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Contrasting genome-size constraints relate to divergent elemental strategies in bryophytes and tracheophytes

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Abstract

Genome size (GS) varies widely across plant lineages, yet its ecological consequences remain unclear. Here, we first examined how GS and climatic variables relate to the size of the reproductive unit and biogeochemical niche (i.e., elemental hypervolume) in bryophytes and tracheophytes (vascular plants). GS is positively associated with pollen and seed size in vascular plants but does not influence spore size in bryophytes. Moreover, GS was positively related to elemental flexibility in bryophytes but not in vascular plants, whereas climatic factors showed the opposite pattern. Elemental and climatic hypervolumes are coupled in vascular plants but decoupled in bryophytes. Overall, regardless of whether GS is an adaptive trait or not, GS can impose ecological and physiological constraints through lineage-specific effects on propagule size and physiological flexibility, reflecting the distinct evolutionary pathways followed by bryophytes and vascular plants during the colonization of land.

Introduction

Genome size (GS) varies approximately 2,440-fold across plants, and much of this variation is caused by polyploidy and the accumulation of repetitive DNA sequences[1–3]. Neutral theories of GS evolution consider GS variation largely as a byproduct of evolutionary processes with limited adaptive significance[4,5]. Alternatively, the “functional” or “(mal)adaptive” hypothesis proposes that GS can influence organismal performance and ecological strategies through its effects on phenotypic and physiological traits[6,7]. Although GS simply represents the total amount of nuclear DNA, it has long been associated with fundamental cellular and developmental properties, including cell size, cell division rates, and developmental timing[8–11]. Through these effects, GS may influence a wide range of phenotypic traits, such as body size, growth rate, and other cell size-related characteristics, potentially shaping species life-history strategies, ecological interactions, and fitness under different environmental conditions[9,12,13]. Despite increasing interest in GS as a potential functional trait, its ecological and evolutionary consequences remain incompletely understood.

Plant colonization of terrestrial habitats was a defining event in Earth’s history, profoundly reshaping the biosphere. This transition gave rise to two major land-plant lineages, bryophytes and tracheophytes (vascular plants), which followed distinct evolutionary pathways during terrestrialization[14]. Bryophytes retain a gametophyte-dominated life cycle, a nutritionally dependent sporophyte, and limited internal regulation of water and nutrient transport, whereas vascular plants evolved dominant autonomous sporophytes, vascular tissues, and stronger physiological control over resource acquisition[15–20]. These contrasting strategies are also reflected in their reproductive propagules. Bryophytes disperse primarily through spores, whereas vascular plants evolved pollen and seeds. Such differences in life-cycle organization, physiological regulation, and propagule biology may influence how GS scales from cellular properties to reproductive traits, physiological flexibility, and ecological niche dimensions. Consequently, bryophytes and vascular plants provide a useful framework for testing whether the ecological consequences of GS are conserved across land-plant lineages.

Previous studies have linked GS to a variety of morphological traits, particularly in vascular plants. For example, the increase in GS is associated with increases in the minimum guard cell size, leading to larger stomatal pore sizes and lower stomatal density, which can reduce water and CO_2 exchange, and leaf maximum photosynthetic rate[21,22]. Larger GS are often associated with larger cell sizes and seed sizes[23–25]. These relationships are commonly interpreted as consequences of cell-size scaling effects, whereby increases in nuclear DNA content constrain minimum cell size and propagate from the genomic to the organ level, the so-called nucleotypic effect[26,27]. Even so, it remains unclear whether this scaling relationship translates into broader ecological or functional consequences. On the other hand, evidence for comparable relationships in bryophytes is still scarce. Because bryophyte sporophytes are developmentally and nutritionally constrained by the gametophyte, it remains unclear whether GS can influence the size of bryophyte reproductive units (spores). Consequently, whether GS-trait relationships observed in vascular plants are conserved across all land plant lineages or are instead lineage specific is not clear.

Beyond morphology, some research has shown that GS can influence growth rates, metabolic demands, and resource-use efficiency of vascular plants[9,28–30]. For example, GS is negatively correlated with potential carbon use efficiency and leaf elongation maximum rate during nighttime, all of which are closely linked to nutrient acquisition and metabolic activity[29,30]. Because plant metabolism ultimately depends on the acquisition and allocation of chemical elements, GS-related physiological constraints may also be reflected in species elemental composition. Elemental traits, such as the concentration of carbon, nitrogen, phosphorus and other elements, often referred to as *elementomes*, reflect fundamental trade-offs in plant function and environmental interaction[31,32]. The multidimensional variation of elemental composition within species, quantified as elemental hypervolumes, can be used to describe species elemental flexibility and thus their biogeochemical niche[31,33–36]. Similarly, climatic hypervolumes describe the range of climatic conditions occupied by species. Integrating these hypervolume-based approaches with GS variation provides a powerful framework for examining how GS may relate to both functional strategies and climatic niche breadth. In addition to GS and physiological constraints, reproductive unit size may also influence elemental strategies through their effects on dispersal. Smaller seeds or spores often disperse farther from their parental environments than larger propagules, potentially exposing species to a broader range of environmental conditions[37,38]. Such dispersal-mediated exposure could, in principle, favor greater elemental flexibility in plants with smaller GS, although this hypothesis has never been evaluated in a multidimensional elemental context. Despite increasing interest in GS and plant functional strategies, no studies have explicitly linked GS to elemental hypervolumes or examined how elemental and climatic hypervolumes relate across major plant lineages.

Here, we address these gaps by conducting a phylogenetic comparative analysis of GS, reproductive unit sizes (seed size, pollen size, and spore size), elemental and climatic hypervolumes in bryophytes and vascular plants. We hypothesized that GS has important ecological consequences across land plants, regardless of whether it is itself adaptive. Specifically, we expect that (1) GS would be positively

associated with reproductive unit size (seeds, pollen, and spores) because of its links to cell size and developmental scaling, and reproductive unit size is associated with climatic and elemental space through dispersal-related processes (2) GS would be associated with elemental flexibility and climatic niche breadth; and (3) these relationships would differ between bryophytes and vascular plants because of their contrasting life histories, physiological organization, and reproductive strategies.

