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1 **Trait-independent habitat associations explain low co-occurrence**
2 **in native and exotic birds on a tropical volcanic island**

3
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21 **ABSTRACT**

22

23 On oceanic islands, strong human impacts on habitats, combined with intro-
24 ductions of exotic species, modify the functional composition of terrestrial
25 bird assemblages and threaten their ecological functions. In La Réunion, an
26 oceanic island located in the Madagascan region, a national park was estab-
27 lished in 2007 to counter the ecosystem-level effects of three centuries of
28 habitat conversion, native species destruction and exotic species introduc-
29 tions. Here, we investigated how bird assemblages were structured in these
30 human-modified landscapes, ten years before the national park set out its
31 first conservation measures. We used a combination of multivariate statistics
32 and generalized additive models to describe variations in the taxonomic and
33 functional composition and diversity of 372 local bird assemblages, encom-
34 passing 20 species, along gradients of habitat composition and configuration.
35 We found that native species were tied to native habitats while exotic species
36 were associated with urban areas and man-modified landscape mosaics, with
37 some overlap at mid-elevations. Species' trophic preferences were segregated
38 along habitat gradients, but ecological traits had an overall weak role in ex-
39 plaining the composition of species assemblages. Hence, at the time of the
40 survey, native and exotic species in La Réunion formed two spatially distinct
41 species assemblages with contrasting ecological trait suites that benefited
42 from antagonistic habitat compositions and dynamics. We conclude that our
43 results support the analysis of historical datasets to establish reference points
44 to monitor human impacts on insular ecosystems.

45 **Keywords** : Insular birds, Ecological traits, Habitat changes, Mascarenes, Oce-

46 anic islands, Species introductions

47

48

49 **INTRODUCTION**

50

51 The Madagascan region is the smallest and the second most distinctive of the
52 world's 11 zoogeographic regions (Holt et al., 2013). Formed exclusively of
53 oceanic islands spread throughout the western Indian Ocean, it is relatively
54 species-poor but displays disproportionately high endemism rates. For in-
55 stance, 41% of the region's 382 native terrestrial bird species are regional en-
56 demics. This percentage even rises to 75% in La Réunion, the second largest
57 island of the region after Madagascar and the largest of the Mascarenes ar-
58 chipelago (Safford et al., 2015). However, assessments of human impacts on
59 insular ecosystems are deficient in the Madagascan region, even on the best-
60 studied islands such as La Réunion, hampering the establishment and evalua-
61 tion of initiatives for the conservation of insular biodiversity.

62

63 On oceanic islands, long-term isolation favoured the evolution of ecosystems
64 involving a low number of endemic species which support non-substitutable
65 ecological functions, notably in birds (Boyer & Jetz, 2014; Kaiser-Bunbury et
66 al., 2010; Sekercioglu et al., 2016). Birds' contributions to insular ecosystems
67 have been particularly well investigated in islands of the Indo-Pacific, such as
68 Hawaii (Barton et al., 2021) or New Zealand (Anderson et al., 2021). Plant-bird
69 interactions likely to support key ecological functions are also documented in
70 the Madagascan region, although case studies remain local and scarce. For in-
71 stance, in La Réunion, the pollination of the endemic orchid *Angraecum brac-*

72 *teosum* by the endemic Reunion olive White-eye *Zosterops olivaceus* recalls
73 the pollination of *Clermontia* (Lobelioideae: Campanulaceae) by endemic Ha-
74 waiian birds (Aslan et al., 2014, Micheneau et al., 2008). However, the extent
75 to which these specialized plant-bird interactions still sustain their ecosystem
76 functions in spite of the human-driven depletion of Madagascan avifaunas
77 remains unknown (Albert et al., 2020; Anderson et al., 2021; Schleuning et al.,
78 2014; Sekercioglu et al., 2016).

79
80 The Madagascan region is sadly famous for its high extinction rates, especially
81 in large frugivorous birds (Heinen et al., 2017). In La Réunion, the first human
82 colonization occurred in the late 17th century, far later than in many other
83 tropical archipelagos. It was accompanied by novel and intense pressures
84 which led many terrestrial bird species to severe range reductions or extinc-
85 tion. Since then, approximately two-thirds of the island's native vegetation
86 has been converted for agriculture or replaced by exotic vegetation (Lagabri-
87 elle et al., 2009; Mourer-Chauvire et al., 1999). Rapid habitat destructions, on
88 top of overhunting and other pressures, were likely the most critical cause for
89 the extinction of all large vertebrates (Albert, Flores, Baider, et al., 2021), in-
90 ducing ecosystem-level cascading effects in a few decades or centuries (Mou-
91 rer-Chauvire et al., 1999; Strasberg et al., 2005; Whittaker & Fernández-
92 Palacios, 2007). In particular, many of the common fleshy-fruited tree species
93 on which frugivorous birds fed declined as lowland native forests were nearly
94 eradicated (Albert et al., 2018). In turn, the extinction of frugivores, which
95 sustained seed dispersal, amplified the decline of most fleshy-fruit plant spe-

96 cies in the 300 years after the first European settlement (Albert et al., 2020;
97 Albert, Flores, Baider, et al., 2021). Conversely, the abundance and diversity
98 of exotic plant species now peaks close to the middle of the elevation gradi-
99 ent (Tassin & Riviere, 2003), and wide extents of high-altitude landscapes
100 have been converted into pastures (Strasberg et al., 2005).

