.

Site name	Elevation (m a.s.l.)	Site type	Size	Citation
Soppensee	596	Lake	24 ha	Hajdas, I., and A. Michczynski. 2010. Age-depth model of Lake Soppensee (Switzerland) based on the high-resolution C14 chronology compared with the varve chronology. Radiocarbon 52:1027-1040. Lotter, A.F. 1999. Late-glacial and Holocene vegetation history and dynamics as shown by pollen and plant macrofossil analyses in annually laminated sediments from Soppensee, central Switzerland. Vegetation History & Archaeobotany 8:165-184.
Sources de l'Yonne	740	Bog	-	Jouffroy-Bapicot, I. 2010. Evolution de la végétation du massif du Morvan (Bourgogne - France) depuis la dernière glaciation à partir de l'analyse pollinique. Variations climatiques et impact des activités anthropiques.. Doctoral dissertation. Université de Franche-Comté, Besançon, France. Jouffroy-Bapicot, I., B. Vannière, E. Gauthier, H. Richard, F. Monna, and C. Petit. 2013. 7000 years of vegetation history and land-use changes in the Morvan Mountains (France): A regional synthesis. The Holocene 23(12):1888-1902.
Tišice	160	Lake	-	Dreslerová, D., E. Břízová, E. Růžičková, and A. Zeman. 2004. Holocene environmental processes and alluvial archaeology in the middle Labe (Elbe) valley. Pages 121-171 in M. Gojda, editor. Ancient landscape, settlement dynamics and non-destructive archaeology. Academia, nakladatelstvi Academie ved ceske republiky, Prague, Czech Republic. Pokorný, P. 2005. Role of man in the development of Holocene vegetation in Central Bohemia. Preslia 77(1):113-128.
Tlstá hora	460	Spring fen	-	Rybníčková, E., P. Hájková, and K. Rybníček. 2005. The origin and development of spring fen vegetation and ecosystems - palaeogeobotanical results. Pages 29-57 in A. Poulíčková, M. Hájek, and K. Rybníček, editors. Ecology and palaeoecology of spring fens of the West Carpathians. Palacký University Olomouc, Academy of Sciences of the Czech Republic, Masaryk University Brno, Olomouc. Rybníček, K., and E. Rybníčková. 2008. Upper Holocene dry land vegetation in the Moravian–Slovakian borderland (Czech and Slovak Republics). Vegetation History and Archaeobotany 17(6):701–711.
Torran Beithe		Blanket peat	-	Davies A (1999). High spatial resolution Holocene vegetation and land-use history in west Glen Affric and Kintail. University of Stirling

Site name	Elevation (m a.s.l.)	Site type	Size	Citation
Vertonne	3	Marsh	-	Joly, C. 2006. Histoire de la végétation dans l'espace centre-ouest atlantique (France): relations Sociétés/Végétation et évolution du trait de côte depuis le Mésolithique récent-final. Doctoral dissertation. Université de Nantes, Nantes, France. Joly, C., and L. Visset. 2009. Evolution of vegetation landscapes since the Late Mesolithic on the French West Atlantic coast. Review of Palaeobotany and Palynology 154:124-179.
Vladař	612	Reservoir	-	Pokorný, P., N. Boenke, M. Chytráček, K. Nováková, J. Sádlo, J. Veselý, P. Kuneš, and V. Jankovská. 2006. Insight into the environment of a pre-Roman Iron Age hillfort at Vladař, Czech Republic, using a multi-proxy approach. Vegetation History and Archaeobotany 15(4):419-433. [DOI: 10.1007/s00334-006-0064-8]
Vrbka	180	Peatland	-	Pokorný, P. 2016. Contributions to the European Pollen Database 29. Vrbka (Czech Republic): pollen record of secondary steppe vegetation development within the Bronze Age agricultural landscape. Grana 55(3):246-249. [DOI: 10.1080/00173134.2015.1120342]
Windmill Rough	263	Spring mire	-	Fyfe, R.M., A.G. Brown, and S.J. Rippon. 2004. Characterising the late prehistoric, "Romano-British" and medieval landscape, and dating the emergence of a regionally distinct agricultural system in South West Britain. Journal of Archaeological Science 31(12):1699-1714.
Zahájí	232	Spring mire	-	Pokorný, P. 2005. Role of man in the development of Holocene vegetation in Central Bohemia. Preslia 77(1):113-128.

Appendix S3: Characteristics of the pollen taxa

Table S3.1 Overview of the available information per pollen taxon and occurrence in pollen records. PPE = pollen productivity estimate from Wieczorek and Herzschuh (2020).

Pollen taxon	PPE	Occurrence in pollen records	Number of trait observations	Number of species in pollen taxon
Abies	6.88	66.67	703	32
Acer	0.23	75.64	1704	24
Alnus	8.46	100	309	14
Apiaceae	2.13	96.15	3129	164
***Artemisia*-type**	11.67	96.15	342	40
Asteraceae	1.42	100	9338	644
Betula	7.2	100	2669	17
Brassicaceae	0.48	96.15	3332	211
Campanulaceae	2.29	75.64	809	92
Carpinus	4.31	78.21	192	9
Caryophyllaceae	21.74	98.72	3680	186
Castanea	5.87	43.59	333	5
Cerealia	3.51	62.82	341	18
Convolvulaceae	0.18	30.77	328	40
Cornaceae	1.72	35.9	386	13
***Corylus*-type**	1.78	100	446	8
Cyperaceae	1.82	100	3939	251
Ericales	0.83	98.72	3063	84
Fabaceae	0.3	93.59	6991	218
Fagus	2.92	100	1120	3
Fraxinus	2.42	97.44	719	8
Humulus	16.43	74.36	30	1
Juglans	3.28	73.08	292	7
***Juniperus*-type**	14.3	67.95	245	15
Lamiaceae	1.06	89.74	3398	181
Larix	3.44	17.95	918	8
Liliaceae-type	1.49	76.92	164	61
Moraceae	1.1	1.28	165	11
Orobanchaceae	0.33	71.79	1084	135
Picea	5.96	66.67	2190	27
Pinus	14.64	98.72	7097	36
Plantaginaceae	3.54	100	2828	127
Poaceae	1	100	11369	380
Populus	1.59	56.41	658	18
Quercus	3.58	100	9077	35
Ranunculaceae	2.4	100	1939	137
Rosaceae	0.88	98.72	6255	388
Rubiaceae	1.67	85.9	1834	68
Rumex	2.01	100	1661	49
Salix	1.3	98.72	2170	106
Sambucus nigra	1.3	28.21	166	1

Table 2 (continued)

Pollen taxon	**PPE**	**Occurrence in pollen records**	**Number of trait observations**	**Number of species in pollen taxon**
***Sanguisorba*-type**	24.07	53.85	248	4
Thalictrum	4.65	79.49	185	14
Thymelaceae	33.05	12.82	114	20
Tilia	1.02	94.87	661	16
Ulmus	2.24	100	401	9
Urtica	10.52	93.59	362	9

Appendix S4: JAGS code

JAGS code for CWM calculation.

```
# Data
# Nyr = number of observations in the pollen data
# Ntax = number of taxa in the pollen data
# Nvar = number of traits in the trait data
# N = number of trait observations, thus the number of rows of zTrait
# Ab = abundance matrix with observations as rows and taxa as species,
in this case a matrix of Nyr rows and Ntax columns
# zTrait = matrix of standardized trait observations of Nvar columns
# Tax = factor of Ntax levels with same length as N
# sdOrig = vector of length Nvar with the standard deviations of the
trait data, for converting to the original scale
# meanOrig = vector of length Nvar with the mean of the trait data,
for converting to the original scale
# zRscal = parameter of the Wisharts distributrion (dwish). zRscal is
a vector of Ntax. zRscal is specified as degrees of freedom + 1 so to
give a flat prior on the correlation parameters
# zRmat = parameter of the Wisharts distributrion (dwish).
# zRmat = a list of covariance matrices of length Ntax. Every matrix
is of size Nvar by Nvar.

model {
## Pollen taxonomic level
# Likelihood
for (i in 1:N) {
           zTrait[i,   1:Nvar]   ~   dmnorm(zMu[Tax[i],   1:Nvar],
           zInvCovMat[1:Nvar, 1:Nvar, Tax[i]])
}

# Priors
for(taxID in 1:Ntax){
    for(varID in 1:Nvar){
      zMu[taxID, varID] ~ dnorm(0, 10^-4)
    }
  zInvCovMat[1:Nvar,  1:Nvar,  taxID]  ~  dwish(zRmat[1:Nvar,  1:Nvar,
taxID], zRscal[taxID])
}

# Convert taxon mean and sd to original scale:
# Convert invCovMat to sd
for(taxID in 1:Ntax){
zCovMat[1:Nvar, 1:Nvar, taxID] <- inverse(zInvCovMat[1:Nvar, 1:Nvar,
taxID])
  for (varID in 1:Nvar ) {
    zSigma[taxID, varID] <- sqrt(zCovMat[varID, varID, taxID])
  }
}

for (taxID in 1:Ntax){
  for (varID in 1:Nvar) {
    sigma[taxID, varID] <- zSigma[taxID,varID] * sdOrig[varID]
    mu[taxID,   varID]   <-   zMu[taxID,   varID]   *   sdOrig[varID]   +
meanOrig[varID]
```

```
  }
}

## Community level
for (i in 1:Nyr){
    zCWM[i,1:Nvar]  ~  dmnorm(zMu[r[i],1:Nvar],  zInvCovMat[1:Nvar,
1:Nvar, r[i]])
    r[i] ~ dcat(Ab[i, 1:Ntax])
}

# Convert cwm to original scale
for (i in 1:Nyr){
    for (varID in 1:Nvar) {
    CWM[i,varID] <- zCWM[i,varID] * sdOrig[varID] +
                           meanOrig[varID]}
```

JAGS code for the general additive model:

$$CWT_{s,y}^{mean} \sim Normal(\beta_0 + f(time) + \alpha_s, CWT_{s,y}^{sd})$$

This model was partly generated by the *jagam* function from the *mgcv* R package (Wood, 2017).

```
model {
# data
# y = mean of CWT (calculated previously)
# sd = standard deviation of CWT (calculated previously)
# n = number of observations, e.g. length of y and sd
# site = factor of nsite levels and length n
# nsite = number of sites

  mu0 <- X %*% b ## expected response
  for (i in 1:n) { y[i] ~ dnorm(mu[i], tau[i])
# parameterize tau
  tau[i] <- 1/sd[i]^2
  }

# random effect of site
  for (i in 1:n) {
    mu[i] <- mu0[i] + re[site[i]]
  }
  for(i in 1:nsite){ re[i] ~ dnorm(0, tau.re)}
  tau.re ~ dgamma(0.001, 0.001)

# Smooths
  for (i in 1:1) { b[i] ~ dnorm(0, 10^-4) }
  # prior for s(Time.BP)
  for (i in 2:9) { b[i] ~ dnorm(0, lambda[1]) }
  for (i in 10:10) { b[i] ~ dnorm(0, lambda[2]) }
  # smoothing parameter priors
  for (i in 1:2) {
    lambda[i] ~ dgamma(.001,.001)
    rho[i] <- log(lambda[i])
  }
}
```

JAGS code for the general additive model:

$$CMW_{s,y}^{mean} \sim Normal\big(\beta_0 + f(agriculture) + f(temperature) + \alpha_s, CMW_{s,y}^{sd}\big)$$

This model was partly generated by the *jagam* function from the *mgcv* R package (Wood, 2017).

```
 model {
# data
# y = mean of CWM (calculated previously)
# sd = standard deviation of CWM (calculated previously)
# n = number of observations, e.g. length of y and sd
# site = factor of nsite levels and length n
# nsite = number of sites

  mu0 <- X %*% b ## expected response
  for (i in 1:n) { y[i] ~ dnorm(mu[i], tau[i])
  # parameterize tau
  tau[i] <- 1/sd[i]^2
  }
   # random effect of site
  for (i in 1:n) {
    mu[i] <- mu0[i] + re[site[i]]
  }
  for(i in 1:nsite){ re[i] ~ dnorm(0, tau.re)}
  tau.re ~ dgamma(0.001, 0.001)

 #  Smooths
  for (i in 1:1) { b[i] ~ dnorm(0,10^-4) }
  ## prior for s(years.since)
  for (i in 2:9) { b[i] ~ dnorm(0, lambda[1]) }
  for (i in 10:10) { b[i] ~ dnorm(0, lambda[2]) }
  ## prior for s(Temperature)
  for (i in 11:18) { b[i] ~ dnorm(0, lambda[3]) }
  for (i in 19:19) { b[i] ~ dnorm(0, lambda[4]) }
  ## smoothing parameter priors
  for (i in 1:4) {
    lambda[i] ~ dgamma(.001,.001)
    rho[i] <- log(lambda[i])
  }
}
```

Appendix S5: Comparison between univariate and multivariate likelihood for CWM calculation

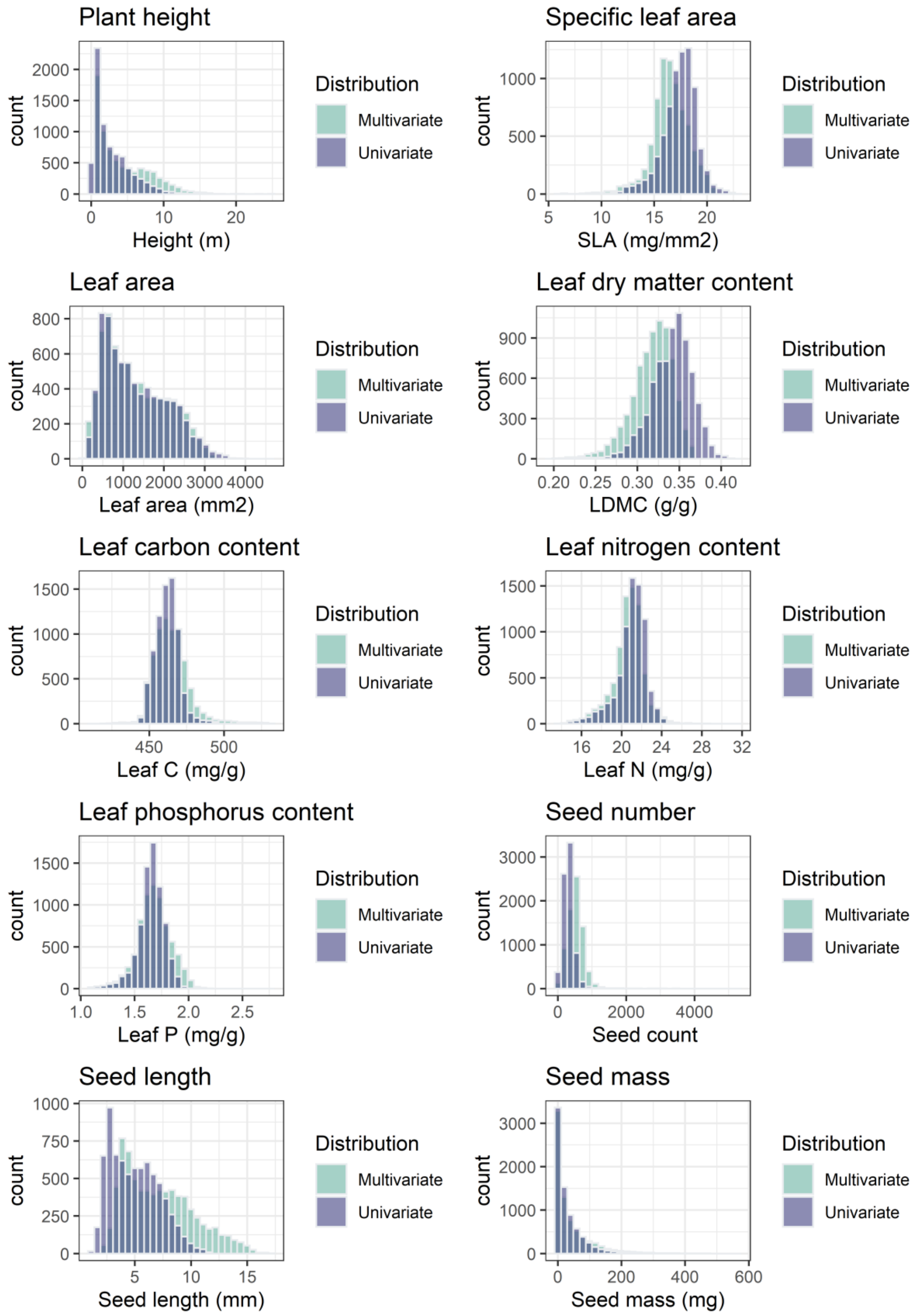

Figure S5.1 Histograms of reconstructed CWM^{mean} trait values using a univariate or a multivariate distribution for the likelihood.

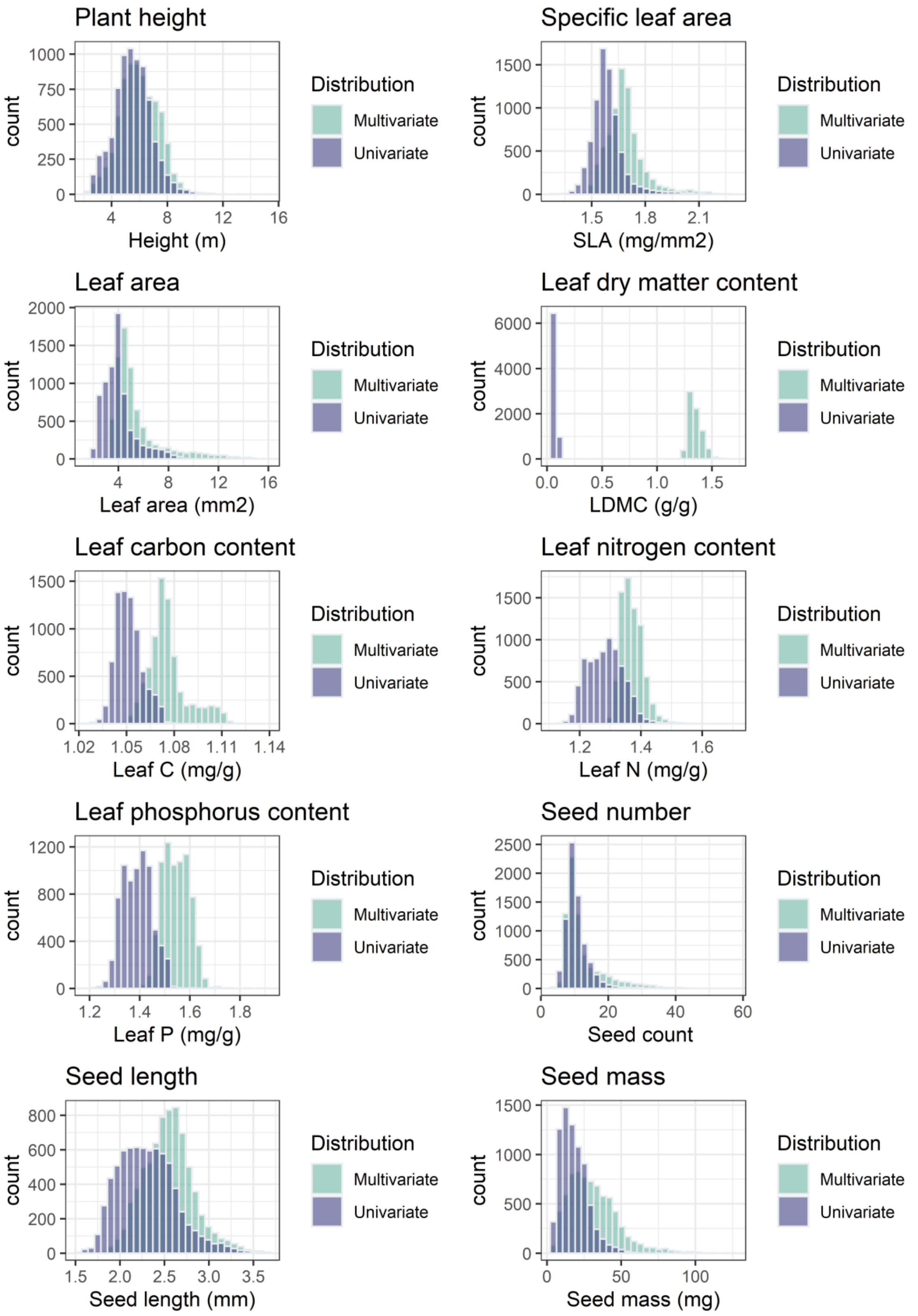

Figure S5.2 Histograms of reconstructed CWM^{sd} trait values using a univariate or a multivariate distribution for the likelihood.

Appendix S6: PCA plots

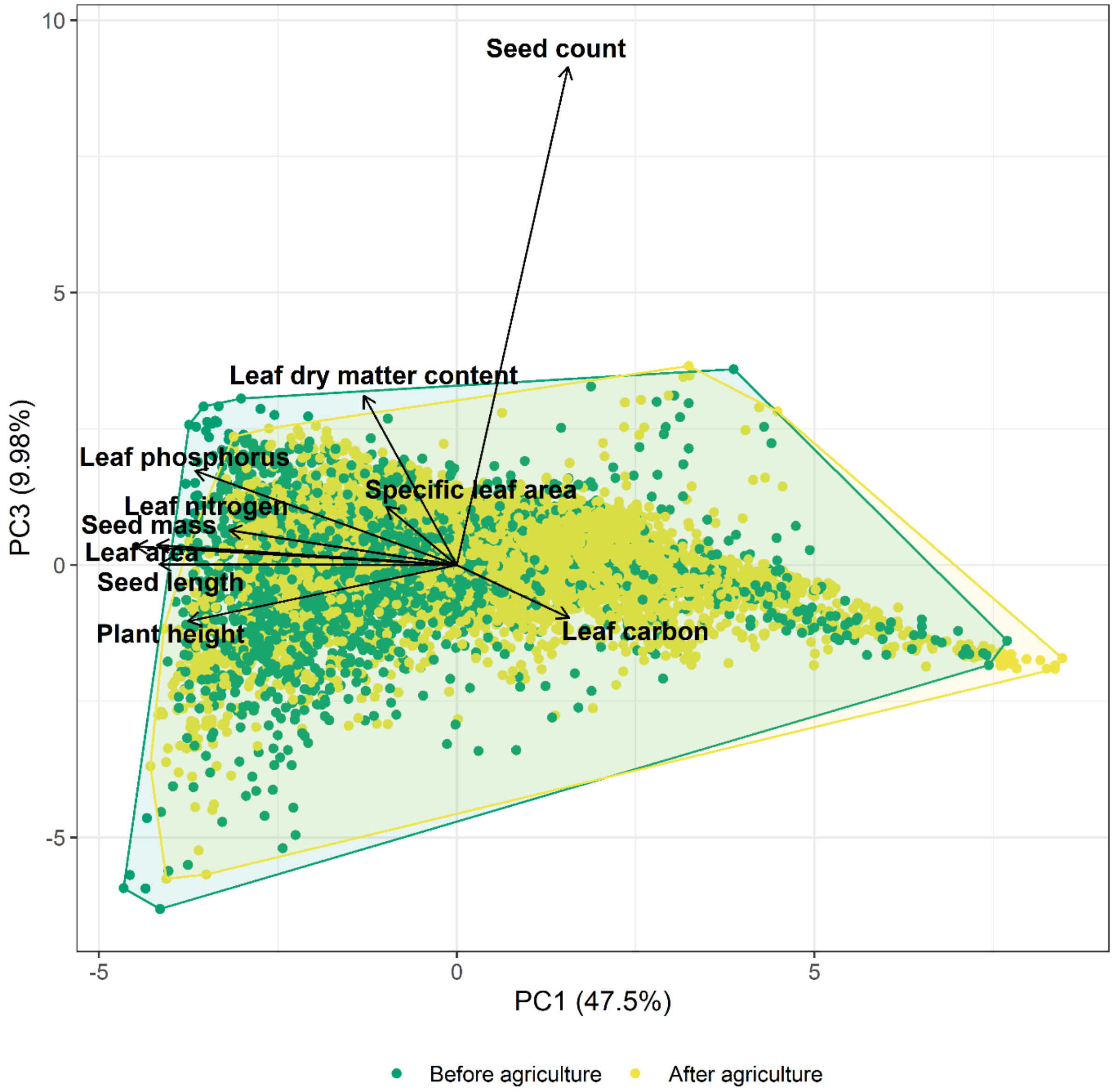

Figure S6.1 Plot of principal component analysis of community level trait values for principal components 1 and 3. Every colored point represents the reconstructed community trait value. The color indicates whether the observation is from before or after agriculture.