Results

We found that genome size (GS), climatic conditions and the elemental composition of photosynthetic tissue were generally important in explaining the size of bryophyte spores and vascular plant seed and pollen (Figure 1). Bryophyte spore size was positively associated with tissue Ca concentration and negatively associated with Mg concentration (Figure 1 a). Bryophyte GS was not significantly associated with spore size, but species with higher sporophyte frequency showed smaller spore sizes. Instead, in vascular plants, seed size was strongly and positively correlated with GS, precipitation seasonality and mean annual precipitation (Figure 1 b). Pollen size was positively related to GS and leaf Ca concentrations and negatively related to leaf P and Mg (Figure 1 c). Variance partitioning further highlighted contrasting drivers among reproductive units (Figure 1 d-f). Spore size variation was dominated by phylogenetic effects (30.6%), with comparatively minor contributions from elemental traits and GS (11.2% and 8.35%, Figure 1 d). Seed size variation was overwhelmingly explained by phylogeny (59.1%), with only small independent effects of climatic variables and GS (5.62% and 5.29%, Figure 1 e). In contrast, pollen size variation was primarily explained by elemental traits and GS (33.5% and 22.5%), whereas phylogenetic effects were relatively weak (14.9%, Figure 1 f). Specifically, we found no significant relationship between GS and spore size in bryophytes (Figure 1g), whereas GS was positively associated with both seed mass ($\beta = 1.39 \pm 0.42$, $P < 0.01$; Figure 1h) and pollen size ($\beta = 0.58 \pm 0.13$, $P < 0.001$; Figure 1i) in vascular plants.

Phylogenetic patterns revealed substantial variation in both elemental hypervolumes and climatic hypervolumes across species within the two major clades of land plants (Figure 2a–b). Species-level hypervolumes showed pronounced heterogeneity within each clade, with no clear phylogenetic clustering of either elemental or climatic hypervolume size. Clade-level comparisons revealed no significant difference in elemental hypervolume between bryophytes and vascular plants (Wilcox test, $P = 0.26$, Figure 2c), and this pattern remained unchanged when different numbers of elements were used to estimate bryophyte hypervolumes (Figure S1). In contrast, climatic hypervolume differed significantly between clades (Wilcox test, $P < 0.001$, Fig. 2d), with bryophytes exhibiting broader climatic niche breadth than vascular plants. In vascular plants, climatic hypervolume sizes exhibited a positive relationship with elemental hypervolume sizes ($\beta = 0.50 \pm 0.13$, $P < 0.001$; Figure 3) while no significant relationship was observed in bryophytes, despite the observed negative trend (Figure 3).

Bryophyte species differed markedly in their elemental hypervolume, as evidenced by their differences in multivariate elemental space and associated hypervolumes (Figure 4a). Species-level elemental spaces along the first two principal component axes revealed substantial interspecific variation in both the

position and spread of elemental values (Figure 4a). Bryophyte elemental hypervolume sizes increased significantly with GS (β = 0.43 ± 0.17, *P* < 0.05; Figure 4b). In contrast, elemental hypervolume sizes declined with increasing temperature seasonality (β = -1.33 ± 0.43, *P* < 0.01; Figure 4c) and MAT (β = -0.91 ± 0.35, *P* < 0.05; Figure 4d). Like bryophytes species, vascular plants showed a substantial interspecific variation as well (Figure 5a). Conversely, elemental hypervolume sizes did not show a significant relationship with GS (Figure 5b). The elemental hypervolume increased with increasing temperature seasonality (β = 0.98 ± 0.21, *P* < 0.001; Figure 5c) and MAT (β = 1.02 ± 0.19, *P* < 0.001; Figure 5d). For bryophytes, elemental hypervolumes were recalculated using different number of elements and elemental combination, the results remained unchanged (Figures S2-S6).

Discussion

The emergence of plants on land was a major evolutionary transition that dramatically transformed Earth's biosphere and ecosystem processes at a global scale. Our results show that the early divergence of the two lineages of land plants resulted in contrasting relationships between the size of the genome, the elemental composition, the size of the reproductive and dispersal units, and the climatic niches of vascular and non-vascular plant species. In bryophytes and vascular plants, GS was associated with traits linked to elemental flexibility, reproductive units, and climatic space relationships, suggesting that GS may impose functional constraints on organismal performance. In this sense, GS may not necessarily evolve as an adaptive trait itself, but it can still shape ecological strategies by influencing physiological and developmental states.

Relationships between genome and reproductive unit sizes

Partial consistent with the first hypothesis, our results indicated that GS significantly and positively affects pollen and seed size in vascular plants whereas it does not influence spore size in bryophytes (Figure 1 a-c, g-i). Although the number of species with complete records for seed and pollen size in our dataset is relatively limited (54 and 21 species, respectively), our findings are consistent with previously published studies in vascular plants[24,39,40], supporting the robustness and reliability of our results. Because reproductive unit size is also likely influenced by plant biomass and allometric scaling, these relationships should be interpreted as broad lineage-level associations rather than direct GS effects alone. This contrast nevertheless underscores the importance of life history in mediating GS and phenotype relationships. In vascular plants, reproductive units develop within an independent, nutritionally autonomous sporophyte, allowing GS-driven increase in cell size and developmental complexity to scale up to organ level and to influence pollen and seed size[26]. In bryophytes, however, sporophyte development is tightly constrained by the gametophyte-dominated life cycle[20]. One possibility is that bryophyte spores already exceed the minimum size constraints imposed by GS, thereby reducing the detectable influence of GS variation on spore dimensions. In addition, although GS is expected to influence cell size and thus set a lower bound on organ dimensions through scaling effects, sporophytes remain physiologically dependent on the parental gametophyte for C and nutrient supply. This dependency imposes an additional resource-based constraint on growth, effectively limiting the

upper size that sporophytes can attain, and hence their spores too. As a result, increases in GS may not translate into larger reproductive structures. This decoupling highlights how developmental constraints can potentially suppress expected GS effects, emphasizing that GS-trait scaling relationships cannot be generalized across terrestrial plant lineages without considering life history traits.

Reproductive traits and the coordination of climatic and elemental hypervolume sizes

Contrary to our expectation that smaller spore size and seed size will exhibit larger elemental or climatic hypervolumes, we found that, in vascular plants, seed size was marginally and positively associated with elemental hypervolumes (Figure S7), suggesting that larger investments in individual reproductive units are associated with greater flexibility in elemental composition. One possible explanation for this weak positive relationship between seed size and elemental hypervolume size is that dispersal distance is influenced by multiple factors, including seed release height, growth form, and dispersal syndrome, in addition to seed size[37,38,41]. Consequently, seed size alone provides only a limited predictor of elemental and climatic strategies. In bryophytes, spore size showed no association with either elemental or climatic hypervolumes (Figure S7 c, d). Although our study encompassed a broad range of climatic conditions, including semi-arid Mediterranean, temperate, and boreal environments, as well as diverse lithologies, all samples were collected within a single geographic region. It therefore remains possible that relationships between spore size and elemental or climatic hypervolumes may emerge at broader spatial scales, where dispersal limitation, historical processes, and stronger climatic contrasts operate. Expanding sampling across larger geographic scales may help clarify whether the absence of association observed here reflects a general feature of bryophyte life history strategies or is scale dependent.

