

Biogeographic patterns of polyploidy in the spleenwort: bridging divergent perspectives over the evolutionary consequences of polyploidy

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Abstract

Despite substantial progress in genomic and phenotypic research on polyploidy, its broader eco-evolutionary implications remain elusive. We thus focused on spleenworts as a model system to investigate the impact of polyploidy on their biogeographic patterns. Contrary to the conventional expectation that polyploids would be more common at higher latitudes, our findings showed a higher prevalence in tropical regions, with their dominance gradually decreasing toward the poles. Both diploid and polyploid species richness in spleenworts displayed similar responses to biogeographic factors such as elevation and isolation from waterbodies that serve as indicators of stress tolerance. This suggested that the potential evolutionary advantages associated with polyploidy at the individual level may not necessarily translate to higher organizational levels. Instead, regional disparities in polyploid formation and extinction rates, particularly influenced by ecological interactions among species, may play a critical role in determining global biogeographic patterns. Our study therefore underscores the importance of understanding the geographic contexts in which polyploidy can either pose an evolutionary risk or contribute to success in plant diversification.

Introduction

Polyploidy, which refers to having multiple sets of chromosomes, is a pivotal process in plant evolution. Since Stebbins' framework on polyploidy in 1940, advances in genetic research have steadily enriched our comprehension of its dynamics and underlying mechanisms^{1,2}. While extensive research has explored the distinct characteristics of polyploids³, the broader evolutionary consequences of polyploidy, particularly within natural populations, have remained relatively understudied¹. This limited attention has resulted in divergent perspectives regarding the implications of polyploidy on plant evolution and diversification. For example, some posit polyploidy as evolutionary noise or dead-ends, citing reduced diversification rate in recently formed polyploid taxa^{4–8}, while others view polyploidy as a high-risk, high-gain path to evolutionary success, akin to sluggers in a baseball game^{9,10}. These divergent perspectives are likely influenced by considerable variations in polyploid traits and ecological prerequisites for their formation and success, which are contingent upon the genetic constitution of parental plants and the specific mode of polyploidization involved¹¹.

The geographic template, constituted by regular variations in environmental conditions, topography, and species interactions, is a critical determinant of how organisms adapt, disperse, and confront the risk of extinction¹². Therefore, analyzing the biogeographic patterns of polyploids can offer valuable insights into how polyploidy operates within specific geographical contexts. For instance, the geographical distribution of polyploidization rates and species richness can elucidate the underlying eco-evolutionary conditions and historical biogeographic processes in operation. Prior research on polyploid biogeography, particularly within the realm of angiosperms, has documented increasing polyploid frequency at higher latitudes and elevations as well as a greater prevalence in extreme environments, such as subarctic, upland, and arid regions^{1,4,13–16}. While these observations may support the role of polyploid vigor in their

tendency to arise and thrive in more challenging conditions^{17,18}, it should be noted that such environments are also often associated with specific lifeforms such as perennial herbs^{1,13}.

To better understand geographic variations in polyploidy, studies should prioritize examining populations of closely related species. This focused approach is essential for effectively controlling confounding factors, such as variations in functional traits and historical biogeography, which may emerge when comparing across higher levels of taxonomic classification¹⁹. We thus directed our attention towards the spleenworts (genus *Asplenium*), due to their global distribution across tropical and temperate regions, their status as one of the most species-rich fern genera (~ 700 species²⁰), their consistent perennial growth form, reliance on abiotic mechanisms for fertilization and dispersal, and extensive evolutionary history dating back to the Paleogene (~ 57 Mya based on fossil records²¹). Furthermore, this group contains an abundance of polyploid taxa, including instances of octoploid or higher ploidy levels^{22,23}. In fact, Lovis (1973) previously suggested that this group held the potential to offer direct evidence of polyploidy dynamics on Earth, despite the challenges faced by researchers of that era due to limited global data and analytical tools²⁴.

In this study, we examined the global biogeographic patterns of polyploidy and corresponding species richness in spleenworts to more deeply understand the underlying biogeographical factors and processes driving these patterns. Our hypothesis posits that the distribution of polyploidy and its species richness is not random but rather highly predictable based on two deterministic processes: (1) spatial autocorrelation with parental cytotypes during the formation of polyploids and their subsequent radiation; and (2) geographic variations that either facilitate or impede the establishment and long-term persistence of polyploid populations. Our investigation encompasses global and regional comparisons of spatiotemporal variations in species richness among cytotypes, considering both ancient and recent polyploidy events. We also assessed various explanatory variables contributing to the observed biogeographic patterns of polyploidy. Our findings elucidate the eco-evolutionary circumstances under which polyploidy may drive either evolutionary success or stagnation in plant diversification, which can help reconcile divergent perspectives on the role of polyploidy in plant evolution.

Results

Global distribution of polyploidy in spleenworts

Polyploid frequency, which represents the proportion of polyploid species relative to the total surveyed species in each biogeographic region, was notably higher in montane forests of tropical and subtropical regions, particularly in the Southern Hemisphere (Fig. 1a). The regions with high polyploid frequency (> 70%) included most islands in Indomalaya (e.g., Java, Sumatra, Borneo, Sundaland, Sulawesi, Seram, and Halmahera), Australasia (e.g., New Guinea, Fiji, Solomon Islands, and New Zealand), and the Afrotropics (e.g., Madagascar), as well as tropical and subtropical moist broadleaf forests in the Neotropics and Afrotropics (e.g., the Congolian coastal forests, Jurua-Purus, and Purus-Madeira moist

forests). In addition, certain desert areas, such as the Sonoran, Chihuahuan, and Sechura deserts, displayed high polyploid frequencies, despite having comparatively low overall species richness.

The pattern of polyploid richness, indicating the number of different ploidy levels in each biogeographic, generally paralleled the pattern observed in polyploid frequency (Fig. 1b). Notable extensions of this pattern (≥ 4) were observed in the Palearctic, including most temperate forests in eastern North America, western Europe, and East Asia. These regions also tended to exhibit the highest ploidy levels as well as phylogenetic endemism (Fig. 1c and Supplementary Fig. 1).

The highest recorded ploidy level among surveyed spleenworts reached 16x, and species with ploidy levels exceeding 12x were found in Southeast US conifer savannas in the Nearctic, in Cuban and Jamaican moist forests, Andean Mountain ranges, and Guianan savanna in the Neotropics, as well as Madagascar humid forests in the Afrotropics (Fig. 1c).

Global species richness patterns

The major hotspots with high species richness for both diploids and polyploids were primarily located in tropic and subtropic moist forests (Fig. 2a). These hotspots included moist broadleaf forests in the Neotropics (e.g., North Central American Highlands, Panama and Costa Rica Highlands, the Andes, and the Caribbean), montane rainforests in Indomalaya (e.g., Jian Nan, South Vietnam Highlands, Sumatra and Peninsular Malaysia, and Taiwan), montane shrub and grasslands in the Afrotropic (e.g., the Great Rift Valley and Madagascar), and temperate broadleaf and mixed forests in the Palearctic (e.g., the Japanese archipelago). The regions with high polyploid but low diploid richness were typically found on the peripheral regions of these hotspots, particularly in the Southern Hemisphere realms of the Neotropics and Afrotropics. In contrast, the regions with high diploid but low polyploid species richness were generally situated in the Northern Hemisphere realms of the Nearctic and Palearctic.

