

Trait-based approaches as ecological time machines: Developing tools for reconstructing long-term variation in ecosystems

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Abstract

1. Research over the past decade has shown that quantifying spatial variation in ecosystem properties is an effective approach to investigating the effects of environmental change on ecosystems. Yet, current consensus among scientists is that we need a better understanding of short- and long-term (temporal) variation in ecosystem properties to plan effective ecosystem management and predict future ecologies.
2. Trait-based approaches can be used to reconstruct ecosystem properties from long-term ecological records and contribute significantly to developing understandings of ecosystem change over decadal to millennial time-scales.
3. Here, we synthesise current trait-based approaches and explore how organisms' functional traits (FTs) can be scaled across time and space. We propose a framework for reconstructing long-term variation in ecosystems by means of analysing FTs derived from palaeoecological datasets. We then summarise challenges that must be overcome to reconcile trait-based approaches with palaeo-datasets. Finally, we discuss the benefits and limitations of trait-based reconstructions of ecosystem temporal dynamics and suggest future directions for research.
4. Reconstructing environmental properties through time vis-à-vis FTs can be separated into two parts. The first is to record trait data for organisms present in modern ecosystems, and the second is to reconstruct temporal variability in FTs from palaeoecological datasets, capturing changes in trait composition over time. Translating palaeoecological datasets into FTs is challenging due to taphonomic,

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taxonomic and chronological uncertainties, as well as uniformitarian assumptions. Explicitly identifying and addressing these challenges is important to effectively calculate changes in FT through time.

5. Palaeo-trait research offers insights into questions related to short- and long-term ecosystem functioning, environmental change and extinction and community assembly rules across time. As work in this area matures, we expect that trait-based approaches integrating palaeoecology and neo-ecology will improve understanding of past ecologies and provide a deeper insight of their implications for present-day and future ecosystem management and conservation.

KEY WORDS

functional diversity, macrofossils, microfossils, neo-ecology, palaeoecological proxies, palaeoecology, quaternary, species equivalents

1 | INTRODUCTION

There is one important certainty in the current anthropogenic age: ecological communities are not stable and are susceptible to change over both short (e.g. diurnal, seasonal, annual) and long (e.g. decadal, centennial, millennial) temporal scales. The Earth is experiencing unprecedented climatic changes not seen for more than 10,000 years (Gulev et al., 2021) and by the end of the 21st century, the Earth's mean global temperature and atmospheric CO₂ concentration are expected to reach levels not seen for more than 10 million years (Burke et al., 2018; Gulev et al., 2021). The consensus among scientists is that we need a better understanding of ecological processes occurring over both the short and long term to plan effective ecosystem management and predict future ecologies, because simply looking at present-day ecologies is insufficient to understand a system's status and can be actively misleading (Kuussaari et al., 2009). Ecosystems change over decadal to millennial time-scales and scientists must be able to track their variability in functioning over equally long periods. Reconstructing ecosystem properties from long-term ecological records has the potential to contribute significantly to this understanding, without having to wait to observe changes occurring in real time.

The past decade of research has shown that observing ecosystem properties and their spatial and temporal variation is an effective approach to investigate the effects of environmental changes on system functioning (e.g. natural variability, resilience, thresholds for state change), contributing to the prediction or mitigation of the effects of global climate change (Hennenon et al., 2018). Palaeoecological records provide a useful source for studying long-term ecosystem responses to both natural (e.g. geological events, glacial-interglacial climatic phases, evolutionary processes) and human-induced (e.g. fire, forest clearance, pollution) drivers at various scales, and extracting palaeoecological measures of ecosystem properties comparable with those from modern ecosystems is a promising area of research (Brussel & Brewer, 2021). An important emerging approach to quantifying ecosystem properties and their

variability uses the functional traits (FTs, defined below) of their component species, although research on how FTs interact with ecosystem properties over medium- to long-term time-scales is still in its infancy. Considering the rapid environmental changes occurring during the Anthropocene and the potential for habitats reaching tipping points for which there are only historical analogues (Burke et al., 2018), FT research needs to evolve into a decadal-scale science with a long-term perspective. While bringing together these approaches to develop and test methods for translating long-term records of community composition into summary metrics of ecosystem properties using species-specific FT information requires careful calibration addressing multiple challenges, it has the potential to transform our ability to address key ecological knowledge gaps vital for effective planning and prediction in a rapidly changing world (see Box 1).

The overarching aim of this paper is to synthesise current understanding of how trait-based approaches can be used to add a long temporal perspective to the study of ecosystem properties. We explore examples of FTs which can be scaled across both time and space and present a framework for reconstructing long-term variation in ecosystems by means of FT analyses of palaeoecological datasets (Figure 1). We then summarise the range of challenges that need to be overcome to reconcile trait-based approaches with palaeo-datasets and consider the current state of research on reconstructing long-term variation in ecosystem properties using FTs. Finally, we summarise the realistic potential and limitations of trait-based reconstructions of ecosystem temporal dynamics and suggest future directions for research (Box 1).

1.1 Definitions and usages (see also Table 1)

This paper focuses on FTs, which are measurable attributes of organisms important for their survival, reproduction and overall fitness (Violle et al., 2007). FTs are, for instance, a bright colour that attracts mates, but also attracts predators (Godin & McDonough, 2003);

