Tansley review

Functional traits of fossil plants

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Summary

A minuscule fraction of the Earth's paleobiological diversity is preserved in the geological record as fossils. What plant remnants have withstood taphonomic filtering, fragmentation, and alteration in their journey to become part of the fossil record provide unique information on how plants functioned in paleo-ecosystems through their traits. Plant traits are measurable morphological, anatomical, physiological, biochemical, or phenological characteristics that potentially affect their environment and fitness. Here, we review the rich literature of paleobotany, through the lens of contemporary trait-based ecology, to evaluate which well-established extant plant traits hold the greatest promise for application to fossils. In particular, we focus on fossil plant functional traits, those measurable properties of leaf, stem, reproductive, or whole plant fossils that offer insights into the functioning of the plant when alive. The limitations of a trait-based approach in paleobotany are considerable. However, in our critical assessment of over 30 extant traits we present an initial, semi-quantitative ranking of 26 paleo-functional traits based on taphonomic and methodological criteria on the potential of those traits to impact Earth system processes, and for that impact to be quantifiable. We demonstrate how valuable inferences on paleo-ecosystem processes (pollination biology, herbivory), past nutrient cycles, paleobiogeography, paleo-demography (life history), and Earth system history can be derived through the application of paleo-functional traits to fossil plants.

I. Introduction

To date, the predominant focus of enquiry in paleobotany has been to document plant diversity and evolution (taxonomy and systematics), and through the development of climatic and atmospheric proxies (paleoclimatology), to examine how long-term environmental change has influenced plant form and diversity across time and space (paleoecology, evolutionary biology). Fewer studies have focused on the capacity of vegetation to 'force' the Earth system through its heterogeneous alteration of the hydrological cycle, weathering rates, and elemental fluxes between land and ocean. It is hypothesized that the magnitude of plant-driven forcing of the Earth system is influenced by the evolution of new plant groups that possess novel traits and trait combinations (Bonan, 1995; Boyce *et al.*, 2010; Boyce & Lee, 2010; Franks *et al.*, 2017; White *et al.*, 2020), yet to date, we lack a robust foundation of functional data on extinct plants to test these hypotheses in sufficient detail.

In this paper, we review a rich resource of paleobotanical and plant trait literature and outline a methodology for bringing fossil and extinct plants 'to life' using a functional trait-based approach pioneered by contemporary plant trait ecologists. We present a critical assessment of fossil plant functional traits that influence Earth system processes in particular. Such traits are referred to as 'effect traits' (Lavorel & Garnier, 2002; Chapin 3rd, 2003; Violle *et al.*, 2007) and are well-established in contemporary ecology. These traits have an 'effect' on ecosystem-scale processes such as carbon sequestration, chemical weathering, and decomposition. In addition to modulating local processes differently across the globe, variation in these traits is a key determinant of global biogeography. Our overarching aim is thus to identify and semi-quantitatively rank a set of fossil plant functional traits that are robust to taphonomic constraints, are relatively easy to measure across various fossil plant preservation modes and which have played a role in shaping Earth's environment, climate, and atmosphere through time via their effect on the carbon, oxygen, nutrient, and hydrological cycles (Fig. 1). We do not focus on 'response traits', such as leaf area, leaf physiognomy and wood growth rings (Lavorel & Garnier, 2002; Chapin 3rd, 2003; Violle *et al.*, 2007; Wright *et al.*, 2017), which are plant traits predominantly shaped by local environmental factors, because they have been extensively used as the fundamental underpinning of fossil plant paleo-climate proxies and reviewed in depth elsewhere (Peppe *et al.*, 2011, 2014; Yang *et al.*, 2011, 2014; Allen *et al.*, 2020; Spicer *et al.*, 2021).

For each paleo-functional trait, we: (1) provide some brief examples of how fossil plant functional traits can elucidate population and ecosystem processes, plant–climate, and plant–atmosphere interactions in Earth's deep past. (2) We highlight relationships between traits and trade-offs that have been robustly established within contemporary global datasets and that could be applied to fossil plants to obtain additional, indirect paleo-functional trait data. In cases where no suitable direct methods or trait–trait relationships have been established, (3) we present opportunities for future research to address these paleo-ecological gaps. Finally, (4) we assess how modes of fossil plant preservation and relevant taphonomic factors may potentially influence paleo-functional trait fidelity to the original trait value and its variability. Using these criteria, the author team has semi-quantitatively scored 26 fossil plant functional traits out of 30 initially assessed (Fig. 1) as a starting point for broader community engagement and to illustrate the relative ranking of paleo-functional traits based on our review.

We have organized the review using the contemporary trait selection in the 'New handbook for standardized measurement of plant functional traits worldwide' (Pérez-Harguindeguy *et al.*, 2013) with a focus first on regenerative traits that can be obtained from fossil palynomorphs and seeds followed by an appraisal of paleo-functional traits of fossil leaves and stems. In the last sections of the paper, we evaluate whole plant traits and trait syndromes that provide critical insights into extant plant ecological strategy and assess which can robustly be applied to plant fossils given their often fragmentary nature. Traits presented by Pérez-Harguindeguy *et al.* (2013) without potential application as paleo-functional traits (4 out of 30 traits) are included along with our assessment and reasoning in Supporting Information Notes S1–S7.

II. Toward the development of fossil plant functional traits

Current Earth system models (ESMs) incorporate vegetation, and biosphere feedbacks and drivers, but generally have not considered how plant-driven feedbacks and forcing over time may have changed with the emergence of new plant evolutionary groups and their associated functional traits (Matthaeus *et al.*, 2023). On geological timescales, the primary drivers of plant trait selection and filtering such as Earth's global mean annual temperature and precipitation, atmospheric composition, wildfire ecology, biota of herbivores, pathogens, symbionts, mutualists, dispersers, pollinators have all changed dramatically. Marked filtering and selection of 'response traits' in an evolving Earth may in turn have changed the forcing strength or capacity of plant traits to have an 'effect' on processes within their ecosystems. For instance, increasing atmospheric CO_2 in the earliest Jurassic selected for plants with lower stomatal conductance (g_{max}). Changes in g_{max} trait values halved evapotranspiration rates of early Jurassic forests impacting run-off in the hydrological cycle, a key Earth system process

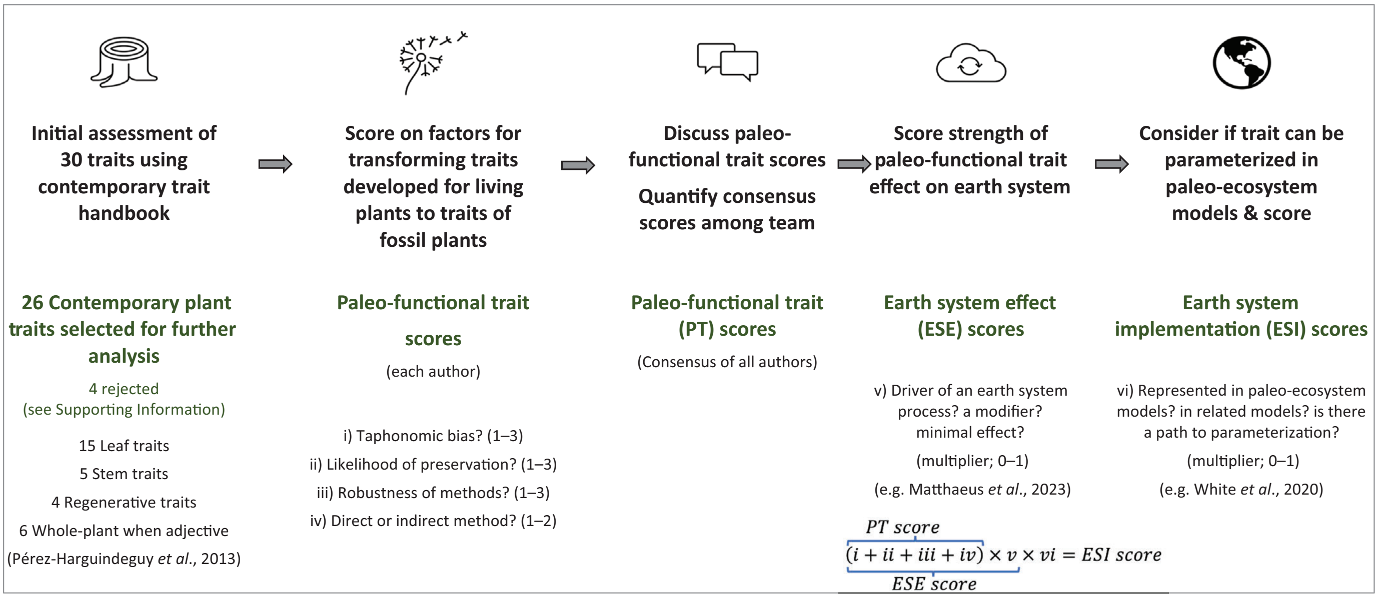

Fig. 1 Methodological framework used to critically evaluate 30 contemporary plant traits (from Pérez-Harguindeguy *et al*., 2013) for their potential application to the plant fossil record as paleo-functional traits. Four traits (leaf water potential, leaf dry matter content, leaf and litter PH, and seedling functional morphology, see Supporting Information Notes S1–S7) were deemed to have low potential applicability to fossil plants and were not evaluated beyond the initial assessment step. The 26 remaining traits were reviewed (Sections V–VII) and semi-quantitatively evaluated by the authors to produce an initial list of paleo-functional traits (Table S1), which we then ranked according to taphonomic bias (i, ii), ease and robustness of trait measurement in fossil plants (iii, iv), strength of the trait's impact on the Earth system (v) and capacity to quantify the impact of the trait on an Earth system process within paleo-ecosystem models (vi; Figs 3, 4).

(Steinthorsdottir *et al.*, 2012). We propose, therefore, that a paleo-functional trait approach in paleobotany will provide an improvement to the representation of vegetation–ESM interactions that is evidence-based, provides testable hypotheses, and is scalable. For example, a linear multiplier has historically been used to account for enhanced plant-driven chemical weathering over geological time (reviewed in Goddéris *et al.*, 2023). This assumption could be tested using fossil functional traits that likely influence weathering rates such as photosynthetic rate, litter decomposability, and xylem conductivity and by tracking changes in their trait values over time. Terrestrial productivity exerts critical influence on the carbon and nutrient cycles (N, P; Lenton *et al.*, 2018), in large part via weathering rates, and is hypothesized to have undergone step-change increases over geological time with more recently derived plant groups (angiosperms) generally being more productive than their ancestors (gymnosperms; Boyce & Zwieniecki, 2012; Boyce *et al.*, 2023). These ideas, however, are challenged by the observation that long-extinct plants (Carboniferous) had similar rates of photosynthesis and transpiration as modern angiosperms (Wilson *et al.*, 2017, 2020; Yiotis & McElwain, 2019) and are ripe for further testing using multiple paleo-functional traits – but which ones should we focus on? The uncertain trajectory of plant functional trait evolution over geological time thereby introduces uncertainty to key Earth system processes (e.g. hydrological cycle and weathering) that exert substantial control on the long-term carbon and oxygen cycles, global temperature, and the habitability of the planet.

A wealth of contemporary ecological studies demonstrates that the functional diversity of plant traits does not map simply to plant evolutionary groups (Diaz *et al.*, 2016; Bruelheide *et al.*, 2018). Global trait-based ecology has emerged in the field of contemporary ecology as a powerful tool to categorize how plants influence their abiotic and biotic environment based on their morphological, anatomical, chemical, physiological, demographic, and/or reproductive traits rather than their species identity or evolutionary relationships (Wright *et al.*, 2004; Cornwell *et al.*, 2008; Diaz *et al.*, 2016; but see van der Plas *et al.*, 2020). A trait-based ecology approach in paleobotany, where species identities are often uncertain compared with contemporary taxonomy, would thus allow the functional characterization of plants, whether long extinct or living, by their functional traits preserved in fossils. In order to critically evaluate the potential of different plant functional traits to inform Earth system science, we have semi-quantitatively evaluated every trait we review in the ensuing sections on the strength of its impact on the Earth system (Earth system effect (ESE) score, Fig. 1) and on the current capacity to quantify this impact using paleo-ecosystem models (Earth System implementation (ESI) score; Fig. 1).

III. Taphonomic constraints for a paleo-functional trait approach

A tree fell in a forest 200 million years ago; no one was there to observe it. Depending on plant type and circumstances, we might still infer how it functioned based on its traits. The plant fossil record is mostly composed of fragmented plant parts (e.g. spores, seeds, leaves, and shoots) that are preserved separately. Broadly, tissue type, preservation mode, and taphonomy (reviewed in Collinson, 1983; Greenwood & Donovan, 1991; Gastaldo, 2001; Ferguson, 2005; Sims & Cassara, 2009) determine the availability of different plant parts on which functional trait measurements can be obtained. Furthermore, each combination of tissue type, preservation mode, and trait requires a unique set of considerations regarding the bias of the resulting trait values (Fig. 1). All fossil preservation types depend on the presence of water, introducing a taphonomic mega-bias favoring plants that grew in or near wet locations or that can survive transport by water to a depositional environment (Ferguson, 2005). Furthermore, because fossil preservation is a rare outcome, robust estimates of the distribution of trait values, and extreme values (i.e. maxima) are likely unavailable most of the time, and require exceptionally preserved floras where thousands of fossil plant parts, including the most delicate (e.g. fossil flowers, pollen tubes, and fern fiddleheads), are available for study. In combination with fragmentation, taphonomy also makes disentangling trait variation from development difficult but not impossible. Part of the solution to the filtering of original trait values by the fossil record is integrating an understanding of the taphonomic factors that transform a living community of plants at some past instance in geological time to a dead assemblage of fossil plant parts, each with their measurable trait values. Taphonomic processes are very well understood for fossil plants and what is required now is that this field is extended to explicitly consider functional traits.

Most often, plant parts are preserved when they are buried quickly, enter anaerobic conditions that hinder decomposition, and are then further altered where the sediment around them becomes rock. This produces compression fossils when original organic material remains, and still-valuable impression fossils when the original matter is lost. Compression/impression fossils allow for the measurement of gross morphological trait values, but deformation due to compression may alter individual traits. Chemical traits may be measured from compressions, though they may be altered in diagenesis (Box 1; Ferguson, 2005) and biased by fossilization potential (Spicer, 1989; Tegelaar *et al.*, 1991; Bacon *et al.*, 2016) likely imposing artifacts in trait values at the plant community/ fossil assemblage scale. This mode of preservation is more likely to preserve tissues that are resistant to fragmentation, deformation, and decomposition, suggesting that functional traits measured from compression/impression fossils will more likely be biased toward trait values of more robust plants and plant parts with dense and/or tough lignin-rich, suberin-rich, or polymer-rich tissues.

In a few special circumstances, anatomy can be preserved in plant fossils. Plant tissues that are flooded with mineral-saturated water or inundated *in situ* by volcanic ash falls (e.g. Wuda Tuff flora), or partially burned in forest fires produce permineralization (see Box 1) and charcoalified fossils, respectively (Schopf, 1975; Wang *et al.*, 2012). These allow measurement of cellular-scale and morphological traits that can be obtained with minimal alteration due to deformation but in most cases, little unaltered organic material remains, precluding ready access to functional traits based on plant chemistry or stoichiometry. Permineralization of fossils allows preservation with less fragmentation, and occasionally of

Box 1 Definition of terms.

Demographic traits: vital rates for the processes of growth, survival, and reproduction that are calculated at a population level. Demographers use life-history traits measured at population levels to model complex attributes of vital rates such as lifespan and maximum age at reproductive maturity.

Diagenesis: the physical and chemical alterations to plants and plant parts and their surrounding sediments that occur during the process of fossilization (before deep metamorphic processes under high temperatures and pressures) and ultimately determine whether the plant/ plant part and its trait values are preserved or destroyed.

Fossil plant (paleo-) functional traits: a measurable property of a plant fossil that is inferred to have influenced the function of the plant while it was alive, and which likely affected its environment or its fitness. These inferences are usually made through relationships between structure or chemistry, and plant function that have been established, and continue to be developed in modern plants.

