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The refuge effect of humid microhabitats for ferns decreases towards more arid regions

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Climate change is expected to intensify biodiversity loss through increasing aridity, but the potential of humid microhabitats to buffer these effects in tropical lowlands remains poorly understood. To address this gap, we surveyed 326 plots across 14 localities along a natural humidity gradient in northeastern Argentina, comparing fern diversity between climatically driven zonal habitats and more humid topographically or edaphically influenced azonal habitats. We found that azonal habitats supported greater fern richness than zonal ones in humid to semihumid regions, but this advantage disappeared towards the arid extreme, where both habitat types hosted equally poor communities. At the species level, only *Christella hispidula* and *Doryopteris pentagona* showed higher frequency patterns in azonal habitats toward drier conditions, whereas most species were more frequent in zonal habitats or showed no clear shift. Annual precipitation best explained variation in species richness, and soil conditions, such as salinity or unsuitable textures, may limit the capacity of azonal habitats to act as refugia under dry climates. Our findings reveal that humid microhabitats can act as refugia for ferns only under favorable moisture conditions, highlighting the need to account for local environmental heterogeneity and edaphic limitations when predicting biodiversity persistence under climate change.

KEYWORDS

climate change, ferns, microclimatic refugia, Northern Argentina, species richness, water regime

1 Introduction

Climate change is one of the main threats to global biodiversity (Omann et al., 2009). Changes in rainfall patterns and rising temperatures are expected to exacerbate physiological and ecological pressures on many species, potentially increasing extinction risks (Parmesan, 2006; Wahid et al., 2007; Pugnaire et al., 2019). Species can react to these changes by adapting to the novel conditions, by shifting their ranges, or by persisting in

microclimatic refugia where local environmental buffering mitigates broader climatic shifts (Dobrowski, 2011; Gould et al., 2015; Meza Torres et al., 2017; Kessler and Kluge, 2022). The strategies employed by species within a given ecosystem will vary depending on many factors such as life history traits, fundamental niche breadth, and habitat heterogeneity, the latter of which may facilitate the availability of microclimatic refugia. Microclimatic refugia are typically defined as locations where topographic, edaphic, or structural features create environmental conditions that differ from and buffer against regional climate (Dobrowski, 2011). Although the term “micro” often evokes very small spatial units (e.g., a rock crevice or treefall pocket), microrefugia can vary widely in extent. Their defining property is not size but their ability to provide locally cooler or moister conditions relative to the surrounding matrix (Kluge and Kessler, 2007; Jones et al., 2011). For example, in mountain systems, plant species have been observed to survive in cool microhabitats at lower elevations where regional climatic conditions are no longer suitable for them (Kluge and Kessler, 2007; Kessler et al., 2011; Gebrehiwot et al., 2019). A similar mechanism may operate in the tropical lowlands, where humid microhabitats could act as refugia under increasing aridity, although this remains poorly explored (Kluge and Kessler, 2007).

Under natural conditions, habitat heterogeneity arises from the spatial distribution of both zonal and azonal vegetation. Zonal habitats reflect broad-scale climatic conditions (Luebert and Plischoff, 2006; Oyarzabal et al., 2018), whereas azonal habitats – driven by localized topography or edaphic factors (Sieben, 2019) – create fine-scale environmental variability. The distinction between zonal and azonal habitats is widely used in ecology to separate environments that primarily reflect the prevailing regional climatic regime (“zonal” sensu Whittaker, 1971; Walter, 1979) from those where local topographic or edaphic conditions generate departures from the regional template (“azonal”; Küchler, 1967). Importantly, azonal habitats are not defined by exposure to different macroclimates, but by local modifiers — such as groundwater influence, riparian corridors, depressions, or shallow ravines — that create buffered or divergent microclimatic conditions (Dobrowski, 2011; Scheffers et al., 2014). Thus, whereas zonal vegetation reflects regional climatic controls, azonal habitats arise from fine-scale geomorphological and hydrological processes that alter soil moisture availability, thermal regimes, and vapor-pressure dynamics (Körner, 2007). Under this framework, differences between zonal and azonal environments stem from microenvironmental variation, not from distinct regional climate regimes. Azonal habitats often deviate markedly from zonal conditions, such as sun-exposed rocky outcrops in humid forests (i.e., drier) or riparian zones in arid landscapes (i.e., wetter), and thus support distinct biotic communities. Moreover, they frequently contribute disproportionately to regional biodiversity by harboring unique species assemblages (Sieben, 2019). In the context of climate change, habitat heterogeneity may prove critical, as azonal habitats that buffer against aridity or warming could serve as microrefugia, enabling species persistence where zonal conditions become unsuitable (Dobrowski, 2011).