Recent studies have explored the biogeochemical niche hypothesis across a range of ecosystems, highlighting how species occupy distinct positions in multivariate elemental space[34,35,42–44]. However, despite this progress, the relationship between multidimensional elemental space and multidimensional climatic space remains largely unexplored. Our study revealed different relationships between climatic and elemental hypervolumes across lineages (Figure 3). In vascular plants, these hypervolumes are positively coupled: species occupying broader climatic niches also exhibit broader elemental strategies. This coordination reflects an adaptive strategy in which climatic expansion is supported by increased elemental space, enabling successful colonization across heterogeneous environments. In bryophytes, however, no significant relationship was detected, suggesting a decoupling between climatic niche breadth and elemental flexibility. This decoupling suggests that broader climatic occupancy in bryophytes does not necessarily require expanded elemental strategies, consistent with the idea that bryophytes rely more strongly on small scale environmental heterogeneity and microhabitat specialization[45,46]. These contrasting patterns point to a fundamentally different mode of ecological adaptation in bryophytes compared to vascular plants, emphasizing microenvironmental specialization rather than coordinated elemental expansion.

Opposite relationships between genome and elemental hypervolume sizes

Our second hypothesis received partial support in bryophytes but not in vascular plants. Genome size was positively associated with elemental hypervolume sizes in bryophytes, indicating increased elemental flexibility with larger genomes (Figure 4b). Since elemental hypervolume reflects flexibility in tissue elemental composition, this association should be closely related to physiological processes such as nutrient uptake, ion balance, metabolic allocation, and elemental homeostasis. In contrast, structural differentiation would require direct evidence from morphological or anatomical traits, such as tissue thickness, cell-wall investment, or growth form. Thus, our results suggest that GS in bryophytes is associated with greater elemental, and potentially physiological, flexibility, rather than providing direct evidence for structural changes like for spore size. Because bryophytes lack real vascular tissues (leaves, stems, and roots) and acquire nutrients largely across their surface, their elemental composition is tightly coupled to local climatic conditions[16,17,19,20,34]. Increased GS may therefore contribute to facilitate broader elemental strategies that buffer metabolic demands under variable microenvironmental conditions. However, the genomic mechanisms underlying this relationship remain unclear and may differ from those reported in vascular plants, where genome expansion is often dominated by non-coding DNA. In contrast, no significant relationship between GS and elemental hypervolume size was detected in vascular plants (Figure 5b). Larger GS species of vascular plants are often linked to slower growth rates, larger cells, and higher metabolic costs, which may support more conservative and tightly regulated nutrient-use strategies[9,13,23,30]. The vascular tissues enable efficient transport and internal regulation of resources, which may strengthen elemental homeostasis by buffering variation in nutrient availability and maintaining relatively stable tissue elemental composition. This stronger homeostatic control could reduce the elemental flexibility of the species. If this interpretation is correct, similar or even stronger relationships might be expected in other lineages with limited internal regulation, such as algae and charophytes, whereas groups characterized by strong homeostatic control may exhibit weaker associations between GS and elemental flexibility.

Climatic controls on elemental hypervolume sizes differ between lineages

Consistent to our third hypothesis, both MAT and temperature seasonality exert contrasting effects on elemental hypervolumes in bryophytes and vascular plants (Figure 4 c, d; Figure 5 c, d). In bryophytes, increasing MAT and temperature seasonality constrain elemental hypervolumes, potentially reflecting more stringent physiological and thermal requirements compared to those with larger elemental flexibility. Due to their poikilohydric nature, bryophytes rapidly lose water when temperature increases and relative humidity declines, leading to direct exposure of cellular structures to thermal and desiccation stress[47,48]. For many temperate bryophyte species, tolerance to elevated temperatures is therefore limited, with long-term decline expected when annual temperatures increase ~2–3 °C above standard ambient conditions[47]. Additionally, the lack of stomata and vascular tissues results in direct exposure to external environmental fluctuations. Consequently, bryophytes have no capacity to modulate water and nutrient exchanges through transpiration or radical systems, which may limit the possible elemental space occupied to cope with environmental conditions of high temperature and seasonality. Rather than compensating through increased elemental flexibility, bryophytes appear to have adapted to

thermal stress by reducing their elemental space, probably remaining only the elemental solutions capable of withstanding those conditions. By contrast, vascular plants show expanded elemental hypervolumes under higher MAT and greater temperature seasonality (Figure 5 c, d). The vascular tissues, stomatal regulation, and complex root systems allow vascular plants to actively regulate water and nutrient acquisition, decoupling internal elemental dynamics from external climatic variability. Consequently, vascular plants may respond to warmer and more seasonal environments not by narrowing their elemental composition, but by exploiting a broader range of resource-use strategies. Higher temperatures are often associated with increased productivity, growth rates, and competitive interactions, potentially promoting greater differentiation in nutrient acquisition and allocation strategies among individuals and species[49,50]. Such processes could contribute to the observed expansion of elemental hypervolumes under warmer and more seasonal climatic conditions.

Limitation and Future Research

Despite the broad environmental variation represented in our dataset, the bryophyte analyses remain based on a regional sampling design. Consequently, the observed relationships should not be interpreted as definitive evidence for all bryophyte lineages or biogeographic regions. Rather than providing definitive evidence for lineage-wide ecological strategies, our results offer initial support for the hypothesis that bryophytes and vascular plants may have followed distinct terrestrialization-associated pathways, with potentially different relationships among genome architecture, physiology, and environmental specialization. Future studies should also integrate experiments, cell-level measurements, and macroevolutionary models to further disentangle causal mechanisms linking GS, physiology, and ecological adaptation. Extending this framework across additional lineages and biogeographic regions will be critical for introducing GS into ecology research and may improve our understanding of how genome-related constraints shape plant responses to environmental change.

Methods

Bryophyte data collection and laboratory analyses

Between August 2020 and May 2024, bryophyte samples were collected from 250 sites distributed throughout the northeastern Iberian Peninsula and the Balearic Islands (Figure S8). The study area covers both lowland and upland regions of Catalonia, encompassing five mountain ranges: the Littoral Mountain Range, the Montseny-Guilleries Massif, the Lluçanès Plateau, the volcanic area of La Garrotxa, and the eastern Pyrenees. The elevation of the locations ranged from 0 to 2300 m. The region exhibits a predominantly Mediterranean climate, which varies from humid and sub-humid conditions in the central and northwestern areas, to a maritime Mediterranean type along the southern coast, and to a Mediterranean pre-Pyrenean regime in the northern zones. Across all sampling sites, mean annual temperature ranged from 2.1 to 16.8 °C, and annual precipitation from 501 to 1231 mm yr^{-1}. Although the bryophytes were collected from a relatively small region (NE Iberian Peninsula), all species have distributions that extend across the continental scale. Furthermore, the environmental gradient across

our sampling locations spans semi-arid, Mediterranean, temperate and boreal ecosystems. The broad geographic distributions of the studied species together with the substantial environmental variability included in our dataset, strengthens the generalizability of our results beyond the study region.

