

1 **A frog adaptive radiation: Ecomorphological evolution in Old-World**
2 **shrub frogs (Rhacophoridae: *Pseudophilautus*)**

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28

29 **Abstract**

30

31 Ecomorphs result from divergent natural selection, leading to species-rich adaptive
32 radiations. Identifying ecomorphs and the resulting adaptive radiations in frogs is
33 challenging due to conserved morphology and high species diversity. In this study, we
34 demonstrate the ecological and climate specializations that have driven the
35 diversification of shrub frogs of the genus *Pseudophilautus* in Sri Lanka, a tropical
36 continental island. We use a time-calibrated phylogeny, morphometric analyses, and
37 climate-niche evolution, and identify five ecomorphological categories, including Tree-
38 shrub, Rock-boulder, Leaf-litter, Habitat Generalists, and Canopy forms, and describe
39 their evolution. Body size is the primary factor separating species, and specific body
40 features correlate with habitat type. Ecomorphs likely evolved multiple times in
41 disparate lineages, and in different regions and altitudes, during cold climatic periods
42 owing to monsoon cycles resulting from the Himalayan-Tibetan orogeny. The common
43 ancestor was a medium-sized, wet-adapted, tree-shrub habitat specialist which
44 originated in the late Oligocene. Extreme size classes (diminutive leaf litter forms and
45 large canopy forms) evolved recently and suggest that morphological disparity arose
46 late in diversification, possibly aided by favorable climates. This work will facilitate
47 understanding of adaptive radiations in frogs, which possibly will help uncover the
48 prevalence of subtle adaptive radiations in frogs, just as in tailed-vertebrates.

49

50 Key words: ecomorphs, adaptive radiation, *Pseudophilautus*, tree frogs, climate niche

51 **Introduction**

52

53 Adaptive radiations play a pivotal role in the phenotypic and ecological diversification
54 of life on Earth. This occurs when species swiftly evolve from a single ancestral lineage
55 into a myriad of distinct forms. Such rapid diversification often transpires when
56 environmental changes present new resources, modify biotic interactions, or unveil
57 previously unoccupied ecological niches [1](Schluter, 2000). The foundations of this
58 process were established by [2]Darwin, (1845) and refined by generations of
59 evolutionary biologists, providing valuable insights into the evolutionary patterns and
60 causal processes seen in various groups of organisms [3-12](Glor, 2010; Losos & Miles,
61 2002; Ole, 2006, Losos & Ricklefs, 2009; Losos & Mahler, 2010, Blackburn et al. 2013,
62 Close et al. 2015, Tokita et al. 2017, Tiago et al. 2020, Swardal et al. 2020). The
63 ecological theory of adaptive radiation suggests that speciation in response to divergent
64 natural selection is primarily ecological [1,3,6](Glor, 2010; Losos & Mahler, 2010;
65 Schluter, 2000). However, studying the processes that lead to ecological speciation is
66 challenging for long-lifespan species, such as vertebrates. Hence, adaptive radiations
67 are typically studied as a macroevolutionary process in deep time, by evaluating the
68 signatures of past or ongoing ecological speciation processes that resulted in
69 reproductive isolation [3,13-15](Glor 2010; Astudillo-Clavijo 2015; Arnold et al. 2008;
70 Revell et al. 2008).

71

72 Ecomorphological clustering is a hallmark of adaptive radiations spurred by ecological
73 speciation. It denotes the interconnected relationship between the physical
74 characteristics (morphology) and ecological roles of closely related species
75 [16,17](Aerts et al. 2000, Schluter, 2001). Ecomorphological clustering is an essential
76 indicator of past or ongoing ecological speciation processes and includes the existence
77 of ecomorphs and divergence in morphology and ecology among sister species
78 [18,19](Erwin, 1994, Moen et al. 2021). In addition to ecomorph evolution, adaptive
79 radiations typically exhibit an 'early burst' pattern, where speciation rates surge in the
80 initial stages of radiation and then decline as ecological niches become saturated over

81 time [4,18,20](Simpson, 1953; Erwin, 1994; Losos and Miles, 2002).

82

83 Frogs and toads (Anura) are one of the most species-rich tetrapod orders with about
84 8000 species [21](AmphibiaWeb, 2023), yet their adaptive radiations are not well
85 understood. Anurans have a conserved body plan [22](Duellman & Trueb, 1986) which
86 results in fewer opportunities for adaptations compared to tailed vertebrates that often
87 display remarkable adaptive radiations. However, frogs can still undergo adaptive
88 radiation and have ecomorphs, although it is more subtle compared to other species
89 [7,23] (Bossuyt and Milinkovitch 2000, Blackburn et al. 2013).

90

91 The species-rich shrub-frog of the genus *Pseudophilautus* [24](Meegaskumbura et al.
92 2002) characterized by direct development, a key evolutionary innovation that allows
93 terrestrial niche occupation [25](Meegaskumbura et al. 2015), provides an opportunity
94 to investigate whether diversification in these frogs constitutes of ecomorphs indicative
95 of ecological speciation.

96

97 The ancestor of *Pseudophilautus* dispersed to Sri Lanka across the ephemeral Palk
98 Isthmus, which provided a terrestrial connection with India during periods of lowered
99 sea level [26](Sudasinghe et al. 2018). Following initial diversification in Sri Lanka, a
100 small component of these frogs back-migrated to India [27,28](Bossuyt et al. 2004,
101 Meegaskumbura et al. 2019). The species remained occupy a diversity of habitats [29-
102 35](Manamendra-Arachchi and Pethiyagoda 2005; Meegaskumbura and Manamendra-
103 Arachchi 2005; Meegaskumbura et al. 2007, 2009, 2012; Wickremasinghe et al. 2013;
104 Meegaskumbura and Manamendra-Arachchi 2011), mostly in the island's aseasonal
105 southwestern wet zone. The wet zone includes a large area of lowland rainforest and
106 three isolated mountain massifs, which combine to provide a climatically and
107 topographically complex region with substantial habitat heterogeneity. Within the wet
108 zone, the vast majority of species are confined to the few remaining fragments of
109 rainforest and tropical montane cloud forest, where they occupy a variety of
110 microhabitats, including rock crevices and boulders in streams, leaf litter, shrubs, open

111 grasslands, and the low, mid- and high canopy of trees [29,30,32,33](Manamendra-
112 Arachchi and Pethiyagoda 2005; Meegaskumbura and Manamendra-Arachchi 2005,
113 2007, 2009, 2012).

114

115 We hypothesize that the ecologically disparate habitat occupation and specialization of
116 *Pseudophilautus* species signals the existence of ecomorphs that underlie a spectacular
117 adaptive radiation. To document such ecomorphs (phenotype-habitat correlation) and
118 outline their evolution, we analyze this species-rich, monophyletic and predominantly
119 insular radiation of tree frogs using a multi-gene, time-calibrated phylogeny, ancestral-
120 state reconstructions, and morphometric analyses. We predict that body size and shape
121 may be influential in explaining the phenotype-habitat correlation of *Pseudophilautus*,
122 and that historical climate may have played a critical role in its diversification.

123

124

125 **Results**

126

127 ***Ecological specialization***

128 Our study of Sri Lankan *Pseudophilautus* showed that these frogs can be classified into
129 five distinct ecomorph categories: Canopy, Generalist, Rock-boulder, Leaf-litter and
130 Tree-shrub in the morphospace (Fig.1, Extended Data Figure 1). Using a principal
131 component analysis (PCA; Fig. 1a), a phylogenetically corrected principal component
132 analysis (pPCA; Extended Data Figure 1) and a linear discriminant analysis (LDA; Fig.
133 1b, 1c), we found that body size and shape can be used to differentiate between these
134 categories (results of LDA analyses are provided in detail in Extended results). In the
135 PCA, the first two principal components explain over 94% of the variance (Table S1,
136 Extended Data Figure 2) with males and females showing a similar pattern within the
137 morphological space. The first PC representing body size explains 93.2% of the
138 morphological variance across species and appears to be the most important feature for
139 separating the five clusters. Leaf-litter species have the smallest body sizes, while
140 Canopy species have the largest. On the second PC axis, although the variance is low

141 1.5%), upper eyelid width (UEW) and palm length (PAL) load strongly mainly
142 distinguishing Rock-boulder species from the others (Fig. 1A). The pPCA suggests that
143 similar morphs have arisen from different lineages pointing towards a convergent
144 evolution in *Pseudophilautus* (Extended Data Figure 1, Table S2).

145

146 The shape analysis based on size-adjusted measurements (residual data) in the PCA
147 retains four principal components, which together explain 64.1% of the variation in
148 shape (Table S3). Finger lengths (FL I-IV), foot length (FOL) and toe lengths (TL I-IV)
149 load strongly on the first principal component. Head length (HL) and mandible–nostril
150 distance (MN), inter-narial distance (IN), and distance between front of eyes (DFE) and
151 inter-orbital width (IO) load strongly along PC2, PC3 and PC4, respectively. Although
152 a distinct differentiation of shape isn't observed among ecomorphs, Canopy forms are
153 clearly separated from Generalists by having greater head length (HL) and mandible–
154 nostril distance (MN) (Extended Data Figure 3, PC1 vs. PC2). Generalists can be
155 distinguished from Rock-boulder forms and Tree-shrub forms by having shorter
156 internarial distance (IN) (Extended Data Figure 3, PC1 vs. PC3). Canopy forms are
157 separated from Rock-boulder forms by having longer fingers (FL), feet (FOL) and toes
158 (TL) (Extended Data Figure 3, PC1 vs. PC4). However, Rock-boulder forms, Tree-
159 shrub forms, Generalists and Canopy forms seem to exist within the ecomorphological
160 space of Leaf-litter forms but, Tree-shrub forms deviate from this pattern along PC4
161 axis.

162

163 ***Phylogenetic analyses***

164 The phylogenetic analysis shows high node support for many taxa and the topology is
165 consistent with [28] Meegaskumbura et al. (2019) (Fig. 2). The results suggest that the
166 most recent common ancestor (MRCA) of the *Pseudophilautus* radiation evolved
167 between 41.8 and 25.2 MYA, with major clade diversification occurring during early to
168 mid-Miocene, 24.1–14.7 MYA. However, most of the extant species evolved during the
169 late Miocene and the Pliocene. Lineage-through-time plots suggest an early, rapid
170 speciation event $\gamma = -3.7077$ ($p=0.04$) over a brief period, which gradually slows down

171 as new lineages accumulate with time (Fig. 2).

172

173 The MRCA of *Pseudophilautus* is predicted to be a medium-sized species (Fig. 3a).
174 Early differentiation in body size (represented by PC1) occurred around 18.9 MYA,
175 followed by an accelerated rate of body size evolution between 10 - 5 MYA,
176 corresponding with the origin of ecomorph categories. Smaller-bodied frogs evolved to
177 become Leaf-litter forms, while larger-bodied forms evolved to become Canopy
178 dwellers, with a few reversals (Fig. 3a). However, there is no comparable trend in PC2
179 towards the evolution of ecomorphs (Extended Data Figure 3), indicating that body size
180 evolution and evolution of morphological characters such as Upper eyelid width (UEW)
181 and Palm length (PAL) were largely decoupled during the diversification of
182 *Pseudophilautus* (Extended Data Figure 3).

183

184 Interestingly, the ‘bayou’ analysis detected evolutionary rate shifts towards a single
185 major adaptive peak (Fig. 3b; the red curve on right). An initial shift towards large body
186 sizes (Fig 3b; large circle on the phylogeny denote rate shifts towards larger body sizes)
187 was followed by shifts towards smaller sizes. The most significant rate shift coincided
188 with the origin of clades A, B and C around 20 MYA (Fig. 2). These clades gave rise to
189 derived ecomorphs such as Canopy forms, Rock-boulder forms and Generalists; the
190 other three clades contain only Leaf-litter forms and Tree-shrub forms.

191

192 The phylomorphospace (Fig 3c) show that species with small-to-medium body sizes
193 belong to the Leaf-litter and Tree-shrub forms, whereas the large-bodied species belong
194 to the Canopy forms. The phylogenetic MANOVA suggest that there is a significant
195 difference ($p = 0.0009$) in the position of ecomorphs in the phylomorphospace,
196 particularly along PC1 (Fig. 3d; Table S4). However, there is some overlap among
197 adjacent ecomorphs. It's worth noting that the evolution of body shape, as represented
198 by size-corrected PC values, doesn't correspond with ecomorph categories. The
199 evolution of body shape was gradual throughout the history of *Pseudophilautus*, and
200 Tree-shrub species span the entire range of body shapes (Extended Data Figure 4).