Fossil plant preservation modes: types of plant fossil preservation are determined by the matrix type (and grain size) the fossil is embedded in as well as the specimens' paleoenvironmental setting. There are six broad preservation categories. Those of two-dimensional preservation are compressions and impressions (Schopf, 1975); the latter lacking any remaining organic material. Three-dimensional preservations are permineralization, casts/molds, and compactions, with permineralizations lacking organic material (except cell walls) as the plant tissue is infiltrated by mineral deposits during formation. These modes have been abundantly described in the literature by case-to-case scenarios and much descriptive work was initially addressed by Schopf (1975). Lastly and of more recent application, molecular preservation retains organic compounds though lack structural remains.

Life-history traits: metrics or quantities that are integrated over a plant's life cycle and usually calculated at population levels (e.g. maximum age at reproductive maturity). Some life-history traits can also be considered as plant functional traits when measured at the level of individual rather than population. Our focus here is on those which can be measured on individuals.

Plant functional traits: broadly defined as any measurable morphological, anatomical, physiological, biochemical, or phenological trait of an individual plant that potentially affects its environment or its fitness (from Pérez-Harguindeguy *et al*., 2013). For the purpose of this review, we focus more on plant functional traits which affect their local, regional and/or global environment (Chapin 3rd's (2003) 'effect' traits) as these are important for Earth system modelling (*sensu* Lavorel *et al*., 2007) in the present and past (Matthaeus *et al*., 2023).

Taphonomy: the fossil record of plants presents a biased representation of living vegetation that once existed. Taphonomy is defined as the processes and factors involved in the transformation of these once-living plant communities to an assemblage of fossil plants preserved within the rock record. According to Greenwood & Donovan (1991), 'plant taphonomy incorporates the processes of the initial abscission of plant parts, their transport (by air and/or water) to a place of eventual deposition, entrapment and eventual burial, and subsequent lithification'.

Trait syndrome: suite of consistently coordinated/correlated traits that occur across multiple scales of biological organization and environmental gradients that result from evolutionary processes (e.g. plant flammability, litter decomposability, and photosynthetic pathway).

herbaceous plants and delicate structures, depending on the process of initial burial. In some exceptional cases, for example, the Rhynie Chert (Trewin, 1994) and Chemnitz Fossil Forest (Rößler *et al.*, 2012) communities are preserved in growth position, allowing measurement of multiple functional traits from the same fossil plant, and whole plant traits in an ecosystem context. In sections V–VIII, we evaluate the research potential of reproductive, leaf, stem, and whole fossil plant functional traits in the context of some of the biases and limitations imposed by preservation mode and taphonomy (i and ii in Fig. 1).

IV. Methodological constraints for a paleo-functional trait approach

The form, development, and taxonomy of plants are increasingly uncertain for extinct plants in deep time. Whereas modern plant ecologists generally begin their investigations with whole plants of known species, plant paleobiologists must start from plant parts. Understanding plant form from a mostly fragmented fossil record requires conceptual reconstruction of plants from fossils containing attachments of one organ to a different kind of organ (e.g. a shoot with an attached seed). Whole plant reconstructions represent a best-case scenario, requiring a comprehensive collection of attachments, often from different fossiliferous beds (e.g. Matsunaga & Tomescu, 2017). The core experimental grouping of the plant paleobiologist, therefore, is not an individual plant, but the plant part available to measure. Furthermore, the co-variation of traits in whole plants is generally unavailable on an individual fossil specimen due to fragmentation and separation of stems, leaves and fruits due to taphonomic processes (Box 1). However, information on the co-variation of traits is often available within a fossil assemblage at the bed level where tens to thousands of different plant organs that originally occurred as litter within the living community are preserved in the same relative abundance ranking as was present in the living vegetation (Burnham *et al.*, 1992). Fossil plant assemblages of this nature enable deep investigation into trait variance within- and between species, assessments of appropriate sample sizes needed to achieve stable trait means, and ultimately the calculation of community-weighted mean trait values.

The limitations of using a paleo-functional trait approach are considerable and multifaceted. Nonetheless, plant fossils represent the one ground-truth record of the foundation of terrestrial ecosystems across deep time. Inferences of trait values from fossil plants may be made more robust by combining estimates from multiple plant parts and using direct measurement alongside biophysical and biochemical relationships between sub-tissue properties and function (e.g. C3/C4 photosynthetic pathways may be distinguished directly using anatomy when it is preserved, and indirectly using C isotopic signatures). Furthermore, the integration of contemporary plant ecology regarding trait trade-offs and economics with the plant fossil record allows for the inference of additional trait values by analogy or through observed trait–trait correlations. For example, six leaf traits (photosynthetic capacity (A_{mass}), dark respiration rate (R_{mass}), leaf mass per area (LMA), leaf lifespan (LL), leaf nitrogen (N_{mass}), and phosphorous content (P_{mass})) co-vary strongly in contemporary global datasets across thousands of species and climate zones; they collectively describe the 'leaf economic spectrum' – the economics of constructing and maintaining a leaf and the trade-offs involved (Wright *et al.*, 2004). Because correlations between some functional traits are so well constrained for extant plants, this opens a window of possibility in paleobotany to infer traits that cannot be measured in fossils, such as P_{mass}, from those that can using multiple methods (e.g. LMA; see leaf economic traits). Variation in trait inferences may then be studied across scales (i.e. within and among fossiliferous bed, horizon, region, biome, and age) to form a picture of vegetation–climate interactions across deep time. We take these methodological considerations (iii and iv in Fig. 1) into account in a semi-quantitative evaluation of every trait in the following sections to ultimately calculate a '-Paleo-functional trait score' for each trait we review. A ranked list of paleo-functional traits is finally produced in the conclusion section by weighting Paleo-functional trait scores for each trait by its ESE and Implementation Scores (see Fig. 1).

V. Functional traits of fossil spores, pollen, and seeds

1. Spores and pollen

The study of functional traits of fossil pollen and spores provides key insights into persistence and resilience of plants, fungi, and ecosystems under environmental change, in particular drought (Abrego *et al.*, 2017; Brussel *et al.*, 2018; Sande *et al.*, 2019; Table 1) as well as inferences on dispersal syndrome and pollination success. Thicker spore walls in forest edge fungi are likely linked to UV-light tolerance, and/or harsher environmental conditions (Norros *et al.*, 2015; Abrego *et al.*, 2017) and habitat characteristics (e.g. moisture) have likely played a substantial role in the evolution of pollen morphology (Ackerman, 2000; Franchi *et al.*, 2011). The presence of pollen wall apertures is related to environments characterized by dry seasons or occasional droughts (Franchi *et al.*, 2011). Although much pollen trait-based research to date tends to be reliant on recently collected data (*c.* 20 yr; Franchi *et al.*, 2011; Nogué *et al.*, 2022), several studies have shown the importance of the incorporation of paleo-ecological and paleontological data into trait frameworks to understand plant performance, fitness, and/or functioning (Reitalu *et al.*, 2015; Brussel *et al.*, 2018; van der Sande *et al.*, 2023). The microscopic size of pollen and spores and their low taxonomic resolution create a challenge to their incorporation as functional traits into global trait analysis. However, potential methodologies have been proposed (reviewed in Reitalu & Nogué, 2023; Table 1). Taphonomic biases in the pollen and spore record are very well constrained compared with other fossilized plant parts, and there is a high likelihood of their fossilization. For these reasons, together with a high potential for direct measurement of trait values from pollen and spores, we attributed a relatively high overall Paleo-functional trait score to spores and pollen (10) (Fig. 3; Table S1). However, lower ESE (3) and ESI (0.3) scores were however assigned (Fig. 1), because although dispersal is a key determinant of biogeographic units, which in turn influence climate and biogeochemical cycles, realized dispersal also relies on vegetative traits. Furthermore, dispersal is

Table 1 Functional traits of fossil pollen.

Trait	Life history/ dispersal syndrome*/climate preference Trait description in relation to drought tolerance and dispersal
Pollen size Small (S), 10–25 μm Medium (M), 26–50 μm Large (L), 51–100 μm	*Tolerance to drought*: Larger pollen grains should have an advantage over smaller ones when desiccation intensity increases: to minimize the rate of water loss due to desiccation, a plant produces larger grains that also have a lower surface-to-volume ratio (Ejsmond *et al*., 2011) *Dispersal*: We expect small and medium pollen grains (e.g. 20-40 μm) to disperse better than those with larger pollen grain (> 40 μm; Vonhof & Harder, 1995). We also expect that small and medium pollen grains to be wind-pollinated and that larger pollen grains to be mostly animal-pollinated. But this is controversial. Smaller sizes are suggested to reduce the settling velocity and, thus, increase the dispersal distance of the pollen (Niklas, 1992). However, various mechanisms exist to increase dispersal distances by reducing pollen mass, such as the presence of air sacs of many conifers (Ackerman, 2000; Schwendemann *et al*., 2007) Pollen size has been found to be affected by chromosome ploidy level, environmental factors, and flower characters, among others (Muller, 1979; Stroo, 2000) and may determine reproductive and seed-siring success as large pollen grains have higher chances of successful fertilization because their size determines the growth rate of pollen tubes (Cruzan, 1990; Ejsmond *et al*., 2011)
Shape oblate, prolate, spheroidal	*Dispersal*: There is evidence that suggests that spherical pollen grains are more present in wind-pollinated plants (Niklas, 1985b; Vaknin *et al*., 2008). In addition, spherical pollen grains dispersed further (Niklas, 1985b; Jackson & Myford, 1999; Ackerman, 2000). The relationship between oblate and prolate pollen grain shapes and dispersal type is not clear. Pollen shape does not seem to play a major role in preferences of forage sources (e.g. honeybees on *Gossypium Hirsutum*; Vaissière & Vinson, 1994)
Aperture types and number Innaparture (0) Colpate (1, 2, 3, > 3) Porate (1, 2, 3, > 3) Colporate (1, 2, 3, > 3)	*Tolerance to drought*: Pollen tolerance to drought may be indicated by the presence of apertures (furrows, pores; Fig. 2; Moore *et al*., 2008, Franchi *et al*., 2011). Apertures are structural elements that allow variation in the pollen volume with changing moisture conditions (Franchi *et al*., 2011) Pollen grains with low desiccation tolerance ('recalcitrant') and furrows are usually absent and there may be an absence of pores (Franchi *et al*., 2011). Recalcitrant plant species are more likely to occur in moist habitats. Pollen grains with high desiccation tolerance ('orthodox'), furrows are usually present
Presence of sculptures (exine) Psilate, Perforate (micro- and macro-); Reticulate; Rugulate; Striate; Gemmate; Verrucate; Echinate	*Dispersal*: Pollen wall sculptures (e.g. perforate, reticulate, and rugulate) may be affected by pollination syndrome (reviewed in Hesse *et al*., 2000; Konzmann *et al*., 2019). Rich ornamentation is associated with entomophily (Vaknin *et al*., 2000; Hu *et al*., 2008). Sculpturing plays an important role in attachment to insect pollinators and to the stigma of the flower Wind-pollinated species often lack elaborate sculptures and appear smooth (i.e. psilate). But, this is controversial as the presence of sculptures on the pollen wall is suggested to be a specific feature for each plant taxon (Pacini & Hesse, 2012)
Dispersal unit (e.g. monad, tetrad)	*Dispersal*: Pollen grains are generally dispersed as monads (single grains) and tetrads (four grains derived from the same meiocyte; Pacini & Franchi, 1999). In addition, some pollen grains present a fluid called pollenkitt. This fluid glues the pollen grains together and forms clumps of both monads and tetrads (e.g. Ericaceae) Monad pollen is a common characteristic for both entomophilous and anemophilous taxa (Chaloner, 1986). However, pollenkitt is typically present in almost all zoophilous plants (Pacini & Hesse, 2005)
Wall thickness (exine) < 2 μm > 2 μm	*Tolerance to drought*: The function of the wall is considered to be mainly protection against adverse environmental conditions such as desiccation and UV radiation (found in fungal spores also). Reduced wall thickness has been considered to be an advantage for taxa living in humid, moist, or even wet environments. The advantage consists of a rapid germination due to the short rehydration time (Pacini & Hesse, 2012)

Terminology used for the six pollen traits (pollen size, shape, apertures, sculptures, dispersal unit, and wall thickness) follows the Palynological Database-PalDat (https://paldat.org) and Halbritter *et al*. (2018).

*We use the concept pollen dispersal to refer to how far for example airborne pollen grains may travel before being deposited (Yao *et al*., 2022).

not currently parameterized within paleo-ecosystem models. Furthermore, many of the key functional traits conferring resilience to drought highlighted below (Table 1) are stronger 'response' traits than 'effect' traits.

2. Seed size and shape

Here, we consider the traits of seeds as they enter the soil or a suitable depositional environment and do not include the fruit or dispersal structures (Fig. 2) associated with the seed as these are much less likely to be preserved in the fossil record. There is an enormous (11 orders of magnitude) variation in seed size among extant plants (Moles *et al.*, 2005a). Still, biases imposed by the fossilization process and factors that influence the movement of seeds into suitable depositional environments are all likely to filter the full range of paleo-seed diversity (Sims & Cassara, 2009). Despite the fact that the fossil record is imperfect, the function of seeds to protect and transport the embryo means that of all plant parts, seeds are very well represented as fossils. Seed size is one of six plant traits selected for its global significance in defining the functional bauplan of extant plants (Diaz *et al.*, 2016); it defines a trade-off between the seedling survival and colonization potential and is strongly correlated with plant height (Diaz *et al.*, 2016). Seeds are usually discrete units but there are exceptions. Seed size, shape, and structure, especially, have been shown to be good indicators of seed persistence in the soil in some biomes

(Thompson *et al.*, 1993; Diaz & Cabido, 1997; Leishman & Westoby, 1998; Peco *et al.*, 2003), which in turn plays a major role in the survival of species in time and space (Christoffoleti & Caetano, 1998). For example, rounder seeds with lower shape values (closer to 0 than to 1) tend to be buried deeper into the soil and seed bank and persist longer (Pérez-Harguindeguy *et al.*, 2013). Interestingly, small seed size is likely underrepresented in the fossil record (Sims & Cassara, 2009), and fossil seed assemblages often contain seeds from species that have travelled long distances and are not therefore representative of the local flora (Collinson, 1983; Burnham, 1990), suggesting considerable taphonomic filtering at play.

In extant plants, seed size (sometimes referred to as mass) is measured by oven-dry mass (Moles *et al.*, 2005a; Pérez-Harguindeguy *et al.*, 2013) and seed shape is defined by its variance in three dimensions (*x*, *y*, *z* – thickness, width, length; Pérez-Harguindeguy *et al.*, 2013). In fossil plants, seed shape can still be defined by its variance in two to three dimensions using a range of microscopy and micro-CT methods (DeVore *et al.*, 2006). Once characterized, seed size and shape can be used beyond taxonomic characterization (DeVore *et al.*, 2006; Matsunaga *et al.*, 2019) and open a window on the functional ecology of the whole plant in the absence of other articulated fossil plant parts. However, taphonomic biases should be considered (Sims & Cassara, 2009). For example, seed mass is strongly correlated with genome size (Beaulieu *et al.*, 2007), growth form (Moles *et al.*, 2005a,b; Beaulieu *et al.*, 2007), dispersal syndrome (Moles *et al.*, 2005a,b), plant lifespan (Moles *et al.*, 2005b), and weakly correlated with net primary production (Moles *et al.*, 2005a). Seed size and shape trait yielded a relatively high paleo-functional trait score in our semi-qualitative analyses (10) but low ESE and ESI scores due to the fact that correlations between this trait and Earth system processes such as photosynthesis are weak and because the functional attributes that correlate strongly with seed size such as dispersal and plant lifespan are not currently parameterized within paleo-ecosystem models (Fig. 3; Table S1).

3. Dispersal syndrome

Dispersal syndromes (Pérez-Harguindeguy *et al.*, 2013) are seed, fruit, or spore morphologies (referred to collectively as disseminules) and the associated modifications that enhance the probability of being dispersed away from the parent plant and characterize a distinct mode of dispersal (Hughes *et al.*, 1994). Such syndromes are known to facilitate dispersal via flotation in water, by animal consumption, or by wind, among other modes. Dispersal by gravity will be excluded from this review as no specialized adaptations are required for this mode (Castro *et al.*, 2010; McLoughlin & Pott, 2019). Where dispersal syndrome can be distinguished based on fossil disseminule morphology, it potentially provides useful insights into fossil species biogeographic limits and biotic interactions within paleo-ecosystems even in the absence of body fossils of the disperser (Robledo-Arnuncio *et al.*, 2014; Aslan *et al.*, 2019; Wojewódzka *et al.*, 2019; Rojas *et al.*, 2022).