Field sampling of bryophytes

A total of 412 bryophyte individuals, representing 107 species, were collected. Among these, 310 samples (90 species) originated from terrestrial habitats and 102 (26 species) from aquatic or semi-aquatic environments (hereafter collectively referred to as hygrophytic bryophytes). Terrestrial bryophytes were sampled from a range of substrates, including tree bark (epiphytic forms), rocks, and soil, across multiple habitat types such as grasslands and both evergreen and deciduous forests. Hygrophytic bryophytes were gathered from semi-natural springs and groundwater discharge areas, where they were either submerged or located within the splash zone. In these environments, contact with water was maintained year-round, except during periods of freezing or extreme drought. The heterogeneous lithology characterizing these springs gave rise to a broad spectrum of water chemical conditions for hygrophytic species[51]. Each sampling location was georeferenced using a GPS device. With these coordinates, we extracted climatic data for mean annual temperature (MAT), mean annual precipitation (MAP), Isothermality, temperature seasonality, and precipitation seasonality from WorldClim 2.0[52]. Temperature and precipitation seasonality were expressed as the coefficient of variation of monthly values to assess how different temperature and precipitation were throughout the year.

Elemental analyses of bryophytes

To determine the elemental composition of terrestrial bryophytes, samples were first thoroughly cleaned with distilled water until all visible particles were removed. After drying at 60 °C to constant weight, the samples were ground to a fine powder using a ball mill (MM400, Retsch, Germany). Concentrations of carbon (C) and nitrogen (N), as well as the stable isotope ratios $\delta^{13}C$ and $\delta^{15}N$, were determined by isotope-ratio mass spectrometry (IRMS) using a Flash EA1112 and TC/EA elemental analyzer coupled to a Delta C stable-isotope mass spectrometer via a ConFlo III interface (Thermo Finnigan, Thermo Electron Corporation, Bremen, Germany). The concentrations of 19 additional elements, including macro- and micro-nutrients and trace elements (P, K, S, Ca, Mg, Na, B, Fe, Al, Cu, Mn, and Zn), were measured using inductively coupled plasma optical emission/mass spectrometry (ICP-OES/MS; ELAN 600 and Optima 8300, Perkin Elmer, Waltham, Massachusetts, USA). Prior to analysis, samples were digested overnight at 90 °C with nitric acid and hydrogen peroxide (2:1, v/v).

Aquatic bryophytes were originally collected for a leaching experiment. This is why for aquatic bryophytes total elemental concentrations were calculated as the sum of the elemental concentrations in the bryophyte tissue and their corresponding leachates. Bryophyte samples were first maintained at room temperature for 24 h, then rinsed under low-intensity agitation for 10 min with distilled water, and subsequently dried at 50 °C for 48 h. To extract leachates, samples were rehydrated in 100 mL of

distilled water for 1 h with gentle agitation. After leachate extraction, samples encrusted with $CaCO_3$ were soaked in acetic acid (pH 2.7) for 1 h to remove carbonate deposits. Elemental concentrations in the leachates, except for C and N, were determined using ICP-OES/MS (ELAN 600 and Optima 8300, Perkin Elmer, Waltham, Massachusetts, USA). Leachate total C and N concentrations were determined with an Analytik Jena multi-N/C 3100 analyzer (Analytik Jena, Jena, Germany). Following leachate extraction, the elemental concentrations of the bryophyte tissue were determined using the same procedures as for terrestrial bryophytes. Total elemental composition of each sample was calculated by summing the elemental masses extracted from bryophyte tissue (concentration × sample dry weight) and their corresponding leachates (concentration × 100 mL) and then divided by the total dry weight of the sample.

Bryophyte genome size and traits

The maximum and minimum spore diameters for each species were obtained from BRYOATT[53] and the Bryophytes of Europe Traits (BET) database[54]. The spore size was estimated as the average of the maximum and minimum spore diameters. For the missing data maximum and minimum of spore diameters (3.7% missing rate), we imputed them with "*funspace*" package in R[55]. Genome size data were retrieved from the GOAT database, expressed as *C-values*[56]. It should be noted that in GOAT database, not all GS estimates were measured directly, in our analysis, only ten out of 107 species were inferred from ancestral or descendant taxa (9.3%). Sporophyte frequency of species was also compiled from Bryophytes of Europe Traits (BET) database[54]. Sporophyte frequency was assessed using a four-level categorical scale (0–3), reflecting how commonly sporophytes are observed (0 = unknown, 1 = rare, 2 = occasional, 3 = common/frequent).

Phylogenetic tree building for bryophytes

The phylogenetic tree was constructed for the species we collected, including 93 moss, one hornwort and 13 liverwort species. The hornwort species (*Anthoceros punctatus*) was designated as an outgroup during tree construction. To obtain gene sequences, we used the R package "rentrez" to retrieve data from GenBank[57], selecting 1 nuclear gene (5.8S) and three plastid genes (rbcL, rps4, and TrnL) (Table S1). These four genes are among the most conserved fragments in the evolutionary process[58]. For species without available sequences in GenBank, we substituted them with sequences from closely related species within the same genus (*Thuidium tamariscium* and *Orthotrichum diphanum* substituting, respectively *Thuidium thermophilum* and *Orthotrichum hallii*). Sequence alignment was performed using MAFFT v7[59,60], and poorly aligned regions were removed using G-blocks with a less stringent selection[61]. We first constructed phylogenetic trees for each gene separately and manually removed long or biologically unreasonable branch sequences. After this sequence cleaning step, the four aligned gene sequences were concatenated. A partition file was generated for the following steps. The final phylogenetic tree was constructed using IQ-TREE web server to generate a consensus tree[62]. Given the different evolutionary rates of nuclear and plastid genes, we used concatenated sequences and partition

file to determine the optimal substitution model for each partition based on the Bayesian Information Criterion (BIC) in IQ-TREE. Finally, the models of TN+F+I+G4, TN+F+G4, K3Pu+F+G4, and TN+F+G4 were selected for 5.8S, rbcL, rps4, TrnL sequences, respectively. The node support analysis was conducted based on 10,000 bootstrap replicates (Ultrafast). The single branch tests were conducted using SH-aLRT with 1000 replications. Each node in the consensus tree was strongly supported, ensuring the robustness of the inferred phylogenetic relationships. We used the R packages phytools[63] and ape[64] to integrate the phylogenetic tree into the analyses.