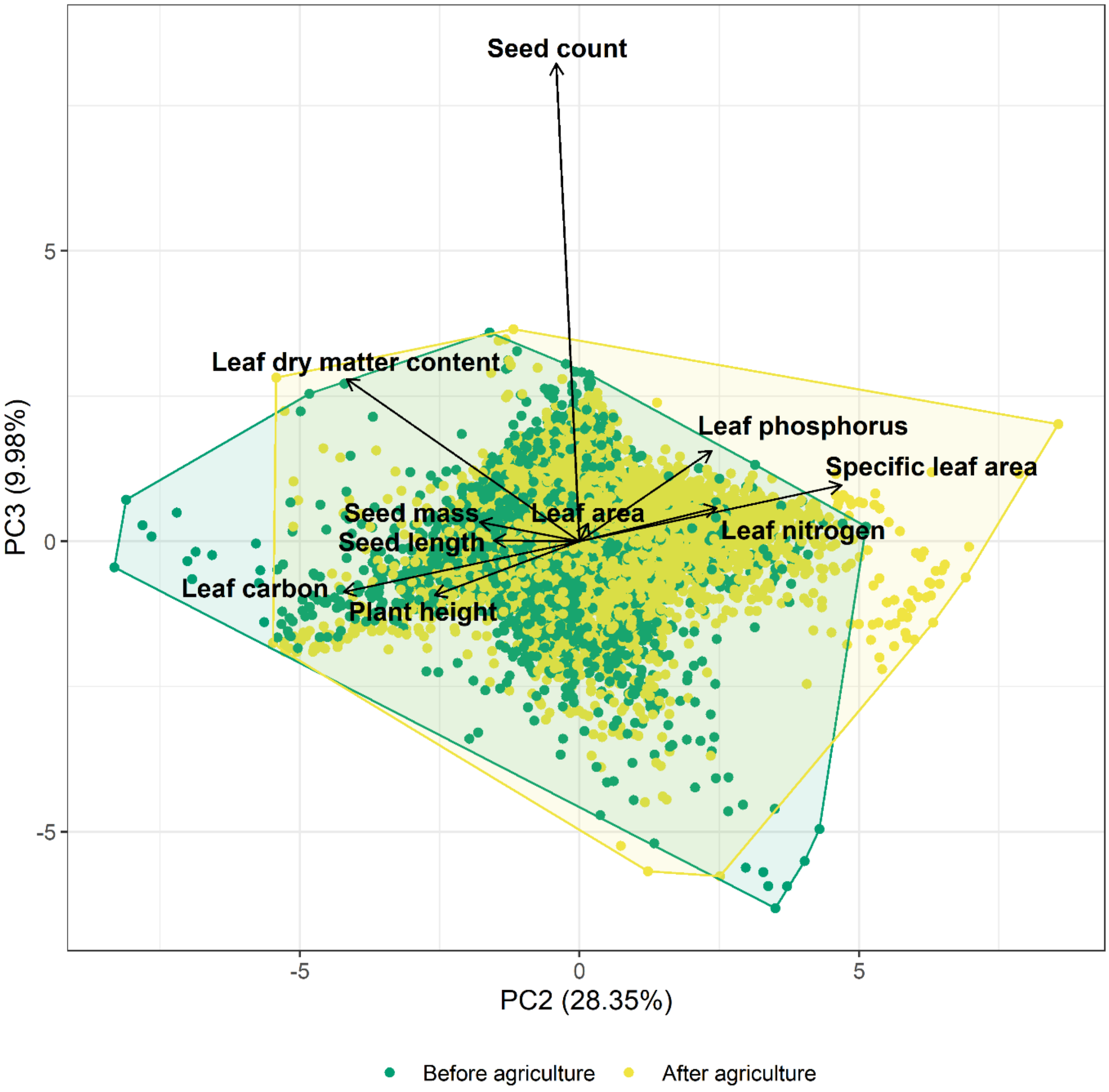

Figure S6.2 Plot of principal component analysis of community level trait for principal components 2 and 3. Every colored point represents the reconstructed community trait value. The color indicates whether the observation is from before or after agriculture.

To test the sensitivity of the analysis to the inclusion of plant height as a functional trait we performed the PCA on CWM calculation that excluded plant height.

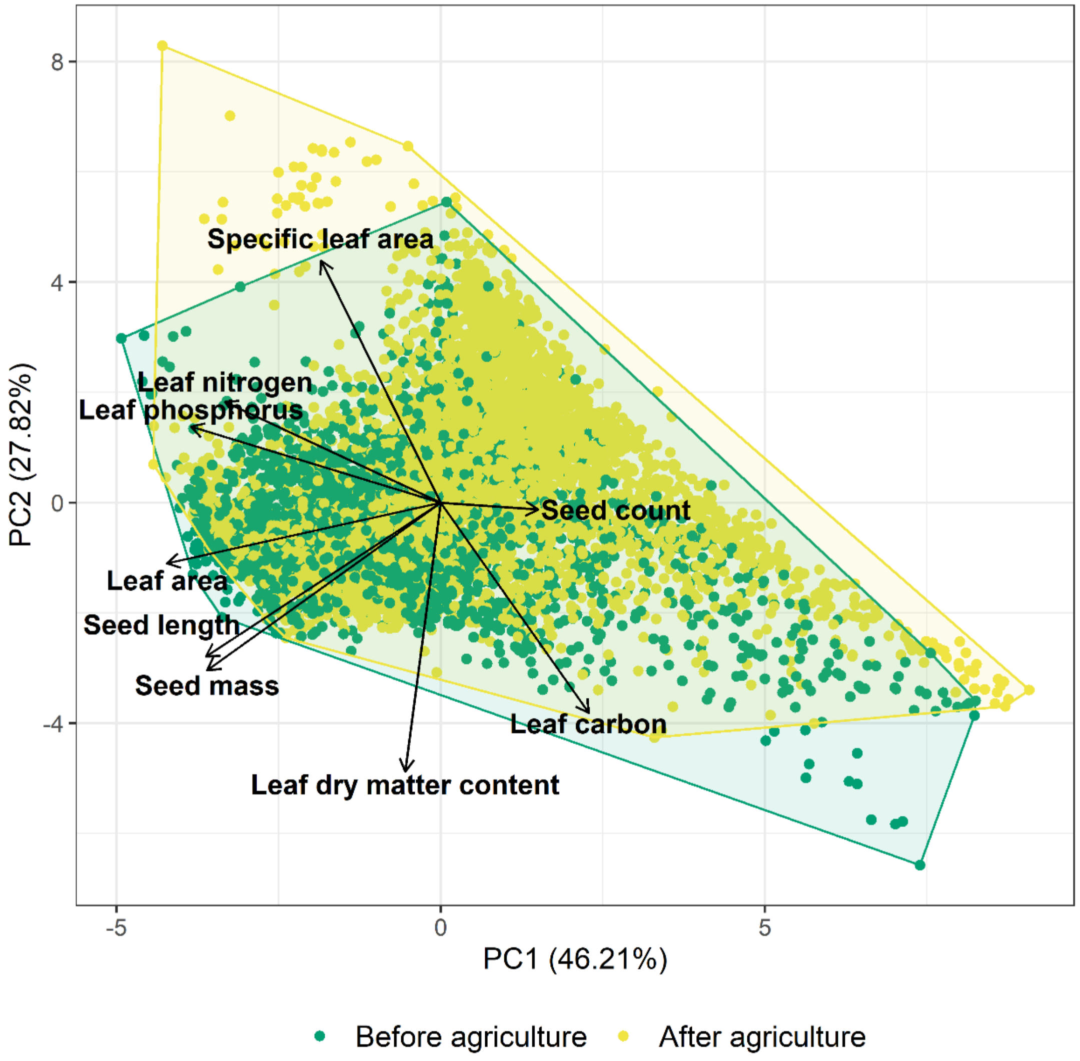

Figure S6.3 Principal component analysis of community level trait values without plant height, principal components 1 and 2. Every colored point represents the reconstructed community trait value. The color indicates whether the observation is from before or after agriculture.

Table S6.1 Loadings of the traits on the principal components for the PCA without plant height.

Trait	PC1	PC2	PC3
Leaf area	-0.469	-0.122	0.011
Leaf phosphorus	-0.428	0.153	0.167
Seed length	-0.402	-0.31	-0.043
Seed mass	-0.4	-0.338	-0.004
Leaf nitrogen	-0.37	0.203	0.096
Specific leaf area	-0.205	0.487	0.118
Leaf dry matter content	-0.061	-0.542	0.259
Seed count	0.167	-0.014	0.934
Leaf carbon	0.253	-0.423	-0.089
Proportion of variance explained (%)	46.2	27.8	10.9

Appendix S7: Evaluation of GAMs

To examine the variability of the smooths, 50 smooth curves from the posterior were drawn (Wood, 2016). Figure 7 shows the results for the first GAM for trait change over time.

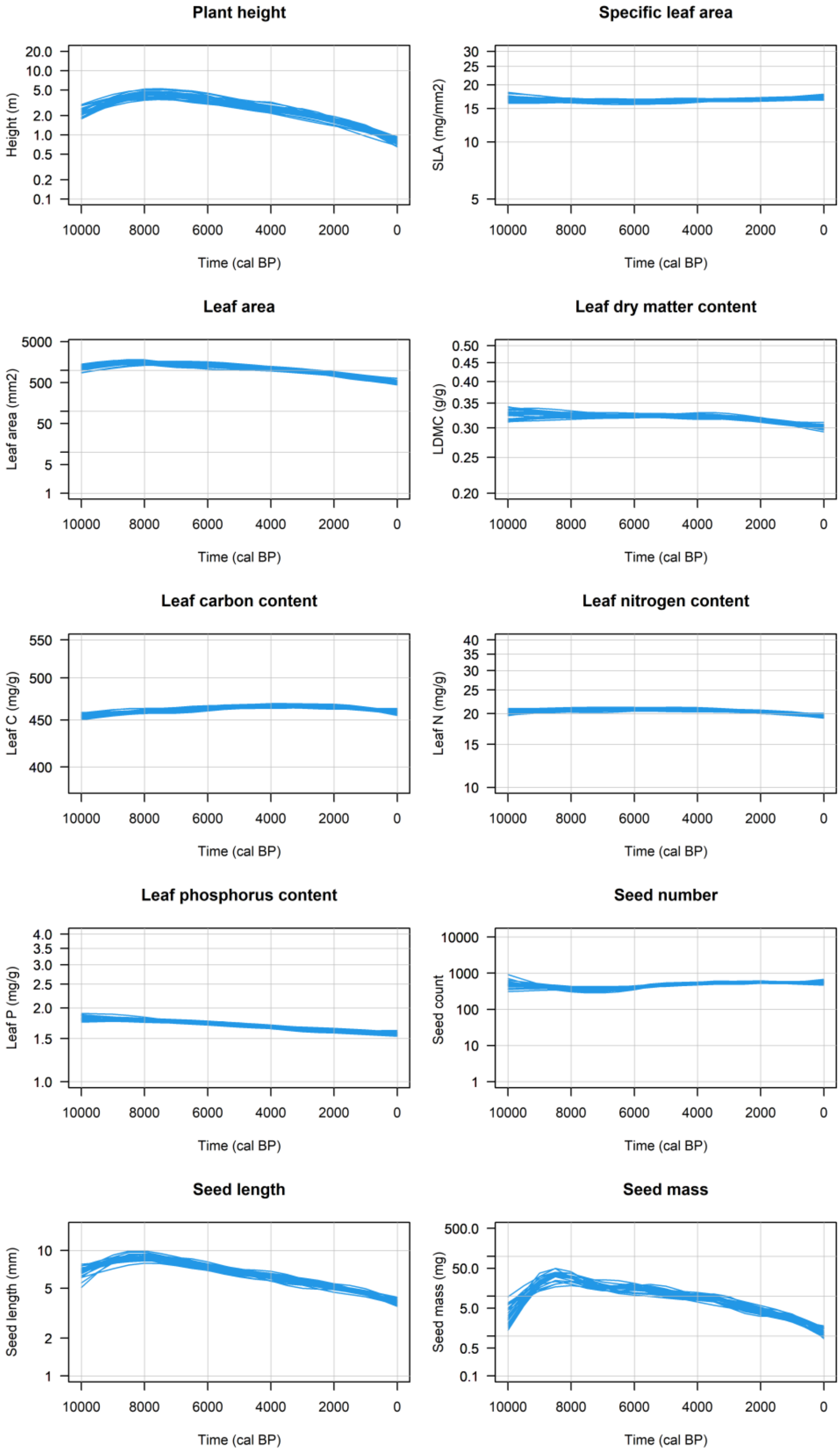

Figure S7.1 50 random draws from the posterior distributions of the GAM for trait change over time. Every line is a draw from the posterior.

To examine the sensitivity of the GAMs to the choice of sites, we performed reruns of the GAM whilst leaving 1 site at the time. Figure 8 shows the results of this model validation for the first GAM for trait change over time.

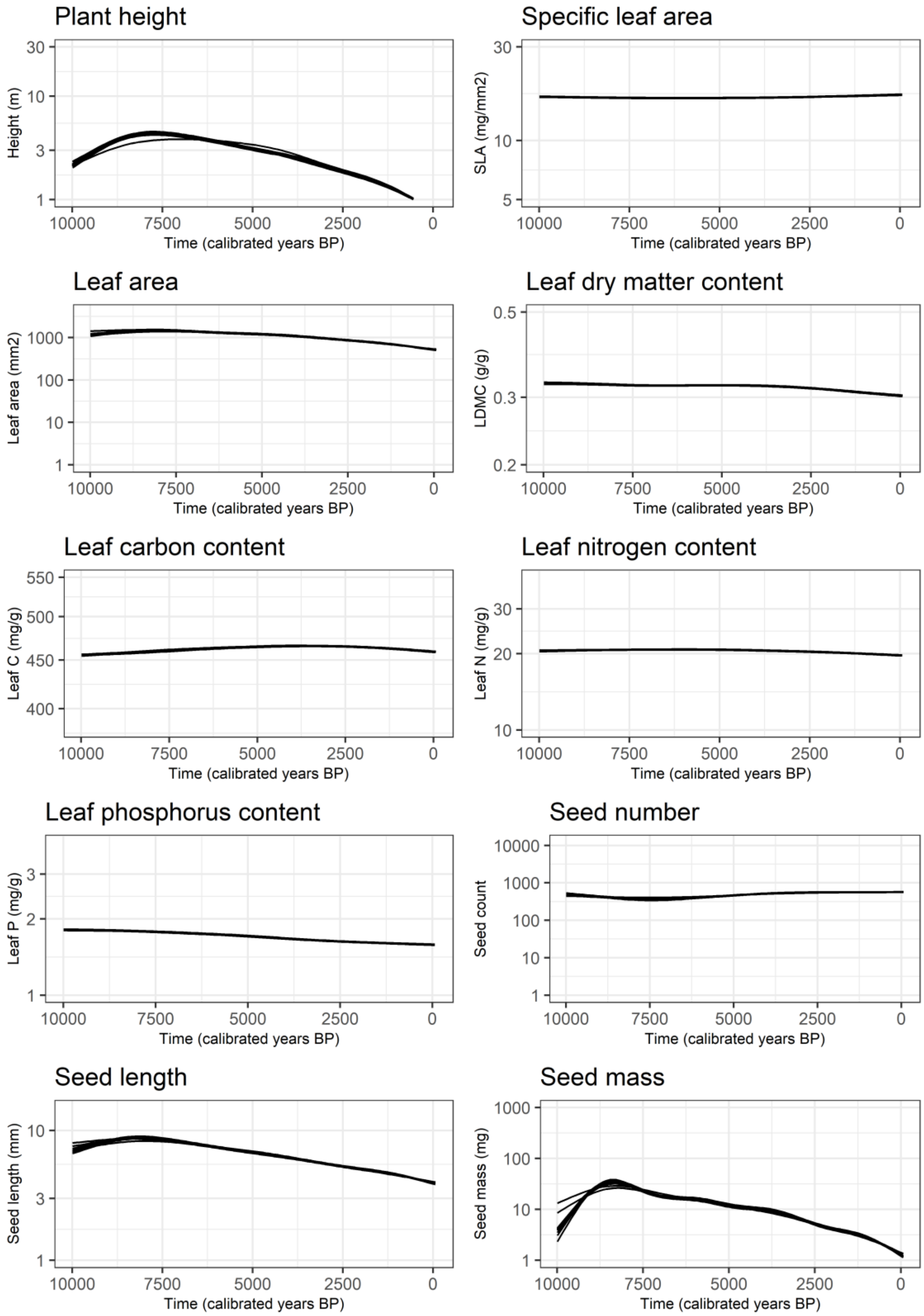

Figure S7.2 Reruns of GAM for trait change over time for testing the effect of site choice on the model. Every line is a run of the GAM while leaving one site from the dataset out.

To examine the sensitivity of the GAMs to uncertainty in the radiocarbon dating, we performed reruns of the GAM with 50 random draws from the *Bchron* age model. Figure 9 shows the results of this model validation for the first GAM for trait change over time.

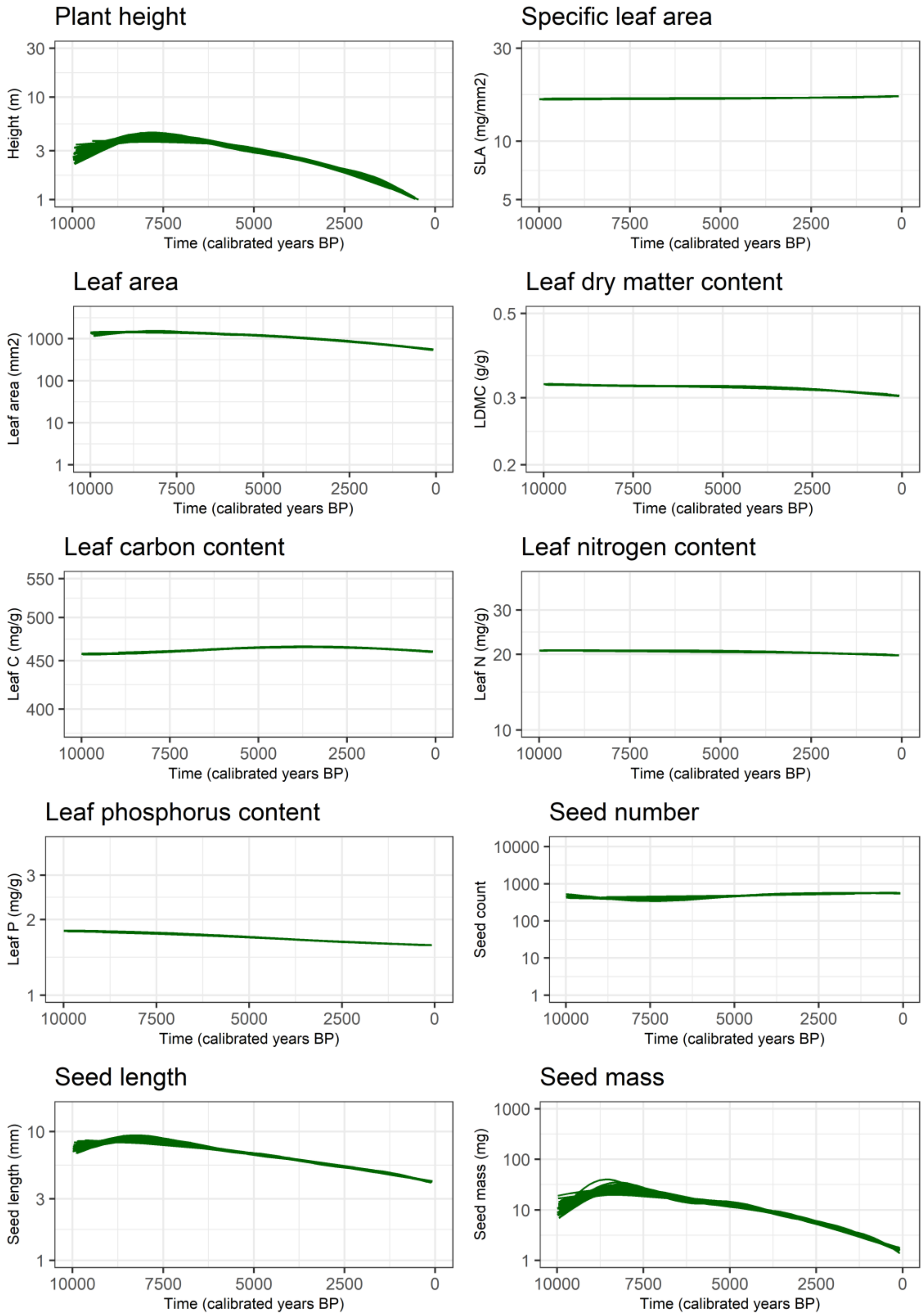

Figure S7.3 50 reruns of the GAM for trait change over time for testing the effect of age uncertainties on the model. Every line is a GAM run on a random draw from the posterior of the Bchron age models.

To examine the variability of the smooths, 50 smooth curves from the posterior were drawn (Wood, 2016). Figure 10 and 11 show the results for the second GAM for trait change since the arrival of agriculture and temperature.

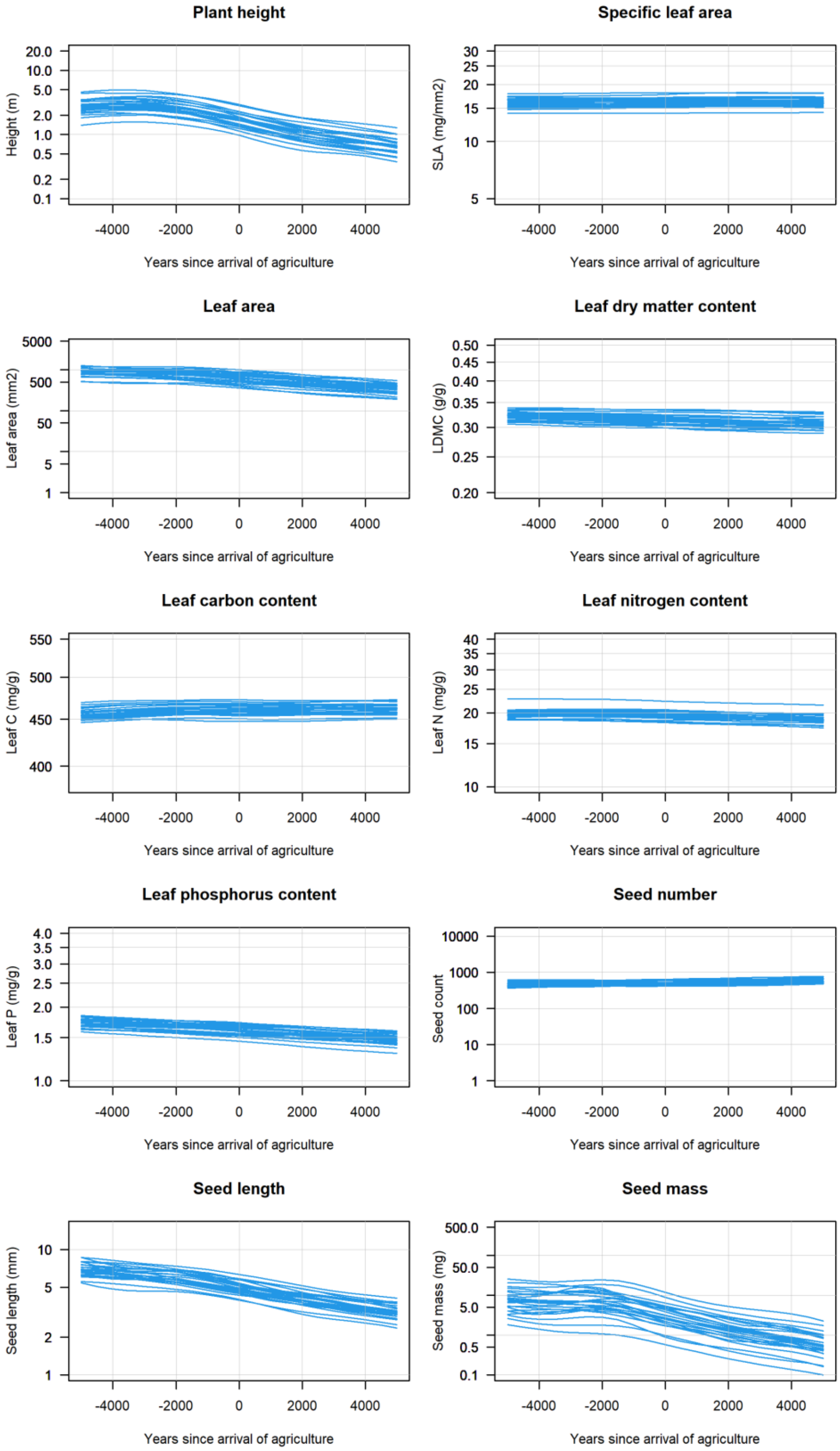

Figure S7.4 50 random draws from the posterior distributions of the GAM for trait change after the arrival of agriculture and temperature. Partial component plot for years since the arrival of agriculture. Every line is a draw from the posterior.

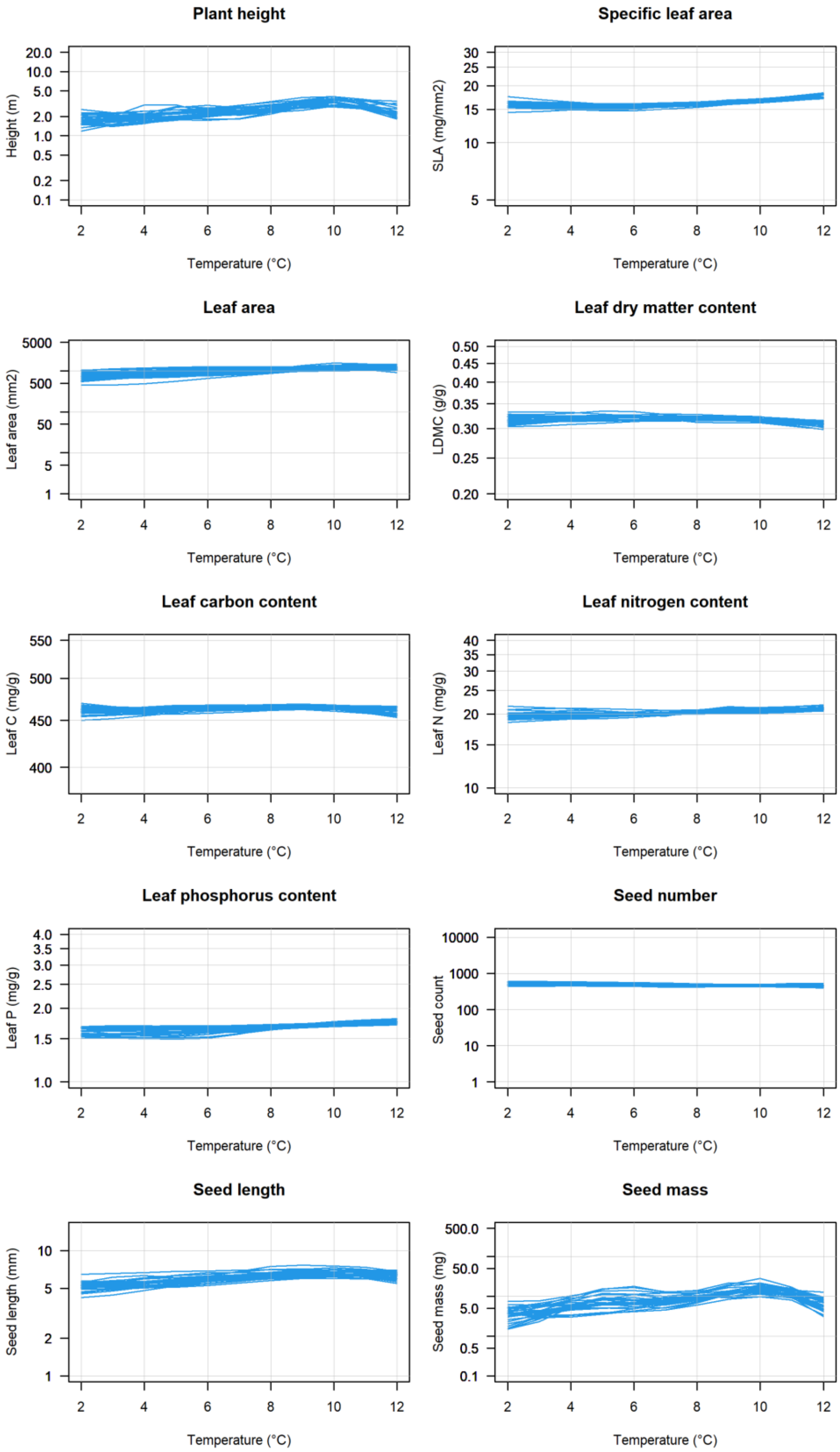

Figure S7.5 50 random draws from the posterior distributions of the GAM for trait change after the arrival of agriculture and temperature. Partial component plot for temperature. Every line is a draw from the posterior.

