Research in Context

TITLE: Why Should We Investigate the Morphological Disparity of Plant Clades?

Jack W. Oyston[1], Martin Hughes[2], Sylvain Gerber[3], Matthew A. Wills[*1]

[1]Milner Centre for Evolution, University of Bath, Bath BA2 7AY, United Kingdom,

[2]Department of Zoology, The Natural History Museum, London SW7 5BD, United Kingdom,

[3]Department of Earth Sciences, University of Cambridge, Cambridge CB2 3EQ, United Kingdom

Running Title: Disparity in Plants

[*]For correspondence. E-mail m.a.wills@bath.ac.uk

ABSTRACT

Background

Disparity refers to the morphological variation in a sample of taxa, and is distinct from diversity or taxonomic richness. Diversity and disparity are fundamentally decoupled; many groups attain high levels of disparity early in their evolution, while diversity is still comparatively low. Diversity may subsequently increase even in the face of static or declining disparity by increasingly fine subdivision of morphological 'design' space (morphospace). Many animal clades reached high levels of disparity early in their evolution, but here have been few comparable studies of plant clades, despite their profound ecological and evolutionary importance. We offer a prospective and some preliminary macroevolutonary analyses.

Methods

Classical morphometric methods are most suitable when there is reasonable conservation of form, but lose traction where morphological differences become greater (e.g., in comparisons across higher taxa). Discrete character matrices offer one means to compare a greater diversity of forms. We explore morphospaces derived from eight discrete data sets for major plant clades, and discuss their macroevolutionary implications.

Key Results

Most of the plant clades in our study show initial, high levels of disparity that approach or attain the maximum levels reached subsequently. These plant clades are characterised by an initial phase of evolution during which most regions of their empirical morphospaces are colonised. Angiosperms, palms, pines and ferns show remarkably little variation in disparity through time. Conifers furnish the most marked exception, appearing at relatively low disparity in the latest Carboniferous, before expanding incrementally with the radiation of successive, tightly clustered constituent subclades.

Conclusions

Many cladistic datasets can be repurposed for investigating the morphological disparity of plant clades through time, and offer insights that are complimentary to more focused morphometric studies. The unique structural and ecological features of plants make them ideally suited to investigating intrinsic and extrinsic constraints on disparity.

Key Words: Disparity, Embryophyta, Morphological diversity, Morphospace, Angiosperms, Conifers, Ferns, Macroevolution, Clade shapes.

INTRODUCTION

The number of species within higher taxa, or within clades of a similar age (Magallón and Sanderson 2001), is hugely variable, even for sister groups diverging (by definition) at the same time. While rates and patterns of extinction are clearly influential, some clades appear much more adept at subdividing nîche space and speciating than others; even in comparison with their closest relatives. Some groups foster enormous radiations in diversity despite maintaining conservative bodyplans and displaying only modest morphological variety relative to that in their parent clades. Insects, as the best example, have a highly constrained body organisation (a fixed number of appendages and tagmata) relative to other groups of arthropods (c.f. crustaceans and branchiopods in particular), yet constitute over half of all described arthropod species (Mayhew 2007). Similarly, beetles display remarkably conservative organisation within insects, despite their notoriously high contribution to global species richness (Erwin 1997). There is no necessary relationship, therefore, between the

number of species within a group (species richness or diversity) and its morphological diversity. Indeed, there are suggestions that a constrained and entrenched bodyplan might actually be conducive to higher diversity (Rabosky *et al.* 2012).

In order to study the relationship between species richness and bodyplan conservation, we need to quantify both diversity and morphological variety or disparity for large groups. Methods for studying diversity are well established (Peet 1974; Gotelli and Colwell 2001; Benton 2009; Ezard *et al.* 2011; Mayhew *et al.* 2012), but approaches for quantifying disparity are less familiar; particularly in the botanical literature (Chartier *et al.* 2014). While it is possible and informative to study diversity and disparity across clades within the extant biota (or, indeed, in any time slice), insights into the dynamics of their interaction are most fruitfully gained by investigating the trajectories of clades throughout their evolution. Most studies to date have focussed on animals (Foote 1994, 1997; Moyne and Neige 2007; Hughes *et al.* 2013), but the long evolutionary history (Wellman 2014) and rich fossil record of land plants (embryophytes) make them ideally suited for comparison. Diversity patterns through time within vascular plants have been studied for many years, typically deriving from species-level compilations of originations and extinctions (Knoll et al. 1979; Niklas et al. 1980; Lidgard and Crane 1990; Kovach and Batten 1993; Cascales-Miñana and Cleal 2012, 2014). Results have differed in some details (Niklas and Tiffney 1994), but are broadly consistent in showing i) a radiation of pteridophytes and gymnosperms in the Late Devonian-Carboniferous ii) a gymnosperm dominated flora in the early-mid Mesozoic of comparatively constant diversity and iii) a mid-late Cretaceous to Tertiary diversity increase, due primarily to the radiation of the angiosperms. The presence of novel morphological features within this group raised the question of whether phases of embryophyte diversification could be explained by the acquisition of 'key innovations' within angiosperms (Endress 2001), seed plants (Rudall and Bateman 2007) and early land plants (Bateman *et al.* 1998; Renzaglia *et al.*

2000). Advances in plant phylogenetics have revealed that the timing of many plant radiations does not match the first appearance of hypothesised innovations (Sanderson and Donoghue 1994; Davies *et al.* 2004; Vamosi and Vamosi 2010), implying instead that the evolution of suites of characters over an extended period of time may enable diversification (Donoghue 2009). The hunt for specific drivers has shifted to focus either on competitive interactions, for example between plants and herbivores (Agrawal 2007; Futuyma and Agrawal 2009), or on environmental factors such as climatic change (McElwain et al. 1999; Beerling et al. 2001; Willis and Niklas 2004; Beerling and Berner 2005; Feild and Arens 2007; Boyce et al. 2009; Willis and McElwain 2013).

In marked constrast to diversity, for which temporal patterns have been investigated for many years (Crane *et al.* 1994; Crisp *et al.* 2011; Donoghue 2008; Kenrick *et al.* 1997; Lupia *et al.* 1999; Schneider *et al.* 2004; Soltis *et al.* 2004), there have been only a handful of studies on the morphological disparity of plants (Lupia 1999; Niklas 1999; Chartier *et al.* 2014). Often these studies have focused on a specific aspect of plant morphology such as leaves (Boyce and Knoll 2002; Boyce 2005) or vascular systems (Wilson and Knoll 2010; Feild et al. 2011). Disparity analyses have furnished an important means of assessing macroevolutionary patterns in animals for some years, and we believe that their application to plants would be equally insightful.

Aims

This paper has two primary aims. The first is to provide an overview of the methods used to quantify morphological disparity, with particular emphasis on their application to plant evolution. We contrast concepts of disparity with those of diversity or species richness, and explain how exploring both trajectories through time can shed light on the evolutionary dynamics of clades. Morphological disparity is usually quantified with reference to the axes

of some form of morphospace; an *n*-dimensional space in which the distances between species or other operational taxonomic units are proportional to some measure of the morphological distances between them. We therefore distinguish between theoretical and empirical morphospaces and discuss their relative advantages and disadvantages for the study of plants. We also explore a variety of potential data sources and consider their relative merits. Particular emphasis is given to character-based empirical methods, which have proved broadly applicable to animal clades at a wide range of taxonomic levels (Hughes *et al.* 2013), but have yet to be utilized in plants. The second objective is to demonstrate the application of these methods to a select number of published character matrices for major plant groups. We compare and contrast the observed patterns of disparity through time with those seen in animals and offer a prospectus for future studies of plant disparity.

What is disparity and why should we study it?

The macroevolution of any major clade through deep time can be characterised in a number of ways. There is perennial interest in how diversity changes (Sepkoski *et al.* 1981; Sepkoski 1997; Sepkoski and Miller 1998), particularly with regards to how species and higher taxonomic richness responds to major physical or biotic changes such as mass extinctions, the opening up of new habitats or the origination of other major groups. Equally fundamentally, we may wish to know how the constituent taxa of a clade are related, and may use phylogeny to better inform the patterns above. Increasingly, however, palaeobiologists are also focussing on the manner in which groups diversified morphologically to give rise to new bodyplans or architectures (Fortey *et al.* 1996). The range or variance of morphological form across species or other taxa is usually referred to as 'morphological variety', 'morphological disparity' or simply 'disparity' in context. Disparity is therefore a property of a sample of taxa rather than of individual species, and is also measured relative to some set of

quantifiable variables. Trajectories of disparity through time are often different from patterns of species and higher taxonomic diversity, and are also difficult to predict from phylogeny.

Although all morphological variety is generated within the context of a phylogeny, diversity and disparity are fundamentally decoupled (Foote 1991; Fortey *et al.* 1996, 1997; Moyne and Neige 2007). Large samples of morphologically very similar species typically have much lower disparity than small groups of morphologically highly dissimilar species. Specifically, numerous basal groups of animals show levels of disparity greater than or equal to their more diverse, derived counterparts (Fig. 1) (Foote 1992, 1994, 1997; Wills *et al.* 1994; Wills 1998) although exceptions exist (Benson *et al.* 2012). At a coarse level, higher taxonomic diversity (e.g., numbers of orders or classes) tends to be a better proxy for disparity than numbers of species or genera (Foote 1990). Plots of relative disparity through time are therefore often used alongside plots of diversity in order to understand the dynamics of clade evolution more fully.

Much of the initial impetus for quantifying levels of disparity came from claims about the evolutionary significance of the fossils from the Middle Cambrian Burgess Shale (Whittington 1985; Conway Morris 1989). In particular, it was claimed (Gould 1989) that the range of morphological variety amongst Cambrian arthropods was far greater than that realised at any time subsequently; an argument couched (at least initially) in the perceived higher taxonomic status (i.e., subphylum or class) of many Burgess Shale genera. Gould (1991) subsequently propounded an 'inverted iconography' model for the evolution of life. An initial phase of experimentation and looser constraint on bodyplan evolution was posited to yield early maximal disparity, followed by a phase of winnowing in which most bodyplans were lost and the survivors consolidated and canalised. Subsequent evolution would typically yield few new bodyplans, but would see increases in diversity; increasing numbers of variations (species) upon a more limited number of constrained themes. However, empirical

studies of marine invertebrates found that the disparity of Cambrian and recent faunas were essentially equivalent (Briggs *et al.* 1992; Wills *et al.* 1994, 2012; Fortey *et al.* 1996) (Fig. 2). Subsequent studies have examined the disparity of clades at numerous successive time intervals, often demonstrating relatively high early disparity even while diversity is low (Foote 1992, 1994; Wills 1998). Recently, this approach has been applied to a larger dataset of exclusively fossil animal clades (Hughes *et al.* 2013). The shape of the disparity profile of a clade through time can be summarised as a centre of gravity index (CG). Clades with precisely symmetrical patterns through time have indices of 0.50, those with higher levels of disparity early in their history have values <0.5 (bottom heavy), while those peaking late tend to > 0.50 (top heavy). In a sample of 98 extinct clades that did not go extinct coincident with one of the 'big five' (Hallam and Wignall 1997, Bambach 2006) mass events, there was a significant bias towards bottom heaviness and early high disparity. Groups persisting to the present tend to have top-heavy profiles; not least because they are artificially truncated by the recent. Those disappearing coincident with one of the big five mass events tend to be top-heavy, and for similar reasons.

Other research agendas have become increasingly important within particular clades. One is the extent to which bodyplans are modular, and comprise units within which changes are relatively tightly correlated, but between which there is greater flexibility (Klingenberg *et al.* 2004; Monteiro and Nogueira 2010; Cooper *et al.* 2010; Drake and Klingenberg 2010) Another is the extent to which developmental versus environmental factors constrain bodyplans over evolutionary time (Allen *et al.* 2008; Anderson *et al.* 2011). Increasingly, there is also interest in quantifying functional disparity, notably in fish and basal tetrapods (Friedman 2010; Anderson *et al.* 2013).

Why study the disparity of plants?

In contrast to animals, there have been few studies investigating the morphological disparity of plant clades. We suspect that the patterns in plants may differ from those in animals; both the trends observed in statistical samples of clades, and the overall pattern of disparity through time for the group as a whole. In this latter context, it may be informative to compare plots of ordinal diversity through time (compiled from Benton, 1993), insofar as counts of higher taxa afford a *very* rough approximation to disparity (Fig. 3). Animals reach relatively high levels of ordinal diversity relatively early in their history; commensurate with the patterns revealed in explicit studies of disparity. The pattern observed in vascular plants differs markedly. Even accounting for the much later origin of vascular plants compared to animals, plants show a much more gradual increase in ordinal diversity, reaching 50% of their maximum relatively late in their evolutionary history. Plants show ordinal diversity increases in three discrete phases: i) the Late Devonian, corresponding to the initial radiation of pteridophytes and gymnosperms; ii) a smaller increase at the start of the Cretaceous, coincident with the appearance of the angiosperms; iii) a Late Cretaceous increase, corresponding to the appearance of many modern angiosperm groups (Niklas and Tiffney 1994).

Ordinal diversity profiles (Fig. 3) suggest that vascular plants have fewer fundamentally different modes of morphological organisation than animals, and acquired novel bodyplans more gradually. Strikingly, plants appear to be relatively unperturbed by the mass extinction events that were catastrophic for animals; or at least the recovery of plants was rapid enough to mask any significant diversity decreases in the fossil record (Rees 2002; McElwain and Punyasena 2007; Cascales-Miñana and Cleal 2014). Plants therefore appear to have greater resilience to certain types of ecological disturbance than animals (Cascales-Miñana and Cleal 2012); a surprising inference given that many aspects of plant morphology are thought to be tightly mechanically and physiologically constrained to optimise

photosynthetic efficiency and structural support (Niklas and Kerchner 1984). Even relatively simple optimization models with a small number of variables can produce the diverse spectrum of habits and gross phenotypes seen across plant groups (Farnsworth and Niklas 1995; Niklas 1999) (Fig. 4); ecological disturbance may actually serve as a driver for increasing phenotypic diversity. Therefore, although basic structural components (eg. phytomers in the case of branches) may be relatively morphologically conserved across taxonomic groups, they can nevertheless produce markedly different gross morphologies, even between closely related species or within species. This scale-dependent disparity is one of the defining characteristics of vascular plants and likely facilitates the unparalleled level of phenotypic plasticity seen within many plant species (Schlichting 1986, 2002; Bradshaw 2006). The hierarchical modularity in many aspects of plant form (Barthélémy and Caraglio 2007; Klingenberg *et al.* 2012) may also have profound implications for plant evolution (Friedman and Williams 2003).