Data collection of vascular plants

Foliar elemental data were compiled from the TRY Plant Trait Database and peer-reviewed publications[65]. All foliar element records were georeferenced, allowing the extraction of corresponding climatic variables from Worldclimate 2.0[52]. Because elemental ecology is a relatively new field, substantial data gaps remain in existing databases, particularly for micronutrients and trace elements. Therefore, our vascular plant analysis focused on C, N, P, K, Ca, and S, which are widely available (compared to bryophytes, for which we used a larger number of elements, see section 2.1.2 above). Finally, 20748 individuals were gathered, referring to 359 species.

Seed size (mass) and pollen size (length) data were obtained from the TRY database[65]. For each species, mean values were calculated and subsequently integrated with the foliar elemental dataset. During data compilation, all species names were taxonomically standardized to ensure consistency across datasets using the Plant List database through the R package "U.Taxonstand"[66]. A total of 54 and 21 species with full elements data and related climatic data were finally collected for seed size and pollen size, respectively. The phylogenetic tree was pruned from a PhytoPhylo megaphylogeny using "V. PhyloMaker2" package to match the species included in our analysis[67].

Statistical analysis

We log10-transformed elemental data (P, K, S, Ca, Mg, Na, B, Fe, Al, Cu, Mn, and Zn), GS, and spore size of bryophytes to reduce skewness in their distributions and then standardized prior to subsequent analyses. We used the *phylolm* function in "phylolm" package to build the saturated models[68]. The predictors we included were climatic variables (MAT, mean annual precipitation, Isothermality, temperature seasonality, and precipitation seasonality), elemental data, as well as habitats (terrestrial or aquatic), genome size and spore frequency. The *phylostep* function in "phylolm" package was used to conduct stepwise regression to explore the best fitted model[68]. The final model was achieved by removing the least significant terms from the full model, in a backwards-forwards direction process until the lowest AICc was achieved. All predictors retained in the final model were further evaluated for multicollinearity using the variance inflation factor (VIF). All variables showed VIF < 10 in the final models[69]. The normality assumption of the final model was assessed using normal Q-Q plots of the regression residuals. Relationships between variables were visualised using partial residuals plots by means of the *visreg* function in "visreg" v.2.7.0 R package[70]. Furthermore, we employed the "phylolm.hp"

package to partition the relative contributions of climatic factors, phylogenetic signal, GS, and elements[71]. Models for vascular plants followed the same procedures as those with bryophytes, and included, as predictors, elemental data (C, N, P, K, Ca, and S), climatic variables (the same with bryophytes), as well as GS.

To quantify the elemental flexibility of each bryophyte and vascular plant species, we used multivariate hypervolumes. All elemental concentrations were log10 transformed. Principal component analysis (PCA) was performed to reduce dimensionality and to eliminate collinearity among elemental variables. We then retained the first three PC axes (k = 3) for hypervolume computation, which together explained at least approximately 68% of the total variance. We did not include additional PC axes to avoid introducing noise and numerical instability rather than biologically meaningful variation. For each species, we calculated the three-dimensional hypervolume in this PCA space using a covariance-based hypervolume estimation approach. This method avoids overfitting in high-dimensional space under limited sample sizes[72]. Specifically, we calculated the square root of the determinant of the covariance matrix of PC scores, which corresponds to the volume of the multivariate Gaussian ellipsoid describing trait dispersion in PCA space. To ensure comparability among species with unequal sample sizes, we performed bootstrap resampling with replacement (n = 300 iterations) using a fixed sample size equal to the minimum number of individuals across species (= 7). For each iteration, a hypervolume was computed and its volume extracted, the mean and 95% confidence interval of these resampled volumes were taken as the expected hypervolume size and its confidence limits, representing the elemental compositional flexibility of each species. A total of 22 bryophyte species and 50 vascular plant species were included in the hypervolume analyses. A sensitivity analysis was conducted with the minimum number of 8, 9, and 10 individuals when estimating each hypervolume. Results were consistent across all three thresholds tested (Table S2). The climatic hypervolumes were estimated following the same method. Finally, we examined the relationship between (1) elemental hypervolumes, GS (*C-value*) and climatic variables (2) elemental hypervolumes, reproductive units (spore size and seed size) and climatic hypervolumes, and (3) elemental hypervolumes, GS (*C-value*) and climatic hypervolumes using phylogenetically informed regressions in the “phylolm” package (v2.6.2), applying a Pagel’s λ model to account for shared evolutionary history among species[68].

Declarations

DATA AVAILABILITY

The data and R code used in this study will be available at Figshare, https://figshare.com/s/f53d2b0d1f78ddd5525f

AUTHOR CONTRIBUTION

X. S.: Conceptualization, Methodology, Formal analysis, Investigation, Data Curation, Writing - Original Draft, Writing - Review & Editing, Visualization, **H. V.**: Writing - Review & Editing, **D. L.**: Writing - Review &

Editing, **R. G.-A.**: Writing - Review & Editing, Investigation, **J. G.-P.**: Writing - Review & Editing, **A. M.**: Investigation**, J. S.**: Investigation**, J. C.**: Data Curation, Investigation, **C. P.**: Writing - Review & Editing**, G. P.**: Writing - Review & Editing**, M. F.-M.**: Conceptualization, Methodology, Data Curation, Writing - Review & Editing, Investigation, Funding acquisition

DECLARATION OF INTERESTS

The authors declare no conflict of interest.