To investigate the role of azonal habitats as microclimatic refugia, we focused on a natural humidity gradient in northeastern Argentina. This region exhibits a pronounced east–west climatic gradient (Karger et al., 2017), mirrored by a transition in zonal vegetation from tall evergreen rainforests in the east to successively lower and more seasonally deciduous forests in the west (Oyarzabal et al., 2018). Embedded within this zonal forest matrix are humid microhabitats such as estuaries, ravines, and forest islets, that may buffer against climatic extremes (Oyarzabal et al., 2018). Our findings will provide critical insights into future vegetation dynamics, as climate projections for the region predict warmer temperatures (particularly in spring), intensified seasonal precipitation contrasts (wetter rainy seasons and drier dry seasons), and heightened water stress (Nuñez et al., 2009; Intergovernmental Panel on Climate Change (IPCC), 2023). Although climate scenarios are relatively well-supported, little is known about how they will affect biotic communities in this region.

Ferns serve as an ideal study group for this project for several reasons. First, they are generally more susceptible to water stress than angiosperms due to less efficient stomatal control (Brodrribb and Holbrook, 2004; Brodrribb and McAdam, 2011; Brodrribb et al., 2017). Second, their efficient spore dispersal limits the effect of dispersal limitation and makes their presence more closely linked to habitat conditions (e.g. Tryon, 1986; Barrington, 1993; Wolf et al., 2001). Their analysis can thus provide evidence on the importance of plasticity and adaptation to climatic fluctuations.

Here, we leverage northeastern Argentina’s natural humidity gradient to test whether fern species use azonal humid microhabitats as microrefugia in areas of reduced water availability. At a broader scale and given the established link between fern diversity and water availability (Kreft et al., 2010), we hypothesize that: a) species richness will be higher in azonal than in zonal habitats, and this richness difference will become more pronounced as regional precipitation decreases; and (b) at a species-specific scale, individual fern species will tend to shift toward more humid microhabitats (azonal) as climatic humidity decreases, such that their relative frequency increases in azonal habitats compared to zonal habitats under drier conditions.

2 Methods

2.1 Sampling sites and data collection

We sampled in 14 localities (listed in Supplementary Figure 1) between 2020 and 2023 across northeastern Argentina, covering the provinces of Chaco, Corrientes, Formosa, and Misiones, prioritizing protected natural areas to avoid human intervention. All maps were produced using QGIS Version 3.28 (QGIS Development Team, 2024). The region exhibits a pronounced precipitation and temperature gradient going from 2150 Kg m⁻² year⁻¹ and 19.3 °C to 781 Kg m⁻² year⁻¹ and 23.5 °C, with more humid and cooler zones in the east and drier, warmer zones in the west (Figure 1). These localities were also selected because the temperature range found between them is not that strong, allowing to test under natural

