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The Evolution of Hutchinsonian Climatic Niche Hypervolumes in Gymnosperms

Fernanda S. Caron[1] | Jānis Lazovskis[2] | David F. R. P. Burslem[3] | Juliano Morimoto[1,4,5]

[1]Programa de Pós-graduação Em Ecologia e Conservação, Universidade Federal Do Paraná, Curitiba, Paraná, Brazil | [2]Institute of Clinical and Preventive Medicine, Faculty of Medicine and Life Sciences, University of Latvia, Riga, Latvia | [3]School of Biological Sciences, University of Aberdeen, Aberdeen, UK | [4]Institute of Mathematics, University of Aberdeen, King's College, Aberdeen, UK | [5]NSF-Simons National Institute for Theory and Mathematics in Biology (NITMB), John Hancock Center in Chicago, Chicago, Illinois, USA

Correspondence: Juliano Morimoto (juliano.morimoto@abdn.ac.uk)

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ABSTRACT

Aim: The niche is a fundamental concept in theoretical and experimental ecology and is used to describe a wide range of ecological processes from species' interactions with the environment to community assemblies. A common way to represent the niche is through a multidimensional geometry known as the Hutchinsonian niche hypervolume. Ecological theory predicts that niche hypervolumes have properties such as holes with broader eco-evolutionary significance, but we lack a comprehensive empirical study of niche hypervolume properties and their evolutionary meaning.

Location: Global.

Time Period: Holocene.

Major Taxa Studied: Gymnosperms.

Methods: We conducted for the first time a systematic and comprehensive test of the evolution of Hutchinsonian climatic niche hypervolume properties (volume and holes) across 418 species, 65 genera, and 12 families of gymnosperms, which includes many species that are endangered or threatened. Using cutting-edge computational algorithms, we measured the evolution of geometric (i. e., volume) and topological (i. e., holes) properties of gymnosperm hypervolumes across a comprehensive calibrated phylogeny.

Results: Our comparative analysis revealed moderate evidence of the non-independent evolution of niche hypervolume and no evidence of the non-independent evolution of holey hypervolumes across gymnosperm species. We also found that species, genera and families with low hypervolume volume, such as monotypic groups like *Gingko*, likely experienced shifts in hypervolume evolutionary rates. However, our analysis of niche positioning showed that climatic distances between co-occurring species did not significantly depart from null expectations, suggesting that their spatial distribution within the climatic space is independent of limiting similarity.

Main Conclusions: Our results indicate that topological properties of gymnosperm climatic niche hypervolumes show little phylogenetic constraint and thus arise as emergent outcomes of species–environment interactions. In contrast, the breadth of environmental occupancy (hypervolume volume) retains a moderate evolutionary signal. These patterns suggest that while the capacity to occupy wider or narrower climatic conditions is moderately shared by evolutionary history, the actual realisation of these niches is not driven by significant climatic divergence.

1 | Introduction

The 'niche' is arguably one of the most important concepts in ecology (Chase 2011; McCann and Gellner 2020). Although definitions are debated (Hutchinson 1957; J. Soberón 2007; Wennekes et al. 2012), the concept of the niche has enabled unprecedented theoretical and empirical advances in our understanding of how species interact with their environment (e. g., Blonder 2016; Soberón and Nakamura 2009; J. M. Soberón 2010; Winemiller et al. 2015; and references therein). In particular, the definition of niche formulated by Hutchinson—the Hutchinsonian niche hypervolume—is widespread in the literature and is simple to apply to the large quantities of ecological data that are increasingly available. In this context, the niche hypervolume can be defined as "an abstract mapping of population dynamics onto an environmental space, the axes of which are abiotic and biotic factors that influence birth and death rates" (verbatim from Holt 2009; see also Hutchinson 1957). Niche hypervolumes have had a major influence on the advancement of ecological theory (Soberón and Arroyo-Peña 2017; Blonder 2018; Jiménez et al. 2019; Mammola and Cardoso 2020; Soberón and Peterson 2020; Carrasco et al. 2022; Conceição and Morimoto 2022), and have uncovered insights into niche evolution (Blonder 2018; Pili et al. 2020; Bates and Bertelsmeier 2021), niche differentiation (Carvalho and Cardoso 2020; Huang et al. 2024), biological invasion (Tingley et al. 2014; Helsen et al. 2020; Zhang et al. 2020), community diversity (Chisholm and Pacala 2010; Loke and Chisholm 2023), ecological specialisation (Bebber and Chaloner 2022), and global biodiversity patterns (Beaugrand et al. 2020; but see Justus 2019).

The niche hypervolume concept has evolved with advances in theoretical and empirical ecology (Chase and Leibold 2003; Holt 2009; Wiens 2011; Kearney et al. 2010; Letten et al. 2017). One aspect of the hypervolume concept that has recently emerged, but remains untested, is the idea that hypervolumes can have holes (Blonder 2016). Specifically, using simulations and a morphological dataset of finches in Galapagos, Blonder (2016) proposed the existence of holes in niche hypervolumes and conjectured that these holes could indicate environmental conditions in which species are vulnerable to be outcompeted in interspecific competition or unaccounted eco-evolutionary processes (e. g., range shifts) that lead to vacant niches. One cannot rule out the possibility of missing data generating artefacts interpreted as holes, but it is plausible—although untested at large scales—that holes have ecological meaning (Blonder 2016; Conceição and Morimoto 2022). Note that, in this conjecture, holes are representative of a fundamental ecological feature that could evolve if, for example, sister lineages share the physiological or morphological vulnerabilities that facilitate invasion of portions of environmental space by other lineages. Blonder (2016) tested the holey niche concept in the morphological niche hypervolumes represented in a community of co-existing finches in the Galapagos and concluded that "well-known datasets may be described in terms of hypervolumes with holey geometries that are potentially consistent with unexplored mechanisms" (Blonder 2016). Thus, Blonder's conjecture could link niche hypervolume properties that exist in high-dimensional space to real-world ecological processes, making the study of hypervolume properties a paramount surrogate and key target of investigations of species' ecology. However, to date, we still lack large scale tests to directly ascertain the evolution of Hutchinsonian climatic niche hypervolume geometric and topological properties. Yet the concept of climatic niche hypervolumes was originally created to represent species' climatic occupancy and is what hypervolumes are widely used for in many applications today (Blonder 2018; Vilas et al. 2022).