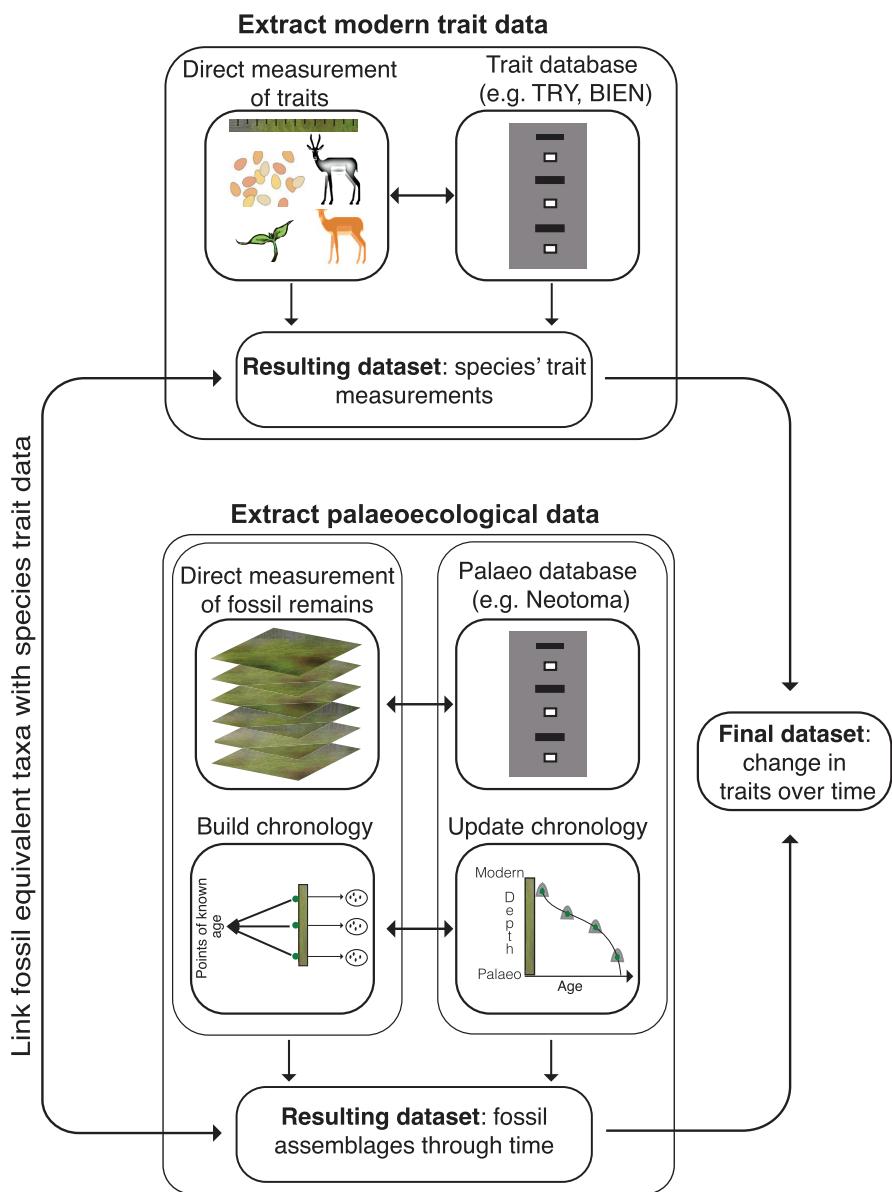


FIGURE 1 Conceptual diagram showing approach for reconstructing long-term variation in functional traits (FTs) using palaeoecological assemblages. The process of reconstructing FT composition can be separated into two interlinked parts. The first (upper box) is focused on extracting trait data from organisms present in modern ecosystems and the second (lower box) is focused on reconstructing temporal variability in FTs from palaeoecological datasets to capture changes in trait composition over time. FT measurements made on organisms found in modern ecosystems can be made directly or extracted from freely available databases (e.g. TRY, BIEN). For palaeoecological datasets, trait estimates are derived from the sedimentary archive by taking assemblages of fossil remains (e.g. plant leaves, testate amoebae) to then either measure FTs directly from the biological remains or align the taxonomy of the remains with modern taxa databases (establishing 'species equivalents'). Sediments from different points in the record can also be dated, and an age-depth model created to add a chronology to the change in traits between assemblages, giving a reconstruction of the variation in FT composition over time.

growing large, thin plant leaves in early succession to capture more energy which then represents a considerable disadvantage as the community gets more crowded; investing in one large seed versus many small seeds (Garnier et al., 2016). FTs often reflect ecological trade-offs; their diversity in an ecosystem regulates biological communities and determines their ability to respond to changes in environmental conditions (Garnier et al., 2016). FTs also provide the means for translating the diversity and abundance of species in a community into measures of both the abiotic environment and the emergent properties of the ecosystem (Green et al., 2022). Current work shows that the functional ecology concept can usefully be applied at a wide range of spatial scales, from local (Bongers et al., 2021) to global (Butler et al., 2017; Carmona et al., 2021), though applying the concept across different temporal scales is less explored (discussed in more detail below).

Quaternary science has a long history (nearly 120 years) of using functional characteristics of species in the interpretation of

palaeoecological datasets (Birks, 2020). Earlier work typically used a range of ecological attributes (e.g. properties of a taxon that described its overall ecology, such as range size, life history, geographic distribution, climate tolerance, habitat types or environmental indicator values) to generate hypotheses about the underlying drivers of past vegetation dynamics (Johs, 1960). Even though these attributes are associated with ecosystem properties, most of these are not FTs in the strict sense (Violle et al., 2007). The FT approach considered in this paper focuses on aggregated trait scores (Table 1) across multiple individuals from multiple species as proxies for ecosystem properties. Aggregated trait scores include both aggregated community trait mean (e.g. community weighted mean, CWM) and functional diversity estimates (e.g. functional richness, functional redundancy, sensu Violle et al., 2007). Ecosystem properties are those which occur as a result of interactions within the community, and between the community and its environment—they broadly include the dynamics of the system and its emergent properties, such as

TABLE 1 Glossary of terminology used in this paper (in alphabetical order; see main text for relevant citations).

Term	Definition
Aggregate trait score	Metrics used to measure FT values across multiple individuals from multiple species as proxies for ecosystem properties (e.g. community weighted mean, functional richness, functional redundancy, functional divergence)
Ecosystem properties	Properties resulting from the functioning of ecosystems due to interactions within communities of species present, as well as between communities and their environment
Functional traits (FTs)	Measurable attributes of organisms important for their survival and reproduction
Long term	A record that extends information about community dynamics beyond existing neo-ecological datasets
Neo-ecology	The study of modern ecosystems (usually based on the interaction between their ecological and environmental characteristics as affected by environmental change and anthropogenic activities)
Palaeoecology	The study of past ecosystems (usually based on the study of sedimentary archives containing the remains of plants, animals and other biological proxies)
Proxy	Biological remains in the sedimentary record that can be used as an indirect representation of a biological parameter in a modern ecosystem
Short term	A record that covers a period for which neo-ecological datasets are available in the same region
Species equivalents	A term referring to the result of taxonomic harmonisation between living organisms and proxies capable of being preserved in the sedimentary record. In many cases, proxies are fragments of the source organism, and cannot be consistently identified to the level of species
Taphonomy	Taphonomy is the study of the incorporation of living organisms into the sedimentary record. It covers all processes, ranging from the discarded parts of an organism (e.g. release of pollen grain, leaf fall) to death of the organism through decomposition, transport into the sedimentary system, deposition within the forming sediment and preservation within sediments over time
Uniformitarianism	The assumption that earth system processes observed in the present day are the same processes that acted in the past. In the context of this article, the main assumptions are that species traits remain stable over time and that the trait–environment relationship is in equilibrium (or actively trending that way)

resilience, sustainability, stability, variability, pollination efficiency or invasion resistance.