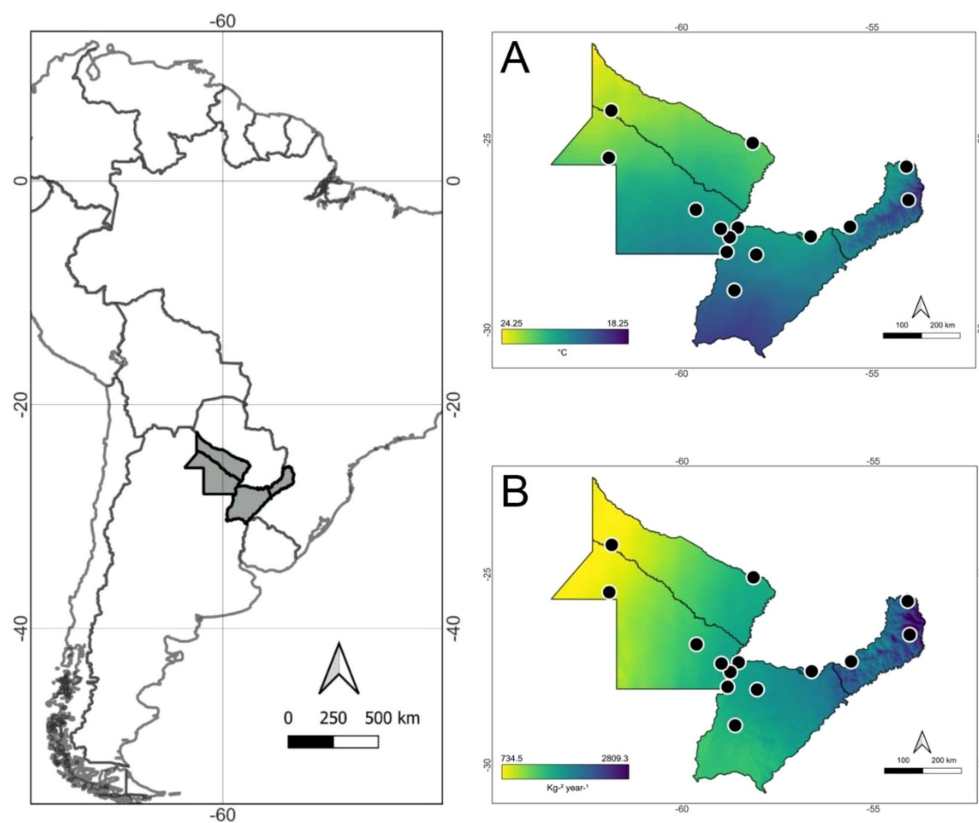


FIGURE 1

Study area and selected bioclimatic variables. Map of sampling localities in northeastern Argentina (dots) overlaid on: (A) Mean annual temperature (BIO1) and, (B) Annual precipitation, selected based on a Pearson correlation analysis to represent independent climatic dimensions related to thermal conditions and water availability. Both variables show clear spatial gradients, with temperatures decreasing toward the east and precipitation decreasing toward the west.

conditions primarily the influence of water availability. At each locality, we distinguished two habitat types following the vegetation unit classification proposed for Argentina by Oyarzabal et al. (2018), which describes the characteristic formations of each phytogeographic province. We defined zonal habitats as formations that represent regional climatic conditions (e.g., Misiones rainforest, Chaco forest), whereas azonal habitats corresponded to environments shaped by local factors such as topography or soil conditions (e.g., riparian forests, wetlands, ravines). This classification, based on a widely used phytogeographic framework, minimized subjectivity in site assignment.

In total, we established 326 plots of 400 m² each, with 8 to 40 plots per locality, distributing them evenly between zonal and azonal habitats. Since the types of habitats vary in heterogeneity and extent, not all localities had the same number of plots. We necessarily applied a lower sampling effort in the western sector of the gradient compared to the east, due to the limited extent and accessibility of humid environments in that region. This methodological decision also relied on available floristic evidence: The Flora of the Ferns of Argentina (Ponce et al., 2016) reports markedly low species diversity in the western Chaco, in contrast with the richness recorded in Misiones and Corrientes. Therefore, the reduced sampling intensity

in the arid sector reflects both logistical constraints and realistic expectations of diversity. To standardize sampling effort, we normalized the number of plots per locality while maintaining the proportion between zonal and azonal habitats. We maintained a minimum distance of 20 meters between plots. To minimize edge effects, we selected plots that were at least 50 meters away from forest boundaries. We applied the standardized sampling method proposed by Kessler and Bach (1999); Karger et al. (2015), recording all ferns species present and counting individuals. Epiphytes were identified and counted with binoculars, looking for fallen branches on the ground, climbing trees, and cutting selected branches. When species could not be identified in the field, we collected specimens for laboratory examination.

2.2 Data analysis

To examine the relationship between species richness and environmental conditions across habitat types, we focused on bioclimatic variables related to temperature and water availability, which are key drivers of fern distribution. We used mean annual

temperature ($^{\circ}\text{C}$; BIO1), annual precipitation ($\text{Kg m}^{-2} \text{ year}^{-1}$; BIO12), precipitation seasonality (Kg m^{-2} ; BIO15), precipitation of driest quarter ($\text{kg m}^{-2} \text{ month}^{-1}$; BIO17), precipitation during the warmest quarter ($\text{Kg m}^{-2} \text{ month}^{-1}$, BIO18), and mean monthly climate moisture index ($\text{Kg m}^{-2} \text{ month}^{-1}$, CMI mean), extracted from CHELSA V2.1 (Karger et al., 2017). Prior to analysis, we assessed collinearity among a broader set of temperature- and precipitation-related variables using a Pearson correlation matrix. Based on this assessment, we retained BIO1 and BIO12 as they capture complementary climatic dimensions while minimizing multicollinearity.