To examine the sensitivity of the GAMs to the choice of sites, we performed reruns of the GAM whilst leaving 1 site at the time. Figure 12 and 13 show the results of this model validation for the second GAM for trait change since the arrival of agriculture and temperature.

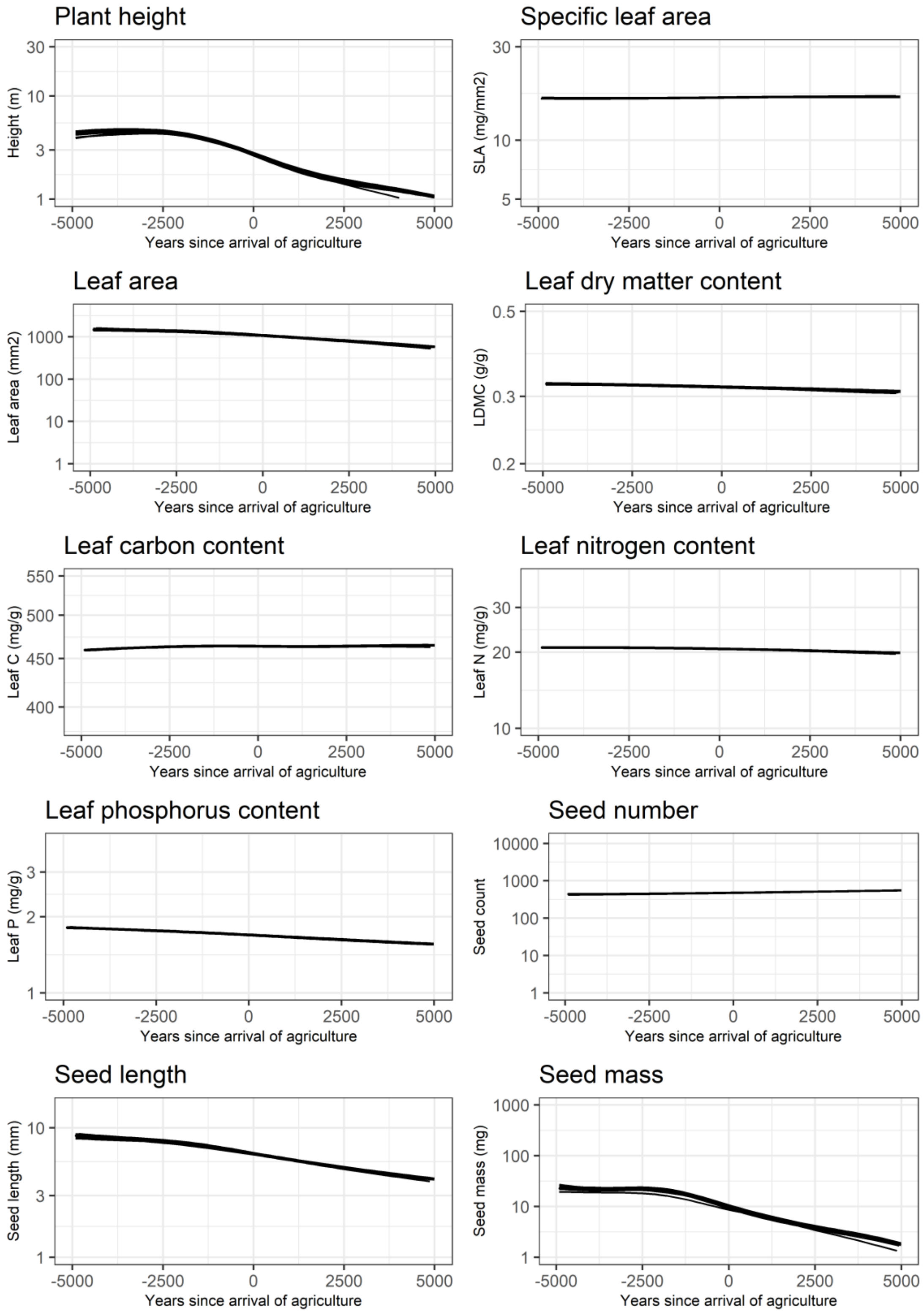

Figure S7.6 Reruns of GAM for agriculture and temperature for testing the effect of site choice on the model. Partial component plot for years since the arrival of agriculture. Every line is a run of the GAM while leaving one site from the dataset out.

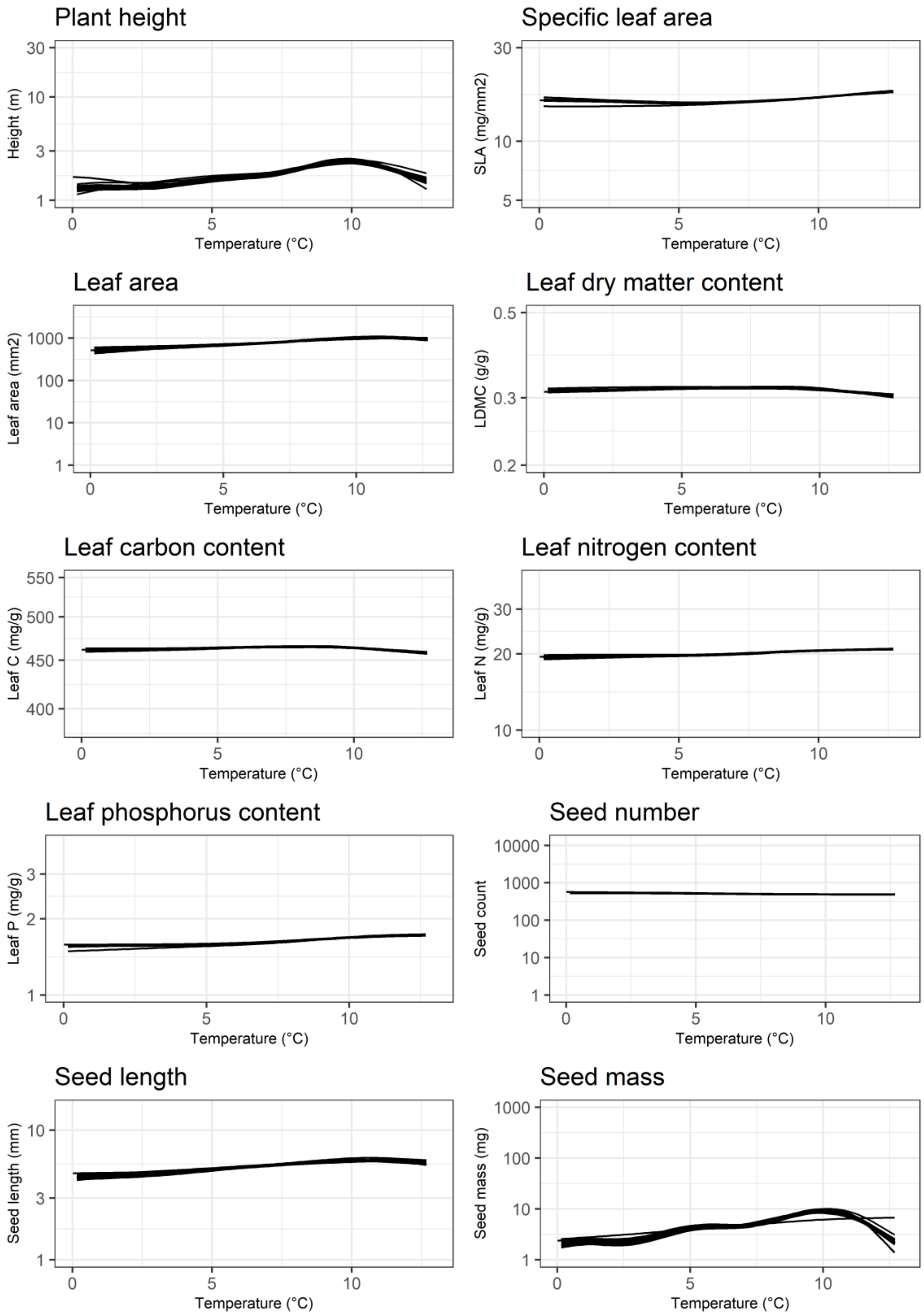

Figure S7.7 Reruns of GAM for agriculture and temperature for testing the effect of site choice on the model. Partial component plot for temperature. Every line is a run of the GAM while leaving one site from the dataset out.

To examine the sensitivity of the GAMs to uncertainty in the radiocarbon dating, we performed reruns of the GAM with 50 random draws from the *Bchron* age model. Figure 14 and 15 show the results of this model validation for the second GAM for trait change since the arrival of agriculture and temperature.

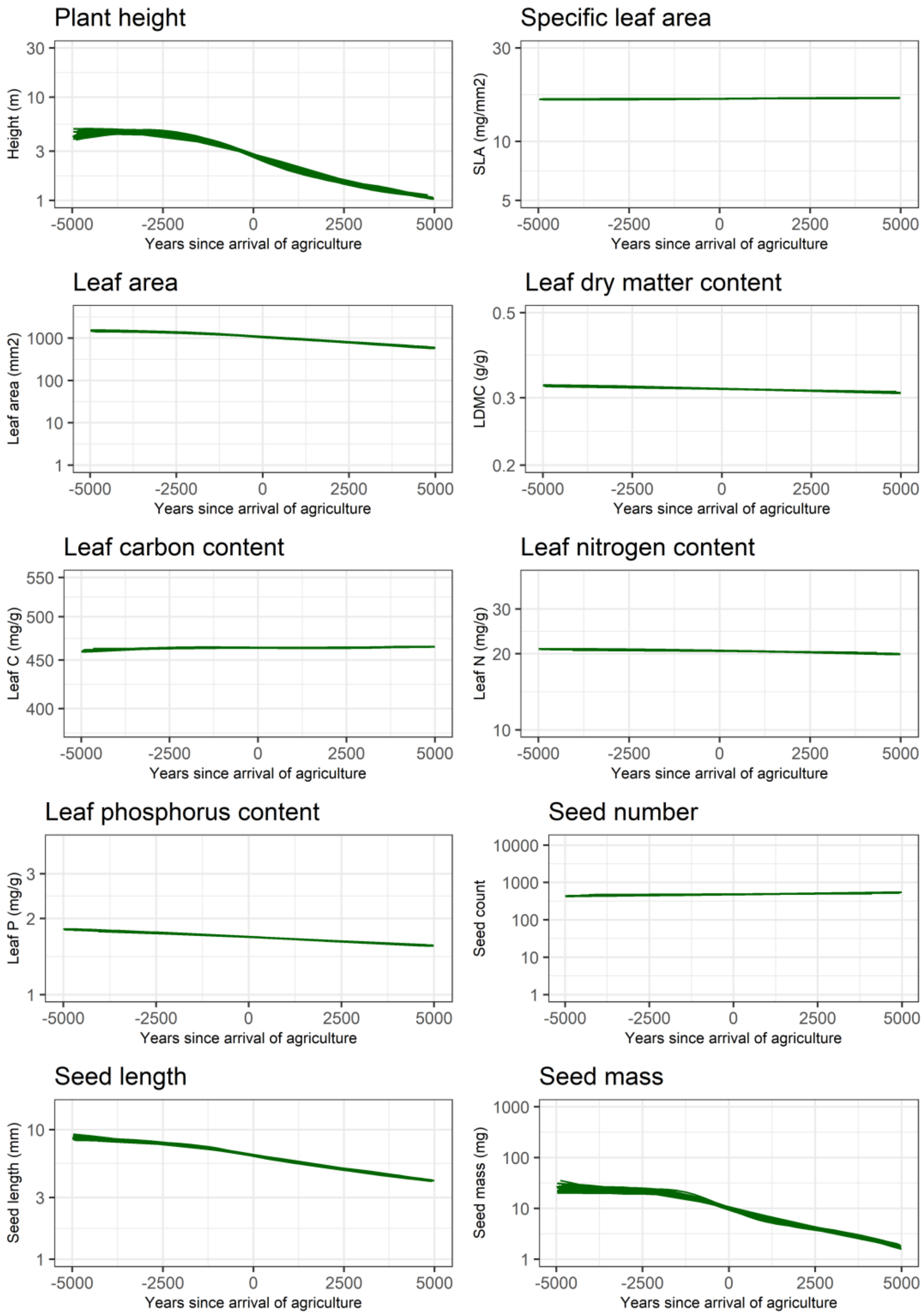

Figure S7.8 50 reruns of the GAM for trait change over time for testing the effect of age uncertainties on the model. Partial component plot for years since arrival of agriculture. Every line is a GAM run on a random draw from the posterior of the Bchron age models.

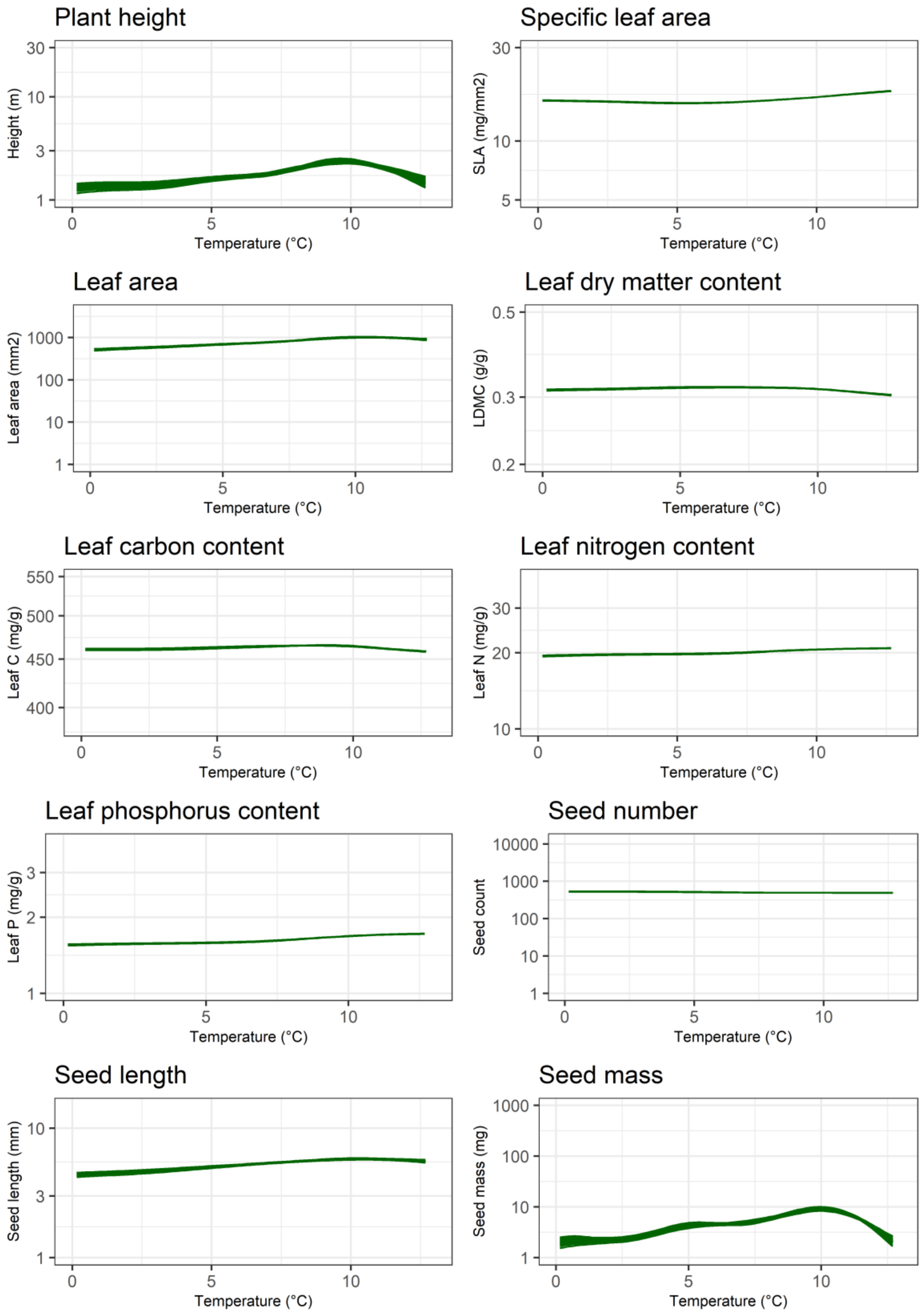

Figure S7.9 50 reruns of the GAM for trait change over time for testing the effect of age uncertainties on the model. Partial component plot for temperature. Every line is a GAM run on a random draw from the posterior of the Bchron age models

Appendix S8: Temperature data

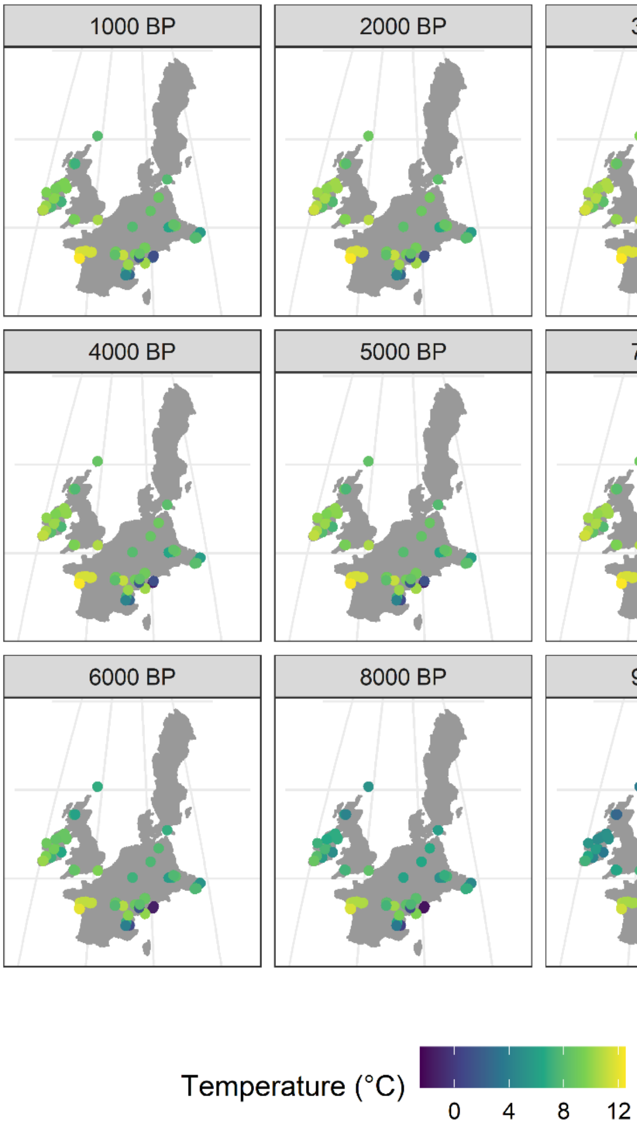

Figure S8.1 Average mean annual temperature at the pollen sites from the CHELSA-Trace21k dataset.

Appendix S9: Correlogram CWM trait values

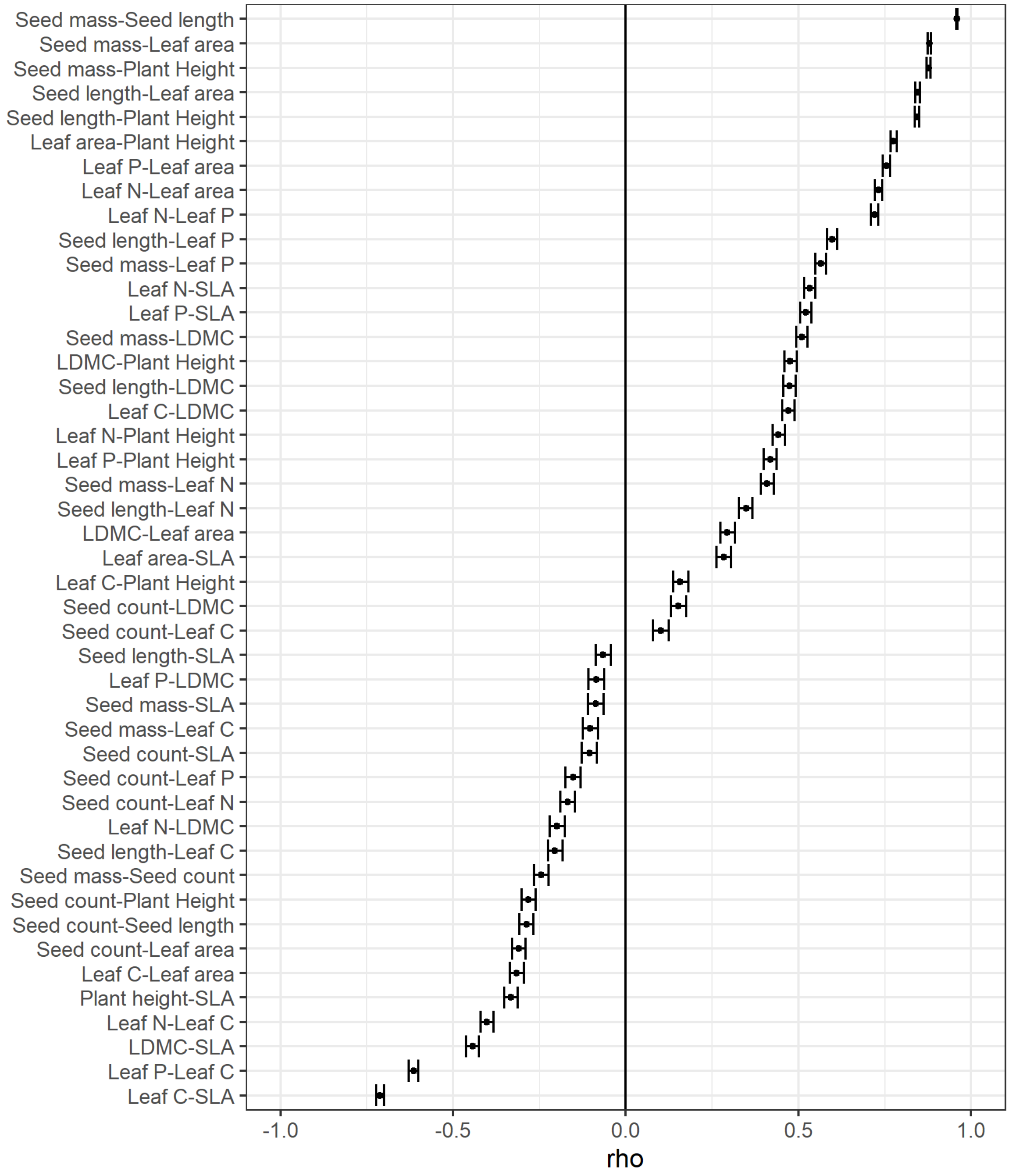

Figure S9.1 Correlogram of CWM trait values.

References

Wood, S. N. (2016). Just Another Gibbs Additive Modeler: Interfacing JAGS and mgcv. *Journal of Statistical Software*, *75*(7), 1-15. https://doi.org/10.18637/jss.v075.i07

Wood, S. N. (2017). *Generalized Additive Models: An Introduction with R* (2 ed.). Chapman and Hall/CRC.

Appendix S10: Taxon level trait estimates

Table S10.1 Trait estimates on the pollen taxonomic level.

