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RESEARCH ARTICLE

Evolutionary causes of global patterns of species richness in regional fern floras across the world

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Abstract

Aim: Globally, biodiversity is unevenly distributed, as a result of varying environmental conditions and regionally different historical processes. The influence of the latter on current diversity patterns is poorly understood. We explore geographic patterns of matches and mismatches between phylogenetic relatedness metrics measuring different depths of evolutionary history and investigate the effects of evolutionary legacy at different evolutionary depths on species density of ferns.

Methods: We divided the globe into 392 geographic regions on land, and collated species lists of ferns for each geographic region. We related species richness to phylogenetic metrics reflecting different depths of evolutionary history (standardized effect sizes of mean nearest taxon distance and mean pairwise distance, $\mathrm{MNTD_{ses}}$ and $\mathrm{MPD_{ses}}$, respectively) for ferns in regional floras across the world.

Location: Global.

Time Period: Current.

Taxon: Ferns.

Results: We show that different centers of fern diversity have strikingly different phylogenetic composition. We find that overall fern species diversity is negatively correlated with both $\mathrm{MNTD_{ses}}$ and $\mathrm{MPD_{ses}}$, so that regions with high species diversity tend to have clustered species assemblages, whereas species-poor regions tend to have overdispersed species assemblages. At the global extent, $\mathrm{MNTD_{ses}}$ and $\mathrm{MPD_{ses}}$ together explained 62.2%, 19.3%, and 65.7% of the variation in species diversity for all ferns as a whole, non-polypod ferns, and polypods, respectively.

Main Conclusions: Our study suggests that current geographic patterns of fern species richness are driven, at least in part, by evolutionary history of ferns, which varies among biogeographic regions.

KEYWORDS
evolutionary legacy, ferns, phylogenetic diversity, phylogenetic relatedness, tropical niche conservatism

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Hong Qian and Michael Kessler contributed equally to this work.

1 | INTRODUCTION

The uneven spatial distribution of biodiversity across the globe results from a combination of environmental factors and historical processes (Rangel et al., 2018; Ricklefs & Schluter, 1993). While the environment determines the availability of resources and the resulting niche space, historical processes, including speciation, extinction, and dispersal, lead to evolutionary legacies in the composition of biotic communities. Whereas present-day environment–biodiversity relationships are relatively straightforward to document, even though unravelling the underlying mechanisms is not (Rosenzweig, 1992; Villalobos & Rangel, 2014), understanding the impact of historical processes on biodiversity is much more challenging, since we only can study the legacies but not the processes themselves (Rangel et al., 2018; Svenning et al., 2015). Nonetheless, documenting evolutionary causes of global biodiversity patterns is fundamental not only to understanding how biodiversity has originated but also to prioritizing conservation efforts in the face of the global biodiversity crisis and limited conservation resources (Robuchon et al., 2021).

The availability of ever more complete and well-resolved phylogenies over the last two decades provides an increasingly powerful tool for unravelling evolutionary legacies in biodiversity patterns. Mean nearest taxon distance (MNTD) and mean pairwise distance (MPD) have been commonly used to quantify evolutionary legacies of biotic assemblages (Webb et al., 2002). MNTD measures the average phylogenetic distance among the closest relatives within an assemblage, whereas MPD measures the mean phylogenetic distance between all pairwise species in an assemblage. MNTD and MPD highlight phylogenetic structure of assemblages at different evolutionary depths: MNTD describes the more 'terminal' structure of the phylogenetic tree whereas MPD is more strongly influenced by the 'basal' structure of the phylogenetic tree (Mazel et al., 2016; Webb et al., 2002). Thus, MNTD represents recent evolutionary history whereas MPD represents relatively deep evolutionary history. A species assemblage with a large MNTD or MPD represents an assemblage with species from different clades far apart in the phylogeny whereas the opposite might represent an assemblage from a single clade or a few clades that recently diversified. When they are standardized using a null model to account for species richness, the resulting values (i.e. standardized effect sizes) become comparable between different assemblages, and can be used to quantify phylogenetic dispersion, so that a negative value represents phylogenetic clustering whereas a positive value represents overdispersion (Cadotte & Davies, 2016; Mazel et al., 2016; Webb et al., 2002). Clustering and overdispersion can result from several different processes, also depending on whether they are detected with metrics that emphasize deep phylogenetic relationships or shallow phylogenetic relationships. For example, clustering of MNTD in an assemblage may reflect recent radiations in one or a few phylogenetic groups, or environmental filtering that only allows for a few closely related phylogenetic lineages to co-occur (Cadotte & Davies, 2016). These cases might be distinguished by comparing patterns of MPD, which can be overdispersed in the first case, but must be clustered in the second case. To unravel the underlying evolutionary processes determining the composition of phylogenetic assemblages, we must thus compare deep and shallow phylogenetic patterns (Webb et al., 2002).