Data on temporal scales beyond a few decades are rarely available from documentary sources and most of our conservation knowledge is derived from short-term data snapshots of ecosystems. Sedimentary records and palaeoecological datasets preserve the remains of ecosystems in stratigraphic sequence over centennial to millennial time-scales but are under-used in developing conservation planning and ecological predictions (Nieto-Lugilde et al., 2021; Słowiński et al., 2019). Palaeoecological datasets (Table 1) usually consist of relative abundances of plant, animal or microorganism remains (e.g. bones, fossil pollen, tests formed by amoebae, diatom frustules), taken to be representative of past communities that formed under (and therefore reflect) past environmental conditions, along with a chronological framework that allows for the ages of assemblages and rates of change to be estimated (Figure 1). Our focus in this paper is comparing studies of living organisms/communities (neo-ecological datasets) with studies based on the palaeoecological/fossil record they leave in the sedimentary archive (palaeoecological datasets). Rather than defining long- and short-term records in terms of numbers of years, we consider a short-term record to be one which covers a period for which neo-ecological datasets are available, and a long-term record to be one which extends the community record beyond existing neo-ecological datasets. In this paper, a palaeoecological record can therefore be short term (fully overlapping with neo-ecological studies) or long term (extending back in time beyond documented ecological datasets).

Standard interpretation of palaeoecological datasets relies on the ecological understanding of groups of organisms based on their modern natural history and ecology to reconstruct past environments. These interpretations can be broadly narrative, or use a range of quantitative techniques such as transfer functions (Juggins & Birks, 2012) to translate assemblages into reconstructions of the environments they lived in (e.g. diatom assemblages to estimate lake water pH or salinity, sensu Vogt et al., 2010; chironomid midge assemblages to estimate July mean temperature, sensu Luoto & Ojala, 2018). However, applying FT approaches to palaeoecological datasets is a useful alternative method to reconstruct past ecosystem properties, which could be developed further both as a new window into the past and as a valuable source of ecological information to improve our understanding of present ecosystem functioning and prediction of future trajectories (Reitalu & Nogué, 2023).

2 | FTs AS PROXIES FOR ECOSYSTEM PROPERTIES: NEO-ECOLOGICAL PERSPECTIVE

The 1992 Earth Summit in Rio de Janeiro, Brazil, was a catalyst for major international research initiatives that aimed to explore questions related to the role of biodiversity in the functioning of ecosystems (Schulze & Mooney, 1993). A critical gap in knowledge was the incomplete understanding of the mechanisms linking biodiversity and ecosystem properties (Grime, 2001). Several studies suggested

that ecosystem properties (e.g. green biomass, soil nutrient stocks) responded strongly to changes in FT community composition rather than to changes in species diversity per se (reviewed by Hooper et al., 2005). This increasing recognition that linking species FTs to ecosystems offered a suitable approach to tackle the impact of biotic loss on ecosystem properties and functioning (Walker, 1992) led some authors to suggest a 'biodiversity revolution' (Cernansky, 2017). The approach that is becoming widely adopted (Díaz et al., 2007; Duffy et al., 2007) is to consider species on a functional basis (Mooney et al., 1997), focusing on what species 'do' rather than on what they 'are'.

Substantial evidence now supports the links between the FT composition of organismal assemblages and ecosystem properties (Chapin III, 2003; Díaz & Cabido, 2001; Fornara & Tilman, 2008; Garnier et al., 2004, 2016; Grime, 2001). One common approach taken by these studies is to model the interactions between individual traits and/or to model trait–environment relationships to describe organisms' fitness in order to determine species' and communities' response to, and effect on, ecosystems (Lavorel & Garnier, 2002). FTs could therefore be considered both as response traits, which respond to variations in environmental conditions (biotic or abiotic), and effect traits, which have the potential to influence the properties of an ecosystem (Figure 2). A conceptual framework of response and effect traits applied to the functional approach should thus allow the responses of species to environmental factors to be linked to the potential effects of these responses on ecosystem properties (Garnier et al., 2016). Such a framework relies on the assumption that environmental filters select the value, range and relative abundance of response traits found in a community which, in turn, affect ecosystem properties through the intermediary influence of effect traits. FTs thus became widely recognised as not only modulating organisms' fitness but also allowing for the quantification of the relationships between the different levels of organisation of ecological systems (Garnier et al., 2016; Lavorel & Garnier, 2002). For instance, the concept of trait convergence may help to predict the range of trait values that will occur after changes in the environment under expected environment–trait relationships, which may help to anticipate species abundances and distributions under changing conditions (de Bello, Carmona, et al., 2021). It should then be possible to anticipate the effects of changes in species compositions (including invasions and/or losses) on the environment from the predicted

direction and magnitude of change in species traits and their effects on ecosystem properties (McGill et al., 2010). These have been the fundamental premises of neo-ecological trait-based approaches for the past two decades and can be regarded as a significant improvement over purely taxonomic-based approaches to predicting community and population responses to environmental change (de Bello, Carmona, et al., 2021) and their subsequent effects on ecosystem functioning (Garnier et al., 2007; Lepš et al., 2006) and services (Lavorel et al., 2011; Lavorel & Grigulis, 2012).

In light of the growing recognition of response–effect trait frameworks, multiple associations have been proposed between traits, ecosystem properties and land management practices to help identify predictable trait–ecosystem relationships that can cascade across trophic levels and support a range of ecosystem services (de Bello et al., 2010; De Deyn et al., 2008; Lavorel et al., 2011; Lavorel & Grigulis, 2012). In addition, it has been argued that 'fast' and 'slow' traits scale-up to faster and slower rates of ecosystem processes such that linkages across plant organs result in an integrated whole-plant economics spectrum (Reich, 2014). A global spectrum of plant form and function has been advanced to offer explanations of evolutionary constraints, support the functional classification of species and ecosystems, and improve predictive vegetation models (Díaz et al., 2016).

The links between FTs and ecosystems can most often be assessed using different measures of trait composition of biological communities (Díaz et al., 2007), including the traits of the dominant species, reflecting the so-called mass ratio hypothesis (Grime, 1998). These measures can be good indicators of ecosystem functioning at a given point in time and useful for examining ecosystem resilience and recovery (de Bello, Lavorel, et al., 2021). The functional diversity of organisms has also been linked to other measures of biodiversity (e.g. phylogenetic diversity), reflecting potential effects of niche complementarity among species on ecosystems (Díaz et al., 2007) or the temporal complementarity in species fluctuations (de Bello, Lavorel, et al., 2021). For instance, ecological differentiation among coexisting species in the form of complementarity may reduce overlap in resource use to increase nutrient cycling (Heemsbergen et al., 2004) and lead to enhanced ecosystem stability (Cadotte et al., 2012) and productivity (Cadotte et al., 2008). Indeed, recent research has shown that functional redundancy within communities is a key factor in the response of ecosystems to future extinction

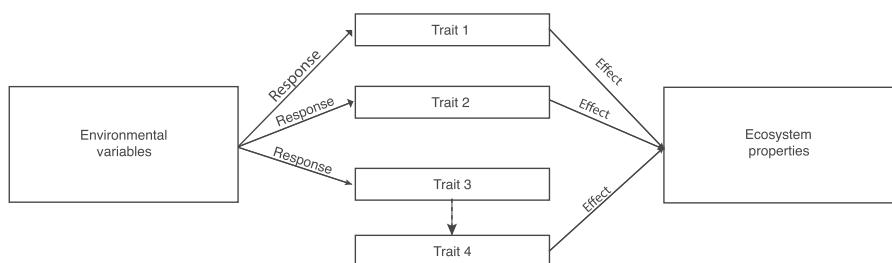


FIGURE 2 Conceptual model linking environmental variables to ecosystem properties via organisms' traits. Traits can respond directly (Traits 1, 2 and 3) or indirectly (Trait 4) to changes in environmental variables. Traits can directly (Traits 1, 2 and 4) or indirectly affect ecosystem properties (effect of Trait 3 mediated through Trait 4).

scenarios, which may cause a significant decline and rearrangement of ecological strategies across trophic levels and subsequent cascading effects on ecosystem properties (Carmona et al., 2021).