201

202 Based on the ancestral reconstruction of the five ecomorphs, it appears that the
203 diversification of *Pseudophilautus* occurred through a Tree-shrub ancestor (Fig. 4a)
204 This ancestor likely inhabited high montane regions (Fig. 4c). Rock-boulder forms
205 arose three times from the common ancestor of [*Pseudophilautus macropus* + *P.*
206 *sordidus*, *P. fergusopnianus* + *P. sarasinorum*]. Leaf litter forms arose five times from
207 [*P. caeruleus*, *P. tanu*, *P. mittermeieri*, *P. zorro* + *P. cuspis* and *P. simba* + *P. semiruber*]
208 common ancestor. The Generalist form may have evolved three times from the common
209 ancestor of [*P. silus* + *P. microtympanum* + *P. lunatus*]. Canopy forms, too, seem to
210 have evolved at least three times from the common ancestor of [*P. reticulatus* + *P.*
211 *stellatus* + *P. cavirostris*]. It is of importance that Rock-boulder, Leaf-litter, Generalists
212 and Canopy forms always evolved from a Tree-shrub ancestor and did so during Mid-
213 Miocene to early Pliocene.

214

215 The 3D phyoecospace (Fig. 4b) suggests that Tree-shrub forms and Leaf-litter forms
216 are distributed at all elevational levels (highlands—above 1500 m, mid elevations—
217 500 to 1500 m, and lowlands—below 500 m, Fig. 4c). Rock-boulder forms and Canopy
218 forms are found at mid-to-low elevations, whereas Generalists are found only at high
219 elevations.

220

221 ***Climatic specializations***

222 The 3D PCA plot depicts the climatic niche occupation in *Pseudophilautus* (Figs. 5a,
223 Extended Data Figure 5) and illustrates how the five ecomorphs occupy different
224 climatic niches, but there is a lot of overlap between them. The first two principal
225 components explain about 88% of the variance (Table S5; Extended Data Figure 5) with
226 PC1 mostly influenced by seasonality in rainfall (bio16, bio17, bio18, and bio19),
227 temperature stability (bio1, bio2, and bio3), and elevation. Tree-shrub forms have
228 expanded their niche along all axes, while Canopy forms and Leaf-litter forms occupy
229 a wider niche along PC1, and Rock-boulder forms and Generalists have expanded
230 niches along PC2. PC2 is mostly a temperature component, dominated by temperature

231 annual range (bio7), which explains about 17.2% of the variance. The third PC, which
232 explains about 6.5% of the variance, also represents environmental temperature
233 (dominated by mean temperature of coldest quarter, bio11, and mean temperature of
234 coldest month, bio6). In the PCA plot, higher PC values correspond to cool and wet
235 conditions, whereas lower PC values indicate warm and dry conditions. The climate
236 niche space of *Pseudophilautus* seem to be determined mainly by temperature variation
237 than rainfall.

238

239 During the early to mid-Miocene, approximately 20 to 12 million years ago, the climatic
240 niche space of ancestral Tree-shrub forms of *Pseudophilautus* expanded (Extended
241 Data Figure 5). However, climatic niche evolution along PC1 was gradual and does not
242 follow a clear pattern among different ecomorphs (Fig. 5b, Extended Data Figure 5;
243 PC1). This suggests that ecomorphs evolved through adaptation to local habitat
244 conditions rather than specific macroclimatic conditions. Nevertheless, deviations from
245 ancestral climatic conditions were minimal along PC2 (Extended Data Figure 5; PC2)
246 and PC3 (Extended Data Figure 5; PC3). Rock-boulder forms evolved towards warmer
247 and drier conditions, with species distributions affected by ranges of extreme
248 temperature conditions and less cold tolerance. Niche expansion along PC2 and PC3
249 was quite recent for *Pseudophilautus*, occurring around the late Miocene and early
250 Pliocene periods (Extended Data Figure 5; PC2 and PC3). The disparity-through-time
251 plots suggest that the rate of evolution of climate niches increased during the second
252 quarter of the evolution along PC2 (Fig. 5c) and during the fourth quarter of along PC3
253 (Fig. 5d). These intervals correspond to the mid Miocene and late Pliocene periods,
254 when conditions became dry and warm during the mid Miocene glaciation (Mi-1
255 glaciation) and wet and cold when Asian monsoons intensified during early Pliocene
256 respectively. However, the rapid expansion of climate niches along all axes seems
257 recent in *Pseudophilautus*.

258

259

260

261 **Discussion**

262

263 The adaptive radiation of *Pseudophilautus* in Sri Lanka is characterized by an early
264 burst radiation, high species diversity and common ancestry, the typical features of
265 recognized adaptive radiations[3,5,6,36,37](Glor 2010; Losos and Ricklefs, 2009;
266 Losos & Mahler 2010; Schluter 2000; Givnish 1997). While strict monophyly of a clade
267 is not always required to be classified an adaptive radiation, recognizing unusual
268 lineages can help identify the processes that limit morphological disparification, species
269 richness, and unusual distributions [38-42](Brandley & De Queiroz, 2004; Johnson et
270 al. 1993; Clarke et al. 1996; Jackman et al. 1999; Rodriguez-Robles et al. 2007). The
271 Indian mainland clade of *Pseudophilautus*, comprising only three species, does not
272 exhibit ecomorph resolution, which suggests that a lack of ecological opportunity in the
273 mainland may have hindered ecological diversification in this clade. In contrast, the
274 island radiation of Sri Lankan *Pseudophilautus* shows a clear morphology-habitat
275 correlation, with recently evolved ecomorphs. Furthermore, the initial colonization
276 from the mainland offered an ecological opportunity for Sri Lankan *Pseudophilautus*.
277 This led to their rapid diversification, as evidenced by the negative gamma value in
278 lineage plots (Fig. 2), during the early phases, and subsequently slowed as ecological
279 niches were occupied.

280

281 The ecomorph diversification of the extant *Pseudophilautus* radiation can be traced
282 back to the late Miocene. This timeline implies that following its initial colonization, a
283 habitat-specialist ancestral species underwent swift diversification, leading to the
284 emergence of ancestral ecomorph types. This initial diversification is marked by a
285 notable shift towards larger body sizes in these ancestors. However, these early
286 ecomorphs eventually faced extinction. Consequently, by the late Miocene, as
287 environmental conditions turned favorable, these niches were occupied by the extant
288 ecomorphs.

289

290 Analysis of morphology reveals distinct morphological groupings (i.e., ecomorphs)
291 associated with each of the habitat types we postulate (Fig 1, Extended Data Figure 1).
292 *Pseudophilautus*, the largest of which are tree canopy forms, require larger hands and
293 feet, and wider disk widths to jump over larger distances. The smallest frogs are leaf
294 litter forms, but there are two distinct types of morphology within this group [43](Bahir
295 et al. 2005). The diminutive forms (less than 15 mm SVL) have short eye-snout
296 distances and almost no disks, while slightly larger frogs (*P. cuspis* and *P. zorro*) have
297 proportionately the largest eye-snout distances and moderately developed disks with
298 flattened bodies, which may aid movement in leaf-litter [29](Manamendra-Arachchi
299 and Pethiyagoda, 2005). The diminutive forms are small enough to move around in leaf
300 litter, while the Generalists also inhabit this habitat [31](Meegaskumbura et al. 2012).
301 Rock-boulder forms have greater head widths and higher internarial and interorbital
302 distances, resulting in lateral widening. These observations affirm that the morphology
303 of *Pseudophilautus* species is highly correlated with specific habitat types. Although,
304 the clades of closely related species are typically composed of similar ecomorphs, there
305 are several instances where ecomorphs have evolved independently from different
306 lineages (Extended Data Figure 1).

307
308 Accelerated phenotypic divergence at the initial stages is a common feature of most
309 adaptive radiations [4,18,20](Losos and Miles, 2002; Erwin, 1994; Simpson, 1953).
310 Within the *Pseudophilautus* radiation, alongside the rapid diversification of various
311 phenotypes, there's a clear surge in early speciation rates, underscoring its adaptive
312 nature. Although earlier ecomorphs appear to have faced extinction, they subsequently
313 paved the way for the emergence of new ecomorphs. This is evident by the ecomorphs
314 (Leaf litter, Rock-boulder and Generalists) deriving from the shrub-tree ecomorph arise
315 only well into the diversification event during the late Miocene, Pliocene and early
316 Pleistocene. The bayou analysis confirms an initial shift towards larger body sizes
317 followed by later shifts towards decreasing body sizes (Fig 3b). This supports a
318 dynamic fitness landscape for *Pseudophilautus* where, during some period of evolution,
319 larger body sizes were selected over smaller; and later, under favorable environmental

320 conditions, smaller body sizes came to be selected for. These changes may have been
321 driven by environmental changes during different periods (e.g.: change in vegetation
322 from broad leaved forests to smaller leaves, extreme climate changes driving conserved
323 body plans for heat conservation). Furthermore, larger body sizes may also have exerted
324 negative selection pressures such as increased predation risk during early evolution
325 such that smaller body sizes were favored later on. However, there is insufficient
326 evidence at present, to validate these arguments.

327

328 The ancestral reconstructions of body size suggest that the adaptive radiation of
329 *Pseudophilautus* species may have originated from a small frog that was likely a shrub
330 dweller (Fig. 3a). As the radiation progressed, there appears to have been an initial burst
331 of diversification to fill micro-niches within the shrubs and eventually into the canopy.
332 However, as the available niches became saturated, competition may have driven
333 adaptive diversification into other ecomorph types, such as the Leaf litter, Rock-ground,
334 and Generalists. This raises an important evolutionary question about the role of
335 interspecific competition in driving phenotypic diversification [44](Svanbäck and
336 Bolnick, 2007).

337

338 During the early stages of radiation, ecological opportunities would be plentiful due to
339 the existence of unoccupied niches [45](Day and Young 2004). However, the likelihood
340 of adaptation to new niches may have decreased if divergent natural selection in the
341 context of competition was weak [46-48](Gavrilets and Vose, 2005; Dayan and
342 Simberloff, 2005, Gavrilets and Losos, 2009). As the empty niches became filled,
343 competition among shrub-tree dwellers increased, potentially leading to diversification
344 into other habitats such as leaf litter (which favored smaller-sized morphs) or rock-
345 boulders (which favored larger-sized species better equipped to compete with near-
346 water typical amphibians). In addition, larger-bodied species may have experienced
347 negative selection pressure due to predation, which could have restricted their
348 diversification and resulted in many smaller species and fewer larger species.

349

350 Ancestral-state reconstructions of the root node of *Pseudophilautus* (Fig. 4a and 4c)
351 suggest that the ancestor was a Tree-shrub species from high elevations, specifically
352 the central-hills of the island [28](Meegaskumbura et al. 2019). Three of the ecomorph
353 types, Tree-shrub, Leaf litter and Rock-boulder, are present in both lowlands and
354 highlands, but the Generalists occur only at higher elevation (above ~700m asl). The
355 Rock-boulder morphs are found along boulder-strewn streams from the highlands to
356 the lowlands; the Leaf litter forms are found in canopy-covered forests of both high and
357 low elevation forests but never in open habitats that lack leaf litter. Tree shrub morphs
358 show the highest distribution, occurring in both open and closed habitats of the
359 highlands and the lowlands. Contrastingly, the Generalists, which occupy all three
360 habitat types, are found only in the cooler and wetter higher elevations (Fig.4b)
361 [29](Manamendra-Arachchi and Pethiyagoda, 2005).

362
363 Since the ancestral-state reconstructions of the root node of *Pseudophilautus* suggests
364 that the ancestor was from high elevations, specifically the central-hills of the island
365 [28](Meegaskumbura et al., 2019), it can be presumed that it was a cool-and-wet-
366 adapted, Tree-shrub-dwelling specialist that seeded the species pump on the island. The
367 Generalists seems to have been derived secondarily; Generalists, in the context of the
368 Sri Lankan *Pseudophilautus* radiation, are species that occupy several habitat types
369 (i.e., Tree-shrub, Rock-boulder and Leaf-litter). In *Pseudophilautus*, the few Generalist
370 species are nested within two disparate clades (Fig. 2). This pattern in habitat utilization
371 of generalists bolsters the notion that terrestrial direct development expresses its full
372 potential in cool and humid habitats. Supporting this hypothesis, the Generalist clade is
373 distributed at high elevations (over 700 m asl) in the perennially wet cloud forests,
374 grasslands, and associated habitats of the three main mountain ranges. It is likely that
375 only in these cool, wet habitats that direct developing species could evolve a more
376 expansive niche breadth, because of their reliance on high humidity for breeding and
377 egg development [25,43,49](Meegaskumbura et al. 2015; Bahir et al. 2005; Schweiger
378 et al. 2017).