Studying niche hypervolume properties is not trivial. The incomplete information available for defining the dimensions of the hypervolume topology poses a challenge. Patchy and heterogeneous observations prevent reconstruction of hypervolume topology from bioclimatic variables with accuracy (e. g., Peterson et al. 2018; Jiménez et al. 2019), and statistical models to "fill" hypervolume topologies are criticised (e. g., Qiao et al. 2017; Mammola 2019; Guillerme et al. 2020). These limitations can be particularly insidious when estimating hypervolume holes as high dimensionality can pose a challenge (Blonder 2016; Conceição and Morimoto 2022). We recently proposed the use of algebraic topology, specifically the concept of persistence homology, to identify holes in hypervolumes and overcome the dimensionality challenge (Conceição and Morimoto 2022). However, neither we nor others have yet used this approach to identify and derive biological meaning from holes and other properties from ecological niche hypervolumes across species within an evolutionary framework. Such comparative studies are needed to better understand if and how ecological niche hypervolume properties, including holes, evolved and are constrained by evolutionary history.

In this paper, we addressed an important knowledge gap about niche hypervolumes, namely, whether niche hypervolume properties evolve non-independently in related species. To achieve this, we present the first comparative study of the evolution of niche hypervolume properties (volume and holes). Understanding evolutionary patterns of niche hypervolume properties can be a way to uncover the eco-evolutionary significance of its properties, such as holes, which have been hypothesised to hold meaningful ecological information but still lack large-scale studies to test this. Plants are excellent models for studying hypervolume properties because they minimise potential confounding effects of range shifts and migration observed in animals (e. g., Valladares et al. 2014; Menchetti et al. 2019; Häfker et al. 2022; and references therein). Many plants are threatened by climate change and understanding the evolution of niche hypervolumes may uncover new insights into how to protect them (Antão et al. 2020; Singh et al. 2023). Moreover, climate niche evolution in plants is representative of similar processes in animals (Liu et al. 2020).

Here, we focused our attention on studying the niche hypervolume properties of gymnosperms. Gymnosperms are non-flowering woody plants with major importance for many ecosystems worldwide. Gymnosperm trees are abundant in many subtropical, temperate, and boreal forests that collectively represent over one-third of the forested regions on the planet (Lesiv et al. 2022). Moreover, many gymnosperms have been assessed as having high extinction risk (~40% of species classified as CR, EN, VU) despite their importance for cultural and provisioning ecosystem services (Forest et al. 2018; Tagliari et al. 2023), whereas other gymnosperms are a primary source of timber (e. g., *Pinus sp*). Gymnosperms are also relatively less diverse than flowering plants, likely due to direct competition (Bond 1989; Coiffard et al. 2012; De Boer et al. 2012), which makes them a tractable but representative group for investigating the evolution of ecological niche hypervolume properties. Given gymnosperms' broad evolutionary and socio-ecological significance, we analysed the environmental niches of 418 species distributed across 65 gymnosperm genera and 12 families, representing 37%, 75% and 93% of all named species, genera and families, respectively (Figure 1A,B) (Yang et al. 2022). We constructed niche hypervolumes with 31 environmental variables and applied a recently developed approach of topological data analysis to estimate hypervolume holes (Conceição and Morimoto 2022). We hypothesised that if niche hypervolume properties captured conserved ecological processes, then hypervolume properties would display strong phylogenetic signals. For example, if closely related species, genera, and families are more likely to have more similar climatic niches (e. g., over- or under-dispersed point clouds in niche space), then this would be captured by our comparative analysis of climatic niche properties such as volume. Our findings advance our conceptual and biological understanding of the multidimensional niche and the evolution of its properties.

2 | Materials and Methods

2.1 | Data Collection and Processing

We obtained occurrence data from the GBIF database (https://www.gbif.org/) for all available gymnosperms. The search was conducted for Cycadopsida (40,554 entries), Ginkgoopsida (57,488 entries), Pinopsida (5,723,563 entries), and Gnetopsida (52,648 entries) (Table S1). We processed the GBIF data to remove duplicated points, points with locations in impossible places (e. g., the sea), and points with large uncertainty. To address potential spatial sampling bias, we applied a spatial thinning procedure using the spThin v.0.2–0 package (Aiello-Lammens et al. 2015). We thinned the occurrence data for each species with a minimum distance threshold of 10 km, ensuring a more balanced representation of geographic space and reducing spatial autocorrelation. We assumed that observations outside native ranges were valid in the construction of the realised niche hypervolume and were therefore maintained. In this respect, we interpreted the realised climatic hypervolume niche as the multidimensional representation of all measured climatic conditions where the species, genera, or families have survived (either within their native range or naturalised in an alien area). Attempting to thin species with the most observations (200 k—300 k data points) required more memory than was available on the HPC being used (4 TB). As a result, we used an alternative sparsification procedure that achieves the same results as thinning using just 16GB of memory (Jamin et al. 2025) as described in Text S1. The resulting data sets produced by the two procedures were nearly identical in size, with maximum interpoint distance among observations in the sparsified versus thinned datasets of 0.24 degrees (~27 km). The details of the sparsification procedure, including its code, can be found in Lazovskis et al. (2025). Recent studies have used hypervolumes to test the differences in climatic niche in invasive vs. native ranges (e. g., Tingley et al. 2014; Zhang et al. 2020), but this is not within the scope of this paper. We only kept points classified as 'human observation' in the GBIF 'basisOfRecord' field with the intention to represent contemporary distribution of extant taxa based on recent climates, thereby excluding fossil records or preserved specimens. The final dataset contained 2,483,316 entries, corresponding to 764 species. The taxonomic classification for the gymnosperms was followed according to the World of Flora Plant List (http://www.worldfloraonline.org/, last accessed Oct 13, 2023).