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Figures

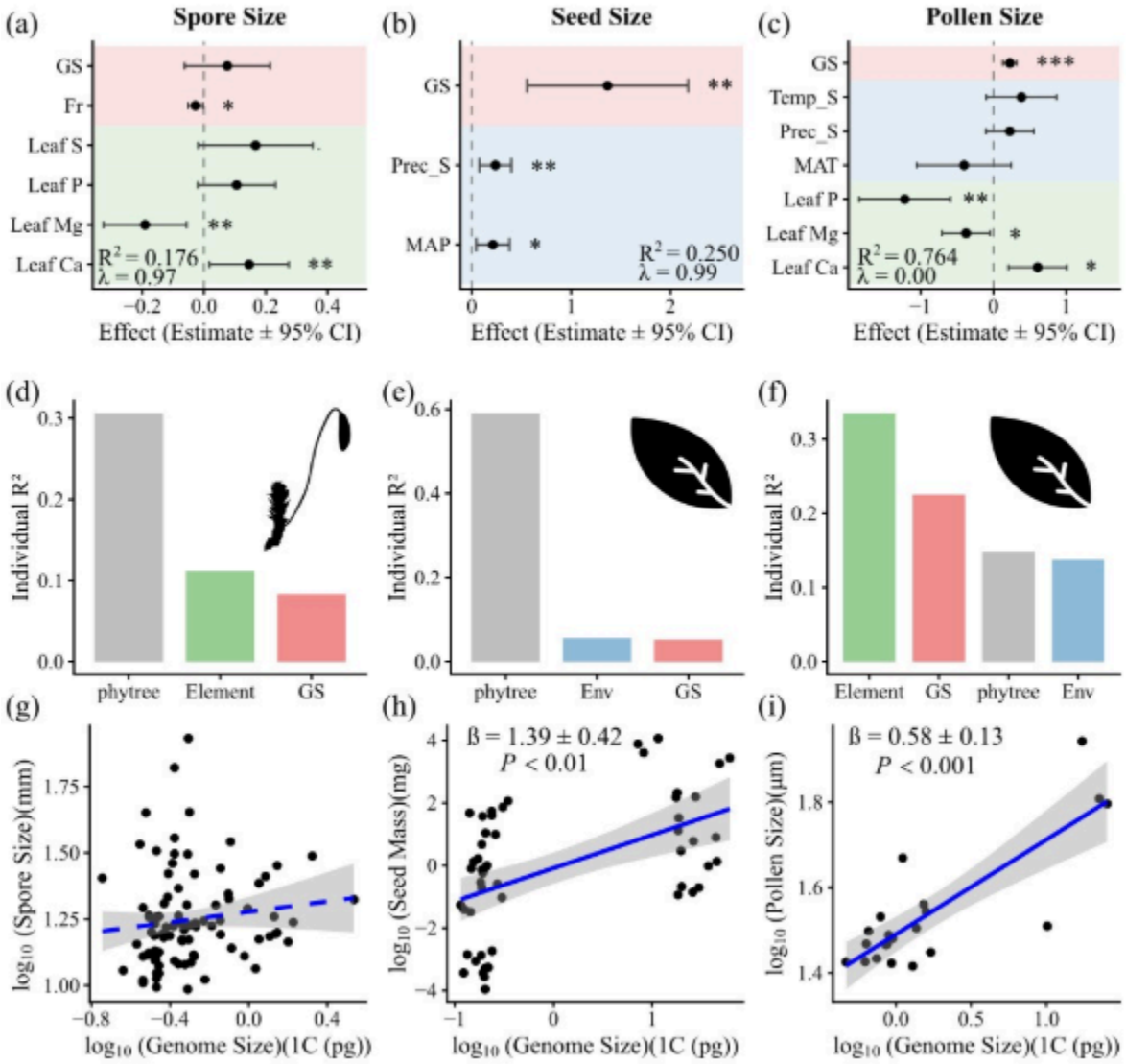


Figure 1

Genome size effects on spore, seed and pollen size. (a-c) Standardized effect sizes (model estimates ± 95% confidence intervals) of genome size (GS), environmental variables (temperature and precipitation), and leaf elemental traits on (a) spore size, (b) seed size, and (c) pollen size based on phylogenetic regression models. Bryophytes elemental concentrations are related to the entire gametophyte, while for vascular plants, elemental concentrations are related to their leaves. Shaded backgrounds indicate different groups of predictors (Fr: Spore frequency, Pre_S: Precipitation seasonality, Temp_S: Temperature seasonality, MAT: Mean annual temperature, MAP: Mean annual precipitation). Dashed vertical lines denote zero effect. Asterisks indicate statistical significance (*P < 0.05, **P < 0.01, ***P < 0.001). Model explanatory power (R^2) and phylogenetic signal (Pagel's λ) are shown within each panel. (d-f) Variance partitioning of residual variation in (d) spore size, (e) seed size, and (f) pollen size, showing the relative contributions of phylogeny (phytree), GS, elemental traits (Element), and environmental factors (Env). Variable categories within each group are indicated using the same color scheme as in the corresponding forest plot. Bars represent the proportion of variance explained by each component. (g-i) Partial residuals plots showing the relationships between GS and (g) spore size, (h) seed size, and (i)

pollen size. Points represent species-level observations. Parameter estimates shown (β ± standard error of the mean) are standardized parameter estimates. The shaded area represents the 95% confidence interval of the slopes.