Dispersal syndrome can be directly inferred from morphological observations of fossils and comparisons with relevant extant examples. Reproductive architectures like the rain-splash cups that accommodate water dispersal seen in liverworts are also found in *Cooksonia*, one of the earliest land plants, although the dispersal syndromes of the spores themselves remain unspecified (Briggs & Crowther, 2008; Murray, 2012; Medina & Estebanez, 2014). Hypothesized plant–insect mutualism is proposed for Permian lycopsid megaspores based on the presences of external starch structures (elaiosomes; Liu *et al.*, 2018). Dispersal syndrome at the ecosystem scale can be indirectly inferred from dental adaptations (Norconk *et al.*, 1998; Guimarães *et al.*, 2008), and coprolites (Habgood *et al.*, 2003). Spore phytophagy in insects is hypothesized for some Carboniferous lycopsids (Chaloner, 1984), providing early evidence for the potential evolution of a dispersal syndrome based on plant–animal interaction. Combinations of direct and indirect evidence, seed morphology, and availability, inferred from the coprolite record, have helped identify deep-time frugivore diets (Dutta & Ambwani, 2007) and contextualize ecological shifts in more recent ecosystems (Boast *et al.*, 2018; Heinen *et al.*, 2023).

Spatial resolution poses a problem for inference of dispersal syndrome. Any disseminule can be transported accidentally via a prevalent dispersal type regardless of the disseminule's adaptive morphology (Pérez-Harguindeguy *et al.*, 2013), and this limitation is magnified for fossils. For example, nonfrugivorous animals consume a wide array of plants and unintentionally disperse fleshy seeds, carrying them long distances regardless of whether the dispersal syndrome is adapted for long or short distances, biasing inferences from the fossil record (Green *et al.*, 2021). Other taphonomic processes such as preburial filtering, reworking, and transport (allochthonous assemblages) can also make the time and place of origin of fossil disseminules unclear. Fossil disseminules may be disintegrated or ruptured, requiring reconstruction, and interfering with syndrome inferences. Nonetheless, evidence of ornamentation or detachment scars from detached fossil appendages (e.g. wings; Fig. 2) can aid in classification (McLoughlin & Pott, 2019). However, even direct morphological inferences of paleo-ecological function may be prone to error (Green *et al.*, 2021). For example, dissimilar fern spore morphologies are anemochorous (Gómez-Noguez *et al.*, 2017), are unexpectedly endozoochorous in certain ecosystems (Lovas-Kiss *et al.*, 2018), and may function in other components of life history (see Table 1). Some important features of dispersal syndromes may be irrecoverable from fossils (i.e. smell, color, sticky textures/substances; Tiffney, 2004). However, successful development of fossil color biomarkers in dinosaur feathers (McNamara *et al.*, 2021) and the observation that nano-surface structures on extant flowers influence petal color (Moyroud *et al.*, 2017) suggest that future advances may allow inference on some of these usually hidden features. In the absence of direct observation of dispersal *per se*, inference of the function of particular structures and dispersal syndromes in the fossil record may therefore be unclear in many cases. This complexity is reflected by the fact that multiple dispersal syndromes have been proposed for some plant groups including Permian *Glossopteris* (Klavins *et al.*, 2001; McLoughlin & Prevec, 2021), fossil *Cycas* (Murray, 2012; Liu *et al.*, 2021), and fleshy seeds in general (e.g. *Ginkgo*; van der Pijl, 1969; Tiffney, 1984; Mack, 2000; Bolmgren & Eriksson, 2005; Del Tredici, 2007; Valenta & Nevo, 2020, 2022). Based on these considerations, we assigned modest paleo-functional trait (7.5) and ESE (5.6) scores for the trait 'dispersal syndrome' and low scores for ESI (0.56), because although undoubtedly the evolution of new dispersal traits through

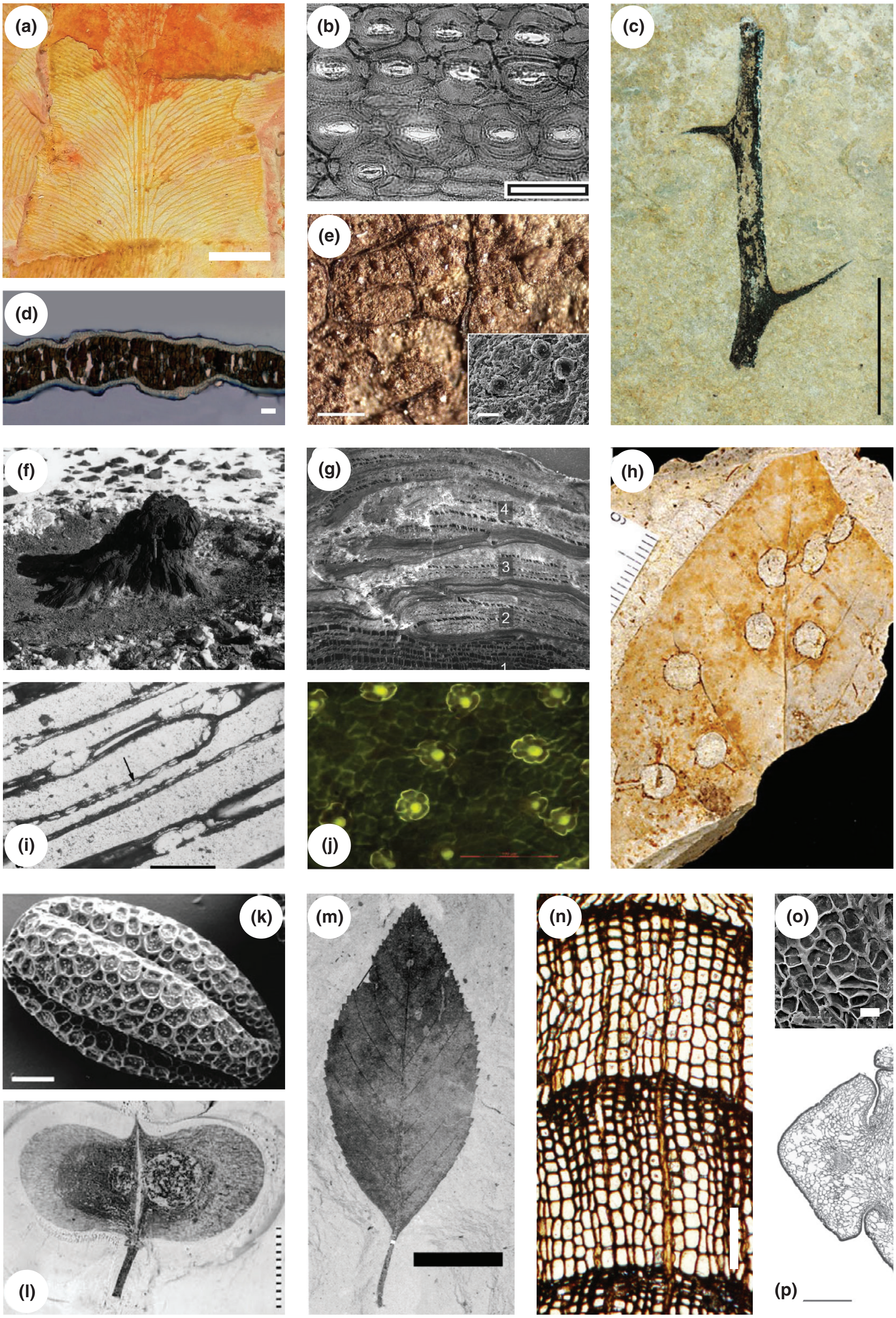

Fig. 2 Examples of fossil plant functional traits. (a) Vein density trait illustrated for Permian *Glossopteris* from Esperança Júnior *et al*. (2023, reused with permission) Bar, 5 mm. (b) Leaf g_{max} trait (a function of stomatal density and pore geometry) illustrated on Cretaceous aged Podocarpaceae compression fossils (Pole & Philippe, 2010, reused with permission) Bar, 50 μm. (c) Spinescence trait (SI) illustrated for Eocene fossil twigs from Tibet (Zhang *et al*., 2022, reused under the terms of a CC-BY 4.0 license) Bar, 10 mm. (d) Leaf mass per area (LMA) trait illustrated on cross-section of Jurassic fossil *Ginkgo* leaf estimated from measurements of cuticle thickness (Soh *et al*., 2017, reused with permission) Bar, 10 μm. (e) Salinity trait illustrated by the ghost presence of CaOx globules (interpreted as druses) on late Oligocene aged *Quercus neriifolia* impression fossils (Malekhosseini *et al*., 2022, reused under the terms of a CC-BY 4.0 license) Bar, 200 μm, inset = 40 μm. (f) Plant height trait can be estimated from fossil trunk diameter on *in situ* fossil tree stumps such as illustrated from the Triassic of Antarctica (Cúneo *et al*., 2003, reused with permission) pen Bar, 14 cm. (g) Bark thickness trait illustrated on Early Carboniferous fossil tree from Australia (Decombeix, 2013, reused with permission) showing successive zones of periderm layers, Bar, 2 mm. (h) Palatability trait measured from the ratio of presence of feeding damage as illustrated by large circular hole feeding on fossil dicot leaf species (Currano *et al*., 2008, reused with permission, copyright (2008) National Academy of Sciences) Bar, 11 mm. (i) Xylem conductivity trait measured from xylem pit membrane (arrow), pit orientation, and abundance shown here on longitudinal sections of polished pyritized Eocene fossil twigs of *Pityoxylon* (Grimes *et al*., 2002, reused with permission). (j) Cuticle trait illustrated using auto-fluorescent properties of Cretaceous aged Angiosperm cuticles (LK-B-55) from West Greenland highlighting secretory trichomes (pellucid dots; C Fay, JC McElwain, & S Robinson, unpublished) Bar, 100 μm. (k) Pollen trait indicating resistance to drought by the presence of furrows illustrated here for recent *Citrus lanatus* (Franchi *et al*., 2011, reused with permission) Bar, 10 μm . (l) Dispersal syndrome illustrated in winged fossil fruits of Eocene aged *Bridgesia bovayensis* (Manchester & O'Leary, 2010, reused with permission) scale bar in mm. (m) LMA trait based on petiole thickness illustrated for Eocene *Alnus parvifolia* from Royer *et al*. (2007), reused with permission) Bar, 1 cm. (n) Life history and maximum plant lifespan can be indirectly inferred from fossil ring width measurements illustrated here in Jurassic permineralized fossil wood *Protophyllocladoxylon* from Vajda *et al*. (2016, reused under the terms of a CC-BY 3.0 license) Bar, 100 μm; (o) Photosynthetic pathway is a syndrome of traits, one of which, cuticle pegs (spandrels) are observed here on the inner surface of the adaxial leaf epidermis of Cretaceous *Frenelopsis teixeirae* compression fossils (Mendes *et al*., 2010; reused with permission) Bar, 200 μm. (p) Mesophyll conductance (g_m) trait can be inferred from mesophyll cell wall thickness within anatomically preserved fossil leaves as illustrated here in a permineralized conifer scale leaf of *Cunninghamia lanceolata* from Brink *et al*. (2009), reused with permission) Bar, 0.5 mm.

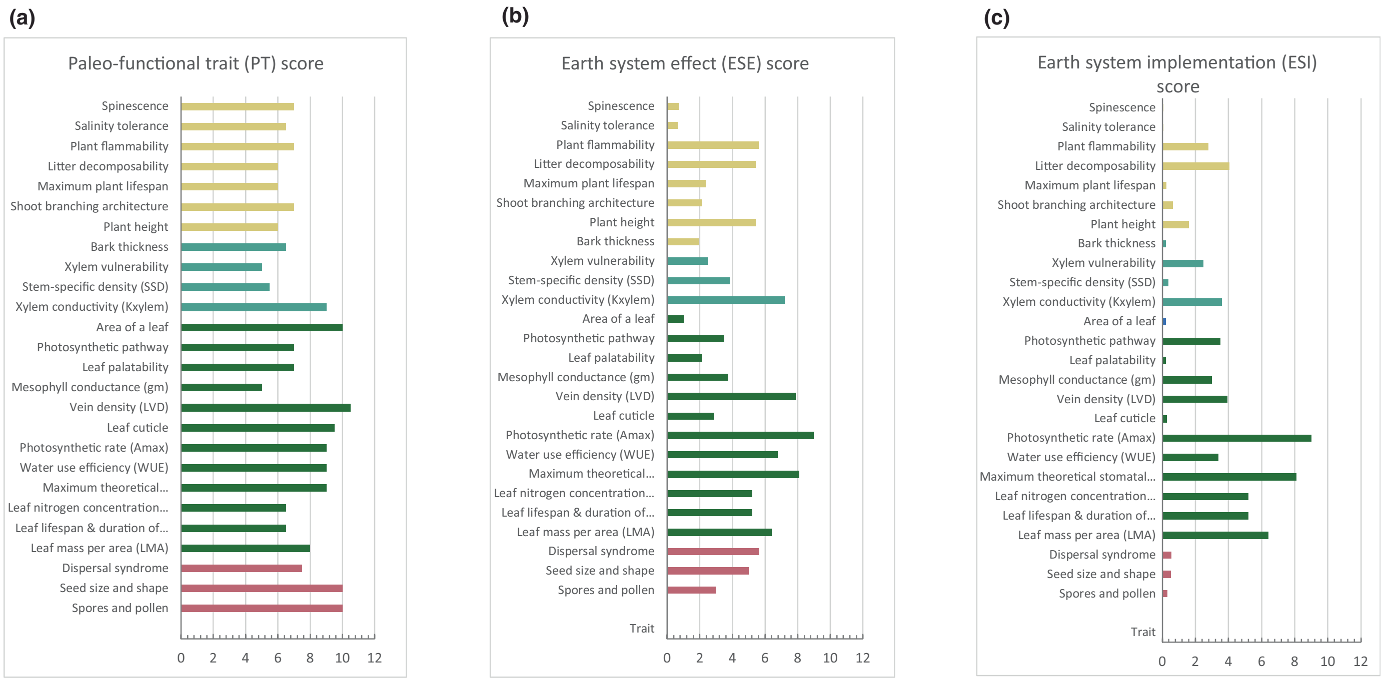

Fig. 3 Comparison of paleo-functional trait scores according to different weighting criteria. (a) Paleo-functional trait (PT in Fig. 1; Supporting Information Table S1) score plots the consensus results of the author team's semi-quantitative evaluation (Fig. 1; Table S1) of how taphonomic bias and methodology of trait measurement influence trait values in fossil plants. Higher PT scores indicate less taphonomic bias and more robust methods of trait estimation. (b) Earth System effect (ESE in Fig. 1; Table S1; ESE = PT × v) score plots the results of the PT score weighted by the author team's semi-quantitative evaluation of the strength of effect of the paleo-trait on the Earth system, with higher scores indicating greater impact. (c) Earth system implementation (Earth system implementation (ESI) in Fig. 1; Table S1; ESI = ESE × vi) score adjusts the results of the ESE score according to the current capacity to parameterize the paleo-trait and its impact on the Earth system within paleo-ecosystem models. Higher ESI scores indicate greater potential application of the paleo-trait to address questions in relation to Earth system processes.

geological time (e.g. the first seed plants in the Devonian and angiosperms in the Cretaceous) influenced biotic interactions and dispersal potential, the 'effect' of such traits on Earth system processes cannot explicitly be quantified within paleo-ecosystem models (Fig. 3; Table S1). This is an interesting research gap that warrants further study.