Apart from the gymnosperm data, we also gathered occurrence data for four outgroup families (see Data analyses section). These families were Psilotaceae (23,865 entries), Calycanthaceae (10,013 entries), Amborellaceae (327 entries), and Matoniaceae (836 entries) (Table S1). For these families, we had a total of 16,361 entries after cleaning and processing the data, corresponding to 23 species. Climatic data were obtained from the WorldClim database using the worldclim_global function in geodata v0 0.6–0.6 (Hijmans et al. 2024), using the argument "var" as "bio" and "tmin". To evaluate the effect of spatial resolution on our results, we obtained this dataset at both 30 arc-seconds (~1 km) and 2.5 min (~5 km) of a degree resolutions (used throughout). Phylogenetic relationships for species, genera, and families for which we had ecological data were retrieved from Stull et al. (2021). Stull et al. (2021) generated two distinct phylogenetic datasets: a transcriptomic/genomic dataset comprising 121 ingroup species, and a broader plastid supermatrix dataset inferred from 78 plastid genes, encompassing 890 gymnosperm species (~82% of recognised species). We used this more comprehensive phylogeny as the basis for our analyses, from which we extracted a pruned subtree retaining only the species included in our dataset that preserved the original topology and branch lengths. In this paper we only considered the climatic component of the niche, as climatic variables represent the primary determinant of variation in plant distributions globally (e. g., Walter 1979). We acknowledge that numerous additional abiotic and biotic factors contribute to niche diversification in plants, including soil properties, elevation and topography, but incorporating these niche dimensions is beyond the scope of the current paper.

Finally, conservation status for each species was retrieved from the IUCN Red List database (https://www.iucnredlist.org/, last accessed Jan 28, 2026) using the *taxize* v.0.10–0 package (Chamberlain and Szöcs 2013). We used the iucn_summary and iucn_status functions to extract the current threat category for each taxon. Species were classified into their respective threat categories: Least Concern (LC), Near Threatened (NT), Vulnerable (VU), Endangered (EN), and Critically Endangered (CR).

2.2 | Data Analyses

We performed analyses of the evolution of the Hutchinsonian niche across gymnosperms primarily at the species level to avoid biases associated with pooling taxa, while also conducting comparative analyses at the level of genus and family. We used 31 environmental variables to construct the climatic niche of each taxon. We conducted a principal component analysis (PCA) with all climatic variables to reduce the dimensionality of these environmental variables to three