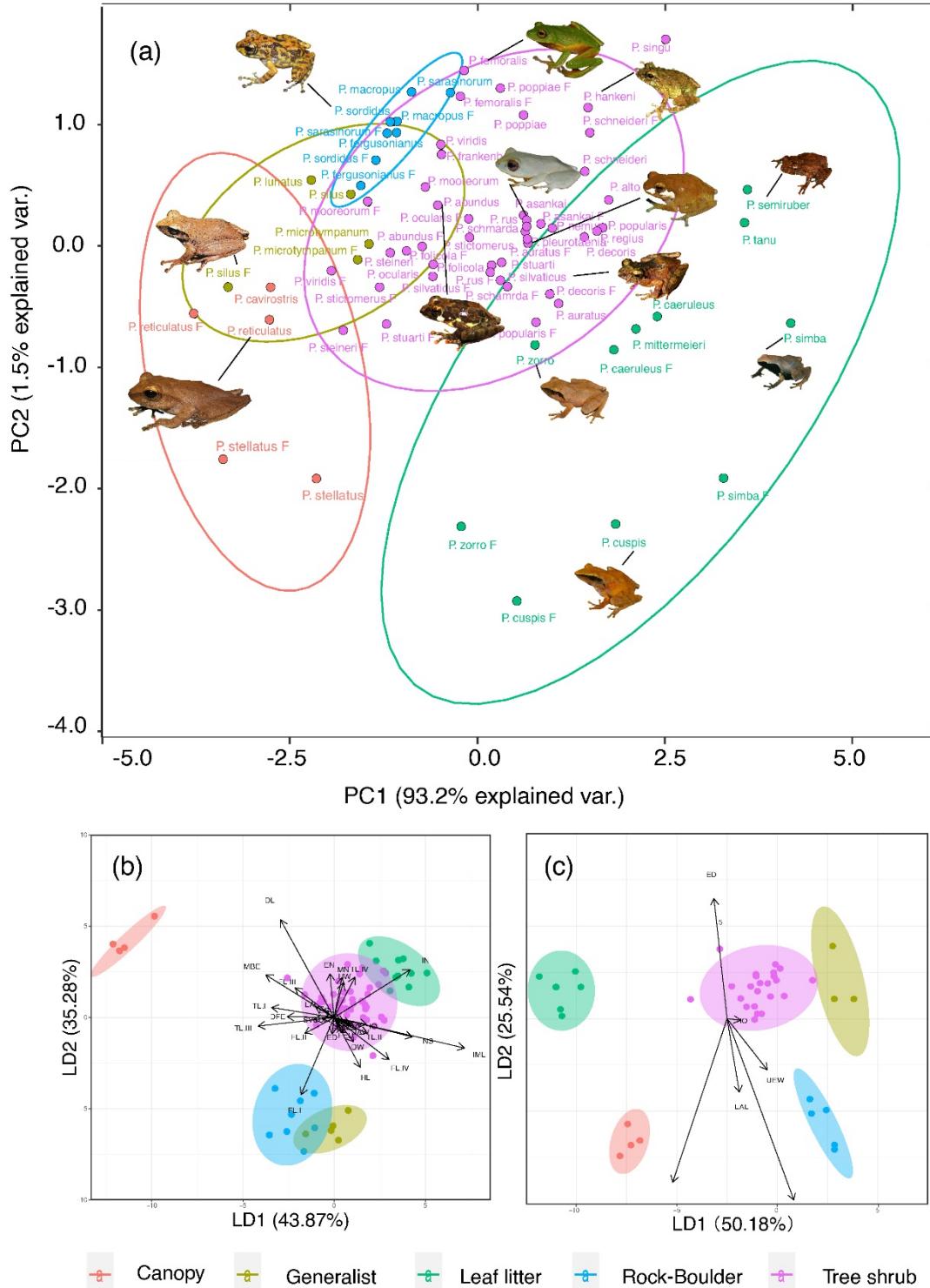
379

380 The late Miocene coincides with the evolution of the climatic niche of *Pseudophilautus*
381 into extreme temperature conditions [50,51](Chatterjee et al. 2013; Ellepola et al. 2022)
382 along PC2 (Fig. 5c), during which the evolution of ecomorphs preceded. However, by
383 the late Miocene, Himalayan-Tibetan orogeny, which started around 30 MYA was well
384 advanced, paving way for two stable monsoons per year [50,52-54](Chatterjee et al.
385 2013; Yin & Harrison, 2000; Gehrels et al .2003, Ellepola and Meegaskumbura, 2023).
386 This in turn aided in the evolution of more ecomorphs during the early Pliocene. Further
387 morphological disparification (formation of other ecomorphs such as Leaf litter,
388 Canopy, Rock-boulder and Generalists) of *Pseudophilautus* seems to have happened
389 during the late Miocene or Pliocene, with the creation and intensification of the two
390 monsoons and lowering of the temperature in the region (Figs. 4 and 5).

391

392 Our analyses sheds light on the evolution of ecomorphs in the *Pseudophilautus*
393 radiation of frogs and suggest that ecomorphs evolved multiple times across the
394 phylogeny, in different geographic regions, and at different altitudes, primarily during
395 a cold climatic period, possibly in association with monsoon cycles arising from
396 Himalayan-Tibetan orogeny. The common ancestor of the radiation was possibly a
397 medium-sized, wet-adapted, tree-shrub-dwelling habitat specialist, and extreme size
398 classes evolved relatively recently. We highlight the importance of considering
399 ecomorphs in understanding the adaptive radiations of frogs and suggest that adaptive
400 radiations, subtler than in tailed vertebrates, may be more prevalent in frogs than
401 previously recognized. Our findings add to the growing body of knowledge on the
402 ecomorphology and adaptive radiations of frogs and underscore the need for further
403 research.

404



405
406 **Fig. 1. The position of Sri Lankan *Pseudophilautus* in morphological space as**
407 **indicated by principal component (PCA—raw data) and linear discriminant**
408 **analyses (LDA).** The PCA conducted on raw data (a) separates species into five habitat
409 categories along the PC1 axis, though with visible overlapping areas. Circles indicate
410 the 95% confidence interval band for each habitat cluster. An 'F' following species

411 names denotes females. Canopy forms and Tree-shrub forms are well separated in
412 morphological space. The LDA conducted on raw data (b) groups all measurements
413 into five habitat categories, with slight overlaps between Generalists and Rock-boulder
414 forms and between Leaf-litter and Tree-shrub forms. Canopy forms are well separated
415 from all others. The LDA conducted on size-corrected measurements (c) also groups
416 species into five categories, with no overlap among groups. Head, finger and toe
417 dimensions are decisive characters in defining their habitat correlation. Coloured circles
418 indicate the 95% confidence interval band for each habitat cluster and each point
419 represents a species. See Extended Data Figure 1 for the results of the pPCA analysis.
420 Frog images indicate the relative size of each species.

421

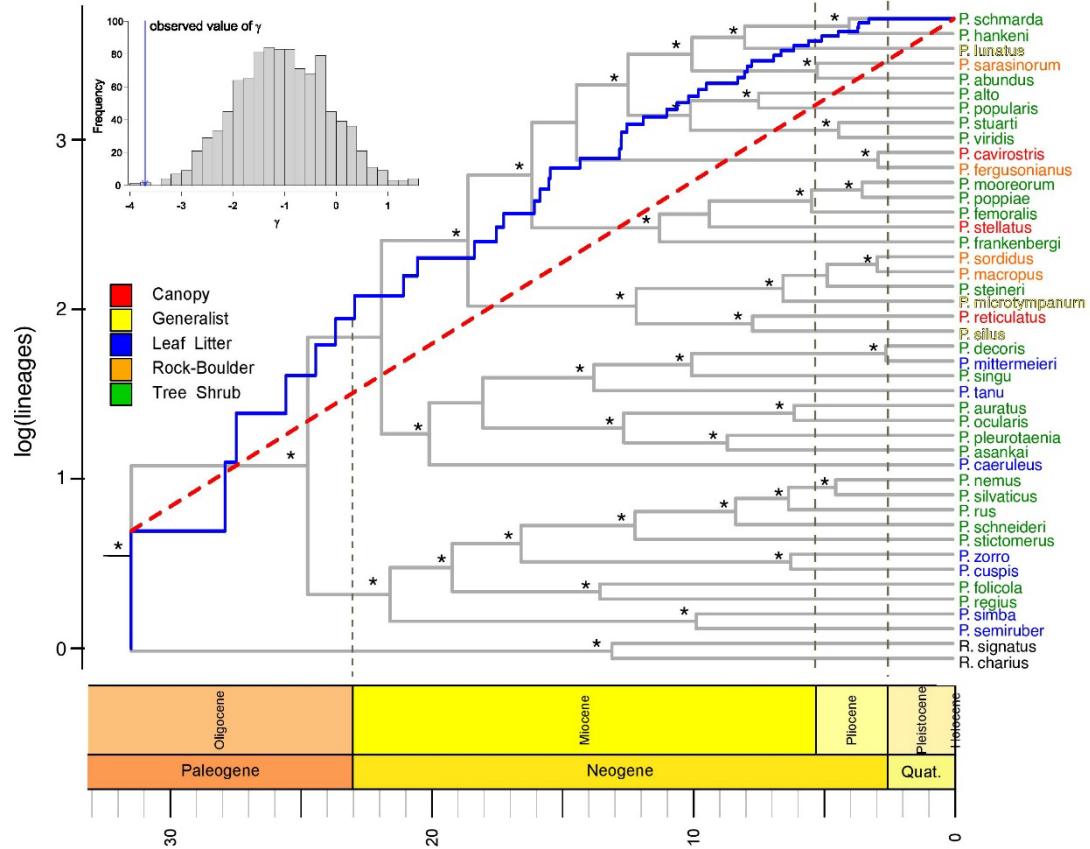
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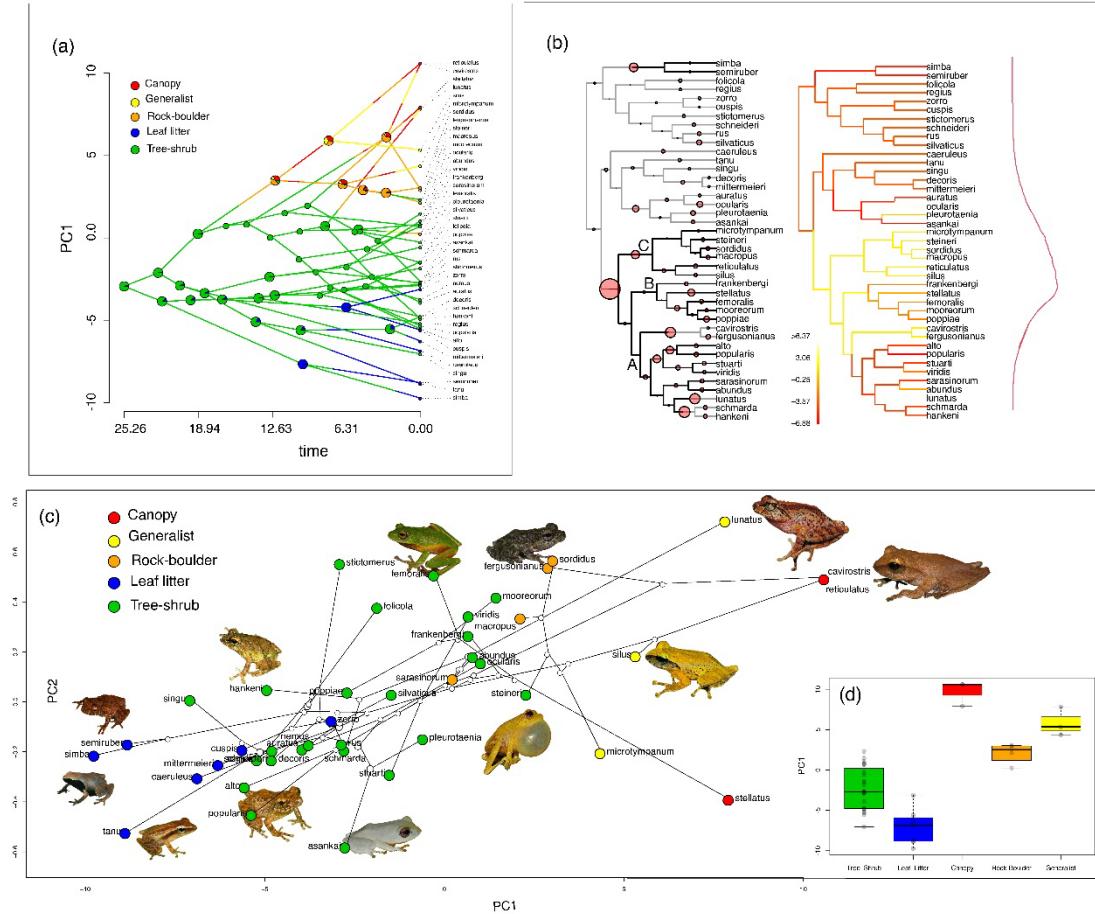
426



427

428 **Fig. 2. Rates of diversification and molecular phylogenetic relationships**
 429 **among extant *Pseudophilautus*, based on Bayesian inference of the concatenated**
 430 **data set of the 16S rRNA + 12S rRNA + CytB +Rag1 (2702 bp) loci.** Asterisks (*)
 431 **above nodes represent $\geq 95\%$ Bayesian posterior probabilities.** The blue line indicates
 432 **the log lineage through time plot, whereas the null (Yule) model is indicated by the red**
 433 **dashed line.** The lineage-through-time plot indicates an early burst of lineages ($\gamma = -$
 434 3.707) followed by a decrease in speciation rate with time. The graph inset shows that
 435 **having accounted for missing taxa, observed value of γ becomes significantly negative**
 436 **to the null model.** Although speciation rates appear higher during the Miocene, Extant
 437 **ecomorphs seem to have emerged during late Miocene and early Pliocene.**