3 | FTs AS PROXIES FOR ECOSYSTEM PROPERTIES: PALAEOECOLOGICAL PERSPECTIVE

A wide range of biological remains can be found in sedimentary archives, reflecting different organismal groups and trophic levels. Like neo-ecologists, palaeoecologists typically specialise in the identification and recording of one or a few groups, and as in neo-ecology, some groups are studied by many researchers and others by few (Lowe & Walker, 2014). Microfossils (Table 2) are usually found in large numbers in suitable sediments, and many records can be collected from a single core with relatively fine time divisions, while macrofossils (visible with the naked eye; Table 2) require larger samples to produce a reasonably sized and hopefully representative assemblage. In some cases, traits can be measured directly from palaeo-proxies. For instance, morphological traits can be measured from bones of animals or shells of microorganisms (Kerr et al., 2017; Marcisz et al., 2020), but most commonly traits assigned to the components of palaeoecological assemblages are derived from trait measurements on modern species (Figure 1; Carvalho, Brown, Waller, Bunting, et al., 2019).

The translation of palaeoecological datasets into assemblages of traits can be partially tested by collecting modern samples of the part found in the palaeoecological record (e.g. seeds, pollen) along with contemporary data on the population creating it and comparing population-derived and palaeo-record-derived values of community traits. This has been applied at different scales, from patches within a habitat (Carvalho, Brown, Waller, Bunting, et al., 2019) to continent-wide studies (Brussel & Brewer, 2021), where pollen-derived functional diversity patterns were shown to adequately track ecological function of contemporary plant communities in both trait space and geographic space, allowing the macroecological pattern of biodiversity to be reconstructed. Comparisons of modern pollen and plant data have shown that traits with relatively low variation within pollen types can be well reflected by pollen data (e.g. specific leaf area, clonality, leaf dry matter content, seed number; Blaus et al., 2020). Table 2 summarises the main palaeoecological proxies which we know to have been used for FT studies (or which have the potential to be used that way). For some groups, such as testate amoebae, palaeoecologists may need to actively collect or measure modern trait data, as well as palaeoecological samples, due to a lack of pre-existing neo-ecological studies, whereas for others (e.g. plants), extensive existing trait databases can be used (Kattge et al., 2020). Palaeoecological data enable researchers to study ecosystems beyond the scope of human observation. However, it is essential to acknowledge that working with these data entails incorporating additional layers of uncertainty from multiple sources. Therefore, it is crucial to identify (and clearly communicate)

strategies for addressing or incorporating such uncertainty (Flantua et al., 2023).

3.1 | Challenges in combining palaeoecological proxies with FT records

Palaeoecological datasets consist of multiple records of the abundance of different organisms, collected from different points across the stratigraphic record, with each record corresponding to a distinct point in time. Calculating aggregated trait scores for each record creates a sequence that indicates how the ecosystem properties linked to traits changed over time (Figure 1). However, there are several differences between neo-ecological and palaeoecological datasets that need to be considered. The three most obvious are taxonomic resolution, taphonomic processing and chronological (un)certainty. In addition, when using modern trait estimates in association with palaeo-proxy data, it is generally assumed that species traits remain stable over time and that the trait–environment relationship is in equilibrium—the assumption of uniformitarianism (but see Peppe et al., 2018).

3.1.1 | Taxonomic challenges

Palaeoecological remains do not always have the same taxonomic resolution as their modern counterparts, since they only consist of part(s) of an organism (e.g. a pollen grain, a diatom frustule, a seed, a leaf, a few bones) and may not include all important identifying features. FTs are usually available for individual species (e.g. TRY, BIEN databases) based on measurements of multiple living individuals and can therefore be applied to species lists from modern ecosystems. Standardisation of a consistent taxonomy is crucial for the success of integrating data from various fields, as noted by Grenié et al. (2023). To achieve this, data analysts require a ‘common currency’ (Rapaciulo & Blois, 2019). Connecting modern FT databases to palaeoecological proxies requires identification of ‘species equivalents’ (Table 1; pollen analysis provides a good example of the process).

Pollen morphotypes can have a range of taxonomic resolutions, with a single type originating from plants of a single species (*Plantago lanceolata*), genus (*Ulmus*), family (Brassicaceae) or other taxonomic unit (e.g. *Ranunculus acris*-type, which in the United Kingdom includes pollen from taxa such as *Anemone nemorosa*, *Pulsatilla vulgaris*, *Clematis vitalba* and all *Ranunculus* species except for *R. parviflorus* and *R. arvensis*, which can be identified to species level when well preserved), the latter encompassing an ecologically highly diverse set of species. When multiple different sites analysed by different researchers are to be combined, there is an additional need to harmonise the palaeoecological taxonomy (i.e. standardise all morphotype synonyms across all the sites; De Klerk & Joosten, 2007; Rull, 2012). There are several underlying issues that contribute to taxonomic uncertainty in pollen analyses, including differences in pollen identifiability, quality of preservation, variation in assumptions for taxon

TABLE 2 Examples of palaeoecological proxies and studies used to reconstruct past ecosystem properties.

Organismal group	Type of remains	Area sampled by proxy	Taxonomic mismatch	Example studies
Plants	Pollen (mic)	SFE and wider surrounding landscape—scale depends on size and nature of SFE	High	Veeken et al. (2022), Blaus et al. (2020), Carvalho, Brown, Waller, Bunting, et al. (2019), Reitalu et al. (2015)
	Phytoliths (mic)	SFE and immediate surroundings	Moderate	Witteveen et al. (2022), Zhang et al. (2022)
	Plant macro-remains (mac)	SFE and immediate surroundings	Moderate	Felde and Birks (2019), Jabłońska et al. (2020), Peppe et al. (2018)
	Leaf Stomata (mac)	Atmospheric CO ₂ and water balance	Low	Woodward (1987), Retallack (2001)
Algae	Diatoms (mic)	SFE water body	Low	Vogt et al. (2010), Grudzinska et al. (2017)
	Organic-walled algal palynomorphs (mic)	SFE water body	Moderate	Stivrins et al. (2022)
Microorganisms	Testate amoebae (mic)	SFE	Low	Marcisz et al. (2020) and references therein
	Fungal spores (mic)	SFE and wider surrounding landscape	High	Saxena et al. (2021)
Insects	Chironomids (mic)	SFE water body	Moderate	Stivrins et al. (2021), Luoto and Ojala (2018)
	Coleoptera (mac)	SFE and immediate surroundings	Moderate	Pilotto et al. (2022), Schweiger and Svensson (2018)
Vertebrates	Bones, teeth, permafrost specimens (mac)	Variable depending on taphonomy (e.g. died in situ, brought by predators)	Low	Seetah et al. (2016), Zhang et al. (2013)
Multiple organismal groups	aDNA and sedaDNA	SFE and immediate surroundings	Moderate	Talas et al. (2021), Alsos et al. (2022)

