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Sticky Innovation, Limited Expansion: Biogeography and Evolutionary Ecology of Toepads in Geckos

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ABSTRACT

Aim: This study investigates the evolutionary diversification and ecological significance of adhesive toepads in geckos. It examines how different toepad configurations (absent, basal, distal and fanlike) have evolved and relate to macroecological patterns. By analysing variation beyond mere presence or absence, it provides a finer-scale understanding of toepad evolution and its links to climate, habitat and biogeographic history.

Location: Global.

Major Taxa Studied: Gekkota.

Methods: Toepad types were assigned based on species descriptions. An ultrametric phylogeny was pruned and calibrated for ancestral state reconstruction via stochastic character mapping. Species distribution, habitat and climate data were compiled from global databases and analysed in R. Species richness, habitat associations and climatic niche space were analysed in relation to toepad configuration.

Results: Toepad configurations are unevenly distributed across gekkotans, with padlessness reconstructed as the ancestral and most common state. Transitions between configurations occurred frequently, including secondary pad loss. Geographic distributions and climatic niche space differ by pad type, with padless species occupying the broadest and most variable conditions. Habitat associations also vary among configurations, with forest being the dominant habitat category across all groups.

Main Conclusions: This study confirms padlessness as the ancestral condition and highlights multiple origins of adhesive toepads. While transitions from padless to basal pads are most frequent, transitions from distal to basal pads are also supported. Climatic niche analysis shows that toepads do not grant access to new climate zones but reflect fine-scale ecological adaptations, particularly to structurally complex habitats. Toepad configurations appear to facilitate ecological diversification within biomes. Geographic patterns seem more influenced by biogeographic history than direct climatic filtering, underscoring the role of historical contingency in shaping functional diversity.

1 | Introduction

One of the central aims in evolutionary biology is to understand why some lineages diversify extensively while others remain species-poor. One widely studied mechanism is adaptive radiation, characterised by elevated rates of lineage diversification and pronounced ecological and morphological disparity driven by access to novel ecological resources (Glor 2010; Mahler et al. 2010; Schluter 2000). A necessary condition for such radiations is ecological opportunity, which may arise from multiple, non-exclusive sources, including geographic dispersal into new environments, climate change, or the extinction of antagonists (Glor 2010; Sternes et al. 2024; Stroud and Losos 2016). Novel traits that can generate or amplify ecological opportunity are often referred to as key innovations (Miller et al. 2023; Rabosky 2017). However, the relationship between key innovations, ecological opportunity and diversification is complex. While key innovations may facilitate adaptive radiation, they do not guarantee it, and their evolutionary significance must be assessed in light of both functional performance and biogeographic history. Thus, integrating macroevolutionary and biogeographic perspectives provides a powerful framework for evaluating how morphological innovations interact with environmental context to shape patterns of lineage diversification.

Adhesive toepads are often cited as a potential key innovation for arboreality in lizards (Miller and Stroud 2021). Within lizards, adhesive toepads are particularly prevalent and diverse within the monophyletic infraorder Gekkota, which includes about 30% of all lizard species (Uetz et al. 2025). Approximately 60% of gekkonid species possess adhesive toepads, facilitating astonishing climbing abilities via reversible dry adhesion (Gamble et al. 2012; Russell et al. 2019). Due to their exceptional efficiency, these toepads have been extensively studied, especially in an attempt to replicate this system for biomimetics (Higham et al. 2019; Russell et al. 2007). The adhesion is generated through a combination of van der Waals forces (Autumn et al. 2002) and frictional adhesion (Autumn et al. 2006). Morphologically, the system relies on microfibrillar stalks on the superficial layer of the sub-digital epidermis known as setae (Gamble et al. 2012), which branch into triangular tips called spatulae (Autumn et al. 2006) for increased surface area. These setae are organised into lamellae or scansors, two types of modified scales that differ in internal anatomy, with scansors allowing fine-scale control via tendinous, adipose, or capillary regulations. Both occur differentially among pad-bearing gekkotans (Bergmann and Russell 2003; Griffing et al. 2022).

Toepad morphologies can strongly differ at the inter-specific level but also intra-specifically, particularly across different digits or among individuals from different populations. This has prompted investigations of their morphology across a number of gekkotan species (Russell 2002; Russell and Bauer 1990). However, studies linking morphology to ecology have been limited. While studies focusing on specific species or genera exist (Riedel et al. 2024; Russell and Delaugerre 2016), studies including the larger gecko phylogeny are limited (but see Zimin et al. 2025) and the need for such studies has been pointed out several times (Gamble et al. 2012; Higham et al. 2019; Russell and Gamble 2019). Additionally, the functional differences between toepad morphologies are not fully explored yet (Russell and Gamble 2019). However, the general idea is that certain morphologies are associated with different structural habitats.

Generally, the development of toepads represents a significant evolutionary innovation among lizards, facilitating enhanced locomotion in vertical environments (Griffing et al. 2022; Miller and Stroud 2021). However, toepads are not a necessary requisite to conquer arboreal habitats, as there are a number of arboreal species lacking pads (Miller and Stroud 2021). Besides aiding in vertical movement, climbing pads provide critical support for gekkotans in various dynamic activities. They serve a crucial function in catching oneself during falls or jumps, enduring substantial forces beyond typical climbing scenarios (Higham et al. 2017). Furthermore, adhesive strength is positively correlated with maximum acceleration, an important trait for escaping predation (Higham 2025). Thus, toepads function as multipurpose adaptations, contributing to both locomotor efficiency and the mitigation of high-impact forces.

Interestingly, adhesive toepads evolved multiple times independently within gekkonids, contrasting the single evolution in the Scincidae and *Anolis* (Anolidae) respectively (Miller and Stroud 2021; Russell and Gamble 2019). Previous studies reconstructed the ancestral state in gekkotans as padless, a condition retained by two families: the Carphodactylidae and the Eublepharidae. The other non-limb-reduced families include species bearing pads (Russell and Gamble 2019). The independent evolution and occasional loss of toepads suggest a complex interplay between environmental demands and locomotor adaptations.

Understanding the origin of toepads and what is driving their diversification has generated considerable research interest (Higham et al. 2016; Riedel et al. 2021, 2024; Russell et al. 2015; Russell and Gamble 2019). Generally, it is hypothesized that the diversification of toepad morphologies occurred rapidly approximately 50–100 million years ago during the early evolution of gekkotans. A closer look at the different morphologies indicates repeated parallel evolution across genera (McCann and Hagey 2024; Russell and Gamble 2019). This suggests that ecological pressures, rather than shared ancestry, may have played a key role in shaping toepad diversity.