The latitudinal peaks of species richness varied across cytotypes, particularly between diploid and polyploid species (Fig. 2b and Supplementary Fig. 2). Polyploid species richness reached its highest point in the tropics (within about $\pm 10^\circ$ of Equator). In contrast, diploid species richness peaked at approximately 40° North. The richness of mixed-ploidy species reached a maximum near 30° North, positioning it between the peaks of polyploid and diploid species richness. Species with unknown ploidy status were primarily located in tropical regions.

However, the relationship between species richness and elevation, as well as isolation from waterbodies, demonstrated a consistent pattern across all cytotypes. The relationship with elevation displayed an inverse parabolic pattern, with the highest species richness occurring at intermediate elevations around 700 meters (Fig. 2c). Species richness generally declined at distances from waterbodies exceeding 2 kilometers (Fig. 2d).

Lineage diversification over time and space

Among all surveyed taxa, 80.9% were identified as polyploids (Fig. 3a and Supplementary Table 1). Notably, the subclades *Erosum*, *Bullatum*, and *Tarachia* exclusively consisted of polyploid taxa. The subclade *Asplenium* had the lowest proportion of polyploids at 38.5%, followed by *Aegaeum* (50.0%), *Pleurosorus* (57.1%) and *Phyllitis* (62.5%). Two other subclades, *Camptosorus* and *Neottopteris*, had more than 70% of their taxa classified as polyploids. All extant spleenworts were inferred to have originated from paleopolyploids (Supplementary Fig. 3).

The diversity of ploidy levels within all spleenwort lineages exhibited a gradual increase over time from $h' = 0.693$ at 60 Mya to $h' = 1.313$ in the present (Fig. 3a). Tetraploids gradually increased their number of lineages, with several fluctuations occurring at around 40, 30, and 15 Mya ($\gamma = -3.889$, $p = 0.001$). Diploid and octoploid lineages emerged relatively late, gradually increasing after approximately 40 Mya (diploids $\gamma = -3.633$, $p = 0.001$; octoploids $\gamma = -0.675$, $p = 0.524$). Other cytotypes remained at relatively low frequencies after their emergence around 25 Mya. The geographic expansion of both diploid and polyploid lineages primarily took place within neighboring biogeographic realms. Their distributions were typically associated with geographic proximity and connectivity. Biogeographic realms where species radiated included the expansion between the Nearctic and Neotropics, Indomalaya-Australasia-Oceania, as well as the Afrotropics and Neotropics.

On a regional scale, the relative frequency among cytotypes and their subsequent diversification varied depending on ecosystem characteristics (Fig. 3b). While tetraploid lineages were dominant overall across time, the number of diploid lineages gradually increased more than those of octoploids in temperate regions covering the Nearctic and Palearctic ($\gamma = -3.252$, $p = 0.001$). The opposite pattern was observed in tropical regions such as the Neotropics, Afrotropics, and Indomalaya ($\gamma = -2.755$, $p = 0.004$). In desert regions, there was a tendency for relatively high diversity in ploidy levels as lineages of different cytotypes similarly increased ($\gamma = -3.447$, $p = 0.002$). Biogeographic regions comprising oceanic islands, such as Indomalaya, Australasia, and Oceania, showed patterns similar to those of tropical regions, with a notable distinction being the persistence and increase of lineages at higher ploidy levels, including dodecaploid levels ($\gamma = -0.632$, $p = 0.486$).

Relative importance of explanatory variables for the species richness patterns

Boosted regression tree (BRT) models demonstrated strong performance, explaining 91.49–98.47% of deviances and cross-validation correlations ranging from 0.74 to 0.91 (Supplementary Table 2). Across all cytotypes, second-order factors, which indicate interactions effects among species, emerged as the most influential variables in explaining the species richness patterns (Fig. 4). Among these factors, phylogenetic diversity (PD) held the highest importance, albeit its relative importance varied for each cytotype. Other second-order factors, such as phylogenetic endemism (PE) and community complexity (NTI), also played notably influential roles, particularly for polyploid species richness.

Diploid species richness was broadly associated with diverse environmental variables, spatiotemporal heterogeneities, and anthropogenic factors. Variables for environmental changes, such as temperature seasonality and average rate of precipitation change, were important explanatory variables for mixed-ploidy species and had positive relationships with species richness. Environmental variability, such as temperature seasonality, explained the distributional patterns of mixed-ploidy species, showing a positive relationship. NTI and Bio4 played a relatively more important role in the richness patterns of species with unknown ploidy status, reflecting their distribution mostly in rainforests in the tropics.

their relative importance values. The x-axis indicates the actual values and the unit of each variable. A smoothed version of the fitted function is added as dashed red lines. PD, phylogenetic diversity; PE, phylogenetic endemism; NTI, nearest taxon index; Bio1, annual mean temperature (°C); Bio4, temperature seasonality (°C); Bio12, annual precipitation (mm); Bio15, precipitation seasonality (mm); Soil_pH, soil pH; Soil_WC, soil water content (kPa), Soil_CEC, Soil Cation exchange capacity (cmol_c/kg); Soil_OC, soil organic carbon (%); HF, human footprint; CV_Bio1, average velocity of temperature change (m/year); CV_Bio12, average velocity of precipitation change (m/year); Ele_het, spatial heterogeneity of elevation (m); Bio1_het, spatial heterogeneity of annual temperature (°C); Bio4_het, spatial heterogeneity of annual precipitation (mm).

Discussion

Our study extensively examined the global distribution patterns of polyploidy in spleenworts. As we hypothesized, the distribution of polyploidy and its species richness was not random but rather highly predictable. Contrary to the conventional expectation that the proportion of polyploid species increases with latitude, our study instead showed that the proportion in spleenworts was much higher in tropical regions. Both diploid and polyploid species richness responded similarly to biogeographic factors such as elevation and isolation from waterbodies, suggesting that the individual-level benefits of polyploidy in stress tolerance may not be the primary driver of these biogeographic patterns. Our findings challenge the commonly held assertion that polyploidy excels in harsher environments that typically occur at higher latitudes and elevations. Alternatively, our findings highlight the importance of considering regional variations in polyploid formation, establishment, and extinction when seeking to comprehend the impact of polyploidy on plant evolution.

The prevalence of polyploids in tropical regions, often considered biodiversity hotspots, suggests a potential link between the abundance of polyploids and the overall diversification rates of their lineages. In tropical regions, most spleenwort clades have formed exclusive polyploid complexes, primarily dominated by tetraploids. This phenomenon likely results from spatial autocorrelation among closely related species during rapid radiation. In particular, the presence of higher phylogenetic endemism in these regions implies that the high polyploid richness is due to the accumulation of species evolving from ancient paleopolyploids. This pattern aligns with the findings of Schneider et al. (2017)²³, which identified whole-genome duplications in the early history of spleenworts that preceded their recent rapid diversification. In this context, the observed patterns, when associated with paleopolyploidy followed by

rapid diversification, appear to support the idea that polyploidy can greatly contribute to plant diversification in a manner analogous to hitting a home run as described by Soltis et al. (2009)²⁵. Indeed, there is substantial corroborating evidence supporting the association between polyploidy and the subsequent rapid diversification of plant lineages, particularly during periods of global climatic upheaval, such as the Paleocene–Eocene transition and the late Miocene^{26–28}.

However, it is imperative to refrain from assuming that polyploidy alone independently propels spleenwort diversification. The observed association between polyploidy and diversification success is primarily prominent in biodiversity hotspots, particularly within tropical and subtropical moist forests. These regions possess unique eco-evolutionary conditions that often promote diversification independently of polyploidy^{29,30}. Hence, continued research should aim to untangle the factors contributing to the prevalence of polyploidy in tropical regions. Such investigations will provide a clearer understanding of how polyploidy interacts with the eco-evolutionary conditions and biogeographic processes unique to specific geographic locations. This necessitates a contextual understanding of the phenomena, recognizing that the effects of polyploidy on diversification cannot be viewed in isolation from other factors.