To analyze patterns of species richness, species richness per plot (count data) was used as the response variable. Because richness exhibited overdispersion, we fitted generalized linear mixed-effects models with a negative binomial error distribution (Venables et al., 2002). Annual precipitation (BIO12) or mean annual temperature (BIO1) were included as continuous predictors, while habitat type was included as a categorical fixed effect with two levels (zonal and azonal). To test whether the relationship between species richness and climate differed between habitat types, we included the interaction between the climatic predictor and habitat type. Locality was included as a random intercept to account for non-independence among plots within the same site.

At the species-specific scale, we analyzed changes in species frequency across the climatic gradient. Species frequency was calculated at the locality level as the proportion of plots occupied by a species within each habitat type, relative to the total number of plots sampled in that habitat type at the same locality. This standardization accounts for unequal sampling effort among localities and allows frequency values to range from 0 to 1. Species frequency was modeled as a function of annual precipitation, habitat type, and their interaction. To allow for potential non-linear responses, we additionally tested quadratic terms for precipitation.

All statistical analyses were performed with the statistical platform R (R Core Team, 2024), mainly using the built-in package stats and the additional package MASS (Venables et al., 2002).

3 Results

In total, we recorded 77 fern species across the study area. Azonal habitats contained 71 species, whereas 52 species were recorded in zonal habitats. Across all localities (Supplementary Table S1), Parque Nacional Iguazú showed the highest overall diversity, with 46 species. *Doryopteris concolor* (Langsd. & Fisch.) Kuhn and *Microgramma vacciniifolia* (Langsd. & Fisch.) Copel were the most widespread species, occurring in 11 localities, followed by *Doryopteris pentagona* Pic.Serm. (9 localities), *Pleopeltis minima* (Bory) J. Prado & R.Y. Hirai (8 localities), and *Adiantopsis chlorophylla* (Sw.) Fée (7 localities).

At the plot scale, the highest species richness values were recorded in the province of Misiones, where several plots contained up to 12 species. In the provinces of Corrientes, Chaco, and Formosa, the richest plot in Corrientes contained 11 species, whereas maximum plot-level richness in the latter two provinces did not exceed three and two species, respectively.

3.1 Climatic effects on species richness in zonal and azonal habitats

We analyzed species richness per plot using negative binomial mixed-effects models. Mean annual temperature (Figure 2A) and annual precipitation (Figure 2B) significantly affected species richness (Table 1), whereas habitat type alone did not. Species richness increased with annual precipitation and decreased with mean annual temperature. We did not detect a statistically

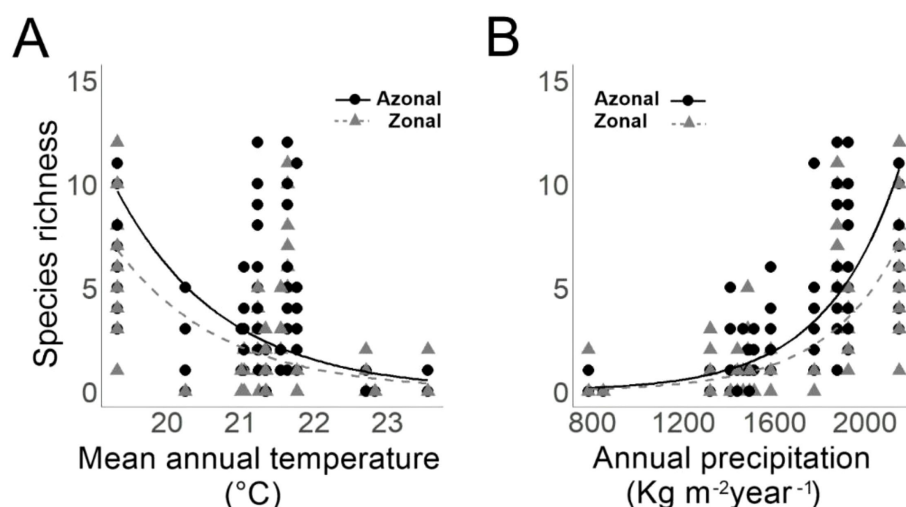


FIGURE 2

Species richness in relation to mean annual temperature (A) and annual precipitation (B) in zonal (grey) and azonal (black) habitats. Points represent individual plots; triangles and grey lines correspond to zonal habitats, whereas circles and black lines correspond to azonal habitats.