Studies of plant disparity to date have mostly focused on specific structures in which shape variation is believed to be of particular functional importance, rather than on holistic analyses of form. Leaf and shoot disparity, in particular, has been extensively studied. Boyce & Knoll (2002) investigated trends in leaf shape in fossil plant lineages, revealing a rapid expansion of leaf morphospace in the Early/Middle Carboniferous. The genetic controls on leaf shape (Langlade *et al.* 2005; Chitwood *et al.* 2014) and compound leaf structures are gradually being better understood (Klingenberg *et al.* 2012). Leaf shape appears to be correlated with shoot morphology (Lacroix *et al.* 2003; Jeune *et al.* 2006), although the importance of selective, functional and historical constraints in the evolution of these hierarchical systems is poorly understood (Burns *et al.* 2008). Floral morphology, despite having long been recognised as a critical component of angiosperm disparity (Stebbins 1951) has received relatively little attention until recently (Whibley *et al.* 2006; Stournaras *et al.*

2013; Chartier *et al.* 2014). Similar considerations apply to the architecture of inflorescences (Prusinkiewicz *et al.* 2007). Other work has investigated the evolution and possible adaptive value of different types of pollen (Lupia 1999; Ressayre and Godelle 2002) as well as physiological properties in the conductive vessels of major seed plant groups (Wilson and Knoll 2010). floral and general. Rather than attempt to assess disparity from large collations of morphological data, more holistic approaches tend to consider habit and gross architecture (Niklas and Kerchner 1984; Niklas 1999; Silva and Batalha 2011).

The decoupling of diversity and disparity within higher plant clades appears every bit as great as that within animal groups (Yu *et al.* 2014) . For example, the true grasses (Poaceae) and the bromeliads (Bromelilaceae) are both families of angiosperms in the order Poales. However, the true grasses are represented by about 10,000 species (The Plant List 2013) of varying size but relatively limited floral disparity, while the bromeliads contain just over 3,000 species but show huge variation in inflorescence morphology (Benzing 2000; Sajo *et al.* 2004). It is clear that a complete picture of plant disparity cannot be captured by focussing exclusively on the disparity of specific structures (as there is strong scale dependence) or by using diversity as a proxy. Holistic approaches that use a broad suite of characters sampled over large numbers of taxa will probably constitute the best way of quantifying plant disparity at macroevolutionary scales. Here, we take some preliminary steps in this direction for a sample of higher plant clades.

Types of data

There are many approaches to quantifying morphology (Moore and Moser 1995; Chapman and Rasskin-Gutman 2001; Lockwood *et al.* 2002), and the most suitable usually depends upon the application and the question being addressed. Where the forms being compared are broadly similar (e.g., typically species within genera or families), a variety of morphometric

approaches can be used to derive sets of continuous variables describing shape and shape change, usually with some implicit standardisation for size and orientation (Rohlf and Marcus 1993; Adams *et al.* 2004) (Fig. 5). Three-dimensional, landmark based approaches operate by identifying biologically (or functionally) homologous points (e.g., intersections between homologous structures) across all of the species or higher taxa (hereafter 'operational taxonomic units' or OTUs) being compared (Marcus 2000; Cramon-Taubadel *et al.* 2007; Mitteroecker and Gunz 2009). Outline based methods describe shapes in more detail. This can either be using a more limited number of discrete points (homologous landmarks), possibly interspersed with semi-landmarks to further specify the form (Bookstein 1997; Perez *et al.* 2006) or using continuous functions (e.g., Fourier analysis) describing shape (Rohlf and Archie 1984; Crampton 1995). Where the forms being compared are more divergent (e.g., across higher taxa) it often becomes difficult to identify a sufficient number of homologous or functional landmarks to capture all but the most limited and conservative aspects of form variation (Bocxlaer and Schultheiß 2010). Here, it is possible to use an array of discretely coded characters, each recognising two or more alternative states, as descriptors of morphological variation (Wills *et al.* 1994; Wills 1998). Such data are more flexible, but entail more assumptions and potential subjectivity concerning the selection and discretisation of characters and states. The morphospaces that they define also have properties that differ from those derived from continuous character data (Gavrilets 1999).

The first studies that addressed the issue of quantifying disparity explicitly with empirical data sets were published about twenty-five years ago (Foote 1990, 1994; Briggs *et al.* 1992; Wills *et al.* 1994) (Fig. 6). The disparity profiles of numerous major animal clades were investigated over the next ten years, before a wane in apparent interest. The last few years, however, have seen the resurgence of empirical studies, with a particular emphasis on the use of discrete character data sets. As a general rule, metazoan clades tend to show an initial rapid

increase in disparity, with early levels of disparity being at or close to the maximum levels observed throughout the group's history.

Biological homology and functional analogy

With all types of data, a distinction can be drawn between those approaches that attempt to capture variation in biologically homologous aspects of morphology (Rohlf 2002; Klingenberg *et al.* 2004), and those that are more concerned with the functional parameters of shape (Nogueira *et al.* 2009; Figueirido *et al.* 2011; O'Higgins *et al.* 2011; Anderson *et al.* 2011, 2013). Morphological disparity can be used to refer to both aspects of variation in form, although the intention is sometimes unspecified (Love 2007). The distinction can be illustrated with reference to the tails of derived sharks and ichthyosaurs, both of which have convergent evolved dorsal and ventral lobes with a relatively high aspect ratio for high-speed aquatic locomotion (Motani 2002; Lingham-Soliar 2005; Lingham-Soliar and Plodowski 2007). In functional terms, the dorsal lobes of both groups are comparable, as are the ventral lobes. However, the vertebral column of sharks extends into the dorsal tail lobe, while that of ichthyosaurs deviates into the ventral lobe. The tip of both dorsal lobes might therefore constitute a valid functional landmark, but the tip of the dorsal lobe of sharks is *biologically* homologous to the tip of the ventral lobe in ichthyosaurs. Similar considerations apply to discrete, character data; much depends upon the manner in which characters and states are defined.

The exclusive use of putatively biologically homologous discrete variables restricts consideration to the same pool of characters used by cladists. In practice, and especially when dealing with fossil taxa, cladistic homology is established on operational grounds of detailed similarity and relationships to other structures (Pinna 1991; Butler and Saidel 2000). Such characters may also be functionally analogous, but are not necessarily so (Ruvinsky and

Gibson-Brown 2000; Shubin *et al.* 2009). Cladistic matrices therefore offer a rich resource for quantifying morphological variety across more conservative suites of putatively biologically homologous characters. Moreover, in the absence of homoplasy, we would expect the inter-OTU morphological distances assessed from such data to correlate closely with the evolutionary or patristic distances inferred on most parsimonious or otherwise optimal phylogenetic trees. With the progressive introduction of more character conflict and homoplasy (Sanderson and Donoghue 1989), this correlation will increasingly break down (Kelly *et al.* 2014), as will the inferred validity of many of the homology statements underpinning the data. Cladograms must account for the distribution of states across taxa by introducing hypotheses of convergence and reversal along branches. The metrics of morphological differences underpinning analyses of morphological disparity do not account for similarity due to the convergent acquisition or loss of traits, and are therefore intrinsically more phenetic in approach. Indeed, as levels of homoplasy increase (and more putative homologies are revealed to be analogies), patterns of morphological variety inferred from homologies and those inferred from statements of functional similarity become progressively more similar.

Morphospaces: theoretical and empirical

Once a set of morphological descriptors or variables has been established for a given group, it is possible to assess the morphological variety of constituent subgroups (e.g., clades) or of chronological subsamples (e.g., taxa from successive geological periods). This can be done directly from the data, but it is more typical to visualise patterns of taxonomic distributions in some form of morphospace; an abstract, multidimensional space in which distances correlate with morphological differences. A distinction (although one not universally embraced; Mitterocker & Huttegger, 2009) can be drawn between theoretical and empirical

morphospaces. Theoretical morphospaces typically have dimensions that each capture a single quantifiable aspect of form, and (despite being parameterised with reference to real organisms) are defined *a priori* without the need for an empirical data set. The most frequently cited examples are those describing mollusc shells, which variously quantify form and growth using a very modest number of variables (Raup and Michelson 1965; Skalak *et al.* 1997; Hammer and Bucher 2005; Urdy *et al.* 2010). Real specimens can be located within theoretical morphospaces, but empirical data are not necessary in order to define them. Empirical morphospaces, by contrast, are constructed from a particular set of empirical morphological data. Their dimensionality tends to be high (Raup and Michelson 1965; Foote 1997; McGhee 1999; Mitteroecker and Huttegger 2009); much higher than that of their theoretical counterparts. For this reason, a number of data reduction techniques (usually multivariate ordination such as principal components or coordinates analysis) are used to condense the dimensionality of the space. This makes it possible to summarise morphological variation using a smaller number of abstracted variables, whilst minimizing distortion. These abstracted axes often cannot be described verbally, but may allow the relative disparity of groups to be visualised and quantified more readily. Many of these approaches necessitate a distillation of the multivariate differences between taxa into a single measure of difference or distance for all possible taxon pairs (often realised as a triangular distance matrix analogous to that used to tabulate distances in a road atlas). The precise distance metric used depends upon the nature of the data and the desired properties of the resultant space and/or disparity indices. These complexities are discussed elsewhere at length (Wills, 1998; Wills, 2001a; Hughes *et al.* 2013).

Two issues deserve emphasis. Firstly, all morphospaces are abstractions, and necessarily based upon a subset of morphological variables. Variable choice inevitably determines the nature of the space. Many practitioners seek to sample variables as widely as

possible from all aspects of morphology, thereby deriving spaces that reflect overall form. This is not always possible, however, as in many cases where only variation in particular organs or aspects of form can be codified across taxa (Pretorius and Scholtz 2001; Lindbladh 2002; Miller and Venable 2003; Neige 2006; Jones *et al.* 2009). Morphospaces derived from particular aspects of form or using data from particular organ systems or modules may be well-suited to addressing particular evolutionary questions. However, 'morphological disparity' is usually conceived as referring holistically to overall form. Secondly, indices of disparity are necessarily relative and comparisons are only possible within the parameters of a given morphospace or underlying data set. Hence, while it is possible to make inferences regarding the relative disparity of a group at different times in its evolutionary history, or to compare the disparity of constituent subgroups within an analysis, it is not possible to make comparisons between groups from independently-constructed morphospaces or data sets. This is also the reason why supermatrices uncritically assembled from multiple published data sets (and containing large blocks of inapplicable codes for large groups of taxa) may lose traction on some of the largest and deepest comparative questions.

A variety of disparity indices have been discussed in the literature (Foote 1991, 1994, 1997; Wills *et al.* 1994; Wills 2001a; Hughes *et al.* 2013), but it is not our intention to rehearse the relative merits of these here. Among the most widely used approaches are those that distil the dispersion of taxa on multiple axes of the morphospace into a single value. The dispersion on a single axis can be quantified either as the range (defined by the outliers) or the variance of scores; the latter has the advantage of a relative insensitivity to sample size differences. Measures on multiple axes can be combined either as their product – effectively calculating the (hyper)volume of a (hyper)cube – or as their sum. While hypervolumes are superficially more intuitive, they effectively give disproportionate weighting to smaller differences on later axes. Most ordination methods sequester progressively smaller fractions

of total variance in later axes, but multiplying the univariate indices of dispersion means that halving the spread on any axis (whether the first or last) will halve the resultant hypervolume. Products also collapse to zero whenever the dispersion of taxa on a given axis is also zero. Summing the univariate indices of dispersion (rather than multiplying them) avoids these problems. The sum of variances has particularly desirable properties, therefore, and has been used throughout the present study.

MATERIALS AND METHODS

Data collection

In general, we followed the protocols set out in Hughes *et al.* (2013). Morphological matrices for six major tracheophyte groups (Angiospermae (Doyle *et al.* 1994; Nandi *et al.* 1998; Doyle and Endress 2014), Arecaceae (Baker *et al.* 2009), Nymphales (Borsch *et al.* 2008), Pinophyta (Hart 1987), Pinaceae (Klymiuk and Stockey 2012) and Polypodiidae (Pryer *et al.* 1995)) were selected from the literature. These represented the most diverse extant higher taxa of vascular plants, in addition to well-sampled subclades within both the angiosperms and conifers. Diversification and extinction patterns within these last two groups have been relatively well-studied. Outgroup taxa were removed from these source matrices in several cases; either because there were missing taxa between the ingroup and outgroup, or because the outgroup OTUs were sampled at a higher taxonomic level than the ingroup. In some datasets, we also had to overcome inhomogeneity of sampling within the ingroup, which we achieved by amalgamating OTUs in such a way as to render them homogeneous at a higher taxonomic level. Character amalgamation utilized modal states. Some characters were rendered uninformative as a result of these condensations, and were therefore removed (specifically Pinaceae - 46, 47, 51; Arecales - 6, 10, 15, 21, 22, 48, 78, 91, 92, 10; Nymphales

- 4, 5, 6, 12, 14, 22, 28, 39, 57). Stratigraphic ranges were assigned to stages using the International Stratigraphic Chart 2009 (Gradstein *et al.* 2004; Ogg *et al.* 2008). Stratigraphic range data were sourced from the *Paleobiology Database* (http://paleodb.org/), *Sepkoski Online* (Sepkoski, 2002) and the *Fossil Record 2* (Benton 1993). Ranges were treated as continuous between first and last occurrences, with data being grouped into stage level time bins. In cases where first and last occurrences were resolved only to intervals above the stage level, we coded for the stage corresponding to the midpoint of the interval. There were very few fossils within the Nymphales, and we therefore estimated ranges using the time calibrated molecular phylogeny of (Yoo *et al.* 2005). Temporal bins with sample sizes of 1 were also amalgamated so that disparity could be calculated for these intervals.

Analyses

For each exemplary clade, intertaxon distance matrices were calculated using the Generalised Euclidean Distance metric (GED) of Wills (1998), and as implemented in Hughes *et al.* (2013). Distance matrices were ordinated in R (R Core Team 2013) using principal coordinates analysis (Wills *et al.* 1994), and incorporating Caillez's correction for negative eigenvectors (Cailliez 1983). Disparity for each time bin was calculated as the sum of variances on all axes of the morphospace, yielding a trajectory of disparity through time. The centre of gravity of each trajectory was used to distinguish between those clades whose temporal mean disparity was located early (bottom-heavy), late (top-heavy) or in the middle of their evolutionary history (symmetrical). A centre of gravity metric (Gould *et al*. 1987; Uhen 1996) in absolute time (*CG*) was calculated for each clade as:

$$CG = \Sigma\, d_i\, t_i \,/\, \Sigma\, d_i$$

Where d_i is the disparity at the ith stratigraphic interval and t_i the temporal midpoint in absolute time (Myr) of the ith stratigraphic interval. This was then scaled between the ages of the oldest (t_{oldest}) and youngest ($t_{youngest}$) intervals to yield an index of observed *CG* (CG_m) between 0 and 1.

The expected CG_m for a clade of constant disparity through time is unlikely to be 0.50, but is determined by the durations of the time bins over which the profile is measured. The observed CG_m was therefore compared with the inherent *CG* (CG_i) for a clade of uniform disparity spanning the same intervals. A bootstrapping procedure was used to generate a distribution of 1,000 resampled differences between CG_m and CG_i, and clades for which >97.5% of bootstrapped replicates lay either above or below the centre of gravity inherent in the timescale (p-value <0.05) were deemed to be significantly top or bottom heavy respectively (Foote, 1991). Observed CG_m was then expressed relative to CG_i as a baseline; hereafter simply *CG*.

An ancillary test from Hughes *et al*. (2013) was used to determine whether the taxa observed in the first two stages had significantly less disparity than the maximum observed in any time bin. The disparity profile of the clade was bootstrapped 1,000 times. For each replicate curve, the difference in disparity between the first two stages and the disparity maximum was calculated, yielding a distribution. If a difference of zero was within the 95% limits of this distribution, we were unable to reject the null hypothesis: namely that there was no difference between the initial disparity and the maximum (early high disparity). In such cases, maximal disparity was achieved in the earliest stages of the clade's evolution. A similar test was applied to the end of each group's history (late high disparity).