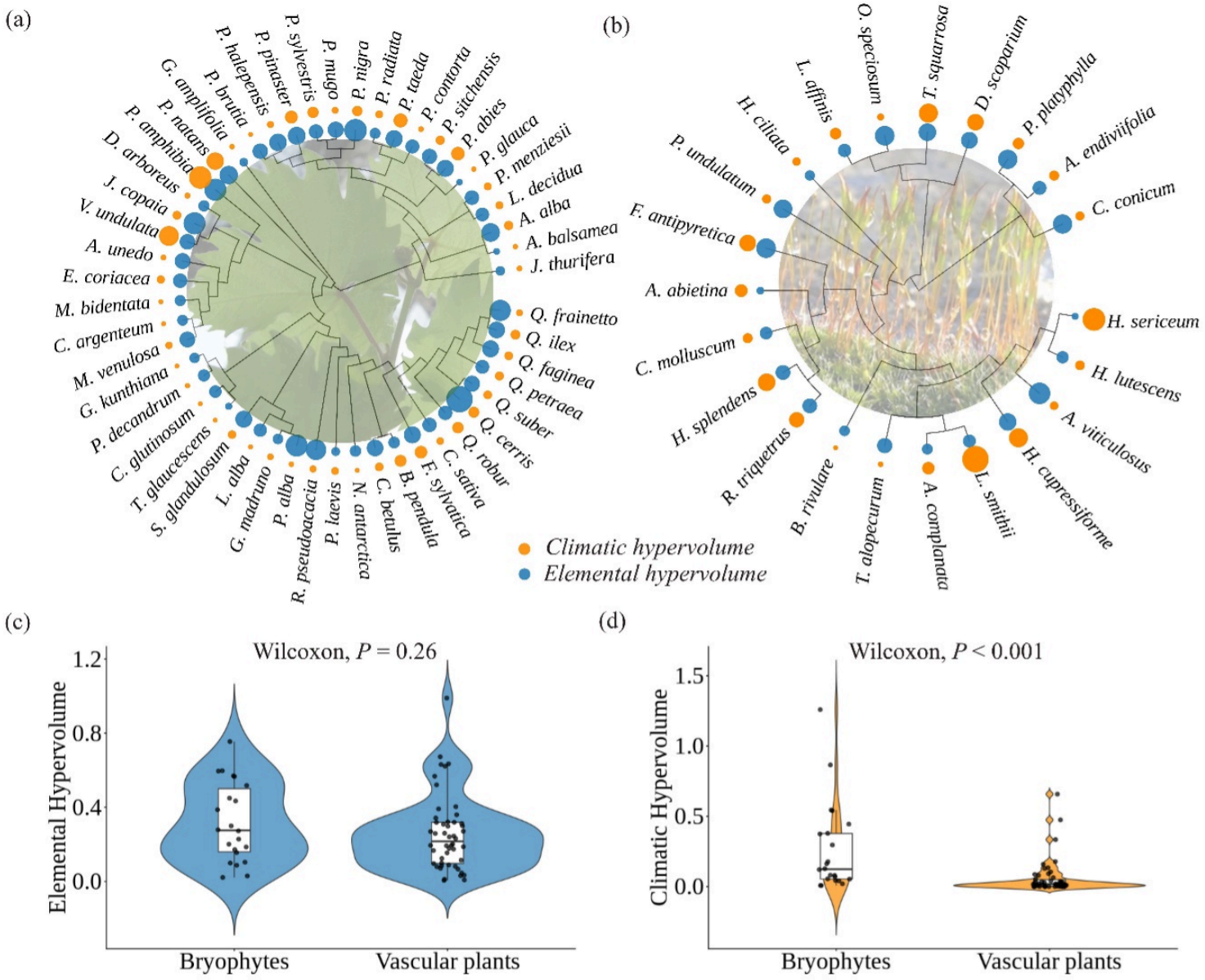


Figure 2

Phylogenetic patterns of elemental and climatic hypervolumes across two major clades of land plants. Circular phylogenies show the relationships among sampled species in (a) vascular plants and (b) bryophytes. For each species, blue circles indicate elemental hypervolumes and orange circles indicate climatic hypervolumes, with circle size proportional to the hypervolume size. Panel (c) shows the distribution of elemental hypervolumes within bryophytes and vascular plants and their clade-level comparison using a Wilcoxon test. Panel (d) shows the distribution of climatic hypervolumes within bryophytes and vascular plants and their clade-level comparison using a Wilcoxon test. Only species

with at least seven sampled individuals were included in this analysis. Points represent species-level estimates, and boxplots summarize the distribution within each clade.

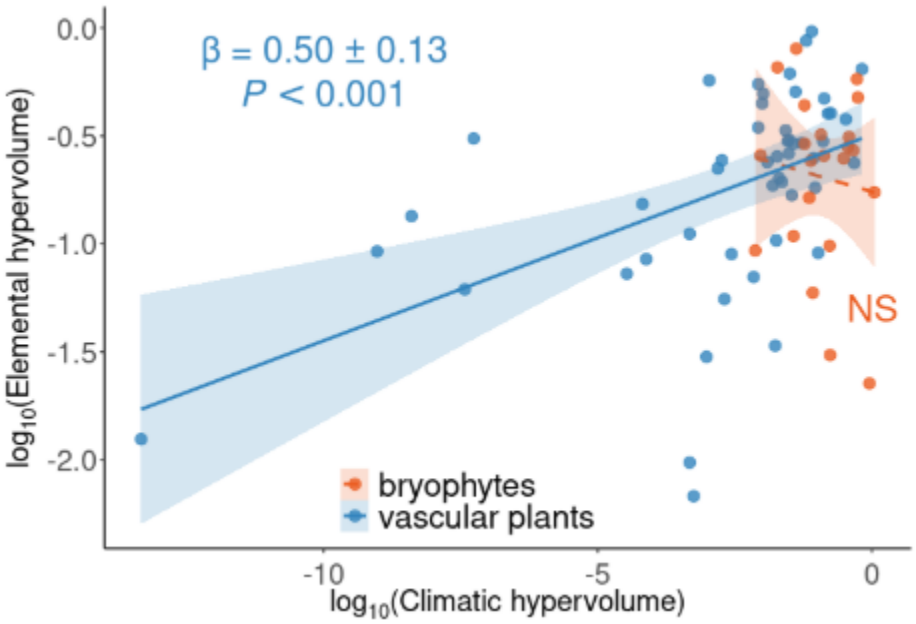


Figure 3

Partial residuals plot showing the relationship between elemental and climatic hypervolume sizes. Points represent species-level observations in bryophytes and vascular plants. Parameter estimates shown (β ± standard error of the mean) are standardized parameter estimates. The shaded area represents the 95% confidence interval of the slopes. NS: Not significant. Leave-one-out analysis showed that removing any single species did not change the direction or significance of the predictors, indicating that the phylogenetic regression results were robust to single-species influence (See details in Table S3 and Table S4 of supporting information).