438



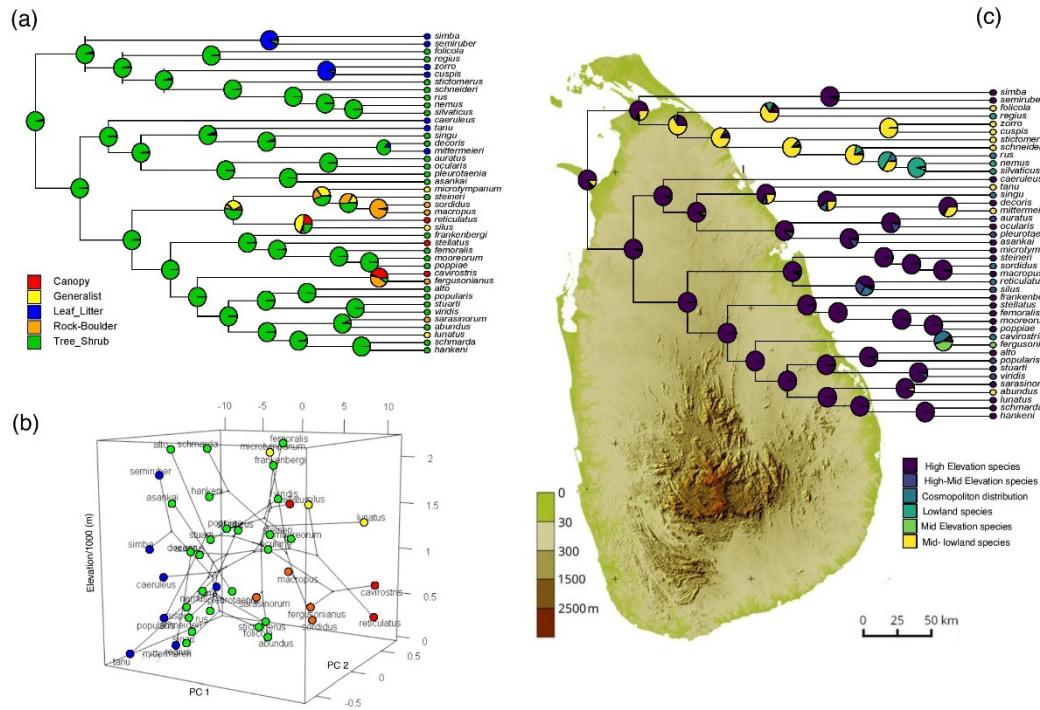
439

440 **Fig. 3. Temporal patterns of morphological evolution along PC1, evolutionary**
441 **shifts in body size and relative position of ecomorphs in the phylomorphospace of**
442 ***Pseudophilautus*.** (A) Traitgrams of PC1 suggest that the different morphs evolved
443 mainly by altering body size. Ancestral state reconstructions traced on traitgram (a)
444 suggest that a medium-sized Tree-shrub form gave rise to the other ecomorphs, which
445 likely evolved 10–5 MYA. (b) Most probable macroevolutionary rate shift
446 configurations for the evolution of body size across the phylogeny. Circles on the left
447 diagram denote shifts in rates of body size evolution. The most significant rate shift
448 occurred near the crown of clades A, B and C. Generally, an initial shift towards larger
449 body size was followed by shifts towards smaller body sizes, ultimately leading to a
450 single adaptive optimum. Branch colors on the right diagram denote instantaneous rates
451 (red = slow, yellow = fast). The probable number of adaptive peaks is denoted by the
452 red curve alongside panel. (c) Different ecomorphs traced on the phylomorphospace
453 indicates clear separation among the five ecomorphs along PC1, while Rock-boulder

454 forms and Leaf-litter forms are clearly separated along PC2. (d) Box plots show
455 separation of different ecomorph categories based on PC1 values (Table S4).

456

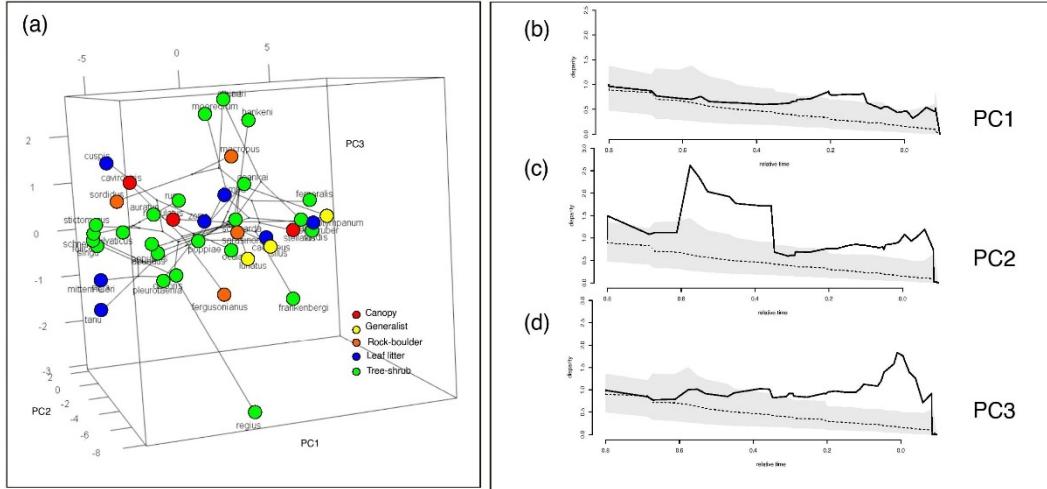
457



458

459 **Fig. 4. Ancestral state reconstructions (ANC) and phyloecospace of Sri Lankan**
460 ***Pseudophilautus*. (a) ANC based on five ecomorph categories of *Pseudophilautus*. (b)**
461 **Phyloecospace of ecomorph categories showing distribution of ecomorphs at different**
462 **elevations. (c) ANC based on the distribution of species at different elevations. Map of**
463 **Sri Lanka in the background depict different elevational ranges: highlands—above**
464 **1500 m, mid-elevations—500 to 1500 m, and lowlands—below 500 m. The likely**
465 **ancestor of *Pseudophilautus* is a Tree-shrub form that inhabited the highlands.**
466 **Elevation subsequently played a role in the evolution of different ecomorphs. For**
467 **example, Generalists are found only at high elevations while Rock-boulder forms are**
468 **found at only mid- to low elevations.**

469



470

471 **Fig. 5. Climate-niche occupation of *Pseudophilautus* ecomorphs in 3D**

472 phyloecospace and the evolution of climate niches of different ecomorphs.

473 Although a dominant pattern is not evident in the occupation of the the climatic niche

474 space, Leaf-litter forms appear to have a wider niche breadth along PC1 and generalists

475 and canopy forms have an expanded niche along PC2. Relative disparity-through-time

476 (DTT) plots of PC scores: PC1 (b), PC2 (c) and PC3 (d) depict change in the rate of

477 climatic niche evolution. Solid lines indicate the observed DTT; dashed lines and

478 corresponding polygons represent averages and 95% confidence intervals of the

479 expectations given a constant accumulation of disparity over time based on 999 pseudo-

480 replicates. A higher rate of climatic niche evolution is observed during the second and

481 fourth quarters of the evolutionary history of *Pseudophilautus*. These intervals

482 correspond to mid-Miocene climatic cinditions and monsoon-driven, wet Pliocene

483 climatic conditions, respectively.

484

485

486 **Methods**

487 The genus *Pseudophilautus* in Sri Lanka represent a spectacular diversification
488 comprised of direct developing frogs. Seventy-two species are recognized at present
489 [21](AmphibiaWeb, 2023) out of which three (*P. wynnaadensis*, *P. amboli* and *P. kani*)
490 represent a subclade from India. The Sri Lankan diversification comprise of 16 extinct
491 species [33](Meegaskumbura et al. 2007) as well as 10 nominal species lacking genetic
492 data [55](Ellepola et al. 2021). We included 41 species of Sri Lankan *Pseudophilautus*,
493 whose validity has been confirmed based on the general lineage concept [56](de Quroz,
494 1999), in the current analysis. These species occupy several habitat types ranging from
495 open grasslands, rock substrates along streams, rainforest canopy, shrubs, leaf litter and
496 anthropogenic habitats, and most are confined to higher elevations of the wet, montane
497 region of the island's southwestern quarter [28,29,33](Manamendra-Arachchi and
498 Pethiyagoda, 2005; Meegaskumbura et al., 2007, Meegaskumbura et al. 2019). To serve
499 as the outgroup, two species from the Indian sister group, *R. charius* and *R. signatus*
500 were included in the phylogenetic analyses.

501

502 **Morphometrics**

503 Thirty-two morphological measurements from adults of both sexes of all species were
504 obtained following the terminology of [29]Manamendra-Arachchi & Pethiyagoda
505 (2005). All measurements were made by the same person to avoid measurement bias
506 (Data S1). Abbreviations: distance between back of eyes (DBE), distance between front
507 of eyes (DFE), length of disk of third finger (DL), width of disk of third finger (DW),
508 eye diameter (ED), eye-to-nostril distance (EN), eye-to-snout distance (ES), femur
509 length (FEL), finger length (FL), foot length (FOL), head length (HL), head width
510 (HW), inner metatarsal tubercle length (IML), internarial distance (IN), interorbital
511 width (IO), lower arm length (LAL), mandible–back of eye distance (distance from
512 angle of jaws to posterior-most point of eye; MBE), mandible–front of eye distance
513 (distance from angle of jaws to anterior-most point of eye; MFE), mandible–nostril
514 distance (distance from angle of jaws to middle of nostril; MN), nostril–snout distance
515 (distance from middle of nostril to tip of snout; NS), palm length (distance from

516 posterior-most margin of inner palmar tubercle to tip of disk of third finger; PAL),
517 snout-vent length (SVL), tibia length (TBL), toe length (TL), tympanum to eye
518 diameter (TYE), tympanum diameter (TYD), upper arm length (UAL) and upper eyelid
519 width (UEW). Digit number is represented by roman numerals I-V (Data S1).

520

521 ***Morphology-habitat correlation***

522 Five main habitat type occupations have been proposed for Sri Lankan *Pseudophilautus*
523 [29-33](Manamendra-Arachchi and Pethiyagoda 2005; Meegaskumbura and
524 Manamendra-Arachchi 2005, 2007, 2009, 2012): Canopy, Generalist, Rock-boulder,
525 Leaf litter and Tree-shrub. These may represent ecomorphs.

526

527 Mean values for all mensural data were calculated for each sex of each species and were
528 \log_{10} -transformed to fulfill assumptions of normality and homoscedasticity. To explore
529 morphological variation among species, multivariate principal component analyses
530 (PCA) were performed using habitat as the grouping variable. Despite the sexual
531 dimorphism evident in *Pseudophilautus* species [29,30](Manamendra-Arachchi &
532 Pethiyagoda 2005, Meegaskumbura & Manamendra-Arachchi 2005), adult males and
533 females were included in the same analyses but identified by sex in the resulting plots.
534 However, because body size may obscure shape variation in interspecific
535 morphological data, we performed a PCA based on size-corrected data as well
536 [57](Velasco and Herrel, 2007). This enabled us to distinguish between size and shape
537 of the species being analysed. To remove effects of body size, residuals were calculated
538 of the regressions of the \log_{10} -transformed morphological variables against \log_{10} -
539 transformed SVL. The residual values were then used in a new principal component
540 analysis, to explore variation in shape among the species. Additionally, to account for
541 the phylogenetic non-independence among species, phylogenetic principal component
542 analyses (pPCA) were also performed on the data sets.

543

544 Linear discriminant analysis (LDA) was performed on normalized measurement data
545 as well as on residual values (i.e., the size-corrected data) to predict the probability of

546 a species belonging to an ecomorph category based on multiple predictor variables.
547 Discriminant analysis maximizes the differences between groups as opposed to
548 maximizing variance along axes in a PCA. The LDA determines group means and
549 computes, for each species, the probability of belonging to a given ecomorph category.
550 The species is then allocated to the category with the highest probability score. Here,
551 60% of the data were treated as training data and 40% were treated as testing data in
552 the LDA model.

553

554 ***Phylogenetic analysis***

555 To infer relationships among *Pseudophilautus*, we constructed a multi-gene phylogeny
556 based on three mtDNA (16S rRNA, 12S rRNA and CytB) and the NucDNA Rag-1
557 molecular loci. The data for CytB gene fragments were newly generated during the
558 current study (others obtained from [28]Meegaskumbura et al. 2019), and for this, DNA
559 was extracted from ethanol preserved tissues using Qiagen tissue extraction kits
560 following manufacturer's protocols. Portions of the CytB genes were amplified by PCR
561 and sequenced directly using dye-termination cycle sequencing. Thermocycling
562 conditions included an initial step at 94 °C for 3 min, followed by 35 cycles at 45 s at
563 94 °C, 1 min at 46–50 °C and 45 s at 48–56 °C, and a final step at 72 °C for 5 min.
564 GenBank accessions used in the analyses are listed in Table S5.