With about 12,000 species worldwide (Hassler, 2004–2021), ferns are the second largest extant clade of vascular plants (Smith, 1972). They originated about 430 million years ago (mya) (Testo & Sundue, 2016) and contain a number of phylogenetically isolated old lineages that trace back to the initial radiation in the Palaeozoic (Lehtonen et al., 2017; Testo & Sundue, 2016). However, about 80% of the current fern diversity is the result of the radiation of polypods (the order Polypodiales), a monophyletic lineage that diversified alongside the rise of angiosperms to ecological dominance starting in the Cretaceous (Du et al., 2021; Schneider et al., 2004), an event that has been called the Angiosperm Terrestrial Revolution because of the massive concomitant changes in biodiversity and ecosystem processes (Benton et al., 2022). Over the evolutionary history of ferns, major extinction events have primarily been caused by global changes in climate and movement of continents, whereas species origination appears to be density-dependent, so that it slowed in periods of high species richness (Lehtonen et al., 2017).

Currently, the global centers of fern species richness are found in southern Central America (Costa Rica and Panama), the tropical Andes from Venezuela to Bolivia, the Hengduan Mountains in China, and Malesia, especially New Guinea, with secondary centers in the Greater Antilles, the Guianas, southeastern Brazil and Madagascar; continental Africa in contrast is very poor in ferns (Qian et al., 2022; Qian, Kessler, Zhang, Jin, & Jiang, 2023; Suissa et al., 2021). These centers reflect globally consistent species richness-environment relationships, with fern richness being highest in regions of moderate temperatures and high humidity and cloud cover, and high environmental heterogeneity, as found especially in tropical mountains (Kessler et al., 2011; Kreft et al., 2010; Suissa et al., 2021; Weigand et al., 2020).

Previous studies on angiosperms (e.g. Qian et al., 2015; Rana et al., 2019) have shown that evolutionary legacy represented by phylogenetic structure is a driver of variation of species richness between areas, but previous studies on ferns (e.g. Qian, Kessler, Zhang, Jin, & Jiang, 2023; Suissa et al., 2021) have not investigated the relationships between fern diversity and phylogenetic structure metrics. Here, we provide the first global analysis to explore the relationship based on a combination of a metric that more strongly reflects ancient evolutionary divergence (MPD) and a metric that reflects relatively recent evolutionary divergence (MNTD). Unlike Qian, Kessler, Zhang, Jin, and Jiang (2023) which focuses on the investigation of the relationships between phylogenetic structure metrics and climatic variables, the present study focuses on the relationships between fern species richness and phylogenetic structure metrics. We find that different regions of high and low fern species richness have strikingly different patterns of phylogenetic diversity which may reflect different histories of species accumulation over time. Considering that different evolutionary processes may lead to similar phylogenetic patterns, we then draw on additional lines of evidence to propose a series of hypotheses to explain the patterns of phylogenetic diversity.

2 | MATERIALS AND METHODS

2.1 | Fern species lists

The globe was divided into geographic units ($N = 392$) as shown in Figure S1, which were primarily level-3 geographic units defined by the Taxonomic Databases Working Group (TDWG) (Brummitt, 2001) and Zhang et al. (2018). These geographic units are commonly called TDWG units (Brummitt, 2001; Zhang et al., 2018). Species assemblages of these geographic units have been frequently used in ecological and biogeographic studies (e.g. Brodie et al., 2021; Guo et al., 2022; Hagen et al., 2021; Qian, Kessler, Zhang, Jin, & Jiang, 2023; Sandel et al., 2020). We used species lists compiled by Qian, Kessler, Zhang, Jin, and Jiang (2023) for the geographic units. As stated in Qian, Kessler, Zhang, Jin, and Jiang (2023), botanical nomenclature in the species lists were standardized following Hassler (Hassler, 2004–2021). The 392 geographic units used in our study included 11,381 species in 324 genera.

2.2 | Fern phylogeny

The time-calibrated megaphylogeny of ferns reported by Nitta et al. (2022; v1.1.0) included 46%, 95% and 100% of the species, genera, and families, respectively, of the extant fern flora of the world. It is the largest and most up-to-date phylogenetic tree for ferns. We used the functions Scenario 3 and build.nodes.1 of the package U.PhyloMaker (Jin & Qian, 2023) and the megaphylogeny of Nitta et al. (2022) as a backbone to generate a phylogeny for the species of the present study. Specifically, branch lengths of added taxa of a family were set evenly between dated nodes and terminals within the family, and a missing species was added at the mid-point of the branch of the genus to which the species belongs. Phylogenetic trees generated by U.PhyloMaker or its sister packages (e.g. Jin & Qian, 2019, 2022) have been commonly used in studies on community phylogenetics (e.g. Cai et al., 2023; Qian, 2023a, 2023b; Qian, Zhang, & Jiang, 2023; Zhou et al., 2023), including studies on ferns (e.g. Qian, Kessler, Zhang, Jin, & Jiang, 2023). Previous studies (e.g. Qian & Jin, 2021) have shown that results derived from phylogenetic trees generated by these packages are robust. Lehtonen et al. (2015) also show that in their study on phylogenetic structure of fern communities, results are qualitatively similar whether phylogenies were resolved to the species or the genus level.