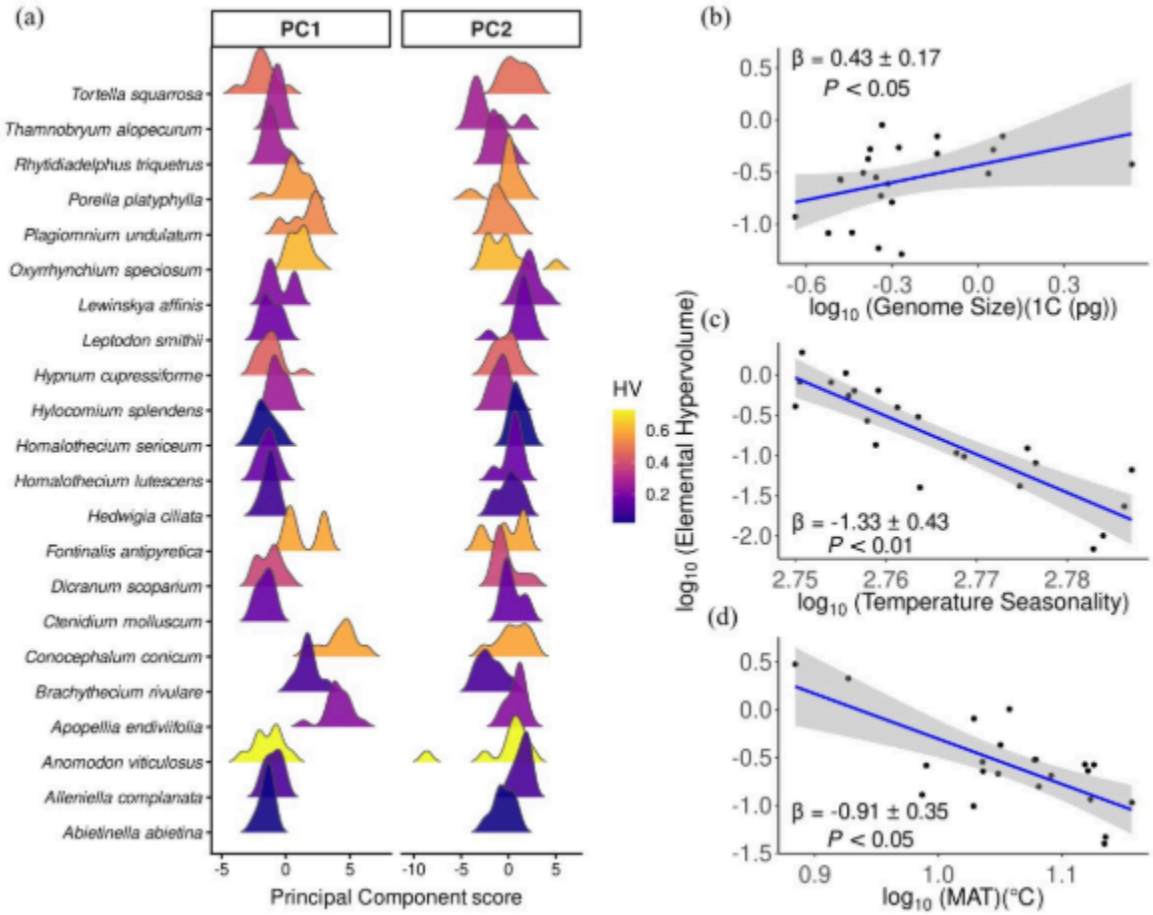


Figure 4

The effects of climate and genome size on elemental hypervolume across bryophytes. (a) Species-level distributions of principal component scores along PC1 (34.3%) and PC2 (25.1%) derived from multivariate elemental space (PC3 explained only 8.9% of variance and was therefore omitted from the main figure). Ridgeline density plots show the distribution of individual observations for each species, colored by hypervolume size (HV), representing the size of the species' occupied elemental space. Warmer colors indicate larger HV. (b-d) Partial residuals plots showing the relationship between species-level HV and genome size, temperature seasonality, and mean annual temperature (MAT). Points represent species-level observations. Parameter estimates shown (β ± standard error of the mean) are standardized parameter estimates. The shaded area represents the 95% confidence interval of the slopes.

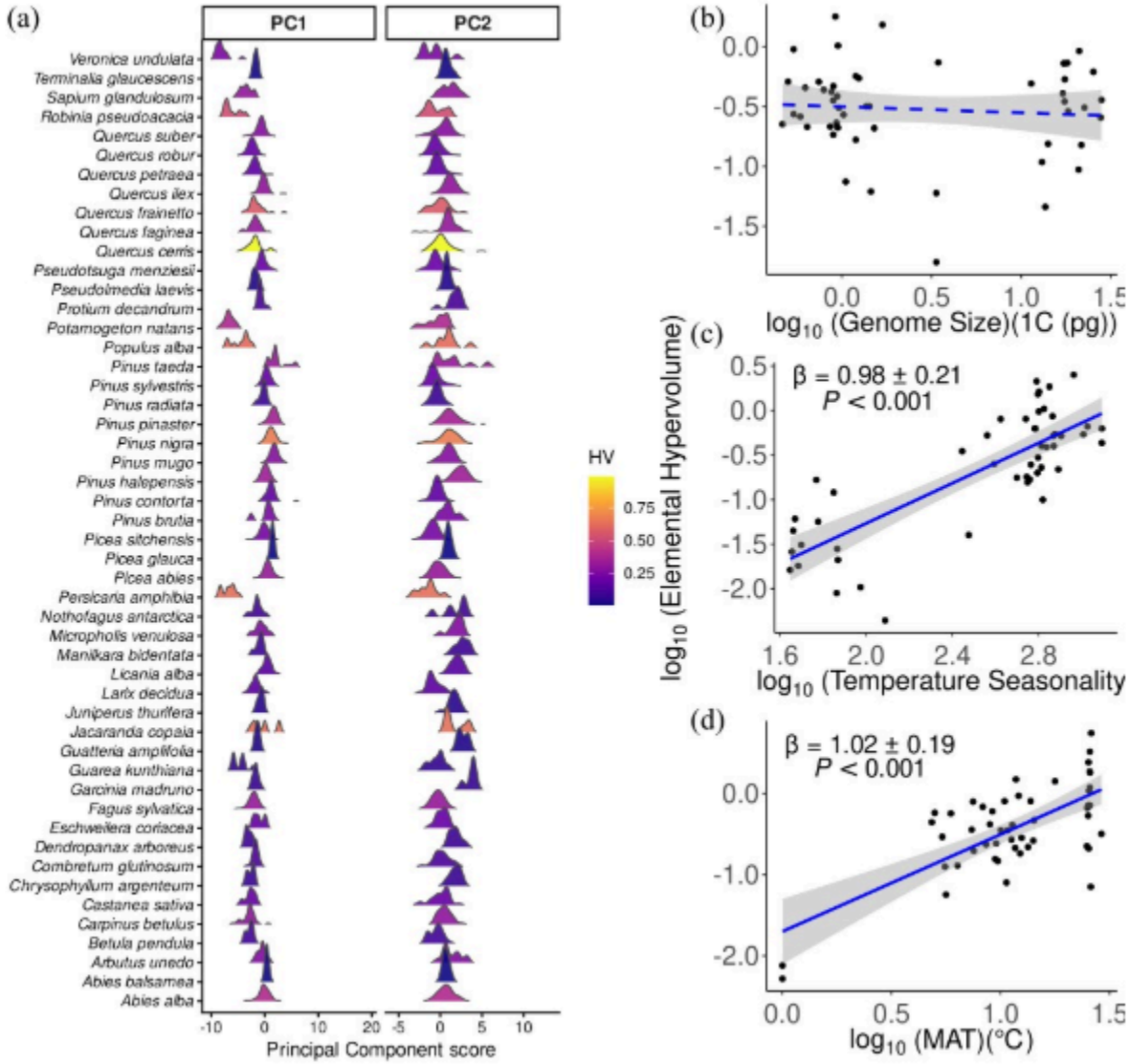


Figure 5

The effects of climate and genome size on elemental hypervolume across vascular plants. (a) Species-level distributions of principal component scores along PC1 (37.8%) and PC2 (27.4%) derived from multivariate elemental space. (PC3 explained only 12.0% of variance and was therefore omitted from the main figure). Ridgeline density plots show the distribution of individual observations for each species, colored by hypervolume size (HV), representing the size of the species' occupied elemental space. Warmer colors indicate larger HV. (b-d) Partial residuals plots showing the relationship between species-level HV and genome size, temperature seasonality, and mean annual temperature (MAT). Points represent species-level observations. Parameter estimates shown (β ± standard error of the mean) are standardized parameter estimates. The shaded area represents the 95% confidence interval of the slope.

Supplementary Files

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