Abbreviations: Mac, macrofossil; Mic, microfossil; SedaDNA, sedimentary ancient DNA; SFE, sediment-forming environment (e.g. lake, mire).

names, inconsistent mapping of taxon names to morphotypes across different regions, plant nomenclature and availability of reference material (i.e. pollen collected directly from an accurately identified plant for comparison with subfossil material), but it is still possible to establish species equivalents allowing connection with modern FT databases.

Establishing FT values for pollen taxa has been attempted using various approaches. A representative plant species can be selected and its traits used for the morphotype (e.g. Connor et al., 2018) or a single value can be calculated for the morphotype from the constituent species (e.g. a mean, median or weighted mean; Carvalho, Brown, Waller, Bunting, et al., 2019; Reitalu et al., 2015). A probabilistic approach can also be used to estimate trait values for pollen types (Veeken et al., 2022). All approaches assume that we know which species contribute to the pollen types at each time and space point in reconstructions, and that the traits of those species have not changed substantially over time (uniformitarianism, see below). It is unclear how far back in time fossil taxa can be interpreted in terms of living taxa. For pollen and spores, as well as plant macrofossils, specimens of Holocene and Pleistocene age are generally

classified in terms of extant plant species or genera, and many Paleogene–Neogene (~66–2.6 Ma) taxa can also be classified in terms of extant genera or at least families. However, further back in time, where plants that are now extinct dominated the landscape, the relationship between fossil and extant taxa is less clear (Mander & Punyasena, 2014).

3.1.2 | Taphonomic challenges

Organismal assemblages in sedimentary systems form through taphonomic processes (Table 1). These can be relatively simple (e.g. a diatom assemblage formed in a closed lake basin consists of the remains of diatoms which died and sank after living in the water column, littoral or benthic zones of the lake when the sediment layer was being laid down) or complex (e.g. a bone assemblage in a cave might reflect a combination of the cave's inhabitants, remains washed in through erosional processes, and remains of prey brought in selectively from the surrounding landscape by predators using the cave). A range of methods, including analysis of the condition of the

remains (e.g. the presence or absence of tooth marks on bones) and use of computer models (e.g. models of pollen dispersal and deposition; Sugita, 1994, 2007a, 2007b), are used to take taphonomy into account when treating a proxy assemblage as a once-living community. In some cases, modern trait spectra can be determined by sampling comparable environments to those where the palaeoecological record formed (e.g. leaf trait studies based on modern forest floor leaf assemblages from wet places, or diatom and chironomid studies based on modern lake surface samples).

With the exception of pollen data, taphonomic biasing of the species spectrum of an ecosystem is not often considered. Quantitative reconstructions of past land cover from pollen records have been a goal for the field since its earliest days, and application of models of the taphonomic relationship between vegetation and pollen assemblages is now used to correct for taphonomic issues and derive more realistic reconstructions of the vegetation community composition (Bunting et al., 2018; Bunting & Middleton, 2009; Sugita, 2007a, 2007b). Thus far, models have only addressed air-borne pollen transport, but they have already been proven effective in northwest Europe (Githumbi et al., 2022) and China (Li et al., 2020) and continue to be developed.

3.1.3 | Chronological uncertainty

In most cases, it is not possible to obtain an age estimate for each sample from a sedimentary sequence directly. Instead, a few points of known age are identified within the sequence, such as tephra layers or radiocarbon age estimates, after which an age-depth model is constructed to provide a chronological framework. From this, individual sample ages can be estimated. Age-depth models can be constructed using a range of statistical methods that allow for the assessment of the uncertainty associated with each age estimate (Blaauw et al., 2018; Trachsel & Telford, 2017). Despite methods being available, palaeoecological studies incorporating age uncertainty into FT analyses are so far rare (but see Veeken et al., 2022), which would be particularly useful when considering ecological questions related to rates of ecosystem change or response (see Box 1).

3.1.4 | Assumption of uniformitarianism in trait–environment relationships

For some types of biological remains, traits are mostly inferred from modern studies of the taxonomic group (e.g. pollen, sedaDNA) but for others, morphological traits can be measured directly from the proxy (e.g. mammal bones, testate amoebae morphology) and thus it is possible to directly measure how a trait has changed over time (see Section 3.2.1 for details). This can then be used as the starting point or evidence for exploring hypotheses about how the environment has changed over time. Different groups will respond to the same environmental triggers in different ways. For instance, annuals and

shrubs respond to aridity with avoidance and tolerance, respectively (Dias et al., 2020), while some traits (e.g. leaf shape) respond near-instantaneously to environmental change (Nicotra et al., 2011). For other traits, there may be lags in responses, or trait response may be complicated by interactions with multiple environmental factors, leading to imperfect correlations between observed trait change and inferred environmental change (Carvalho, Brown, Waller, & Boom, 2019). Therefore, it is particularly important in palaeoecological studies to ensure clear differentiation between observed change in traits and inferred changes in drivers of traits. This is because various kinds of flexibility or evolutionary or chronological disequilibrium between trait and environment may affect this relationship (Damuth & Janis, 2011; Hall & Cote, 2021; Pardi & Desantis, 2021; Strömberg et al., 2013; Tütken et al., 2013).

When traits are inferred from modern studies of the taxonomic group (e.g. pollen), uniformitarian assumptions are also made. Pollen-derived estimates of traits begin with the measurement of an individual plant property (e.g. seed size) in modern plants. Measurements from multiple individuals are combined to give a species mean trait measurement. These measurements are then aggregated to give a mean trait measurement to a specific pollen type, requiring assumptions about the species mixture that generated the pollen type identified in the record. If the goal is a CWM (see Table 1) trait measurement, the values need to be combined a third time with the trait estimate of all other pollen types, which requires assumptions of how the relative proportions of pollen types in an assemblage relate to the abundance of different plants in the community or communities that created the assemblage. It is possible to map changes in CWM trait values (or other functional diversity metric) over time, which can form the basis of testable hypotheses as to the environmental causes of the trait change. However, the added layers of assumptions and/or uncertainties need to be clearly considered, as well as the potential disequilibrium between CWM (or other metric) estimates and the environmental drivers of that trait.