VI. Fossil leaf functional traits

1. Leaf mass per area

Leaf mass per area (in g m^{-2}), also referred to as specific leaf area (SLA = 1/LMA), is calculated for extant plants by dividing the dry mass by the area of one side of a fresh leaf (Pérez-Harguindeguy *et al.*, 2013). LMA is a leaf economic trait, which, together with LL, leaf nitrogen concentration (LNC), photosynthetic rate (A_{mass}), and respiration rate collectively, reflect the spectrum of ways in which a leaf can be constructed, maintained, and operated as primary photosynthetic structure (Wright *et al.*, 2004; Reich, 2014). LMA is one of the most readily measured and useful plant functional traits within the leaf economic spectrum. Broadly speaking, low LMA leaves such as those of extant deciduous trees (median = 75 g m^{-2}) tend to grow faster, have higher A_{mass} and stomatal conductance (g_s), have less carbon investment in structural tissues, shorter LL, and higher LNC; the corollary is observed for leaves with high LMA such as evergreen gymnosperms (median = 227 g m^{-2}), which invest heavily in structural tissues, have long LLs but the trade-off is lower LNC and A_{mass} per mass (Wright *et al.*, 2004; Poorter *et al.*, 2009). Collectively, leaf economic spectrum traits, including LMA, are important predictors of ecosystem-scale processes such as productivity (Chapin 3rd, 2003; Poorter & Bongers, 2006), decomposition and nutrient cycling (see Decomposition; Cornwell *et al.*, 2008), herbivory (see Leaf Palatability; Currano *et al.*, 2008), and water use efficiency (WUE; Soh *et al.*, 2019). They have already been utilized in fossil plants to infer paleo-life history (e.g. pace of life; Blonder *et al.*, 2014) and whole plant ecological strategy (e.g. stress tolerator, Soh *et al.*, 2019), but such inferences are complex (Kelly *et al.*, 2021; see Section VII).

Fresh leaf area and dry mass cannot be directly measured in fossils due to dehydration, shrinkage, compression, and selective loss of internal leaf tissues that occur during fossilization. Furthermore, taphonomic factors likely strongly bias the fossil record against the preservation of low LMA taxa due to the low abundance of carbon-rich structural compounds resulting in greater mechanical damage during transport to a depositional environment (Bacon *et al.*, 2016). Despite these challenges, numerous independent proxy methods have been developed to quantify paleo-LMA from adaxial epidermal density (Haworth & Raschi, 2014), leaf petiole width (Royer *et al.*, 2007, 2010; Peppe *et al.*, 2014; Fig. 2), and leaf cuticle thickness (Soh *et al.*, 2017; Fig. 2), all of which scale positively with LMA. Multiple trait models that include leaf ^{13}C, petiole width, and epidermal cell area have also been developed to predict paleo-LMA and paleo-canopy position (Cheesman *et al.*, 2020). High LMA leaves have a greater investment in structural tissues, higher densities of smaller cells, larger petioles to mechanically support leaves that have thicker tissue layers (including cuticle), and/or more dense tissue. Application of paleo-LMA methods to fossil plants has enabled functional classification of extinct genera (Soh *et al.*, 2017; Wilson *et al.*, 2017), assessment of extinction selectivity associated with mass extinction events (Blonder *et al.*, 2014; Soh *et al.*, 2017; Butrim *et al.*, 2022), and appraisal of herbivore-plant interactions (Currano *et al.*, 2008) among many others. Not surprisingly, therefore, LMA scored highly as a paleo-functional trait (8) and ESE Trait (6.4) and yielded high ESI scores in our evaluation as it is among a few functional traits currently parameterized in paleo-ecosystem models (Fig. 3; Table S1).

2. Leaf lifespan and duration of green foliage

Leaf lifespan, or the period of time for which a leaf is alive and physiologically active, as well as duration of green foliage, is useful in understanding a plant's nutrient use strategy, life history, leaf decomposability, palatability, and canopy position (Aerts, 1995; Wright *et al.*, 2004). Leaf lifespan covaries with LMA, A_{mass}, and g_s (Wright *et al.*, 2004; Poorter *et al.*, 2009). The duration of green foliage is important in the hydrological cycle, for productivity and Earth albedo effects, and should be included where possible within paleo-ecosystem models (Matthaeus *et al.*, 2023). Shorter-lived leaves tend to show resource allocation toward high photosynthetic rates and have lower investment in C-rich lignified tissues, whereas longer-lived leaves are often lignin-rich and tend to allocate resources toward leaf protection (Reich *et al.*, 1991). Longer-lived leaves decompose more slowly due to a higher proportion of structurally complex tissue, but they tend to sink in water faster than leaves with lower LMA (Greenwood & Donovan, 1991; Gastaldo, 2001). This may provide a taphonomic bias toward leaves with a long lifespan in fossil litter deposits preserved *in situ* (Bacon *et al.*, 2016; e.g. volcanic ash deposits) but toward leaves with a much shorter lifespan in fossil assemblages filtered by transport via water (e.g. lake deposits).

Leaf physiognomy (size and shape) and abscission scars (Thomas & Cleal, 1999) have traditionally been used to characterize whether a fossil leaf is deciduous or evergreen; however, these parameters provide mixed signals in relation to LL. Thick leaves, small leaf surface area, and thick cuticles in combination are typically associated with an evergreen habit (Thomas & Cleal, 1999; Falcon-Lang & Cantrill, 2001), but there are many exceptions and leaf thickness cannot be measured easily in fossils. Entire margins, drip tips, and leaf size are associated with tropical rainforests, which have an evergreen canopy but with varied LL (Burnham & Johnson, 2004). Fossil growth ring anatomy may be a better way to assess LL in fossils; leaf traces within the rings of juvenile stems or branches differ between deciduous and evergreen conifers (Falcon-Lang & Cantrill, 2001). In some cases, anatomically preserved leaf traces can show a number of growth ring increments indicating the longevity of a particular leaf (Falcon-Lang & Cantrill, 2001). However, this method is not widely applicable due to difficulties associated with preservation and sample preparation (Falcon-Lang & Cantrill, 2001). Furthermore, a precise age estimate is not possible for LLs of < 1 yr. The markedness of the growth ring boundary in trunk woods may also be used to estimate LL in anatomically preserved coniferopsids (Falcon-Lang, 2000a,b; Falcon-Lang & Cantrill, 2001), but the method requires well-preserved specimens, which lack growth abnormalities (Falcon-Lang & Cantrill, 2001). Both methods using growth ring anatomy also require the assumption that distinct growth rings represent annual increments, which may not be the case.

The most fruitful route for obtaining LL estimates from fossils comes from leaf trait relationships within the leaf economics spectrum; in particular with LMA (Wright *et al.*, 2004; Poorter *et al.*, 2009; see LMA section above). While the leaf LL–LMA relationship is significant (positive), it is also noisy, showing a shallower response along an environmental gradient (e.g. increasing aridity, temperature, and irradiance; Wright *et al.*, 2004; Royer *et al.*, 2010). Therefore, it is more appropriate to infer LL from LMA at an assemblage level to avoid over-interpreting LMA estimates of individual taxa (Royer *et al.*, 2010; Soh *et al.*, 2017). Chemical characterization of fossil leaf waxes may also prove useful in the development of novel LL proxies in the future (García-Plazaola *et al.*, 2015; Leide *et al.*, 2020). Large differences are observed between n-alkane abundance in angiosperms and gymnosperms, and within these groups, a higher abundance of n-alkanes is associated with longer-lived leaves (Diefendorf *et al.*, 2011). However, when considered in a broader phylogenetic context, these differences appeared to be less pronounced (Diefendorf *et al.*, 2015). Further work incorporating more detailed descriptors of LL (as opposed to just 'evergreen' or 'deciduous'; Diefendorf *et al.*, 2015), as well as a more comprehensive leaf chemical characterization (Leide *et al.*, 2020) are thus needed. High scores were assigned to LL across all the categories in our semi-quantitative analyses as although taphonomic biases toward certain LL trait values are highly probable, because these biases are well known for different depositional environments, associated errors can be constrained (Fig. 3; Table S1). Overall, the potential of using LL as a paleo-functional trait (score = 5.2) ranked slightly lower than LMA because the methods of estimating LL trait values from fossils are not as well developed as those for LMA despite both traits having equal strength of impact on the Earth system (Figs 3, 4; Table S1).

3. Leaf nitrogen concentration

Leaf nitrogen concentration (LNC) refers to the total amount of N per unit dry leaf mass expressed in mg g^{-1} (or sometimes as % dry leaf mass; Pérez-Harguindeguy *et al.*, 2013). N is essential for protein (such as photosynthetic enzymes) and nucleotide synthesis (Moreau *et al.*, 2019). Despite its abundance in the environment, N is one of the most limiting plant nutrients, often existing as forms inaccessible to plants such as N_2, NO_3^-, and NH_4^+ (Aerts & Chapin, 1999; Jia & von Wiren, 2020). As such, LNC measurements can provide valuable insights into plant ecology and physiology (Chapin, 1980) and it is considered an important plant functional trait. Leaf N concentration correlates negatively with LL (Reich *et al.*, 1992; Wright *et al.*, 2004), positively with A_{mass} (Field & Mooney, 1986; Wright *et al.*, 2004), and negatively with LMA (Wright *et al.*, 2004). These relationships within the leaf economic spectrum represent the trade-off between investment in structural tissue and allocation of N to RuBisCO, though long-lived leaves tend to have lower LNC and vice versa (Wright *et al.*, 2004; Luo *et al.*, 2021).

LNC can be measured directly from extant and compression fossil plant material using elemental analysis (White *et al.*, 2020). Currently, however, the fate of LNC during diagenesis and fossilization is not well known. Loss of internal leaf structures and leaching of solutes during the fossilization process (Haworth & Raschi, 2014) could severely alter the original trait values. Pyrolysis experiments have been used to simulate the chemical changes that take place within leaves due to diagenesis (Mosle *et al.*, 1997) and would be equally valuable to assess the fate of LNC during fossilization. Pilot LNC measurements on compression fragments of Late Pennsylvanian fossil taxa have yielded promising results that plot within the trait values of modern LNC (Matthaeus *et al.*, 2023) and are in line with expectations based on their other paleo-leaf economic spectrum traits but further systematic investigation is required. A likely future challenge in establishing direct protocols for measuring fossil LNC will be to collect adequate amounts of compression fossil material (a minimum of 1 mg of ground-up sample material is required; Aslam *et al.*, 2012). Fossil LNC could also be estimated indirectly using trait relationships with LMA. However, paleo-LMA is also subject to diagenetic effects and reliance on indirect inference could mask the detection of unusual trait combinations that may have arisen during plant evolution but are no longer present in extant plants Based on these considerations, the authors attributed paleo-functional trait, ESE, and ESI scores of 6.5, 5.2, and 5.2, respectively (Figs 3, 4; Table S1).

4. Maximum theoretical stomatal conductance

Maximum theoretical stomatal conductance (g_{max}, sometimes referred to as G_{max} or g_{smax}) is a measure of the total diffusive stomatal area available for the exchange of CO_2 and water vapor into and out of the leaf respectively and assumes that all stomatal pores on the leaf (or photosynthetic stem) are open to their maximum geometry (circle or ellipse). g_{max} can be calculated from extant and fossil plants by combining measurements of stomatal density, stomatal pore length (to calculate maximum pore area), and guard cell width into the equation of Parlange & Waggoner (1970) modified by Franks & Beerling (2009; Fig. 2). Maximum geometry of the stomatal pore is estimated by fitting an ellipse (Lawson *et al.*, 1998) or circle, using stomatal pore length (m) as the long axis (diameter) and m/2 as the short axis. Because all stomata on a leaf surface are never fully open to a maximum circular or elliptic geometry in field conditions, g_{max} is considered a theoretical maximum rate (Dow *et al.*, 2014; McElwain *et al.*, 2016). Stomatal opening behavior is dynamic (Lawson & Vialet-Chabrand, 2019) and patchy (Weyers & Lawson, 1997) across the leaf surface and the degree of dynamism, coordination, and patchiness varies across evolutionary groups (Brodribb & McAdam, 2011), meaning that no living plant operates at its theoretical maximum. Extensive field surveys of woody angiosperm trees and laboratory-based measurements of a broad range of evolutionary groups demonstrate that living plants operate (g_{op} and referred to as g_s) at around from 25% (Franks) to 26% (Murray *et al.*, 2020) of their g_{max} value. It is therefore possible to estimate the operational stomatal conductance (g_{op}) of extinct fossil plants to both CO_2 (g_{CO2}) and water vapor (g_{H2O}; 1.6 times g_{CO2}) using the g_{max} trait (McElwain *et al.*, 2016). As functional plant traits, g_{max} and g_{op} provide vital insights into a fossil plant's likely ecological strategy within a paleo-community as g_{op} correlates strongly with photosynthetic rate (reviewed in Berry *et al.*, 2010; Medlyn *et al.*, 2011) and other key traits in the leaf economic spectrum (Kröber *et al.*, 2015) including LMA (Soh

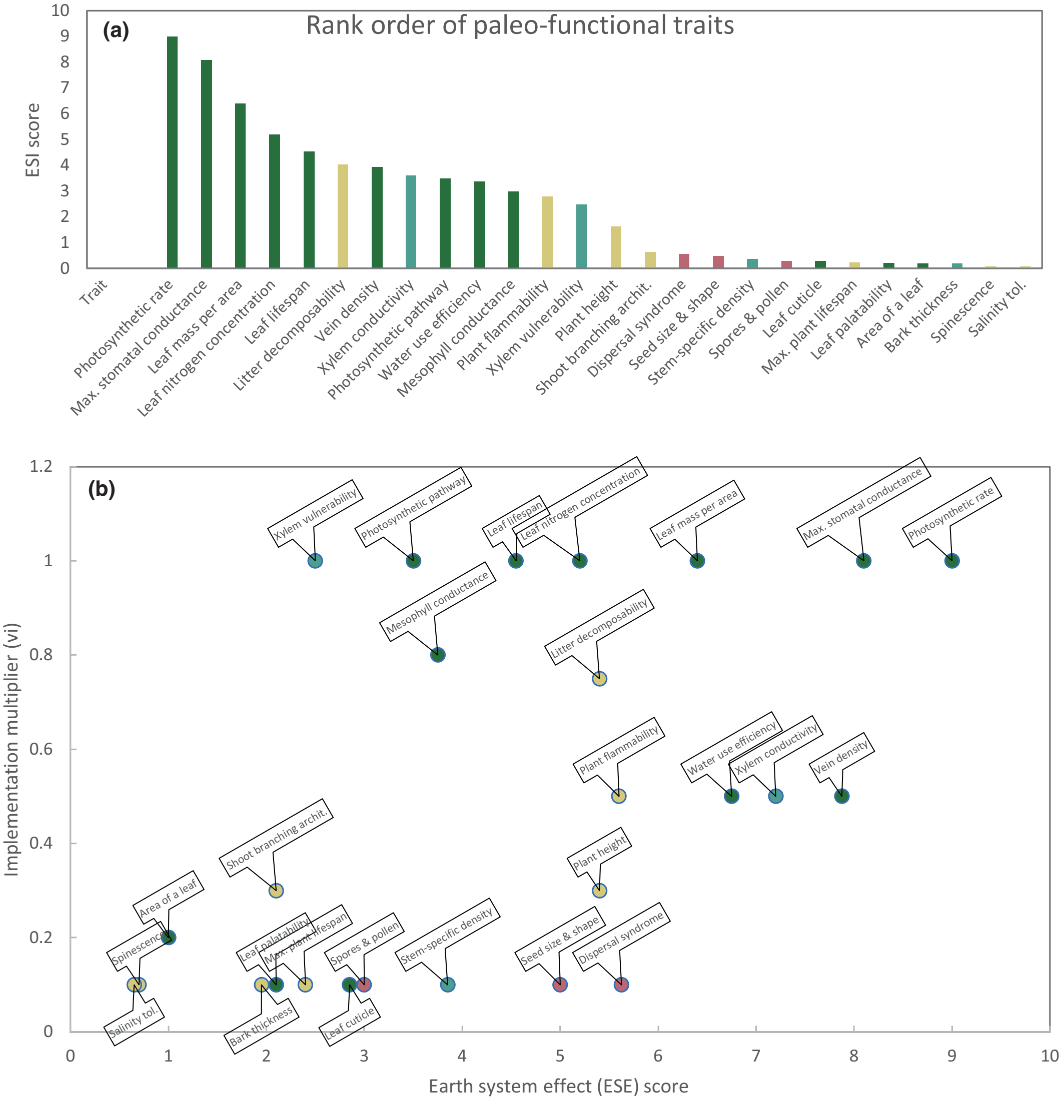

Fig. 4 A ranked list of paleo-functional traits that can be applied to fossil plants. (a) Ranked list of paleo-functional traits based on Earth system implementation (ESI) scores illustrating the rank order of traits with the highest (photosynthetic rate) to lowest (salinity tolerance) potential application to the plant fossil record as evaluated by the author team. (b) Bi-plot illustrating the breakdown of components within the final trait ranking shown in panel a, where the horizontal axis shows the Earth system effect (ESE) score (in Fig. 1; Supporting Information Table S1; ESE = PT × v) and the vertical axis is the implementation multiplier (vi in Fig. 1; Table S1).

et al., 2019; Wu *et al.*, 2020), LNC (Schulze *et al.*, 1994; Juhrbandt *et al.*, 2004), and LL (Poorter & Bongers, 2006), and also whole plant WUE (Soh *et al.*, 2019). Based on the relative ease with which g_{max} can be measured across various modes of plant fossil preservation (McElwain & Steinthorsdottir, 2017) and the fact that it constrains understanding of paleo-productivity (Franks & Beerling, 2009; Wilson *et al.*, 2015; McElwain *et al.*, 2016), the hydrological cycle at local to global levels (Steinthorsdottir *et al.*, 2012; Jasechko *et al.*, 2013; White *et al.*, 2020), and fossil plant WUE (Reichgelt *et al.*, 2020), we evaluate it here as a paleo-plant functional trait with strong potential application to a range of research questions relating to plant–climate and plant–atmosphere evolution and Earth system processes in general (Matthaeus *et al.*, 2023). Paleo-functional trait, ESE, and ESI scores of 9, 8.1, and 8.1 were, respectively assigned (Fig. 3; Table S1).