2.3 | Phylogenetic diversity and dispersion metrics

We calculated mean nearest taxon distance (MNTD) and mean pairwise distance (MPD) (Webb, 2000) for each geographic region. We calculated standardized effect size for both MPD and MNTD for each geographic region. The standardized effect size of MPD (MPD_{ses}) and the standardized effect size of MNTD (MNTD_{ses}) were calculated using the following formula based on global species pool: $X_{\text{ses}} = (X_{\text{obs}} - \text{mean}(X_{\text{null}}))/\text{SD}(X_{\text{null}})$, where X_{obs} is the observed value, X_{null} is the average expected value for randomized assemblages, and SD (X_{null}) is the standard deviation of expected values among randomized assemblages. MPD_{ses} and MNTD_{ses} measure the phylogenetic dispersion of assemblages at different evolutionary depths, and thus represent the legacy of evolutionary histories at different phylogenetic depths (Mazel et al., 2016). For both metrics, a negative value reflects relative phylogenetic clustering of species while a positive value reflects relative phylogenetic overdispersion of species. We used the R package PhyloMeasures (Tsirogiannis & Sandel, 2016) to calculate the metrics. Defining MPD_{ses} and MNTD_{ses} requires a null model and a defined species pool. The null model used in PhyloMeasures considers all possible combination of S species from the species pool (where S is the richness of a sample to be standardized) to be equally likely (see Tsirogiannis & Sandel, 2016 for details).

There are 11 orders of ferns in the world (PPG I, 2016). The order Polypodiales, which are commonly called 'polypods', account for 82% of extant fern species, and originated and diversified much later than nearly all the other orders (Lehtonen et al., 2017). Qian, Kessler, Zhang, Jin, and Jiang (2023) showed that geographic and ecological patterns of phylogenetic metrics of the polypods substantially differ from a combination of the other 10 orders, nine of which are older than the order Polypodiales while the other order is as old as Polypodiales. Consequently, we also calculated the metrics for polypods and non-polypods (i.e. all fern orders except for the polypod order) separately, in addition to calculating the above-noted phylogenetic metrics for all ferns as a whole.

2.4 | Data analysis

Because area varies among the geographic regions and because species richness is often linearly correlated with log-transformed sampling area (Rosenzweig, 1995), to account for the effect of area variation on species richness, we followed previous studies (e.g. Guo et al., 2021; Qian, Kessler, Zhang, Jin, & Jiang, 2023) in dividing the number of species in each geographic region by the $\log_{10}$-transformed area (in square kilometre) of the geographic region (hereafter, species diversity or species density).

To explore consistency versus discrepancy in geographic patterns between MNTD_{ses} and MPD_{ses} based on significance of clustering versus overdispersion at the threshold level of $\alpha = 0.05$, a value of MNTD_{ses} or MPD_{ses} is considered significant clustering if it is < -1.96, non-significant (neutral) if it is ≥ -1.96 but ≤ 1.96, or significant overdispersion if it is > 1.96 (Hortal et al., 2011; Mazel et al., 2016). For either of the two phylogenetic metrics, we divided the 392 geographic units into three classes: significant clustering (c), non-significant or neutral (–) or significant overdispersion (o). The full combination of the three classes of the two metrics resulted in nine categories (Figure 1).

Because phylogenetic metrics represent evolutionary histories and because evolutionary histories are considered among drivers of species diversity (Algar et al., 2009), phylogenetic metrics representing evolutionary histories have been considered as drivers of species diversity in statistical models (e.g. Algar et al., 2009; Rana et al., 2019). Accordingly, using regression analysis, we explored the degree to which the variation in species diversity among geographic regions can be explained by the variation in each of the phylogenetic metrics examined in this study.

Previous studies have shown that for a given group of organisms, evolutionary histories can differ substantially between biogeographic regions (Ricklefs, 2004; Rosenzweig, 1995). Accordingly, in addition to exploring the relationship between species diversity and each of the phylogenetic metrics at the global extent, we also explored the relationship for each biogeographic realm. We divided the globe into six biogeographic realms, which are either continents or continent-like regions, as shown in Figure S1.