RESULTS AND DISCUSSION

Patterns of plant disparity through time

Our results are presented as preliminary explorations of the manner in which our selected clades have explored one form of morphospace through time. While more detailed work will certainly follow, our findings highlight several general patterns and permit certain conclusions.

For extinct clades with homogeneous birth/death dynamics and characters evolving under a Brownian model, the null expectation is that clade disparity profiles should be somewhat top heavy on average (a mean clade centre of gravity greater than 0.5) (Foote 1991). This is because the morphology of new lineages is contingent upon the morphology of those from which they have evolved; clades would therefore be expected to explore morphospaces in a progressive manner. The extinction of lineages, by contrast, can occur in any pattern with respect to the morphospace. Random extinction, in particular, will tend to maintain a relatively wide morphospacial distribution, introducing a fundamental asymmetry into clade evolution. This is an over-simplistic model for the clades studied here, because all are extant; the Recent effectively truncates their evolution. As demonstrated by Hughes *et al.* (2013), extant clades (as well as those becoming extinct coincident with one of the 'big five' mass events) have a much greater tendency towards top-heaviness merely by virtue of their persistence to the Recent. It is therefore unsurprising that most of our exemplar clades (with the exception of two of the three angiosperm data sets: Doyle *et al.* 1994; Nandi *et al.* 1998) show significantly top-heavy (CG > 0.5) profiles (Table 1). More remarkably, several of

these clades show initial disparity levels close to their maxima, or reach this level early in their history. Arecaceae (palms) (Baker *et al.* 2009) first appeared *at* their maximum disparity, while all three of our angiosperm data sets (Nandi *et al.* 1998; Doyle *et al.* 1994; Doyle and Endress 2014) showed initial disparity levels over 90% of the maxima in each case. Polypodiales (ferns) (Pryer *et al.* 1995) and Pinaceae (pines) (Klymiuk and Stockey 2012) both reached their maxima within three time bins. The Nymphales (water lilies) (Borsch *et al.* 2008) are represented by a small data set (just 22 taxa) partitioned into larger time bins. Despite their apparently slow start, early disparity levels were not significantly different from the maximum (Table 1).

Conifers (Hart 1987) have the most dynamic disparity trajectory, with initial Carboniferous and Permian levels significantly lower than at any subsequent times (Fig. 7). These modest levels persisted until after the end of the Permian, whereupon there were significant increases into the early Mesozoic. Although disparity appears to decline between the Middle and Late Triassic, it increases subsequently to reach maximum levels at the end of the Jurassic. Levels then decline gradually until the Recent, with extant disparity being significantly lower than the maximum levels observed at the end of the Jurassic. Conifers also show more intensive clustering of taxa in the morphospace at a variety of spatial scales than do the other clades in our study (Fig. 8). Disparity within the pine family (Fig. 9) shows broad similarities with conifers as a whole from their origins in the Jurassic; a reassuring finding given that pines represent a significant proportion of conifer diversity from this time. The initial increase in disparity for pines occurs slightly later than the corresponding increase in conifers as a whole, and is maintained until the present day.

Both angiosperms as a whole (Doyle *et al.* 1994) (Fig. 10) and the palm subclade (Baker *et al.* 2009) (Fig. 11) show approximately constant disparity through time. Palm disparity undergoes a slight decrease through the end of the Mesozoic and the early

Palaeogene, such that the disparity of living taxa is lower than the realised maximum of the past. In contrast, our results suggest that the water lilies (Borsch *et al.* 2008) did not reach present levels of disparity until the Neogene (Fig. 12), with markedly lower levels for the first 10 My of their history. We note that this is our smallest data set (22 taxa), resulting in large estimates of error relative to observed fluctuations in disparity.

In polypod ferns, disparity increases through the Permian and Triassic, reaching or slightly exceeding modern levels by the Early Jurassic (Fig. 13). Disparity increased slightly thereafter to peak levels around the K-Pg but subsequently declined significantly in the last few million years.

An unexpected observation is that high levels of disparity were maintained for the past 80+ My in our largest clades (conifers, pines, ferns and angiosperms), despite successive radiations of subgroups and catastrophic environmental and faunal upheavals over this time, including the K/Pg event (Ehleringer and Sage 1991; Cerling *et al.* 1997; Zachos *et al.* 2001). Indeed, while there is evidence of significant local faunal turnover in plants (McElwain and Punyasena 2007), recent work suggests that only two major extinction pulses are supported in the plant fossil record: one at the Carboniferous-Permian transition and another during the middle-late Permian (Cascales-Miñana and Cleal 2014). Of the groups analysed, only conifers spanned this second event and actually show a significant increase in disparity during this time. It is therefore possible that conifers were evolving into areas of ecospace formerly occupied by other plant groups that declined at the end of the Permian (Retallack 1995).

The high initial disparity of many of the plant groups investigated here results from the appearance of a small number of morphologically highly distinct taxa close to the base of each clade. In most of our groups, fossils quickly define the extremes of the empirical envelope as soon as they appear, with subsequent lineages gradually filing the intervening

morphospace rather than colonising more eccentric regions of it. Conifers exhibit a rather different pattern (Fig. 7), with the gradual appearance of subclades that each occupy distinct regions of the space (Fig. 8). Rather than rapid morphospace occupation followed by subsequent saturation, conifers appear to show several phases of morphospace colonisation and subsequent diversity increase in tightly defined regions centred around pioneers with novel character combinations. This suggests that the evolution of conifers may have been characterised by the intermittent acquisition of novel morphologies or 'key' innovations, followed by subsequent diversification. Such events may include the radiation of the pines in the Jurassic and the cypresses in the Cretaceous and early Palaeogene. The high degree of morphospace clustering may result from competition with other groups (such as angiosperms), constraining the available morphospace. However, it is more likely to be a function of greater structural or developmental constraints acting upon suites of characters within the conifer dataset (moreover, conifers appear to show relatively tight clustering in the Triassic and Jurassic, prior to the inferred appearance of basal angiosperms). Pines show much weaker clustering than conifers as a whole. Characters within the pine dataset (Klymiuk and Stockey 2012) were derived from cone morphology, strongly implying that Pinacae were able to explore the majority of possible cone forms rapidly and early in their evolution in a relatively unconstrained manner.

Because most of the discrete character matrices analysed here included a broad sample of characters from many different anatomical regions, it is reasonable to assume that the gross morphology of the taxa in the sample was reasonably represented. Our three angiosperm matrices had marked differences in character and taxon composition (Fig. 14), but showed similar overall patterns of disparity through time

Why are there so few studies of plant disparity?

There are a number of possible reasons why empirical morphospace approaches have been underutilised within the plant sciences, aside from the usual methodological considerations underpinning the choice of data and indices (Rohlf 1998). Many morphometric approaches entail time-consuming data collection, which may limit tractable sample sizes. There are also difficulties in establishing variable or character sets that can be measured or coded across higher taxa. Most studies therefore focus upon smaller plant clades or else derive data from particular structures (Chartier *et al.* 2014) rather than investigating overall morphological disparity. Moreover, the often fragmentary nature of fossil material may mean that holistic treatments are impractical, or that many types of morphometric data cannot be obtained (Adams *et al.* 2004).

Utilising existing discrete morphological data matrices

New morphological character matrices for plants are becoming increasingly rare (Gottlieb 1988; Sytsma *et al.* 1991); mounting evidence from molecular phylogenetics implies that morphological convergence is obfuscating our understanding of plant relationships (Bowe and Coat 2000; Donoghue and Doyle 2000; Schneider *et al.* 2009). However, we believe that morphological character data has important uses beyond that of inferring phylogeny (Thorne *et al.* 2011); not least for quantifying patterns of disparity change throughout morphologically and taxonomically diverse clades with long evolutionary histories. In this context, the problems of homoplasy and convergence that bedevil phylogenetic inference are less marked, since morphospaces are conceived for a variety of purposes and can be intended to reflect a variety of aspects of evolution. Discrete character morphospaces offer a framework for quantifying patterns of morphological disparity within large clades, but also highlight questions that can be addressed in a more focussed manner using other morphometric techniques (Goodman 2002). More comprehensive analyses of existing plant character

matrices would represent an efficient use of legacy data, allow some of the commonalities suggested in this paper to be properly tested and would powerfully complement existing and future morphometric studies.

Despite the abundance of discrete, morphological data in the literature, there are a number of considerations when using explicitly cladistic matrices for disparity studies. Morphological cladists usually seek to resolve phylogeny (Forey *et al.* 1998), but are not always concerned with representing accurate branch lengths and evolutionary distances. Even in the extreme approach adopted by pattern cladistics, which views the cladistic method as being divorced from evolutionary assumptions of descent through modification (Brady 1982; Brower 2000), there is still an imperative to recognise hierarchical groupings within sets of taxa (Hennig 1966; Estabrook *et al.* 1975). There may therefore be a tendency to subdivide morphological variety more finely within taxa that are morphologically conservative overall in order to resolve their relationships or structure. Conversely, taxa supported by long evolutionary branches may be morphologically very distinct from their nearest sampled relatives, but there may be no imperative to quantify all of these differences to the same degree of resolution as in highly diverse and morphologically similar groups. More generally, it is reasonable to expect character matrices to be biased towards distinctive features and/or those which have been demonstrated to be good at distinguishing groups in previous studies. An allied issue is the assumption that all characters should be treated equally. This may not always be desirable, particularly in cases where some groups are characterised by a limited number of highly distinctive and variable characters while others are defined by broader suites of gross morphological features that are nevertheless coded as a single character. For example, it is probably simplistic to treat the presence or absence of sclereids in the leaves on an equal footing with scandent versus arborescent growth habits (Foster 1956; Rury and Dickison 1984) . While there are a variety of objective approaches for the differential weighting of

characters in phylogenetic studies, these are derived from predictions or empirical estimates of levels of homoplasy or the phylogenetic information content of characters (Farris 1969; Sharkey 1989; Goloboff 1993, 2014) . In disparity analyses, what may be required is rather some weighting derived from the ontogenetic priority, developmental (Riedl 1977; Arthur 1984, 1988; Wimsatt 1986) or structural depth (Stebbins 1969; Pettersson 2009) of characters, although such weights are notoriously difficult to assign.

Some cladistic matrices are constructed in order to address particular questions; most commonly sequences of character acquisition across important evolutionary transitions: for example, tetrapods from fishes (Wagner and Chiu 2001; Long and Gordon 2004; Ruta *et al.* 2006; Wagner *et al.* 2006) and birds from dinosaurs (Garner *et al.* 1999; Xu 2006; Heers *et al.* 2014; Brusatte *et al.* 2014). Such data intentionally focus on the taxa and characters bracketing these changes, with deliberately much sparser sampling outside of this. More generally, outgroup taxa – often included for rooting purposes – are more sparsely sampled than those of the ingroups (Graybeal 1998; Heath *et al.* 2008). Morphological cladistic characters may therefore sample morphological variation unevenly across taxa and through time. Not all data sets are suitable for investigating temporal and taxonomic patterns of morphological variation therefore, and many require some form of moderation. Hughes *et al.* (2013), for example, standardised sampling according to higher taxonomy, and removed outgroups.

One final issue is the inclusion or otherwise of autapomorphic character states; those present in just a single taxon (Yeates 1992; Bryant 1995). Such states cannot influence inferred cladistic branching structure, but they do affect branch lengths (without introducing homoplasy) and indices of morphological difference. In two state characters, an autapomophic state renders the entire character cladistically (but not phenetically) uninformative. This property is flagged by most phylogenetic software, which usually results

in their removal from cladistic matrices. Autapomorphic states are more likely to be retained in multistate characters (those with three or more states), since the character remains informative overall. More generally, cladists do not actively seek to include autapomorphic states, such that cladistic matrices usually omit this aspect of morphological variation. Empirically, however, the inclusion/exclusion of autapomorphies makes relatively little difference to assessments of morphological variety (Wills 2001a,b). The precise effect of autapomorphic states will depend upon the overall properties of the data set and the mode of analysis, but in general they merely cause the taxa possessing them to appear marginally more divergent from the overall mean morphology than they would otherwise be.

There is an increasing desire for large, complete phylogenies to underpin various forms of evolutionary and ecological analyses (Guyer and Slowinski 1993; Phillimore and Freckleton 2006; Tamura *et al.* 2012). Large matrices of molecular characters (supermatrices) are frequently assembled *de novo* using open data resources and automated algorithms (Liu *et al.* 2001; Davies *et al.* 2004; Bininda-Emonds 2004; Davis and Page 2008). There are no similar repositories or tools for morphological matrices. Assembling large matrices comprising hundreds or thousands of OTUs and characters from first principles would ensure greater consistency, but is hugely time-consuming. Hence, morphological supermatrices are often assembled by amalgamating the largest data sets or synthetic treatments available for constituent groups. However, this approach may entail its own set of problems. The first is alluded to above; the differential sampling of taxa and characters. Taxon sampling can be standardised more readily, but uniform character sampling requires more detailed knowledge and entails greater subjectivity. More problematically, it is often difficult or impossible to code many of the characters in the constituent matrices for the 'outgroup' taxa (those represented in the other matrices), thereby resulting in large blocks of inferred plesiomorphies (typically '0' or absent) and inapplicable codings ('?'). Depending upon the

manner in which such inapplicabilities are treated, this phenomenon can result in artificially distinct clusters of taxa, strongly but spuriously demarcated by these discontinuities in knowledge and character sampling (Wilkinson *et al.* 2005; Cotton *et al.* 2006). For these reasons, large published cladistic matrices compiled from first-hand observations of specimens (or from careful treatments of the primary literature) have many potential advantages over those assembled by conjoining data from disparate published sources (de Dequeiroz and Gatesy 2007).

CONCLUSIONS

1. The concept of morphological disparity is distinct from those of diversity and species richness (Wills 2001) . Indices of disparity attempt to codify the morphological variety of a sample of taxa, are calculated relative to some set of morphological variables or characters, and often utilise a plot of taxa in a multidimensional morphospace. Morphospaces are abstract spaces in which the geometric distances between taxa are proportional to some measure of the morphological differences between them. The nature of a morphospace is entirely contingent upon the underlying data, the manner in which differences between taxa are summarised as distances, and the methods used to project these distances into an *n* dimensional space. The precise approach will depend upon the purpose for which the morphospace is intended. It follows that there is no objective morphospace (in the sense that there is an objective phylogeny), and that the dispersion of taxa in different spaces cannot be compared directly (comparisons between subgroups within the space are possible, but these are necessarily only relative). Morphospaces derived from large samples of characters or variables encompassing most aspects of form are most likely to offer

insights into overall morphological variety. Indices of disparity variously assess the relative dispersion of samples of taxa within a morphospace, or provide some distillation of the morphological differences between them.