Pollen taxon	**SLA**	**Plant height**	**LA**	**LDMC**	**Leaf carbon**	**Leaf phosphorus**	**Leaf nitrogen**	**Seed length**	**Seed count**	**Seed mass**
	mg/mm^2	m	mm^2	g/g	mg/g	mg/g	mg/g	mm		mg
Abies	5.07 ± 1.33	33.24 ± 2.33	31± 2.11	0.3 ± 1.17	501.81 ± 1.04	1.43 ± 1.34	13.14 ± 1.3	9.25 ± 1.49	4936 ± 2.73	19.25 ± 4.03
Acer	17.66 ± 1.38	16.88 ± 2.27	4143± 2.21	0.35 ± 1.15	465.19 ± 1.03	1.65 ± 1.3	20.42 ± 1.27	32.7 ± 1.36	50 ± 4.71	44.9 ± 2.89
Alnus	16.49 ± 1.52	17.24 ± 3.4	2762± 2.99	0.31 ± 1.27	496.82 ± 1.07	1.83 ± 1.38	30.59 ± 1.29	2.41 ± 1.72	1563 ± 4.32	1.12 ± 5.04
Apiaceae	21.92 ± 1.53	0.59 ± 2.19	2445± 4.43	0.2 ± 1.3	438.76 ± 1.05	2.78 ± 1.45	25.81 ± 1.29	5.04 ± 1.66	1466 ± 9.97	2.53 ± 3.25
Artemisia-type	20.12 ± 1.62	0.76 ± 3.48	294± 4.5	0.24 ± 1.34	437.98 ± 1.05	2.3 ± 1.41	25.12 ± 1.41	1.25 ± 1.77	18184 ± 9.26	0.15 ± 7.71
Asteraceae	20.59 ± 1.42	0.58 ± 2.17	1236± 3.8	0.18 ± 1.4	434.69 ± 1.06	2.24 ± 1.43	22.08 ± 1.31	3.87 ± 2.08	1334 ± 6.17	0.63 ± 5.95
Betula	13.82 ± 1.31	8.96 ± 5.48	630± 4.76	0.38 ± 1.16	525.57 ± 1.05	1.94 ± 1.34	24.31 ± 1.23	3.01 ± 1.43	1646 ± 3.24	0.23 ± 2.87
Brassicaceae	24.03 ± 1.4	0.37 ± 2.21	798± 5.55	0.13 ± 1.4	396.16 ± 1.06	2.91 ± 1.28	31.31 ± 1.26	1.61 ± 1.79	1110 ± 9.05	0.69 ± 6.02
Campanulaceae	31.03 ± 1.55	0.43 ± 2.43	334± 5.39	0.18 ± 1.38	461.01 ± 1.04	1.77 ± 1.29	27.3 ± 1.26	1.02 ± 1.62	2402 ± 6.92	0.09 ± 3.58
Carpinus	22.54 ± 1.68	12.74 ± 4.69	1767± 3.95	0.25 ± 1.34	463.13 ± 1.06	1.8 ± 1.65	19.95 ± 1.37	19.97 ± 2.01	6300 ± 6.6	22.75 ± 7.98
Caryophyllaceae	22.21 ± 1.47	0.22 ± 2.37	83± 6.85	0.17 ± 1.31	444.86 ± 1.04	1.81 ± 1.73	23.4 ± 1.24	1.1 ± 1.8	483 ± 6.95	0.26 ± 5.09
Castanea	13.35 ± 1.66	26.46 ± 4.48	8338± 4.09	0.34 ± 1.36	495.61 ± 1.06	1.83 ± 1.53	22.18 ± 1.39	4.55 ± 2.02	1 ± 6.49	5583.06 ± 7.74
Cerealia	23.3 ± 1.49	1.16 ± 3.32	2589± 6.82	0.23 ± 1.35	403.39 ± 1.08	1.85 ± 1.84	24.91 ± 1.36	13.57 ± 2.16	157 ± 5.16	26.51 ± 7.24

Pollen taxon	**SLA**	**Plant height**	**LA**	**LDMC**	**Leaf carbon**	**Leaf phosphorus**	**Leaf nitrogen**	**Seed length**	**Seed count**	**Seed mass**
	mg/mm^2	m	mm^2	g/g	mg/g	mg/g	mg/g	mm		mg
Convolvulaceae	26.26 ± 1.57	0.59 ± 4.35	1455± 3.89	0.17 ± 1.29	446.34 ± 1.05	1.92 ± 1.42	30.02 ± 1.35	2.68 ± 2.16	141 ± 5.83	5.86 ± 9.3
Cornaceae	20.1 ± 1.53	2.78 ± 4.39	1990± 3.22	0.32 ± 1.28	444.38 ± 1.05	1.86 ± 1.5	18.58 ± 1.28	8.26 ± 1.77	13 ± 4.55	54.77 ± 5.42
Corylus	19.07 ± 1.65	4.45 ± 3.5	3733± 3.12	0.38 ± 1.28	448.41 ± 1.05	2.16 ± 1.35	20.9 ± 1.3	16.54 ± 1.76	1439 ± 4.62	786.07 ± 5.27
Cyperaceae	16.36 ± 1.49	0.34 ± 2.03	427± 3.37	0.32 ± 1.22	453.15 ± 1.05	1.35 ± 1.47	18.04 ± 1.26	2.73 ± 1.62	128 ± 6.71	0.71 ± 2.77
Ericales	10.89 ± 1.55	0.48 ± 3.89	63± 12.46	0.35 ± 1.24	542.2 ± 1.05	1.02 ± 1.46	13.75 ± 1.3	1.83 ± 2.35	378 ± 11.18	0.11 ± 8.64
Fabaceae	21.31 ± 1.44	0.54 ± 3.29	211± 4.49	0.23 ± 1.28	473.81 ± 1.04	1.65 ± 1.33	36.05 ± 1.23	2.88 ± 1.86	121 ± 5.76	6 ± 6.43
Fagus	14.44 ± 1.47	29.57 ± 2.35	2352± 2.27	0.33 ± 1.25	493.39 ± 1.04	1.29 ± 1.32	23.33 ± 1.24	7.39 ± 1.5	246 ± 3.25	226.81 ± 3.25
Fraxinus	14.18 ± 1.58	16.29 ± 3.17	2612± 4.15	0.34 ± 1.22	446.28 ± 1.05	2.02 ± 1.32	20.48 ± 1.27	31.07 ± 1.57	580 ± 3.68	52.57 ± 3.81
Humulus	24.39 ± 3.38	4.29 ± 39.02	5602± 29.98	0.29 ± 2.08	475.2 ± 1.16	1.02 ± 2.31	18.05 ± 2.04	2.51 ± 5.62	38 ± 93.6	3.36 ± 143.93
Juglans	15.16 ± 1.76	28.21 ± 5.26	3718± 4.78	0.3 ± 1.4	510.95 ± 1.07	2.38 ± 1.58	22.24 ± 1.43	3.5 ± 2.22	143 ± 7.85	9915.4 ± 9.61
***Juniperus*-type**	4.55 ± 2.12	5.78 ± 4.5	21± 3.63	0.47 ± 1.3	512.12 ± 1.08	1.02 ± 1.52	11.05 ± 1.39	5.09 ± 1.86	240 ± 5.39	21.6 ± 6.8
Lamiaceae	23.8 ± 1.59	0.37 ± 2.13	423± 4.53	0.2 ± 1.34	449.43 ± 1.05	2.15 ± 1.61	21.32 ± 1.38	1.6 ± 1.57	303 ± 5.72	0.7 ± 3.61
Larix	9.78 ± 1.49	39.33 ± 3.2	18± 3.12	0.36 ± 1.27	511.08 ± 1.05	1.83 ± 1.43	18.51 ± 1.33	8.44 ± 1.73	131645 ± 4.41	4.53 ± 5.11
Liliaceae-type	21.58 ± 1.7	0.38 ± 5.44	776± 5.45	0.12 ± 1.46	439.25 ± 1.07	2.24 ± 1.5	32.83 ± 1.51	4.66 ± 2.4	127 ± 10.52	2.7 ± 9.62

Pollen taxon	**SLA**	**Plant height**	**LA**	**LDMC**	**Leaf carbon**	**Leaf phosphorus**	**Leaf nitrogen**	**Seed length**	**Seed count**	**Seed mass**
	mg/mm^2	m	mm^2	g/g	mg/g	mg/g	mg/g	mm		mg
Moraceae	18.62 ± 2.07	10.96 ± 5.34	7758± 4.67	0.3 ± 1.39	439.68 ± 1.07	1.75 ± 1.7	25.22 ± 1.43	2.23 ± 2.09	977 ± 8.53	4.07 ± 11.99
Orobanchaceae	20.75 ± 1.38	0.24 ± 2.52	147± 3.13	0.2 ± 1.27	452.99 ± 1.06	2.32 ± 1.55	29.63 ± 1.45	1.84 ± 2.45	276 ± 8.95	0.47 ± 11.2
Picea	4.03 ± 1.28	39.28 ± 1.67	33± 1.69	0.42 ± 1.15	494.74 ± 1.02	1.36 ± 1.34	11.41 ± 1.25	8.03 ± 1.31	115524 ± 1.91	4.99 ± 2.15
Pinus	4.55 ± 1.24	27.56 ± 1.51	67± 1.61	0.37 ± 1.09	510.08 ± 1.03	1.09 ± 1.33	11.72 ± 1.19	7.93 ± 1.2	1092 ± 1.73	13.97 ± 2.68
Plantaginaceae	22.57 ± 1.45	0.25 ± 2.19	366± 5.27	0.18 ± 1.35	455.57 ± 1.08	2.09 ± 1.47	20.99 ± 1.28	1.35 ± 1.54	829 ± 7.51	0.24 ± 3.58
Poaceae	20.45 ± 1.47	0.47 ± 2.03	454± 3.51	0.31 ± 1.28	444.99 ± 1.04	1.56 ± 1.61	19.54 ± 1.33	4.11 ± 1.89	847 ± 7.73	0.54 ± 4.18
Populus	13.49 ± 1.43	22.7 ± 2.86	2654± 2.85	0.38 ± 1.26	495.68 ± 1.06	1.76 ± 1.43	22.18 ± 1.34	1.68 ± 1.64	1588 ± 3.65	0.25 ± 5.18
Quercus	10.12 ± 1.53	24.42 ± 1.76	1973± 2.34	0.36 ± 1.15	483.86 ± 1.04	1.21 ± 1.37	18.12 ± 1.31	19 ± 1.27	176 ± 2.64	1903.49 ± 2.19
Ranunculaceae	22.5 ± 1.42	0.4 ± 3.12	1730± 4.01	0.18 ± 1.32	453.25 ± 1.04	2.32 ± 1.49	24.41 ± 1.24	3.24 ± 1.65	196 ± 6.35	1.9 ± 3.76
Rosaceae	15.96 ± 1.45	1.1 ± 5.26	1063± 3.46	0.34 ± 1.2	467.73 ± 1.04	1.91 ± 1.35	21.27 ± 1.22	4.99 ± 2.35	71 ± 16.74	5.18 ± 13.4
Rubiaceae	29.38 ± 1.5	0.35 ± 2.31	61± 3.79	0.22 ± 1.33	441.17 ± 1.05	1.89 ± 1.39	22.05 ± 1.29	1.67 ± 1.6	201 ± 13.3	1.24 ± 5.01
Rumex	24.61 ± 1.38	0.56 ± 2.63	1858± 4.98	0.13 ± 1.23	460.14 ± 1.04	2.87 ± 1.29	34.05 ± 1.21	2.27 ± 1.56	2070 ± 6.78	0.85 ± 3.3
Salix	12.14 ± 1.35	1.33 ± 7.44	418± 3.27	0.35 ± 1.2	491.27 ± 1.05	1.55 ± 1.48	23.53 ± 1.24	1.81 ± 1.7	8176 ± 40.58	0.09 ± 3.58
Sambucus nigra	21.34 ± 1.76	5.41 ± 4.85	920± 4.58	0.23 ± 1.38	424.91 ± 1.06	2.65 ± 1.46	37.4 ± 1.37	5.29 ± 2.08	6 ± 7	6.4 ± 8.68

Pollen taxon	**SLA**	**Plant height**	**LA**	**LDMC**	**Leaf carbon**	**Leaf phosphorus**	**Leaf nitrogen**	**Seed length**	**Seed count**	**Seed mass**
	mg/mm^2	m	mm^2	g/g	mg/g	mg/g	mg/g	mm		mg
***Sanguisorba*-type**	20.48 ± 1.64	0.44 ± 4.62	318± 4.12	0.29 ± 1.35	444.08 ± 1.08	1.38 ± 1.44	20.9 ± 1.35	3.24 ± 1.99	611 ± 9.1	4 ± 7.88
Thalictrum	20.68 ± 1.85	0.39 ± 5.84	1802± 14.58	0.28 ± 1.43	447.39 ± 1.07	2.31 ± 1.58	22.94 ± 1.4	3.52 ± 2.29	412 ± 32.51	1.26 ± 9.66
Thymelaceae	18.25 ± 2.14	0.75 ± 7.06	351± 6.15	0.23 ± 1.47	449.37 ± 1.08	2.39 ± 1.81	24.4 ± 1.48	7.65 ± 2.46	9 ± 16.63	18.57 ± 18.01
Tilia	26.47 ± 1.64	16.27 ± 4.45	4266± 3.64	0.21 ± 1.31	462.98 ± 1.05	2.57 ± 1.45	25.86 ± 1.33	7.82 ± 1.89	1 ± 5.58	54.96 ± 6.43
Ulmus	14.74 ± 1.72	24.56 ± 3.57	2982± 3.57	0.31 ± 1.36	415.68 ± 1.05	1.73 ± 1.42	22.18 ± 1.33	22.19 ± 1.8	0 ± 4.73	8.04 ± 5.53
Urtica	30.43 ± 1.65	0.98 ± 4.15	1152± 3.9	0.21 ± 1.33	375.67 ± 1.06	4.11 ± 1.43	46.62 ± 1.35	1.7 ± 1.93	823 ± 8	0.23 ± 7.34

Paper 3: The effect of plant life-history strategy on population and community responses to human impact

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Author contributions: AV designed the study supervised by MJS, SM and FS. MJS, SM, FS, MD, RF, IM and MM all provided feedback on the analysis and design of the study. AV conducted the analysis and wrote the manuscript. IM provided R code for preparation of BioTIME data.

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Code and data availability: R-scripts of this analysis are available at https://github.com/sTeTra-Working-Group/LifeHistory

5 The effect of plant life-history strategy on population and community responses to human impact

Abstract

Community-level dynamics culminate from the abundance changes of the species that make up that community. Understanding the factors that cause different rates of change among species in the community may help explain current and future biodiversity changes. Life-history traits may be crucial in explaining how species respond to human activity. Here, we used the biodiversity database BioTIME to study plant species' response to human impact in isolation, by studying population changes, and relative to the community, by calculating species' turnover contribution. We found that population level changes could not be explained by life-history or human impact. Species' turnover contribution was related to life-history, but the context matters. Species with a slow life-history contribute more to turnover in areas that have become warmer and drier due to climate change. Species with a high reproductive output have a higher turnover contribution in areas of relatively high land use change. Knowing why species may contribute disproportionately to turnover is important for understanding turnover metrics and the underlying mechanisms that shape biodiversity.

5.1 Introduction

Rates of biodiversity change differ vastly between taxa and biomes. For instance, taxonomic compositional change is more rapid in the marine realm and among small-bodied organisms (Blowes et al., 2019; Korhonen et al., 2010). Understanding the factors that cause such different rates of change is essential for choosing appropriate metrics of biodiversity change, forecasting biodiversity changes and setting realistic timeframes for ecosystem management. Although much of the dynamics in community composition are caused by extrinsic factors (e.g. environmental fluctuations) (Newbold et al., 2015), the role of intrinsic factors such as species characteristics are yet poorly understood (Soininen, 2010; Watts et al., 2020). Indeed, if biodiversity changes were an inherent property of the ecosystem, changes due to extrinsic factors might be overestimated (O'Sullivan et al., 2021). Conversely, if such intrinsic properties do not affect biodiversity change, a more robust attribution of biodiversity change to extrinsic factors is warranted.

Community-level dynamics culminate from the abundance changes of the species that make up that community (Shimadzu et al., 2015). These dynamics might be strongly driven by changes in a single population or a species group with similar traits (Di Cecco & Hurlbert, 2022). The life-history traits of species (e.g. traits relating to survival, growth and reproduction) may play a vital role in explaining community-level dynamics because they partly determine population growth rates (Salguero-Gomez et al., 2018). 55% of the variation in life-history traits in plant species can be characterised in two axes: the fast-slow continuum (traits related to longevity and growth) and the reproduction strategy axis (traits such as the number of sexual recruits and degree of iteroparity) (Salguero-Gomez et al., 2016).

Under environmental change, different responses of plant species can be expected from life-history traits. High extinction risk has been found for K-strategists, i.e., species with a long lifespan, late age of maturity and low fecundity (Chichorro et al., 2022). However, environmental change drivers are complex and diverse, and different traits might determine species' sensitivity to drivers. For instance, long-living, stress-tolerant herbaceous plants are potentially less vulnerable to droughts (Wilcox et al., 2021). The same might be true for long-living, slow-growing trees such as conifers (Choat et al., 2012; Locosselli et al., 2020). On the other hand, population growth rates of short-living herbaceous plants respond more strongly to climate anomalies (Compagnoni et al., 2021). High intensity of human impact might favour weedier species, i.e. species with high fecundity that are good dispersers but bad competitors (Tilman & Lehman, 2001)

Here, we use the biodiversity database BioTIME to examine if population-level and community-level changes can be explained by life-history traits and human impact (Dornelas et al., 2018)(Figure 5.1). The BioTIME database contains data on species identities and abundances on a community-level through time. Using community-level data, instead of data from population monitoring studies such as the Living Planet Database (LPI, 2016), allows for examining population trends in isolation and in the context of the community. We test population change can be explained by life-history and human impact. We expect species with short life spans and high fecundity to have the highest population changes when exposed to high human impact. Long-living species might be able to cope with high climate change intensity but not with high human impact. Furthermore, we test if species with particular life-histories may contribute disproportionally to turnover. We expect fast-living species to contribute the most to turnover because their population growth rates can fluctuate more with greater environmental variability under human impact (Le Coeur et al., 2022). Slow-living species might contribute the least to turnover because of their stable or slow population growth. Alternatively, slow-living species could contribute the most to turnover because of their vulnerability to global change (Chichorro et al., 2022).

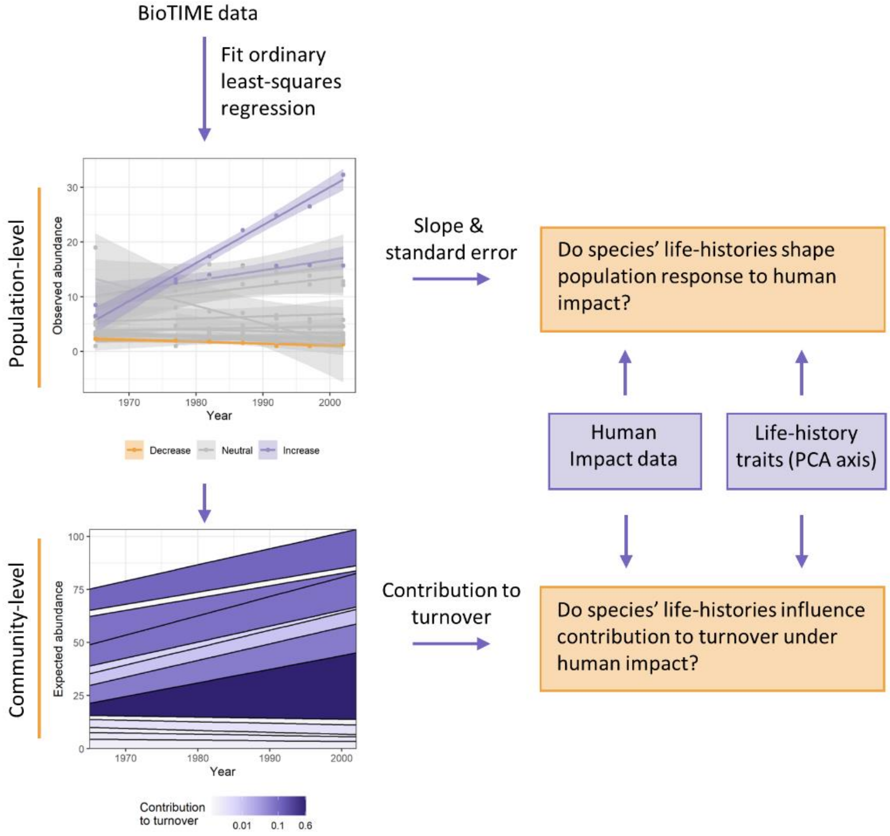

Figure 5.1 Diagram explaining the structure of the analysis. 1) Ordinary least-squares regression (OLS) was fitted to the populations in every assemblage in the BioTIME data, slope and standard error were carried through in the following analysis. Colour of the lines indicate if the population significantly changes according to the OLS regression 2) Contribution to turnover was calculated using the fitted OLS models and the method of Shimadzu et al. (2015). Colour in the stacked graph represents the contribution to turnover, darker colours indicate higher contribution to turnover. The abundance data shown in the plots are from 1 of the 184 assemblages in the dataset - Forest Inventory of a Northern Hardwood Forest Watershed 6 (study ID 234, Battles et al. (2019)).

5.2 Methods

5.2.1 BioTIME data selection

Before filtering for relevant studies, the dataset contained the records of 5741 terrestrial plant species from 96 studies. To account for differences in spatial extent between studies, the database was gridded in 96 km^2 hexagonal cells, meaning studies with a large spatial extent were assigned to multiple. We selected time series with a time span of 5 years or more and discarded studies that only contained presence/absence data. We only included populations for which the binomial names were known, thus discarding taxa that were only determined to genus or family level. For calculating population trends, we needed a minimum of 3 observations of a species per time series, thus transient species were excluded from the analysis. Before matching with trait data, these selection criteria resulted in the inclusion of 2641 species from 184 assemblage series and 64 studies, forming 4455 population records with an average time span of 33 years (Appendix figure S1.1). The time series were mainly distributed in Europe and North America (Appendix figure S2.1). Because BioTIME is a compilation of multiple studies, there is no common taxonomy. Therefore, we harmonised taxonomy using the R-package *lcvp* (Freiberg et al., 2020).

5.2.2 Human impact data

To assess population exposure to anthropogenic pressures, we used driver data created by Bowler et al. (2020) because this data was previously processed for the time series in BioTIME (Daskalova et al., 2021). This dataset has a grid resolution of 100 km^2 and is a compilation of 16 spatially explicit global change driver layers. Temporally explicit data on human pressure were not available for the time span of the biodiversity data. Every variable in this dataset is scaled, ranked and summed across five main anthropogenic drivers of biodiversity change: climate change, human use, human population density, pollution and alien potential (Bowler et al., 2020). We focussed on two of the five main drivers, climate change and human use (Table 5.1). The climate change metric is based on five variables: temperature trend, temperature divergence, change in climate extremes, velocity of climate change and aridity trend. Higher values represent the increased intensity of climate change, particularly in relation to warming and drying. The human use metric is compiled from five variables: crop cover, pasture cover, urban cover, forest loss and livestock density. Higher values of this metric relate to increased intensity of human use, particularly land use.

Table 5.1 Variables included in the calculation of the two biodiversity change drivers that are used in this study. See Bowler et al. (2020) for the full details on the compilation of these metrics.

Driver	Variable	Interpretation
Climate change	Temperature trend Temperature divergence Change in climate extremes Velocity of climate change Aridity trend	Higher climate change impact particular in relation to warming and increased aridity
Human use	Crop cover Pasture cover Urban cover Forest loss Livestock density	Increased human use, especially more land use change

5.2.3 Trait data

We used two sources of life-history data in this study, the TRY database and the COMPADRE database (Kattge et al., 2020; Salguero-Gómez et al., 2014). Whilst high-quality life-history trait data can be obtained from the COMPADRE database, a database of matrix population models, the species cover of TRY data is much greater. Four traits from the COMPADRE database were selected: Net reproduction, generation time, age of maturity and longevity. Generation time, age of maturity and longevity are traits that relate to the fast-slow spectrum of life histories, while net reproduction is one of the main traits differentiating species along the reproductive strategy axis (Salguero-Gomez, 2017). We calculated these traits from the COMPADRE database using the *Rcompadre* and *Rage* R-packages (Jones et al., 2021). From the TRY database, we downloaded longevity and the three functional traits that may be a proxy to life-history: seed number per reproductive unit, seed mass and vegetative plant height. Plant height correlates with key life-history traits such as reproductive rate and longevity (Brown et al., 2004; Gaillard et al., 2005). Seed mass influences seedling survival and seed count the number of recruits (Moles et al., 2005). To improve matching with the BioTIME database, the nomenclature of the trait databases was also harmonised using the *lcvp* package (Freiberg et al., 2020).

Because woody and herbaceous plants have distinctive traits and life-history strategies, we classified species into two functional groups using data from TRY: woody plants and forbs and graminoids (Kattge et al., 2020).

Data availability on life-history traits data from the COMPADRE trait data was too low to proceed with the analysis. Only 0.01 % of the woody species and 0.03 % of forbs and graminoids matched the population data from the BioTIME database. Therefore, we only included TRY data in the following analysis since 25% of woody species and 21% of forbs and graminoids had trait data available (Appendix figure S3.1 and S3.2). To test the appropriateness of using TRY data as a proxy for life-history traits, we calculated the correlation between the TRY and COMPADRE traits (Appendix figure S3.3).

Because organisms balance their allocation to survival, development, and reproduction with the availability of resources, traits are fundamentally correlated (Diaz et al., 2016). Therefore, we performed a principal component analysis (PCA) and used the first two principal components as predictors in the following analysis. We calculated the mean trait value per species and log-transformed and scaled trait data before running the PCA.

5.2.4 Population trend analysis

We tested the effect of trait, human use and climate change on population change using a two-step analysis. First, we estimated the abundance trend of every population time series. Population data was square-rooted and scaled to reduce variance and allow comparison between different estimates of abundance and growth forms (Dornelas et al., 2019). Leading and lagging zeros were removed, so the trend was only fitted over the time the species was observed. We fitted ordinary least squares regression to the population time series, with year as the sole predictor, to estimate long-term trends in population abundance. The slope and the standard error were carried through to the following analysis.

We used the *brms* R package to test the effect of life-history traits, human use and climate change on the estimated population slopes following the approach of Antao et al. (2020) (Antão, 2020; Bürkner, 2017). The benefit of this approach is that it considers the uncertainty in the estimated slopes of population abundance. Specifically, in the *brms* package, the function se() can be used to specify known standard errors to observations, in this case the standard errors of the population slopes. We assumed that the population trends followed a student's t-distributed likelihood and used normally distributed, vague priors for the predictors and intercept. The model structure was defined as follows:

$$\begin{aligned}\Delta Abundance \sim\ & PC1 + PC2 + climate\ change + human\ use + growth\ form \\ & + PC1{:}\ climate\ change + PC1{:}\ human\ use + PC2{:}\ climate\ change \\ & + PC2{:}\ human\ use + (1|study)\end{aligned}$$

Where $\Delta Abundance$ is the population slope estimated by the ordinary least squares regression and 1|study the random effect for study. The colons ":" indicate the interaction terms between the principal components and human impact variables from Bowler et al. (2020). Chain convergence was checked by inspecting trace plots and using R-hat values.