5. Water use efficiency

Water use efficiency is a measure of how water saving a plant is in relation to photosynthesis. Low values in the 20 to 40 µmol mol^{-1} range are typically observed in modern angiosperm trees of tropical everwet forest biomes while higher values (60 to 80 µmol mol^{-1}) are recorded from desert plants and those from seasonally dry biomes (Soh *et al.*, 2019).Water use efficiency is an informative functional trait in relation to the hydrological cycle and hydroclimate generally in the deep past (White *et al.*, 2020) and allows broad characterization of paleo-biomes from fossil iWUE estimates of dominant taxa within paleo-ecosystems (Matthaeus *et al.*, 2023). Intrinsic water use efficiency (iWUE) is expressed as the ratio of photosynthesis (*A*) and leaf conductance to water vapor transfer (*g*) of which g_s is the dominant component. It can be calculated using stable carbon isotope ratios of modern and fossil plants according to the equation of Farquhar *et al.* (1982) below. However, in the case of fossils both the concentration and $\delta^{13}C_{air}$ of CO_2 cannot be measured directly and need to be inferred from proxies. Furthermore, differential preservation of fossil plant tissue can bias $\delta^{13}C_{plant}$ samples toward lighter or heavier values and must also be taken into account along with other sources of variability (Sheldon *et al.*, 2020). $\delta^{13}C_{air}$ in the geological past is estimated from temperature-sensitive equations (Romanek *et al.*, 1992) applied to measurements of $\delta^{13}C_{calcite}$ of marine brachiopods and their estimated paleo-temperature at the time of growth. Paleo-CO_2 concentration can be obtained from stomatal-based proxies applied to the same leaf or fossils within the same assemblage (McElwain & Steinthorsdottir, 2017) or other proxy CO_2 methods (CenCO$_2$PIP Consortium, 2023).

An isotope ratio mass spectrometer is used to determine the ratio of $C^{13} : C^{12}$ in a living and fossil plant sample ($\delta^{13}C_{plant}$) (Farquhar *et al.*, 1982).

$$\begin{aligned}\mathrm{iWUE} &= A/g = c_a(1-c_i/c_a)/1.6\\ &= c_a\left(1-\left(\Delta_{plant}-a\right)/(b-a)\right)/1.6\end{aligned}$$

where $\Delta_{plant} = (\delta 13C_{air}–\delta 13C_{plant})/1 + (\delta 13C_{plant}/1000)$; c_i/c_a is calculated according to $\Delta_{plant} = a + (b–a)\ (c_i/c_a)$, where a is fractionation due to diffusion in air (=4.4‰) and b is net fractionation caused by carboxylation (=27‰); $\delta^{13}C_{air}$ = the stable isotope ratio of CO_2 in the air at the time the leaf developed; $c_a = CO_2$ concentration of the atmosphere at the time of leaf development.

An alternative method of estimating iWUE of fossil taxa is from model estimates of photosynthesis (A) and stomatal conductance (g_s) (A/g_s = WUE) that can be derived from biochemical proxy CO_2 models (Franks *et al.*, 2014) using a methodology fully described in Reichgelt *et al.* (2020) or inferred from multiple traits that are directly measurable on fossilized stems (stem hydraulic conductance; Wilson *et al.*, 2015) and leaves (vein density (VD) to infer A and G_{max}; McElwain *et al.*, 2016; Murray *et al.*, 2019, 2020) and integrated to get a picture of the whole plant WUE (see detailed discussion in Wilson *et al.*, 2015). Our semi-quantitative analysis of iWUE yielded high paleo-functional trait scores (9) as this trait can be measured using multiple independent methods but lower ESE scores (6.75) because the trait is a ratio, and it is difficult to quantify its impact on the Earth system as this requires disentangling the combined impacts of photosynthesis and transpiration. A lower ESI score (3.37) reflects the fact that the trait is an output of paleo-ecosystem models rather than an input.

6. Photosynthetic rate

The light-saturated CO_2 assimilation rate (A_{max}) represents the theoretical potential of a leaf's photosynthetic capacity. Canopy-scale assimilation, which influences the organic C cycle, is proportional to A_{max} (Wilson *et al.*, 2017). Well-established correlations with other parameters of the world-wide leaf economics spectrum (Wright *et al.*, 2004), such as LMA (see leaf mass per area) and N_{mass} (see leaf nitrogen concentration) allow indirect estimation of A_{max} from plant fossils. The mechanistic model proposed by Franks *et al.* (2014) may also be used to estimate A_{max} from plant fossils based on the photosynthetic activity of a modern ecophysiological analog (A_0) under ambient conditions (C_{a0}), diffusive estimates of g_{max} (see Section V), and c_i/c_a as estimated from fossil carbon isotopes. Methods of estimating paleo-functional trait values which do not rely on the use of, or comparison with, modern ecophysiological analogs are preferable, however, especially for extinct species with unusual trait combinations that have no appropriate modern equivalents. Alternatively, A_0 can be indirectly estimated from fossils by measuring leaf venation properties (D_v, D_m; McElwain *et al.*, 2016) and g_{max}. The Franks model relies on a linear correlation between photosynthetic carbon gain and C_a, which may not be physiologically accurate in some cases (McElwain, 2018). This trait was identified as the trait with the highest potential as a paleo-functional trait (score = 9) as it can be estimated from multiple methods and is currently parameterized in paleo-ecosystem models, yielding a high ESI score (9) (Figs 3, 4; Table S1).

7. Leaf cuticle traits

The leaf cuticle membrane is denser than wood (Onoda *et al.*, 2012) and because of its unique acid and enzymatic-resistant qualities is exceptionally well preserved in the plant fossil record (McElwain & Chaloner, 1996). The cuticle of all plants functions to protect the plant against water loss via transpiration (Zeisler & Schreiber, 2016). Although cuticular conductance (g_{min}) is low relative to stomatal conductance (g_{op}), it varies widely among extant plants (Duursma *et al.*, 2019; Slot *et al.*, 2021) and is critical to whole plant function and survival during heatwaves and drought when stomata are closed but low quantities of transpiration water loss still occur. Ultimately, the permeability of cuticle to water molecules and resistance of cuticles to water loss is dependent on both physical and chemical (e.g. waxes) attributes, which can be readily determined in fossils. The chemical composition of waxes and their distribution are considered the most important determinants of cuticular water loss, with long-chain n-alkanes playing a particularly important role (Leide *et al.*, 2007), and both can be measured in compression fossils. Additional cuticular traits can be determined for fossil cuticle samples using their auto-fluorescent properties (Fig. 2j); these analyses yield chemo-ecological data in relation to plant–insect interactions via chemical signaling to pollinators, seed dispersers, and prey and on secondary metabolites defense against UV-B radiation (reviewed in García-Plazaola *et al.*, 2015; Leide *et al.*, 2020). For example, strong autofluorescence in the blue (emission at 475 nm) under excitation with UV light (360 nm) can signal the presence of UV-protecting compounds such as coumarin (García-Plazaola *et al.*, 2015; Jardine *et al.*, 2019).

Physical cuticle traits including thickness, density, and mechanical properties (tensile strength and modulus of elasticity) vary substantially across evolutionary groups (Onoda *et al.*, 2012) and show strong correlations with whole-leaf functional traits such as LMA and LL. Interesting trait trade-offs have been observed for cuticle alone. For example, cuticle thickness is not correlated with cuticular conductance, suggesting that thickness does not play a role in reducing water loss; however, thick cuticles have higher tensile strength (Onoda *et al.*, 2012) and are positively correlated with LL. This suggests that thick cuticles contribute to the overall mechanical strength of long-lived leaves (Onoda *et al.*, 2012) and could therefore be a route to estimating LL of fossils from cuticle fragments. Despite the fact that the cuticle membrane of leaves is thin compared with the total leaf thickness, because it is dense, it contributes substantially to overall LMA (Onoda *et al.*, 2012). It is unsurprising, therefore, that cuticle thickness has been developed as a paleo-LMA proxy (Soh *et al.*, 2017; Fig. 2d). Techniques for extracting and observing fossil cuticle are reviewed in Kerp & Bomfleur (2011). The abundance of cuticle in the fossil record and the range of significant functional characteristics that can be inferred for the whole plant from fossil cuticle fragments resulted in a high paleo-functional trait score (9.5) but low ESE score (2.85) because its influence on reflectivity and water relations cannot be easily quantified currently, nor are these attributes parametrized within paleo-ecosystem models (Fig. 3; Table S1).

8. Vein density

Venation architecture shows diverse patterns across different phylogenetic groups and across evolutionary time, applying functional constraints on hydraulic conductance and indirectly on photosynthetic rate, as well as providing mechanical stability (Roth-Nebelsick *et al.*, 2001; Boyce *et al.*, 2009; Pérez-Harguindeguy *et al.*, 2013; Sack *et al.*, 2013). Leaf VD (the length of veins per unit leaf area) is therefore a functional, measurable leaf trait in megaphyll leaves playing an important role in ecosystem processes such as transpiration and productivity. On a global scale, VD influences the carbon and hydrological cycle (Boyce *et al.*, 2009). Vein density shows a high degree of phenotypic plasticity, showing adaptations to resource gradients (e.g. light, nutrient, and soil water availability) and environmental conditions (e.g. humidity and wind speed; Roth-Nebelsick *et al.*, 2001; Sack & Scoffoni, 2013), and emerging work has demonstrated that vein conductivity can compensate for lower VD (Rockwell & Holbrook, 2017). Given these caveats, taphonomic biases should be taken into consideration when measuring VD traits in the geological past. The paleobotanical record is biased toward the preservation of certain leaf types (e.g. sun leaves) and toward the preservation of plants growing near lacustrine or fluvial environments (Van der Burgh, 1994; Ferguson, 2005). As VD is affected by both light and soil water availability, these taphonomic factors may lead to an overrepresentation of certain vein network traits in the fossil record. These can be controlled for, in part, by using proxies for leaf canopy placement such as epidermal undulation index (Kürschner, 1997), leaf ^{13}C (Carvalho *et al.*, 2021), and number of vein endings per leaf perimeter (Boyce, 2009).

Vein density is measurable on compression/impression leaf fossils and has been used extensively in taxonomic work and to infer paleo-ecophysiology (Uhl & Mosbrugger, 1999; Boyce *et al.*, 2009; Boyce *et al.*, 2010; Esperança Júnior *et al.*, 2023; Fig. 2a). VD can also be estimated on cross-sections of anatomically preserved leaf specimens from trait correlations with interveinal distance (Uhl & Mosbrugger, 1999). However, this is a less reliable parameter than leaf vein length per area (Uhl & Mosbrugger, 1999). Relatively unaltered fossil leaf remains can be prepared for VD measurements by clearing, following similar methods for modern material (Dilcher, 1974; Evans-FitzGerald *et al.*, 2016). For compression/impression fossils, various photography and lighting techniques can be employed (Kerp & Bomfleur, 2011) as well as latex or silicone molds (Barbosa & Muchagata, 2021) and transfers (Dilcher, 1974; Kouwenberg *et al.*, 2007). Vein density can be measured from photographed fossil specimens using digital tracing in image processing software provided there is sufficient contrast between the leaves' nonvenal tissue and vein network (Sack *et al.*, 2014). Additional difficulties can be caused by the surrounding matrix not being sufficiently fine to preserve small morphological features.

A denser vein network provides greater mechanical stability (Roth-Nebelsick *et al.*, 2001). Therefore, VD may be useful to consider in the context of leaf strength and palatability traits (Vincent, 1990; Sack & Scoffoni, 2013). VD measurements are also used to model assimilation rates of fossil plants (Boyce & Zwieniecki, 2012; Blonder *et al.*, 2014; McElwain *et al.*, 2016; Wilson *et al.*, 2017), to reconstruct paleo hydroclimate, to infer canopy position (Carvalho *et al.*, 2021), and to estimate leaf size from fossil fragments (Sack *et al.*, 2012). Vein density may also have some application as a paleo-functional trait in distinguishing different photosynthetic pathways as it is generally higher for C4 than C3 and crassulacean acid metabolism (CAM) plants (Sack & Scoffoni, 2013). Vein networks can however be highly three-dimensional in the succulent leaves of CAM plants suggesting that VD would likely underestimate their conductive capacity (Ogburn & Edwards, 2013). Overall, VD is a thoroughly useful trait and our semi-quantitative assessment yielded high paleo-functional trait (10.5) and ESE scores (7.8) but lower ESI scores (3.9) (Fig. 1) because although this trait is important for the hydrological cycle/productivity, it is not currently directly parameterized within paleo-ecosystem models (Fig. 3; Table S1).

9. Mesophyll conductance

Mesophyll conductance (g_m; mol CO_2 m^{-2} s^{-1}) is the measure of CO_2 diffusion from the substomatal cavity through the mesophyll tissue to the site of carboxylation. Low mesophyll conductance can limit photosynthesis, and its relative importance varies significantly between different phylogenetic lineages and under different atmospheric compositions (Gago *et al.*, 2019; Yiotis & McElwain, 2019). In bryophytes, lycophytes, and in some CAM plants, g_m is the predominant limiting factor in photosynthetic capacity, whereas more evolutionarily recent lineages show a co-limitation between g_m and g_{op} (Males & Griffiths, 2017; Gago *et al.*, 2019; Yiotis & McElwain, 2019). As a functional trait, therefore, g_m has a bearing on the productivity of past ecosystems that depends on prevailing climatic and atmospheric conditions and dominant plant evolutionary group.

It should be measured using multiple different approaches in modern-day plants to obtain robust trait values (Flexas *et al.*, 2013). The principal methods to estimate g_m in living plants include chlorophyll fluorescence and gas exchange (Harley *et al.*, 1992), carbon isotope analysis (Evans *et al.*, 1986), and A/Ci curve fitting

(Ethier & Livingston, 2004), none of which can be applied to fossils. However, anatomical features, such as leaf mesophyll cell wall thickness and exposure of chloroplasts to cell perimeter (S_c/S), play an important role in constraining g_m and have been used as a basis to develop g_m proxies for permineralized and charcoalified fossil plants (Tomas *et al.*, 2013; Veromann-Jurgenson *et al.*, 2017; Carriqui *et al.*, 2019; Fig. 2p).

Anatomical data such as porosity, mesophyll cell width, cell wall thickness, and thickness of mesophyll tissue have also been used to model mesophyll conductance for well-preserved fossils (Roth-Nebelsick & Konrad, 2003; White *et al.*, 2020). However, this type of preservation is exceptionally rare, and anatomically preserved specimens may also have undergone postburial deformation. Furthermore, while there is a good correlation between anatomy-based models and chlorophyll fluorescence/gas exchange approaches for extant plants, there are some discrepancies. Anatomical modelling tends to overestimate g_m in species with high LMA and underestimate it in species with low LMA (Tomas *et al.*, 2013). In addition, uncertainties with anatomical approaches are increased when applied to fossils, as fewer parameters can be directly measured, and must be inferred from extant plants (e.g. using a scaling relationship between S_c/S and mesophyll surface area exposed to intercellular air spaces per unit of leaf area (S_m/S) in White *et al.* (2020)).