565

566 Mitochondrial gene fragments were aligned using MUSCLE as implemented by MEGA
567 v.11 [58](Tamura et al. 2021); regions for which there was low confidence in positional
568 homology were removed from the analysis. Nuclear gene sequences were aligned using
569 MEGA v.11 with translated amino-acid sequences. The complete concatenated dataset
570 included 43 valid taxa [55](Ellepola et al., 2021) and a total of 2702 base pairs (bp).
571 Two species of *Raorchestes* (*R. charius* and *R. signatus*), the sister group of
572 *Pseudophilautus*, were included as outgroup taxa.

573

574 Tree topology was inferred both using a maximum likelihood approach (IQ-TREE;
575 [59]Nguyen et al. 2015) and a bayesian approach (BEAST v.2.5; [60]Drummond and

576 Rambaut, 2007) of which both yielded similar results, hence the tree topology obtained
577 from BEAST were used in subsequent analyses. Both analyses were performed for both
578 partitioned and unpartitioned datasets as well as for each gene individually. The dataset
579 was partitioned into specific gene regions by specifying character sets (charset 12S
580 rRNA = 1–308; charset 16S rRNA = 309–776; charset CytB = 777–1310; charset Rag-
581 1 = 1311–2702). The partitioned dataset was used for the phylogenetic analyses. The
582 best-fitting nucleotide substitution model for each dataset was chosen using jModelTest
583 v.2.1.4 [61](Darriba et al. 2012). Model GTR+I+G as the nucleotide substitution model,
584 Yule model as the tree prior, and lognormal relaxed clock as the molecular clock were
585 assigned in BEAST and the analysis was run on the Cipres Science Gateway Server
586 [62](Miller et al. 2015) for 50 million generations in two consecutive runs. Burnin was
587 defined by observing the log-output file in Tracer v.1.6 [63](Drummond et al. 2012);
588 90% of post-burnin trees were analysed using Tree Annotator and a final maximum
589 clade credibility tree constructed (Data S2).

590
591 To examine the temporal context of divergence, we estimated divergence times among
592 lineages on the partitioned dataset by using BEAST v.2.5 [60](Drummond and Rambaut,
593 2007). The Yule model was given as the tree prior, the GTR+I+G model of evolution
594 specified, and other parameters estimated for all gene partitions. Over 10 million
595 generations of Markov chain Monte Carlo (MCMC) simulations were run, with one
596 tree saved per 1000 generations. The analysis was run using the uncorrelated lognormal
597 relaxed clock. We calibrated the tree using a literature-based, molecular-estimated
598 secondary calibration point from [64](Chen et al. (2020) (i.e., the age of the most recent
599 common ancestor (MRCA) of extant *Pseudophilautus*, 16.48–24.92 Mya) which was
600 derived based on different calibration prior-combinations that included fossil
601 calibrations as well as secondary calibrations on a Anchored Hybrid Enrichment data
602 set.

603
604 We analysed the accumulation of lineages through time to discern the tempo of
605 diversification in the radiation [65](Harmon et al., 2008). Lineage-through-time plots

606 were constructed by plotting the log number of lineages against the divergence time as
607 implemented in phytools 2.0 [66](Revell, 2023). A null model was also developed
608 wherein the tree was simulated with a total of 72 taxa (to account for the missing taxa-
609 [21]Amphibiaweb (2023) records 72 species for *Pseudophilautus*) and assuming a
610 constant rate of speciation across the lineages (under a pure birth model) with no
611 extinctions. A Monte Carlo Constant Rate test (MCCR) was used to calculate the
612 gamma (γ) statistic in phytools 2.0, which compares the general shape of the lineage
613 through time curve to a null pure birth model. If $\gamma < 0$, the radiation shows an early,
614 rapid speciation event; if $\gamma = 0$, the radiation undergoes a constant diversification rate;
615 and if $\gamma > 0$, the diversification rate increases towards the present [67](Pybus and
616 Harvey, 2000).

617

618 We visualized the evolution of traits of *Pseudophilautus* defined by PC1 and PC2 axes
619 in a phylomorphospace [68](Sidlauskas, 2008) using the phylomorphospace function
620 in PHYTOOLS [69](Revell, 2012). Further, by using principal component values, we
621 tested whether there are significant differences among ecomorphs in their morphospace
622 positions by performing a phylogenetic MANOVA. This was backed by phylogenetic
623 ANOVA and post hoc tests performed on each PC axis treated with ‘ecomorph’ as the
624 categorical variable [69](Revell, 2012).

625

626 Morphological variation in *Pseudophilautus* was described by estimating ancestral
627 states of PC1 and PC2 and visualizing them using traitgrams [70](Evans et al. 2009)
628 under a browninan motion model, implemented with the phenogram function in
629 PHYTOOLS [69](Revell, 2012). Ancestral states were reconstructed separately based
630 on different ecomorphs, and elevational level (primarily: highlands—above 1500 m,
631 mid-elevations—500 to 1500 m, and lowlands—below 500 m; species sharing two or
632 more levels were categorized as high-mid, mid-low or cosmopolitan; Data S3). To infer
633 the number and timing of evolutionary shifts within ecomorphs, we used stochastic
634 character mapping [71,72](Neilson 2002; Heulsenbeck et al. 2003) implemented with
635 the make.simmap (model="ER") function in PHYTOOLS [69](Revell, 2012). We

636 tested multiple models for the ancestral state reconstruction; the ER model gave the
637 highest likelihood. On each of the 1000 post burnin trees obtained from BEAST, we
638 used stochastic character mapping to generate 100 potential histories. This approach
639 considers uncertainty in both the evolutionary history of the traits as well as the inferred
640 topology of the phylogeny.

641

642 To identify evolutionary shifts in body size (defined by PC1 axis), the bayou v. 2.1.1
643 analysis [73](Uyeda and Harmon 2014) was implemented in R v. 4.2.1 [74](R Core
644 Team 2022). The ‘bayou’ approach detects evolutionary shifts towards different optima
645 without influence by a priori groupings on the tree. Bayou uses a reversible-jump
646 Bayesian approach that uses univariate data to estimate the placement and magnitude
647 of evolutionary shifts [73](Uyeda and Harmon 2014). We used an unconstrained bayou
648 analysis on PC1 values using an OU model with different priors. The model having the
649 prior values alpha = 0.09, sig2 = 0.09, k = 0.25, theta = 0.32, and loc = 0.01 was selected
650 as a reasonable OU model for the analysis, and shifts with a posterior probability (pp)
651 of 0.5 were regarded as significant. We used PC1 values, which explain 93.2% of the
652 variance, as the continuous variable, as it mostly represents body size.

653

654 ***Climatic niche evolution***

655 We obtained from published literature present-day geographical occurrences in the
656 form of GPS coordinates for all extant *Pseudophilautus* species, which we
657 supplemented with geocoordinates from our own field data. Location data are provided
658 in Data S3. Our final data set includes a total of 363 occurrence records.

659

660 Information on 19 bioclimatic variables and elevation for each occurrence point (at a
661 spatial resolution of 0.5 arcsec) was obtained from WORLDCLIM 2.0 [75](Ficks and
662 Hijmans 2017) using the “extract” function in RASTER 3.0-7 [76](Hijmans et al. 2015).
663 Mean values for each bioclimatic variable for each taxon are provided in Data S4.

664

665 We used the average bioclimatic conditions in a PCA based on their correlation matrix

666 to illustrate climatic niche occupation of different ecomorphs. The axes to be retained
667 for further analyses were determined using the broken-stick method as implemented in
668 VEGAN 2.5-6 [77](Oksanen et al. 2017). We assumed that measured species means are
669 a reasonable approximation of the realized climatic niche of the species [78](Wiens et
670 al. 2007). We constructed the 3D phyloecospace for all ecomorphs by using the
671 calculated PC scores to show the climatic niche occupation of ecomorphs. We then
672 assessed the extent to which traits (climatic niche evolution along each PC axis) had
673 accumulated over time in each biogeographic region using disparity-through-time
674 (DTT) plots [79](Harmon et al. 2003), with expected disparities calculated based on
675 1000 resampling by using the ‘dtt’ function in GEIGER 2.0.6.2 [65](Harmon et al. 2008)
676 and with phenograms (projections of the phylogenetic tree in a space defined by
677 phenotype/PC axis and time) constructed with the ‘phenogram’ function in
678 PHYTOOLS [69](Revell, 2012).

679

680 **Data availability**

681 The authors declare that data supporting the findings of this study are available within
682 the Data files S1, S2, S3 and S4. Additional data that support the findings of this study
683 are publicly available online at <https://www.ncbi.nlm.nih.gov/genbank/>,
684 <http://www.iucnredlist.org/technical-documents/spatial-data>, <https://www.gbif.org> and
685 <https://www.worldclim.org>. For Genbank accession numbers see Table S5.

686

687 **Code availability**

688 All codes used in support of this publication are publicly available in specific R
689 packages which we have mentioned in the reference list.

690

691 **References**

- 692 1. Schluter D. 2000 Ecological character displacement in adaptive radiation. *Am. Nat.* **156**, S4-S16. (doi:10.1086/303412).
- 693 2. Darwin C. 1845 *Journal of researches into the natural history and geology of the countries visited during the voyage of H.M.S. beagle round the world under the Command of Capt. FitzRoy, RN.* London: John Murray.
- 694
- 695
- 696

697 3. Glor RE. 2010 Phylogenetic insights on adaptive radiation. *Annu. Rev. Ecol. Evol. Syst.* **41**, 251-270. (doi:10.1146/annurev.ecolsys.39.110707.173447).

698 4. Losos JB, Miles DB. 2002 Testing the hypothesis that a clade has adaptively radiated: iguanid lizard clades as a case study. *Am. Nat.* **160**, 147-157. (doi:10.1086/341557).

699 5. Losos JB, Ricklefs RE. 2009 Adaptation and diversification on islands. *Nature* **457**, 830-836. (doi:10.1038/nature07893).

700 6. Losos JB, Mahler DL. 2010 Adaptive radiation: the interaction of ecological opportunity, adaptation, and speciation. In *Evolution since Darwin: the first 150 years* (eds Bell MA, Futuyma DJ, Eanes WF, Levinton JS), pp. 381-420. Sunderland, UK: Sinauer Associates.

701 7. Blackburn DC, Siler CD, Diesmos AC, McGuire JA, Cannatella DC, Brown RM. 2013 An adaptive radiation of frogs in a Southeast Asian island archipelago. *Evolution* **67**, 2631-2646. (doi:10.1111/evo.12145).

702 8. Close Roger A, Friedman M, Lloyd Graeme T, Benson Roger BJ. 2015 Evidence for a Mid-Jurassic adaptive radiation in mammals. *Curr. Biol.* **25**, 2137-2142. (doi:10.1016/j.cub.2015.06.047).

703 9. Tokita M, Yano W, James HF, Abzhanov A. 2017 Cranial shape evolution in adaptive radiations of birds: comparative morphometrics of Darwin's finches and Hawaiian honeycreepers. *Philos. Trans. R. Soc. B: Biol. Sci.* **372**, 20150481. (doi:10.1098/rstb.2015.0481).

704 10. Simões TR, Vernygora O, Caldwell MW, Pierce SE. 2020 Megaevolutionary dynamics and the timing of evolutionary innovation in reptiles. *Nat. Commun.* **11**, 3322. (doi:10.1038/s41467-020-17190-9).

705 11. Svardal H, Quah FX, Malinsky M, Ngatunga BP, Miska EA, Salzburger W, Genner MJ, Turner GF, Durbin R. 2020 Ancestral hybridization facilitated species diversification in the Lake Malawi cichlid fish adaptive radiation. *Mol. Biol. Evol.* **37**, 1100-1113. (doi:10.1093/molbev/msz294).

706 12. Seehausen O. 2006 African cichlid fish: a model system in adaptive radiation research. *Proc. R. Soc. B: Biol. Sci.* **273**, 1987-1998. (doi:10.1098/rspb.2006.3539).

707 13. Astudillo-Clavijo V, Arbour JH, López-Fernández H. 2015 Selection towards different adaptive optima drove the early diversification of locomotor phenotypes in the radiation of Neotropical geophagine cichlids. *BMC Evol. Biol.* **15**, 77. (doi:10.1186/s12862-015-0348-7).

708 14. Arnold SJ, Bürger R, Hohenlohe PA, Ajie BC, Jones AG. 2008 Understanding the evolution and stability of the G-Matrix. *Evolution* **62**, 2451-2461. (doi:10.1111/j.1558-5646.2008.00472.x).

709 15. Revell LJ, Harmon LJ, Collar DC, Oakley T. 2008 Phylogenetic signal, evolutionary process, and rate. *Syst. Biol.* **57**, 591-601. (doi:10.1080/10635150802302427).