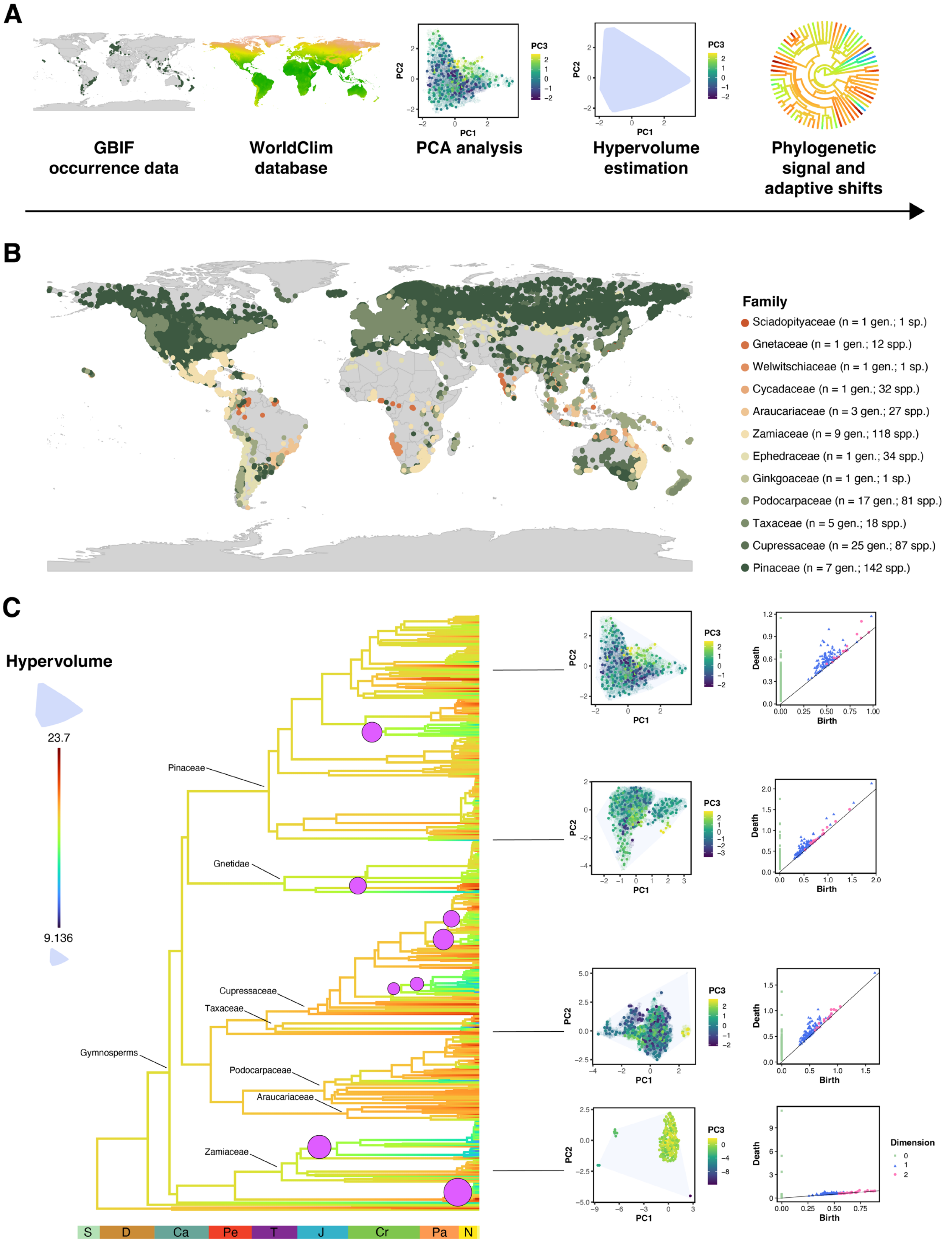

FIGURE 1 | Legend on next page.

FIGURE 1 | Overview of the analyses performed in the present study. (A) Steps to analyse the data: Collection of the occurrence data in GBIF database; extraction of the bioclimatic variables for each occurrence; PCA analysis with the bioclimatic data; estimation of the climatic niche hypervolume volume and properties; calculation of the phylogenetic signal of the hypervolume properties. (B) Occurrence data for each species, genus and family that were studied. Legend indicates the number of species and genera in each family. (C) Hypervolume properties, phylogenetic signal, and adaptive shifts were estimated. Phylogeny is mapped with hypervolume, in which blue corresponds to small hypervolume and red to large volumes. Time scale is represented at the base of the phylogeny. Circles represent the adaptive shifts with a posterior probability higher than 0.3. Graphs at the right represent examples of hypervolumes estimated and the persistence homology diagrams. Green: Dimension 0, Blue = dimension 1, and Pink: Dimension 2 homology.

orthogonal axes (i. e., PC1-3), which captured a high proportion of the cumulative environmental variance (mean > 82%; Table S2). A PCA was conducted for each gymnosperm species, genus, and family separately using the function prcomp in R (R Core Team 2024). For each taxon, we also calculated its centroid in the first three PC axes. For this, we calculated the mean of each PC axis for the taxa individually and for the gymnosperms. Then, we estimated the Euclidean distance between each taxon centroid to the gymnosperm centroid. While the hypervolume volume is based on the extreme values of the PCA, the distance between centroids can be regarded as a measure of the uniqueness of the taxon's climatic niche (Figures S2–S4).

Hypervolumes were estimated using the hypervolume_gaussian function in *hypervolume* v.3.1–4 (Blonder 2024) with default parameters. This algorithm provides random points that "fill" the hypervolume space (see Blonder et al. 2014) and from which properties of the hypervolumes can be estimated. As the hypervolume analyses are computationally intensive, we had to reduce the dataset for the species, genera and families that had more than 50,000 locality entries. The species that had their occurrences reduced were *Abies alba*, *Amborella trichopoda*, *Calycanthus floridus*, *Juniperus communis*, *Juniperus oxycedrus*, *Matonia pectinate*, *Picea abies, Pinus halepensis*, *Pinus nigra*, *Pinus pinaster*, *Pinus pinea*, *Pinus sylvestris*, *Psilotum nudum*, and *Tmesipteris tannensis*; the genera were *Abies*, *Juniperus*, *Larix*, *Picea*, *Pinus*, and *Taxus*; and the families were Cupressaceae and Pinaceae. Inspection of the occurrence points derived from the entire and reduced datasets showed that this reduction in the locality entries did not affect the coverage of the taxon occurrence (Figure S1). Furthermore, we performed a linear regression between the number of species within each genus or family and its estimated hypervolume volume (log-transformed) to evaluate if the richness of each taxon influenced the hypervolume estimation. We also estimated whether mean species-level hypervolume volume was related to genus richness. In addition, to ensure that the choice of spatial resolution and the spatial thinning procedure did not significantly affect the hypervolume estimation, we calculated the bottleneck distance between the persistence diagrams of the hypervolumes generated for each case. This approach allowed us to confirm that the underlying structure of the climatic niche remained consistent across different data resolutions and sampling densities.