5.2.5 Contribution to turnover analysis

We use the turnover measure developed by Shimadzu et al. (2015) to test if species with specific traits contribute disproportionately to species turnover. This measure, called D, is designed specifically to quantify temporal turnover. The turnover measure D is population based, not based on dissimilarity measures like commonly used turnover metrics such as the Jaccard index or the Bray-Curtis metric (Magurran & McGill, 2010). Community-level changes are modelled as the cumulative consequence of abundance changes of the species within a community. In other words, the turnover of a whole community is the additive of the "turnover", i.e. the abundance change, of each species in the community (Shimadzu et al., 2015). D is comprised of D_1, the part of turnover due to changes in species composition, and D_2, the total abundance change (Figure 5.2). D_1 is defined as the sum of logarithmic change rates of the species in the community weighted by their initial abundance. So that D_1 from the beginning *t* to the end of the time series *u* is

$$D_1(t{:}u) = -\sum_{i=1}^{s} log\left(\frac{p_i(t)}{p_i(u)}\right) p_i(t)$$

Where p_i is the relative abundance of species *i*. D_2 is described as the logarithmic change in the total abundance of the community

$$D_2(t{:}u) = log\left(\frac{\lambda(\mathrm{u})}{\lambda(\mathrm{t})}\right)$$

Where λ is the total abundance of the community. Finally, total turnover D is defined as the sum of D_1 and D_2

$$D(t{:}u) = D_1(t{:}u) + D_2(t{:}u)$$

Contribution to turnover (*r*) of species *i* is the absolute turnover of the species (d_i) divided by the absolute total turnover of the community so

$$r_i(t{:}u) = \frac{|d_i(t{:}u)|}{\sum_{i=1}^{s} |d_i(t{:}u)|}$$

We used the same ordinary least square models that we defined for the population change models for the calculation of the expected species abundances at the beginning (*t*) and the end of the time series (*u*).

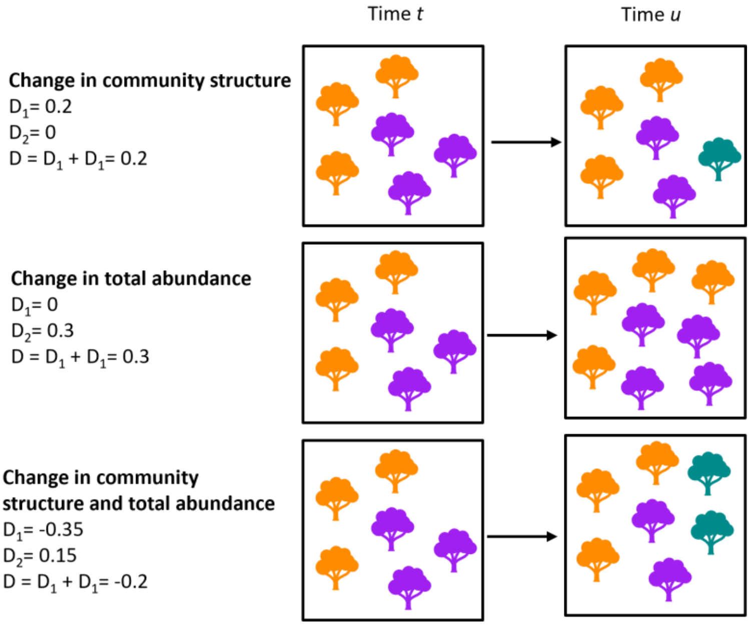

Figure 5.2 Three scenarios in which the two components of D might change. 1) change in community structure, between and u a new species enters the community, in this scenario only D1 will change. 2) Change in total abundance, between t and u both species increase in abundance, but their relative abundance does not change, in this scenario only D2 changes. 3) Change in community structure and total abundance, in this scenario both D1 and D2 will change.

To test if life-history traits, human use and climate change affect species' contribution to turnover, we followed a similar model structure as defined for the population-level analysis:

$$\begin{aligned} Contribution\ to\ turnover \sim PC1 + PC2 + \ climate\ change + human\ use + growth\ form \\ + PC1{:}\, climate\ change + PC1{:}\, human\ use + PC2{:}\, climate\ change \\ + PC2{:}\, human\ use + (1|study) \end{aligned}$$

Where 1|study is the study-level random effect. The colons ":" indicate the interaction terms between the principal components and human impact variables. Because contribution to turnover is a proportion, and thus bounded between 0 and 1, we used a beta-distributed likelihood. The model was fitted using the *brms* package (Bürkner, 2017). Chain convergence was checked by inspecting trace plots and using R-hat values.

Species' contribution to turnover does not only depend on the population trend, but also on the context of the community. Even though a population remains stable over time in absolute terms, its contribution to turnover might change because of changes in the community, consequently changes in species relative abundance. To understand how characteristics of the population and the context of the community and affect species' contribution to turnover, we performed a simulation study. We tested for the influence of four factors, population trend, dominance, species richness and community evenness. We used the code from Avolio et al. (2019) to simulate communities with three levels of species richness and three levels of evenness, thus having nine scenarios in total. For each of the nine scenarios we simulated a hundred communities. Then, we calculated contribution to turnover using this simulated abundance data.

5.3 Results

5.3.1 Principal component analysis

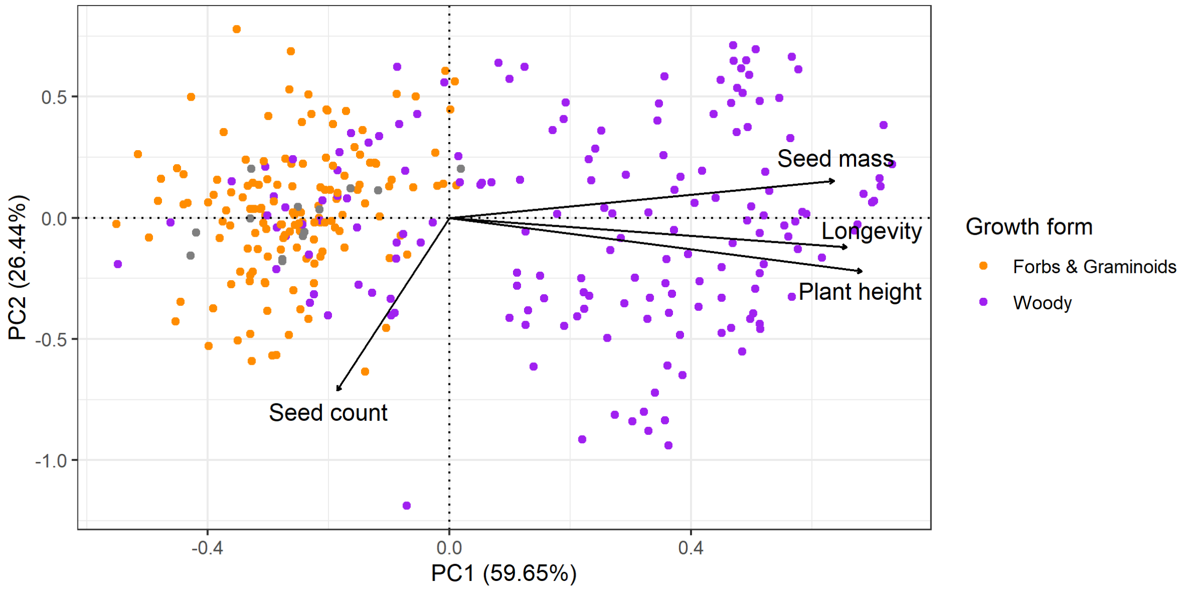

Figure 5.3 PCA of life history traits. Different colours, orange for forbs and graminoids and purple for woody plants indicate growth forms.

86% of the variation in life-history is explained by the first two axes of the PCA (Table 5.2, Figure 5.3) The first principal component (59.65%) describes the variation in longevity, plant height and seed mass. Higher scores on this axis correspond to tall, long-living species with big seeds, at this end most woody species are found. On the other end of the first principal component, all herbaceous species and some woody species are situated. The second principal component expresses differences between species in seed count, with more negative scores corresponding to higher seed count.

Table 5.2 Loadings of the traits on the principal components.

Trait	**PC1**	**PC2**	**PC3**
Longevity	2.63	-0.48	1.23
Plant height	2.73	-0.88	-0.02
Seed count	-0.74	-2.85	-0.50
Seed mass	2.55	0.61	-1.39
Proportion of variance explained (%)	59.65	26.44	10.30

5.3.2 Population changes

Of the 4455 populations in the data set, we found 969 (21.8%) were significantly decreasing, 496 significantly increasing (11.1%) and 2990 (67.1%) without a significant change in abundance. A high number of populations are situated in areas of high climate change and human use intensity. Also at relatively low climate change but intermediate to high human use, there is an increased number of populations. Few sites are in areas of low climate change impact and low human use (Figure 5.4).

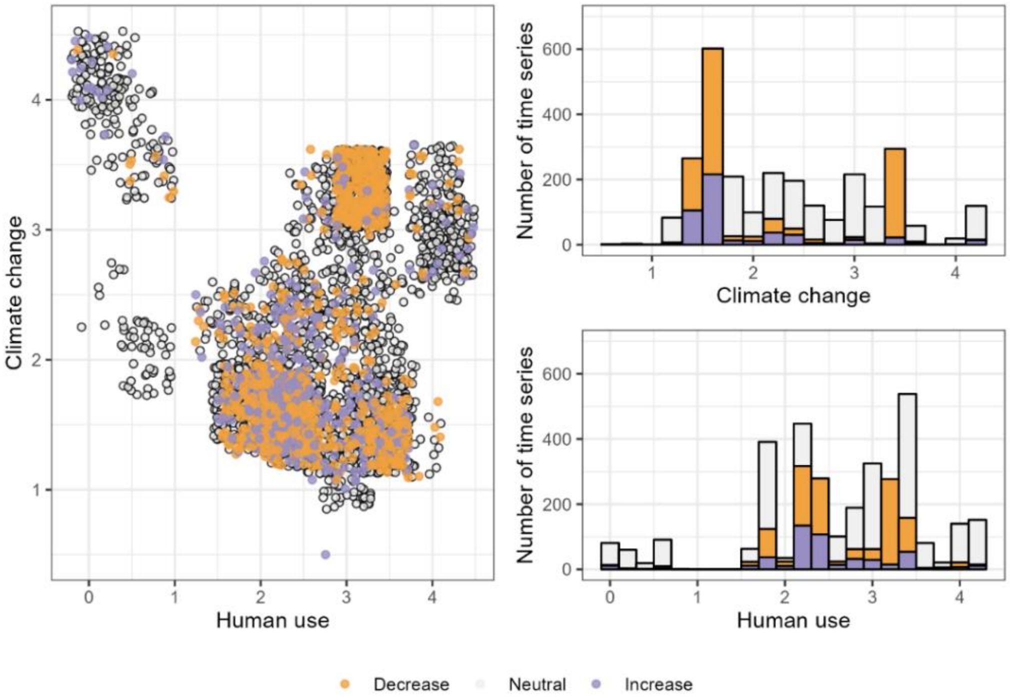

Figure 5.4 Representation of the population trends along the two global change drivers of (Bowler et al., 2020). Random jitter was added to the scatter plot to increase the visibility of points. Colours indicate if the estimated slopes are significantly positive (purple, slope positive, $p < 0.05$), significantly negative (orange, slope negative, $p < 0.05$) or neutral ($p > 0.05$)

None of the predictor variables included in this study could explain population changes, as all 95% credibility intervals cross zero (Figure 5.5, Appendix figure S6.3). Thus, we demonstrate no systematic population change of species with particular traits here. We also do not find consistent population changes with increased climate change intensity or human use.

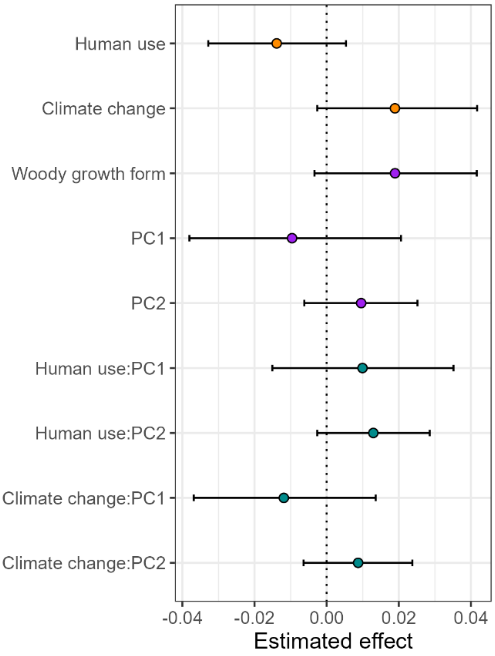

Figure 5.5 Effect of life-history traits (purple), human use and climate change intensity (orange) and their interaction (cyan) on population change. Whisker plots show the mean estimated slope and the 95% credibility interval. Complete model outputs and marginal effect plots are presented in Appendix S6.

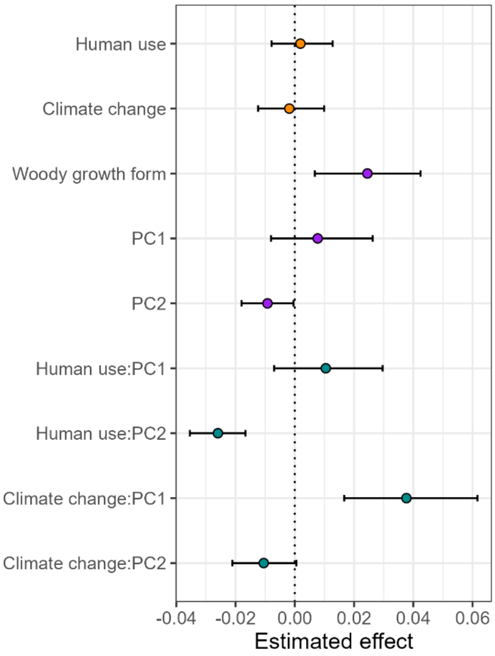

Figure 5.6 Effect of life-history traits (purple), human use and climate change intensity (orange) and their interaction (cyan) on contribution to turnover. Whisker plots show the mean estimated slope and the 95% credibility interval. Complete model outputs and marginal effect plots are presented in Appendix S6.

5.3.3 Contribution to turnover

The simulation study we performed shows that the abundance of species and the evenness of community affect the contribution to turnover metric. Contribution to turnover increases with the initial abundance of species. A greater range of contribution to turnover values can be attained in uneven communities. Species richness has a minor effect on contribution to turnover (Appendix figure S5.2). Population trends affect contribution to turnover too, species with great population change generally get higher contribution to turnover values (Appendix figure S5.3).

Turnover contribution is low for most species with available trait data (median 0.006) but relatively high for some (third quantile 0.04). Woody species contribute, on average, 2.5% more to turnover than forbs and graminoids (estimated effect 0.025, 95% credibility interval; [0.007,0.042]). Life-history traits are predictors of contribution to turnover, but these effects are conditional on the degree of human use and climate change intensity (Figure 5.6, Appendix figure S6.4). We find a significant positive interaction between PC1 and climate change intensity (estimated effect 0.038, 95% credibility interval; [0.017, 0.062]). This means tall and long-living species contribute more to turnover when conditions are warmer and drier (Table 5.1, Table 5.2). We find a small but significant effect of PC2 (estimated effect -0.009, 95% credibility interval; [-0.018,-0.0004]) and a significant negative interaction effect between human use and PC2 (estimated effect -0.026, 95% credibility interval; [-0.035, -0.017]). This indicates turnover can be attributed to species with high seed numbers, especially when there is more land cover change (Table 5.1, Table 5.2).

5.4 Discussion

To mitigate biodiversity changes, it is essential to understand the ways species and communities respond to anthropogenic impact. Life history strategy is a key determinant of species' vulnerability to anthropogenic impact (Chichorro et al., 2022; Locosselli et al., 2020; Wilcox et al., 2021), and therefore potentially important in explaining population and community composition changes. This study aimed to test if life-history traits can explain population-level and community-level changes with environmental change. We find evidence of the significance of life-history strategy in explaining community-level changes in areas of human impact, but there is no indication that it influences population changes. We find that the contribution to turnover of species' life-history is context-specific. The fast-slow continuum explains species' contribution to turnover with increasing climate change impact and reproductive strategy influences contribution to turnover with increased human use.

We do not find an effect of life-history on population changes. Rather than being a predictor of long-term population change, species' life-history strategy might be more informative in predicting variability in population growth rates (Le Coeur et al., 2022; McDonald et al., 2017). Here we fitted an ordinary linear regression to the population data, so we could not pick up any variability in population size over time. Our analysis might be confounded by the choice of traits and trait data availability. Only about 25% of the populations were analysed for their traits and we only included longevity as a true life-history trait (Appendix figure S3.1 and S3.2). The three other traits, plant height, seed mass and seed number, are functional traits that not necessarily reflect species' life-history.

Although three out of four traits we analysed are functional traits, not life-history traits, the PCA does show similar trade-offs in life-history as demonstrated by Salguero-Gomez et al. (2016]). The first principal component describing species' pace-of-life and the second relates to species' reproductive strategy (Figure 5.3, Table 5.2). Previous research has shown that functional traits are related to life-history strategy (Adler et al., 2014), but that they do not match exactly (Kelly et al., 2021)(Appendix figure S3.3). For instance, plant height and seed size positively correlate in warm environments but less so in cold climates because of the high resource cost (Kelly et al., 2021). We here also show that plant height correlates with generation time in woody, but not in herbaceous plants (Appendix figure S3.3). Also, seed number might not be a good proxy for reproduction across the lifespan of an organism, as it does not encompass seedling survival, degree of iteroparity or clonal growth (Janovský & Herben, 2020; Moles & Westoby, 2004). Reproductive traits also vary within species and between years (Cochrane, 2015). More data on life-history traits is essential to allow more comprehensive global analyses of the effect of life-history traits on population changes.

Contribution to turnover is a measure of population change relative to the turnover in the community (Shimadzu et al., 2015). It cannot distinguish if populations increase, decrease or if there is a compositional change in the rest of the community. A high turnover contribution of single populations could indicate an invasive species but similarly a species-specific decline because of disease (Di Cecco & Hurlbert, 2022). In this study there does not seem to be a relationship between strong population decreases or increases and high turnover contribution, but further tests are necessary to make inferences from this (Appendix figure S5.1e).

We find significant evidence that species' turnover contribution is influenced by life-history strategy with increased human use and climate change. Because the direction of change is unknown, the exact reasons for these significant results are challenging to tease out and are just suggested here. The higher turnover contribution of tall and long-living species with increased climate change could be because of their heightened vulnerability (Chichorro et al., 2022). Increased human activity might have caused greater turnover contribution of species with high seed count because it positively impacts weedier species (Tilman & Lehman, 2001). It should be noted that the human impact data we used is spatially, but not temporally explicit, therefore it is assumed here that current human impact can be used as a proxy for past human impact.

Further analysis is needed to test what population and community trajectories lead to a high contribution to turnover under environmental change. Knowing why species may contribute disproportionately to turnover is important for mitigating the biodiversity crisis for two reasons. First, if turnover is due to single species undergoing a change rather than the whole community, ecosystem management approaches will be different (Di Cecco & Hurlbert, 2022). Second, knowing the traits and population trajectories of species that are strong contributors to turnover, could lead to a better understanding of the processes that drive biodiversity change (Gotelli et al., 2022).

5.5 References

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Appendix S1 - Duration and interval of the population time series

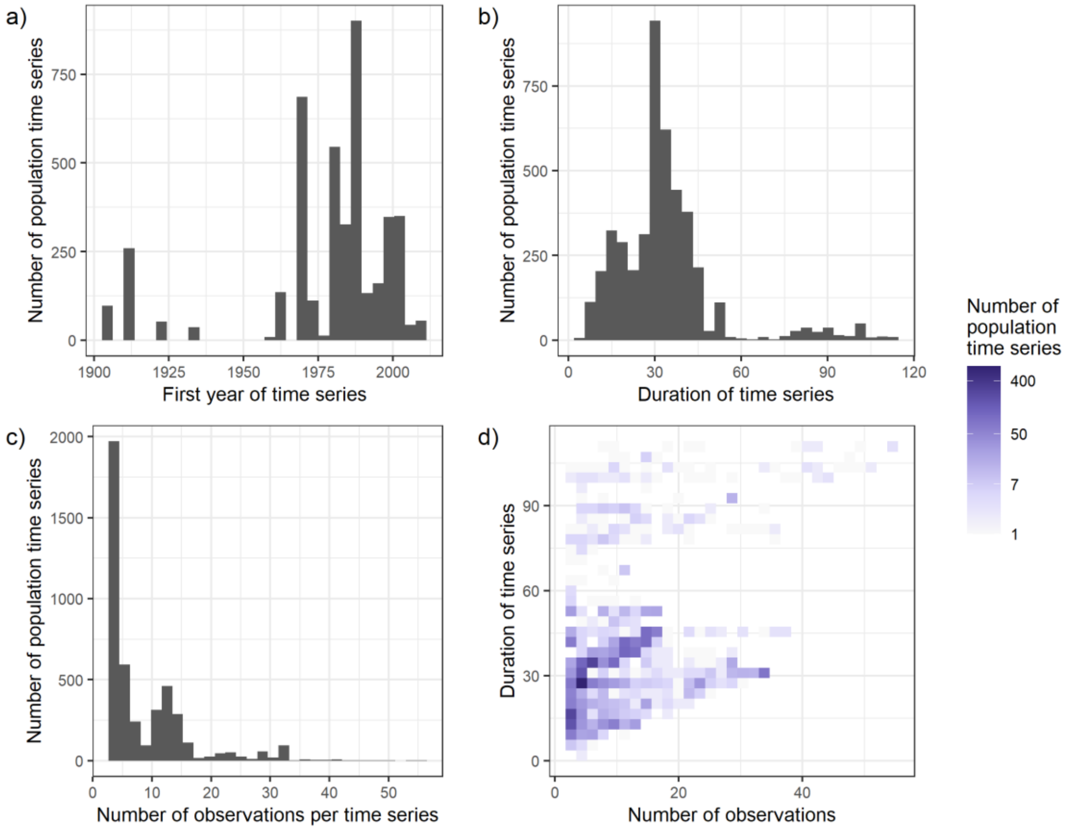

Figure S1.1 Temporal sampling of the population time series. a) First year of sampling. b) Duration of the time series. c) Number of observations per time series. d) Number of observations and duration of the time series, darker colours indicate higher number of population time series (note the log scale).

Appendix S2 - Map of study sites

Figure S2.1 Location of study sites.

Appendix S3 -Trait data coverage and trait correlations

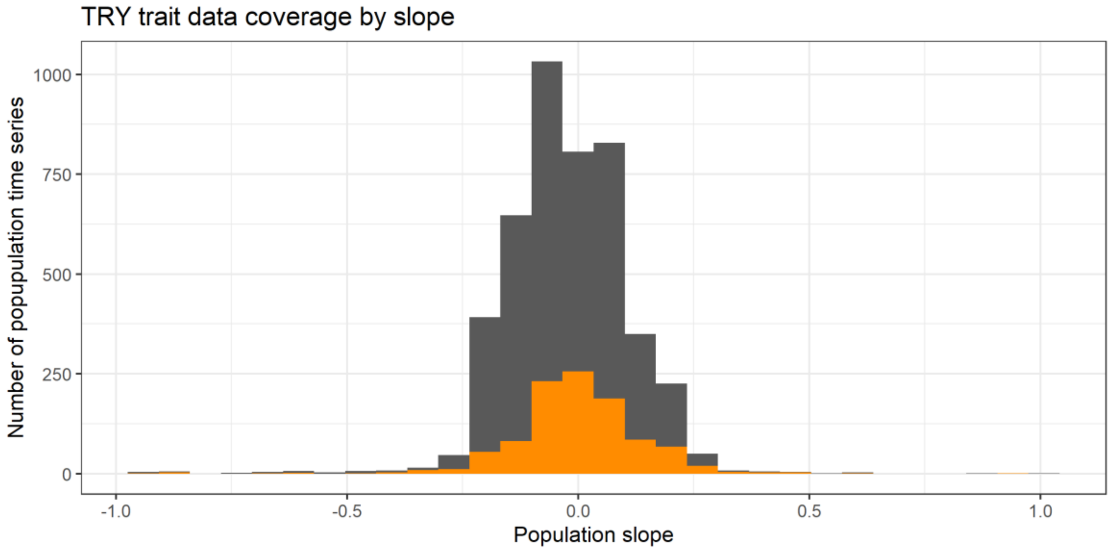

Figure S3.1 Distribution of population slopes (grey) and coverage of the TRY trait data by slope (orange).

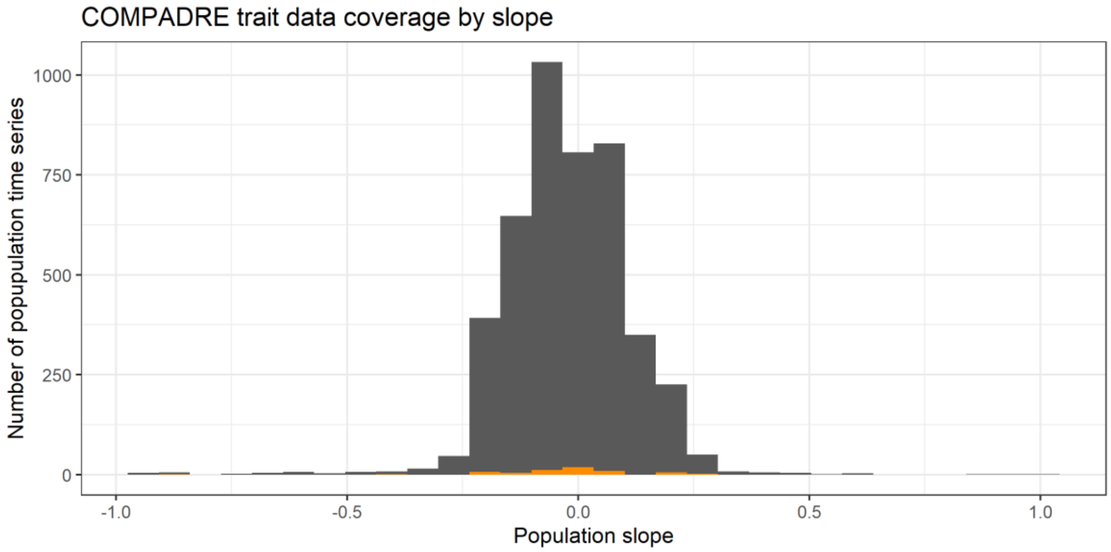

Figure S3.2 Distribution of population slopes (grey) and coverage of the COMPADRE trait data by slope (orange).