2. Diversity and disparity appear to be fundamentally decoupled. A significant majority of the animal clades investigated show relatively high disparity early in their evolution (Hughes *et al.* 2013) at times when diversity is still comparatively low (i.e., there are modest numbers of taxa but these are morphologically highly distinct from each other). The subsequent evolution of such groups often sees an increase in diversity with little or no concomitant increase in disparity; there are increasing numbers of taxa within a restricted number of morphological 'themes'. Disparity may even decline as diversity is rising, since some of the most speciose clades have particularly constrained bodyplans but are able to partition ecospace and morphospace particularly finely. A substantial minority of animal clades show other patterns, including high initial disparity at low diversity (Foote 1990).
3. There have been relatively few studies of morphological disparity in plants, and no studies have attempted to assess patterns of overall disparity in major clades through time. Temporal patterns of diversity in plants and animals show significantly different patterns (Knoll *et al.* 1979), with plants counterintuitively being less affected at times of global mass extinction (Cascales-Miñana and Cleal 2014). An assessment of patterns of disparity in major plant clades is therefore overdue, and may provide insights into plant macroevolution to complement those being obtained for animals.
4. There are numerous morphometric methods that allow shape and shape change to be quantified across taxa. However, as the morphogical variety of the forms being compared increases (usually in tandem with the taxonomic scope of the study), the ability of such approaches to compare increasingly disparate forms becomes more

limited. Discrete character data sets have certain advantages in this context. There are rich resources of discrete character matrices already available for numerous plant clades, and although initially intended for inferring phylogeny, these data sets can be repurposed for disparity studies within certain strictures.

5. Our preliminary disparity analyses for 6 exemplary plant clades demonstrate that initial levels of disparity are usually high, if not indistinguishable from (or at) the maximum ultimately achieved by the group. Most regions of the morphospace are colonised early in the history of each plant clade, with subsequent evolution serving merely to increase diversity within these regions. The notable exception are the conifers, in which subclades appear intermittently, and progressively colonise distinct regions of the space. This results in conifer disparity increasing incrementally over the first half of the group's history. All of our exemplary plant clades have disparity profile shapes with a centre of gravity higher than the intrinsic null (significantly so in all save two angiosperm datasets). This is unsurprising, however, since all are extant groups, with profiles truncated by the Recent (Hughes *et al.* 2013) (Hughes *et al.*, 2013). Combining detailed empirical morphometric studies of specific anatomical regions with the more holistic approach illustrated here will likely be reciprocally illuminating, and offer insights into plant macroevolution.

ACKNOWLEDGEMENTS

This paper evolved from a presentation by MAW at Euro Evo Devo 2014 in Vienna, and we thank Rainer Melzer and Günter Theißen for their invitation to speak at their symposum. We are grateful to the authors who generated the cladistic matrices repurposed and reanalysed

herein. This work was generously supported by grant 43915 from the JTF, which funds JWO's PhD work.

CONTRIBUTIONS

JWO wrote the manuscript, collated plant morphological and stratigraphic datasets, drafted figures and analysed data. MH ran disparity analyses and statistics, summarized the disparity literature and drafted figures. SG produced clustering plots. MAW conceived and designed the study, wrote the manuscript and drafted one figure.

LITERATURE CITED

Adams DC, Rohlf FJ, Slice DE. **2004**. Geometric morphometrics: ten years of progress following the "revolution." *Italian Journal of Zoology* **71**: 5–16.

Agrawal AA. **2007**. Macroevolution of plant defense strategies. *Trends in Ecology and Evolution* **22**: 103–109.

Allen CE, Beldade P, Zwaan BJ, Brakefield PM. **2008**. Differences in the selection response of serially repeated color pattern characters: standing variation, development, and evolution. *BMC Evolutionary Biology* **8**: 94.

Anderson PSL, Friedman M, Brazeau MD, Rayfield EJ. **2011**. Initial radiation of jaws demonstrated stability despite faunal and environmental change. *Nature* **476**: 206–209.

Anderson PSL, Friedman M, Ruta M. **2013**. Late to the table: diversification of tetrapod mandibular biomechanics lagged behind the evolution of terrestriality. *Integrative and comparative biology* **53**: 197–208.

Arthur W. **1984**. *Mechanisms of morphological evolution*. New York: Wiley.

Arthur W. **1988**. *A theory of the evolution of development*. New York: Wiley.

Baker WJ, Savolainen V, Asmussen-Lange CB, Chase MW, Dransfield J, Forest F, Harley MM, Uhl NW, Wilkinson M. **2009**. Complete generic-level phylogenetic analyses of palms (Arecaceae) with comparisons of supertree and supermatrix approaches. *Systematic Biology* **58**: 240–256.

Barthélémy D, Caraglio Y. **2007**. Plant architecture: a dynamic, multilevel and comprehensive approach to plant form, structure and ontogeny. *Annals of Botany* **99**: 375–407.

Bateman RM, Crane PR, DiMichele WA, Kenrick PR, Rowe NP, Speck T, Stein WE. **1998**. Early evolution of land plants: phylogeny, physiology, and ecology of the primary terrestrial radiation. *Annual Review of Ecology and Systematics* **29**: 263–292.

Beerling D, Berner R. **2005**. Feedbacks and the coevolution of plants and atmospheric CO2. *Proceedings of the National Academy of Sciences* **102**: 1302–1305.

Beerling D, Osborne C, Chaloner W. **2001**. Evolution of leaf-form in land plants linked to atmospheric CO2 decline in the Late Palaeozoic era. *Nature* **410**: 352–354.

Benson RBJ, Evans M, Druckenmiller PS. **2012**. High diversity, low disparity and small body size in plesiosaurs (Reptilia, Sauropterygia) from the Triassic–Jurassic boundary. *PLoS One* **7**: e31838.

Benton MJ. **1993**. *The Fossil Record 2*. London: Chapman & Hall.

Benton MJ. **2009**. The Red Queen and the Court Jester: species diversity and the role of biotic and abiotic factors through time. *Science* **323**: 728–732.

Benzing DH. **2000**. *Bromeliaceae: profile of an adaptive radiation*. Cambridge: Cambridge University Press.

Bininda-Emonds ORP. **2004**. The evolution of supertrees. *Trends in Ecology & Evolution* **19**: 315–322.

Bocxlaer B Van, Schultheiß R. **2010**. Comparison of morphometric techniques for shapes with few homologous landmarks based on machine-learning approaches to biological discrimination. *Paleobiology* **36**: 497–515.

Bookstein FL. **1997**. Landmark methods for forms without landmarks: morphometrics of group differences in outline shape. *Medical Image Analysis* **1**: 225–243.

Borsch T, Löhne C, Wiersema J. **2008**. Phylogeny and evolutionary patterns in Nymphaeales: integrating genes, genomes and morphology. *Taxon* **57**: 1052–1081.

Bowe L, Coat G. **2000**. Phylogeny of seed plants based on all three genomic compartments: extant gymnosperms are monophyletic and Gnetales' closest relatives are conifers. *Proceedings of the National Academy of Sciences of the United States of America* **97**: 4092–4097.

Boyce CK. **2005**. Patterns of segregation and convergence in the evolution of fern and seed plant leaf morphologies. *Paleobiology* **31**: 117–140.

Boyce CK, Brodribb TJ, Feild TS, Zwieniecki M a. **2009**. Angiosperm leaf vein evolution was physiologically and environmentally transformative. *Proceedings of the Royal Society of London, Series B: Biological Sciences* **276**.

Boyce CK, Knoll AH. **2002**. Evolution of developmental potential and the multiple independent origins of leaves in Paleozoic vascular plants. *Paleobiology* **28**: 70–100.

Bradshaw AD. **2006**. Unravelling phenotypic plasticity–why should we bother? *New Phytologist* **170**: 644–648.

Brady RH. **1982**. Theoretical issues and " pattern cladistics ." *Systematic Zoology* **31**: 286–291.

Briggs DEG, Fortey RA, Wills MA. **1992**. Morphological disparity in the Cambrian. *Science* **256**: 1670–1673.

Brower AVZ. **2000**. Evolution is not a necessary assumption of cladistics. *Cladistics* **16**: 143–154.

Brusatte SL, Lloyd GT, Wang SC, Norell MA. **2014**. Gradual assembly of avian body plan culminated in rapid rates of evolution across the dinosaur-bird transition. *Current Biology* **24**: 2386–2392.

Bryant HN. **1995**. Why autapomorphies should be removed. *Cladistics* **11**: 381–384.

Burns JH, Munguia P, Nomann BE, Braun SJ, Terhorst CP, Miller TE. **2008**. Vegetative morphology and trait correlations in 54 species of Commelinaceae. *Botanical Journal of the Linnean Society* **158**: 257–268.

Butler AB, Saidel WM. **2000**. Defining sameness: historical, biological, and generative homology. *BioEssays* **22**: 846–853.

Cailliez F. **1983**. The analytical solution of the additive constant problem. *Psychometrika* **48**: 305–308.

Cascales-Miñana B, Cleal CJ. **2012**. Plant fossil record and survival analyses. *Lethaia* **45**: 71–82.

Cascales-Miñana B, Cleal CJ. **2014**. The plant fossil record reflects just two great extinction events. *Terra Nova* **26**: 195–200.

Cerling TE, Harris JM, MacFadden BJ. **1997**. Global vegetation change through the Miocene/Pliocene boundary. *Nature* **389**: 153–158.

Chapman R, Rasskin-Gutman D. **2001**. Quantifying morphology. In: Briggs E, Crowther P, eds. *Palaeobiology II*. Malden: Blackwell Science, 489–492.

Chartier M, Jabbour F. **2014**. The floral morphospace–a modern comparative approach to study angiosperm evolution. *New Phytologist* **204**: 841–853.

Chartier M, Jabbour F, Gerber S, Mitteroecker P, Staedler Y, Crane PR, Schonenberger J. **2014**. The floral morphospace – a modern comparative approach to study angiosperm evolution. *New Phytologist* **204**: 841–853.

Chitwood DH, Ranjan A, Martinez CC, Headland LR, Thiem T, Kumar R, Covington MF, Hatcher T, Naylor DT, Zimmerman S, Downs N, Raymundo N, Buckler ES, Maloof JN, Aradhya M, Prins B, Li L, Myles S, Sinha NR. **2014**. A modern ampelography: a genetic basis for leaf shape and venation patterning in grape. *Plant Physiology* **164**: 259–272.

Conway Morris S. **1989**. Burgess Shale faunas and the Cambrian explosion. *Science* **246**: 339–346.

Cooper WJ, Parsons K, McIntyre A, Kern B, McGee-Moore A, Albertson RC. **2010**. Bentho-pelagic divergence of cichlid feeding architecture was prodigious and consistent during multiple adaptive radiations within African rift-lakes. *PloS One* **5**: e9551.

Cotton JA, Slater CSC, Wilkinson M. **2006**. Discriminating supported and unsupported relationships in supertrees using triplets. *Systematic Biology* **55**: 345–350.

Cramon-Taubadel N Von, Frazier BC, Lahr MM. **2007**. The problem of assessing landmark error in geometric morphometrics: theory, methods, and modifications. *American Journal of Physical Anthropology* **35**: 24–35.

Crampton JS. **1995**. Elliptic Fourier shape analysis of fossil bivalves: some practical considerations. *Lethaia* **28**: 179–186.

Davies TJ, Barraclough TG, Chase MW, Soltis PS, Soltis DE, Savolainen V. **2004**. Darwin's abominable mystery: insights from a supertree of the angiosperms. *Proceedings of the National Academy of Sciences of the United States of America* **101**: 1904–1909.

Davis KE, Page RDM. **2008**. Reweaving the tapestry: a supertree of birds. *PLoS Currents* **6**.

De Dequeiroz A, Gatesy J. **2007**. The supermatrix approach to systematics. *Trends in Ecology & Evolution* **22**: 34–41.

Donoghue MJ. **2009**. Key innovations, convergence, and success: macroevolutionary lessons from plant phylogeny. *Paleobiology* **31**: 77–93.

Donoghue MJ, Doyle JA. **2000**. Seed plant phylogeny: demise of the anthophyte hypothesis? *Current Biology* **10**: 106–109.

Doyle JA, Donoghue MJ, Zimmer EA. **1994**. Integration of morphological and ribosomal RNA data on the origin of angiosperms. *Annals of the Missouri Botanical Garden* **81**: 419–450.

Doyle JA, Endress PK. **2000**. Morphological phylogenetic analysis of basal angiosperms: comparison and combination with molecular data. *International Journal of Plant Sciences* **161**.

Doyle JA, Endress PK. **2014**. Integrating Early Cretaceous fossils into the phylogeny of living angiosperms: ANITA lines and relatives of Chloranthaceae. *International Journal of Plant Sciences* **175**: 555–600.

Drake AG, Klingenberg CP. **2010**. Large-scale diversification of skull shape in domestic dogs: disparity and modularity. *The American Naturalist* **175**: 289–301.

Ehleringer JR, Sage RF. **1991**. Climate change and the evolution of C4 photosynthesis. *Trends in Ecology and Evolution* **6**: 95–99.

Endress PK. **2001**. Origins of flower morphology. *Journal of Experimental Zoology* **115**: 105–115.

Erwin TL. **1997**. Biodiversity at its utmost: tropical forest beetles. In: Reaka-Kudla ML, Wilson DE, Wilson EO, eds. *Biodiversity II: Understanding and Protecting Our Biological Resources*. Joseph Henry Press, 27–40.

Estabrook G, Johnson CS, Morris FM. **1975**. An idealized concept of the true cladistic character. *Mathematical Biosciences* **212**: 263–272.

Ezard THG, Aze T, Pearson PN, Purvis A. **2011**. Interplay between changing climate and species' ecology drives macroevolutionary dynamics. *Science* **25**: 16–19.

Farnsworth KD, Niklas KJ. **1995**. Theories of optimization, form and function in branching architecture in plants. *Functional Ecology* **9**: 355–363.

Farris J. **1969**. A successive approximations approach to character weighting. *Systematic Biology*: 374–385.

Feild TS, Arens NC. **2007**. The ecophysiology of early angiosperms. *Plant, Cell & Environment* **30**: 291–309.

Feild TS, Brodribb TJ, Iglesias A, Chatelet DS, Baresch A, Upchurch GR, Gomez B, Mohr BAR, Coiffard C, Kvacek J, Jaramillo C. **2011**. Fossil evidence for Cretaceous escalation in angiosperm leaf vein evolution. *Proceedings of the National Academy of Sciences* **108**: 8363–8366.

Figueirido B, MacLeod N, Krieger J, De Renzi M, Pérez-Claros JA, Palmqvist P. **2011**. Constraint and adaptation in the evolution of carnivoran skull shape. *Paleobiology* **37**: 490–518.

Foote M. **1989**. Perimeter-based Fourier analysis : a new morphometric method applied to the trilobite cranidium. *Journal of Paleontology* **63**: 880–885.

Foote M. **1990**. Nearest-neighbor analysis of trilobite morphospace. *Systematic Biology* **39**: 371–382.

Foote M. **1991**. Morphological and taxonomic diversity in clade's history: the blastoid record and stochastic simulations. *Contributions From the Museum of Paleontology* **28**: 101–140.

Foote M. **1992**. Paleozoic record of morphological diversity in blastozoan echinoderms. *Proceedings of the National Academy of Sciences of the United States of America* **89**: 7325–7329.

Foote M. **1994**. Morphological disparity in Ordovician-Devonian crinoids and the early saturation of morphological space. *Paleobiology* **20**: 320–344.

Foote M. **1997**. The evolution of morphological diversity. *Annual Review of Ecology and Systematics* **28**: 129–152.