Next, to evaluate the evolutionary association between hypervolume properties and extinction risk, we employed Phylogenetic Generalised Least Squares (PGLS) models (Table S3). IUCN conservation statuses were converted into a numerical ordinal scale (LC = 0, NT = 1, VU = 2, EN = 3, CR = 4). Species listed as Data Deficient (DD) or Not Evaluated (NE) were excluded from these analyses. For genus and family-level analyses, we calculated the proportion of threatened species (VU, EN, and CR) within each taxon as the response variable. All models were fitted using Maximum Likelihood (ML) to estimate the phylogenetic signal, ensuring that the correlation structure appropriately accounted for phylogenetic relatedness (Stull et al. 2021). Niche volume data were log-transformed before the analyses. Additionally, to further investigate the ecological mechanisms underlying niche evolution, we tested the competitive exclusion hypothesis by calculating the Net Relatedness Index (NRI) using climatic niche distances. We used a null model approach via the sesmpd function in *picante* v1.8–2 (Kembel et al. 2010), with 999 randomisations using the "taxa.labels" null model. Niche distances were calculated as the Euclidean distance between hypervolume centroids in the climatic space (PC1–3). Significant negative *z*-scores ($p < 0.05$) were interpreted as evidence of phylogenetic overdispersion, indicating that co-occurring species occupy more divergent portions of the climatic space than expected by chance.

Finally, we estimated the phylogenetic signal and adaptive shifts for the hypervolume properties and the distance of centroids. The phylogenetic signal was calculated using the phylosig function in *phytools* v2.3–0 (Revell 2024). The statistics used were Pagel's λ (Pagel 1999), with 1000 iterations, and Blomberg's K (Blomberg et al. 2003), with 1000 simulations. We also mapped the hypervolume properties in the phylogeny using the contMap function in *phytools* v2.3–0 (Revell 2024). As a final analysis, we estimated adaptive shifts in the evolution of the hypervolume volume using the *bayou* package v2.3–0 (Uyeda and Harmon 2014). This package fits Bayesian reversible-jump multi-optima Ornstein–Uhlenbeck (OU) models to phylogenetic comparative data, identifying the location and magnitude of adaptive shifts (Uyeda and Harmon 2014). We ran the analyses at the species, genus, and family levels using the default prior configurations. We ran the models two times at each level for 10 million generations, considering 30% as burn-in. All variables were log-transformed prior to the calculations. Besides the species-level analysis, the phylogeny was manipulated to be used at the genus and family level, keeping either one random representative per genus or family for this. In addition, we also estimated the dimension 2 holes in the 3D ecological hypervolumes using a state-of-the-art topological data analysis approach (Conceição and Morimoto 2022) and the *TDAstats* package (Wadhwa et al. 2018). We focused on dimension 2 holes because they represent the boundaries of 3D sub-volumes within the 3D hypervolume. Ecologically, this indicates that while trait combinations along a curved boundary are viable, the interior region is systematically

TABLE 1 | Phylogenetic signal using Blomberg's K (Blomberg et al. 2003) and Pagel's **λ** (Pagel 1999) of hypervolume and holes at the species level. LogL (logL0) refers to the log-likelihood estimates of the (null) models.

Trait	λ	logL	logL0	*p*	K	*p*
Hypervolume	**0.492**	−892.753	−922.367	**0.000**	0.017	0.293
Mean distance	**0.093**	33.021	27.149	**0.001**	**0.030**	**0.003**
Maximum distance	0.052	−120.328	−122.184	0.054	0.012	0.512
SD distance	**0.071**	−50.876	−53.690	**0.018**	0.019	0.162

Note: Bold: $p < 0.05$.

unoccupied, implying multivariate constraints on species' occupancy. This structure reflects joint physiological, energetic, and/or ecological limitations that exclude intermediate environments from being suitable for species' occupation. We estimated maximum niche hypervolume hole size (i. e., largest hole size) as the maximum "survival" (i. e., persistence) of dimension 2 holes upon Vietoris-Rips filtration and the average and standard error as the mean and standard error of the survival of all dimension 2 holes identified for a given hypervolume (Conceição and Morimoto 2022). Our motivation for studying these holes was that, if holes exist in ecological niche hypervolumes and evolve non-independently, we could infer their biological significance from the shared ecological properties among species. We did not focus on dimension 0 (holes which emerge based on distance among data points) or dimension 1 (holes in the faces of the hypervolumes) because they are dependent on the distribution of datapoints which defines the hypervolume rather than holes in the structure of our 3D hypervolumes (see Conceição and Morimoto 2022 and references therein). Importantly, our approach captured the persistent dimension 2 holes that emerge from the species' biotic and abiotic interactions and not from the lack of climatic variable combinations or the topology of the environmental space (E-space) as shown in Text S1. It is also important to note that we cannot rule out that hypervolumes constructed using principal components could distort the holes that exist thereby adding noise to our phylogenetic analysis (false negative) (see Discussion). We currently lack a systematic study to ascertain whether our approach, which is common practice in ecology, conserves the topological structures of the niche hypervolume. Such knowledge will have far-reaching implications for ecological studies as many studies rely on the ability of computational algorithms to estimate the topology of niche hypervolumes accurately. All analyses were performed in R v4.4–0 (R Core Team 2024).

3 | Results

Taxonomic richness had no statistically significant influence on hypervolume volume at either the genus ($R^2 = 0.037$, $p = 0.122$) or family levels ($R^2 = 0.254$, $p = 0.094$). Sensitivity analyses further confirmed that these topological features were not artefacts of the resolutions of our climatic data (30 s vs. 2.5 min), as dimension 2 persistence diagrams remained robust to both occurrence thinning (mean Bottleneck Distance = 0.081) and changes in spatial resolution (mean Bottleneck Distance = 0.076).

We also found a significant negative relationship between hypervolume volume and IUCN threat status ($\beta = -0.103$, SE = 0.025, $t = -3.961$, $p < 0.001$, $R^2 = 0.037$), indicating that species with narrower climatic tolerances are consistently associated with higher extinction risk categories. This pattern was also supported at the genus and family levels (Genus: $\beta = -0.07$, SE = 0.032, $t = -2.234$, $p = 0.029$, $R^2 = 0.059$; Family: $\beta = -0.102$, SE = 0.033, $t = -3.073$, $p = 0.013$, $R^2 = 0.458$). Conversely, hypervolume dimension 2 holes metrics were not correlated with IUCN threat status (Table S4), suggesting that holey hypervolumes are not indicators of extinction risk as measured by the IUCN threat status.