710 16. Aerts P, Van Damme R, Vanhooydonck B, Zaaf A, Herrel A. 2000 Lizard locomotion: how morphology meets ecology. *Neth. J. Zool.* **50**, 261-277. (doi:10.1163/156854200505865).

741 17. Schluter D. 2001 Ecology and the origin of species. *Trends Ecol. Evol.* **16**, 372-
742 380. (doi:10.1016/s0169-5347(01)02198-x).

743 18. Erwin DH. 1994 Early introduction of major morphological innovations. *Acta*
744 *Palaeontol. Pol.* **38**, 281-294.

745 19. Moen DS, Ravelojaona RN, Hutter CR, Wiens JJ. 2021 Testing for adaptive
746 radiation: A new approach applied to Madagascar frogs. *Evolution* **75**, 3008-
747 3025. (doi:10.1111/evo.14328).

748 20. Simpson GG. 1953 The major features of evolution. *Columbia University Press*.

749 21. AmphibiaWeb. Information on amphibian biology and conservation
750 (AmphibiaWeb, 2023).

751 22. Duellman WE, Trueb L. 1986 Biology of Amphibians. Mc Graw-Hill Book
752 Company, 1221 Avenue of the Americas, New York, New York 10020, U.S.A.;
753 Mc Graw-Hill Book Company GmbH, Postfach 630520, D-2000 Hamburg 63,
754 Bundesrepublik Deutschland. 670 pp. many figures and tables, price: \$ 40,-,
755 D.M. 128. *Amphib-reptil.* **9**, 319-321. (doi:10.1163/156853888x00459).

756 23. Bossuyt F, Milinkovitch MC. 2000 Convergent adaptive radiations in
757 Madagascan and Asian ranid frogs reveal covariation between larval and adult
758 traits. *Proc. Natl. Acad. Sci. USA* **97**, 6585-6590.
759 (doi:10.1073/pnas.97.12.6585).

760 24. Meegaskumbura M, Bossuyt F, Pethiyagoda R, Manamendra-Arachchi K, Bahir
761 M, Milinkovitch MC, Schneider CJ. 2002 Sri Lanka: an amphibian hot spot.
762 *Science* **298**, 379-379. (doi:10.1126/science.298.5592.379).

763 25. Meegaskumbura M, Senevirathne G, Biju SD, Garg S, Meegaskumbura S,
764 Pethiyagoda R, Hanken J, Schneider CJ. 2015 Patterns of reproductive-mode
765 evolution in Old World tree frogs (Anura, Rhacophoridae). *Zool. Scr.* **44**, 509-
766 522. (doi:10.1111/zsc.12121).

767 26. Sudasinghe H, Ranasinghe RHT, Goonatilake SdA, Meegaskumbura M. 2018
768 A review of the genus *Labeo* (Teleostei: Cyprinidae) in Sri Lanka. *Zootaxa* **4486**,
769 201-235. (doi:10.11646/zootaxa.4486.3.1).

770 27. Bossuyt F *et al.* 2004 Local endemism within the Western Ghats-Sri Lanka
771 biodiversity hotspot. *Science* **306**, 479-481. (doi:10.1126/science.1100167).

772 28. Meegaskumbura M, Senevirathne G, Manamendra-Arachchi K, Pethiyagoda R,
773 Hanken J, Schneider CJ. 2019 Diversification of shrub frogs (Rhacophoridae,
774 *Pseudophilautus*) in Sri Lanka-Timing and geographic context. *Mol.*
775 *Phylogenetics Evol.* **132**, 14-24. (doi:10.1016/j.ympev.2018.11.004).

776 29. Manamendra-Arachchi K, Pethiyagoda R. 2005 The Sri Lankan shrub-frogs of
777 the genus *Philautus* Gistel, 1848 (Ranidae: Rhacophorinae), with description of
778 27 new species. In *Contributions to biodiversity exploration and research in Sri*
779 *Lanka* (eds Yeo CJ, Ng PKL, Pethiyagoda R), *Raffles Bull. Zool. Supplement*
780 *12*, pp. 163-303.

781 30. Meegaskumbura M, Manamendra-Arachchi K. 2005 Description of eight new
782 species of shrub frogs (Ranidae: Rhacophorinae: *Philautus*) from Sri Lanka.
783 *Raffles Bull. Zool.* **12**, 305-338.

784 31. Meegaskumbura M, Manamendra-Arachchi K, Bowatte G, Meegaskumbura S.

785 2012 Rediscovery of *Pseudophilautus semiruber*, a diminutive shrub frog
786 (Rhacophoridae: *Pseudophilautus*) from Sri Lanka. *Zootaxa* **3229**, 58-68.
787 (doi:10.11646/zootaxa.3229.1.4).

788 32. Meegaskumbura M, Manamendra-Arachchi K, Pethiyagoda R. 2009 Two new
789 species of shrub frogs (Rhacophoridae: *Philautus*) from the lowlands of Sri
790 Lanka. *Zootaxa* **2122**, 51-68. (doi:10.5281/zenodo.188147).

791 33. Meegaskumbura M, Manamendra-Arachchi K, Schneider CJ, Pethiyagoda R.
792 2007 New species amongst Sri Lanka's extinct shrub frogs (Amphibia:
793 Rhacophoridae: *Philautus*). *Zootaxa* **1397**, 1-15.
794 (doi:10.11646/zootaxa.1397.1.1).

795 34. Wickramasinghe LJM, Vidanapathirana DR, Airyarthne S, Rajeev G, Chanaka
796 A, Pastorini J, Chathuranga G, Wickramasinghe N. 2013 Lost and found: one
797 of the world's most elusive amphibians, *Pseudophilautus stellatus* (Kelaart 1853)
798 rediscovered. *Zootaxa* **3620**, 112-128. (doi:10.11646/zootaxa.3620.1.5).

799 35. Meegaskumbura M, Manamendra-Arachchi K. 2011 Two new species of shrub
800 frogs (Rhacophoridae: *Pseudophilautus*) from Sri Lanka. *Zootaxa* **2747**, 1-18.
801 (doi:10.11646/zootaxa.2747.1.1).

802 36. Schlüter D. (Oxford Univ. Press, 2000) *The ecology of adaptive radiation*.

803 37. Givnish TJ. 1997 Adaptive radiation and molecular systematics: aims and
804 conceptual issues. In *Molecular evolution and adaptive radiation* (eds Givnish
805 TJ, Sytsma KJ), pp. 1-54. New York, USA: Cambridge University Press.

806 38. Brandley MC, de Queiroz K. 2004 Phylogeny, ecomorphological evolution, and
807 historical biogeography of the *Anolis Cristatellus* series. *Herpetol. Monogr.* **18**,
808 90-126. (doi:10.1655/0733-1347(2004)018[0090:Peeahb]2.0.Co;2).

809 39. Johnson MS, Murray J, Clarke B. 1993 The ecological genetics and adaptive
810 radiation of *Partula* on Moorea. *Oxford Surv. Evol. Biol.* **9**, 167-238.

811 40. Clarke BC, Johnson MS, Murray J. 1996 Clines in the genetic distance between
812 two species of island land snails: how 'molecular leakage' can mislead us about
813 speciation. *Philos. Trans. R. Soc. Lond., B, Biol. Sci.* **351**, 773-784.
814 (doi:10.1098/rstb.1996.0072).

815 41. Rodríguez-Robles JA, Jezkova T, García MA. 2007 Evolutionary relationships
816 and historical biogeography of *Anolis desechensis* and *Anolis monensis*, two
817 lizards endemic to small islands in the eastern Caribbean Sea. *J. Biogeogr.* **34**,
818 1546-1558. (doi:10.1111/j.1365-2699.2007.01718.x).

819 42. Jackman TR, Larson A, de Queiroz K, Losos JB, Cannatella D. 1999
820 Phylogenetic relationships and tempo of early diversification in *Anolis* lizards.
821 *Syst. Biol.* **48**, 254-285. (doi:10.1080/106351599260283).

822 43. Bahir MM, Meegaskumbura M, Manamendra-Arachchi K, Schneider CJ,
823 Pethiyagoda R. 2005 Reproduction and terrestrial direct development in Sri
824 Lankan shrub frogs (Ranidae: Rhacophorinae: *Philautus*). *Raffles Bull. Zool.* **12**,
825 339-350.

826 44. Svanbäck R, Bolnick DI. 2007 Intraspecific competition drives increased
827 resource use diversity within a natural population. *Proc. R. Soc. B: Biol. Sci.*
828 **274**, 839-844. (doi:10.1098/rspb.2006.0198).

829 45. Day T, Young KA. 2004 Competitive and facilitative evolutionary
830 diversification. *Bioscience* **54**, 101-109. (doi:10.1641/0006-
831 3568(2004)054[0101:Cafed]2.0.Co;2).

832 46. Gavrilets S, Vose A. 2005 Dynamic patterns of adaptive radiation. *Proc. Natl.
833 Acad. Sci. USA* **102**, 18040-18045. (doi:10.1073/pnas.0506330102).

834 47. Dayan T, Simberloff D. 2005 Ecological and community-wide character
835 displacement: the next generation. *Ecol. Lett.* **8**, 875-894. (doi:10.1111/j.1461-
836 0248.2005.00791.x).

837 48. Gavrilets S, Losos JB. 2009 Adaptive radiation: contrasting theory with data.
838 *Science* **323**, 732-737. (doi:10.1126/science.1157966).

839 49. Schweiger S, Naumann B, Larson JG, Möckel L, Müller H. 2017 Direct
840 development in African squeaker frogs (Anura: Arthroleptidae: *Arthroleptis*)
841 reveals a mosaic of derived and plesiomorphic characters. *Org. Divers. Evol.* **17**,
842 693-707. (doi:10.1007/s13127-017-0335-5).

843 50. Chatterjee S, Goswami A, Scotese CR. 2013 The longest voyage: tectonic,
844 magmatic, and paleoclimatic evolution of the Indian plate during its northward
845 flight from Gondwana to Asia. *Gondwana Res.* **23**, 238-267.
846 (doi:10.1016/j.gr.2012.07.001).

847 51. Ellepola G, Pie MR, Pethiyagoda R, Hanken J, Meegaskumbura M. 2022 The
848 role of climate and islands in species diversification and reproductive-mode
849 evolution of Old World tree frogs. *Commun. Biol.* **5**, 347. (doi:10.1038/s42003-
850 022-03292-1).

851 52. Yin A, Harrison TM. 2000 Geologic evolution of the Himalayan-Tibetan orogen.
852 *Annu. Rev. Earth Planet. Sci.* **28**, 211-280. (doi:10.1146/annurev.earth.28.1.211).

853 53. Gehrels GE, DeCelles PG, Martin A, Ojha TP, Pinhassi G, Upreti BN. 2003
854 Initiation of the Himalayan orogen as an early Paleozoic thin-skinned thrust belt.
855 *GSA Today* **13**, 4-9. (doi:10.1130/1052-5173(2003)13<4:Iothoa>2.0.Co;2).

856 54. Ellepola G, Meegaskumbura M. 2023 Diversification and biogeography of
857 Rhacophoridae – a model testing approach. *Front. Ecol. Evol.* In review.

858 55. Ellepola G, Herath J, Manamendra-Arachchi K, Wijayathilaka N, Senevirathne
859 G, Pethiyagoda R, Meegaskumbura M. 2021 Molecular species delimitation of
860 shrub frogs of the genus *Pseudophilautus* (Anura, Rhacophoridae). *PLoS ONE*
861 **16**, e0258594. (doi:10.1371/journal.pone.0258594).

862 56. De Queiroz K. 1999 The general lineage concept of species and the defining
863 properties of the species category. In *species: new interdisciplinary essays* (ed
864 Wilson RA), pp. 49-89. Cambridge, MA: MIT Press.

865 57. Velasco JA, Herrel A. 2007 Ecomorphology of *Anolis* lizards of the Choco'
866 region in Colombia and comparisons with Greater Antillean ecomorphs. *Biol. J.
867 Linn. Soc.* **92**, 29-39. (doi:10.1111/j.1095-8312.2007.00885.x).

868 58. Tamura K, Stecher G, Kumar S, Battistuzzi FU. 2021 MEGA11: molecular
869 evolutionary genetics analysis version 11. *Mol. Biol. Evol.* **38**, 3022-3027.
870 (doi:10.1093/molbev/msab120).

871 59. Nguyen L-T, Schmidt HA, von Haeseler A, Minh BQ. 2015 IQ-TREE: A Fast
872 and Effective Stochastic Algorithm for Estimating Maximum-Likelihood

873 Phylogenies. *Mol. Biol. Evol.* **32**, 268-274. (doi:10.1093/molbev/msu300).

874 60. Drummond AJ, Rambaut A. 2007 BEAST: Bayesian evolutionary analysis by
875 sampling trees. *BMC Evol. Biol.* **7**, 214. (doi:10.1186/1471-2148-7-214).

876 61. Darriba D, Taboada GL, Doallo R, Posada D. 2012 jModelTest 2: more models,
877 new heuristics and parallel computing. *Nat. Methods* **9**, 772.
878 (doi:10.1038/nmeth.2109).