4 | EXAMPLES OF PALAEOECOLOGICAL PROXIES

In this section, we present examples of how FTs can be combined with palaeoecological data taken from studies of plant leaves (macrofossils), testate amoebae (microfossils) and vertebrate macrofossils to illustrate the potential value of the FT approach for understanding ecosystem functions.

4.1 | Example: Plant leaves

Plant macrofossils like leaves and reproductive structures are widely employed in palaeoecological studies (Birks & Birks, 2000). Given that leaves are primary sites of photosynthesis and play a central role in plant growth and survival, leaf fossils represent a potentially rich record of FTs through time. Leaf traits

include morphological characteristics like shape and area (Hang et al., 2021), specific leaf area (Liu et al., 2019) and its inverse, leaf mass per area (LMA; Wright et al., 2004), chemical characteristics such as leaf nitrogen and phosphorus concentrations (Rawat et al., 2021), and physiological characteristics like vein (Blonder et al., 2014) and stomata (McElwain & Steinhorsdottir, 2017) density. Leaf traits have been widely studied in modern ecosystems and it has been shown that variation in some of these traits can reflect ecological trade-offs and environmental factors (Blonder et al., 2014; Poorter et al., 2009; Wright et al., 2004). A central challenge when estimating leaf traits directly from palaeoecological records is the variable occurrence of plant macrofossils through time. The patchy distribution of leaf fossils means that a continuous record is rarely preserved. Instead, there are often discrete intervals within a core or a stratigraphic section that contain leaves, but these are separated by gaps in time (Boyce, 2008; Jackson & Booth, 2007; Mander et al., 2010), meaning it is rarely possible to generate long data time series derived from fossil leaves from a single location.

Connecting macrofossil taxon finds with modern trait estimates only allows for the rough estimation of taxon averages of trait values. Estimating traits directly from fossil material poses a different challenge, as the quality of preservation needs to be extremely good, and the preservation of whole intact leaves is the exception rather than the rule in the fossil record. In response, proxies that do not rely on the preservation of entire leaves have been developed for certain traits (e.g. Butrim et al., 2022; Soh et al., 2017). For example, Soh et al. (2017) reconstructed the LMA of fossil leaves preserved in a series of discrete fossiliferous horizons in East Greenland spanning the period of major climate warming ca. 200 million years ago during the Triassic–Jurassic transition using a proxy for LMA based on a scaling relationship between the thickness of leaf cuticle (which can be measured on a leaf fragment) and LMA. This study found that forests prior to Triassic–Jurassic global warming ~200 million years ago were dominated by plants with short leaf lifespans, but that forests following the warming were dominated by plants with high LMA thought to have had slower metabolic rates (Soh et al., 2017). Similar deep-time work has been undertaken on other traits (e.g. leaf vein density) and has shown that Neotropical rainforests in the late Cretaceous (~72–66 million years ago) were characterised by an open canopy, whereas those in the Palaeocene (~66–56 million years ago) more closely resembled modern rainforests with a closed canopy and multi-stratal structure (Carvalho et al., 2021). Several leaf traits have been used frequently to reconstruct environmental conditions (Royer et al., 2005). For example, the frequency of stomata on fossil leaves has been used to reconstruct atmospheric CO₂ concentrations (Wagner et al., 2004). In an interesting use of pollen data to reconstruct a foliar trait, pollen data (associated with modern leaf area estimates) have been used to reconstruct leaf area index in relation to changes in climate (Gonzales et al., 2008). Changes in leaf traits can have significant impacts on vegetation structure and ecosystem function (Boyce et al., 2010) and, as the examples above show, the reconstruction of leaf traits through time represents a promising

means of understanding how ecosystems have responded to past environmental change.

4.2 | Example: Testate amoebae

Reconstructing long-term environmental changes based on microbial communities is particularly challenging, since most functionally diverse microbial groups (e.g. ciliates, naked amoebae, flagellates; Weisse, 2017; Weisse et al., 2016) do not preserve well in sediments. Testate amoebae are an exception. These unicellular amoeboid organisms possess species-specific, decay-resistant tests (shells) that protect the amoeba from the influence of various environmental stressors and are well preserved in a range of sediments after death (e.g. peat, soil, lake sediments and marine sediments like salt-marshes), making them well suited for palaeoecological analyses. Individual species' tests vary in size, shape and composition and can be used to identify species in both neo-ecological and palaeoecological studies (Meisterfeld, 2000; Mitchell et al., 2008).

FTs present in testate amoebae can provide relatively detailed environmental reconstructions (Marcisz et al., 2020). Examples include FTs connected to morphology (e.g. test size, construction and aperture parameters), trophy (e.g. species trophic status or trophic position within communities) and species ecological preferences for microscale hydrology or pH (Marcisz et al., 2020). Knowledge of the ecological implications of specific FTs can come from both observational and experimental ecological studies (Basińska et al., 2020; Fournier et al., 2012; Koenig et al., 2018; Krashevská et al., 2016; Macumber et al., 2020; Marcisz et al., 2014; Mulot et al., 2017; Payne et al., 2016), as well as from palaeoecological investigations through information gained from other proxies (Fournier et al., 2015; Lamentowicz et al., 2015; Marcisz et al., 2016).

Training sets of modern testate amoebae data are often combined with palaeoecological data using transfer function models to reconstruct past environmental conditions like water-table depth and pH from peatlands (Amesbury et al., 2016; Lamentowicz et al., 2008; Qin et al., 2021). Adding information from FTs can strengthen and broaden these numerical analyses (Marcisz et al., 2020). Specific features of the tests carry a large amount of information about ecological preferences of testate amoeba species. For instance, morphological traits of assemblages such as test aperture metrics can give information about ecosystem disturbance regimes (an opening in the test through which the amoeba feeds and locomotes). The size and location of the aperture are determined by feeding preferences and hydrological conditions (Lamentowicz et al., 2015). In general, the larger the aperture size, the larger the prey that can be eaten by the amoeba. Shifts in the aperture spectrum of a community often indicate changes in the microbial food web structure or the destabilisation of trophic interactions (Hamard et al., 2019), which in palaeoecological datasets can point to disturbance events affecting ecosystem functioning (e.g. peat extraction in peatlands or substantial natural or anthropogenic drying events; Lamentowicz et al., 2015; Marcisz et al., 2016). The location of the aperture also

seems to relate to adaptation to hydrological conditions; species with smaller, more protected apertures show a preference for lower water-tables (Lamentowicz et al., 2015) where large-apertured amoebae are at risk of desiccation. A rapid drop in water-table can lead to species turnover (Marcisz et al., 2016). In contrast, lacustrine testate amoebae aperture sizes vary in response to water temperature and length of growing seasons (Dallimore et al., 2000).