The goal of the current study is twofold. Firstly, the categorization and ancestral state reconstruction of the larger gecko phylogeny will offer insights into the evolutionary background, continuing the work of Russell and Gamble (2019). More importantly, by examining the climatic and geographical space occupied by different toepad categories, along with their associated habitat types, we test the hypothesis that variation in toepad morphology may have facilitated access to novel habitat niches, as we expect a close link between locomotor performance, habitat use, and climate. While the general presence or absence of toepads has already been considered in terms of structural microhabitat selection (Zimin et al. 2025), the inclusion of specific toepad types allows for a finer-scale understanding. Here, we take a first step by addressing the broadest ecological and biogeographical patterns, providing a baseline from which more detailed analyses (e.g., looking at more fine-scaled patterns of niche partitioning) can build. By integrating biogeography, climate and habitat information, this study explores how different toepad configurations correspond to specific environmental conditions, offering a foundation for understanding the connection between repeated morphological adaptation, biogeography and ecology.

2 | Materials and Methods

2.1 | Study Species

This study includes all the recognised non-limb-reduced Gekkota species as of September 30, 2023 (2230 species) based on the Reptile Species Checklist by the Reptile Database (Uetz et al. 2023). Species names from other data sources were reconciled against this list by consulting the Reptile Database species name history.

2.2 | Data Collection and Preparation

Each species was assigned a toepad category [absent, basal, distal, fanlike (see illustrations Figure 2)] based on original species descriptions, following the classification system of Russell and Gamble (2019). Habitat data following the International Union for Conservation of Nature (IUCN) Habitats Classification Scheme (Version 3.1) (considering only the highest hierarchy) for 1497 species were obtained through the R package 'rredlist' (Gearty and Chamberlain 2024). Distribution ranges of 1833 gecko species were accessed through GARD 1.7 (Global Assessment of Reptile Distributions) (Roll and Meiri 2022).

Climate data (mean annual air temperature [bio1], annual precipitation amount [bio12], net primary productivity [npp], climate moisture index [cmi]) were obtained from CHELSA (Climatologies at high resolution for the earth's land surface areas) (Karger et al. 2021) as averages for the years 1981–2010. These variables were selected for their ecological relevance and low intercorrelation and represent metrics that are useful to differentiate between different biomes (Whittaker 1970).

All data preparation and analysis steps were performed using R (R Core Team 2023) version 4.3.3 and the 'dplyr' package (Wickham et al. 2025) was used for data manipulation. An ultrametric Gekkota phylogeny was computed from a fully sampled squamate phylogeny (Tonini et al. 2016). The tree was subset to include the non-limb-reduced Gekkota, with species names aligned to the most recent taxonomy as provided by the Reptile Database (Uetz et al. 2023). Polytomies were resolved using 'RRphylo' (Castiglione et al. 2018), with all multifurcating nodes randomly resolved and a numerical tolerance of 1e-10. The resulting tree was rendered ultrametric by a semi-parametric penalised likelihood approach with a smoothing parameter of $\lambda = 0.1$ using the 'ape' package (Paradis and Schliep 2019).

2.3 | Phylogenetic Modelling

Using the 'picante' package (Kembel et al. 2010), the toeapd categories were matched to the phylogenetic tree. Via the 'phytools' package (Revell 2012), three transition models (equal rates [ER], all rates different [ARD], symmetric [SYM]) were compared through Akaike information criterion (AIC). The best-fitting model was used to generate 1000 stochastic character maps to infer evolutionary transitions. Using the same methods, hidden states models were fit using the 'corHMM' package (Beaulieu et al. 2025) on the non-resolved tree, once without hidden states and once with two rate categories.

2.4 | Ecological and Climate Niche Space Analyses

Species richness maps were computed by rasterizing distribution polygons from GARD 1.7 using the 'terra' (Hijmans 2023a) and 'raster' package (Hijmans 2023b) with a spatial resolution of 2.5 min in equal earth Greenwich projection (EPSG: 8857). Species richness maps were generated per toepad configuration.

Climate niche space was analyzed through principal component analysis (PCA) using median and standard deviation values of the CHELSA climate variables across species ranges, accessed with the 'exactextratr' package (Baston 2023). The PCA was performed through the 'ade4' package (Dray and Dufour 2007), and principal components (PC) with eigenvalues > 1 were retained (Table S2). Hypervolumes sensu (Blonder et al. 2024) were constructed for each toepad category using the support vector machine (svm) approach and compared using hypervolume overlap statistics to assess differences in climatic niches with the 'hypervolume' package.

IUCN habitat types were aggregated to the highest level, retaining only suitable habitats according to the assessments while marginal habitat categories were excluded. Through combination with the toepad data, the proportion of habitat category per toepad configuration was assessed. 95% confidence intervals (CIs) were calculated in each toepad category for every habitat. The seven most common habitat categories were considered.

3 | Results

Toepad configurations are unevenly distributed across gekkotan families (Figure S1). The absence of toepads is the ancestral and most common state, present in 941 species, followed by basal toepads (849 species), distal toepads (407 species) and fanlike toepads (33 species). No carphodactylid and eublepharid species possess adhesive toepads. Among the remaining families, the basal and distal configurations are widespread, but fanlike toepads are only present in the Gekkonidae and the Phyllodactylidae.

Based on model comparison, the ARD model was selected as the best-fitting model of trait evolution (Table S1). When including hidden states (rate.cat = 2), simpler ER and SYM parameterizations were favoured while ARD performed poorly (Table S5). Although the hidden-state models fit better statistically, they did not alter the biological interpretation: transitions between states are still consistent with the asymmetries identified under ARD. Importantly, ER and SYM do not allow estimation of directional biases, which are present at least at the level of toepad gain versus toepad loss (Higham et al. 2015; Russell and Gamble 2019).

Therefore, we present ARD results in the main text as it allows for a biologically more meaningful interpretation and provide hidden-state model fits as Appendix (Figures S3 and S4).

Ancestral state reconstruction supports absent toepads as the ancestral condition (Figure 1), retained by the two padless families. The pad-bearing families show transitions from the absent configuration to a pad-bearing configuration. Additionally, transitions between pad-bearing types and toepad losses are reconstructed (Figure 2). Specifically, 31.237 transitions occurred on average; the most common transition is from padless to a pad-bearing configuration. The transition towards basal toepads is hypothesized to be the most frequent (15.915 times on average). Additionally, 4.346 toepad losses from the basal and distal configuration are reconstructed. No changes from the fanlike state into another are reconstructed.