TABLE 1 Pearson correlation matrix of temperature- and precipitation-related bioclimatic variables used to assess collinearity prior to model fitting.

Bioclimatic variables	BIO1	BIO12	BIO15	BIO17	BIO18	CMImean
BIO1	1.00	-0.72	0.65	-0.60	-0.74	-0.74
BIO12	-0.72	1.00	-0.98	0.96	0.94	0.98
BIO15	0.65	-0.98	1.00	-0.95	-0.88	-0.95
BIO17	-0.60	0.96	-0.95	1.00	0.88	0.95
BIO18	-0.74	0.94	-0.88	0.88	1.00	0.96
CMImean	-0.74	0.98	-0.95	0.95	0.96	1.00

Based on this analysis, mean annual temperature (BIO1) and annual precipitation (BIO12) were retained as they represent complementary climatic dimensions while minimizing multicollinearity.

significant interaction between annual precipitation and habitat type, indicating that the relationship between precipitation and species richness did not differ between zonal and azonal habitats. Likewise, mean annual temperature did not interact significantly with habitat type. Locality accounted for a substantial proportion of the variance as a random effect.

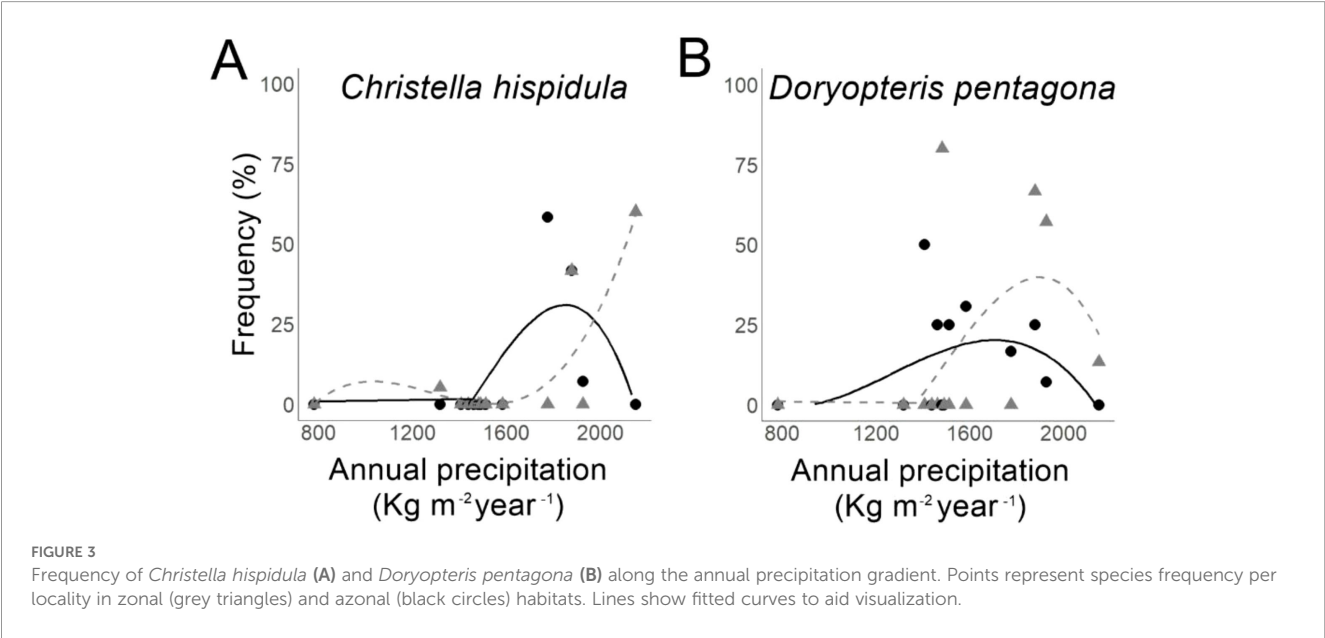
3.2 Species frequency patterns along the precipitation gradient

Thirteen fern species were recorded in four or more localities. Species frequency varied widely among species and across the precipitation gradient. For most species, frequency did not show a consistent relationship with annual precipitation across habitat types. Two species, *Christella hispidula* (Decne.) Holttum (Figure 3A) and *Doryopteris pentagona* (Figure 3B), showed higher relative frequencies in azonal habitats toward drier conditions, whereas several species displayed higher frequencies in zonal habitats or no clear differences between habitat types. For most species, the

interaction between annual precipitation and habitat type was not statistically significant. In the two driest localities (L13 and L14), species richness was low in both habitat types, with two species recorded in each. *Anemia tomentosa* (Savigny) Sw. var. *tomentosa* and *Cheilanthes obducta* Mett. ex Kuhn occurred in both zonal and azonal habitats, with higher frequencies in zonal plots.