Understanding the specific conditions that promote the formation, establishment, and persistence of polyploids remains a challenge^{31,32}. Nonetheless, our study highlights that the key factors explaining the global patterns of polyploid richness are the phylogenetic diversity and community complexity of each region. Those with a diverse array of lineages, such as tropical regions, seem to have a greater potential to support higher polyploid richness. This relationship becomes evident when considering second-order spatial effects such as ecological interactions among spleenwort species. In such regions, intensified interactions among closely related taxa can profoundly stimulate polyploid formation, particularly promoting the emergence of allopolyploids through hybridization²⁷. In addition, high rates of niche partitioning driven by intense competition within complex communities can facilitate their rapid diversification³³. Therefore, the global disparities in overall species richness and phylogenetic diversity are likely foundational to the uneven distribution of polyploid species, as they result in geographically unequal potential for species interactions and hybridization.

Ecological conditions that support micro-allopatric speciation emerged as another important factor contributing to the long-term viability of polyploids as they can set the conditions for successful establishment while adhering to minority cytotype exclusion (MCE). According to this principle, populations with minority cytotypes inevitably face selective disadvantages due to frequency-dependent effects, including limited mating opportunities³⁴. These endogenous forces at the population level often lead to the dominance of the majority cytotype over stable coexistence, although mixed ploidy populations can temporarily persist through various reproductive isolation mechanisms such as assortative mating within ploidy levels, self-fertilization, and asexual recruitment^{35,36}. In this sense, regions rich in microhabitats and geographical barriers are expected to facilitate cytotype separation, which prevents parental introgression and allows emerging cytotype populations to persist.

Tropical regions offer particularly large potential for micro-allopatric speciation in ferns due to their diverse microhabitats and environmental heterogeneity³⁷. The presence of three-dimensional microhabitats with stable water resources creates novel niches that promote the successful establishment of newly formed polyploid populations. In addition, the dynamic interplay between elevation and climatic conditions, particularly in Neotropical mountain ranges, lead to greater climatic heterogeneity that may increase regional species richness³⁰. The presence of stable climatic conditions and minimal disturbance in these regions may also provide sufficient time for the long-term persistence and diversification of ancient polyploid lineages. For example, the tropical Andes, known for its dynamic orogenic processes in which geographic barriers can shift over time³⁸, is thought to experience a higher occurrence of hybridization followed by allopolyploidy. Our findings corroborated this expectation, as these areas displayed elevated levels of polyploid richness.

Intriguingly, regions with high polyploid but low diploid species richness were often located adjacent to hotspots of overall species richness, particularly in the Southern Hemisphere. This pattern can be attributed to biogeographic processes in which polyploids disperse into new spaces with ecological niches similar to those of their immediate ancestors but not yet occupied by them. Polyploidy, particularly in allopolyploids, can also facilitate niche divergence, enabling the colonization of habitats that were previously inaccessible to their progenitors^{39,40}. Given that allopolyploid evolution could result in niche intermediacy and expansion^{4,40}, the process of filling available vacant niches would involve an outward movement from their places of origin. This phenomenon suggests a geographic pattern of “polyploid radiation” driven by endogenous forces. However, this process notably hinges on the availability of unoccupied niches within geographic proximity, which allows for stochastic dispersal and subsequent establishment of polyploid populations³⁹. The tropical ecosystems in the Neotropics, Afrotropics, and Indomalaya align with these conditions and have the potential to accommodate more polyploid species due to their greater habitat diversity. This suggests that a geographic template sets the boundaries and regulates the process of polyploidy radiation, thus influencing the global patterns of polyploid frequency.

In such scenarios, polyploids may find themselves pushed into less favorable neighboring regions, including arid areas such as the Sonoran Desert in North America and parts of Australia where they might be mistakenly viewed as having initially colonized these areas due to antecedent novel adaptive traits acquired from polyploidization. However, these traits are more likely to have developed gradually after their displacement into these less hospitable environments. In other words, the novel morphological and physiological traits they acquire are the result of gradual adaptations over time, rather than immediate outcomes of polyploidy. Nonetheless, the long-term persistence of these polyploids may still rely on the availability of niches that can offer protection and time for further evolutionary adaptations to occur. Future time-series analysis may be necessary to fully understand these spatial dynamics of polyploidy evolution within a geographic framework.

This perspective challenges the commonly held assertion that polyploids are more common at higher latitudes and possess an inherent superiority under stressful conditions^{3,13}. Studies have consistently

highlighted that polyploidy can confer advantages in adapting to different environments or ecological niches³. This phenomenon, known as polyploid or hybrid vigor, stems from increased genetic diversity and novel gene combinations arising from polyploidy. Such enhanced fitness can manifest in various ways, including larger size, improved resistance to stressors such as diseases or drought, and greater fertility. Nevertheless, this phenomenon remains unverified in natural populations and our findings indicate that both diploid and polyploid species richness show similar responses to key biogeographic variables related to stress tolerance, such as elevation and isolation from water bodies. These findings suggest that polyploid vigor may have little impact on species richness patterns. This prompts intriguing questions regarding whether any individual-level advantages of polyploidy truly outweigh the potential drawbacks that may emerge at the population or higher organizational levels, including reproductive disadvantages related to minority cytotype exclusion.

Within an evolutionary framework, the strategies adopted by diploids and polyploids are likely influenced by their geographic locations and the selective pressures they encounter, rather than being determined by their inherent adaptive potentials. In cases where minor cytotypes disperse into less populated areas, these founding populations tend to establish in more challenging environments. In response to these challenges, they are likely to develop stress-adaptive strategies. Conversely, populations with major cytotypes may have adaptations that allow them to thrive in more favorable environments, capitalizing on their higher frequency within this area. Therefore, any variations in evolutionary transformations among cytotypes can be attributed to frequency-dependent phenomena, influenced by their original locations, historical biogeographic processes, and population-level eco-evolutionary drivers. While polyploidy can expedite modifications, it is less likely to determine the specific strategies that populations must evolve to successfully establish and radiate.

This perspective may elucidate the latitudinal patterns of polyploidy observed in spleenworts. Their diploid and polyploid species showed somewhat distinct latitudinal distributions. Regions at higher latitudes, such as the Nearctic and Palearctic, showed relatively higher diploid species richness, while the tropics hosted a greater proportion of polyploid species. This contrasts with prior observations in angiosperms wherein polyploids tend to be more prevalent at higher latitudes^{13,41,42}. More importantly, our findings challenge several traditional views regarding the causes of the uneven polyploid distribution in angiosperms, such as that polyploids possess greater colonization ability and that high rates of unreduced gametes and hybridization in fluctuating environments contribute to the prevalence of polyploidy in such regions^{13,17,18,43}.

We hypothesize that historical biogeography underpins the latitudinal occurrence pattern of polyploidy. In spleenworts, during the early stages of a recent radiation that occurred roughly 30 million years ago, diploids in the Nearctic and Palearctic regions are estimated to have gained a relative advantage over polyploids with ploidy levels higher than tetraploids^{19,23}. Conversely, in the southern continents, the original diploid forms were estimated to have become extinct much earlier due to the geologically earlier onset of glaciation and the associated disturbances in the Southern Hemisphere. Therefore, the observed latitudinal pattern in polyploid frequency in spleenworts has likely been shaped by the dominant cytotype

and their diversification in specific regions⁴⁴. This suggests that the latitudinal patterns in polyploid frequency are not primarily determined by inherent characteristics of polyploidy but are instead contingent on the historical biogeographic processes specific to particular lineages.