Other methods include the use of scaling relationships between g_m and photosynthetic rate (A_n) to estimate g_m from paleo-assimilation rate (see A_n; Niinemets *et al.*, 2009; Franks *et al.*, 2014; Veromann-Jurgenson *et al.*, 2017; Gago *et al.*, 2019), carbon isotopic technique which require measurements of g_{max} and $\delta^{13}C$ of a leaf fossil and $\delta^{13}C$ of the prevailing atmospheric CO_2 (Pons *et al.*, 2009), and neurofuzzy logic model approaches for defining g_m from the inputs of leaf hydraulic conductance (K_{leaf}) and LMA (Flexas *et al.*, 2013). Isotopic approaches may be too difficult to resolve in the fossil record given that discrimination by g_m is so small compared with other drivers of variability in leaf $\delta^{13}C$. In the case of the latter method as more traits (K_{leaf} and LMA and VD) are required to model g_m and those traits are typically observed in different fossil plant preservation modes, they may have weak predictive power (Flexas *et al.*, 2013). Given some of the limitations to inferring g_m in fossils and its indirect impact on the Earth system (via photosynthesis), our analysis yielded relatively low scores for the g_m trait across all of the indicators developed (Fig. 3; Table S1).

10. Leaf palatability

Leaf palatability is one of the most widely studied functional traits in fossils (Royer *et al.*, 2007; Currano *et al.*, 2008). It is important for understanding biotic interaction, ecosystem productivity, and nutrient recycling in the deep past because palatable leaves are usually more nitrogen-rich (Currano & Jacobs, 2021). In modern plants, palatability is the measure of a model herbivore's preference for the leaves of certain plants, or the proportion of leaf area eaten (Dostalek *et al.*, 2020). This preference is affected by numerous underlying leaf-quality traits (Pérez-Harguindeguy *et al.*, 2003, 2013). The suite of leaf traits that influence palatability also affect decomposability due to their similar constraints (low LNC, high concentration of lignin, and secondary metabolites); as a result, they are positively correlated (Grime *et al.*, 1996; Pérez-Harguindeguy *et al.*, 2013). There is a correlation between LMA and palatability: high LMA has been linked to lower nutrient concentrations and tougher leaves, which makes them less palatable to herbivores (Coley & Barone, 1996; Wright *et al.*, 2004; Royer *et al.*, 2007; Currano *et al.*, 2008).

It is important that herbivory damage in fossils is first distinguished from detritivory before palatability measurements are undertaken (Labandeira & Allen, 2007), as palatability only concerns the former. The four main criteria used to differentiate between the two are reviewed in Labandeira (1998). Palatability is quantified by the percentage or ratio of leaf area consumed vs total leaf area and then compared between species (Pérez-Harguindeguy *et al.*, 2013; Dostalek *et al.*, 2020). Williams & Abbott (1991) proposed using the total proportion damaged for a tree or stand instead of the average proportion damaged:

$$\mathrm{TPD} = \sum_{i=1}^{n} D_i / \sum_{i=1}^{n} T_i, D = \text{Damaged area}, T = \text{Total area}$$

Alternatively, for fossil leaves, Currano *et al.* (2008) calculated the ratio of leaves with/without feeding damage instead of measuring the consumed leaf area ratio. This metric can be compared among fossil species for assemblages with diverse and well-preserved fossil floras, and between assemblages from the same depositional environments and likely similar taphonomic filtering of palatable/unpalatable leaf categories. The Currano *et al.* (2008) method is better suited to paleobotanical studies due to the general incompleteness of the fossil record and because true preference tests on leaf palatability cannot be undertaken for extinct herbivores.

On average, gap demanders are more palatable than shade-tolerant plants, due to lower concentrations of tannins, lower tensile strength, and lower fiber content (Coley, 1987), whereas taxa with high LMA and LL are more well-defended (Wright *et al.*, 2004). Ultraviolet-B absorbing compounds can also make plants unpalatable (Liu *et al.*, 2023) and because UV-B dosage has changed dramatically in the geological past, especially at mass extinction boundaries and before the establishment of an ozone layer, it is important to couple palatability traits with those that allow inferences on canopy position (e.g. Carvalho *et al.*, 2021) and UV-B dose (Jardine *et al.*, 2019). Leaf palatability scored relatively highly in our analysis as a paleo-functional trait (7) because the taphonomic processes which can under- or overrepresent certain leaf categories in the fossil record are well studied. A lower ESE score was assigned because its impact on Earth system processes is difficult to quantify and implement within paleo-ecosystem models (Figs 3, 4; Table S1).

11. Photosynthetic pathway

There are three well-recognized photosynthetic pathways in terrestrial plants, C3, C4, and CAM, each of which is characterized by a broadly distinctive suite of associated biochemical, physiological, anatomical, and carbon isotopic traits that are collectively referred to as trait syndromes (reviewed in Sage, 2017; Edwards, 2019, Box 1). CAM and C4 are carbon-concentrating photosynthetic pathways that originated and diversified in the Cenozoic according to molecular clock estimates (Sage, 2017; Edwards, 2019) but may have had multiple pre-Cenozoic origins in extinct lineages (Raven & Spicer, 1996; Green, 2010; Looy *et al.*, 2021). Identifying the likely photosynthetic pathway of fossil plants relies mainly on anatomical (C4, C3, and CAM) and carbon isotopic (C4 and C3) traits; however, these can only rarely be measured from the same fossil sample and distinguishing CAM from C4 in fossils remains a challenge. Determining photosynthetic pathway is important from a functional traits perspective, because as a trait syndrome, it has consequences for overall productivity within the paleo-ecosystem, the timing and magnitude of water flux to the atmosphere (at night for CAM and in the day for C4 and C3), and for both the timing (in the day for C3 and C4 and night for CAM) and optimal conditions for photosynthesis (Sage, 2017; Edwards, 2019). C4 photosynthesis is found in hot, high-light, and dry environments, where photorespiration is increased due to high temperatures, while CAM photosynthesis is found in arid environments where mesophyll CO_2 concentrations are low due to stomatal closure and tissue succulence. In general, C4 plants have higher photosynthetic rates and productivity than C3 plants, while the opposite trend is found in CAM plants (Sage, 2017).

C4 photosynthesis takes place in modified, thickened bundle sheath cells that surround veins, which are rarely observable in fossils. High leaf bundle sheath : mesophyll ratio in C4 plants (Christin *et al.*, 2013; Edwards, 2019) could be indirectly inferred from high vein densities (see section V). C4 plants can also be distinguished from C3 plants based on their distinctive carbon isotopic signatures which range from − 10‰ to −14‰ under modern atmospheric $\delta^{13}C$ values of *c.* −8‰ compared with the C3 plants range of −21‰ to −35‰ (Pérez-Harguindeguy *et al.*, 2013).

Detecting CAM plants in the fossil record is more complex because their C isotopic values overlap with the ranges of both C3 and C4 depending on whether they are obligate (−10‰ to −15‰) or facultative CAM (−10‰ to −30‰; Winter *et al.*, 2015; Edwards, 2019). Extant CAM plants typically have very high LMA values, which overlap with those of evergreen gymnosperms (Poorter *et al.*, 2009). Despite this apparent complexity in definitively detecting CAM in the fossil record, there is a suite of leaf traits associated with obligate and 'strong' CAM plants (i.e. those with C3 + CAM that predominantly use CAM), which are potentially highly recognizable in a myriad of fossilization modes that warrant future coordinated research. These traits are functionally associated with either reducing water loss in arid environments (high iWUE) or facilitating water transport from water storage tissue and veins in succulent leaves and stems that have low leaf and/or stem g_m (Edwards, 2019). They include leaf succulence, long LL, large mesophyll cell size, low stomatal density, low intercellular air space and low g_m, thick cuticles with high hydrophobicity, thick inter-epidermal cuticular pegs (spandrels; Fig. 2o) and intra-cuticular wax and often with Calcium oxalate crystals (druses), 3D leaf venation, leaves that are terete or oblong in cross-section, extra-xylary vascular bundles (xylem and phloem tissue that are grouped into units of vascular tissue occurring in the pith outside of the main grouping of vascular bundles that occur in the stele) and photosynthetic phylloclades (modified flattened, usually photosynthetic, stem that is often subtended by a scale-like leaf; Bernardino-Nicanor *et al.*, 2012; Ogburn & Edwards, 2013; Males & Griffiths, 2017; Edwards, 2019; Niechayev *et al.*, 2019; Fig. 2). The extinct Cheirolepidiaceae conifers that were widespread in saline, arid, and humid environments in the Jurassic and Cretaceous (Gomez *et al.*, 2002; Mendes *et al.*, 2023) possess a number of potential CAM functional traits and may be a good target for further research. This syndrome of traits scored highly as paleo-functional traits and moderately as ESE traits in our semi-quantitative analysis (Fig. 3; Table S1).

VII. Fossil stem functional traits

1. Xylem conductivity

Xylem conductivity (K) is a measure of the capacity of xylem tissue to transport and supply water from roots to leaves. It is considered a master regulator of photosynthesis and plant productivity (Sperry *et al.*, 2008; Brodribb, 2009) and damage to stem water-transport capacity plays an outsized role in plant mortality. Many plants can survive the temporary loss of conductivity in leaf and branch xylem, whereas stem damage can be fatal (Choat *et al.*, 2012). The movement of water through xylem is a function of the anatomy of the xylem conduits and how resistant they are to flow (measured as plant, stem, or leaf conductance) and the negative water potential gradient between soil and leaves (Sperry *et al.*, 2008). As water potential cannot be measured or inferred from fossil plants and multiple studies on extant plants have demonstrated the importance of xylem anatomy for whole plant water movement (Hacke *et al.*, 2004; Pittermann *et al.*, 2005, 2011; Feild *et al.*, 2009, 2011; Schulte & Hacke, 2021), it follows that xylem conductivity (*K*) has emerged as a key functional trait in paleobotany (Cichan, 1986; Wilson & Knoll, 2010). Fossilized xylem conduits provide a timeline on both the evolution of xylem conductivity and on the appearance of novel safety-giving anatomies, which evolved to maintain water flow under changing environmental stressors (Niklas, 1985a; Kenrick & Crane, 1991, 1997; Friedman & Cook, 2000; Edwards *et al.*, 2006; Wilson & Fischer, 2011; Strullu-Derrien *et al.*, 2013; Wilson, 2016; Decombeix *et al.*, 2019; Olson *et al.*, 2021). Fossilized xylem anatomy has also been measured to infer potential vulnerability in water-conducting tissues to drought, aridity, and freezing (Wilson & Knoll, 2010; Matthaeus *et al.*, 2022).

Xylem conductivity (*K*) describes water flow through the vascular system, and it can be expressed on several anatomical or spatial scales. For example, *K* can be expressed as either *Ks* (stem-specific conductivity) or *Kl* (conductivity including selected leaf area measured *Kl* = *Ks*/leaf area : sapwood cross-sectional area) per unit of pressure gradient (kg m^{-1} s^{-1} MPa^{-1}) in living plants. Detailed guidance on how to perform measurements of K in living plants can be found in Jarvis & Whitehead (1981), Gleason *et al.* (2012) and Pérez-Harguindeguy *et al.* (2013). Although *K* cannot be directly measured in fossil plants, xylem cells are well preserved and common in the fossil record dating back to the early Devonian (Kenrick & Crane, 1997; Kenrick *et al.*, 2012). Moreover, mature xylem conduits are dead cells in living plants; therefore, estimating *K* for fossil specimens is facilitated with less taphonomic filtering than for live tissues. Estimating *K* in paleobotany is broadly achieved by measurements of xylem conduit area, diameter, and length, paired with cell wall morphology/dimensions, while considering decay, and diagenesis (Cichan, 1986; Kenrick & Crane, 1991; Wilson *et al.*, 2008; Strullu-Derrien *et al.*, 2013). Estimations of *K* in all plants are grounded in adaptations of the Hagen–Poiseuille equation (Cichan, 1986; Wilson *et al.*, 2008) and Ohm's Law (van den Honert, 1948), applied at the cellular level rather than per whole plant. This is also ideal for paleobotanical research given the frequent disarticulation of plant specimens (Wilson *et al.*, 2008; Wilson & Knoll, 2010; Wilson & Fischer, 2011; Wilson, 2013, 2016). In these, xylem flow is estimated as conductance on a single-cell scale, where *Ksc* (cross-section conductivity) and *Ksp* (conduit-specific conductivity) represent *K*, normalized by transverse lumen and tracheid wall areas rather than by rate of flow, allowing for quantitative functional comparison of plants across genera independent of individual pressure gradients and environmental conditions.

Ultimately, the objective of representing conductance in extinct plants requires models and theory capable of piecing together the missing and perhaps *unknown* anatomical features of the whole plant. Therefore, a prominent focus in deep-time xylem conductivity studies over the past decade has been the role of pits, their membranes, and how their resistance and safety ultimately impact *K* and xylem transport. Pit membranes and pit apertures are preserved in the fossil record (Fig. 2i), and can be of use in estimating extinct plant hydraulics (Jones & Chaloner, 1991; Duerden, 1993; Wilson *et al.*, 2008; Pittermann, 2010; Wilson, 2013; Matthaeus *et al.*, 2022; Wilson *et al.*, 2023); xylem conductivity scored highly in our semi-quantitative assessment as a paleo-functional trait (9) and as an ESE trait (7.2) but achieved lower scores for ESI because it cannot currently be parameterized in a paleo-ecosystem model (Table S1; Figs 3, 4).

2. Stem-specific density

Stem-specific density (SSD) is the dry mass of a stem segment divided by the fresh volume of the same segment (Pérez-Harguindeguy *et al.*, 2013) and is of primary importance in the herbaceous-woody plant divide in global plant trait variation (Diaz *et al.*, 2016). Most of the carbon in the extant biosphere is incorporated into the stems of woody plants (Zanne *et al.*, 2010), and although the carbon concentration of stems is generally *c.* 50% across species and climates, the total carbon stocks stored in an individual tree is largely a function of the diameter of the tree at chest height and SSD (Chave *et al.*, 2005, 2009). Large-scale changes in SSD over geological time and space therefore influence the long-term carbon cycle. Burial of woody biomass with different SSD values would in turn influence the long-term oxygen cycle by preventing decomposition and oxidation processes. Increased SSD is associated with stem resistance to biomechanical and hydraulic failure (King *et al.*, 2006; Diaz *et al.*, 2016; Meinzer *et al.*, 2016; Fu *et al.*, 2019), at the cost of decreased growth rate due to increased stem carbon requirements. Plants with higher SSD tend to be more resilient to environmental stressors, have lower mortality rates, wider ecological niches, and achieve greater heights. In paleobotany, manoxylic (low SSD), and pycnoxylic (high SSD) wood types correspond to the two end members of the SSD continuum (Galtier & Meyer-Berthaud, 2006), and opportunities remain to tease out finer paleo-ecological strategies of fossil taxa using quantitative proxies for SSD (proposed below). Applying standard techniques for direct measurement of modern SSD (*sensu stricto*) to stem fossils is not possible due to the inaccessibility of fresh volume. Morphological distortions during fossilization (e.g. compression) further complicate the direct measurement of SSD. However, SSD and related quantities like wood density might be reconstructed based on stem biochemistry, anatomy (xylem lumen diameter), and compared with SSD in modern plant taxa to develop paleoproxies for this trait.

Stem-specific density can be decomposed into wood and bark density. These tissues serve different functions and are expected to have different chemical compositions, physical structures, and densities (Pérez-Harguindeguy *et al.*, 2013). In woody plants, structural support is provided by the secondary xylem, necessitating enrichment with biomolecules like lignin, while phloem and stem parenchyma perform biochemical functions, bark protects the tree from water loss, herbivory, and fire (Rosell, 2019). Because wood density is a commercially important property, a considerable body of literature exists on the patterns and causes of wood density variation in commercial forestry species. This literature might be leveraged to establish relationships between areal fractions of wood tissues and density, which could then be applied to the fossil record. In tropical angiosperm trees, for example, wood density is positively correlated to vessel wall fraction, and negatively correlated to fiber lumen fraction, vessel area, and pith area (Ziemińska *et al.*, 2013; Zieminska *et al.*, 2015).