Within the global gekkotan distribution, geographical differences in the occurrences according to the toepad configuration are visible (Figure 3). Padless species are widely distributed, with richness hotspots in Northern Africa, the Middle East, Central Asia and Australia, though absent from Madagascar. Basally padded species dominate in Africa (including Madagascar) and Southeast Asia, with a notable hotspot in western Namibia. Distal toepads are concentrated in Australia, with scattered occurrences elsewhere. Fanlike toepads have the narrowest range, restricted to Madagascar, North Africa and the Arabian Peninsula.

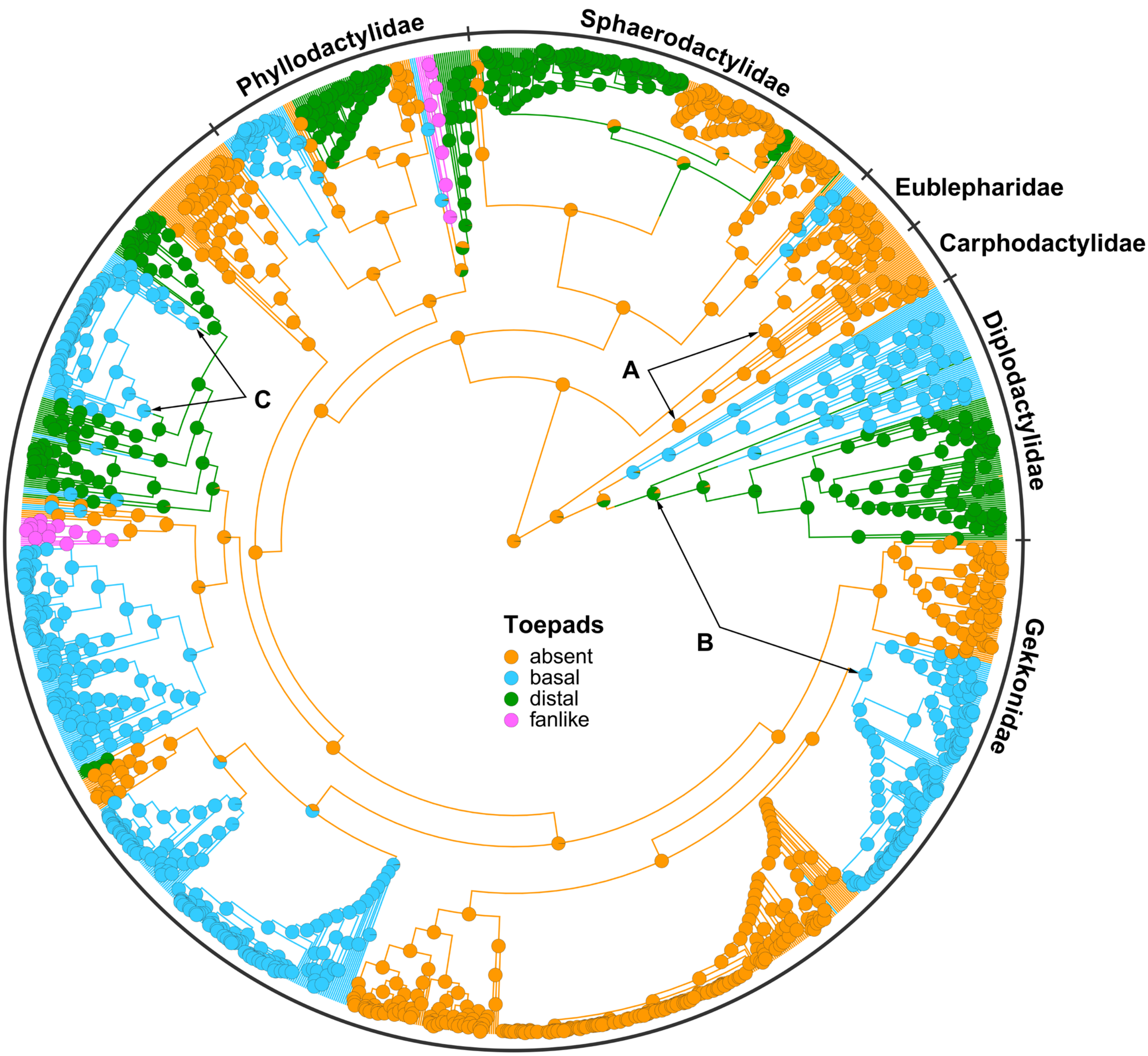

FIGURE 1 | Phylogenetic fan tree of 1512 Gekkota species with four toepad configurations mapped as discrete characters under an all-rates-different transition model. Branch colours correspond to a single representative tree randomly selected from 1000 stochastic character mapping simulations. Pie charts at internal nodes indicate the proportion of inferred character states across all simulations. Marked transitions show (A) retention of ancestral padless configuration in Eublepharidae and Carphodactylidae, (B) examples of independent origins of adhesive toepads, (C) examples of transition from the distal to the basal configuration.

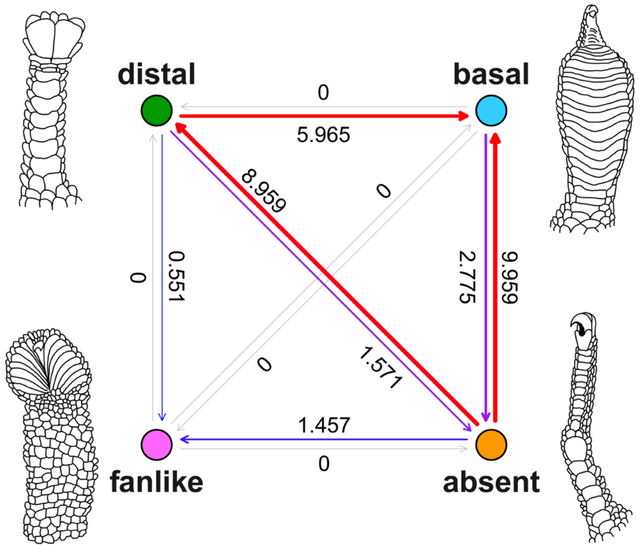

FIGURE 2 | Average transition rates between four toepad configurations across 1000 simulations using an all-rates-different transition model. Illustrations depict the ventral view of digit IV from representative species: Left pes of *Cyrtodactylus khasiensis* (absent), right pes of *Gekko smithii* (basal), left pes of *Ebenavia inunguis* (distal), and left pes of *Uroplatus ebenaui* (fanlike). Illustrations modified from Riedel et al. (2024) and Russell and Gamble (2019).