In addition, when assessing the geographic variation of polyploidy, confounding factors unrelated to polyploidy must be considered, including life strategies, drought tolerance, and herbivore resistance. These factors often exhibit their own distinct latitudinal patterns and could potentially confound our understanding of the biogeographic processes responsible for the latitudinal pattern of polyploidy frequency. For example, the higher prevalence of perennial herbs at higher latitudes, which often have a larger proportion of polyploid species⁵, could create misleading associations between polyploid frequency and latitude because functional traits of these lifeforms, rather than any inherent advantages of polyploidy, could be responsible for the observed latitudinal pattern. This consideration is particularly important because our understanding of polyploid biogeography is primarily based on angiosperm studies that involve comparisons across higher levels of taxonomic classification. These studies often do not focus on populations of closely related species although this is necessary to control confounding factors irrelevant to polyploidy. Therefore, further studies are required to disentangle the latitudinal patterns seen in angiosperm polyploidy from those of other confounding factors.

In the Northern Hemisphere's higher latitudes, new cytotypes may encounter greater challenges, primarily due to limited ecological niches for cytotype separation and higher introgression risk as species tend to expand their geographic ranges in line with Rapoport's rule^{45–47}. These factors may help explain the reduced overall ploidy richness of spleenworts in the Northern Hemisphere. As previously discussed, if diploid lineages in spleenworts possessed a frequency advantage in founder populations over those with higher ploidy levels during the initial stages of recent radiation in the Northern Hemisphere, the pressures of introgression are likely to have favored continued diversification of diploids over that of other cytotypes. In the case of angiosperms, perennial herbs, which tend to have high rates of polyploidy, usually dominate these regions. This implies that the higher prevalence of polyploidy in angiosperms in these regions results from the diversification or introgression of existing polyploid perennial herbs rather than broadly higher rates of polyploidization. Latitudinal patterns in polyploidy frequency therefore vary among plant lineages depending on the specific historical biogeographic processes and evolutionary dynamics within their respective areas.

The distributional patterns of intraspecific variations in ploidy levels, including the presence of intermediate odd ploidies, likely reflect dynamic processes involving the polyploid formation, establishment, and extinction⁴⁸. Mixed-ploidy species exhibited the highest species richness near 30° North, positioning this peak between those of polyploid and diploid species richness. Environmental variability, such as temperature seasonality, played a substantial role in shaping this distributional pattern. As ferns typically have low reproductive barriers, these areas with many mixed-ploidy species may represent conditions in which rare cytotypes recurrently emerge within a species through hybridization. Considering the historical latitudinal range shifts of biomes and major floral turnover in the

Northern Hemisphere, including those during the Paleocene-Eocene Thermal Maximum⁴⁹, these regions likely serve as secondary contact zones among differing cytotypes that promote the recurring formation of additional polyploids through frequent hybridization. Autopolyploidization, along with apomixis, may also be favored as mechanisms to restore fertility after hybridization⁵⁰. Thorough investigations into the spatial segregation patterns and genetic divergence of these mixed-ploidy species could provide insights into the influences of ecological conditions and biogeographic processes on the specific modes of polyploidization in these regions.

Specific ecosystems, such as deserts, present an intriguing case with notably high polyploidy diversity. This is likely attributable to the unique environmental stressors and population dynamics within these harsh environments. Interestingly, various cytotypes within these desert ecosystems showed a similar increasing trend in lineage numbers over time, which provides valuable opportunities to explore how different cytotypes can form and coexist in such regions. Of particular interest is the persistence of rare intermediate cytotypes such as triploidy and hexaploidy within desert ecosystems. Their presence suggests that intercytotype hybridizations have occurred across different ploidy levels in these environments, leading to the formation of these uncommon cytotypes. The demographic stochastic forces typical of harsh environments may also suppress the dominance of certain cytotypes, thereby facilitating the coexistence of multiple cytotypes³⁴. Studying the mechanisms that facilitate the coexistence of differing cytotypes, such as asexual reproduction and assortative mating, could be a focus of future research in these regions.

Biogeographic regions with many oceanic islands, such as Indomalaya, Australasia, and Oceania, showcased the persistence of species with high ploidy levels, including octoploids and dodecaploids. Oceanic islands often present unoccupied ecological niches and maintain stable climatic conditions with minimal disturbances^{51,52}, which are conducive to successful colonization by polyploid species. Furthermore, the isolation provided by these islands, along with their depauperate and less diverse communities, effectively reduces the risk of introgression from preexisting progenitors. Islands undergo distinct biogeographic processes, including taxon cycles that involve adaptive shifts driven by successive range expansions and contractions over time, as well as the progression rule patterns governing dispersal between adjacent islands. These processes can influence population dynamics, thus promoting the emergence and persistence of polyploid species. For instance, Hawaiian polyploid species show traces of ancient polyploid complexes with high basic chromosome numbers, suggesting the involvement of ancient polyploidization events in their evolutionary history⁵³. To deepen our understanding, future studies could explore the relationship between insularity and the prevalence of (paleo)polyploidy, which may also include atypical insular settings such as edaphic, montane, and anthropogenic islands.

Overall, our findings showed diverse aspects of polyploid richness influenced by various geographical and ecological factors. Location- and frequency-dependent phenomena in polyploid frequency helps bridge the gap among divergent hypotheses regarding when and where polyploidy either puts a lineage at risk or leads to success in diversification. In spleenworts, lineages in the Northern Hemisphere tend to

display relatively lower polyploid species richness, indicating a gradual reduction in polyploids likely due to a higher risk of extinction compared to diploids, which supports the extinction-risk hypothesis⁷. Conversely, tropical lineages tend to show a higher proportion of polyploids due to both increased diversification rates and lower extinction rates. These polyploids are primarily concentrated in biodiversity hotspots, supporting the high-gain path hypothesis². The observed uneven distribution of polyploid frequency can thus be explained by the regional differences in turnover rates between the formation, establishment, and extinction of polyploids, highlighting the importance of understanding geographical context and the complex role of polyploidy in plant evolution. Varying predispositions to polyploid evolution and varying accumulation timelines across lineages add further complexity when assessing the impacts of polyploidy in broader taxonomic groups.

Our findings also emphasize the pressing need for comprehensive exploration of polyploid dynamics across various spatiotemporal scales. Currently, cytological data is largely collected at the species level, rather than at the population level. This limitation presents challenges in connecting the distributional patterns of polyploidy with the underlying causal conditions and biogeographic processes. In particular, other pivotal factors thought to affect polyploidy distribution, including varying rates of unreduced gamete production, adaptive potentials, and invasiveness, are predominantly operating at the individual or population level. To establish a solid foundation for understanding the spatial dynamics of polyploidy, we recommend conducting cytological studies at finer spatial resolutions with a focus on micro-allopatric speciation within specific populations and their subsequent radiation into adjacent areas. This research should be conducted in conjunction with an exploration of mechanisms particular to polyploidy, such as minority cytotype exclusion. In addition, differential rates of formation and extinction within specific polyploidization modes can introduce biases into their biogeographic patterns, particularly concerning the recurring formation and rapid extinction of autopolyploids. Therefore, research with more precise time intervals over which polyploidization occurs could further advance our comprehension of the temporal dynamics of polyploid evolution. Lastly, future studies should consider addressing potential biases arising from uneven data distribution across lineages and geographic locations, particularly within tropical taxa.