Tests are constructed from different types and sources of environmental mineral material reflecting the availability of substrates in a given ecosystem (Fiąłkiewicz-Kozięt et al., 2015; Marcisz et al., 2020) and environmental conditions, such as heavy metal contamination (Fiąłkiewicz-Kozięt et al., 2015; Nasser et al., 2020) or cultural eutrophication (Macumber et al., 2020). In peatlands, where mineral material is sparse, xenosomes (species with agglutinated tests made from environmental debris) are less common and communities are often dominated by idiosomes (species with tests made of secreted biosilica plates like *Euglypha* species) and species producing proteinaceous tests. Increasing numbers of xenosomes can reflect increased runoff into the peatland (Marcisz et al., 2021). Lamentowicz et al. (2009) showed that anthropogenic deforestation that increased catchment erosion and input of nutrients into a peatland habitat led to high abundance of xenosomes.

4.3 | Example: Vertebrates

The palaeoecological record of past faunas is, like the fossil leaf record, fragmented and patchy (Benson et al., 2021) but well suited to FT studies since a subset of FTs can be measured on individuals' bones directly. Widespread evidence has emerged to suggest that in the late Quaternary, as modern humans spread across the last ice-age world, a profound change in terrestrial faunas took place, with widespread, severe and selective losses of large-bodied species (the late Quaternary megafaunal extinction, LQME; Sandom et al., 2014). For example, in previous interglacials, species of elephant, rhinoceros and hippopotamus were present in temperate northern Europe along with cattle, horse and deer, creating faunas of much higher functional diversity than at present. Trends during the last ice age and Holocene have resulted in terrestrial mammal assemblages that are considerably smaller than they have been throughout the tens of millions of years of mammalian evolution (Smith et al., 2018). Given the substantial impact of large mammals on the structure of the ecosystems they inhabit, the functioning of such ecosystems is now likely very different compared to most of the time modern biota has evolved (Fricke, Hsieh, et al., 2022; Fricke, Ordonez, et al., 2022). For example, a global study of body size and diet showed widespread downsizing and a common shift from mixed grazer-browser to browser-dominated assemblages across the Late Pleistocene to the present (Schowanek et al., 2021).

Trait-based macroecological analyses show that reintroductions of large herbivores have potential to substantially modify ecosystem functioning in ways that increase system diversity and resilience (Lundgren et al., 2020; Schowanek et al., 2021), in line

with neo-ecological evidence from real-world rewilding projects (Konvička et al., 2021; Ratajczak et al., 2022). Other studies have observed changes in mammalian community FTs and considered wider ecological effects within regions and across the globe (Dantas & Pausas, 2022; Doughty et al., 2016). For example, estimates of assemblage-level home range metrics from body size and trophic level (diet) of mammal and bird faunas show strong declines in assemblage-level mean and maximum home range (Berti & Svensson, 2020), with trait-estimated potential reductions in biotic connectivity via vertebrate-mediated dispersal of plants and other organisms (Albert-Daviaud et al., 2020; Fricke, Hsieh, et al., 2022). In addition, trait-based explorations of mammalian predator-prey food web structures have documented severe declines in food web complexity over the LQME (Fricke, Ordonez, et al., 2022). These losses are proportionally stronger than expected from the level of global species extinctions, reflecting the disproportionate impact of selective removal of particular species or functional groups (Fricke, Ordonez, et al., 2022).

5 | NEW PERSPECTIVES: REALISING THE POTENTIAL OF TRAITS FOR ALL ECOLOGICAL TIME-SCALES

5.1 | New avenues for the use of FTs in long-term studies

Palaeoecological estimates of traits carry with them a range of uncertainties, whether measured directly on preserved pieces of individual organisms (e.g. leaf shape, bone length, test shape) or derived through matching trait measurements of extant organisms with palaeo-records. Acknowledging and recording these sources of uncertainty is an important step in integrating a long-term perspective into studies of trait variation (Figure 3). For FT research to evolve and incorporate a temporal perspective, new FTs will have to be formulated and adapted as conceptualisations and generalisations about temporal ecology develop, alongside the use of conventional FTs developed first for understanding spatial variation in ecosystem properties. This remains true whether FTs are measured directly on subfossil remains, extrapolated from scaling relationships, or calculated from taxonomically matched modern trait database entries. New and expanded FT datasets are increasingly being developed to inform a temporal perspective on past ecosystem properties. These include, for instance, FTs for testate amoebae, which can be used to reconstruct present and past local hydrology (van Bellen et al., 2017), or as indicators of long- and short-term changes in the health, disturbance and water-table status of a site (Jassey et al., 2015; Marcisz et al., 2016, 2020), as well as to understand the changing degree of past landscape openness and amount of peatland overgrowth with low stature vascular vegetation or trees (Creevy et al., 2018; Payne et al., 2016).

One rapidly developing area of research is genomic ecology, and since genetic data can be used to identify potential FTs that are not

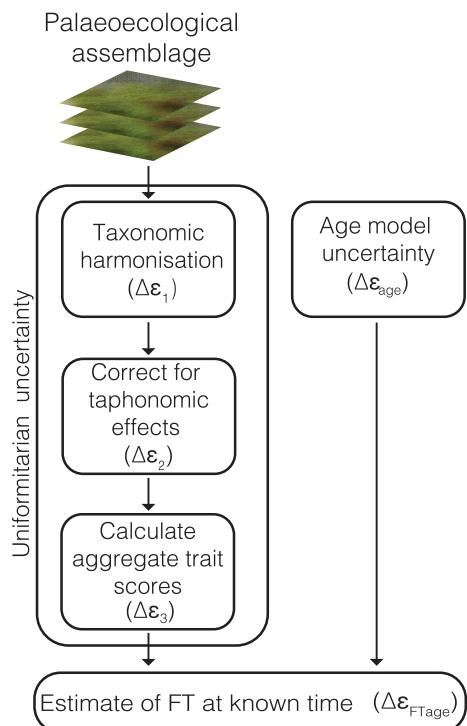


FIGURE 3 Conceptual diagram showing sources of uncertainty associated with reconstructing long-term variation in functional traits (FTs). This figure shows how errors associated with taxonomic ($\Delta\epsilon_1$), taphonomic ($\Delta\epsilon_2$) and trait scores ($\Delta\epsilon_3$) propagate when reconstructing FTs using palaeoecological datasets. Assemblages in sedimentary systems form through taphonomic processes, which are subject to errors. Therefore, adjusting for taphonomic effects is vital. Taxonomic harmonisation is accomplished either by taxonomic matching using trait databases or via direct measurements of traits from proxies. An aggregate trait score (e.g. functional diversity index) can then be calculated since $\Delta\epsilon_1$ and $\Delta\epsilon_2$ have been accounted for during the process of taxonomic harmonisation but will nonetheless also have errors. Uniformitarian uncertainty will affect all three sources of error. Constructing an age-depth model ($\Delta\epsilon_{age}$) provides the chronological framework for estimating ages of samples, though uncertainties in the process must be quantified. Distinguishing between observed changes in traits and inferred changes in drivers of traits is particularly important in palaeoecological studies ($\Delta\epsilon_3$) and is a crucial step prior to combining all uncertainties and calculating changes in FT through time ($\Delta\epsilon_{FTage}$).