Forey PL, Humphries CJ, Williams DM. **1998**. *Cladistics: the theory and practice of parsimony analysis*. Oxford: Oxford University Press.

Fortey RA, Briggs DEG, Wills MA. **1996**. The Cambrian evolutionary "explosion": decoupling cladogenesis from morphological disparity. *Biological Journal of the Linnean Society* **57**: 13–33.

Fortey R, Briggs D, Wills M. **1997**. The Cambrian evolutionary "explosion" recalibrated. *BioEssays* **19**: 429–434.

Foster AS. **1956**. Plant idioblasts : remarkable examples of cell specialization comparative morphology of idioblasts. *Protoplasma* **46**: 184–193.

Friedman M. **2010**. Explosive morphological diversification of spiny-finned teleost fishes in the aftermath of the end-Cretaceous extinction. *Proceedings of the Royal Society of London, Series B: Biological Sciences* **277**: 1675–1683.

Friedman WE, Williams JH. **2003**. Modularity of the angiosperm female gametophyte and its bearing on the early evolution of endosperm in flowering plants. *Evolution* **57**: 216–230.

Futuyma DJ, Agrawal AA. **2009**. Macroevolution and the biological diversity of plants and herbivores. *Proceedings of the National Academy of Sciences of the United States of America* **106**: 18054–18061.

Garner JP, Taylor GK, Thomas ALR. **1999**. On the origins of birds: the sequence of character acquisition in the evolution of avian flight. *Proceedings of the Royal Society of London, Series B: Biological Sciences*: 1259–1266.

Gavrilets S. **1999**. Dynamics of clade diversification on the morphological hypercube. *Proceedings of the Royal Society of London, Series B: Biological Sciences* **266**: 817–824.

Goloboff P. **1993**. Estimating character weights during tree search. *Cladistics* **9**: 83–91.

Goloboff P a. 2014. Extended implied weighting. *Cladistics* **30**: 260–272.

Goodman N. **2002**. Biological data becomes computer literate: new advances in bioinformatics. *Current Opinion in Biotechnology* **13**: 68–71.

Gotelli NJ, Colwell RK. **2001**. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* **4**: 379–391.

Gottlieb LD. **1988**. Towards molecular genetics in *Clarkia*: gene duplications and molecular characterization of PGI genes. *Annals of the Missouri Botanical Garden* **75**: 1169–1179.

Gould SJ. **1989**. *Wonderful life*. New York: WW Norton.

Gould S, Gilinsky N, German R. **1987**. Asymmetry of lineages and the direction of evolutionary time. *Science* **236**: 1437–1441.

Gradstein FM, Ogg JG, Smith AG. **2004**. *A Geologic Time Scale*. Cambridge University Press.

Graybeal A. **1998**. Is it better to add taxa or characters to a difficult phylogenetic problem? *Systematic biology* **47**: 9–17.

Guyer C, Slowinski JB. **1993**. Adaptive radiation and the topology of large phylogenies. *Evolution* **47**: 253–263.

Hammer Ø, Bucher H. **2005**. Models for the morphogenesis of the molluscan shell. *Lethaia* **38**: 111–122.

Hart JA. **1987**. A cladistic analysis of conifers: preliminary results. *Journal of the Arnold Arboretum* **68**: 269–307.

Heath TA, Hedtke SM, Hillis DM. **2008**. Taxon sampling and the accuracy of phylogenetic analyses. *Journal of Systematics and Evolution* **46**: 239–257.

Heers AM, Dial KP, Tobalske BW. **2014**. From baby birds to feathered dinosaurs: incipient wings and the evolution of flight. *Paleobiology* **40**: 459–476.

Hennig W. **1966**. *Phylogenetic systematics*. Urbana: University of Illinois Press.

Hughes M, Gerber S, Wills MA. **2013**. Clades reach highest morphological disparity early in their evolution. *Proceedings of the National Academy of Sciences of the United States of America* **110**: 13875–13879.

Jeune B, Barabé D, Lacroix C. **2006**. Classical and dynamic morphology: toward a synthesis through the space of forms. *Acta Biotheoretica* **54**: 277–293.

Jones D, Purnell MA, von Bitter PH. **2009**. Morphological criteria for recognising homology in isolated skeletal elements: comparison of traditional and morphometric approaches in conodonts. *Palaeontology* **52**: 1243–1256.

Kelly S, Grenyer R, Scotland RW. **2014**. Phylogenetic trees do not reliably predict feature diversity. *Diversity and Distributions* **20**: 600–612.

Klingenberg CP, Duttke S, Whelan S, Kim M. **2012**. Developmental plasticity, morphological variation and evolvability: a multilevel analysis of morphometric integration in the shape of compound leaves. *Journal of Evolutionary Biology* **25**: 115–129.

Klingenberg CP, Leamy LJ, Cheverud JM. **2004**. Integration and modularity of quantitative trait locus effects on geometric shape in the mouse mandible. *Genetics* **166**: 1909–1921.

Klymiuk AA, Stockey RA. **2012**. A lower Cretaceous (Valanginian) seed cone provides the earliest fossil record for *Picea* (Pinaceae). *American Journal of Botany* **99**: 1069–1082.

Knoll AH, Niklas KJ, Tiffney BH. **1979**. Phanerozoic land-plant diversity in North America. *Science* **206**: 1400–1402.

Kovach WL, Batten DJ. **1993**. Diversity changes in lycopsid and aquatic fern megaspores through geologic time. *Paleobiology* **19**: 28–42.

Lacroix C, Jeune B, Purcell-Macdonald S. **2003**. Shoot and compound leaf comparisons in eudicots: dynamic morphology as an alternative approach. *Botanical Journal of the Linnean Society* **143**: 219–230.

Langlade NB, Feng X, Dransfield T, Copsey L, Hanna AI, Thébaud C, Bangham A, Hudson A, Coen E. **2005**. Evolution through genetically controlled allometry space. *Proceedings of the National Academy of Sciences of the United States of America* **102**: 10221–10226.

Lidgard S, Crane PR. **1990**. Angiosperm diversification and Cretaceous floristic trends: a comparison of palynofloras and leaf macrofloras. *Paleobiology* **16**: 77–93.

Lindbladh M. **2002**. Morphometric analysis of pollen grains for paleoecological studies: classification of *Picea* from eastern North America. *American Journal of Botany* **89**: 1459–1467.

Lingham-Soliar T. **2005**. Caudal fin allometry in the white shark *Carcharodon carcharias*: implications for locomotory performance and ecology. *Naturwissenschaften* **92**: 231–236.

Lingham-Soliar T, Plodowski G. **2007**. Taphonomic evidence for high-speed adapted fins in thunniform ichthyosaurs. *Naturwissenschaften* **94**: 65–70.

Liu F-GR, Miyamoto MM, Freire NP, Ong PQ, Tennant MR, Young TS, Gugel KF. **2001**. Molecular and morphological supertrees for eutherian (placental) mammals. *Science* **291**: 1786–1789.

Lockwood CA, Lynch JM, Kimbel WH. **2002**. Quantifying temporal bone morphology of great apes and humans: an approach using geometric morphometrics. *Journal of Anatomy* **201**: 447–464.

Long JA, Gordon MS. **2004**. The greatest step in vertebrate history: a paleobiological review of the fish tetrapod transition. *Physiological and Biochemical Zoology* **77**: 700–719.

Love AC. **2007**. Functional homology and homology of function: biological concepts and philosophical consequences. *Biology & Philosophy* **22**: 691–708.

Lupia R. **1999**. Discordant morphological disparity and taxonomic diversity during the Cretaceous angiosperm radiation: North American pollen record. *Paleobiology* **25**: 1–28.

Magallón S, Sanderson MJ. **2001**. Absolute diversification rates in angiosperm clades. *Evolution* **55**: 1762–1780.

Marcus LF. **2000**. Application of landmark morphometrics to skulls representing the orders of living mammals. *Hystrix* **11**: 27–47.

Mayhew PJ. **2007**. Why are there so many insect species? Perspectives from fossils and phylogenies. *Biological Reviews of the Cambridge Philosophical Society* **82**: 425–454.

Mayhew PJ, Bell MA, Benton TG, McGowan AJ. **2012**. Biodiversity tracks temperature over time. *Proceedings of the National Academy of Sciences of the United States of America* **109**: 15141–15145.

McElwain JC, Beerling DJ, Woodward FI. **1999**. Fossil plants and global warming at the Triassic-Jurassic boundary. *Science* **285**: 1386–1390.

McElwain JC, Punyasena SW. **2007**. Mass extinction events and the plant fossil record. *Trends in Ecology and Evolution* **22**: 548–557.

McGhee GR. **1999**. *Theoretical morphology: the concept and its applications*. Columbia University Press.

Miller JS, Venable DL. **2003**. Floral morphometrics and the evolution of sexual dimorphism in *Lycium* (Solanaceae). *Evolution* **57**: 74–86.

Mitteroecker P, Gunz P. **2009**. Advances in geometric morphometrics. *Evolutionary Biology* **36**: 235–247.

Mitteroecker P, Huttegger SM. **2009**. The concept of morphospaces in evolutionary and developmental biology: mathematics and metaphors. *Biological Theory*.

Monteiro LR, Nogueira MR. **2010**. Adaptive radiations, ecological specialization, and the evolutionary integration of complex morphological structures. *Evolution* **64**: 724–744.

Moore KJ, Moser LE. **1995**. Quantifying developmental morphology of perennial grasses. *Crop Science* **35**: 37–43.

Motani R. **2002**. Scaling effects in caudal fin propulsion and the speed of ichthyosaurs. *Nature* **415**: 309–312.

Moyne S, Neige P. **2007**. The space-time relationship of taxonomic diversity and morphological disparity in the Middle Jurassic ammonite radiation. *Palaeogeography, Palaeoclimatology, Palaeoecology* **248**: 82–95.

Nandi OI, Chase MW, Endress PK. **1998**. A combined cladistic analysis of angiosperms using rbcL and non-molecular data sets. *Annals of the Missouri Botanical Garden* **85**: 137–214.

Neige P. **2006**. Morphometrics of hard structures in cuttlefish. *Vie et Milieu* **56**: 121–127.

Niklas KJ. **1999**. Evolutionary walks through a land plant morphospace. *Journal of Experimental Botany* **50**: 39–52.

Niklas KJ, Kerchner V. **1984**. Mechanical and photosynthetic constraints on the evolution of plant shape. *Paleobiology* **10**: 79–101.

Niklas KJ, Tiffney BH. **1994**. The quantification of plant biodiversity through time. *Philosophical Transactions of the Royal Society of London. Series B, Biological sciences* **345**: 35–44.

Niklas KJ, Tiffney BH, Knoll AH. **1980**. Apparent changes in the diversity of fossil plants. a preliminary assessment. *Evolutionary Biology* **12**: 1–89.

Nogueira MR, Peracchi AL, Monteiro LR. **2009**. Morphological correlates of bite force and diet in the skull and mandible of phyllostomid bats. *Functional Ecology* **23**: 715–723.

O'Higgins P, Cobb SN, Fitton LC, Gröning F, Phillips R, Liu J, Fagan MJ. **2011**. Combining geometric morphometrics and functional simulation: an emerging toolkit for virtual functional analyses. *Journal of Anatomy* **218**: 3–15.

Peet RK. **1974**. The measurement of species diversity. *Annual Review of Ecology and Systematics* **5**: 285–307.

Perez SI, Bernal V, Gonzalez PN. **2006**. Differences between sliding semi-landmark methods in geometric morphometrics, with an application to human craniofacial and dental variation. *Journal of Anatomy* **208**: 769–784.

Pettersson M. **2009**. *Complexity and evolution*. Cambridge: Cambridge University Press.

Phillimore AB, Freckleton RP. **2006**. Ecology predicts large-scale patterns of phylogenetic diversification in birds. *The American Naturalist* **168**: 220–229.

Pinna MGG. **1991**. Concepts and tests of homology in the cladistic paradigm. *Cladistics* **7**: 367–394.

Pretorius E, Scholtz CH. **2001**. Geometric morphometrics and the analysis of higher taxa: a case study based on the metendosternite of the Scarabaeoidea (Coleoptera). *Biological Journal of the Linnean Society* **74**: 35–50.

Prusinkiewicz P, Erasmus Y, Lane B. **2007**. Evolution and development of inflorescence architectures. *Science* **316**: 1452–1457.

Pryer KM, Smith AR, Skog JE. **1995**. Phylogenetic relationships of extant ferns based on evidence from morphology and rbcL sequences. *American Fern Journal* **85**: 205–282.

Rabosky DL, Slater GJ, Alfaro ME. **2012**. Clade age and species richness are decoupled across the eukaryotic tree of life. *PLoS Biology* **10**: e1001381.

Raup DM, Michelson A. **1965**. Theoretical morphology of the coiled shell. *Science* **147**: 1–2.

Rees PM. **2002**. Land-plant diversity and the end-Permian mass extinction. *Geology* **30**: 827–830.

Renzaglia KS, Duff RJ, Nickrent DL, Garbary DJ. **2000**. Vegetative and reproductive innovations of early land plants: implications for a unified phylogeny. *Philosophical Transactions of the Royal Society of London. Series B, Biological sciences* **355**: 769–793.

Ressayre A, Godelle B. **2002**. Aperture pattern ontogeny in angiosperms. *Journal of Experimental Zoology* **135**: 122–135.

Retallack GJ. **1995**. Permian-Triassic life crisis on land. *Science* **267**: 77–80.

Riedl R. **1977**. A systems-analytical approach to macro-evolutionary phenomena. *The Quarterly Review of Biology* **52**: 351–370.

Rohlf FJ. **1998**. On applications of geometric morphometrics to studies of ontogeny and phylogeny. *Systematic Biology* **47**: 147–158.

Rohlf FJ. **2002**. Geometric morphometrics and phylogeny. *Morphology, Shape and Phylogeny*. CRC Press, 175–193.

Rohlf FJ, Archie JW. **1984**. A comparison of Fourier methods for the description of wing shape in mosquitoes (Diptera: Culicidae). *Systematic Biology* **33**: 302–317.

Rohlf FJ, Marcus LF. **1993**. A revolution in morphometrics. *Trends in Ecology and Evolution* **8**: 129–132.

Rudall PJ, Bateman RM. **2007**. Developmental bases for key innovations in the seed-plant microgametophyte. *Trends in Plant Science* **12**: 317–326.

Rury P, Dickison W. **1984**. Structural correlations among wood, leaves and plant habit. *Contemporary problems in plant anatomy*. Orlando: Academic Press, 495–540.

Ruta M, Wagner PJ, Coates MI. **2006**. Evolutionary patterns in early tetrapods. I. Rapid initial diversification followed by decrease in rates of character change. *Proceedings of the Royal Society of London, Series B: Biological Sciences* **273**: 2107–2111.

Ruvinsky I, Gibson-Brown JJ. **2000**. Genetic and developmental bases of serial homology in vertebrate limb evolution. *Development* **127**: 5233–5244.

Sajo MG, Rudall PJ, Prychid CJ. **2004**. Floral anatomy of Bromeliaceae, with particular reference to the evolution of epigyny and septal nectaries in commelinid monocots. *Plant Systematics and Evolution* **247**: 215–231.

Sanderson MJ, Donoghue MJ. **1989**. Patterns of variation in levels of homoplasy. *Evolution* **43**: 1781–1795.