Methods

Biogeographic regions

We hierarchically categorized biogeographic regions across multiple scales based on the Terrestrial Ecoregions of the World (TEOW) framework developed by Olson et al. (2001)⁵⁴ (www.worldwildlife.org/publications/terrestrial-ecoregions-of-the-world). At the broadest scale, we delineated eight distinct biogeographic realms: Antarctic, Oceania, Indomalaya, Australasia, the Neotropics, the Afrotropics, the Nearctic, and the Palearctic. On an intermediate level, we identified and defined 14 terrestrial biomes, including tundra, tropical and subtropical forests, temperate forests, deserts, and others. For the smallest scale, we identified 867 terrestrial ecoregions. These ecoregions were defined

based on the presence of distinct biotas and substantial immigration barriers, offering a finer-grained perspective on terrestrial biogeographic units⁵⁴.

Phylogenetic tree

We acquired a global phylogenetic tree containing 5,685 extant fern species using the R package *FTOL* v.1.4.0⁵⁵. This phylogenetic tree was constructed based on plastid DNA sequences through maximum likelihood estimation. The tree was rooted by designating *Zygnema*

circumcarinatum as an outgroup, and molecular dating was performed with the aid of 53 fossil constraints. We extracted the clade within the genus *Asplenium* using the R package *ape* v. 5.7–1⁵⁶. The final tree comprised 310 taxa in the genus *Asplenium*, representing approximately 44.3% of the total *Asplenium* species as recognized by Smith (2006)²⁰.

Occurrence data

We retrieved 1,304,516 georeferenced occurrence records from the Global Biodiversity Information Facility for the species listed in the phylogenetic data (GBIF Occurrence Download, <https://doi.org/10.15468/dl.rm2cj>). These records underwent filtering by GBIF querying systems to only include herbarium specimens with precise geospatial information. We further removed flagged entries featuring duplications, coordinate errors (e.g., country centroids and capitals, zero or identical coordinates, and locations of biodiversity institutions), as well as taxonomically unverified records. These filtering processes were conducted using the R package *CoordinateCleaner* v.2.0-20⁵⁷. To address geographical sampling bias and prevent model overfitting, we applied rarefaction to the spatially autocorrelated occurrences at a 10 km resolution using the R package *humboldt* v. 1.0.0.0420121⁵⁸. Furthermore, we visually inspected entries at the species level using ArcGIS Pro 2.8.3 to identify and remove any outliers. Outliers were determined based on the native ranges of each taxon identified using data from the Plants of the World Online of Royal Botanic gardens of Kew (<https://powo.science.kew.org/>). As a result, we retained 44,656 records representing 282 species. Accordingly, we removed taxa lacking adequate georeferenced occurrence records from the phylogenetic tree, leading to a total of 279 species (Supplementary Data 1).

Cytotype data

We collected information regarding chromosome numbers and ploidy levels for the species with both phylogenetic and occurrence data from multiple databases, including the Chromosome Counts Database (CCDB, <http://ccdb.tau.ac.il/>), the Index to Plant Chromosome Numbers database (IPCN, <http://legacy.tropicos.org/Project/IPCN>), as well as primary research papers (Supplementary Data 2). To ensure consistency, we normalized species names from each dataset with the occurrence data using the GBIF name matching tool (<https://www.gbif.org/tools/species-lookup/>). Taxonomic uncertainties were further resolved by referring to the Checklist of Ferns and Lycophytes of the World (<https://www.worldplants.de/world-plants-complete-list/complete-plant-list>). We manually excluded the

records with irregular chromosome counts, including those of hybrids and varieties. Ploidy levels were determined using the base chromosome number (x) of 36^{20} . Species were subsequently categorized into four groups: diploid ($2x$), mixed-ploidy species (species composed of multiple ploidy levels), polyploid (above $2x$), and unknown ploidy level. To streamline data analysis, we substituted the ploidy levels of $34x$, $35x$, $37x$ with diploids, as they are presumed to have undergone dysploidy. In addition, we treated apogamies as having identical ploidy levels in both gametophyte (n) and sporophyte stages ($2n$). We did not differentiate between allo- and autopolyploids due to the challenges associated with applying this distinction across the entire dataset. Complete cytotype information was available for 172 species. There were 157 taxa that possessed complete information on phylogeny, occurrence, and cytotypes, representing 56.3% of the surveyed dataset, while there were 122 with unknown cytotypes, comprising 43.7% of the total.

Explanatory data

We assessed 20 potential predictors, encompassing 17 environmental (first-order) and three biological (second-order) factors (Supplementary Data 3). The environmental factors included current climatic conditions, the magnitude of past climatic change, topographic variables, spatial heterogeneity, edaphic conditions, and anthropogenic impacts. We obtained current climate raster data and elevation at a 30 arc-second spatial resolution from WorldClim 2.0 (<https://www.worldclim.org/>). We estimated the magnitude of historical temperature and precipitation variations by computing the distance between a grid cell with past climate values representative of the Last Glacial Maximum (LGM, ca. 21ka) and an adjacent grid cell with current climate values matching those of the LGM period⁵⁹. We sourced both LGM and current (covering the period 1979–2013) temperature and precipitation raster data at a 10-minute resolution from PaleoClim (<http://www.paleoclim.org/>). We estimated the spatial heterogeneity of temperature, precipitation, and elevation by computing the coefficient of variation between a focal cell and its neighboring cells, using the Focal Statistics tool in ArcGIS Pro 2.8.3. Soil raster data with 250m spatial resolution were downloaded from the ISRIC Soil Data Hub, including pH, water content, cation exchange capacity, and organic carbon (<https://www.isric.org/>). The human footprint raster data, which estimated recent anthropogenic pressures on natural ecosystems by incorporating information about population density, human land use, and infrastructure, were obtained from the NASA Socioeconomic Data and Applications Centre (<https://earthdata.nasa.gov>). We homogenized these spatial data from various sources, and all values of these explanatory variables were summarized for each geographic unit using the Zonal Statistics as Table tool in ArcGIS Pro 2.8.3.

In our assessment of biotic variables, we included phylogenetic diversity (PD), phylogenetic endemism (PE), and nearest taxon index (NTI) for each ecoregion. To quantify phylogenetic diversity, we used the Faith's PD metric, which calculates the sum of branch lengths for all co-occurring species within a specific region⁶⁰. Higher PD values are attributed to communities comprising more evolutionarily divergent taxa with older evolutionary histories, whereas lower PD values denote assemblages with taxa that have more recent evolutionary origins. PE quantifies the extent to which a particular lineage is found exclusively within a particular ecoregion. We used the NTI to evaluate the phylogenetic structure of

communities, which helps determine whether species within a community are phylogenetically clustered or dispersed. This index is derived from the calculation of the mean nearest neighbor phylogenetic distance (MNTD). Higher values of NTI indicate phylogenetic clustering and lower values of NRI indicate phylogenetic overdispersion. Both PD and PE for each region were calculated using the *r* package *canaperv* v. 1.0.1⁶¹, and the PE was calculated using the *r* package *picante* v. 1.8.2⁶².