To distinguish the relative importance of evolutionary legacy representing deep evolutionary histories (e.g. measured by $\mathrm{MPD}_{\mathrm{ses}}$) from that representing shallow evolutionary histories (e.g. measured by $\mathrm{MNTD}_{\mathrm{ses}}$) in affecting species diversity, we conducted a series of partial regressions (Legendre & Legendre, 2012) to partition the variation in species diversity explained by $\mathrm{MPD}_{\mathrm{ses}}$ and $\mathrm{MNTD}_{\mathrm{ses}}$ into three portions: explained uniquely by $\mathrm{MPD}_{\mathrm{ses}}$, explained uniquely by $\mathrm{MNTD}_{\mathrm{ses}}$, and explained jointly by $\mathrm{MPD}_{\mathrm{ses}}$ and $\mathrm{MNTD}_{\mathrm{ses}}$.

We conducted regression analyses to assess the relationships among variables. We used simultaneous autoregressive (SAR) error models, which account for spatial autocorrelation (Kissling & Carl, 2008), to estimate the coefficient of determination of a regression. We used Spatial Analysis in Macroecology (www.ecoevol.ufg.br/sam/; Rangel et al., 2006) for statistical analyses.

3 | RESULTS

Species diversity (SD; defined here as the number of species in a geographic region being divided by $\log_{10}$-transformed area in km^2 of the geographic region) of ferns was highest in the well-known diversity hotspots in southern Central America (Costa Rica and Panama), the tropical Andes from Venezuela to Bolivia, the Malesian region (especially New Guinea), and the Hengduan Mountains of southwestern China and adjacent regions (e.g. India, Myanmar, and Vietnam) (Figure S2a). Secondary centers of species diversity were found in northern Central America, southeastern Brazil, Madagascar, and eastern Asia (especially Taiwan and Japan). When we mapped non-polypod ferns (Figure S2b) and polypods (Figure S2c) separately, subtly different patterns emerged. While the pattern of polypods closely mirrored that of overall ferns, non-polypod ferns were more strongly concentrated around the equator and showed no center of diversity in the Hengduan Mountains and surrounding areas.

At the global scale, SD was negatively correlated with standardized effect size of mean nearest taxon distance ($\mathrm{MNTD}_{\mathrm{ses}}$, which reflects relatively recent evolutionary divergence) and the standardized effect size of mean phylogenetic distance ($\mathrm{MPD}_{\mathrm{ses}}$, which reflects ancient evolutionary divergence and measures assemblage-wide phylogenetic dispersion) (Pearson's correlation: $r = -0.789$ and -0.299, respectively, $p < 0.001$).

When $\mathrm{MNTD}_{\mathrm{ses}}$ was used to quantify phylogenetic dispersion of each assemblage, that is phylogenetic dispersion reflecting shallow evolutionary history, regions with very high phylogenetic dispersion for ferns as a whole were primarily located in Africa, whereas regions