SSD may be inaccessible for fossil tissues where there is a high degree of density variation, or for which function is expected to be different between extinct and modern plants. For example, lycopsids were likely structurally supported by bark rather than secondary xylem (DiMichele *et al.*, 2013), and medullosan stelar and parenchyma arrangements are unlike any modern tree (Wilson *et al.*, 2017). In such cases, biochemical analyses combined with inferences about potential tissue function may be applied as an additional lens for estimating SSD. For example, modern-stem bulk C : N is associated with the proportion of the tissue in various structural and functional tissue types that have well-characterized densities. A database of these associations would allow bulk stem compression C : N ratios to serve as a proxy for SSD that is more broadly applicable to the fossil record. Taphonomy experiments would however be required to test the robustness of the original stem C : N signal through temperature and pressure changes associated with fossilization (*sensu* McNamara *et al.*, 2021). In summary, therefore, although SSD is undoubtedly important for Earth system processes and woody fossils are well preserved in the fossil record, given the highly preliminary nature of methodology to estimate this trait from fossils, SSD achieved relatively low paleo-functional (5.5), ESE (3.85), and ESI scores (0.38) (Table S1; Figs 3, 4).

3. Xylem vulnerability

Xylem of vascular plants facilitates the transport of water to plant tissues from the soil and the maintenance of plant function (Zanne *et al.*, 2014). Water is drawn from soil through tracheary conduits in xylem by negative water potential (Ψ) induced by transpiration from leaves. During dry periods, water potential may exceed the physiological limits of xylem, causing water-transport failure, also known as hydraulic failure. The primary mode of failure is thought to be embolism via air-seeding (Venturas *et al.*, 2017): Under extreme negative potential air is pulled into water-filled conduits from adjacent tissues resulting in conduit blockage and reduction of total xylem water-transport capacity (Mayr *et al.*, 2014). Ecosystem functions like transpiration and photosynthesis depend on xylem water transport, and the physiological limitations of xylem are associated with tree mortality and vegetation distribution in modern ecosystems (Sperry, 2000; Sperry *et al.*, 2002; McDowell *et al.*, 2008; Choat *et al.*, 2012; Adams *et al.*, 2017). Therefore, xylem vulnerability to failure has likely had an impact on ecosystems and Earth surface processes since the initial diversification of vascular plants in the Devonian (Banks, 1975; Chaloner & Sheerin, 1979; Niklas, 1980, 1983, 1985a; Bouda *et al.*, 2022).

Xylem physiology has been inferred from morphological and anatomical measurements of deep-time fossils (e.g. Niklas, 1985a; Wilson *et al.*, 2008; Wilson & Knoll, 2010; Wilson, 2013), and has largely focused on the conductivity allowed by conduits and pit apertures. Pits are openings in the xylem secondary cell wall that leave only the middle lamella between adjacent conduits (i.e. the pit membrane; Choat *et al.*, 2008). Pit characteristics are a good target for estimating xylem hydraulic vulnerability from fossil conduit anatomy. Recent work has shown that the pit-membrane area-to-thickness ratio is a strong predictor of the hydraulic limitations of xylem (Kaack *et al.*, 2021). Unfortunately, pit membranes are challenging to measure, and measurements at the nanometer scale (i.e. of pit-membrane thickness) would be subject to considerable preservation biases. Though this has not yet been tested, fossil pit-membrane thickness may not be representative of *in vivo*-pit thickness. Another anatomical character, pit-area per conduit, also informative on xylem vulnerability to embolism (Pittermann *et al.*, 2006; Hacke *et al.*, 2007; Brodersen *et al.*, 2014), has been applied to late Pennsylvanian-aged fossil plants (Matthaeus *et al.*, 2022; Wilson *et al.*, 2023). Inferring absolute water-transport properties and ecosystem impacts based on conduit anatomy, however, requires assumptions about tissue-scale properties – of xylem as a whole (e.g. size distribution of conduits and sapwood area), which is accessible from stem permineralizations based on network connectivity (Bouda *et al.*, 2022) – along with the whole plant architecture and the whole plant coordination of traits. We evaluated xylem vulnerability as having lower potential as a paleo-functional trait because of the reliance on fossilized pit-membrane anatomy, the difficulty of obtaining trait values from fossilized pit membranes and due to the complexity of incorporating the trait within paleo-ecosystem models (Figs 3, 4; Table S1).

4. Bark thickness

Bark is a complex tissue with diverse physiological and ecological functions (Rosell, 2019). In extant plants, bark thickness is simply measured with calipers. There is a robust relationship between bark thickness and stem diameter in many tree taxa (Borger, 1973; Williams *et al.*, 2007; Rosell *et al.*, 2017), suggesting that it might be used as a proxy for stem diameter in fossil plants where whole stems are not preserved. However, the relationship between bark thickness and stem diameter varies among taxa, bark types, and between main stem and twigs – as bark thickness is also associated with a number of different environmental factors and physiological functions (Rosell *et al.*, 2017; Rosell, 2019; see flammability). In the most extreme cases – for species with decorticating bark (Gill & Ashton, 1968; Borger, 1973) or bark shed in strips (Williams *et al.*, 2007) – there may be little or no allometric relationship between bark thickness and stem diameter. Attempts to account for the factors influencing bark thickness in contemporary ecology have considered different parts of bark (e.g. inner and outer) and varied environments (e.g. tropical rainforest, temperate forest, or savannah), and they have made progress in disentangling interactions (Paine *et al.*, 2010; Hempson *et al.*, 2014; Rosell *et al.*, 2015, 2017). These studies have also laid the foundations for using fossil bark thickness as a paleo-functional trait to infer wildfire frequency and intensity (Uhl & Kauffman, 1990; Hoffmann *et al.*, 2003; Lawes *et al.*, 2013; Pausas, 2015). Stem photosynthesis and herbivory defense may be inferred from the proportion of inner and outer bark, and the presence or absence of rhytidome (outermost bark which is characterized by multiple layers of periderm tissue interspersed by phloem-rich layers; Rosell *et al.*, 2015; Rosell, 2019). Bark (wound periderm) has also been observed in extant CAM plants as a defense against high UV-B flux (dos Santos Nascimento *et al.*, 2015).

The fossil record contains bark components (i.e. periderm; Fig. 2g; vascular cambium) as early as the Lower Devonian, and may coincide with the earliest appearance of secondary growth (Banks, 1981; Hoffman & Tomescu, 2013). Functional inferences based on bark thickness traits and constituent structures require the preservation of complete sections of bark which can be achieved when the bark type (i.e. its physiology) is known, and the delimiting structures are identifiable (e.g. vascular cambium and periderm). Even in these cases, the actual thickness of the outermost structures will likely be thinner than *in vivo* due to alteration during burial. These processes may be indistinguishable from normal, *in vivo* shedding from periderm. Furthermore, the considerable differences in the physiological function of bark in some extinct taxa that completely lack any living structural analogs (e.g. all extant lycopsids are herbaceous but many ancestral taxa were arborescent with extensive bark) may make high-confidence inferences difficult for those taxa. Chemical components of fossil bark (dos Santos Nascimento *et al.*, 2015; Angyalossy *et al.*, 2016) may, however, provide broadly useful information on the paleo-function of the individual even in the absence of phylogenetically related modern analogs. Considering all of the factors reviewed above, we assessed bark thickness as having lower potential as a paleo-functional and ESE trait relative to many of the other traits reviewed here with scores of 6.5 and 1.95 respectively (Figs 3, 4; Table S1).

5. Plant height

Plant height is the shortest distance between the upper boundary of the main photosynthetic tissues and the ground level, expressed in meters (Pérez-Harguindeguy *et al.*, 2013). Direct measurement of height is not usually possible within the fossil record due to fragmentation (Niklas, 1994). Rare fossilization events can lead to whole tree stumps being preserved *in situ* (Cúneo *et al.*, 2003; Wang *et al.*, 2012) and whole-body fossils being preserved intact (Sun *et al.*, 1998; Fig. 2f). In such cases, fossil plant height can be measured directly. For the most part, fossil plant stems and trunks are not intact. However, their height can be estimated indirectly. Niklas has developed formulae for estimating fossil plant height based on the allometric scaling relationships of diameter at chest height across phylogenetic and ontogenetic differences (Niklas, 1994; Enquist & Niklas, 2001). Height has also been estimated based on the shape of permineralized logs by projecting to vanishing point (Falcon-Lang & Scott, 2000). However, this methodology may underestimate tree height where the base width of trunks is unknown (Falcon-Lang & Scott, 2000).

Height is a key trait in the global spectrum of plant form and function (Diaz *et al.*, 2016). It represents the economic trade-off between investment in structural tissues, stem maintenance, and access to light (Falster & Westoby, 2003). Taller plants are linked to increased biomass, acting as carbon sinks (Moles *et al.*, 2009), and woody debris of taller plants such as trees slows decomposition (Gora *et al.*, 2019 and references therein). Taller canopies provide niche partitioning by opening up understory and aerial habitats. Increased plant height is therefore associated with greater plant and animal diversity in contemporary ecosystems (August, 1983; Moles *et al.*, 2009). Maximum plant height is also associated with an ability to disperse reproductive propagules and can thus provide useful insights on reproductive success (Beckman *et al.*, 2018). Therefore, particularly since the acquisition of arborescence in the late Devonian (Stein *et al.*, 2007), plant height can tell us a great deal about total ecosystem function (Moles *et al.*, 2009), and has been used extensively to provide key ecological contexts for swamp dwelling plants of the Carboniferous (Philips & DiMichele, 1992; DiMichele *et al.*, 2013). However, the light-competitive advantage of height depends on the relative height of other species within the paleo- or modern plant community rather than the absolute height of a species (Falster & Westoby, 2003), complicating inferences for fossil communities. Although plant height scored modestly as a potential paleo-functional trait (6) in our semi-quantitative evaluation, because of its importance in affecting ecosystem-scale and Earth system processes outlined above it ranked relatively highly as an ESE trait (score = 5.4; Figs 3, 4; Table S1). We suggest this paleo-functional trait has good potential for further development of methods to quantify trait values from fossils and to parameterize within paleo-ecosystem models.

VIII. Whole plant functional traits applied to fossils

1. Life history and maximum plant lifespan

Life-history strategies are described by the timing and intensity of the demographic processes of growth, survival, and reproduction (Stearns, 1992). Life-history strategies are indicators of ecological strategy and give insights into how populations respond to abiotic and biotic drivers, including climate (Csergo *et al.*, 2017) and variation in these traits is strongly associated with environmental stress (Pérez-Harguindeguy *et al.*, 2013). As an example, extant gymnosperm and angiosperm trees with high longevity (high maximum lifespan) are slow-growing and usually occupy sites that are harsh (cold, nutrient-poor, frequently flooded etc.) but are subject to little storm disturbance (reviewed in Di Filippo *et al.*, 2015). Quantification of life-history strategies thus informs potential responses of populations to environmental change (Buckley *et al.*, 2019). Contemporary life-history metrics, however, cannot usually be calculated directly for extinct populations, as demography is usually unavailable. Nonetheless, life history has been considered for even the oldest, most basal plants using whole plant concepts (Matsunaga & Tomescu, 2017).

Direct morphological and anatomical evidence of life-history strategies for fossils are generally lacking. For instance, counting permineralized annual growth rings of woody stems and roots merely elucidates a plant's age at the time of death (Creber & Chaloner, 1984; Weaver *et al.*, 1997; Luthardt *et al.*, 2017) not the tree or species potential longevity. Long sequences of fossil growth rings are also rare (Chapman, 1994; Luthardt *et al.*, 2017). Growth rate estimates based on mean annual ring widths from the same fossil trunks/roots (Fig. 2n) could however, be used to infer longevity using scaling relationships between mean ring width and longevity that have been developed for living taxa (Di Filippo *et al.*, 2015), although they are biome specific. Population-level surveys of mean ring width from *in situ* preserved fossil forests provide some of the best data sources to model the longevity of fossil taxa (e.g. Cúneo *et al.*, 2003) but it is acknowledged that these are exceptionally rare. For taxa that lack annual growth rings (e.g. most wet tropical taxa), plant lifespan is more difficult to interpret (Chaloner & McElwain, 1997; Boyce & DiMichele, 2016).

Counting the mean size of the annual increments on the stolon or rhizome may be the only way to indirectly assess maximum lifespan via growth rate in nonwoody fossil plants (Hotton *et al.*, 2001; Gensel & Berry, 2016). In cases without clear annual increments, detailed analysis of morphology, including the presence of perennating roots and shoots, counting the number of annual stem growth increments in woody shoots, presence of leaf scars on shoots and shoot scars on roots, will at least determine whether the fossil is an annual or perennial. Alternatively, if LL and plant height can be estimated for the fossil taxon, and leaves with axial attachment are available, a rough estimate of axial growth rate can be compared with overall tree height to estimate age at death (Boyce & DiMichele, 2016).

Most current inferences of paleo-life-history rest on plant form (e.g. woodiness and seed size), leaf economics, and trait–climate associations (e.g. leaf shape). However, interpretation of lifespan for taxa that lack living relatives or equivalents (NLEs) or those that have extinct combinations of physiological traits can result in vastly different estimates for the plant's lifespan (Philips & DiMichele, 1992; Cleal & Thomas, 2005; Boyce & DiMichele, 2016; Thomas & Cleal, 2018). For example, lifespan estimates for the iconic late Pennsylvanian *Lepidodendron*, which reached an estimated height of 45 m, range from decades (Thomas & Cleal, 2018) to centuries (Boyce & DiMichele, 2016). For fossil taxa with no obvious NLEs, studies have relied on observations that extant plant life histories are structured by two major axes – a 'pace of life' axis and a reproductive axis (Salguero-Gomez *et al.*, 2016). Furthermore, maximum plant lifespan is strongly aligned with the pace of life dimension of life-history strategies (Salguero-Gomez *et al.*, 2016). These principles have been applied to early angiosperms, where a fast-paced 'weedy' life strategy has been inferred from single paleo-functional traits such as seed size (Wing & Boucher, 1998) and LMA (Royer *et al.*, 2010). Recent studies, however, demonstrate the complexity of inferring demography from individual functional traits; seed size and plant height are positively correlated with maximum lifespan in extant plants but only in hot relatively invariable climates (Kelly *et al.*, 2021). Furthermore, very different life forms, such as herbs and trees, can give rise to similar life histories (Salguero-Gomez *et al.*, 2016), and divergent life forms can converge on similar trait and life-history profiles depending on environment and phylogeny (Kelly *et al.*, 2021). Thus, combinations of paleo-functional traits, with information from multiple plant organs as well as the sedimentary and paleo-climatic environment context of the fossils may improve our understanding of the life-history strategy of fossil plants in the future. Based on these myriad considerations and obvious complexity, we assessed this syndrome of traits with a relatively high Paleo-functional trait value (6) but low ESE (2.4) and even lower ESI scores (0.24) due to the difficulty of integrating ecosystem models and demography models for current living vegetation let alone developing a paleo-demography model for fossils (Figs 3, 4; Table S1).

2. Litter decomposability

Decomposition of plant litter is important for nutrient recycling, soil fertility, and productivity. It regulates terrestrial biogeochemical cycles at both a global and local ecosystem scale (Zhang *et al.*, 2021) by restoring nutrients from dead plant parts into the soil and CO_2 to the atmosphere, while slow decomposition provides fuel for wildfires (Cornwell *et al.*, 2008). Decomposition involves the breakdown of plant litter, both physically and chemically, into its elements through progressively simpler compounds (Aerts, 2006). In contemporary ecosystems, the majority of aboveground litter is leaf litter, and broadly, chemical trait–decomposability relationships are preserved both across organs (leaves, roots, and stems) of different species and within organs in the same species (Freschet *et al.*, 2012).

Experimentally, the rate of decomposition is the percentage of mass loss over time with k (decomposition constant) defining a mass loss curve (Pérez-Harguindeguy *et al.*, 2013). Litter decomposition is the result of interactions between climate and the community of decomposers (Berg & McClaugherty, 2008). Global litter decomposition is primarily driven by environmental conditions such as temperature and precipitation (Aerts, 1997), which are relevant to environmental change in geological time. Plant traits affect decomposition rate, primarily via their influence on usefulness as a resource for decomposer organisms (i.e. chemical composition and morphology), referred to as litter quality. Litter quality varies significantly among living plant lineages, so patterns of plant effects on nutrient cycling probably varied through deep time (Liu *et al.*, 2014). For instance, the leaves of gymnosperms generally decompose 44% slower than eudicots, and ferns and bryophytes decompose more slowly again (Liu *et al.*, 2014).