Spatial patterns of polyploid richness

We computed polyploid frequency (the proportion of polyploid species to the total surveyed species), ploidy richness (the number of different ploidy levels), and maximum ploidy level within each biogeographic region using the 'Pairwise Dissolve' tool in ArcGIS Pro 2.8.3. To assess the relationship between species richness and biogeographic variables, we extracted the values of latitude and elevation for each occurrence point datum using the 'Extract Multiple Values to Points' tool. The isolation values from waterbodies, as an indirect indicator of water stress, were calculated using the 'Near' tool, utilizing the base maps for world water bodies downloaded from ESRI Maps and Data group (<https://www.arcgis.com>). All scatter plots were generated using the *r* package *ggplot2* v.3.4.3⁶³.

Ploidy evolution inference

To provide an overview of polyploidy evolution within the spleenworts phylogeny and their geographic distribution, we estimated ploidy levels for ancestral nodes through stochastic character mapping, using the *r* package *phytools* v.1.9–16⁶⁴. Ploidy levels were treated as a discrete character, and we performed 1,000 simulations for each analysis using transition matrix values generated by an equal-rates (ER) model. Major subclades were identified following Schneider et al. (2017)²³, and the proportion of polyploid taxa in each subclade was estimated based on the current ploidy levels of each taxon (Supplementary Data 4). We determined the current geographic ranges of each species by aggregating their occurrences within specific biogeographic realms (Supplementary Data 5). To visualize the phylogenetic tree along with these traits, we utilized the *r* package *phytools* and the iTOL tool⁶⁵.

Lineage diversification over time and space

Based on the phylogenetic tree and cytotype information, we generated lineage-through-time plots using the *r* package *phytools* v.1.9–16⁶⁴. We calculated the γ test statistic to assess the variations in diversification patterns based on cytotype and across different biogeographic regions. The γ statistic is specifically designed to determine whether the observed pattern adheres to a standard normal distribution in trees generated under a pure-birth speciation model⁶⁶. We performed each test using 1,000 simulated pure-birth phylogenies for each analysis. In addition, we constructed a two-column matrix consisting of time points and the corresponding lineage counts, encompassing both overall data and a geographical subset using the *r* package *ape* v.5.7–1⁵⁶. With this matrix, we computed the Shannon diversity of polyploidy within all spleenwort lineages over specific time intervals. This polyploidy diversity analysis was conducted using the *r* package *vegan* v.2.6–4⁶⁷. In the case of mixed-ploidy species, we selected the highest ploidy level for analyses to streamline the methodology. In addition, we organized

major ecosystems to simplify the process of deconstructing data for lineage-through-time plots based on distinct ecosystem types. The temperate ecosystem category encompassed temperate grasslands, savannas and shrublands, as well as temperate conifer forests, temperate broadleaf and mixed forests, and boreal forests. In the tropical ecosystems, we included tropical and subtropical grasslands, savannas, and shrublands, along with coniferous forests, dry broadleaf forests, and moist broadleaf forests. Furthermore, we categorized the realms of Indomalaya, Oceania, and Australasia as island ecosystems.

Relative importance of explanatory variables

The relative importance of explanatory variables was assessed using boosted regression tree (BRT) models. BRT models utilize a boosting technique to adaptively combine large numbers of predictions derived from multiple regression decision trees, thus enhancing predictive accuracy. These models excel at capturing intricate nonlinear associations while demonstrating robustness in the presence of outliers and collinear predictor variables^{68,69}. Using the R package *dismo* v.1.3–14⁷⁰ and *ggBRT* v.0.0.0.9000⁷¹, we performed BRT modeling using the datasets divided into the four groups of diploids, polyploids, mixed-ploidy species, and species with unknown ploidy status. Each model was fitted with a Gaussian distribution, tree complexity of 5, learning rate of 0.01, and bag function of 0.7. Final models were validated using 10-fold cross-validation. The relative importance of each predictor variable was estimated based on the number of times a variable was selected for each decision tree and scaled to a percent, with a higher number indicating a stronger influence on the response^{69,72}. Differences in the relative importance of explanatory variables by the groups were visualized with a heatmap using the R package *ggplot2* v.3.4.3⁶³. The fitted functions of a BRT model that showed the effect of an explanatory variable on the response were displayed as partial dependence plots.

Declarations

Competing interests

The authors have no conflicts of interest associated with this publication.

Data availability

All the datasets used in this study are available in the Supplementary Dataset.

Supporting information

Appendix 1. Supplementary dataset 1–4.

Appendix 2. Supplementary tables and figures.

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Figures

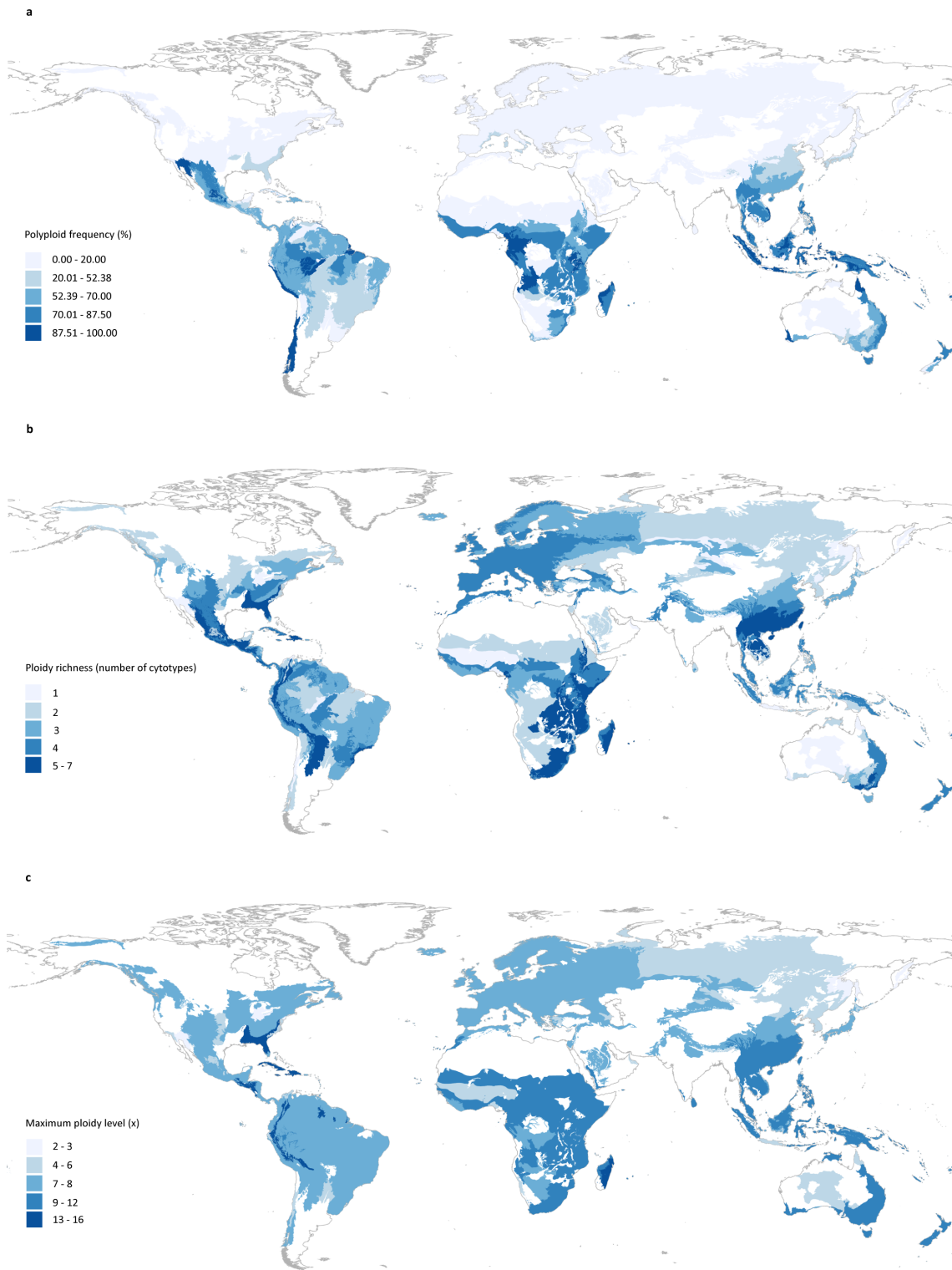


Figure 1

Global distribution of polyploidy in the spleenworts. **a**, Polyploid frequency (proportion of polyploid species relative to total surveyed species), **b**, Ploidy richness (number of different ploidy levels). **c**, Maximum ploidy level of sporophytes ($2n$) in each ecoregion. The legend is displayed using natural break intervals to more clearly categorize and represent the data.