Hypervolumes show clear differences in the climatic space occupied by toepad categories (Figure 4), with three PC-axes representing 89.24% of the variation in climate space. On PC1 (43.06%) all toepad categories overlap on the positive side, which is associated with lower median values and variability of the climate variables. Species with basal pads and padless species tend to dominate the negative side, representing regions with higher overall climate values and variability. PC2 (33.22%) reflects a contrast between stable and variable climates. Fanlike and distally padded species cluster near zero, indicating occupation of narrower climate ranges. In contrast, basally and especially non-padded species are more widely dispersed along this axis, suggesting representation in both stable and highly variable climates. The final axis, PC3 (12.96%), captures temperature structure, largely independent of other climate variables. All padded species cluster around zero, while non-padded species extend along the positive end, indicating association with cooler but more variable thermal environments. The absolute volumes resemble the species numbers per category. Accordingly, species with absent toepads occupy the largest space and species with fanlike toepads the smallest. Generally, hypervolumes overlap extensively (Table 1). Absent toepads show the largest unique fraction of climate space (51%–86%), while basal toepads overlap minimally with absent toepads (19% unique). Distal and fanlike configurations show limited unique space (3%–6%) and overlap extensively with each other. However, fanlike toepads have a larger unique fraction relative to distal toepads (28%).

The proportion of IUCN habitat types varies with toepad configuration (Table 2). Forest is the most frequently associated habitat across all groups, with observed proportions consistently exceeding the 95% CIs. Rocky areas represent the second most common habitat, also showing proportions above the CI in all groups, most notably in species with basal (31.9%) and distal (31.4%) pads. Artificial terrestrial habitats are more evenly distributed across toepad types, though slightly less common in species lacking toepads (14.3%). Distinct differences emerge in more open and arid habitats: savanna and shrubland are more frequently associated with species possessing basal and distal toepads, with proportions exceeding the upper bounds of the CI. Grassland, though generally less common, is most prevalent in species with distal toepads (14.0%). Desert habitats are primarily associated with fanlike species (19.0%) and, to a lesser extent, those without adhesive pads (12.5%).

4 | Discussion

4.1 | Ancestral State Reconstruction and State Transitions

This is the first toepad categorization of all the recent non-limb-reduced Gekkota species (as of September 2023). About 42% of the non-limb-reduced Gekkota species do not possess adhesive toepads (Figure S1).

The ancestral form, absent toepads, was retained by two families: the Eublepharidae and the Carphodactylidae, in line with previous studies (Gamble et al. 2012; Russell and Gamble 2019). Phylogenetic reconstructions suggest the Diplodactloidea (Diplodactylidae, Carphodactylidae, Pygopodidae) represent the sister group to all remaining gekkotans (Gamble et al. 2012). The divergence of Eublepharidae from the lineage comprised of the Sphaerodactylidae, the Gekkonidae and the Phyllodactylidae likely occurred during the Jurassic (around 179 MYA) and may have been associated with the breakup of Pangea into Laurasia and Gondwanaland (Jonniaux and Kumazawa 2008). This is consistent with the independent origins of adhesive toepads within the Gekkonidae and the Diplodactylidae (Figure 1B). Meanwhile, the carphodactylid–pygopodid lineage, part of the Australasian diplodactyloid radiation, likely originated following the West–East Gondwanan divide, with extant representatives now restricted to Australasia (Oliver and Sanders 2009; Skipwith et al. 2019).

The remaining four non-limb-reduced families include padded as well as padless species. Within the Gekkonidae, 46.7% lack toepads, mostly by retaining the ancestral state. However, some lineages show signs of secondary toepad losses. For example, within the southern African clade containing *Chondrodactylus*, *Pachydactylus* and *Rhoptropus* (among others, Heinicke et al. 2017), all species bear basal toepads, except *Pachydactylus rangei* and *Chondrodactylus angulifer*. For both species, morphological evidence points towards a secondary toepad loss (Gamble et al. 2012; Russell and Gamble 2019). The only diplodactylid species lacking pads, *Lucasium damaeum*, shows similar morphological evidence (Russell and Gamble 2019), matching a secondary loss reconstructed in this study. All padless phyllodactylids and sphaerodactylids (46.3%) seem to have retained the ancestral state, in line with previous evidence (Russell and Gamble 2019).

The basal configuration is present in all four pad-bearing families. It is the most common pad type within the Gekkonidae (45%), while in the remaining three families the distal configuration