Next, we examined the ecological mechanisms of species coexistence and whether niche differentiation has been driven by limiting similarity. Contrary to expectations, we found no consistent pattern of niche overdispersion across the studied genera (Table S3). Most genera exhibited niche distances that did not significantly depart from null expectations ($p > 0.05$), with a few clades (*Encephalartos*, *Ephedra*, and *Widdringtonia*) even showing patterns of niche clustering. Moreover, the average hypervolume volume was not correlated with genus richness ($\beta = 0.110$; SE = 0.184; $t = 0.600$; $p = 0.551$; $R^2 = -0.010$). These patterns indicate that co-occurring species maintain their climatic requirements without significant divergence or reduction in niche breadth driven by limiting similarity.

We also tested whether ecological niche hypervolume evolved non-independently across gymnosperms. We found a significant but moderate Pagel's λ for niche hypervolume (Table 1). At broader taxonomic scales, we found weak evidence to support the non-independent evolution of ecological niche hypervolume as only Blomberg's *K* at the genus level was statistically significant (Table S5). Estimates of Pagel's λ at the genus and family levels and Blomberg's K at the family level were not statistically significant (Table S4).

We also analysed the evolution of hypervolume holes (Blonder 2016). At the species level, although the Pagel's λ for mean and SD distances for dimension 2 holes were statistically significant, the estimates were notably low (Pagel's $\lambda < 0.1$; Table 1). Our analyses of the average size of dimension 2 holes (Figures S2A, S3B, S4B), standard error of estimates of dimension 2 holes (Figures S2B, S3C, S4C), and maximum size of dimension 2 holes (Figures S2C, S3D, S4D) at the genus and family levels revealed independent evolution of hypervolume holes. And while the overall shape and associated persistence diagrams differed among themselves (e. g., Figure 1C), pairwise distance matrices of the dimension 2 holes did not reveal any clusters of pairwise distances which appeared similar (Figures S2E, S3F, S4F). In fact, there was no difference between the observed and randomised pairwise distance matrices (Figure S5).

Next, we measured adaptive shifts in evolutionary rates for the hypervolume volume. Comparing the value of the adaptive regime (θ) in the root of the phylogeny with the adaptive regimes leading to other lineages, it is possible to assess if these new adaptive regimes suffer an increase or decrease in value. Thus, this can indicate if a smaller or larger hypervolume has been favoured in these lineages relative to the ancestral state. In gymnosperms at the species level, the root value of the adaptive regime (θ) of the hypervolume volume was estimated as 18.457. The model identified a complex evolutionary dynamic characterised by 17 major shifts in adaptive regimes. The most robust shifts ($PP > 0.90$) indicated strong selective pressures on specific lineages. Notably, we observed a sharp reduction in niche volume for *Torreya taxifolia* ($\theta = 10.745$; $PP = 0.99$) and *Taxus floridana* ($\theta = 11.734$; $PP = 0.84$), representing the lowest estimated θ values. Conversely, the clade comprising *Cycas* (*C. angulata*, *C. armstrongii*, *C. megacarpa, C. maconochiei, C. orientis, C. ophiolitica*, *C. canalis*, *C. calcicola*) showed a highly consistent shift ($PP = 0.99$) toward an intermediate volume regime ($\theta = 14.820$). Large-scale niche diversification events were detected in multi-species clades, suggesting the conservation of new adaptive regimes (Figure 1C). This is exemplified by shifts in *Macrozamia*, *Encephalartos*, and *Lepidozamia* ($\theta = 14.957$; $PP = 0.83$) and in the *Parrya* section of *Pinus* ($\theta = 16.172$; $PP = 0.72$). The highest adaptive regime value was found in a *Gnetum* clade (*G. africanum*, *G. gnemon*, *G. nodiflorum, G. gnemon, G. edule*), where the niche expanded to $\theta = 21.005$ ($PP = 0.60$), surpassing the ancestral root value. Other conifer clades, such as *Juniperus* ($\theta = 16.817$) and *Cupressus* ($\theta = 16.503$), also converged toward similar volume regimes.

Lastly, we tested if the relative distinctiveness of the niche of each genus and family of gymnosperms evolved non-independently, but the results were not statistically significant (Text S1). At the species level, we found a significant, albeit weak, phylogenetic signal for centroid distances, although this pattern was not maintained at the genus or family levels (Table S6). These results suggest that while niche distinctiveness retains some evolutionary heritage among closely related species, ecological niche hypervolume holes, like hypervolume volume, likely capture more dynamic ecological processes that evolve independently among lineages.

4 | Discussion

All species have a niche, and these niches are often represented as niche hypervolumes. Thus, the niche hypervolume remains one of the most significant concepts in ecology today (Chase 2011; McCann and Gellner 2020). Despite its significance to theoretical and empirical ecology, we lacked a comprehensive understanding of hypervolume properties and whether they evolve non-independently in related species. Here, we answer this question by studying the evolution of the Hutchinsonian climatic niche hypervolume properties in gymnosperms, by mapping how climatic niche hypervolume geometrical and topological properties, such as volume and holes, evolved across this group.