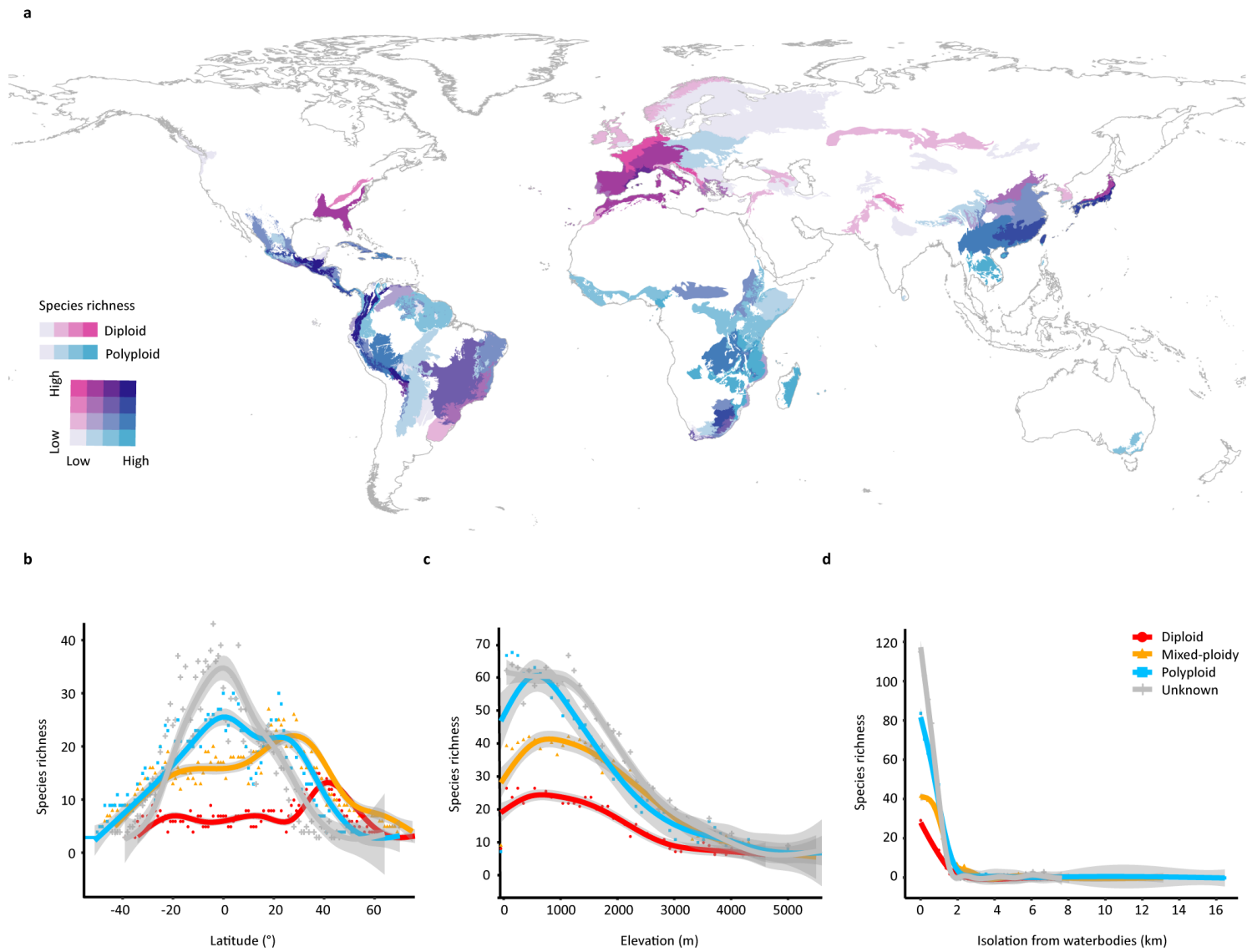


Figure 2

Global species richness of spleenworts along key biogeographic variables. **a**, Global bivariate map of diploid and polyploid species richness. **b**, Species richness by latitude, **c**, species richness by elevation. **d**, Species richness by isolation from waterbodies. The solid regression lines in the scatter plots depict the overall trend, while the shaded areas surrounding these lines indicate one standard deviation.