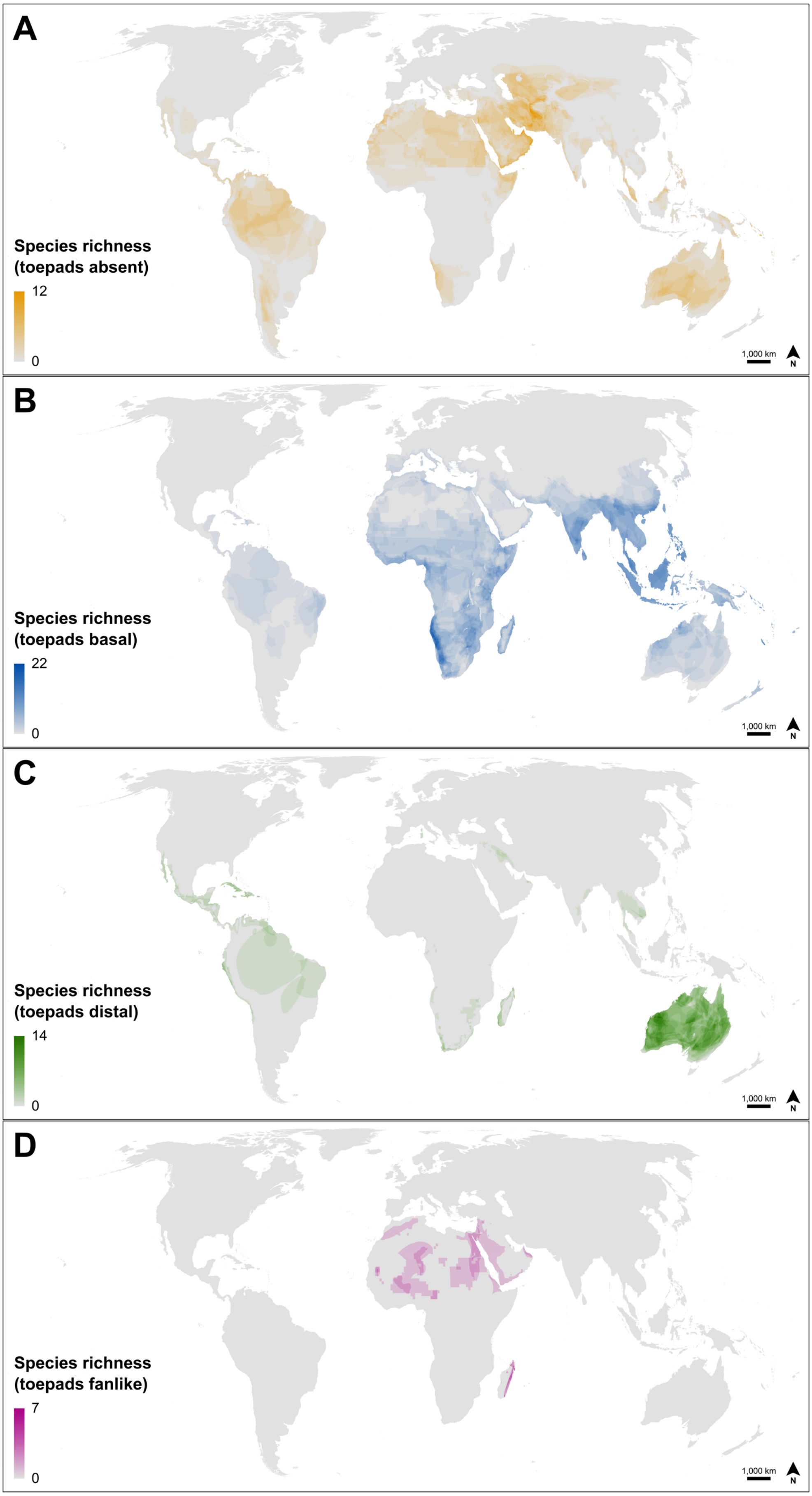

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FIGURE 3 | Global species richness maps for each toepad category: (A) absent, (B) basal, (C) distal, (D) fanlike. Species richness is shown using a colour gradient.

dominates: Phyllodactylidae (52.4%), Sphaerodactylidae (49.8%) and Diplodactylidae (51.3%). The rarest configuration, fanlike, is present in only 33 species from two genera: *Ptyodactylus* (Phyllodactylidae—7.3%) and *Uroplatus* (Gekkonidae—1.3%).

Previously, when considering fewer gekkonid species, multiple gains of adhesive toepads have been hypothesized (Gamble et al. 2012; Russell and Gamble 2019), consistent with the results of the current study. However, the hypothesized transitions between toepad configurations differ. The 2019 study favours transitions from the basal to distal configuration, arguing that the distal configuration is often nested within clades possessing the basal configuration (Russell and Gamble 2019). Conversely, the transition model of the current study hypothesizes an average of about six transitions from distal to basal toepads and no transitions from basal toepads. The differences in the hypothesized transitions can be attributed to the use of differing transition models. While the current study applied the ARD model, a previous study (Russell and Gamble 2019) applied a single-parameter model with equal rates. The ER model was a better fit (determined by AIC) for the smaller dataset of 149 non-limb-reduced Gekkota species. However, the current analysis includes 1512 species, leading to the better support of the ARD model (Table S1), which needs larger datasets to provide the necessary information to estimate the multiple parameters.

Although basal toepads are the most common in terms of absolute numbers, the distal configuration is more common proportionally within the individual families (excluding the Gekkonidae). Since there is compelling evidence for independent gains of toepads in various families, they should be considered individually. Excluding the Gekkonidae, gains of distal toepads are hypothesized more often than gains of basal toepads, suggesting their evolution is more likely. This is supported by the developmental patterns of the different toepad configurations. Truncating embryonic development of digital adhesive pads appears to result in more distally situated pads, both in distal pads (e.g., *Sphaerodactylus*) and basal pads (*Hemidactylus*) (Griffing et al. 2022, 2024). Additionally, the development of toepads is accomplished through derived distal-to-proximal morphogenesis of the digital scales (Griffing et al. 2022, 2024), suggesting distal pad development is less complex. Earlier studies looking at the internal digit anatomy of distally and basally padded species have hypothesized the development from distal to basal pads as well (Russell and Bauer 1990).

Importantly, the question of whether basal or distal toepads are ancestral within clades expressing both types might be clade-specific. For example, a study on terrestrial and saxicolous lineages of *Heteronotia binoei* (padless) found enlarged terminal subdigital scales in the saxicolous lineages (Riedel et al. 2021), arguing for an evolution from absent to distal toepads. When looking at a similar study working on the padless genus *Cyrtodactylus*, trends towards the expression of basal toepads in response to specific habitats exist (Riedel et al. 2024). Additionally, the possibility of the joint evolution of both pad types cannot be excluded (Gamble et al. 2012). While comparative anatomy and genetic studies (Gamble et al. 2012; Russell and Gamble 2019) can offer some insights, these methods often provide indirect evidence that can lead to conflicting interpretations. One reliable way to answer such questions is through an examination of the fossil record (Jablonski and Shubin 2015). Although the gekkotan fossil record is limited and soft tissue preservation, such as toepads, is rare, initial discoveries (Bauer et al. 2005; Arnold and Poinar 2008) offer promising potential for future research.

4.2 | Global Distribution and Climate Niche Space

The integration of ecological data into the evolutionary history of gekkotan toepads offers a promising chance to unravel the patterns driving their immense diversification (Higham et al. 2019; Riedel et al. 2024). The hypervolumes of each toepad type reflect their distribution and species numbers, with species lacking adhesive pads occupying the largest and most diverse environmental range, followed by those with basal, distal and fanlike pads, which inhabit more homogeneous conditions.

Due to the large hypervolume of species with no adhesive pads, they have the highest amount of space unique to them (at least 51%), corresponding to their wide geographic range with the southern- and northernmost distribution of any configuration. This is underlined by having the highest variability of climate values.

The northernmost distribution areas of padless gecko species tend to coincide with arid and desert-like environments (Figure S2). Although specific ecological data on these northern species may be limited, their occurrence in such habitats can be interpreted through existing literature on gecko morphology and habitat specialisation. Studies on pedal specialisations in dune-dwelling geckos showed that certain desert species have evolved digit morphologies better suited for loose, sandy substrates. In such environments, adhesive toe pads may be less effective or even disadvantageous compared to clawed digits or reduced subdigital structures, which facilitate digging and stable locomotion in shifting sand (Bauer and Russell 1991). This pattern is further supported by evidence of independent reductions in subdigital lamellae among Namib–Kalahari geckos of the genus *Pachydactylus* (Lamb and Bauer 2006). Generally, the loss or reduction of adhesive structures can result in biomechanical and functional adaptations that enhance running and burrowing, traits particularly advantageous for terrestrial species inhabiting loose substrates (Higham et al. 2015). Thus, the prevalence of padless geckos in the far north can be predicted as an adaptive response to the physical and ecological demands of arid desert habitats, where adhesive pads are less functional.