Sanderson MJ, Donoghue MJ. **1994**. Shifts in diversification rate with the origin of angiosperms. *Science* **264**: 1590–1592.

Schlichting CD. **1986**. The evolution of phenotypic plasticity in plants. *Annual Review of Ecology and Systematics* **17**: 667–693.

Schlichting CD. **2002**. Phenotypic plasticity in plants. *Plant Species Biology* **17**: 85–88.

Schneider H, Smith AR, Pryer KM. **2009**. Is morphology really at odds with molecules in estimating fern phylogeny? *Systematic Botany* **34**: 455–475.

Sepkoski JJ. **1997**. Biodiversity: past, present, and future. *Journal of Paleontology* **71**: 533–539.

Sepkoski JJ, Bambach RK, Raup DM, Valentine JW. **1981**. Phanerozoic marine diversity and the fossil record. *Nature* **293**: 435–437.

Sepkoski JJ, Miller AI. **1998**. Analysing diversification through time. *Trends in Ecology and Evolution* **13**: 158–159.

Sharkey MJ. **1989**. A hypothesis-independent method of character weighting for cladistic analysis. *Cladistics* **5**: 63–86.

Shubin N, Tabin C, Carroll S. **2009**. Deep homology and the origins of evolutionary novelty. *Nature* **457**: 818–823.

Silva IA, Batalha MA. **2011**. Plant functional types in Brazilian savannas: The niche partitioning between herbaceous and woody species. *Perspectives in Plant Ecology, Evolution and Systematics* **13**: 201–206.

Skalak R, Farrow D, Hoger A. **1997**. Kinematics of surface growth. *Journal of mathematical biology*: 869–907.

Stebbins GL. **1951**. Natural selection and the differentiation of angiosperm families. *Evolution* **5**: 299–324.

Stebbins GL. **1969**. *The basis of progressive evolution*. Chapel Hill: University of North Carolina Press.

Stournaras KE, Lo E, Bohning-Gaese K, Cazetta E, Dehling DM, Schleuning M, Stoddard MC, Donoghue MJ, Prum RO, Schaefer HM. **2013**. How colorful are fruits? Limited color diversity in fleshy fruits on local and global scales. *New Phytologist* **198**: 617–629.

Sytsma KJ, Smith JF, Berry PE. **1991**. The use of chloroplast DNA to assess biogeography and evolution of morphology, breeding systems, and flavonoids in *Fuchsia* sect, *Skinnera* (Onagraceae). *Systematic Botany* **16**: 257–269.

Tamura K, Battistuzzi FU, Billing-Ross P, Murillo O, Filipski A, Kumar S. **2012**. Adaptive radiation and the topology of large phylogenies. *Proceedings of the National Academy of Sciences of the United States of America* **109**: 19333–19338.

The Plant List. **2013**. The Plant List. *Published on the internet*.

Thorne PM, Ruta M, Benton MJ. **2011**. Resetting the evolution of marine reptiles at the Triassic-Jurassic boundary. *Proceedings of the National Academy of Sciences of the United States of America* **108**: 8339–8344.

Uhen M. **1996**. An evaluation of clade-shape statistics using simulations and extinct families of mammals. *Paleobiology* **22**: 8–22.

Urdy S, Goudemand N, Bucher H, Chirat R. **2010**. Allometries and the morphogenesis of the molluscan shell: a quantitative and theoretical model. *Journal of Experimental Zoology. Part B, Molecular and Developmental Evolution* **314**: 280–302.

Vamosi JC, Vamosi SM. **2010**. Key innovations within a geographical context in flowering plants: towards resolving Darwin's abominable mystery. *Ecology Letters* **13**: 1270–1279.

Wagner GP, Chiu C. **2001**. The tetrapod limb: a hypothesis on its origin. *Journal of Experimental Zoology* **291**: 226–240.

Wagner PJ, Ruta M, Coates MI. **2006**. Evolutionary patterns in early tetrapods. II. Differing constraints on available character space among clades. *Proceedings of the Royal Society of London, Series B: Biological Sciences* **273**: 2113–2118.

Wellman CH. **2014**. The nature and evolutionary relationships of the earliest land plants. *New Phytologist* **202**: 1–3.

Whibley AC, Langlade NB, Andalo C, Hanna AI, Bangham A, Thebaud C, Coen E. **2006**. Evolutionary paths underlying flower color variation in *Antirrhinum*. *Science* **313**: 963–966.

Whittington HB. **1985**. *The burgess shale*. New Haven: Yale University Press.

Wilkinson M, Pisani D, Cotton JA, Corfe I. **2005**. Measuring support and finding unsupported relationships in supertrees. *Systematic biology* **54**: 823–831.

Willis KJ, McElwain JC. **2013**. *The Evolution of Plants*. Oxford: Oxford University Press.

Willis KJ, Niklas KJ. **2004**. The role of Quaternary environmental change in plant macroevolution: the exception or the rule? *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* **359**: 159–172.

Wills MA. **1998**. Crustacean disparity through the Phanerozoic: comparing morphological and stratigraphic data. *Biological Journal of the Linnean Society* **65**: 455–500.

Wills MA. **2001**. Disparity vs. diversity. In: Briggs DEG, Crowther PR, eds. *Palaeobiology II*. Oxford: Blackwell Science, 495–500.

Wills MA, Briggs DEG, Fortey RA. **1994**. Disparity as an evolutionary index: a comparison of Cambrian and Recent arthropods. *Paleobiology* **20**: 93–130.

Wills MA, Gerber S, Ruta M, Hughes M. **2012**. The disparity of priapulid, archaeopriapulid and palaeoscolecid worms in the light of new data. *Journal of evolutionary biology* **25**: 2056–2076.

Wilson JP, Knoll AH. **2010**. A physiologically explicit morphospace for tracheid-based water transport in modern and extinct seed plants. *Paleobiology* **36**: 335–355.

Wimsatt W. **1986**. Developmental constraints, generative entrenchment, and the innate-acquired distinction. In: Bechtel W, ed. *Integrating scientific disciplines*. Dordrecht: Martinus-Nijhof, 185–208.

Xu X. **2006**. Feathered dinosaurs from China and the evolution of major avian characters. *Integrative Zoology* **1**: 4–11.

Yeates D. **1992**. Why remove autapomorphies? *Cladistics* **8**: 387–389.

Yoo M-J, Bell CD, Soltis PS, Soltis DE. **2005**. Divergence times and historical biogeography of Nymphaeales. *Systematic Botany* **30**: 693–704.

Yu Y, Heinrichs J, Schäfer-Verwimp A, Zhu R-L, Schneider H. **2014**. Inferring the accumulation of morphological disparity in epiphyllous liverworts. *Organisms Diversity & Evolution* **14**: 151–162.

Zachos J, Pagani M, Sloan L, Thomas E, Billups K. **2001**. Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* **292**: 686–693.

TABLES

Table 1. Expected (or inherent) and observed centres of gravity (CG_{scaled}) for clade disparity profiles, along with the results of bootstrapping tests (*CG p*-value) to determine if these differ. The expected *CG* is that determined for a clade with uniform disparity through time, and deviates from 0.5 because stratigraphic intervals and bins are of variable length. Relative *CG* is adjusted relative to the expected or inherent *CG* as a baseline. Clades that persist to the Recent typically have top-heavy profiles, since they are effectively truncated. Early high and late high columns indicate the results of bootstrapping tests to determine if the disparity observed in the first and last intervals is distinguishable from the overall maximum for the clade ('no' indicates a difference with $p < 0.05$)

Clade	Dataset	Expected CG	Observed CG	Relative CG	CG p-value	Early high	Late high
Angiosperms	Doyle & Endress 2014	0.757	0.759	0.502	0.001	no	no
Angiosperms	Doyle *et al.* 1994	0.718	0.722	0.504	0.228	yes	yes
Angiosperms	Nandi *et al.* 1998	0.714	0.718	0.504	0.846	no	no
Conifers (Pinophyta)	Hart 1987	0.556	0.712	0.655	0.001	no	no
Leptosporangiate Ferns (Polypodiidae)	Pryer *et al.* 1995	0.546	0.669	0.622	0.001	no	no
Palms (Arecaceae)	Baker *et al.* 2009	0.690	0.761	0.571	0.001	yes	no
Pines (Pinaceae)	Klymiuk & Stockey 2012	0.604	0.753	0.649	0.001	no	yes
Water Lilies (Nymphaeales)	Borsch *et al.* 2008	0.626	0.794	0.668	0.001	yes	yes

Appendix 1: Distribution of characters in our plant data sets

Publication	Nandi et al. 1998	Doyle & Endress 2000	Doyle & Endress 2013	Hart 1987	Klymiuk & Stockey 2012	Pryer et al. 1995	Borsch 2008	Baker et al. 2005
Group	Extant Angiosperms	Basal Angiosperms	Angiosperms	Conifers	Pine Family	Polypod Ferns	Water Lilies	Palms
Growth & Habit	0	1	1	4	0	1	5	5
Cellular	22	0	4	2	0	2	0	6
Chemical	104	0	0	5	0	0	1	1
Stem	24	18	23	22	0	18	4	0
Leaf	17	17	13	16	0	19	7	14
Ovules/Seeds/Fruit	30	38	30	9	3	NA	6	15
Floral	37	23	54	NA	NA	0	28	52
Embryo & Development	7	0	0	27	0	1	1	3
Pollen	11	11	17	15	0	NA	10	9
Gametophyte	NA	NA	NA	NA	NA	11	NA	NA
Strobilus	NA	NA	NA	23	31	NA	NA	NA
Spores & Sporangia	NA	NA	NA	NA	NA	25	NA	NA
Total	252	108	142	123	34	52	62	105

FIGURE CAPTIONS

Figure 1. Diversity and disparity are often decoupled, particularly when sampling at lower taxonomic levels. Data for crinoids from Foote (1999). When crinoids first appear in the Ordovician, there are relatively few genera (A), but the mean morphological distances between them (as an index of disparity) are relatively large (B). Part of their subsequent history entailed a systemic increase in diversity through to the early Carboniferous, which paradoxically coincided with a decline in disparity over the same interval. Conversely, disparity remained relatively high for much of the Mesozoic despite a low diversity following the Permo-Triassic mass extinction. Many groups show a similar overall pattern, with relatively small numbers of morphologically distinct species or genera typifying the early phase of a clade's radiation.

Figure 2. Simplified models of the pattern of morphological disparity through the Phanerozoic. The 'traditional' model assumes that patterns of disparity loosely track diversity, which increases (albeit irregularly) through time. Gould (1989) espoused an inversion of this model, derived largely from his own interpretation of the significance of fossils from the Middle Cambrian Burgess Shale. Cambrian genera were believed to represent numerous, highly distinct bodyplans, between which there were morphological differences comparable to those distinguishing the living phyla. Most of these Cambrian bodyplans were lost arbitrarily in the early Palaeozoic, resulting is a marked reduction in disparity ('decimation'). Subsequent evolution entailed increasing diversity within this more limited number of themes, but disparity was belived to persits unchanged. Fortey *et al.* (1996) summarised findings from the then-published empirical studies of disparity, which revealed comparable levels of disparity amongst Cambrian invertebrate groups and their living counterparts. Subsequent studies have largely confirmed the validity of the latter picture.

Figure. 3. Ordinal diversity of animals (Eumetazoa) and plants (Embryophta) through the Phanerozoic. Numbers of orders per geological stage have been tallied from Benton (1993) for animals and from Cascales-Minãna & Cleal (2014) for plants. The 'Big Five' mass extinctions are marked with vertical arrows.

Figure 4. Simulation of bifurcate branching structures capturing aspects of vascular plant morphology (after Niklas 1999). (A) illustration of the three parameters used: the bifurcation angle ϕ, the rotation angle Υ and the probability of apical bifurcation P. Separate numerical values can be used for each parameter for each axes (e.g. P_1 and P_2). (B) Simplified three-dimensional morphospace created from the orthogonal alignment of the three parameters of the simulation, showing the spectrum of branching structures produced. *Cooksonia*-type Y-shaped branching structures occupy the upper left region, more complex overtopped structures occupy the lower right rearground and planated lateral 'branches' occupy the lower right foreground. Figures redrawn from Niklas (1999).

Figure 5. Types of data underpinning disparity analyses. (A) Landmarks (in red) from Webster & Zelditch (2008) situated on homologous points of a trilobite cephalon. (B) Equidistant semi-landmark points (in red) from MacLeod (2010), defining the outline of a trilobite cephalon (shown in grey). (C) Measurements taken for a Fourier analysis of a trilobite cranidium, from Foote (1989). X is the starting point, XY is the midline, point C is the centroid, L is the length from X to Z, D is the distance from the centroid to Z and θ is the angle XCZ.

Figure 6. The resurgence of disparity analyses for animal clades and the paucity of plant studies. (A) Bar chart of the number and taxonomic distribution of focal clades in disparity analyses from 1990 to 2014. (B) The decline in the use of outline data and the ascendance of discrete character and landmark based studies since 2010. We espouse the use of discrete

character data for producing empirical morphospaces of disparate plant clades. Underlying data in Appendix 1, although we have removed studies in Hughes *et al.* (2013) from the figure (this further increases the number of discrete character studies in the last five years).

Figure 7. (A) Disparity profile and morphospace plots for conifers from Hart (1987). Disparity (black circles) calculated as the sum of variances on all principal coordinate axes within several time bins. Values are the mean of 1,000 bootstrap replicates ±SE. Diversity per stage is indicated by open, red circles. (B) Distribution of taxa on the first two principal coordinate axes of the empirical morphospace at four of the period time bins.

Figure 8. To what extent are taxa clustered within their respective morphospaces at different levels of granularity? Highly clustered, spatially heterogeneous distributions can be approximated with smaller numbers of principal points than can diffuse, spatially homogenous distributions. The extent to which a principal point distribution matches the empirical distribution is given by the sample mean squared deviation (SMSD). Open circles indicate the observed SMSD with an increasing number of principal points. Solid lines denote the expected, null SMSD curve for a multivariate homogeneous distribution containing the same number of points within the same spatial bounds as the observed distribution. Dashed lines are lower and upper bounds of the 95% confidence interval around this null. Where the observed lines (circles) fall below the dashed interval, the empirical distribution is significantly more tightly clustered than expected. Analyses of four plant morphospaces. (A) conifers (Hart 1987). (B). pine family (Klymiuk and Stockey 2012). (C) angiosperms (Doyle and Endress 2014) (D) leptosporangiate ferns (Pryer *et al.* 1995). Note the particularly tight clustering of conifers over a large range of principal point numbers.

Figure 9. (A) Disparity profile and morphospace plots for the pine family from Klymiuk & Stockey (2012). Disparity (black circles) calculated as the sum of variances on all principal

coordinate axes within several time bins. Values are the mean of 1,000 bootstrap replicates ±SE. Diversity () per stage is indicated by open, red circles. (B) Distribution of taxa on the first two principal coordinate axes of the empirical morphospace at four of the period time bins.

Figure 10. (A) Disparity profile and morphospace plots for angiosperms from Doyle & Endress (2014). Disparity (black circles) calculated as the sum of variances on all principal coordinate axes within several time bins. Values are the mean of 1,000 bootstrap replicates ±SE. Diversity () per stage is indicated by open, red circles. (B) Distribution of taxa on the first two principal coordinates of the empirical morphospace at four of the period time bins.