879 62. Miller MA, Schwartz T, Pickett BE, He S, Klem EB, Scheuermann RH,
880 Passarotti M, Kaufman S, O'Leary MA. 2015 A Restful API for access to
881 phylogenetic tools via the CIPRES Science Gateway. *Evol. Bioinform.* **11**, 43-
882 48. (doi:10.4137/ebo.S21501).

883 63. Drummond AJ, Suchard MA, Xie D, Rambaut A. 2012 Bayesian phylogenetics
884 with BEAUTi and the BEAST 1.7. *Mol. Biol. Evol.* **29**, 1969-1973.
885 (doi:10.1093/molbev/mss075).

886 64. Chen JM *et al.* 2020 An integrative phylogenomic approach illuminates the
887 evolutionary history of Old World tree frogs (Anura: Rhacophoridae). *Mol.*
888 *Phylogenetics Evol.* **145**. (doi:10.1016/j.ympev.2019.106724).

889 65. Harmon LJ, Weir JT, Brock CD, Glor RE, Challenger W. 2008 Geiger:
890 investigating evolutionary radiations. *Bioinformatics* **24**, 129-131.
891 (doi:10.1093/bioinformatics/btm538).

892 66. Revell LJ. 2023 phytools 2.0: An updated R ecosystem for phylogenetic
893 comparative methods (and other things). *bioRxiv*.
894 (doi:10.1101/2023.03.08.531791).

895 67. Pybus OG, Harvey PH. 2000 Testing macro-evolutionary models using
896 incomplete molecular phylogenies. *Proc. R. Soc. B: Biol. Sci.* **267**, 2267-2272.
897 (doi:10.1098/rspb.2000.1278).

898 68. Sidlauskas B. 2008 Continuous and arrested morphological diversification in
899 sister clades of characiform fishes: a phylomorphospace approach. *Evolution* **62**,
900 3135-3156. (doi:10.1111/j.1558-5646.2008.00519.x).

901 69. Revell LJ. 2012 phytools: an R package for phylogenetic comparative biology
902 (and other things). *Methods Ecol. Evol.* **3**, 217-223. (doi:10.1111/j.2041-
903 210X.2011.00169.x).

904 70. Evans Margaret EK, Smith Stephen A, Flynn Rachel S, Donoghue Michael J.
905 2009 Climate, niche evolution, and diversification of the “bird-cage” evening
906 Primroses (Oenothera, Sections Anogra and Kleinia). *Am. Nat.* **173**, 225-240.
907 (doi:10.1086/595757).

908 71. Nielsen R, Huelsenbeck J. 2002 Mapping mutations on phylogenies. *Syst. Biol.*
909 **51**, 729-739. (doi:10.1080/10635150290102393).

910 72. Huelsenbeck JP, Nielsen R, Bollback JP, Schultz T. 2003 Stochastic mapping of
911 morphological characters. *Syst. Biol.* **52**, 131-158.
912 (doi:10.1080/10635150390192780).

913 73. Uyeda JC, Harmon LJ. 2014 A Novel Bayesian Method for Inferring and
914 Interpreting the Dynamics of Adaptive Landscapes from Phylogenetic
915 Comparative Data. *Syst. Biol.* **63**, 902-918. (doi:10.1093/sysbio/syu057).

916 74. R Core Team. 2022 R: A language and environment for statistical computing. R

917 Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.

918

919 75. Fick SE, Hijmans RJ. 2017 WorldClim 2: new 1-km spatial resolution climate
920 surfaces for global land areas. *Int. J. Climatol.* **37**, 4302-4315.
921 (doi:10.1002/joc.5086).

922 76. Hijmans RJ, Phillips S, Leathwick J, Elith J. 2015 Dismo: species distribution
923 modeling. R package version 1.0-12, <http://CRAN.R-project.org/package=dismo>.

924

925 77. Oksanen J, Simpson GL, Blanchet FG, Kindt R, Legendre P, Minchin PR,
926 O'Hara RB. 2017 Vegan: community ecology package. R package Version 2.4-
927 3, <https://CRAN.R-project.org/package=vegan>.

928 78. Wiens JJ, Parra-Olea G, García-París M, Wake DB. 2007 Phylogenetic history
929 underlies elevational biodiversity patterns in tropical salamanders. *Proc. R. Soc.
930 B: Biol. Sci.* **274**, 919-928. (doi:10.1098/rspb.2006.0301).

931 79. Harmon LJ, Schulte JA, Larson A, Losos JB. 2003 Tempo and mode of
932 evolutionary radiation in iguanian lizards. *Science* **301**, 961-964.
933 (doi:10.1126/science.1084786).

934

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947 **Author contributions**

948 Conceptualization, M.M., M.P., G.E. and G.S.; methodology, M.P. and G.E.; formal
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950 curation, G.E., G.S., D.S ; writing—original draft preparation, M.M., G.E.,

951 G.S., K.M., N.W. M.P., D.S., R.P. and C.S; writing—review and editing, M.M., G.E.,
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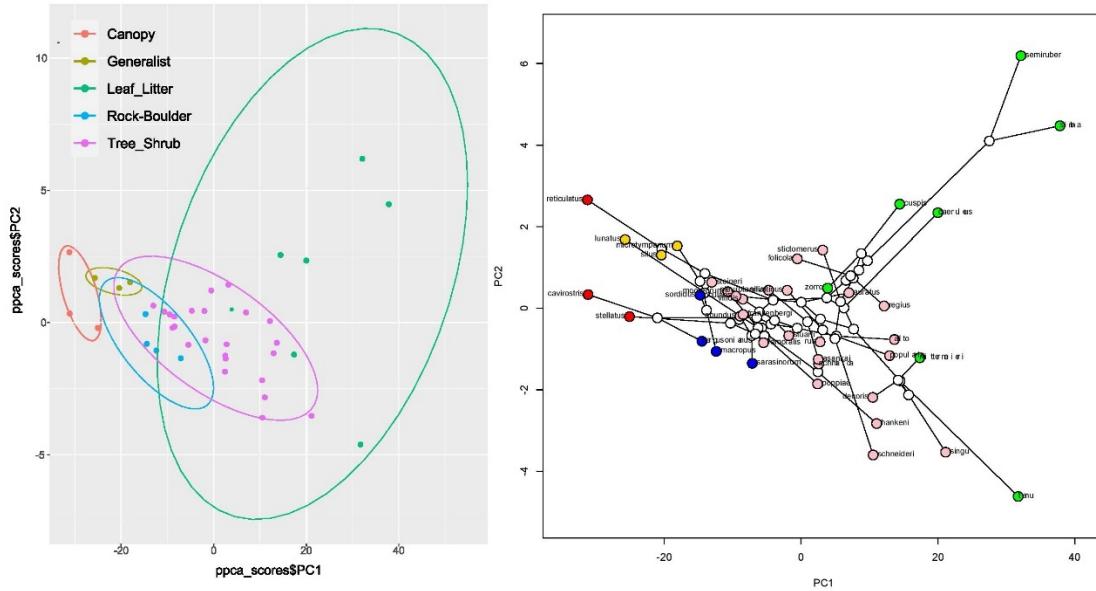
954 Competing interests

955 The authors declare no competing interests.

956

957 Extended data Figures

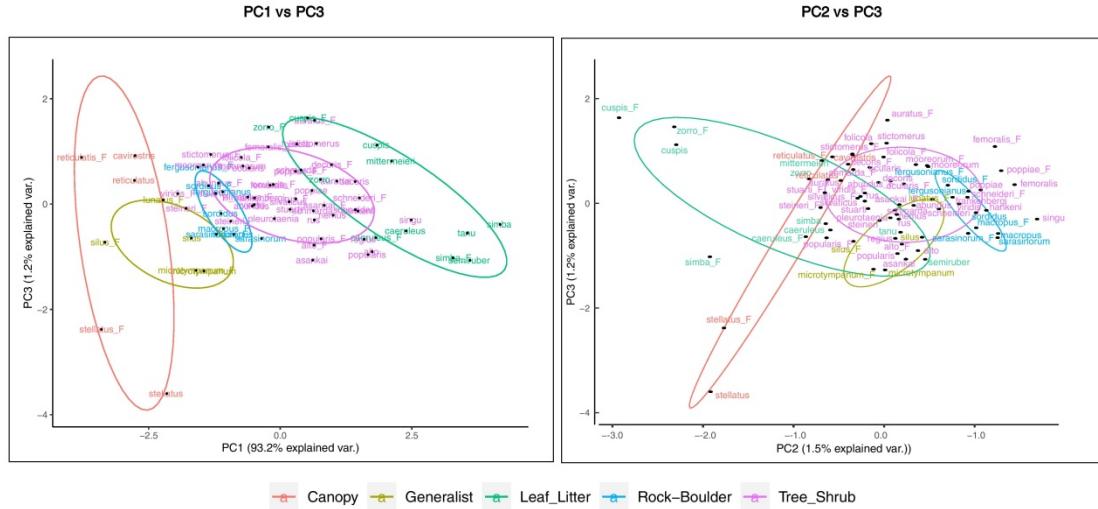
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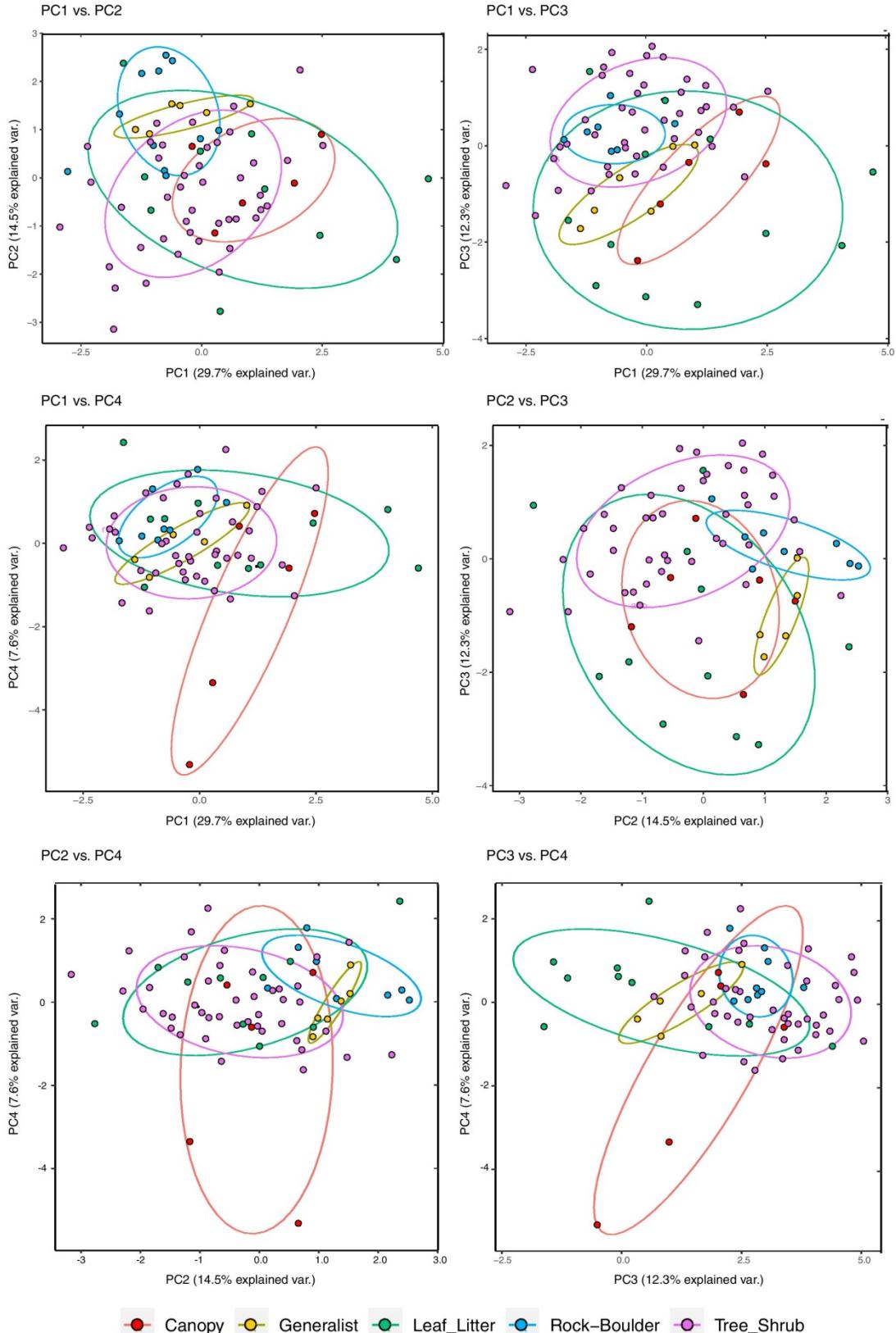
960 **Extended Data Figure 1. The position of Sri Lankan *Pseudophilautus* in**
961 **morphological space as indicated by the first two axes of the phylogenetic principal**
962 **component analysis (pPCA).** Ecomorphs categories are distinguished mainly along
963 pPC1 axis (left). pPC1 is primarily defined by body size (SVL), foot length (FOL)
964 and head length (HL) whereas PC2 is mainly defined by upper eyelid width (UEW),
965 lower arm length (LAL) and interorbital width (IN). The phlomorphaspace laid on the
966 pPC axes shows that ecomorphs cluster despite being phylogenetically unrelated hence
967 pointing towards a convergent adaptive radiation in *Pseudophilautus*.