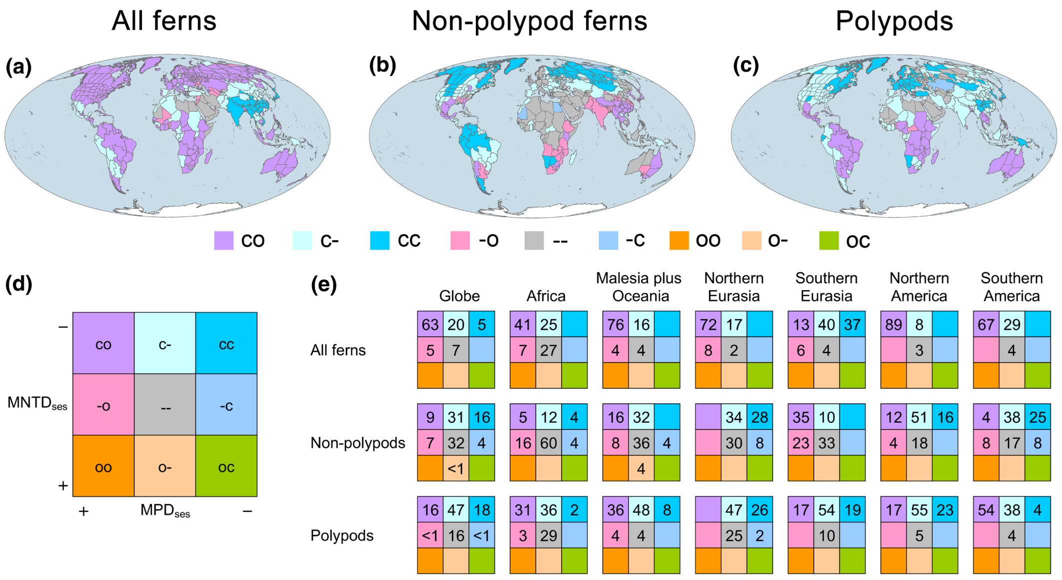

FIGURE 1 Geographic patterns of all possible combinations of three classes representing tip-weighted phylogenetic relatedness ($\mathrm{MNTD}_{\mathrm{ses}}$) and three classes representing basal-weighted phylogenetic relatedness ($\mathrm{MPD}_{\mathrm{ses}}$) for (a) all ferns as a whole, for (b) non-polypod ferns, and (c) polypods separately. For each phylogenetic relatedness metric, a value smaller than −1.96 represents significant phylogenetic clustering (c), a value falling in the range from −1.96 to 1.96 represents non-significant (neutral) phylogenetic relatedness (–), a value greater than 1.96 represents significant phylogenetic overdispersion (o). Panel (d) shows codes for the nine categories of all possible combinations of the two phylogenetic relatedness metrics (the left letter of each code for $\mathrm{MNTD}_{\mathrm{ses}}$ and the right letter for $\mathrm{MPD}_{\mathrm{ses}}$). Panel (e) presents the proportion (%) of geographic regions (assemblages) for each of the nine categories in the globe and in each of the six biogeographic realms.

with low phylogenetic dispersion were located in the Hengduan Mountains and surrounding areas (Figure S2d). When non-polypod ferns and polypods were considered separately, the geographic pattern of MNTD_{ses} for polypods was generally similar to that for all ferns (compare Figure S2f with S2d) but the geographic pattern of MNTD_{ses} for non-polypod ferns differed substantially from those for ferns as a whole and for polypods (compare Figure S2e with S2d and S2f).

When MPD_{ses} was considered, regions with high phylogenetic dispersion for ferns as a whole included North America, Europe, eastern South America and eastern Australia (Figure S2g). In general, tropical areas in Asia, Africa and North America tended to have lower phylogenetic dispersion (and thus higher phylogenetic clustering), and India and eastern Asia had the lowest phylogenetic dispersion (Figure S2g). However, when polypods and non-polypod ferns were considered separately, they differed substantially from those for ferns as a whole (compare Figure S2g with Figure S2h and S2i). For example, India and eastern Asia, along with tropical North America, and tropical Africa, had relatively high MPD_{ses} for non-polypod clades, but these areas had relatively low MPD_{ses} for ferns as a whole (compare Figure S2g with S2h). For polypods, areas with high MPD_{ses} included much of South America, much of Sub-Saharan Africa and Australia. There was only a small portion of the world that had congruent geographic patterns for MPD_{ses} among all ferns, polypods and non-polypod ferns (e.g. eastern Australia).

Comparing geographic patterns of MNTD_{ses} and MPD_{ses} revealed that geographic patterns in variation of MNTD_{ses} were similar in some regions and different in other regions, compared with those of MPD_{ses} (compare Figure S2d with S2g), regardless of whether ferns as a whole were considered or polypods and non-polypod ferns were considered separately. For example, for ferns as a whole, most of temperate North America had relatively low MNTD_{ses} (Figure S2d) but relatively high MPD_{ses} (Figure S2g). In contrast, areas across nearly whole Africa had high MNTD_{ses} (Figure S2d) but mostly had low MPD_{ses} (Figure S2g). Areas with congruent patterns between MNTD_{ses} and MPD_{ses} included most of Asia and eastern South America.

We found that, globally, over half (63%) of the geographic regions showed a combination of clustered MNTD_{ses} and overdispersed MPD_{ses} (category co; Figure 1a,e) followed by 20% regions with clustered MNTD_{ses} and neutral MPD_{ses} (category c-; Figure 1a,e). Regions falling into the other seven combinations of MNTD_{ses} and MPD_{ses} were rare or absent. However, the combination of both clustered MNTD_{ses} and MPD_{ses} (category cc), although present in only 5% of the regions, showed a distinctive geographic pattern, being found only in the center of diversity in the Himalaya, the Hengduan Mountains, and surrounding regions, as well as Japan. Among the non-polypod ferns, the combinations of neutral or clustered MNTD_{ses} and neutral MPD_{ses} (category -- or c-, respectively) was most common (32% and 31%, respectively), but five of the other seven combinations were also found (Figure 1b,e). In contrast, among the polypods, the clustered MNTD_{ses} was dominant, mostly in combination of neutral MPD_{ses} (47%; category c-; Figure 1c,e), the combination of both clustered MNTD_{ses} and MPD_{ses} (category cc; 18%) dominated in the temperate Northern Hemisphere. The centers of fern species diversity largely showed patterns consistent with the overall patterns, although there were some conspicuous deviations. For example, southern Eurasia had mainly clustered MNTD_{ses} and neutral MPD_{ses} (category c-) for all ferns (40%) and a predominance (35%) of clustered MNTD_{ses} and oversdispersed MPD_{ses} (category co) for the non-polypods.