Within the pad bearing groups, basally padded species have the largest proportion of their hypervolume unique to species lacking adhesive pads (19%). This can be explained by their

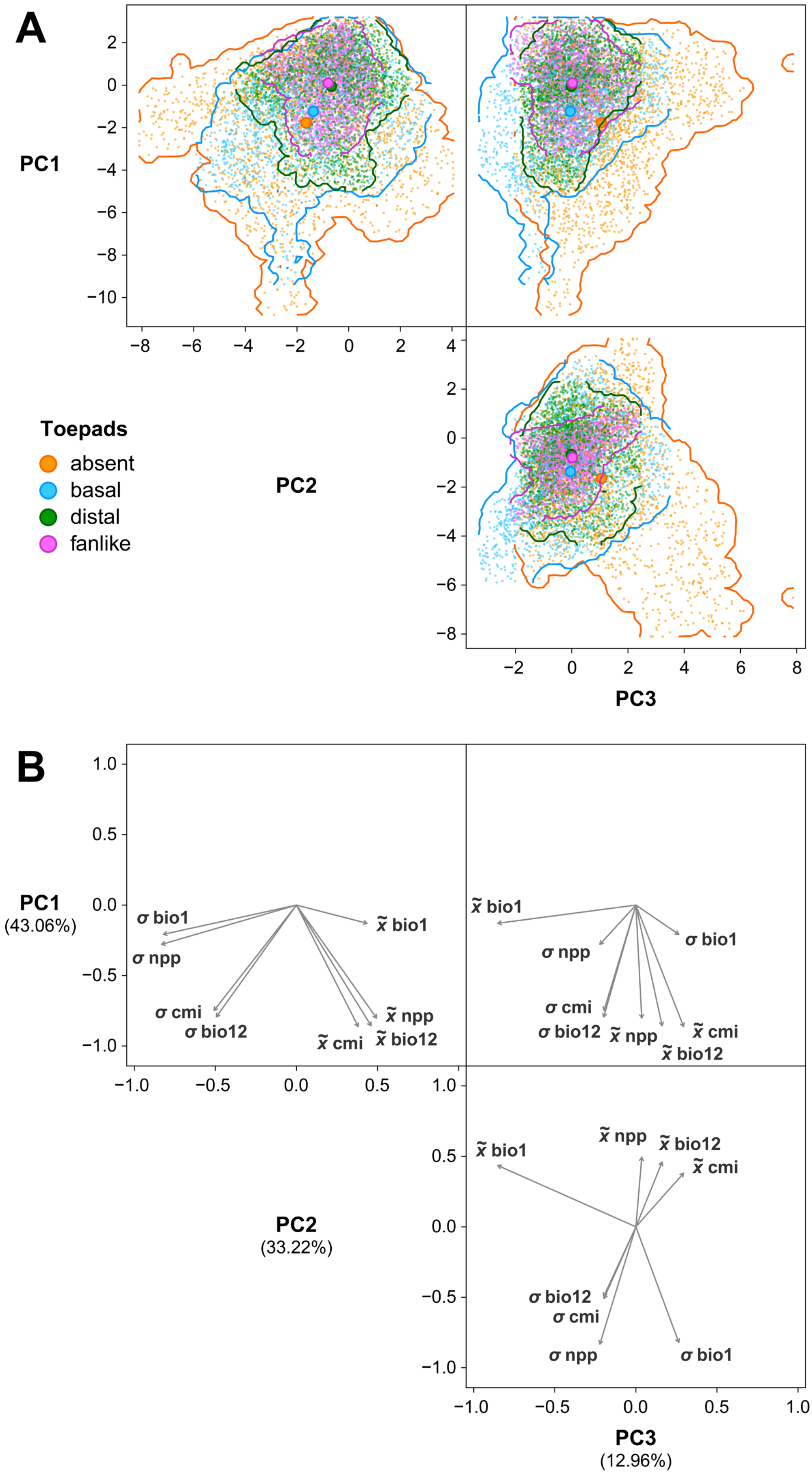

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FIGURE 4 | (A) Climatic niche hypervolumes for each toepad configuration, plotted along the first three principal component axes (Eigenvalues > 1) derived from median and standard deviation values of four CHELSA (Climatologies at high resolution for the earth's land surface areas) (Karger et al. 2021) climate variables: Annual mean temperature (bio1), annual precipitation (bio12), net primary productivity (npp), and climate moisture index (cmi). (B) Variable loadings of the four climatic variables on the first three principal components, illustrating the contribution of each to the observed climatic variation (for exact values see Table S2).

TABLE 1 | Pairwise climatic niche overlap between toepad configurations based on hypervolume comparisons.

Overlap statistics	Jaccard	Sørensen	Frac_ unique_1	Frac_ unique_2
absent–distal	0.222	0.364	0.776	0.038
absent–fanlike	0.132	0.233	0.867	0.061
absent–basal	0.428	0.600	0.522	0.195
fanlike–distal	0.396	0.568	0.249	0.544
basal–distal	0.371	0.542	0.623	0.041
fanlike–basal	0.231	0.376	0.025	0.767

Note: Values represent Jaccard and Sørensen similarity indices, as well as the fraction of unique climatic space occupied by each configuration in the pair. Higher Jaccard and Sørensen values indicate greater overlap; higher fractional uniqueness indicates greater distinctiveness.

geographic distribution; the focus in the tropics correlates with the unique fraction in hypervolume compared to species lacking toepads, which are notably absent from Central Africa.

In Central Africa, basal pads are the sole toepad configuration, predominantly represented by species of the genus *Hemidactylus* (Gekkonidae). This genus, one of the most species-rich and widely distributed among reptiles, is believed to have originated in Asia before dispersing to the Arabian-African region early in its diversification (Carranza and Arnold 2006). Their early colonisation and subsequent diversification within Central African rainforests (Šmíd et al. 2013) likely established unique preconditions for their current dominance. First, the dense Central African forest block may have acted as a biogeographic barrier, limiting the arrival of arid-adapted species (Chirio and Ineich 2006), such as many padless geckos. Second, *Hemidactylus* species are known to be strong ecological competitors, often displacing native gecko fauna where they are introduced (Agarwal et al. 2021; Weterings and Vetter 2017; Yang et al. 2012). This competitive advantage could have further contributed to their persistence and ecological dominance. Thus, the prevalence of basally padded species in Central Africa may be linked to not only dispersal history but also ecological exclusion. Unlike regions with similar climates, such as Southeast Asia and northern Australia, which host species with a variety of toepad configurations, Central Africa's unique ecological and evolutionary history may have favoured the persistence and dominance of basal pad configurations.