visible in morphology or easily measurable through other means, its development will likely improve understanding of trait–environment relationships (Kjær et al., 2022). Genetic approaches can also be used to map the origin of certain physiological traits to contribute to knowledge of the limits of uniformitarian assumptions and enable reconstruction of ecosystem properties in the deeper past. In palaeoecology, development of methods for extracting aDNA (ancient DNA) from individual fossils and sedaDNA (sedimentary DNA—genomic data from fragments shed by the past community and preserved within sediments) from sedimentary archives offers additional ways to use genetic information to explore variations in traits in space and time (Talas et al., 2021). SedaDNA-based studies

of past vegetation change (Alsos et al., 2022; Parducci et al., 2017) show that this technique offers great potential to reveal the community composition (and thus trait composition) of organismal groups that do not leave reliable visible fossil evidence (Kisand et al., 2018). SedaDNA-based community reconstructions face the same challenges as other palaeo-proxies (i.e. taxonomic resolution, taphonomic processes and chronological certainty), but exploring this future avenue of research in more detail is beyond the scope of this paper.

5.2 | Grand challenges for palaeo-trait research

Developing a better palaeo-trait methodology by addressing the methodological obstacles identified in this paper could help answer fundamental and pressing questions in ecology, palaeoecology and biological conservation, such as those outlined in **Box 1**. For instance, Sutherland et al. (2022, 2023) identified the protection and long-term resilience of wetland ecosystems and the expansion of mangrove habitats as emerging issues of concern for global biodiversity conservation. Palaeo-trait studies can elucidate historical processes of vertical accretion/subsidence and sedimentation of wetland and mangrove habitats to inform future conservation policies and actions. Moreover, some of the fundamental ecological questions for the 21st century (Sutherland et al., 2013) sit at the interface between neo-ecology and palaeoecology (Davies & Bunting, 2010), requiring palaeo-trait research to attain a true temporal perspective on past ecosystem properties: how susceptible are ecosystems to tipping points? What factors and mechanisms determine ecosystem resilience and an ecosystem's sensitivity to changes in community composition? In addition to these general questions, we pose our own key questions for palaeo-trait research to address in the coming years in **Box 1**, not only to elucidate past environmental change, but also to provide essential knowledge to help predict the future of ecosystems and habitats across different regions and develop more effective management strategies.

5.3 | Concluding remarks

Throughout this paper, we have argued that FTs offer a valuable tool for translating palaeoecological datasets into formats that can be directly compared to neo-ecological assessments, adding a much-needed temporal dimension to ecological synthesis and understanding. Long-term experiments and monitoring studies can only proceed at the same rate as the systems being studied, while palaeoecological approaches allow for the collection of datasets spanning centuries, millennia or even millions of years based on a few months or years of study. We have explored a range of issues that must be addressed to translate palaeoecological datasets into estimates of species- or community-level traits and identified taxonomy, taphonomy, chronological uncertainty and uniformitarian assumptions as the main challenges (**Figure 3**). The extent to which these challenges

BOX 1 Key questions for a palaeo-trait framework

Ecosystem functioning and the reconstruction of palaeo-trait variation

- Can FTs provide insights into the functioning of past ecosystems, including processes that are difficult to capture (e.g. ecosystem consequences of herbivory rates, plant and nutrient dispersal rates)?
- To what extent have different diversity components of past FT composition (e.g. CWM, functional diversity) driven the stability of biomes in the face of environmental fluctuations, including resistance and resilience?
- What are the legacies of anthropogenic impact on ecosystem functioning where human influence has ceased or been considerably diminished (i.e. notably as mediated via FT changes)?
- Can existing modelling approaches be used to overcome the methodological obstacles to reconstructing FTs through time and assigning FTs to palaeoecological proxies?

Environmental change and extinction

- To what extent can FTs be used to track the trajectory of environmental change through time?
- Are there FTs that can confer a degree of resistance to extinction? If so, how might they be quantified and how do they relate to properties that are thought to affect extinction risk at geological time-scales (e.g. geographic range size, rarity, reproductive specialisation)?

Community assembly rules across time

- Are community assembly rules (e.g. FT convergence and divergence) different across different eras?
- Can community assembly rules be determined through the FTs of palaeoecological proxies to enable palaeoecological studies to transition from taxonomic units to FTs?
- What can FT studies tell us about the emergence of non-analogue communities and ecosystems at times of rapid environmental change, and the effects on both species and ecosystem function in the wider earth system?

are difficult to resolve depends on the palaeoecological proxy of interest. Active research continues to explore better ways of bringing together existing but imperfect records (e.g. spatial-interpolation statistical methods, taxonomic harmonisation processes, age modelling, pollen taphonomic modelling).

Palaeoecological records potentially offer consistent, temporally coherent data spanning ecologically meaningful timeframes

from a wide range of terrestrial and marine contexts. They have considerable potential to complement and enhance neo-ecologically derived understanding of ecosystem properties and functions and to overcome some of the 'environmental myopia' diagnosed by Lindenmayer et al. (2010). This natural human tendency to fit changes into existing frameworks, conceptual models, or ecosystem typologies can actively interfere with effective understanding and adaptation to effective science and action in a rapidly changing world. It is increasingly important to move beyond the familiar environmental boundaries of the last few centuries, within which our current ecological understanding developed, and being open to 'ecological surprises', unexpected outcomes and the emergence of novel ecosystems. Overcoming the barriers between neo-ecological and palaeoecological studies which arise from differences in spatial, temporal and taxonomic sampling methodologies, data formats and analytical approaches will increase awareness of the diversity of possible trajectories for present-day systems in a changing future. FT approaches are well suited to this synthesis and can play a vital role in developing ecological studies that go beyond the particular to a more general understanding of how ecosystems function and species interact, and how important emergent properties like resilience and persistence arise in diverse systems. As work in this area matures, we expect that trait-based approaches integrating palaeoecology and neo-ecology will create a much richer understanding of past ecologies and a deeper insight of their implications for present-day and future ecosystems and their management.

AUTHOR CONTRIBUTIONS

Kerry A. Brown, M. Jane Bunting and Fabio Carvalho convened the symposium and had the original idea for this review. Francesco de Bello, Luke Mander, Katarzyna Marcisz, Ondrej Mottl, Triin Reitalu and Jens-Christian Svenning participated in the symposium. Kerry A. Brown, M. Jane Bunting and Fabio Carvalho outlined the manuscript and led the writing and revisions. Fabio Carvalho and Francesco de Bello wrote Section 2, M. Jane Bunting wrote Section 3, and Luke Mander, Katarzyna Marcisz and Jens-Christian Svenning wrote Section 4. Kerry A. Brown, M. Jane Bunting and Fabio Carvalho developed the concepts for all figures and Kerry A. Brown constructed all figures. All other authors contributed substantially to all sections, and all draft versions and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

There are no data to archive for this manuscript.

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