4 Discussion

Our results indicate that species richness in the studied environments is strongly influenced by water availability, a key factor in shaping biodiversity and ecosystem resilience under climate change (Kessler and Kluge, 2022; Harrison et al., 2020). Among the analyzed variables, annual precipitation and mean monthly precipitation of the warmest quarter best explained species richness variation, which aligns with previous studies highlighting water input as a critical driver of fern diversity and distribution (Kreft et al., 2010; Kessler and Kluge, 2022; Weigand et al., 2019; Suissa et al., 2021). In contrast, mean annual



temperature had the weakest relationship with species richness, likely due to the relatively narrow temperature range among localities. This pattern is consistent with previous studies indicating that precipitation and water availability have a stronger influence than temperature on fern species richness, particularly in tropical and montane regions where thermal variation is limited and moisture becomes the main limiting factor (Kluge et al., 2006; Kluge and Kessler, 2007; Hietz, 2010).

Our study was built on the premise that azonal habitats function as humid microclimatic refugia for ferns under drier conditions (Dobrowski, 2011). Accordingly, we predicted that the species richness of azonal habitats should increase relatively to zonal ones as it gets drier, and therefore, individual species should shift their habitat preferences from zonal to azonal habitats. However, neither of these predictions are met when we analyze the study gradient as a whole. While azonal habitats host greater fern species richness than zonal habitats, this difference only emerges at the more humid end of the climatic gradient. The same was observed at species level, where only 2 of the 12 most abundant ferns followed the predicted shift to azonal habitats towards arid conditions.

This unexpected result is largely driven by our two westernmost study locations, which are located in a very arid region and where azonal habitats likely exhibit humid conditions only seasonally. However, they often develop on loamy and saline soils, which are generally unsuitable for fern establishment (Pennington et al., 2001; Oyarzabal et al., 2018). Excluding these two locations, brings our results more in line with our expectations, so that under humid to semihumid climatic conditions, humid azonal habitats do indeed play a certain role as habitat refugia for fern species requiring humid habitat conditions. This is in accordance with higher fern richness in ravines in Bolivian mountain forests (Kessler, 2001).

This suggests that humid microhabitats may indeed act as refugia for some fern species under conditions of increasing aridity and temperatures during climate change, but only until a certain threshold, when it gets too dry in general for ferns, and when even humid microhabitats have too extreme climatic and edaphic conditions to support most fern species. Thus, our findings challenge the notion of a universal role of microrefugia and highlight the need to integrate edaphic factors and environmental heterogeneity into predictions of species persistence under climate change. Furthermore, the effectiveness of microhabitat refugia depends on the temporal and spatial scales of analysis (Gould et al., 2015) and may also be influenced by biotic interactions (Olsen and Klanderud, 2014). Statements in this regard need to be made with care and have to take into consideration the local habitat conditions (Kluge and Kessler, 2007; Dobrowski, 2011), including environmental heterogeneity and soil properties, both of which are likely to play increasingly important roles under climate change (Pugnaire et al., 2019).

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found in the article/Supplementary Material.

Author contributions

SP: Methodology, Writing – review & editing, Formal analysis, Validation, Data curation, Conceptualization, Writing – original draft, Investigation, Resources, Software, Visualization. DA-M: Investigation, Visualization, Software, Formal analysis, Validation, Conceptualization, Supervision, Writing – review & editing, Methodology. MK: Visualization, Resources, Validation, Formal analysis, Project administration, Conceptualization, Writing – review & editing, Methodology, Investigation, Software, Funding acquisition, Supervision. JK: Software, Formal analysis, Investigation, Visualization, Supervision, Validation, Conceptualization, Methodology, Writing – review & editing, Data curation. EM-T: Supervision, Investigation, Resources, Conceptualization, Funding acquisition, Writing – review & editing, Project administration, Visualization, Methodology, Validation.

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Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2026.1719536/full#supplementary-material>

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