The hypervolume of distally padded species largely overlaps with the hypervolumes of species with absent and basal pads. Their concentration in Australia stems from diplodactylid gekkotans. Unlike many other Australasian squamates, diplodactylids are believed to have originated in Australia before its final separation from Antarctica, which has contributed to their significant presence in the region (Skipwith et al. 2019). In the Caribbean, the prevalence of distal pads is largely attributed to *Phyllodactylus* (Phyllodactylidae) and *Sphaerodactylus* (Sphaerodactylidae). The diversification of *Phyllodactylus* likely began in the early Oligocene, coinciding with the period when the Greater Antilles and the Caribbean had increased connectivity with South America (Gamble et al. 2008). Thus, similarly to basally padded species, evolutionary history appears to be a key factor driving the current distribution of species with distal pads.

This observation supports the hypothesis that the differences between basal and distal toepad configurations do not reflect adaptations to fundamentally distinct climatic conditions. Instead, it appears that historical biogeographic contingencies—such as which lineage arrived first in a given region—played a more significant role in shaping their current distributions. Once established, these lineages diversified within the available environmental space, rather than expanding into entirely new climatic zones. This interpretation aligns with the largely overlapping habitat types occupied by both pad configurations, with distal pads being slightly more associated with desert and shrubland habitats, possibly a consequence of Australia's increasing aridification (Fujioka and Chappell 2010).

The hypervolume of fanlike species also lies within the hypervolumes of absent and basal species; they can only be found in northern Africa and Madagascar, represented by one genus, respectively. Their hypervolume is most unique from distal pads (28%), mostly in terms of temperature structure (PC3), similarly to basal pads with which they geographically have more overlap with. The genus *Uroplatus* (Gekkonidae) originated in Madagascar in the mid-Tertiary, during which the island had already been isolated from all other landmasses. Interestingly, this genus was never successful in oceanic dispersal (Raxworthy et al. 2008), suggesting that the fanlike toepad configuration might be a very specific adaptation. This is supported by the patchy distribution area of the strictly rock-dwelling north African genus *Ptyodactylus* (Phyllodactylidae) (Metallinou et al. 2015). This implies that the distribution of the fanlike toepad configuration is driven by the dispersal history of the clades as well as their specialisation to specific environments.

In summary, the climatic niches of different toepad types reveal considerable overlap, with species lacking adhesive pads occupying the broadest range of environmental conditions. While species with adhesive pads share much of the same climatic space, the various toepad configurations do not grant access to entirely new climatic niches. Instead, the ecological differences between toepad types seem to manifest more prominently at smaller ecological scales, such as within specific regions or microhabitats (Zimin et al. 2025; Riedel et al. 2024)—a pattern

TABLE 2 | Habitat associations of 1497 species based on toepad configurations.

	Forest		Savanna		Shrubland		Grassland		Rocky areas		Desert		Artificial—terrestrial	
Absent	0.694	▲▲▲	0.052	▲	0.154	▲	0.038	—	0.281	▲▲	0.125	▲	0.143	▲
Basal	0.568	▲▲▲	0.227	▲▲	0.283	▲▲	0.067	▲	0.319	▲▲▲	0.054	▲	0.268	▲▲
Distal	0.581	▲▲▲	0.168	▲	0.352	▲▲▲	0.140	▲	0.314	▲▲	0.089	▲	0.222	▲▲
Fanlike	0.667	▲▲▲	0.048	—	0.190	—	0.048	—	0.286	—	0.190	—	0.190	—

Note: Values represent the proportion of species within each toepad category occurring in each habitat type, based on IUCN habitat classification data. Upward-facing triangles (▲) indicate proportions significantly higher than expected based on the 95% confidence interval, with ▲ = just outside 95% CI (+0.01), ▲▲ = moderately outside (+0.05), and ▲▲▲ = strongly outside (+0.1 or more). A dash (—) indicates proportions within the 95% confidence interval.

particularly evident in species with fanlike pads. These findings highlight the need for further research into the fine-scale ecological and evolutionary processes that shape the distribution and specialisation of the toepad adaptations.

4.3 | Habitat Patterns and Ecological Specialisation

Toepad patterns by IUCN habitat categories(Jung et al. 2020) show that most occurrences are higher than expected by the 95% CIs, which is unsurprising, considering the major habitat types of gekkotans were analysed. The dominant habitat type across all toepad categories is forest, which is expected as this is the most common habitat type in the tropics (Keith et al. 2020) (Figure S2), which is where geckos are mostly concentrated (Meiri 2019). Interestingly, padless species show a higher proportion of forest habitats than either basal or distal types—a pattern that appears counterintuitive given previous assumptions about pad functionality. This may reflect differences in microhabitat use within forests (e.g., ground-dwelling vs. arboreal), lineage-specific dispersal histories, or the limitations of broad habitat classifications like "forest" in capturing relevant ecological variation (Grismer et al. 2020; Riedel et al. 2020).

The Savanna habitat is dominated by pad-bearing species. According to the IUCN Habitats Classification Scheme (Version 3.1) (IUCN 2024), it represents the transitional zone between grasslands and forests, characterised by grass ground cover and an overstorey of widely spaced trees and shrubs. Open areas like these are often associated with a higher predation risk (Smith and Ballinger 2001), which may create selective pressures for escape strategies such as climbing. Since arboreality is regularly present in gekkotans with adhesive pads (Zimin et al. 2025), their dominance in savanna habitats may reflect both the structural availability of elevated microhabitats and the adaptive advantage of vertical escape from predators. Savannas are structurally heterogeneous, providing a variety of climbing surfaces favouring climbing generalists. An ecological survey of Australian gecko communities showed that species richness of the Diplodactylidae with distal or even reduced distal toepads is significantly higher in savanna woodlands than in tropical rainforests (Riedel et al. 2020), suggesting a link between pad type and ecological opportunity in structurally varied habitats. A notable example is *Heteronotia binoei* (Gekkonidae), an Australian savanna species with absent toepads, which shows clear morphological differences between its ground-dwelling and saxicolous lineages. The latter exhibits adaptations towards distal toepads (Riedel et al. 2021), indicating that adhesive structures may aid movement on rocky substrates, while padless morphologies may benefit ground-dwelling species, as they have to run more often or faster to escape predators. This is supported by terrestrial species often having longer hindlimbs (Zimin et al. 2025). Overall, the dominance of pad-bearing species in Savanna habitats underscores the adaptive significance of adhesive toepads in these environments, where species with adhesive pads, particularly those adapted to climbing rocks and trees (Salvi et al. 2023), are better suited to the varied terrain and heightened predation pressures.