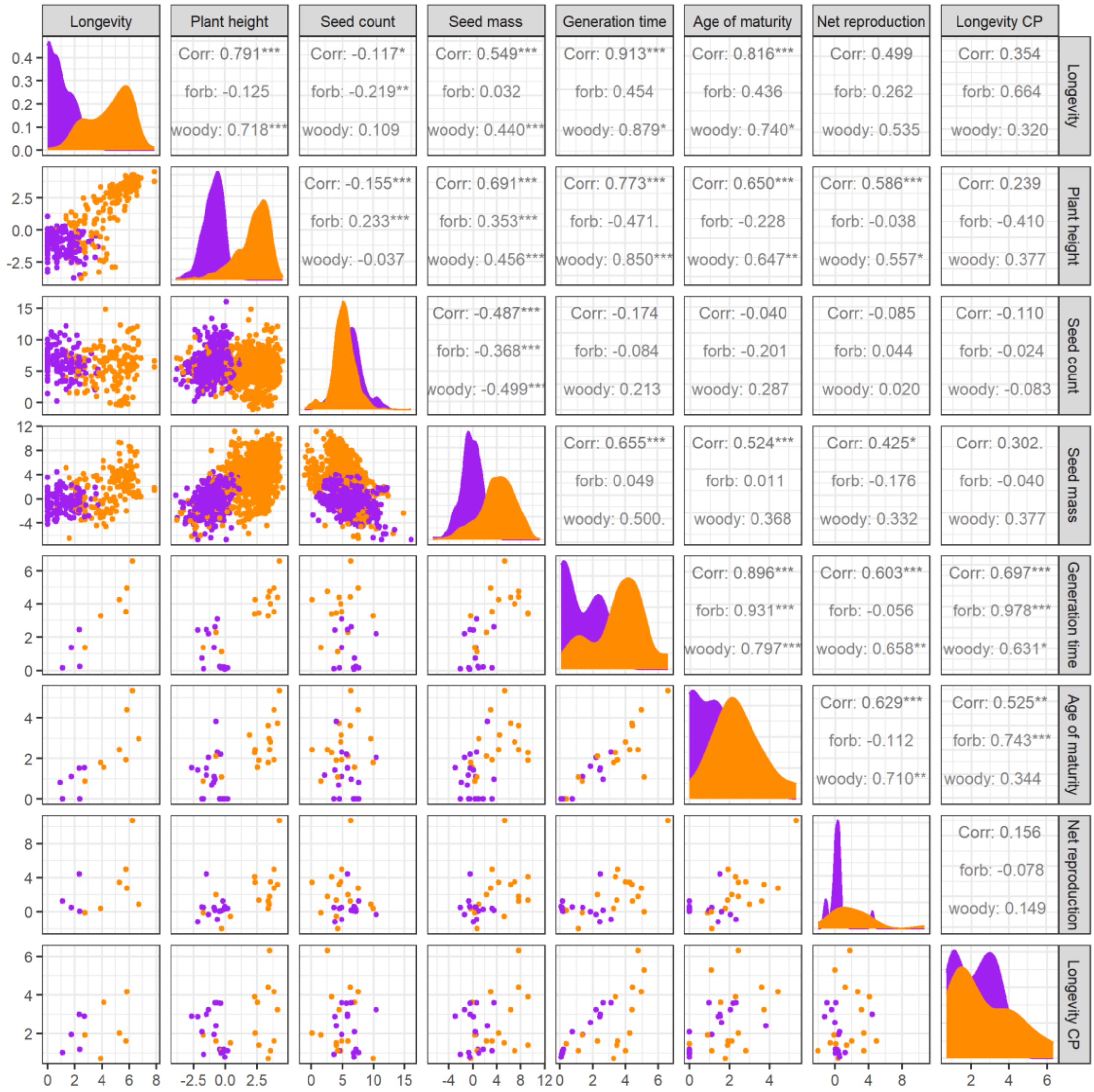

Figure S3.3 Correlations between the traits from the TRY data and COMPADRE. colour indicated the plant functional type, woody (orange) or forbs and grasses (purple).

Appendix S4 - Standard error of the estimated slope

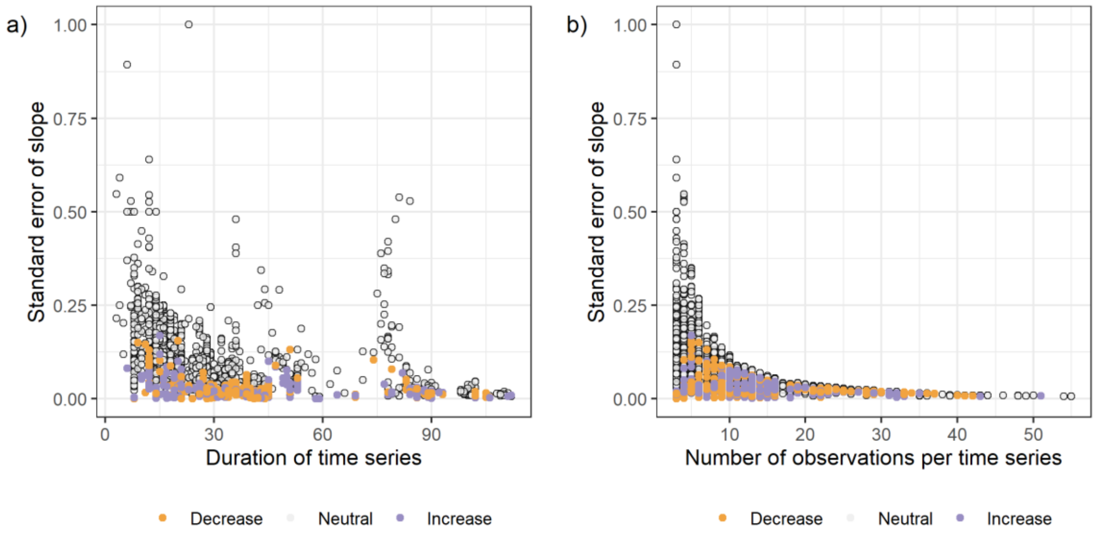

Figure S4.1 Standard error of the estimated population slopes, as a function of number of observations per time series (a) and duration of the time series (b). Colours indicate if a population significantly increases (purple), significantly decreases (orange) or does not change significantly ($p > 0.05$, grey).

Appendix S5 - Contribution to turnover

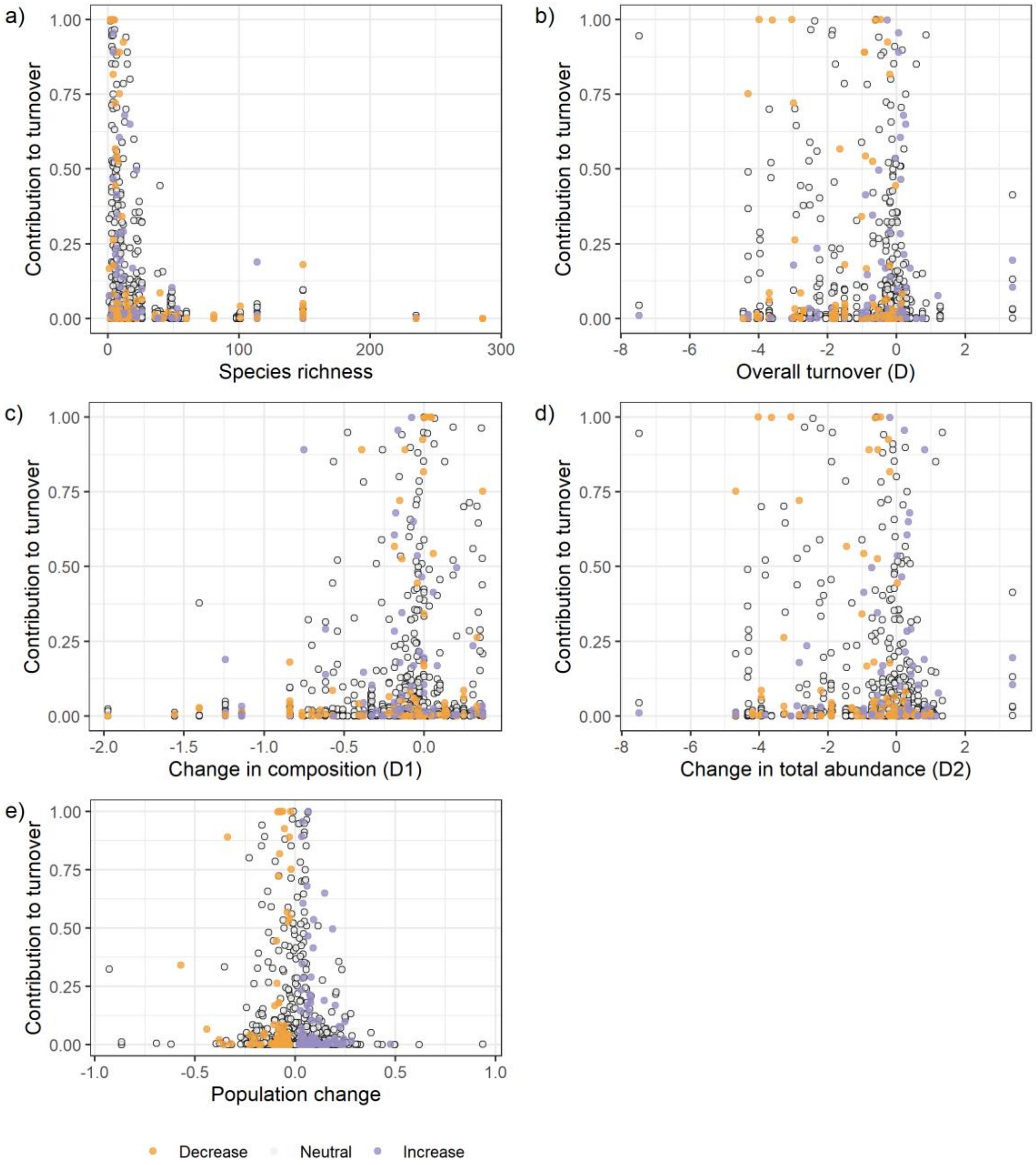

Figure S5.1 Contribution to turnover as a function of: species richness (a), overall turnover (b), change in composition (c), total abundance change (d) and population slope (e). Only species with trait data are plotted. Colours indicate if a population significantly increases (purple), significantly decreases (orange) or does not change significantly ($p > 0.05$, grey).

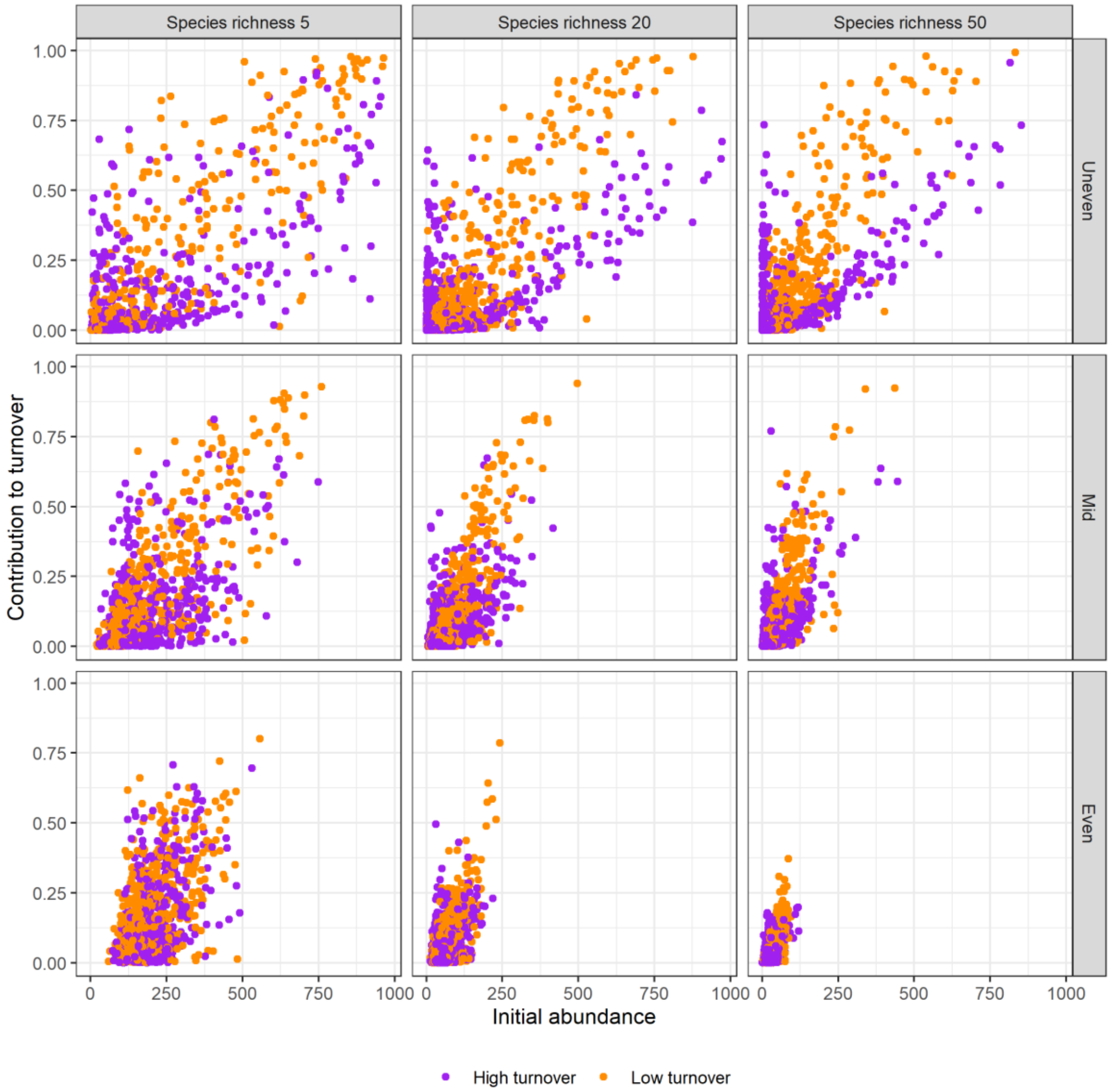

Figure S5.2 Effect of species abundance at the start of a time series on contribution to turnover in 100 simulated communities with different species richness and evenness. The total number of individuals is held constant at 1000 individuals. Code for simulating communities comes from Avolio et al. (2019).

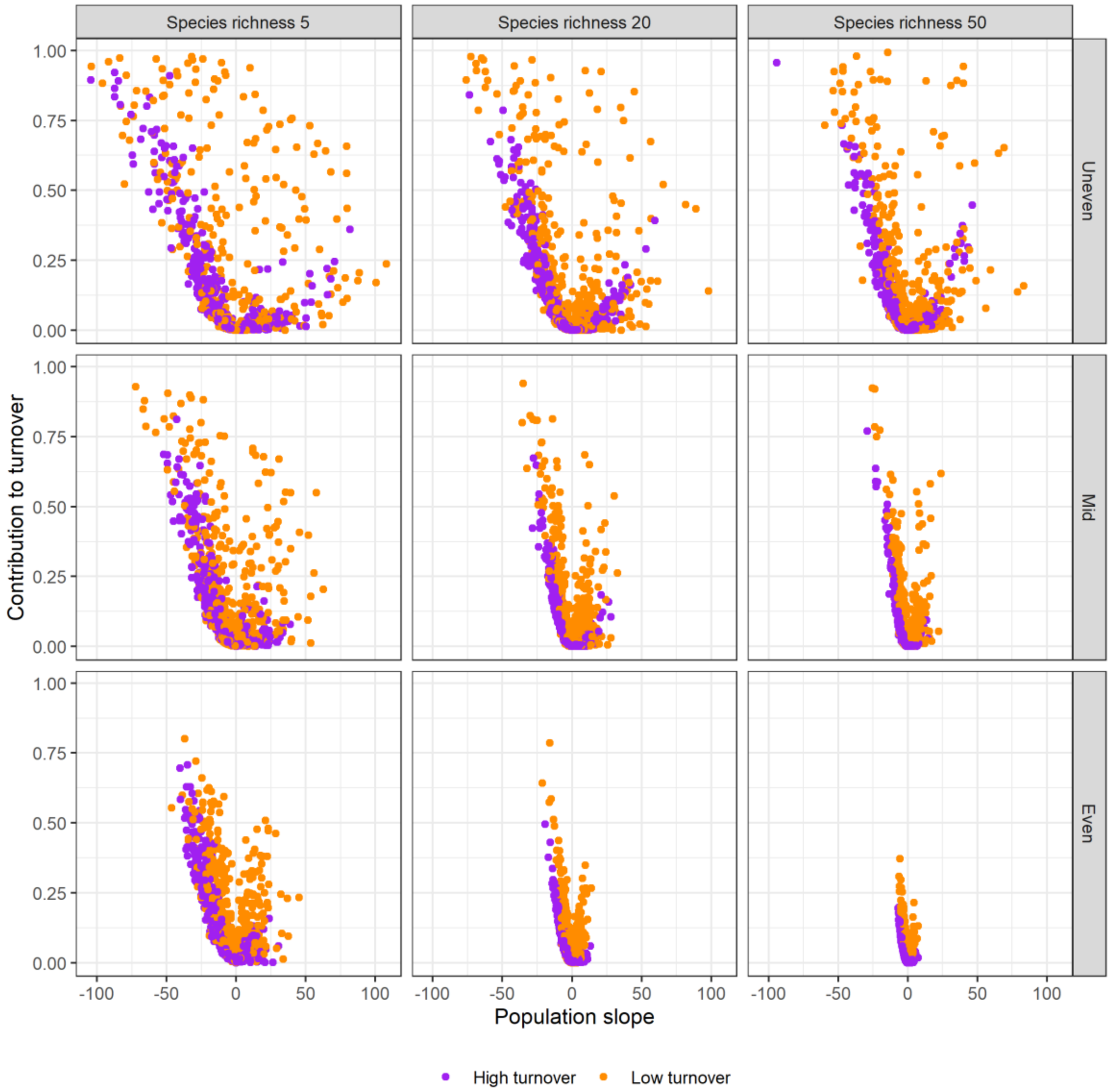

Figure S5.3 Effect of population slope on contribution to turnover in 100 simulated communities with different species richness and evenness. The total number of individuals is held constant at 1000 individuals. Code for simulating communities comes from Avolio et al. (2019).

Appendix S6 - Model outputs

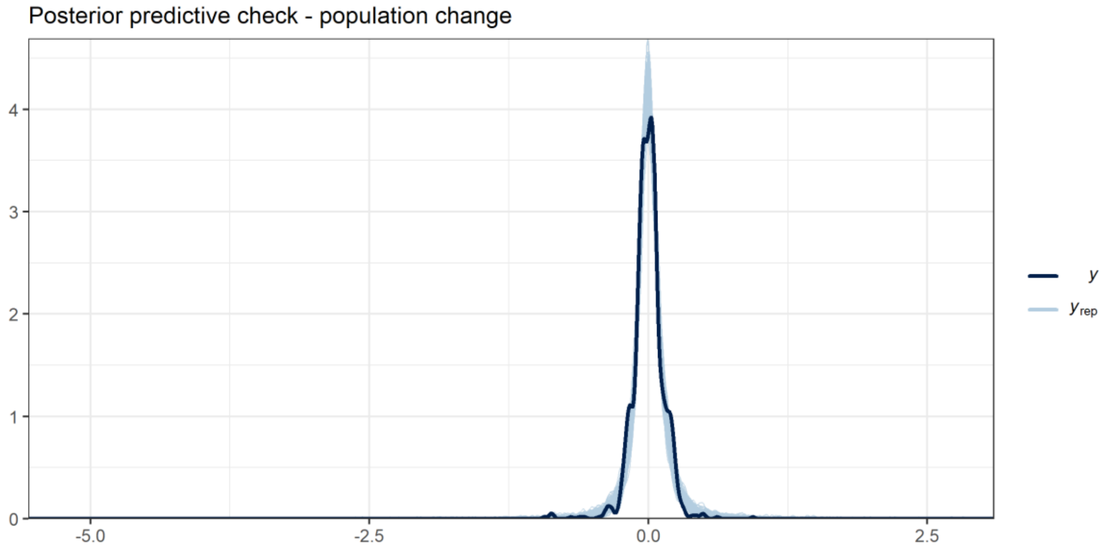

Figure S6.1 Posterior predictive check for the population change model. Light blue lines present random draws from the posterior, dark blue line is the original data.

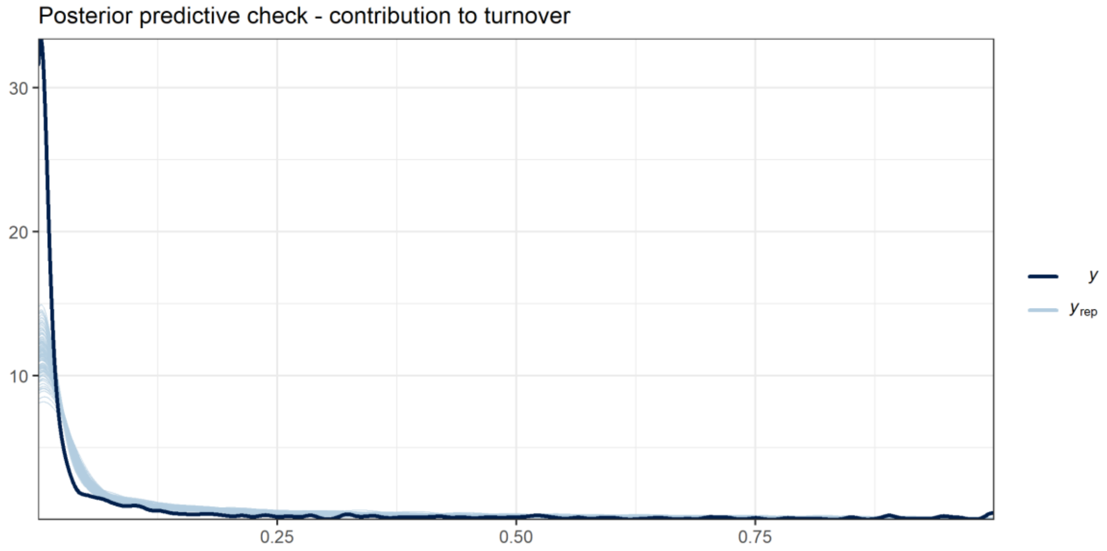

Figure S6.2 Posterior predictive check for the contribution to turnover model. Light blue lines present random draws from the posterior, dark blue line is the original data.

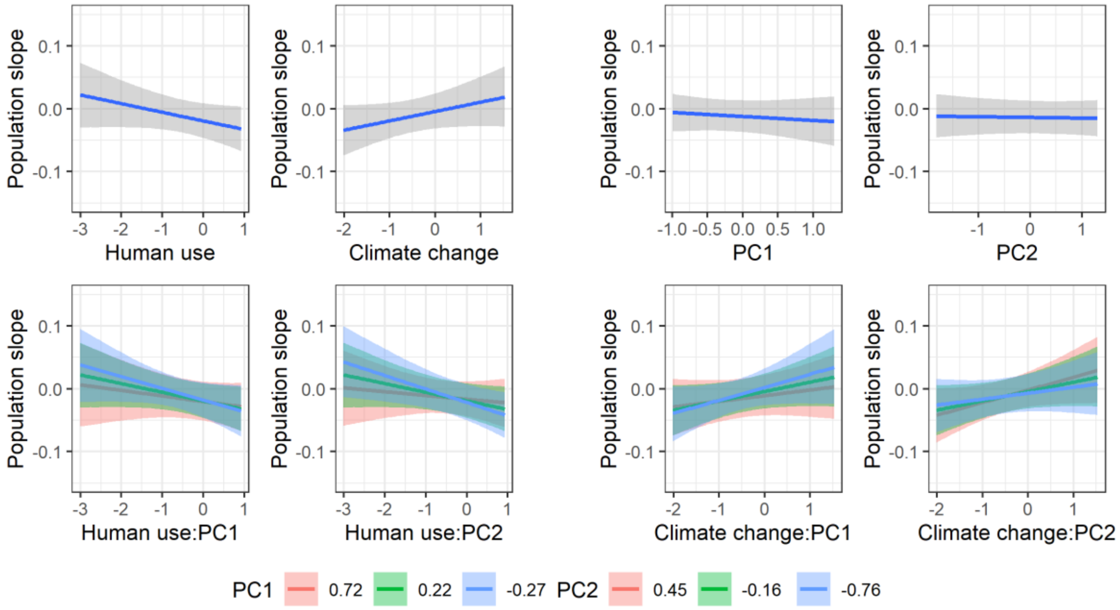

Figure S6.3 Marginal effect plots of the population change model.