The most important traits contributing to litter quality are chemical traits that can be assessed in fossils. These are N content, lignin content, toughness (can be inferred from VD and cuticle thickness), and LMA (see section V; Cornwell *et al.*, 2008; Freschet *et al.*, 2012). Other leaf traits that go beyond the scope of fossil taxa such as N form (Rosenfield *et al.*, 2020) and phenolics also influence the decomposition rate. Morphological traits further impact decomposability. At the very least size/volume (S/V), ratios affect the area exposed to decomposers in the early stages of decomposition. Consequently, overall prediction of decomposition relies on a relatively full picture of taxon traits. Litter quality is, therefore, a trait syndrome that is relevant for past environmental change but accessible from fossils only via correlations with chemical traits (available from compression fossils and coal balls) and morphological and anatomical traits (available from most fossil preservation modes). Detailed taphonomic studies suggest that most compression leaf fossils and leaves preserved in carbonaceous coal balls were likely preserved rapidly by covering recent falls of undecomposed leaf litter (Greenwood & Donovan, 1991; Gastaldo, 2001), making them the best targets for relatively unbiased assessment of paleo-litter decomposability in future studies.

For litter decomposition and biomass turnover, it is important to note that plants are made up of multiple organs that may have different geochemical effects; for instance, stem and root litter typically decompose slower and contain more lignin, so they have a disproportionate role in humus formation (Swift, 1977). Particular traits may also vary in their contribution to litter quality per organ; for instance, lignin content is important for wood decomposition. The effect of chemical traits may also change due to differing access to decomposers; for instance, N is found in enzymes in leaves and roots for CO_2 assimilation/absorptive capacity, while it is primarily found in storage and defense compounds in stems (Freschet *et al.*, 2012). Lignin is in itself notable because it is a complex polymer fundamental to the lignin–cellulose structural matrix of wood and relevant to co-evolution of enzymatic mechanisms in decomposers. It is hypothesized that the evolution of wood-degrading enzymes was a key event ending coal formation at the end of the Carboniferous (Floudas *et al.*, 2012) although this is disputed based on evidence of from the fossil record of fungi and plants (Nelsen *et al.*, 2016). Chemical derivatives of lignin are readily preserved and extractable from fossils (Niklas, 1981; Logan & Thomas, 1987) throughout the geological record although to our knowledge no paleo-decomposability metric for fossil lignin content has been developed. Overall, interactions with both decomposers and other species in litter mixtures (Porre *et al.*, 2020) are a key modulator of the effects of traits on decomposition and may act differently on different traits. Hence, litter decomposability should be cautiously inferred from the fossil record and we have attributed relatively low paleo-functional trait scores accordingly (6), although the Earth system score (5.4) and ESI (4.05) scores are high because of the quantifiable impacts on biogeochemical cycling (Figs 3, 4; Table S1). Our assessment is that this paleo-functional trait syndrome is a good target for further study because of its high potential value to address interesting questions on plant evolution–Earth system interaction.

3. Plant flammability

Wildfire has occurred for > 400 million years (Ma; Edwards & Axe, 2004; Glasspool *et al.*, 2004; Belcher, 2016) and has likely been relevant to Earth system processes for at least 350 Ma (Scott & Glasspool, 2006). Plants host many traits that either influence fire or respond to fire, many of which can be, or have the potential to be, observed in the fossil record. These can be linked to variations in environmental conditions such as weather, seasonality, climate, and the abundance of oxygen in the atmosphere and therefore, have the potential to clarify a broad range of Earth system processes across deep time (Archibald *et al.*, 2018). Of critical importance and often overlooked in deep-time research is the influence of plant traits on flammability (the propensity of plant material to ignite, given an ignition source, and then propagate a fire) and the nature of the subsequent fire behavior (rate of spread and intensity), which interacts with ecosystem processes to determine the effects that a fire may have. While other proxies such as charcoal abundance may serve as indicators of fire frequency, we can utilize fire-linked plant traits to make the best-informed interpretations of fire effects (*sensu* the ‘effect’ trait concept) in the ancient past (Belcher, 2016).

Plant traits influence flammability and fire behavior at the leaf level, the whole plant level, and the physiological/phenological level (Archibald *et al.*, 2018) and act together to determine whether fires may burn in the canopy of forests, in the surface fuels (the understory) in litter or in ground fuels (such as organic soils and peat). There is a considerable literature describing the variety of plant traits that impact fire regimes (Kane *et al.*, 2008; Schwilk & Caprio, 2011; Cornwell *et al.*, 2015; Grootemaat *et al.*, 2015), many of which are observable in the fossil record. Perhaps the most obvious are the leaf morphological traits of leaf length and leaf area (Notes S1), which are particularly important in determining the nature of fires in leaf litter because they influence the bulk density of the litter. The bulk density of leaf litter decreases with leaf area and length such that litters that have leaves with larger areas or longer needles will carry more rapidly spreading fires (de Magalhães & Schwilk, 2012). Such measurements have been linked to the energy production from paleo-litter fires where leaves that pack tightly in high bulk density litter beds will burn more slowly but with an overall high total energy release that can damage soils and seed banks, while those of larger leaves or longer needles that pack less densely will run rapidly through litter beds but impart little heat downward (Belcher, 2016).

The opposite tends to be true for tree or shrub canopies, where small leaves increase the ease of heat transfer and tend to form dense canopies (Schwilk & Ackerly, 2001; Archibald *et al.*, 2018). LMA likely also influences flammability, where higher LMA leaves ought to contain overall more energy to give to a fire (both crown, surface, and litter fires) but will also affect litter fires via their influence on rates of decomposition (Cornwell *et al.*, 2008). Other traits that enhance canopy flammability include dead branch retention (Bond & Midgley, 1995; Schwilk & Ackerly, 2001) and the retention of dead leaves (He *et al.*, 2011). Low canopy base heights and dead branch retention influence the ability of surface fires to climb into the canopy. Hence, whole plant reconstructions are of importance to understanding the likely potential fire behavior that might exist in an ancient ecosystem. Other observations – such as branch or shoot shedding, a trait observed in many extant Pinaceae – tend to be associated with surface fire regimes. This trait has been noted using careful observations of Permian age conifer fossils (Looy, 2013). Similarly, thick bark tends to be associated with survival in surface fire regimes, where thick bark protects the trees’ cambium from the heat of surface fires, while thinner bark is associated with traits such as canopy seed storage (serotiny) and tends to be linked to crown fire regimes (Pausas, 2014). The evolution of thick bark and serotiny in *Pinus* appears to date back to the Cretaceous, a time of enhanced flammability (He *et al.*, 2012). It has also been suggested that a woody rachis that supports a compact cone with bracts/scales covering winged seeds are traits that might be considered as characteristic of serotinous cones (He *et al.*, 2016). Such observations demonstrate the potential of using paleo-functional traits to indicate the likely fire regime operating in ancient ecosystems. Similarly, variations in leaf biochemical traits (such as terpene content) have been linked to flammability and being capable of driving different fire regimes. For example, conifers in surface fire regimes appear to have higher needle terpene contents, which appears to enhance litter flammability, encouraging frequent surface fires (Dewhirst *et al.*, 2020).

Ancient ecosystems have been reconstructed using plant traits and included in models that make fire behavior predictions for time periods such as the Permian (He *et al.*, 2016), the Triassic–Jurassic (Belcher *et al.*, 2010; Belcher, 2016; Baker *et al.*, 2022), the Cretaceous (Belcher & Hudspith, 2017), and the Miocene (Boulton & Belcher, 2019). More recently, global dynamic vegetation models have been used to answer deep-time questions regarding atmospheric oxygen that rely on consideration of plant functional types (Vitali *et al.*, 2022). Therefore, the study of fossil plant traits has a significant potential to inform novel understanding of paleo wildfires and their effects, and we have scored this trait highly as a paleo-functional trait (7) accordingly (Table S1). Flammability has significant but complex impacts on the carbon and oxygen cycles, resulting in an ESE score of 5.6 (Figs 3, 4). Furthermore, although paleofire can be modelled currently within paleo-ecosystem models, flammability is a trait syndrome made up of many individual traits and it is not a simple task to parameterize at individual trait level, thus resulting in a lower ESI score (2.8) (Figs 3, 4; Table S1).

4. Salinity tolerance

Salinity tolerance is a complex trait consisting of the ability of plants to grow in saline environments. Saline-tolerant plants (halophytes) appear to be present as early as the Devonian (Channing & Edwards, 2009); however, the fossil record of halophytes is often based on the sedimentary context indicating a marine influence (Vakrahmeev, 1991; Gomez *et al*., 2002; Mendes *et al*., 2023) rather than more direct evidence based on fossil plant functional traits. Stable carbon isotopic analysis of leaf compression fossils has been used to indicate likely salinity gradients among fossil plant taxa from the same depositional setting (Nguyen Tu *et al*., 1999) with greater discrimination against C^{13} (less negative ^{13}C values) used to indicate higher salinity sub-environments. Variability in stable carbon isotopes can also be influenced by photosynthetic syndrome (see section V), light intensity, aridity, and many other factors, so it is not a straightforward salinity indicator (Arens *et al*., 2000; Diefendorf *et al*., 2011; Cernusak *et al*., 2013). Nowadays, only a small fraction of terrestrial plants exhibit salinity tolerance. Plants use three main mechanisms by which they deal with excess environmental NaCl: (1) salt exclusion, (2) salt excretion, and (3) salt compartmentalization.

Roots of many salt-tolerant plants maintain K^+ uptake, discriminating against Na^+, resulting in an increased K^+/Na^+ ratio compared with the growing medium. K : Na selectivity (S) can be calculated as: $S = ([K^+]/[Na^+])_{plant}/([K^+]/[Na^+])_{soil}$ (Pérez-Harguindeguy *et al*., 2013). Ion concentrations in living plants and modern soils can be measured by atomic emission spectrometry (AES) and atomic absorption spectrometry (AAS) but are not currently available in fossils due to unknown effects of diagenesis on the original K/Na ratios. Other salt-tolerant plants excrete salt through special salt glands. These glands, found mostly on leaves and sometimes on stems, show different structural and functional diversity (Dassanayake & Larkin, 2017; Grigore & Toma, 2020). Microscopic observation of fossil plant cuticle with epifluorescence (see Cuticle Traits) may reveal their presence as many have auto-fluorescent properties and are superficially similar in size and structure to ordinary trichome bases which are readily observed on fossil leaves. Some salt-tolerant species compartmentalize Na^+ in vacuoles and these are often succulent. Although direct observation of this type of compartmentalization is currently not possible to study in fossils, which typically lack cellular level preservation, LMA (reviewed in detail in section V) is a good general predictor of succulence (Poorter *et al*., 2009). However, LMA cannot be used in isolation as values for evergreen gymnosperms and succulent overlap (Poorter *et al*., 2009). Traits associated with salt excretion which are observable in fossils include the presence of regularly spaced crystals (salt recreation) and their anatomical excretory structures (sclereids, tracheo-ideoblasts; Grigore & Toma, 2020). For example, salt tolerance is often associated with the presence of calcium oxalate (CaOx) crystals in idioblasts of leaves and roots (Santos *et al*., 2016; Karabourniotis *et al*., 2020). SEM EDX analysis of Oligocene fossil leaves has confirmed the presence of ghost accumulations of CaOx crystals (druses; Malekhosseini *et al*., 2022), suggesting that additional underutilized traits are now available to study paleo salinity tolerance in fossil plants (Fig. 2e). Overall, however, salinity tolerance achieved low scores across all categories (Table S1; Figs 3, 4), suggesting that it ranks low in terms of future development potential as a paleo-functional trait compared with others reviewed here.

IX. Concluding remarks

Measurement of fossils forms the primary record of vegetation–climate interactions across deep time. Traditionally, fossil plants have been used to document paleodiversity and plant evolution and as proxies of past environmental change. Less often have individual fossils been used to measure trait values as a means to evaluate their functioning within paleo-ecosystems. Incorporation of trait values within paleo-ecosystem models provides a powerful tool with which to evaluate the impact of newly evolved traits and suites of traits on the Earth system. Our critical review and semi-quantitative assessment of plant traits have resulted in a ranked list of paleo-functional traits (Fig. 4) that we identify as having the greatest potential to use in further studies investigating how plant evolution has shaped their environment, Earth surface, and Earth system processes through deep time. We have focused on and attempted to rank 'effect' traits; however, we view our ranked list as a working hypothesis and preliminary rather than a final and definitive outcome. Our methodological framework outlined in Fig. 1 provides a means for others to re-assess our scores and re-evaluate our ranking or to develop new paleo-functional trait evaluations that align better with the specific questions being asked. For example, we expect that an entirely different paleo-functional trait ranking will emerge if the traits are evaluated for their 'response' to rather than 'effect' on their paleo-environment. Response traits that have been strongly filtered by paleo-environment are the foundation stone of paleo-climate and paleo-atmospheric proxies. Pollen, spore, and leaf area traits would rank highly under a 'response to environment' evaluation.

Where relevant in the review, we highlighted particular traits that are ripe for further development but have scored relatively low under our ranking criteria because they require systematic approaches to quantify their trait values from fossils and further control for bias and error (e.g. plant height, CAM photosynthesis, LNC, SSD). Our critical assessment of paleo-functional traits has also revealed a constellation of traits (flammability, iWUE, xylem conductivity, VD, plant height, and dispersal syndrome) that are measurable in the fossil record and critically important for Earth system processes but are not yet parameterized within paleo-ecosystem models (Fig. 4). We highlight these, in particular, as excellent targets for future data-model integration. Perhaps somewhat unsurprisingly, leaf traits in the leaf economic spectrum rank among the highest paleo-functional traits (Figs 3, 4), which is encouraging as their application to fossil plant assemblages is growing and methodologies for their estimation are improving.

While individual paleo-functional traits provide interesting quantitative insight into the function of individual plant parts, a paleo-ecosystem-scale network of traits using multiple traits from different organs and community-weighted plant trait values (calculated as the product of relative taxon abundance and average trait values; e.g. Soh *et al*., 2017) should be our ultimate goal. Trait-based whole-plant understanding of plant function should incorporate existing knowledge about architecture, growth form, life history, and phenology from the rich literature of paleo-ecological inference as a framework for checking the robustness of individual trait values. Synthesizing all available paleo-functional traits in this way also provides a framework for integration with processes, global constraints, and trade-offs observed in modern plant ecology to allow the understanding of global vegetation effects across deep time and plant evolution.

Inference of vegetation function across deep time is a major outcome of interest for paleo-functional trait analysis. A parallel goal is obtaining a deeper understanding of the tempo of plant trait evolution and an overview of the functional traits that confer ecological resilience in a changing global climate (e.g. through xylem vulnerability, spore, and pollen traits). The impact of improving the resolution of trait spaces within phylogenetic and ecological groupings, as well as clarification of plant and ecosystem processes by modern plant scientists will expand understanding of deep-time vegetation processes. Coordination between paleo- and contemporary plant scientists is warranted, for example, to promote the measurement of traits that have a high degree of ecological impact and are measurable from both living and fossil plants (Fig. 4). We hope that our review and semi-quantitative assessment of fossil plant functional traits will provide ideas and 'fossil for thought' toward this endeavor. Equally, we hope that our proposed methodological framework to evaluate paleo-functional traits will provide a useful basis for the development of new paleo-functional trait metrics and trait rankings in the future that are aligned with the specific questions being asked.

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Competing interests

None declared.

Author contributions

JCM and SN conceived the project. JCM and WJM designed the review structure and approach. JCM, WJM, BJ, AK, CC, SN, CB, KO'D, KK, CMB, IPM, JDW, YMB and RN drafted the manuscript. JCM, WJM, CC, YMB, JPW, JDW and SN prepared the figures and tables. KK, AK, KO'D and CB prepared the bibliography. All authors participated in the discussion and editing of the manuscript, figures, and tables.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Notes S1 Area of a leaf.

Notes S2 Leaf water potential.

Notes S3 Leaf dry matter content.

Notes S4 Leaf and leaf litter PH.

Notes S5 Seedling functional morphology trait.

Notes S6 Spinescence.

Notes S7 Shoot branching architecture.

Table S1 Assessment of contemporary plant traits for potential utilization as paleo-traits.