Rocky areas represent a dominant habitat type across all toepad configurations (Table 2). For example, the non-padded genus *Cyrtodactylus* (Gekkonidae) contains numerous karst-dwelling species (Grismer et al. 2020), with evolutionary trends within the genus pointing to an enlargement of the subdigital scale area in saxicolous species, contrasting with a reduction in terrestrial species (Riedel et al. 2024). This underlines the tendency of toepad formation when inhabiting rocky areas. Generally, the saxicolous lifestyle is common among Gekkota (Zimin et al. 2025), and no specific toepad type seems to be favourable. Differences in performance might emerge when looking at a smaller scale and considering factors like surface size or roughness (Higham et al. 2019; Huber et al. 2007; Pillai et al. 2020; Russell and Johnson 2014). For instance, a study comparing a basally and distally padded species found that on dusty parsinite rock, the basal toepads were disadvantaged due to fouling by small particles (Russell and Delaugerre 2016), suggesting that specific toepad types may be more advantageous depending on the substratum.

The desert habitat does not belong to the dominating habitat types for geckos independent of pad configuration. Although lizards are often better adapted to the arid conditions compared to other reptiles (Lewin et al. 2016), it remains a challenging habitat. It is proportionally the most common among species with fanlike pads. This can be explained by *Ptyodactylus*, which is distributed in northern Africa, including the desert regions like parts of the Sahara Desert or the northern Eastern Desert (Metallinou et al. 2015). As mentioned previously, they seem to be particularly adapted to these types of environments, potentially due to the functional advantages of their fanlike pads on specific rock surfaces. Similar to distally padded species studied by Russell and Delaugerre (2016), *Ptyodactylus* may benefit from reduced pad fouling on dusty or coarse substrates. In contrast, basally padded species—although dominant across much of sub-Saharan Africa—are less common in northern Africa, which may reflect their reduced performance under dusty desert conditions.

A surprisingly common IUCN habitat type is Artificial Terrestrial, which includes arable land, pastureland, plantations, rural gardens, urban areas, and heavily degraded former forest (IUCN 2024). Artificial land, strongly associated with human structures, can be disturbing for most reptile species (Doherty et al. 2020), yet some gekkonids thrive in these environments. A great example of this is the basally padded genus *Hemidactylus* (Gekkonidae), of which many species are very well adapted to living in close proximity with humans, which has led to some becoming exceptionally invasive species (Weterings and Vetter 2017). Similarly, species of the basally padded genus *Phelsuma* (Gekkonidae) have successfully broadened their niche by utilising artificial structures as new habitats (Augros et al. 2017). The success of basally padded species may be attributed to their ability to exploit vertical surfaces, such as walls and buildings (Weterings and Vetter 2017), which are abundant in human-altered landscapes. Urban populations of basally padded *Anolis* lizards showed increased toepad size and number of lamellae compared to forest populations (Howell et al. 2022), indicating that adhesive toepads may pose a selective advantage in urban environments. Other padded and non-padded gekkotan species, though less dominant, also find opportunities in artificial terrestrial habitats. Overall, the prevalence of basally padded species in artificial terrestrial habitats highlights the importance of morphological and behavioural flexibility in adapting to human-dominated landscapes. The unique challenges of these environments, such as surface texture and thermal properties, need to be further studied in order to explore the distribution of different toepad types.

Generally, studies focusing on narrow phylogenetic frameworks are helpful to disentangle possible evolutionary and ecomorphological patterns in the Gekkota lineages. The gradual evolution of adhesive structures on padless species has been discussed before (Russell et al. 2015), and relating such observations to habitat structure has recently gained attention. Studies considering padless genera or species have shown that trends towards the evolution of basal (Riedel et al. 2024) or distal (Riedel et al. 2021) toepads in response to more saxicoline or arboreal lifestyles exist. Future research focusing on specific lineages and incorporating surface structure analysis will be crucial in uncovering deeper evolutionary patterns. Such focused studies may allow for empirical testing and refining of the patterns proposed in this study, providing a framework to validate or challenge the broader hypotheses presented here.

5 | Conclusion

In conclusion, this study provides critical insights into the evolution, ecological significance and climatic distribution of toepad configurations in gekkonids. We confirmed the multiple independent origins of adhesive toepads and supported the ancestral state of padlessness. Our transition model suggests a novel pathway from distal to basal pads, emphasising the importance of dataset size and analytical models in evolutionary research. Additionally, the exploration of climatic niches revealed that toepads do not open access to entirely new climatic niche spaces. Instead, differences between toepad types appear to reflect fine-scale ecological adaptations, particularly in relation to microhabitats and substrate specificity. Our findings show that pad-bearing geckos occupy a wide range of habitat types within their climatic niche, suggesting that while adhesive toepads may not expand the niche at biome and climate level, they do facilitate niche expansion at the structural level within habitats. Another key conclusion is that the global distribution patterns of toepad types appear to be shaped more by biogeographic history and dispersal dynamics than by direct adaptation to specific macrohabitats or climatic niches. With the possible exception of padless species, our results show no strong climatic separation between pad types. Instead, the predominance of certain toepad configurations in particular regions seems to reflect historical colonisation events and subsequent in situ diversification. This underlines the importance of historical contingency and regional evolutionary pathways in shaping present-day functional diversity, rather than strictly ecological filtering based on climate. These findings underscore the intricate interplay of evolutionary history, ecological pressures and environmental constraints in shaping the diversity of gekkotan toepads. Future research integrating fossil evidence, developmental studies, and detailed ecological analyses will be pivotal in unraveling the complex dynamics of toepad evolution and their ecological drivers.

Author Contributions

Conceptualization: D.R., J.R.; Methodology: D.R., J.R., Y.K.; Software: Y.K.; Validation: D.R., J.R., Y.K.; Formal analysis; Investigation: D.R., J.R., Y.K.; Resources: D.R.; Data Curation: Y.K.; Writing – original draft: Y.K.; Writing – review and editing: D.R., J.R., Y.K.; Visualization: Y.K.; Supervision: D.R., J.R.; Project administration: D.R.; Funding acquisition: Y.K., J.R.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All used original data sources were open source and are cited in Section 2. Compiled data on toepad category and the R code used can be accessed in the Supporting Information.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** jbi70087-sup-0001-DataS1.zip.