At the global extent, MNTD_{ses} and MPD_{ses} together explained 66.2%, 19.3% and 65.7% of the variation in species diversity for all ferns, non-polypod ferns, and polypods, respectively (Figure 2). In all the three groups of ferns, MNTD_{ses} uniquely explained much more variation in species diversity than explained uniquely by MPD_{ses}, and the variation in species diversity uniquely explained by MNTD_{ses} was more than that explained jointly by MNTD_{ses} and MPD_{ses} (Figure 2).

When the six biogeographic realms were analysed separately, MNTD_{ses} and MPD_{ses} collectively explained 11.2%–88.7% (52.0% on average) of the variation in species diversity in the 18 cases (i.e. three fern groups by six biogeographic realms) (Figure 2). MNTD_{ses} uniquely explained more variation in species diversity than that uniquely explained by MPD_{ses} in 16 out of the 18 cases, including all cases for Africa, Asia, Malesia plus Oceania, and South America (Figure 2).

Relating species diversity to MNTD_{ses} and MPD_{ses} revealed much more variation between continents (Figure 3a,b). For MNTD_{ses}, all continents showed negative relationships between species diversity and MNTD_{ses}, although the slopes of the relationships differed markedly, being very steep in southern and northern Americas, but very shallow in Africa. In contrast, a clear negative relationship between species diversity and MPD_{ses} was found for northern America, Malesia and southern Eurasia, whereas southern America and northern Eurasia showed almost no relationship, and Africa showed a strongly positive one. When polypods and non-polypod ferns were considered separately, the afore-noted general patterns held (compare Figures S3 and S4 with Figure 3).

4 | DISCUSSION

This study is sister to the study by Qian, Kessler, Zhang, Jin, and Jiang (2023). These two studies use the same set of regional fern floras but address two different sets of questions. The study of Qian, Kessler, Zhang, Jin, and Jiang (2023) focuses on the relationships of species density and phylogenetic metrics with climate conditions, and found that temperature-related variables explained more variation in these metrics than did precipitation-related variables, and that climate extremes have a stronger relationship with phylogenetic structure of ferns than does climate seasonality. In contrast, the present study focuses on the exploration of geographic patterns of matches and mismatches between a phylogenetic relatedness metric reflecting deep evolutionary history (MPD_{ses}) and another one reflecting shallow evolutionary history (MNTD_{ses}), and the investigation of the effects of evolutionary history represented by MPD_{ses} and MNTD_{ses} on species density. Thus, these two studies address different sets of questions on the one hand, and are complementary to each other on

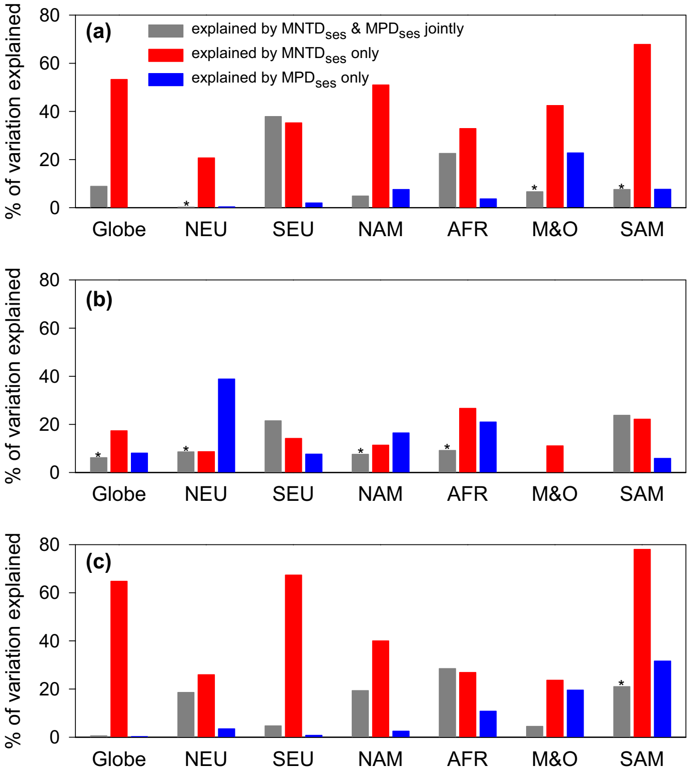

FIGURE 2 Variation in species diversity (SD; i.e. the number of species in a geographic unit being divided by $\log_{10}$-transformed area in km^2 of the geographic unit) explained only by MNTD$_{ses}$, only by MPD$_{ses}$, or jointly by MNTD$_{ses}$ and MPD$_{ses}$ for (a) all ferns as a whole, (b) non-polypod ferns, and (c) polypods in the globe and in each of the six biogeographic realms (NEU, northern Eurasia; SEU, southern Eurasia; NAM, northern America; SAM, southern America; AFR, Africa; M&O, Malesia plus Oceania; SAM, southern America). An asterisk above a bar represents a negative value resulting from the variation partition (see Legendre and Legendre (2012) for statistical interpretation of a negative value). Note that in each panel each biogeographic realm included three bars (grey on the left, red in the middle, blue on the right) but some bars may not be visible because the explained variations that they represented were close to zero.

the other hand. Interpretation of patterns of species diversity is challenging because they can result from different evolutionary processes (Cavender-Bares et al., 2009). Our aim here is to document the global patterns, to provide a framework for hypothesis-driven in-depth studies of individual clades, in which actual cases of extinction, speciation, and dispersal are identified, which allow us to fully understand how fern diversity has been accrued in different geographic regions.