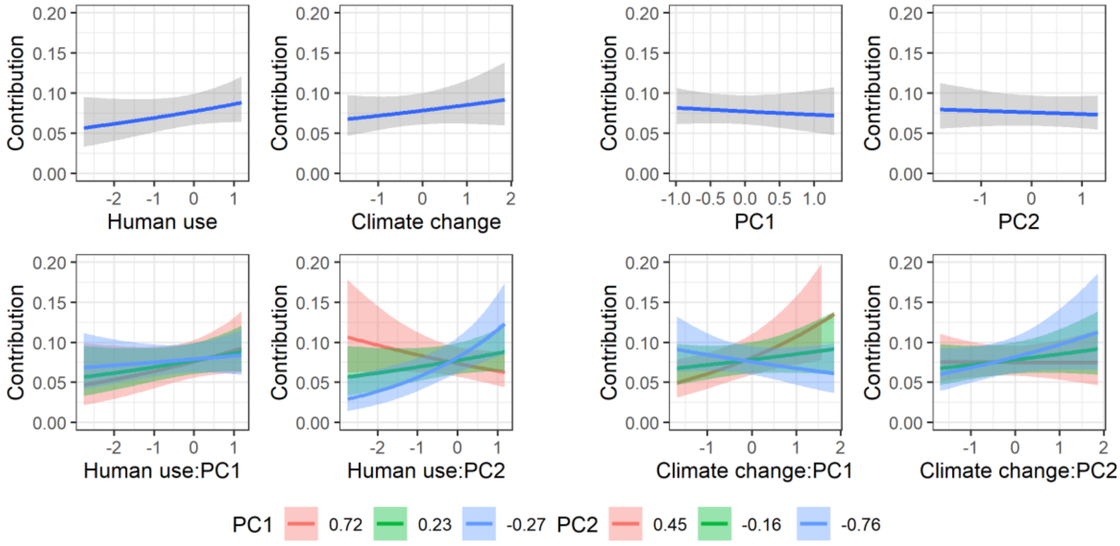

Figure S6.4 Marginal effect plots of the contribution to turnover model.

Table S6.1 Output for population change model, including all estimated parameters. Sigma is the scale parameter of the student’s t-distribution and nu the degrees of freedom.

Term	Estimate	Estimated Error	Q2.5	Q97.5
Intercept	-0.006	0.016	-0.037	0.026
Human use	-0.014	0.010	-0.033	0.005
Climate change	0.019	0.011	-0.003	0.042
PC1	-0.010	0.015	-0.038	0.021
PC2	0.010	0.008	-0.006	0.025
Growth form-woody	0.019	0.012	-0.003	0.042
Human use:PC1	0.010	0.013	-0.015	0.035
Human use:PC2	-0.012	0.013	-0.037	0.014
Climate change:PC1	0.013	0.008	-0.003	0.029
Climate change:PC2	0.009	0.008	-0.006	0.024
Random effect study	0.062	0.010	0.044	0.083
Sigma	0.048	0.003	0.041	0.054
Nu	5.050	0.803	3.747	6.895

Table S6.2 Output for contribution to turnover model. Values are on the logit scale. Phi is the precision parameter of the beta distribution.

Term	Estimate	Estimated Error	Q2.5	Q97.5
Intercept	-2.492	0.130	-2.748	-2.236
Human use	0.021	0.086	-0.152	0.186
Climate change	-0.033	0.099	-0.230	0.160
PC1	0.096	0.132	-0.160	0.358
PC2	-0.140	0.082	-0.300	0.020
Growth form-woody	0.305	0.135	0.041	0.569
Human use:PC1	0.133	0.142	-0.143	0.411
Human use:PC2	0.436	0.137	0.170	0.703
Climate change:PC1	-0.446	0.106	-0.651	-0.235
Climate change:PC2	-0.163	0.103	-0.367	0.041
Random effect study	0.446	0.072	0.318	0.603
Phi	1.437	0.086	1.276	1.613

References

Avolio, M. L., Carroll, I. T., Collins, S. L., Houseman, G. R., Hallett, L. M., Isbell, F., Koerner, S. E., Komatsu, K. J., Smith, M. D. & Wilcox, K. R. (2019). A comprehensive approach to analyzing community dynamics using rank abundance curves. Ecosphere, 10(10). https://doi.org/10.1002/ecs2.2881

Appendix S1 - Duration and interval of the population time series

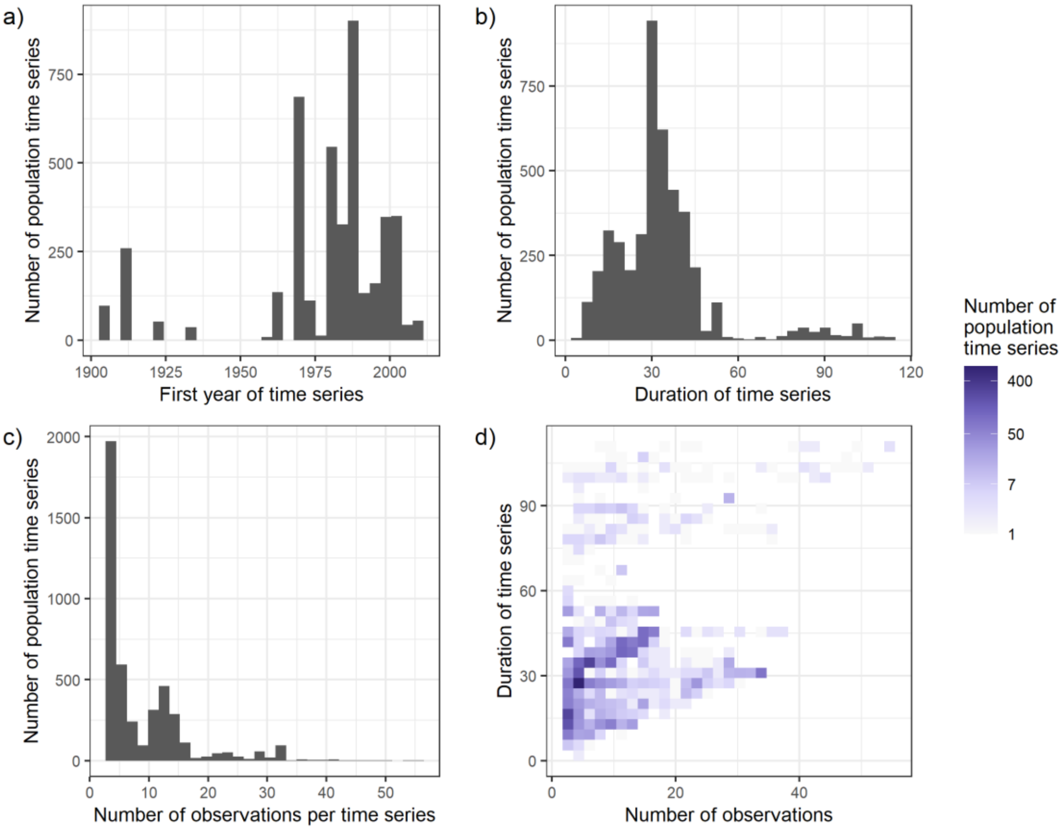

Figure S1.1 Temporal sampling of the population time series. a) First year of sampling. b) Duration of the time series. c) Number of observations per time series. d) Number of observations and duration of the time series, darker colours indicate higher number of population time series (note the log scale).

Appendix S2 - Map of study sites

Figure S2.1 Location of study sites.

Appendix S3 -Trait data coverage and trait correlations

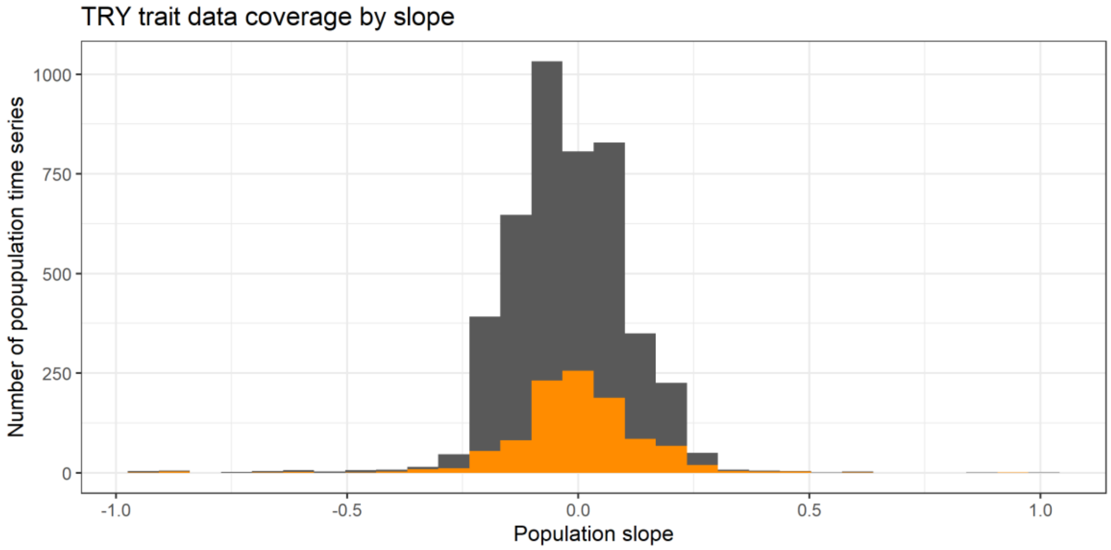

Figure S3.1 Distribution of population slopes (grey) and coverage of the TRY trait data by slope (orange).

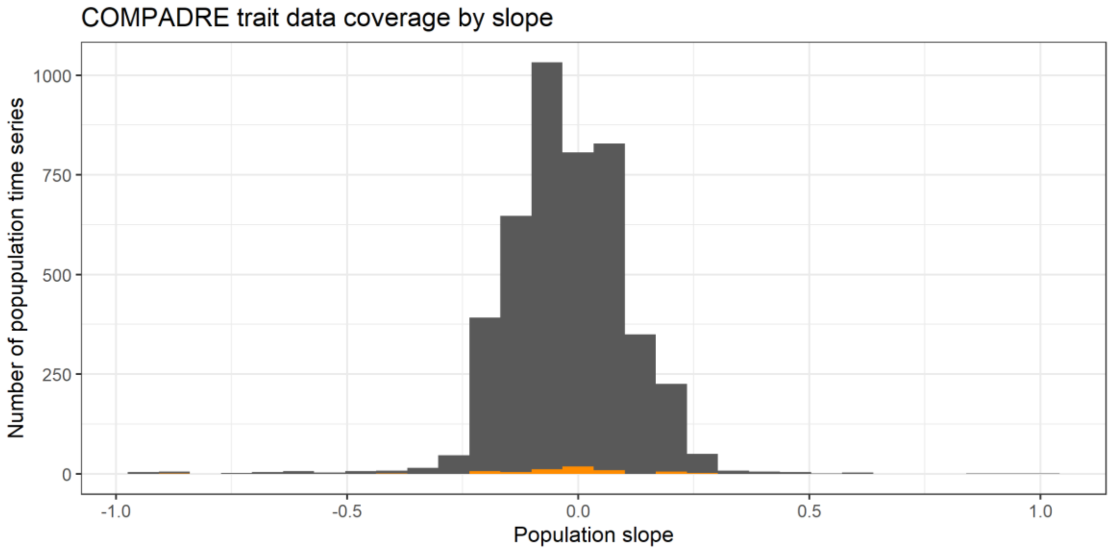

Figure S3.2 Distribution of population slopes (grey) and coverage of the COMPADRE trait data by slope (orange).

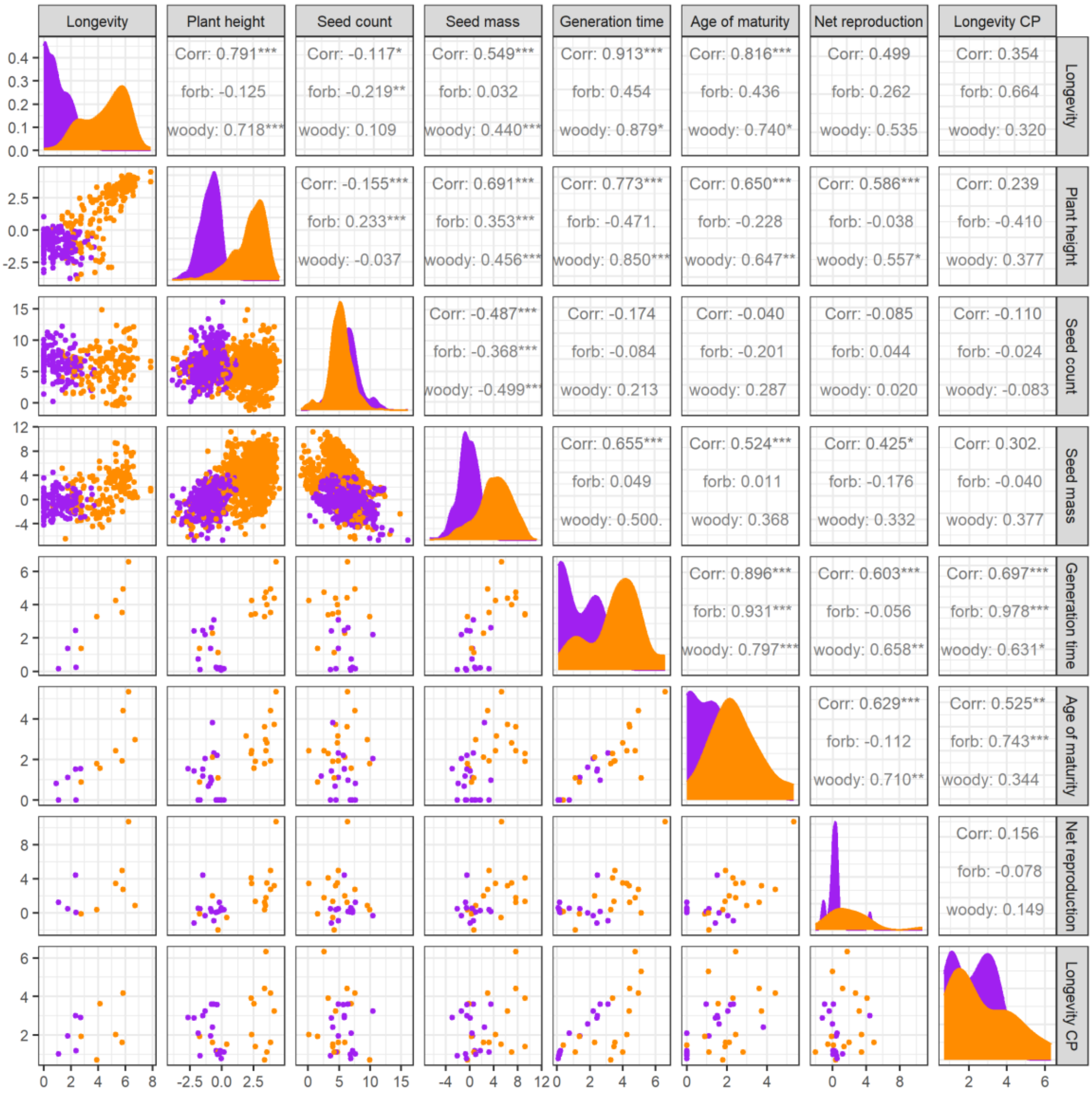

Figure S3.3 Correlations between the traits from the TRY data and COMPADRE. colour indicated the plant functional type, woody (orange) or forbs and grasses (purple).

Appendix S4 - Standard error of the estimated slope

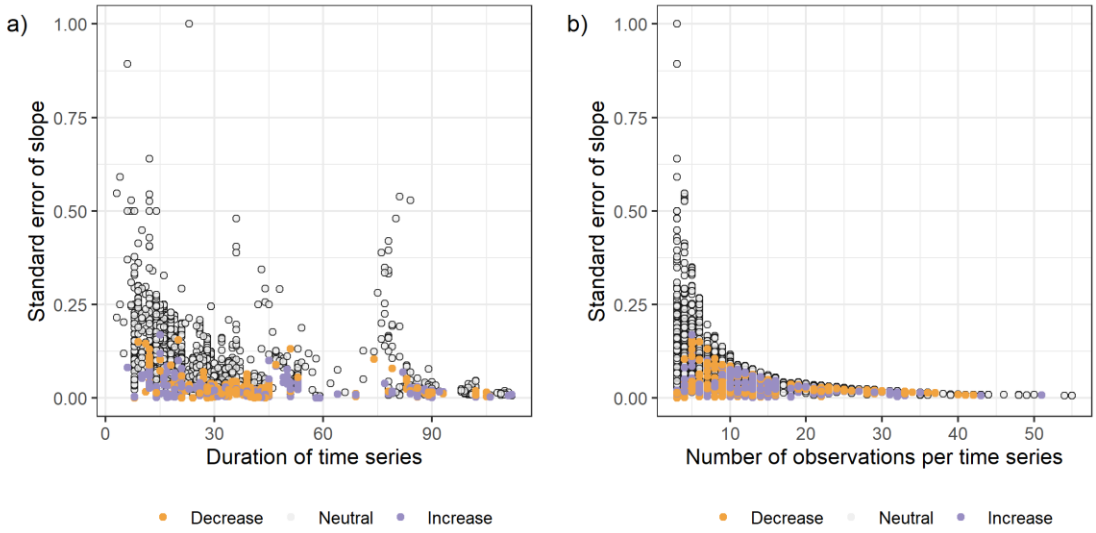

Figure S4.1 Standard error of the estimated population slopes, as a function of number of observations per time series (a) and duration of the time series (b). Colours indicate if a population significantly increases (purple), significantly decreases (orange) or does not change significantly ($p > 0.05$, grey).

Appendix S5 - Contribution to turnover

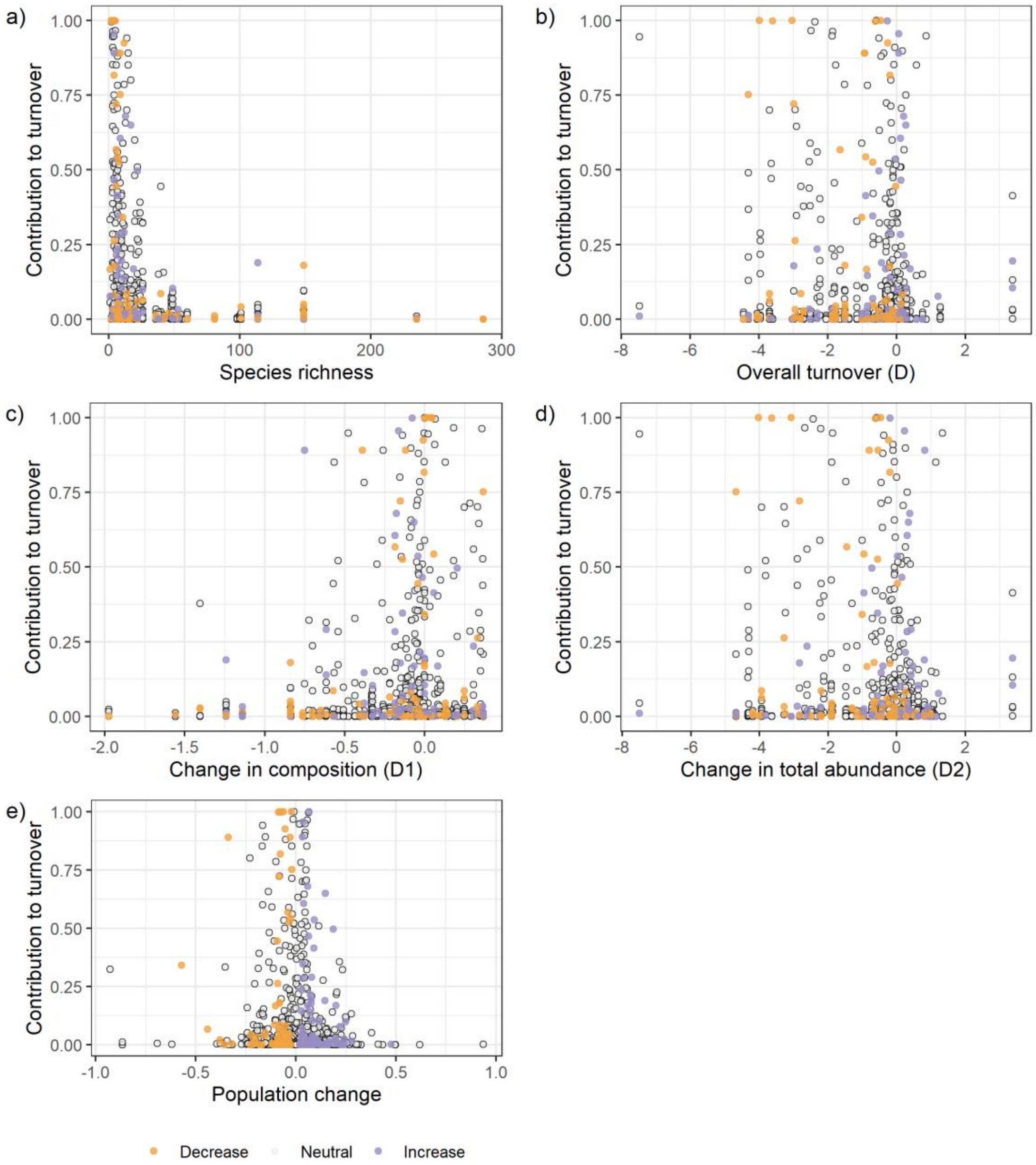

Figure S5.1 Contribution to turnover as a function of: species richness (a), overall turnover (b), change in composition (c), total abundance change (d) and population slope (e). Only species with trait data are plotted. Colours indicate if a population significantly increases (purple), significantly decreases (orange) or does not change significantly ($p > 0.05$, grey).

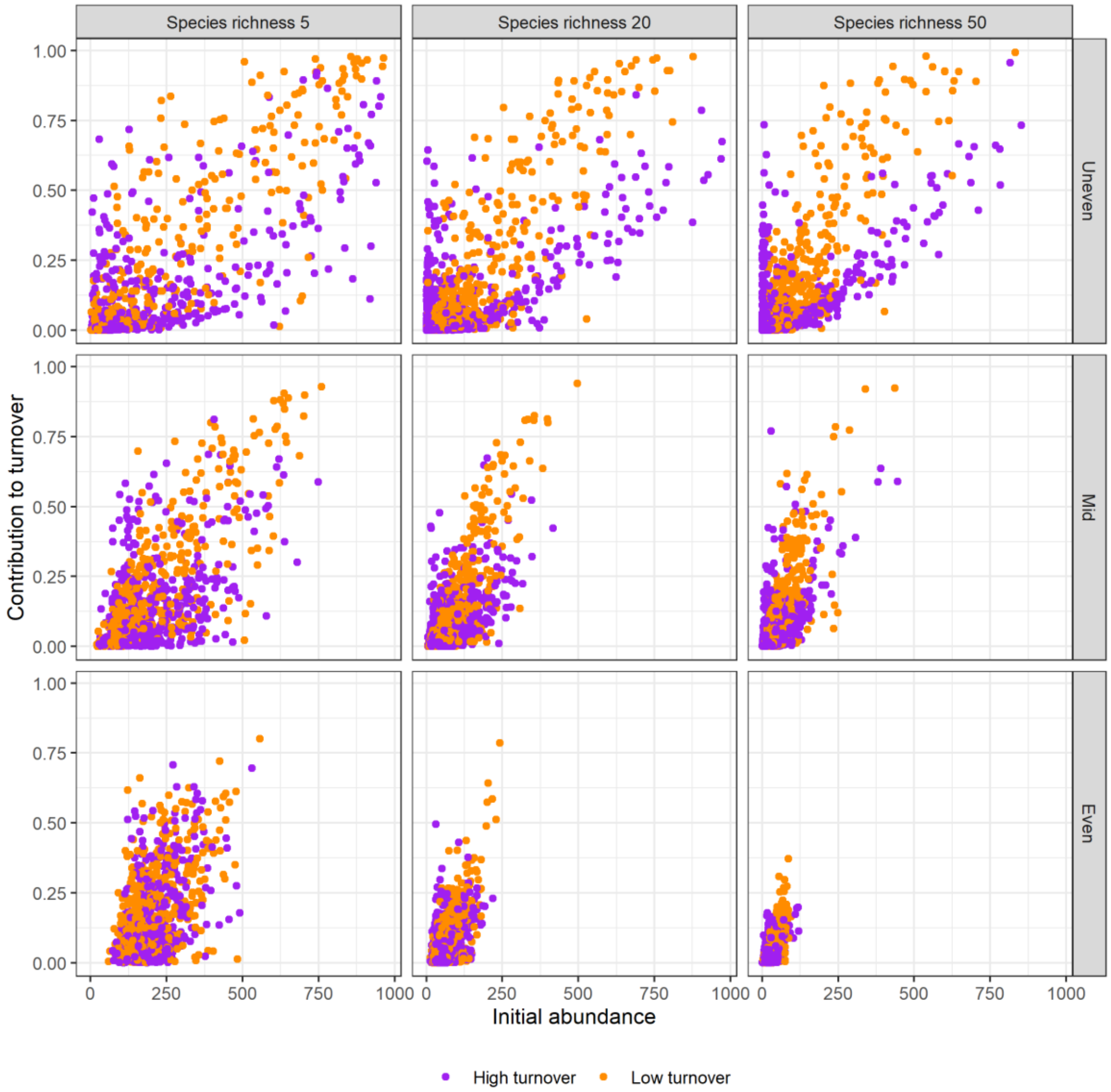

Figure S5.2 Effect of species abundance at the start of a time series on contribution to turnover in 100 simulated communities with different species richness and evenness. The total number of individuals is held constant at 1000 individuals. Code for simulating communities comes from Avolio et al. (2019).