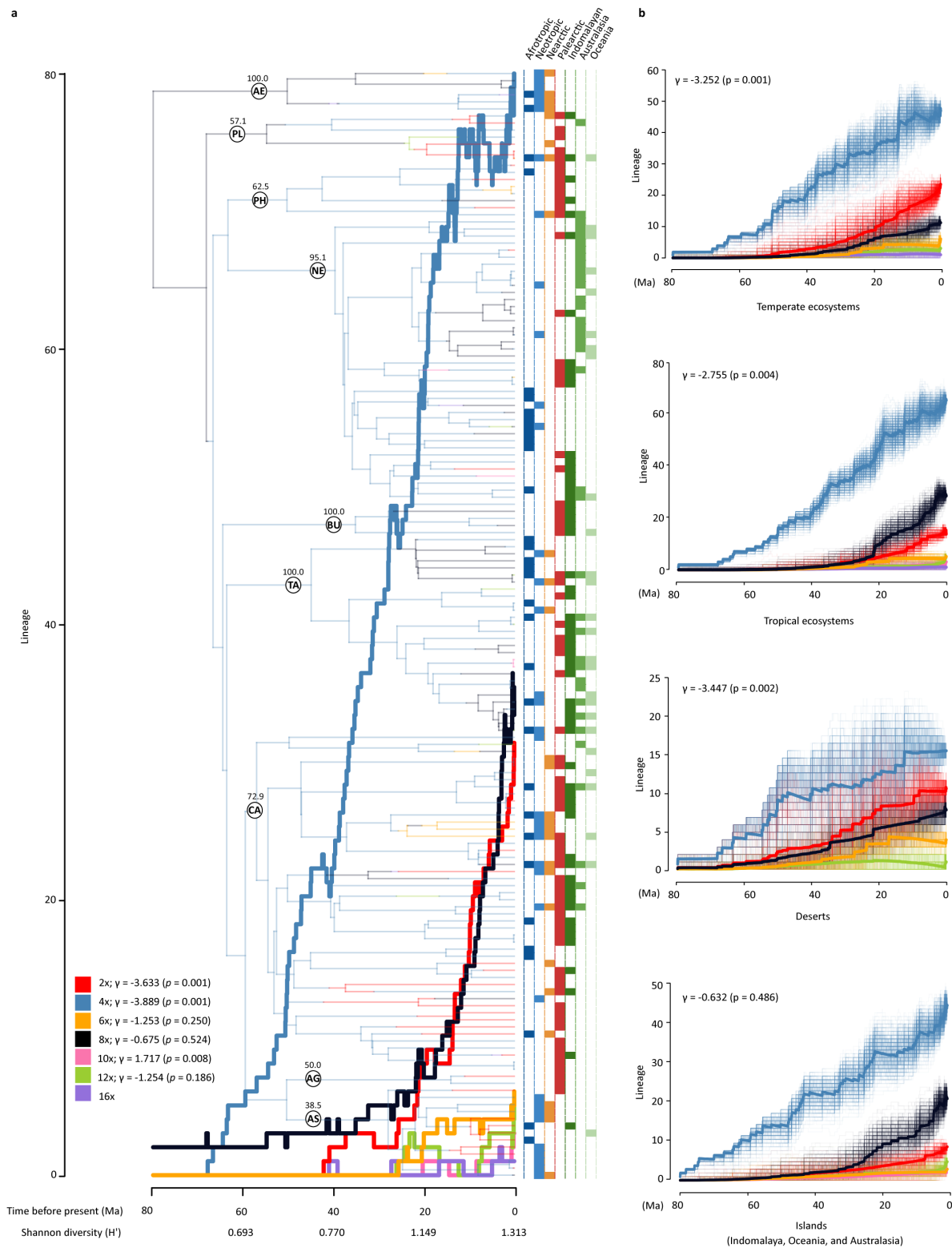


Figure 3

Lineage-through-time plots. **a**, Overall spleenworts lineages. The underlying phylogenetic tree incorporates a hypothesis of stochastic sporophyte ploidy evolution (colored branches). The posterior probabilities of each internal node generated from 1,000 stochastic character maps are shown in Supplementary Fig. 3. The geographic distribution of each taxon is shown by colored tiles positioned to the right of the branch tips. The numbers beneath the geological years on the x-axis denote the Shannon

diversity within all spleenwort lineages during specific time periods. Major subclades are denoted by circled two letter abbreviations, along with the proportion of polyploid lineages they contain, which is determined by the current ploidy levels of each taxon (Supplementary Table 1). AE, *Erosium*; PL, *Pleurosorus*; PH, *Phyllitis*; NE, *Neottopteris*; BU, *Bullatum*; TA, *Tarachia*; CA, *Camptosorus*; AG, *Aegaeum*; AS, *Asplenium*. **b**, Across major ecosystems. Each plot was generated by using 1,000 stochastic character maps.

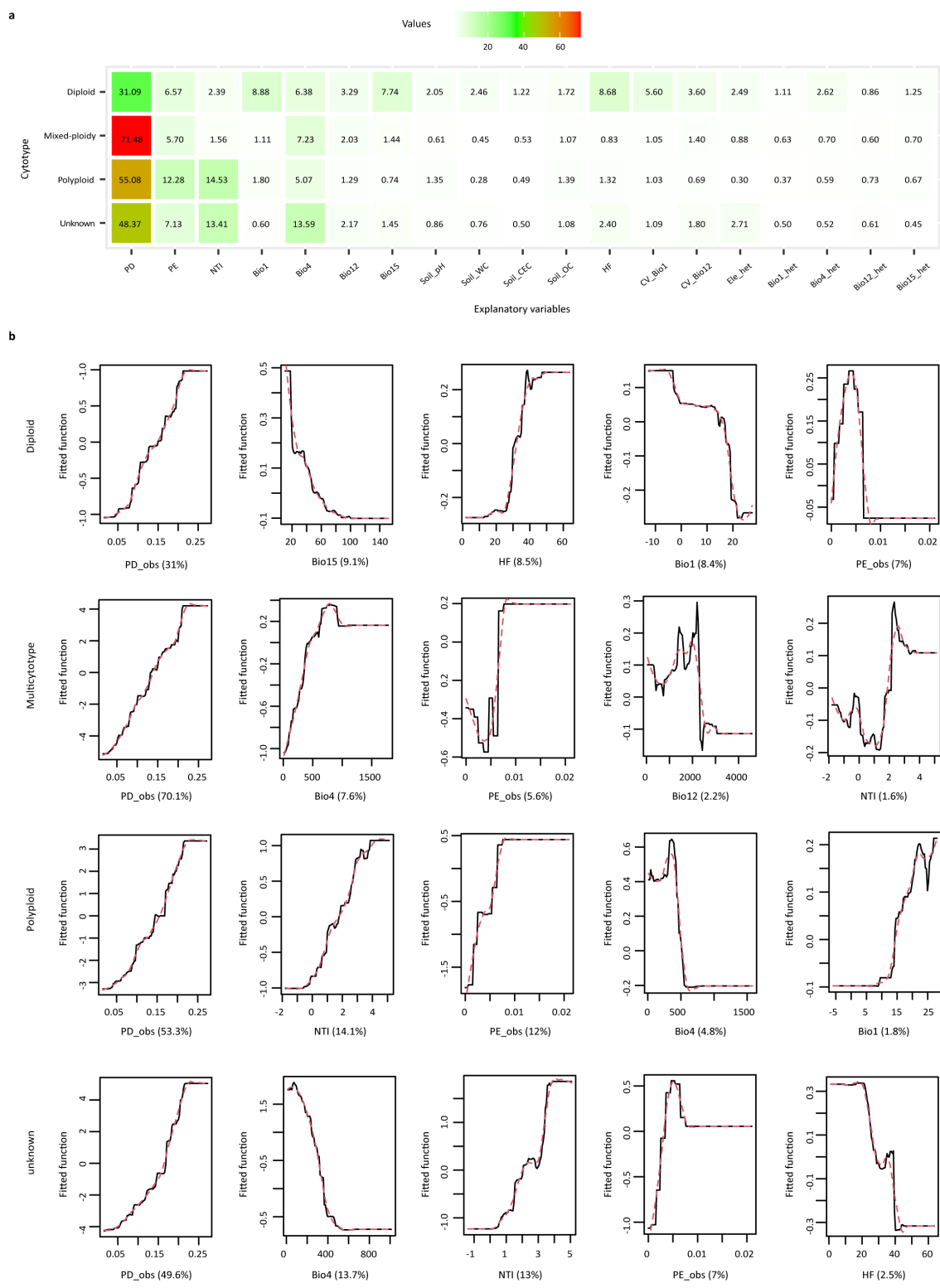


Figure 4

a, Relative importance of explanatory variables. **b**, Partial dependence plots for species richness patterns across cytotypes. The top five significant explanatory variables are shown with their relative importance values. The x-axis indicates the actual values and the unit of each variable. A smoothed version of the fitted function is added as dashed red lines. PD, phylogenetic diversity; PE, phylogenetic endemism; NTI, nearest taxon index; Bio1, annual mean temperature (°C); Bio4, temperature seasonality (°C); Bio12, annual precipitation (mm); Bio15, precipitation seasonality (mm); Soil_pH, soil pH; Soil_WC, soil water content (kPa), Soil_CEC, Soil Cation exchange capacity (cmol_c/kg); Soil_OC, soil organic carbon (%); HF, human footprint; CV_Bio1, average velocity of temperature change (m/year); CV_Bio12, average velocity of precipitation change (m/year); Ele_het, spatial heterogeneity of elevation (m); Bio1_het, spatial heterogeneity of annual temperature (°C); Bio4_het, spatial heterogeneity of annual precipitation (mm).

Supplementary Files

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