The patterns of phylogenetic diversity revealed by combining the phylogenetic metrics of MPD$_{ses}$ (which more strongly reflects ancient evolutionary divergence) and MNTD$_{ses}$ (which reflects relatively recent evolutionary divergence) are more complex than those of species density. For ferns as a whole, the dominant pattern worldwide is a combination of overdispersed MPD$_{ses}$ and clustered MNTD$_{ses}$ (purple in Figure 1d). This pattern likely reflects that deep evolutionary lineages such as families tend to be widespread, with many fern families occurring on several continents, resulting in overdispersion. In contrast, many fern groups have undergone recent regional species radiations, as known, for example, for the relatively old tree fern family Cyatheaceae (Loiseau et al., 2020) and therelatively young families Polypodiaceae (Sundue et al., 2015) and Dryopterideaceae (Le Péchon et al., 2016). Also, we find that overall fern species diversity is negatively correlated with both MNTD$_{ses}$ and MPD$_{ses}$, so that regions with high species diversity tend to have clustered species assemblages, whereas species-poor regions tend to have overdispersed species assemblages. We propose that this reflects that regions with low species diversity tend to mainly include phylogenetically scattered families and species, without a strong signal of regional radiations, and vice versa.

This rather simple general pattern does not hold, however, if we look into more detail, especially regarding MPD$_{ses}$, which reflects deep evolutionary divergence. Comparing the four global centers of fern diversity, we find that only one of them (Malesia) corresponds to the global pattern with overdispersed MPD$_{ses}$, whereas southern Mesoamerica and the tropical Andes largely have neutral MPD$_{ses}$, whereas the Hengduan Mountains even have clustered MPD$_{ses}$. We hypothesize that these differences suggest that despite comparable levels of current species diversity, the origination and accumulation of this diversity has followed different pathways in these regions. Whereas southern Malesia appears to have gradually accumulated their fern diversity over time, Mesoamerica and the Andes also show a signal of mixing of lineages. We propose that this reflects the fact that these regions are easily accessible for dispersal to and from other regional centers of fern diversity (Central America, eastern Brazil, southern Andes, Guianan highlands). Dispersal into the Andes by boreotropical fern elements during the Great American Biotic Interchange following the contact of the North and South American continental masses, has been shown, for example, in the genus *Diplazium* (Wei et al., 2015). As