968



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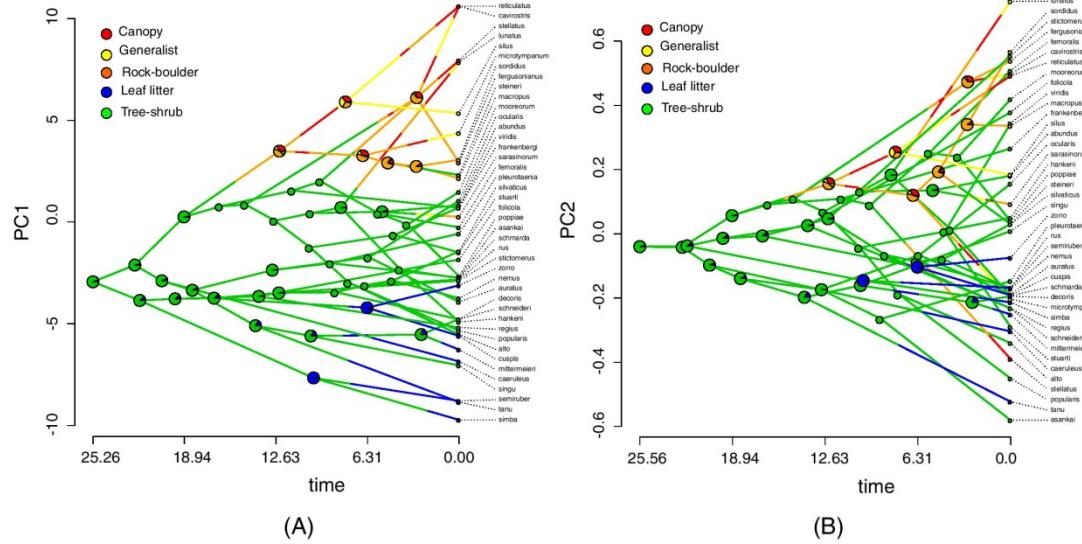
970 **Extended Data Figure 2. The position of Sri Lankan *Pseudophilautus* in**
971 **morphological space as indicated by principal component analysis (PC2 and PC3)**
972 **conducted on the raw data.** Ecomorph categories are clearly separated along the PC1
973 axis. PCA defined by PC2 and PC3 explains only about 2.7% of the variance. PC2 and
974 PC3 do not distinguish between ecomorph categories, although Upper eyelid width
975 (UEW) and Palm length (PAL), and distance from eye to nostril (NE) and Nostril–snout
976 distance (NS), load heavily on PC2 and PC3, respectively (see Table S1).



Extended Data Figure 3. The position of Sri Lankan *Pseudophilautus* in morphological space as indicated by different axis combinations of the principal component analysis, using size-adjusted data. Overall, different ecomorph categories

981 are not well defined along any axis. However, Canopy and Generalist forms segregate
982 along PC2, while Rock-boulder forms segregate from Canopy forms along PC1 and
983 PC3. A general pattern indicates that all other ecomorphs exist within the morphological
984 space of Leaf-litter forms but Tree-shrub forms being an exception along PC4. The
985 relationships between different principal component axes are shown by sub plots.
986

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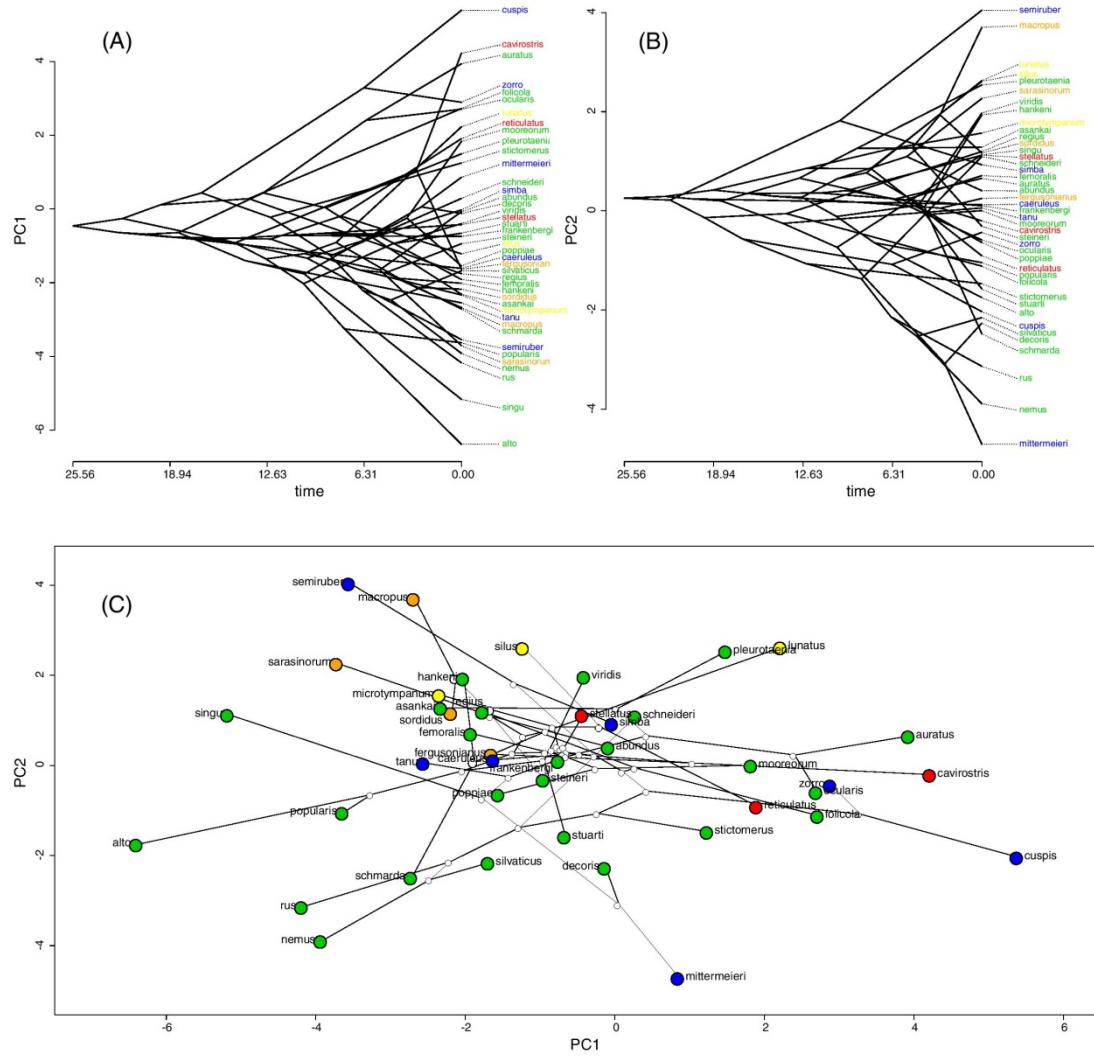
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(A)

(B)

989 **Extended Data Figure 4. Temporal patterns of morphological evolution in**
990 **ecomorphs along PC1 and PC2.** The traitgram of PC1 (A) suggests that the evolution
991 of different morphs is attained mainly by altering body size, whereas a clear pattern is
992 not evident by the traitgram of PC2 (B). Overall, these patterns suggest that body size
993 evolution and evolution of morphological characters such as Upper eyelid width (UEW)
994 and Palm length (PAL) were largely decoupled during the history of *Pseudophilautus*.
995 Ancestral-state reconstructions traced on traitgrams suggest that a medium-sized tree
996 shrub form has given rise to other ecomorphs. Other ecomorphs likely evolved between
997 10 and 5 MYA.

998



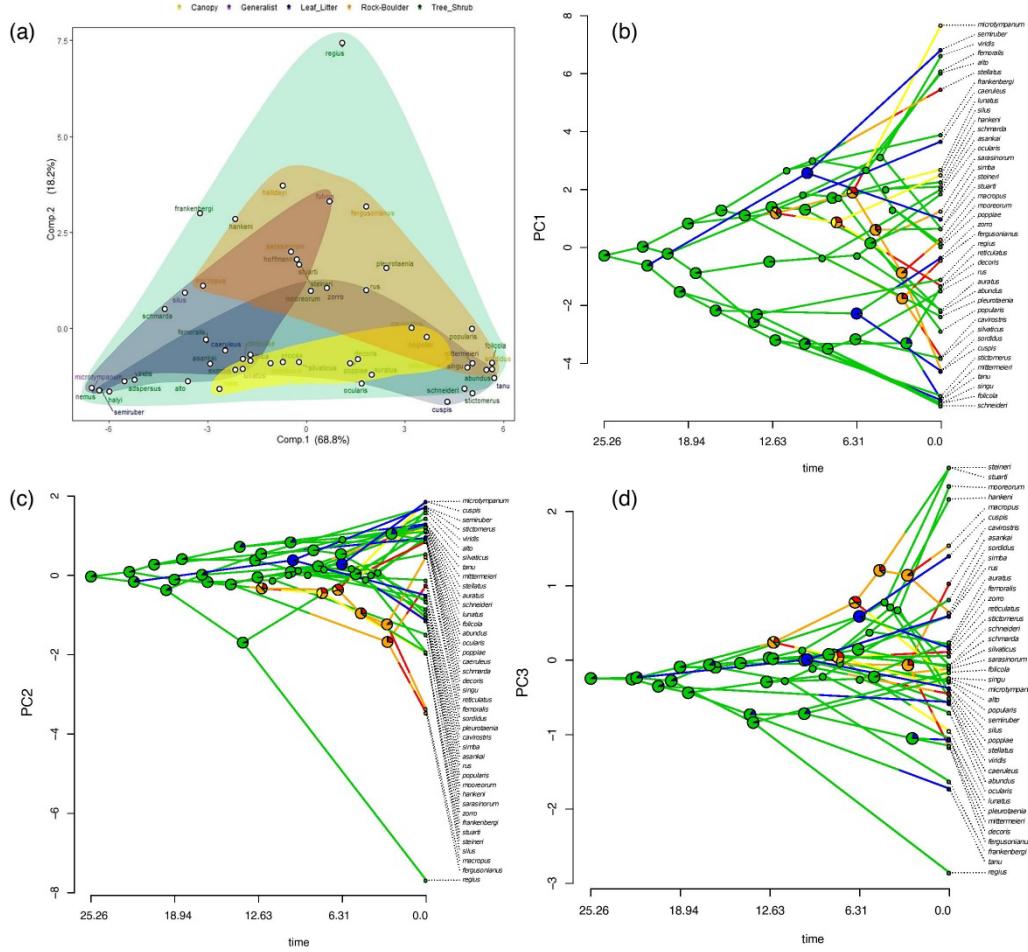
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1000 **Extended Data Figure 5. Temporal patterns of morphological evolution along PC1**
1001 **and PC2, and ecomorphs as phylomorphospace-traitgrams in *Pseudophilautus***
1002 **(using size-corrected residual data).** A clear correlation of body shape and ecomorphs
1003 are not evident from the traitgrams. Traitgram of PC1 (A); Traitgram of PC2 (B);
1004 Different ecomorphs traced on the phylomorphospace (C) indicating tree shrub forms
1005 spanning the entire range of body shapes.

1006

1007

1008



1009

1010 **Extended Data Figure 6. Climatic niche space occupation and climatic niche**
1011 **evolution in *Pseudophilautus* ecomorphs.** (a) Climatic niche occupation of
1012 Pseudophilautus ecomorphs. Minimum convex polygons for different ecomorphs are
1013 shown by different colours. Climatic niches of the ecomorphs largely overlap, although
1014 there is some separation among Canopy forms, Rock boulder forms and Generalists.
1015 Canopy forms and Leaf litter forms appear to have expanded their climatic niche along
1016 PC1, whereas Generalists and Rock boulder forms have expanded their climatic niches
1017 along PC2. Tree-shrub forms have expanded their climatic niche along all axes.
1018 Evolution of the climatic niche of ecomorphs along PC1 (b), PC2 (c) and PC3 (d). ANC
1019 of the ecomorphs are depicted on nodes. A dominant pattern of climate niche evolution
1020 is not evident along PC1 but a slight correspondence is shown in PC2 and PC3. Rock-
1021 boulder forms show a pattern of evolving towards extreme temperature conditions
1022 while a single species of Tree-shrub ecomorph, *Pseudophilautus regius* seems
1023 evolving towards extreme warm and dry conditions as well (see PC2 and PC3).