Holes in niche hypervolumes have been conjectured as ecologically meaningful (Blonder 2016). Our data provide the most comprehensive assessment of hypervolume holes in climatic niche hypervolumes and show that holes in niche hypervolumes are not influenced by evolutionary history in gymnosperms. This means that, if holes are indeed ecologically meaningful, they emerge because of species-environment interactions without priming effects from evolutionary history. Thus, the ecological significance of holey hypervolumes depends on individual life-histories and the population and community level interactions that shape species' climatic occupancy, with evolutionary legacies being of secondary importance. This is important because niche hypervolumes can be studied dynamically (i. e., changes through time) where the appearance of holes could signal responses to stressors that affect species' niches. For example, holes could be a direct reflection of landscape fragmentation that modulates and even prevents species from persisting or colonising suitable environments (Quiroga and Souto 2022). This aligns with the rationale underlying the original hypothesis of holey niches by Blonder (2016) but does not bring us closer to understanding if holey niches are meaningful ecologically. Future studies on the dynamics of niche hypervolumes could provide useful insights.

Our data suggest that climatic niche hypervolume evolved with only a moderate degree of phylogenetic dependence at the species level (Pagel's $\lambda = 0.492$; Table 1), whereby related species share more similar niche volumes than expected by chance. This could indicate that the ability to tolerate the breadth of climatic conditions is influenced at least partly by evolutionary history. However, our analysis of niche positioning shows that climatic distances between co-occurring species do not significantly depart from null expectations (Table S3). These results suggest that while the capacity to occupy narrower or wider climatic conditions is moderately conserved, the realisation of these niches within the climatic volume is independent of limiting similarity. Therefore, while the ability to occupy narrower or wider climatic conditions is moderately influenced by evolutionary legacies, its realisation does not support the competitive exclusion hypothesis in the climatic dimensions studies here. Note that Blomberg's K was not statistically significant at the species or family levels (see Table 1 and Table S5), and statistically significant only at the genus level (Table S5). Blomberg's K captures the degree of variation within and among lineages, and a non-significant value of K suggests that within-lineage variation is high relative to the phylogenetic expectation (Meireles et al. 2020). The statistically significant results at the genus but not species or family level were driven by the relatively homogenous hypervolume of genera within the Pinaceae, Araucariaceae, and Podocarpaceae families (Figure 1B). These are genera and families with widespread climatic tolerances which are represented by hypervolumes with comparatively higher volumes in our analysis. Contrastingly, Pagel's λ is a scalar that correlates a trait matrix with a phylogenetic matrix and was not statistically significant at the genus or family levels. The statistical significance observed at the species level but not at the genus and family levels is likely a combination of the number of species in our analysis and the variation of hypervolume within genera and families of gymnosperms.

Climatic niche hypervolume volume—but not holes—is correlated with species' IUCN threat status. Our data revealed a statistically significant relationship between hypervolume volume and IUCN threat status, with species with narrower niches consistently associated with higher vulnerability levels. This shows that hypervolume volume can be a proxy for species' threat levels. Similar patterns were observed at the genus and family levels suggesting that taxonomic level alone is not responsible for—and cannot override—the effect. We found no evidence that holey hypervolume properties were correlated with IUCN threat status at any taxonomic level (Table S4). While this does not directly test the conjecture in Blonder (2016) that holey hypervolumes can represent vulnerability to invasion, it does show that IUCN threat status is not linked to holey niche properties.

It is important to highlight that our analysis at the genus and family levels, despite combining species with different hypervolume characteristics and in different numbers, still capture known ecological features in gymnosperms. This opens the possibility that hypervolume properties can be studied at higher taxonomic levels. For instance, we found a nearly 2-fold difference between the smallest and largest hypervolume by volume in our dataset. *Gingko, Stangeria*, and *Welwitschia* genera had the lowest hypervolume volume estimates (Figure 1C). *Ginkgo* is a living fossil that has been deemed one of the most critically endangered gymnosperms in the world and, therefore, has a relatively narrow ecological distribution reflected in its hypervolume volume (Forest et al. 2018). Although not classified as (critically) endangered by the IUCN Red List, *Welwitschia* has a unique ecology and occupies arid and semi-arid environments in sub-Saharan Africa with relatively narrow ecological distribution, also being considered a living fossil. Likewise, *Stangeria* is not classified as (critically) endangered by the Red List but has a unique ecology and is endemic to southern Africa (Schönland 1918). These findings highlight that our hypervolume approach captures relevant ecological characteristics of the genera and families and, thus, that the lack of evidence for the non-independent evolution of ecological niche hypervolume properties is meaningful. The causes of such shifts are unknown and multifactorial, but the direct competition and diversification of angiosperms likely contributed, although cannot fully explain, this pattern (Fragnière et al. 2015).

The complexity of the high-dimensional geometries of hypervolumes poses challenges for the visualisation and computations of their properties. To study climatic niche hypervolume properties across gymnosperms, we needed to make simplifying assumptions to guarantee the feasibility of the analysis. One such assumption was that PCA transformation and dimensionality reduction of our point cloud preserved ecological information. This assumption is shared with most studies using the concept of niche hypervolumes (e. g., Pianka et al. 2017; Zhang et al. 2020; Ellis 2022) but it is worth highlighting that no systematic study has yet tested the implications of PCA on point cloud structure and hypervolume properties (but see also Mahony et al. 2017; Lu et al. 2021). PCA acts as a projection of the point cloud into lower dimensions and can introduce biases such as for example "filling in" holes which are present in higher dimensions. However, it is important to highlight that the opposite is not true: we cannot have artificial holes or topological structure emerging after PCA. Thus, our study provides a conservative estimate of the evolution of climatic niche hypervolume properties. We are currently working to develop algorithms which directly test the influence of PCA on climatic niche hypervolume properties, and which would allow the computation of hypervolume properties (particularly holes) more efficiently (Lazovskis et al. 2025). This is the scope of future work.