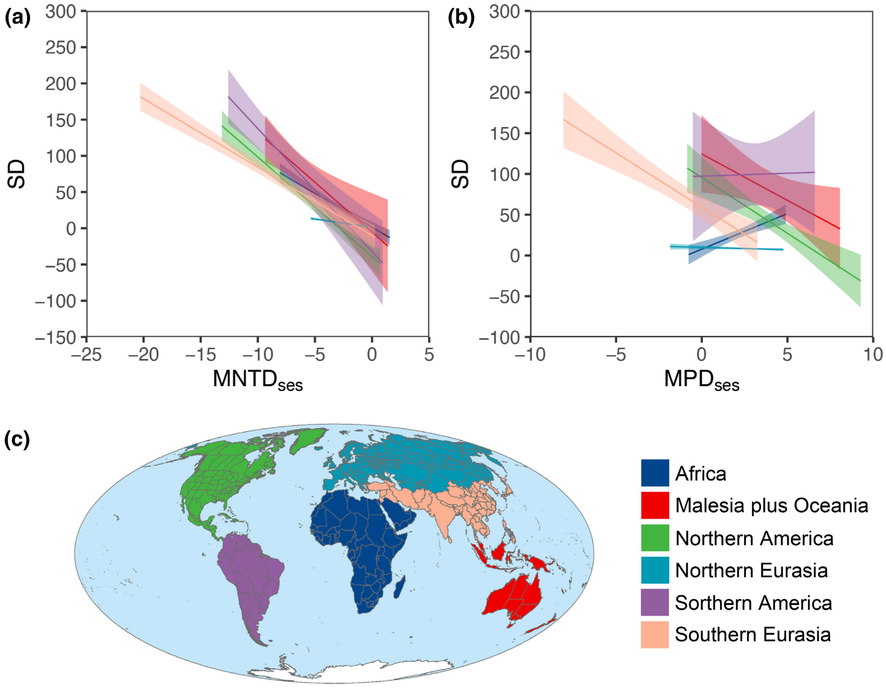

FIGURE 3 Relationships between the species diversity (SD; i.e. the number of species in a geographic unit being divided by $\log_{10}$-transformed area in km^2 of the geographic unit) of all ferns and phylogenetic relatedness metrics (MNTD$_{ses}$, MPD$_{ses}$; (a) and (b)) for each of the six biogeographic realms shown in (c). Colours in panels (a) and (b) correspond to colours for biogeographic realms in panel (c). Lines indicate best-fit linear regressions with 95% confidence intervals. The slope and statistic significance of each of the relationships were assessed based on simultaneous autoregressive error models, which were shown in Table S1. The relationships for non-polypod ferns and polypods were shown in Figures S3 and S4.

a result of this, the Andean representatives of fern clades are intermixed with those from the adjacent regions. On the other hand, the Hengduan Mountains appear to have accumulated their fern diversity as a result of both combining a nonrandom subset of families and of recent radiations. This may reflect the fact that this is the only non-tropical center of fern diversity, so that some major tropical fern lineages are absent or poorly represented. The recent radiations in turn are likely due to the exceptional topographical and climatic complexity of the region, as shown for several major angiosperm radiations in the region (Favre et al., 2015; Xing & Ree, 2017; Yan et al., 2015).

The diversity of evolutionary pathways shaping current patterns of fern diversity becomes even more evident when we not only compare ferns as a whole, but also distinguish between non-polypod fern clades that originated prior to the Angiosperm Terrestrial Revolution and the more recent polypod radiation. Thus, the pattern of overdispersed MPD$_{ses}$ in all ferns is lost when we separate non-polypods and polypods, where non-significant (neutral) patterns dominate. This shows that the overdispersion results from the comparison of phylogenetically distantly related fern lineages, and that it disappears when we restrict the analyses to more closely related families.

Looking at individual continents, in Africa the non-polypod fern clades tend towards overdispersed MPD$_{ses}$ and MNTD$_{ses}$, whereas among polypods there is a strong signal of clustered MNTD$_{ses}$. We propose that this is a signature of major extinctions in Africa as a result of past arid conditions, for example during the globally hot Miocene climate optimum Africa (Couvreur et al., 2021), as also shown for angiosperms (Qian, Kessler, Zhang, Jin, Soltis, et al., 2023), followed by more recent diversification from the few lineages that survived or colonized the continent from America or Asia (Bauret et al., 2017).

The Northern Hemisphere as a whole has a tendency towards regional fern floras that are clustered for both phylogenetic diversity metrics when separating non-polypods and polypods. This likely reflects that only a few lineages have adapted to these conditions as a result of phylogenetic niche conservatism, both among and within families. For example, the families Equisetaceae, Osmundaceae and Ophioglossaceae are best represented in temperate regions. The Equisetaceae has a rich fossil record of highly diverse growth forms under tropical climatic conditions in the Palaeozoic (Lehtonen et al., 2017; Ryberg et al., 2008), reflecting massive extinctions in the Mesozoic, resulting in the survival of the sole genus *Equisetum* with about 15 species. A similar case is seen for the family Osmundaceae, although its diversification and major extinction happened at a somewhat later time (Cheng et al., 2020). Interestingly, these families currently occupy mainly moist, aquatic and semiaquatic habitats (Equisetaceae, Osmundaceae) or open, often disturbed herbaceous vegetation (Ophioglossaceae) that have few other fern species, which would be in accordance with the notion that these are relict groups that survive in regions with low species richness and low direct competition. The Southern Hemisphere does not show this pattern, presumably because of the less extensive land area at higher latitudes combined with milder, more oceanic climates.

Concluding, ferns are a fascinating study group to address questions of how species diversity has accumulated over time, and how different evolutionary processes have influenced the current composition of regional plant assemblages. Our study highlights these differences and proposes some hypotheses as a background for future in-depth studies.

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CONFLICT OF INTEREST STATEMENT

None.

DATA AVAILABILITY STATEMENT

Plant data used in this study are available at World Plants (https://www.worldplants.de) and Plants of the World online (http://www.plantsoftheworldonline.org). Climate data used in this study are available at the CHELSA climate database (https://chelsa-climate.org/bioclim).

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BIOSKETCHES

Hong Qian's research is multidisciplinary and particularly lies at the interface of ecology and biogeography (https://www.researchgate.net/profile/Hong_Qian3/publications).

Author Contributions: HQ initiated the research; JZ and YJ prepared the data; HQ and MJ analyzed the data; HQ and MK wrote the manuscript; all authors participated in revising the manuscript.-

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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