Figure 11. (A) Disparity profile and morphospace plots for palms from Baker *et al.* (2009). Disparity (black circles) calculated as the sum of variances on all principal coordinate axes within several time bins. Values are the mean of 1,000 bootstrap replicates ±SE. Diversity () per stage is indicated by open, red circles. (B) Distribution of taxa on the first two principal coordinate axes of the empirical morphospace at four of the period time bins.

Figure 12. (A) Disparity profile and morphospace plots for water lilies from Borsch *et al.* (2008). Disparity (black circles) calculated as the sum of variances on all principal coordinate axes within several time bins. Values are the mean of 1,000 bootstrap replicates ±SE. Diversity () per stage is indicated by open, red circles. (B) Distribution of taxa on the first two principal coordinate axes of the empirical morphospace at four of the period time bins.

Figure 13. (A) Disparity profile and morphospace plots for extant leptosporangiate ferns from Pryer *et al.* (1995). Disparity (black circles) calculated as the sum of variances on all principal coordinate axes within several time bins. Values are the mean of 1,000 bootstrap replicates ±SE. Diversity () per stage is indicated by open, red circles. (B) Distribution of taxa

on the first two principal coordinate axes of the empirical morphospace at four of the period time bins.

Figure 14. Disparity profiles for three cladistic angiosperm datasets. Disparity (black circles) calculated as the sum of variances on all principal coordinate axes within several time bins. Values are the mean of 1,000 bootstrap replicates ±SE. Despite the inclusion of different taxa and characters, all three profiles show a rapid initial increase in disparity followed by relatively constant disparity over the rest of their history.