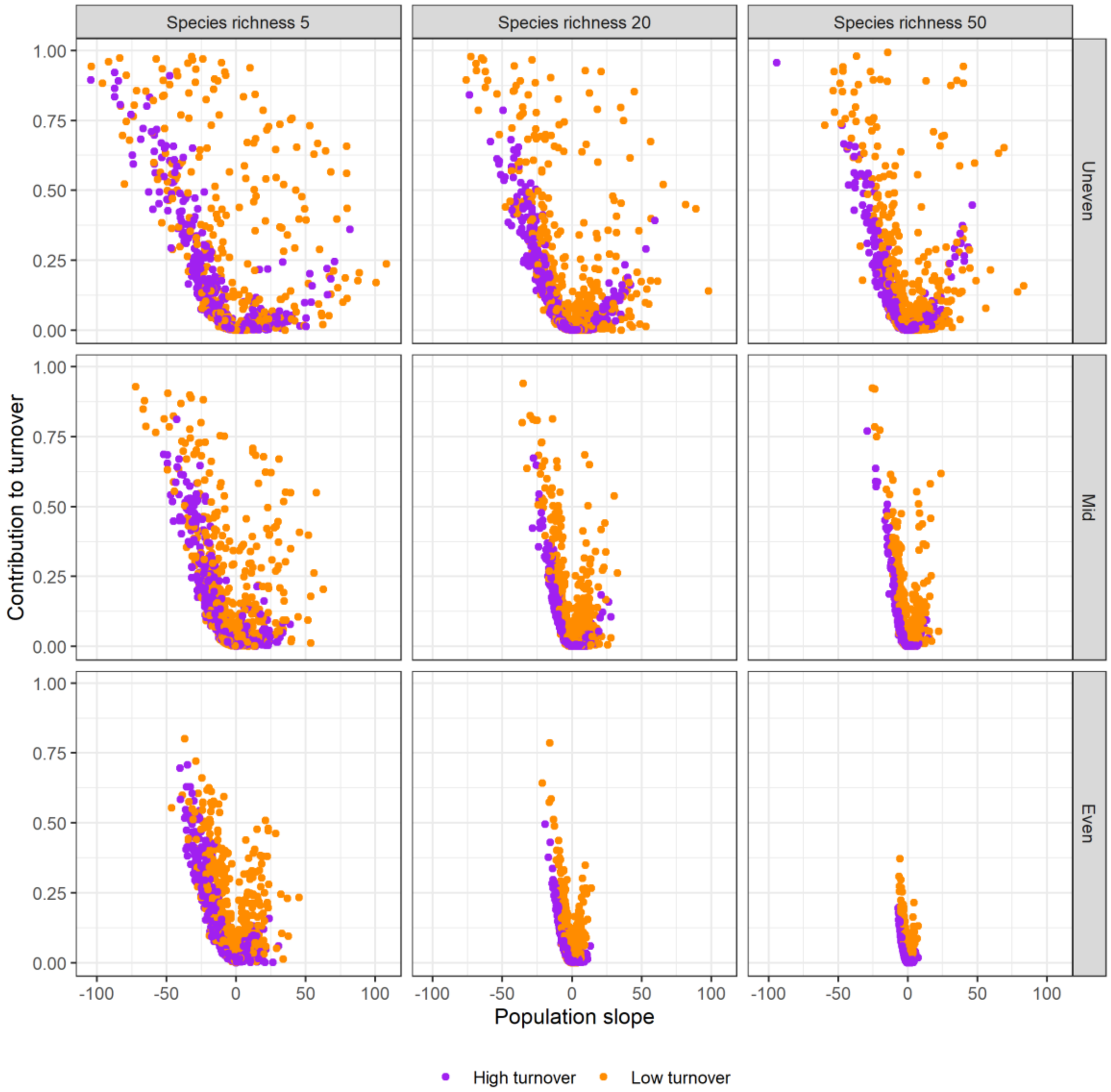

Figure S5.3 Effect of population slope on contribution to turnover in 100 simulated communities with different species richness and evenness. The total number of individuals is held constant at 1000 individuals. Code for simulating communities comes from Avolio et al. (2019).

Appendix S6 - Model outputs

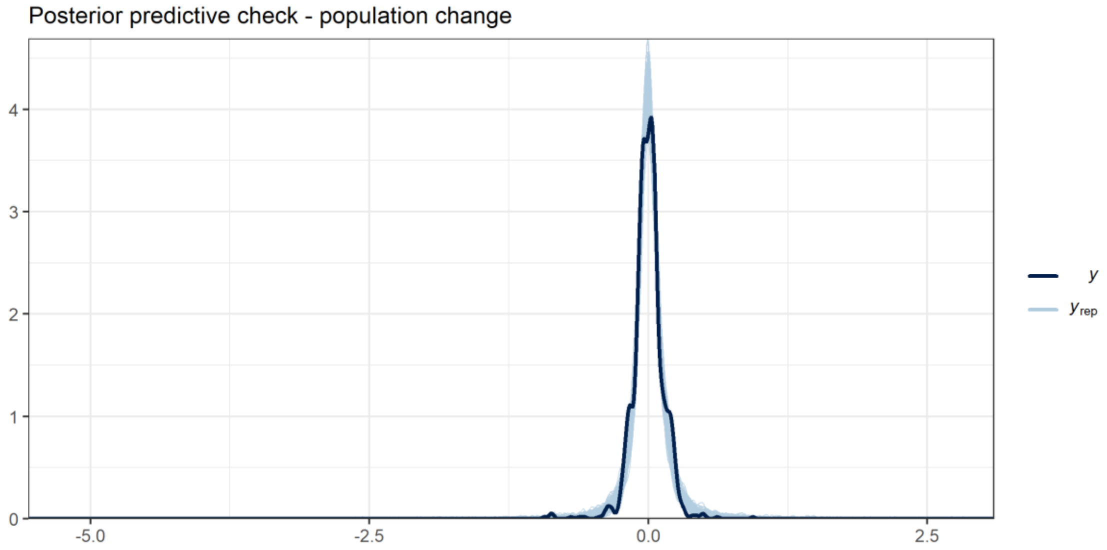

Figure S6.1 Posterior predictive check for the population change model. Light blue lines present random draws from the posterior, dark blue line is the original data.

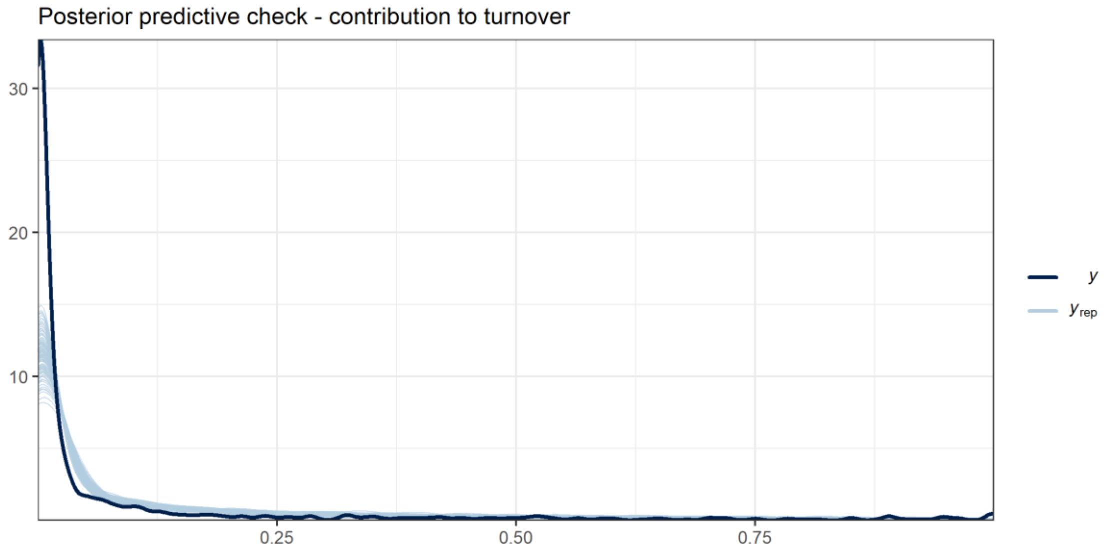

Figure S6.2 Posterior predictive check for the contribution to turnover model. Light blue lines present random draws from the posterior, dark blue line is the original data.

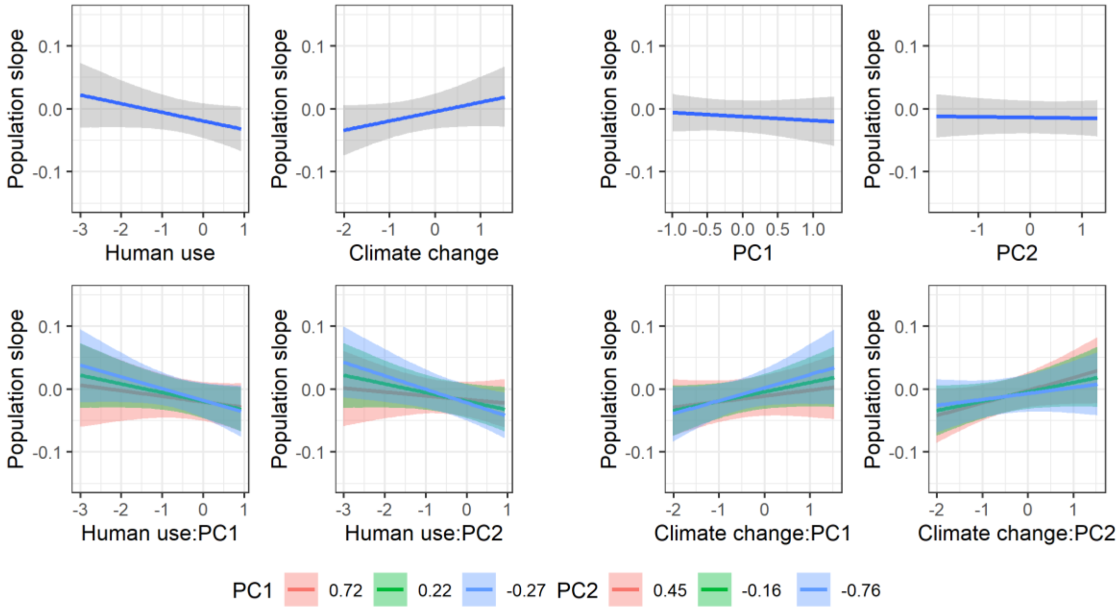

Figure S6.3 Marginal effect plots of the population change model.

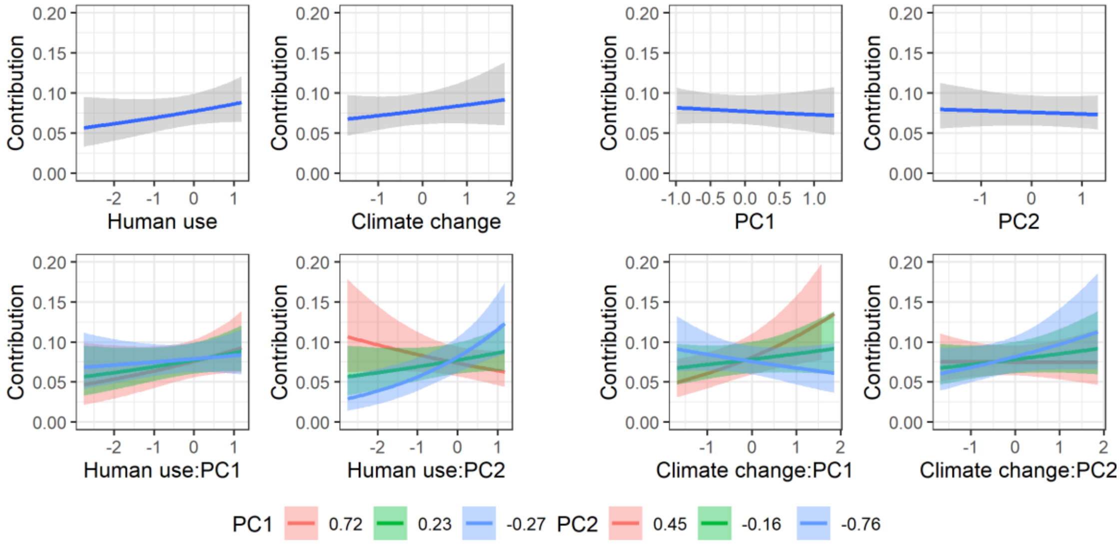

Figure S6.4 Marginal effect plots of the contribution to turnover model.

Table S6.1 Output for population change model, including all estimated parameters. Sigma is the scale parameter of the student’s t-distribution and nu the degrees of freedom.

Term	Estimate	Estimated Error	Q2.5	Q97.5
Intercept	-0.006	0.016	-0.037	0.026
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Human use:PC2	-0.012	0.013	-0.037	0.014
Climate change:PC1	0.013	0.008	-0.003	0.029
Climate change:PC2	0.009	0.008	-0.006	0.024
Random effect study	0.062	0.010	0.044	0.083
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PC1	0.096	0.132	-0.160	0.358
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Random effect study	0.446	0.072	0.318	0.603
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6 Synthesis

6.1 Summary of main findings

In this thesis trait-based approaches were applied in novel ways with the ultimate goal of understanding how humans shape plant composition over long time scales. Below I summarise the key findings of the three papers in this thesis.

Paper 1 tested the reliability of using pollen records for reconstructing past plant trait composition. I reconstructed trait composition from pollen data using a novel Bayesian method that allows for the consideration of trait variability within pollen taxa. I compared plant trait composition reconstructions based on modern pollen samples with the trait composition of the surrounding vegetation. In general, there was a high uncertainty in the estimated relationship between vegetation trait composition and pollen-based trait reconstructions. This high uncertainty is most likely caused by variation in pollen taxa and differences in pollen productivity and dispersal. Because of the low sample size in this study, a possible positive relationship between pollen-based reconstructions and vegetation trait composition is not ruled out. However, these results advocate carefully considering trait variation within pollen taxa and encourage further testing of the trait-based approach in palaeoecology.

Paper 2 examined how the start of agriculture changed plant functional composition in Europe. I demonstrated a four-fold decrease in whole plant size since the beginning of agriculture. Especially in the last 2000 years, a trend towards the acquisitive end of the leaf economic spectrum was shown. Both agriculture and climate may have played a role in this trend. These results indicate that by modifying vegetation functional composition, early agriculture might have significantly impacted biogeochemical cycles.

Paper 3 used life-history traits to understand recent population changes and examined if species with particular traits contribute disproportionately to turnover. I found that species life-history is an important predictor of contribution to turnover but did not demonstrate a relationship with population change. Knowing why species may contribute disproportionately to turnover is important for understanding turnover metrics and the underlying mechanisms that shape biodiversity.

Overall, I consider the main contributions of this thesis as follows. 1) It shows the potential of the trait-based approach in palaeoecology and gives insights into methodological challenges of the approach, thereby providing a stepping-stone for further advances in the field of functional palaeoecology. 2) I demonstrated the insights that can be obtained by studying how individual species contribute to long-term changes and I showed the potential of the use of life-history traits to understand these contributions.

6.2 Limitations and ways forward

This thesis has drawn theories and techniques from functional ecology, palaeoecology and population ecology. Below I suggest ways to overcome limitations for further integration of these ecological disciplines to advance our understanding of how humans shape plant communities and, ultimately, ecosystem functioning.

6.2.1 The application of the trait-based approach in palaeoecology

Situation: The field of functional palaeoecology is rapidly developing and some recent studies show the potential of the approach to understand long-term vegetation changes. For instance, reconstructions from fossil pollen show relationships between trait composition and human impact and climate (Adeleye et al., 2023; van der Sande et al., 2019). However, the trait-based approach in palaeoecology remains to be thoroughly tested. Previous research has shown positive relationships between pollen-based trait compositions and the trait composition of the vegetation (Blaus et al., 2020; Carvalho et al., 2019; van der Sande et al., 2020). These studies also shed light on some of the main factors controlling the reliability of pollen-based reconstructions, such as the plant functional type and spatial scale. For instance, the functional composition of herbaceous plant is best represented up to 6 m radius (Blaus et al., 2020). However, these studies rarely incorporate the trait variation within pollen types into the trait composition reconstructions (but see Brussel and Brewer (2021)).

Contribution: In this thesis I developed a Bayesian hierarchical modelling approach to reconstruct trait composition from pollen data. Using this modelling approach I demonstrated in Paper 1 the importance of considering trait variation in the reconstruction of functional composition from pollen data. Paper 1 also indicated that taphonomic differences between pollen taxa are important to consider when reconstructing trait composition from pollen data. In general, Paper 1 advocated caution for the use of the trait-based approach in palaeoecology. The main methodological challenges that were identified in Paper 1, were to an extent addressed in Paper 2. I used the same hierarchical model to incorporate trait variation within pollen taxa and corrected for taphonomic differences between taxa using pollen productivity estimates. Furthermore, I also tested for the effect of chronological uncertainties. The sample size in Paper 2 was much greater than in Paper 1, about 7000 versus 16 observations respectively. This high sample size will likely have created enough support to find significant relationships in Paper 2, despite high uncertainty in the CWM estimates. Paper 2 demonstrated the informativeness of the application of the trait-based approach in palaeoecology. I confirmed that the use of functional traits in palaeoecology has the potential to characterise broad spatial and temporal changes in plant composition. I showed intuitive changes: Plant height decreased even though there was a high variation in plant height within pollen types.

Ways forward: While Paper 2 shows the potential of the trait-based approach in palaeoecology, the findings of Paper 1 urge that further testing of the trait-based approach in palaeoecology is necessary. To advance functional palaeoecology, our understanding of the relationship between the trait composition of the vegetation and pollen-based reconstructions needs to be improved. I propose two ways. Firstly, pollen-based reconstructions of vegetation abundance used in trait reconstruction should be improved. Existing models for the quantitative reconstruction of past vegetation, such as REVEALS, could be applied for this purpose (Sugita, 2016). The effect of spatial scale and plant functional group should be explicitly considered in trait reconstructions. Further development of pollen productivity estimates specific to habitats and taxa can also aid in more reliable reconstructions of past vegetation (Bunting & Farrell, 2022). Secondly, it is crucial to integrate trait variation in estimating taxon-level trait values and reduce uncertainty from trait variation wherever possible. This can be done by improving the taxonomic precision of pollen data by integrating aDNA (Alsos et al., 2022), species distribution modelling (Svenning et al., 2011) and macro-botanical information (Birks & Birks, 2000).

6.2.2 Data situation on long-term ecological data

Situation: The growing availability of time series on biodiversity in open databases such as the LPI (LPI, 2016), BioTIME (Dornelas et al., 2018) and Neotoma (Williams et al., 2018) is significantly aiding the assessment and understanding of global biodiversity changes (IPBES, 2019; Woodbridge et al., 2020). Accessible long-term ecological and palaeoecological data were also crucial to this thesis. However, the generalizability of the results shown here is inherently dependent on the representativeness of the included data. There are pervasive biases in biodiversity and palaeoecological data that might have shaped the trends and conclusions drawn in this thesis.

Contribution: In Paper 2, I used pollen data from 78 sites across North-Western Europe. The initial systematic search I conducted identified 210 relevant publications, but the data for only 74 sites were openly available, while four were acquired from a collaborator. Therefore, my analyses are biased towards studies with openly available data. Palaeoecological data, in general, is also biased because of the availability of fossil sites and physical conditions that influence preservation (Inman et al., 2018). Biodiversity data in general is biased spatially towards countries with a high GDP and towards protected areas (Hughes et al., 2021). The BioTIME data used in Paper 3 mainly contains studies performed in places of medium to high human impact (Daskalova et al., 2021). Therefore, this study did not consider the full range of intensity of human impact, making the inferences restricted towards areas with human presence.

Ways forward: While the persistence of long-term ecological studies is threatened by decreasing funding to hold up monitoring, long-term data is essential for understanding environmental change impacts on plant communities (Hughes et al., 2017). The data situation of long-term ecological data could be improved in several ways (Hughes et al., 2021). First, targeted sampling of underrepresented areas could reduce biases. Secondly, funding and recognition for data generation, archiving and digitization could improve data availability (Sommer et al., 2019) (Hughes et al., 2021). Lastly, increased appreciation and use of palaeoecological data in ecology could reduce temporal biases.

6.2.3 Trait data situation

Situation: Like other types of ecological data, biases and gaps exist in trait data. These gaps are non-random, equatorial regions are under-represented, and more data is available for species with high SLA and low plant height (Cornwell et al., 2019; Sandel et al., 2015). The data situation is also biased towards relatively easy-to-measure traits, such as leaf traits (Streit & Bellwood, 2022). These easily measured traits are also the subject of critique, as these traits might not be regarded as "functional" because their link with species fitness and ecosystem functions might be hazy (Laughlin et al., 2020; van der Plas et al., 2020).

Contribution: Functional traits in this thesis were insightful in characterising broad changes in plant composition on large temporal and spatial scales (Paper 2). The changes in plant trait composition could be linked to climate and the start of agriculture. Thereby, I have mostly looked at traits from the perspective characterising community response to drivers. The second use of traits in ecology is to infer ecosystem processes from the functional composition of communities. The relationship between ecosystem functioning and plant functional composition is untested in the palaeoecological record and only implied in this thesis.

In Paper 3, I showed that life-history traits could be important predictors of community changes under human impact. While functional traits are important in determining species tolerance to biotic and abiotic constraints, they might not directly link to demography (Laliberte & Tylianakis, 2012; Paniw et al., 2021; Wilcox et al., 2021). Thus, for a full picture of community response to human impact, combining the strength of functional and life history traits might be necessary.

Ways forward: The data situation on functional traits could be improved by collecting data in underrepresented regions. More importantly, however, is that data coverage of relevant traits will be improved, for instance for root traits and life history traits (Guerrero-Ramírez et al., 2021). Collecting demographic data for the calculating of life-history traits is highly time intensive, as studies need time spans of 4 years or more, depending on the species (Salguero-Gomez et al., 2018). Potentially, the data situation on life-history traits can be improved understanding of the relationships between life-history, functional traits, climate and phylogeny, allowing for gap-filling (Kelly et al., 2021).

Furthermore, methodological advances might allow demographic processes to be inferred from community data (Paniw et al., 2023).

6.2.4 Incorporating uncertainty in ecological studies

Situation: The use of Bayesian inference in ecology has steadily grown in the past two decades (Anderson et al., 2021). The flexibility and hierarchical way the models can be built and the explicit handling of uncertainty explain the appeal of Bayesian analysis. Furthermore, Bayesian analyses have become easier and more accessible through the development of R-packages as *brms* and *runjags* (Bürkner, 2017; Denwood, 2016).

Contribution: Keeping track of and incorporating uncertainty in the analysis was particularly important in this thesis. In Papers 1 and 2 Bayesian models were used to propagate the uncertainty caused by trait variation in pollen types to estimates of functional composition on the community level. In Paper 3 I used a Bayesian meta-analytical framework to handle measurement errors in population change estimates.

Ways forward: In this thesis, I have not used one of the most significant assets of Bayesian analysis, the ability to incorporate prior knowledge in the form of priors. Using informative priors, rather than vague priors used here, might improve the precision of the functional composition estimates in Papers 1 and 2. Some suggestions of information to include for constructing more informative priors are, at the risk of becoming “subjective”, using known trait covariance (Shiklomanov et al., 2020) and plant functional composition data from modern analogues (Williams & Shuman, 2008).

6.2.5 Quantifying human impact

Situation: Anthropogenic impact on biodiversity is diverse and challenging to quantify because multiple drivers can act in additive, synergistic and antagonistic ways (Bowler et al., 2020). When using pollen records, it is especially complicated because of the need for independent data, while often specific pollen taxa are used as human impact indicators (Izdebski et al., 2022). Existing data on human impact are of low temporal and spatial resolution (such as Klein Goldewijk et al. (2017) or insufficient temporal coverage (Mu et al., 2022).

Contribution: In this thesis, I used human impact indicators that are not temporally explicit. Therefore, in Paper 2, I could not quantify the effect of differences in agricultural trajectories between sites on changes in plant functional composition. In Paper 3, I could not account for changing intensities of human impact over the time span of the studies.

Ways forward: There is a need for independent proxies to study human impact on plant functional composition. Proxies based on archaeological remains could offer a solution on palaeoecological time scales. Demographic reconstructions based on archaeological remains are of relatively high spatial and temporal resolution and coverage, although they are generally not available at great spatial scales (Woodbridge et al., 2018). Also on the shorter time scales of Paper 3, understanding plant composition changes could be improved by increasing the temporal coverage of human impact data. Combining data sources from remote sensing and national statistics as done by Winkler et al. (2021) could be a way forward.

6.3 Conclusion and future directions

Anthropogenic impact on plant communities is altering ecosystem functions, ecosystem services and ultimately human well-being (Diaz et al., 2006). Anticipating potential (undesirable) changes requires a thorough understanding of the natural dynamics of ecosystems and how those dynamics are changed by humans (Gillson et al., 2021; Lindenmayer et al., 2012). This thesis has employed novel ways to use traits for understanding human impacts on plant communities in the temporal domain. I suggest two major lines of inquiry for future research that have emerged from this thesis.

6.3.1 Extending the timescales of ecosystem functioning research

To my knowledge, functional palaeoecology has only focused on the assessment of the interaction between drivers and plant functional composition (Adeleye et al., 2023; van der Sande et al., 2019). In ecology, trait-based approaches are also used for assessing the effect of plant composition on ecosystem functions. The palaeoecological record provides a rich source of proxies on past ecosystem functioning which could be harnessed for the examination of the influence of plant functional composition on long-term ecosystem functioning (Dearing et al., 2012; Jeffers et al., 2015). Natural and anthropogenic drivers that have their primary impact on land affect the aquatic environment through coupled biogeochemical cycles and physical processes. For example, plant functional composition changes on the land may result in an increase of sediment or nutrients moved to the aquatic environment and affect abiotic and biotic components of the lake system (McLauchlan et al., 2013). Because of this aquatic-terrestrial coupling, palaeoecological proxies might provide a way of studying the effect of plant functional composition on ecosystem functioning (Dearing et al., 2012; Jeffers et al., 2015; Mills et al., 2017).

6.3.2 Improving integration between palaeoecology and ecology

Although collaboration between ecology and palaeoecology is growing, the historical divides still remain. Some barriers to the further integration of these two disciplines are the mismatches in scale, temporal and taxonomic resolution (Dillon et al., 2023). Also differences in commonly used statistical techniques and measures of change might hamper further integration (Dillon et al., 2023). So increased use or development of statistical methods that can applied in palaeoecology and ecology, such as generalized additive models, could promote integration. In both ecology and palaeoecology measures of temporal species turnover are used (Magurran et al., 2019; Mottl et al., 2021). By my knowledge, it is unknown how these turnover metrics relate to each other and are influenced by taxonomic resolution and temporal uncertainties. Finally, shared research agendas, such as seen for restoration, resilience and here functional trait composition, might increase opportunity for the integration of palaeoecological and ecological research (Goodenough & Webb, 2022).

6.4 References

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