It is also worth noting that our study focused on climatic variables, but the concept of niche hypervolume can be extended to n-dimensions and represent a comprehensive set of conditions where species persist (Hutchinson 1957). The availability of nutrients and water in the soil is particularly relevant to plants and gymnosperms are known to respond and adapt to edaphic conditions at a global scale (Wang et al. 2019; Wang et al. 2023). The absence of phylogenetic signal for holey climatic niche hypervolumes does not imply that niche hypervolumes in other dimensions are convex or that their holey niches evolve non-independently. Gymnosperms occupy nutrient-poor, acidic and harsh soils in temperate regions (Bond 1989; Berendse and Scheffer 2009). Some edaphic traits have low variability in temperate regions (e. g., pH; Zhao et al. 2019), which would likely translate into convex (non-holey) edaphic hypervolumes if most species are occupying the narrow range of conditions available. Other edaphic traits such as C:N ratios are more variable and could underlie holey edaphic niche hypervolumes. Future studies should address this gap. We advise edaphic hypervolumes to be analysed independent of climatic niches especially if PCA is to be employed as the projection of climatic niches shown here to evolve non-independently could incorporate noise into the analysis of holey edaphic niches. We currently lack the computational tools to identify holes in high-dimensional niche hypervolumes using raw data and thus, dimensionality reduction such as PCA provides the only viable solutions. We are currently developing new tools to overcome this (Lazovskis et al. 2025).

5 | Conclusion

The niche is a cornerstone concept in ecology which has stimulated unprecedented advances in theoretical and empirical studies. Hutchinsonian climatic niche hypervolume is widespread in the literature and likely to become increasingly common for modelling ecological niches from open data. We studied the properties of the climatic niche hypervolumes of gymnosperms and found evidence that the climatic niche hypervolume volume is moderately influenced by evolutionary history whilst holes evolve independently. These are the first results to systematically probe how Hutchinsonian hypervolumes properties evolved, and to show that ecological niche hypervolume properties likely capture dynamic ecological characteristics of the niche. This probably limits the range of evolutionary inferences which can be made from Hutchinsonian climatic niche hypervolumes, especially if the goal is to identify the ecological significance of holey niches. Future work in other taxa for which phylogenetic relationships have been well established (e. g., vertebrates) will provide further insights into the evolutionary insights that can be gained from the concept of the (holey) niche hypervolume.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in Raw data and code area available in Zenodo: at https://doi.org/10.5281/zenodo.18509493.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Text S1:** Table S1. Families and genera used in the study with the respective DOI numbers from GBIF. **Table S2:** Cumulative variance explained by the first three principal components (PC1–3) across different taxonomic levels. **Table S3:** Climatic niche dispersion patterns (NRI) based on centroid distances of niche hypervolumes for each gymnosperm genus. **Table S4:** Phylogenetic linear regression models of hypervolume properties and IUCN threat status across different levels of organisation. **Table S5:** Phylogenetic signal using Blomberg's K (Blomberg et al. 2003) and Pagel's λ (Pagel 1999) of hypervolumes and holes at the genus and family level. **Table S6:** Phylogenetic signal using Blomberg's K (Blomberg et al. 2003) and Pagel's **λ** (Pagel 1999) of PCA centroids at the species, genus, and family level. **Figure S1:** Occurrence points for the genera and families with more than 50,000 data points. At the left (green) are all available occurrence points in GBIF. At the right (orange), the subset of 50,000 data points for this study is shown. (A) Occurrence points at the genus level. (B) Occurrence points at the family level. **Figure S2:** Phylogenetic signal and centroid analysis at the species level. (A) Character mapping of mean distance of points at dimension 2. (B) Character mapping of the standard deviation of distance of points at dimension 2. (C) Character mapping of the maximum distance of points at dimension 2. (D) Centroids of the PCA analysis for each species. Circles represent each species centroid, while the star represents the centroid for all species. (E) Bottleneck pairwise distance of persistence diagrams. Darker values represent closer bottleneck distances. **Figure S3:** Phylogenetic signal, adaptive shifts, and centroid analysis at the genus level. (A) Character mapping of the hypervolumes. Circles represent the adaptive shifts with a posterior probability higher than 0.3. (B) Character mapping of mean distance of points at dimension 2. (C) Character mapping of the standard deviation of distance of points at dimension 2. (D) Character mapping of the maximum distance of points at dimension 2. (E) Centroids of the PCA analysis for each family. Circles represent each family centroid, while the star represents the centroid for all families. (F) Bottleneck pairwise distance of persistence diagrams. Darker values represent closer bottleneck distances. **Figure S4:** Phylogenetic signal, adaptive shifts, and centroid analysis at the family level. (A) Character mapping of the hypervolume. Circles represent the adaptive shifts with a posterior probability higher than 0.3. (B) Character mapping of mean distance of points at dimension 2. (C) Character mapping of the standard deviation of distance of points at dimension 2. (D) Character mapping of the maximum distance of points at dimension 2. (E) Centroids of the PCA analysis for each family. Circles represent each family centroid, while the star represents the centroid for all families. (F) Bottleneck pairwise distance of persistence diagrams. Darker values represent closer bottleneck distances. **Figure S5:** Differences between the pairwise distance matrix calculated with the empirical data and a random pairwise matrix. (A) Family level analysis. (B) Genus level analysis. Solid line = mean, dashed = mean + or—1 standard deviation.