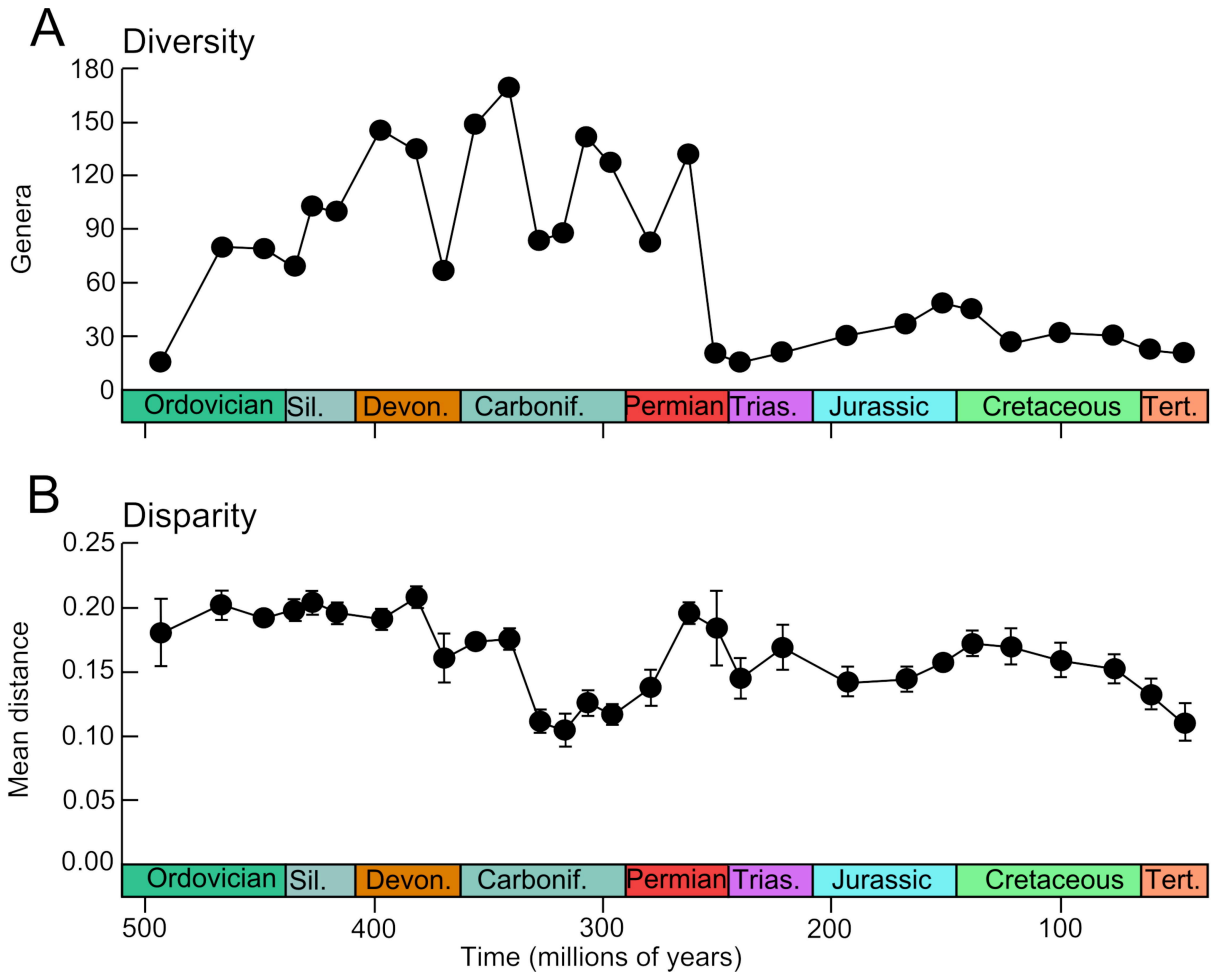

Figure 1

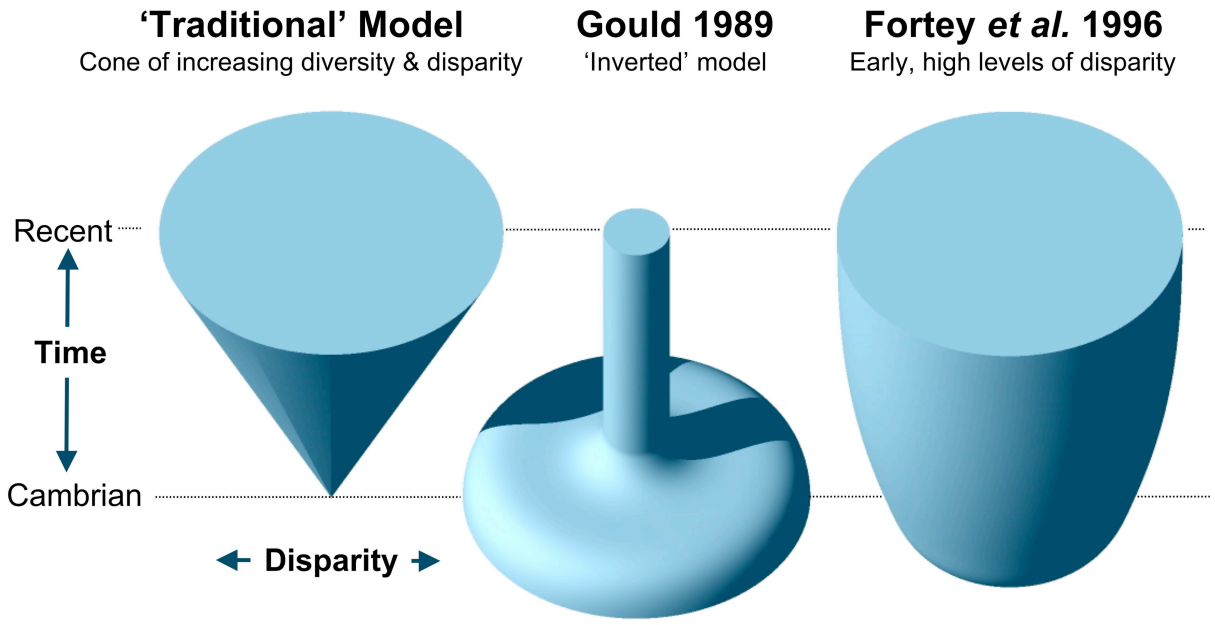

Figure 2

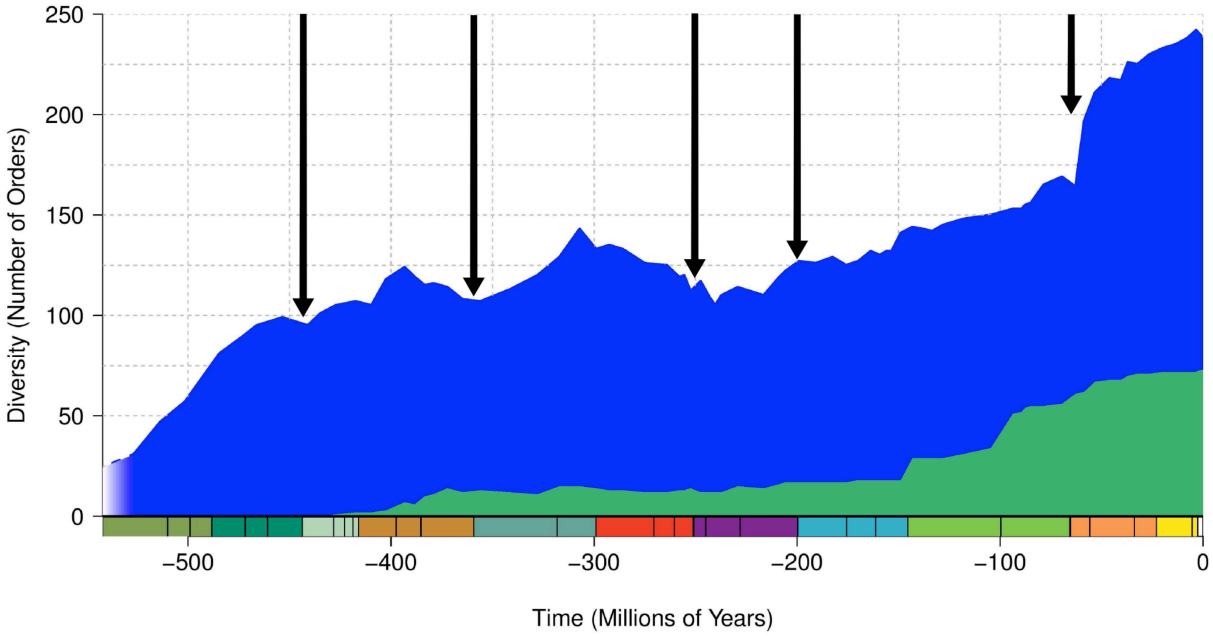

Figure 3

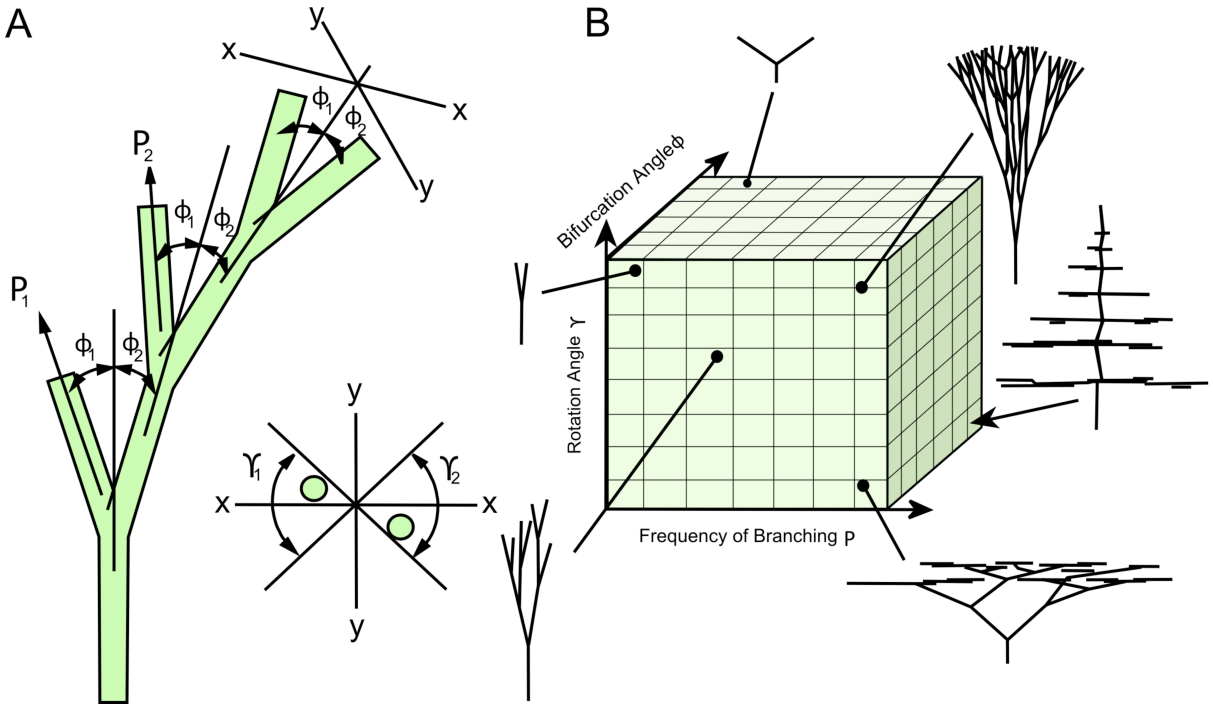

Figure 4

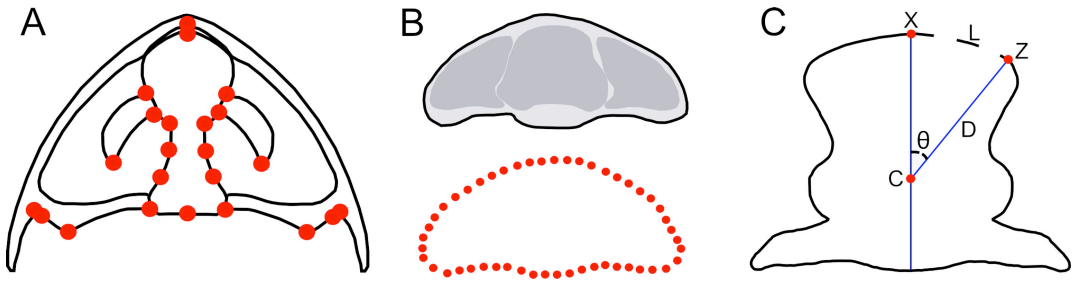

Figure 5

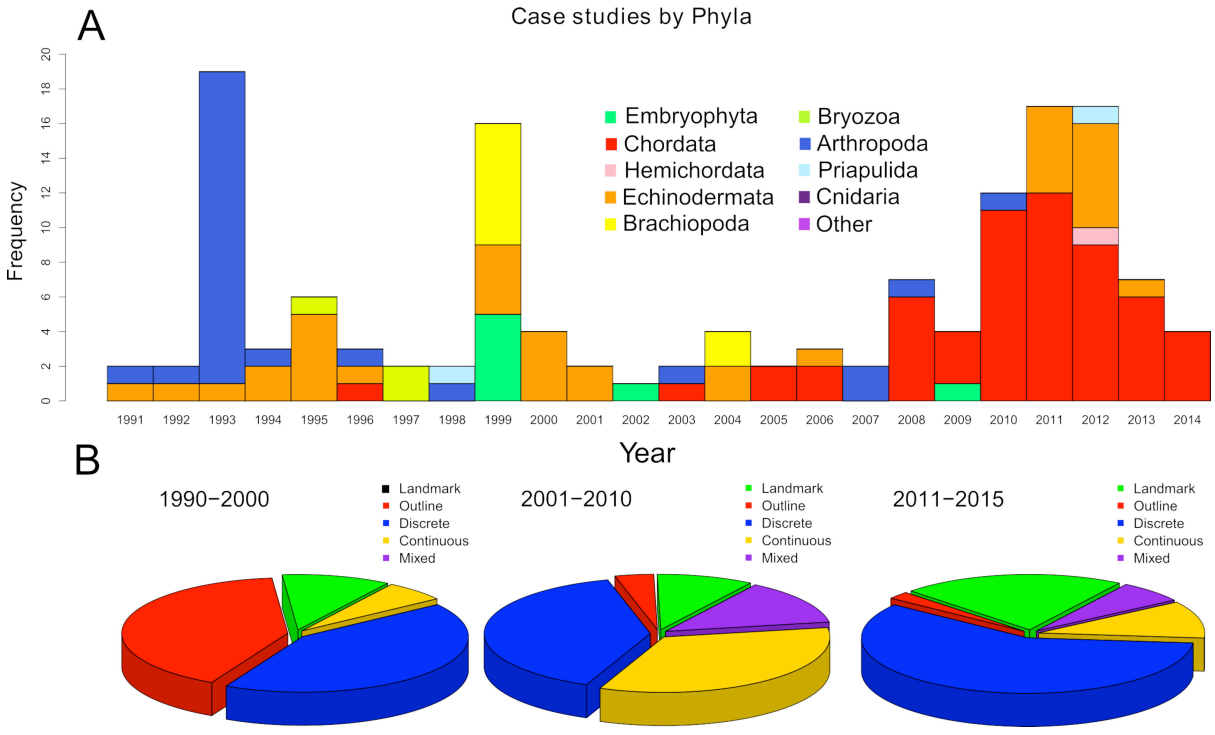

Figure 6

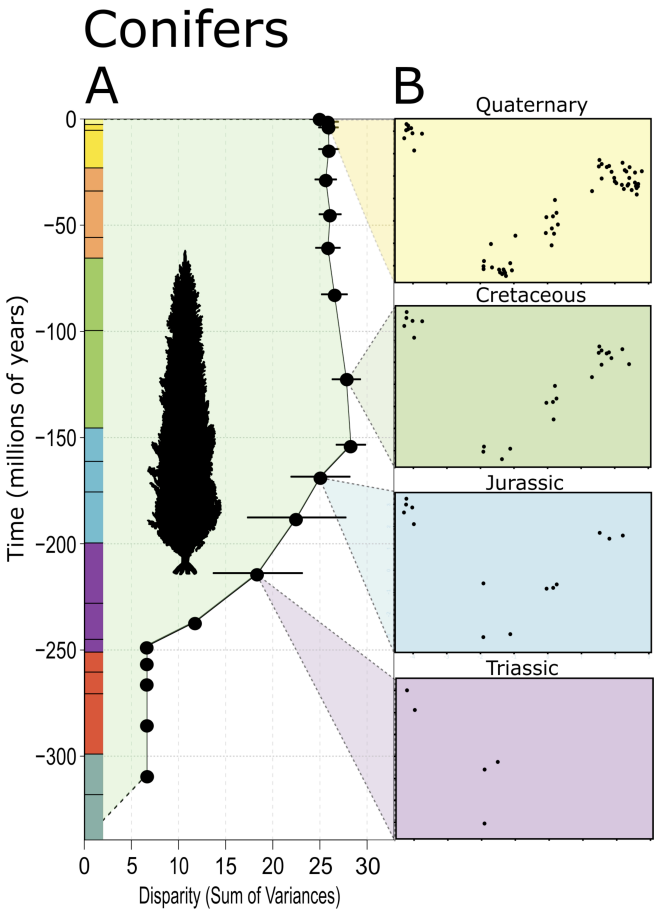

Figure 7

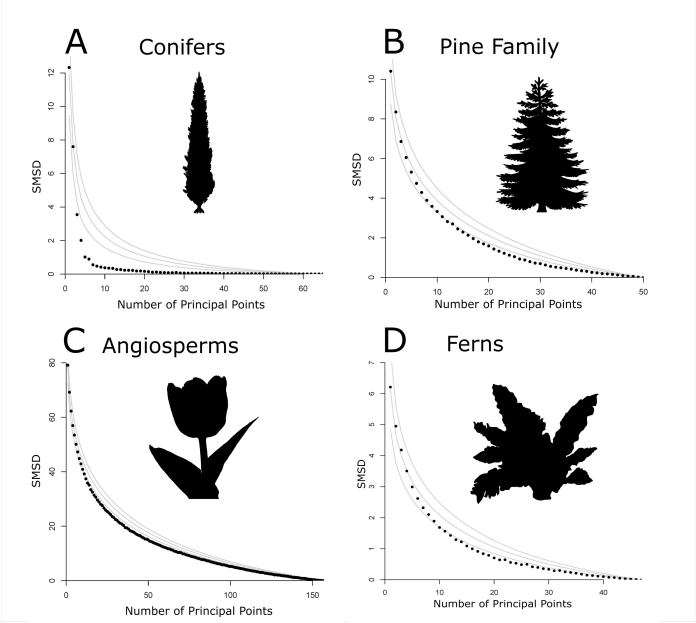

Figure 8

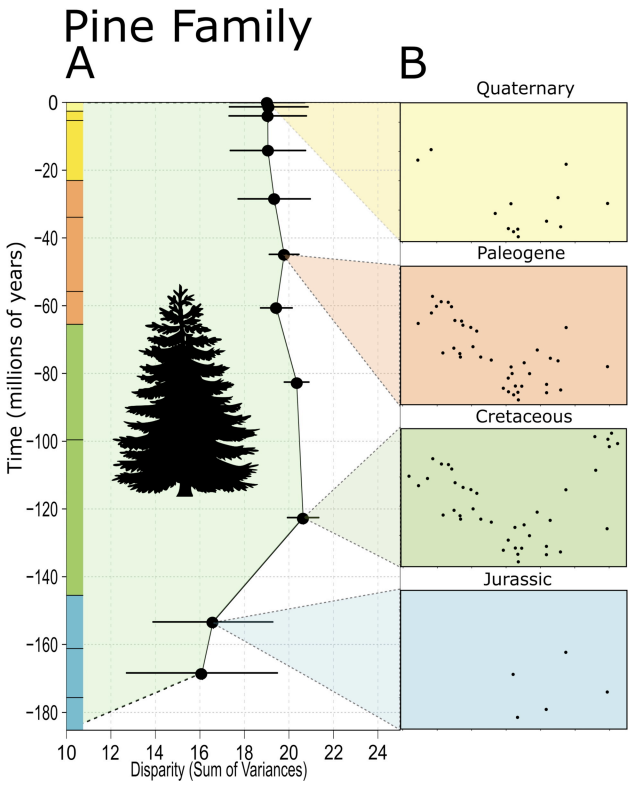

Figure 9

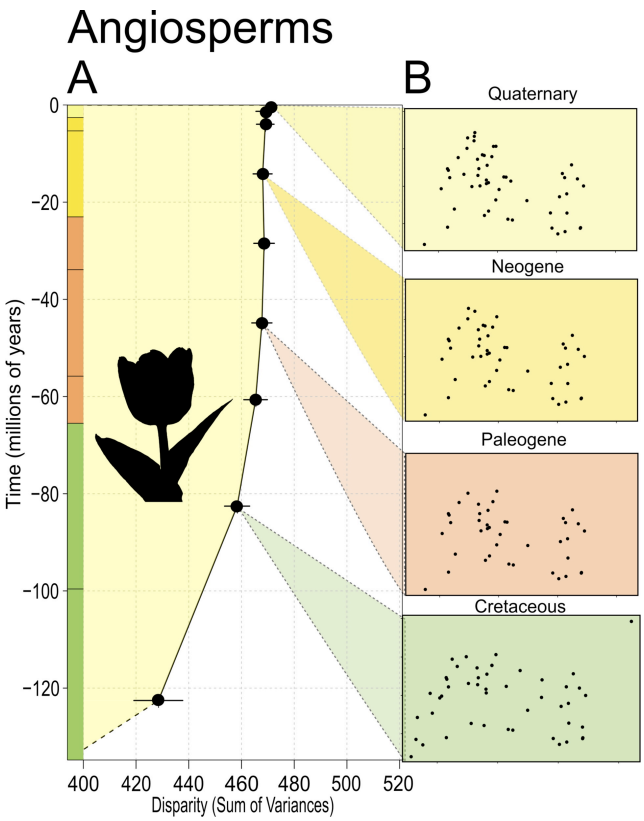

Figure 10

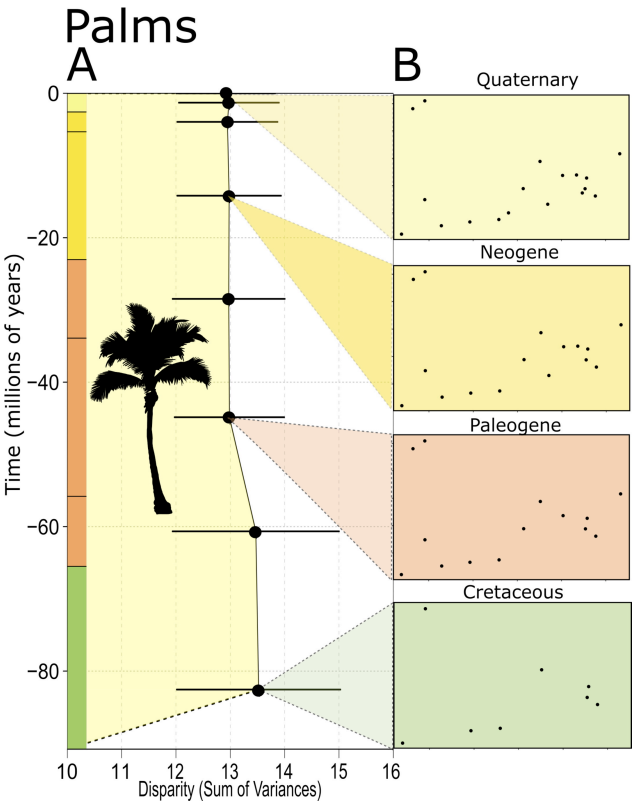

Figure 11

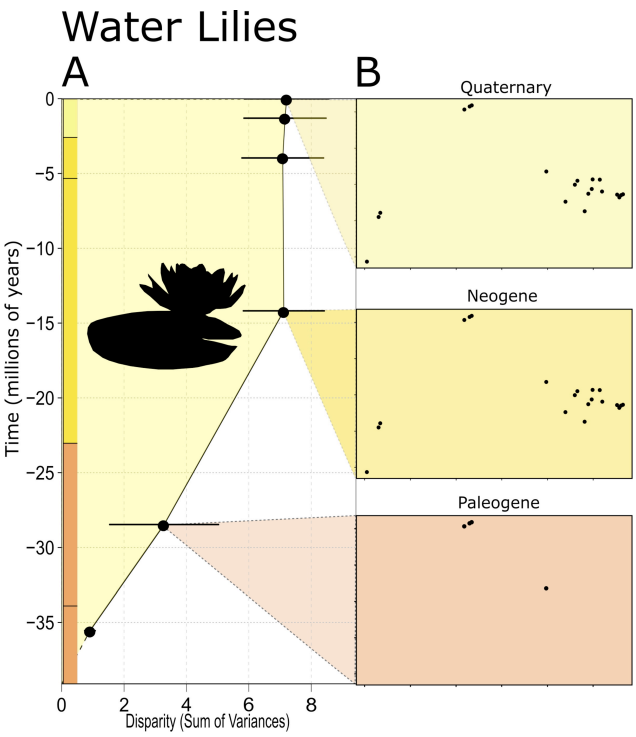

Figure 12

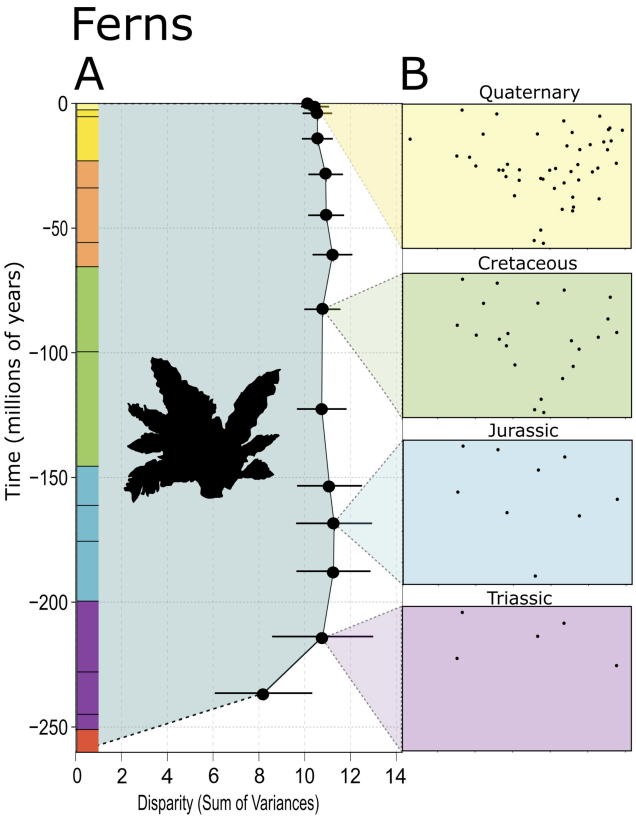

Figure 13

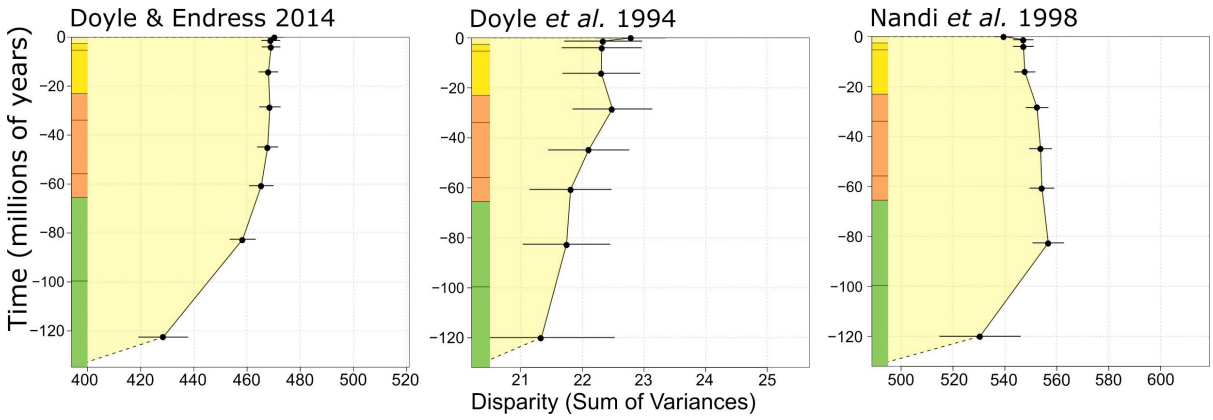

Figure 14