101

102 Island endemic birds are characterized by low dispersal abilities, failure to
103 cope with the lack of native food resources in human modified habitats, and
104 high mortality rates due to introduced mammalian predators such as cats or
105 rats. Conversely, exotic species that establish feral populations on islands un-
106 surprisingly exhibit ecological traits associated with ecological opportunism,
107 use of human resources and ability to colonize novel environments (Blackburn
108 et al., 2009; Cassey, 2002; Duncan et al., 2003). Accordingly, the propensity of
109 exotic bird species to invade islands from their initial introduction locations
110 depends on an interaction between the invasibility of non-converted native
111 habitats and species' propensity for colonization, determined by their eco-
112 logical traits and the conditions of their introduction (Alpert et al., 2000;
113 Blackburn et al., 2009). The introduction of exotic species has in some in-
114 stances compensated, or even exceeded in number, the man-mediated ex-
115 tinction of native and endemic species (Sax et al., 2002; Whittaker et al.,
116 2014). However, native and exotic bird species exhibit low functional redun-
117 dancy, and are segregated among habitats along elevational and anthropo-
118 genic disturbance gradients (Barnagaud et al., 2014, 2022; Fischer & Linden-
119 mayer, 2007; Whittaker & Fernández-Palacios, 2007).

120

121 Because of their trait and habitat differences, exotic species do not usually
122 replace native species' lost ecological functions (Anderson et al., 2021; Dun-
123 can et al., 2003; Vila et al., 2011), except in idiosyncratic situations such as the
124 replacement of *Clermontia's* native pollinators by introduced *Zosterops* in Ha-
125 waii (Aslan et al., 2014, but see Pejchar, 2015 for a contrasting example on
126 seed dispersal also in Hawaii). Hence, although bird introductions increase
127 taxonomic diversity (the diversity of species) and functional diversity (the di-
128 versity of ecological traits) at the island scale (Whittaker et al., 2014), their ef-
129 fect on the composition of local species assemblages and ecosystem functions
130 remains unclear. For instance, among the 20 exotic bird species established in
131 La Réunion since the 19th century, the Red-whiskered Bulbul (*Pycnonotus jo-*
132 *cosus*) is the only one known to enter native forests, thus liable to modify the
133 composition of native plant assemblages through the endozoochorous disper-
134 sal of exotic plants (Clergeau & Mandon-Dalger, 2001; Mandon-Dalger et al.,
135 1999). Although these novel mutualistic interactions are identified, the extent
136 to which they may favour plant invasions and ultimately trigger long-term
137 changes in the composition of plant communities remains unknown.

138

139 Unlike many oceanic islands with comparable sizes, the land use patterns in
140 La Réunion partly disentangle the distribution of native and converted habi-
141 tats from altitudinal variation, offering the possibility to distinguish their re-
142 spective influences on the distribution, composition and diversity of species

143 assemblages. Depending on the scale at which species respond to their envi-
144 ronment and resources, the island's fine-grained mosaics of man-modified
145 and native vegetation may either inflate contrasts in the functional composi-
146 tion of species assemblages within local habitats, or trigger biotic homogeni-
147 zation at the landscape scale (Byamungu et al., 2021; Cadotte et al., 2011;
148 Diaz & Cabido, 2001; McGill et al., 2006). These features, concentrated on a
149 relatively small study region, makes La Réunion a particularly favourable study
150 area to investigate the determinants of spatial variations in the composition
151 of local bird assemblages. In particular, the weak correlation between altitude
152 and human impact, at least up to the upper third of the elevation gradient, al-
153 lows separating their respective roles on the co-occurrence or separation of
154 exotic and native bird species among local assemblages.

155
156 Building on this specificity, we investigated spatial patterns in the distribution
157 of bird species and their ecological traits in La Réunion, aiming to *(i)* describe
158 native and exotic species' distributions along habitat and elevational gradi-
159 ents, *(ii)* investigate the resulting distributions of ecological traits on these
160 gradients and *(iii)* assess the outcome of these patterns in terms of taxonomic
161 and functional diversity patterns. To our knowledge, we thus perform the
162 first comparison of the distributions of native and exotic terrestrial bird spe-
163 cies within landscapes on an oceanic island of the Madagascan biome outside
164 Madagascar. From an applied viewpoint, the unpublished data analyzed here
165 were gathered during an extensive bird point count survey conducted in the
166 austral summer 1997-98, 30 years after the last exotic bird introduction and

167 10 years before the establishment of La Réunion National Park. Our results
168 therefore provide a useful point of reference for a future evaluation of con-
169 servation measures aimed to reduce human imprint of native ecosystems
170 within the national park (McNellie et al., 2020).

171

172 **MATERIAL AND METHODS**

173

174 **Study location**

175

176 La Réunion Island is a three-million years old volcanic island, part of the Mas-
177 carene archipelago (Western Indian Ocean, 55°30' E and 21°05' S, Fig.1). Ad-
178 ministratively, it is a french “département d’Outre-Mer”, which warrants the
179 feasibility of long-term studies with the support of well-established local re-
180 search institution and conservation stakeholders, a relatively rare feature in
181 the Madagascan region. In the centre of the island, a plateau (Plaine des Ca-
182 fres, *ca.* 1500 m above sea level) is flanked by two volcanoes (Piton de la
183 Fournaise, 2631 m, active, and Piton des Neiges, 3069 m, extinct), descending
184 into the coastal plain with an elevation change of 2000 m in 10-30 km. This
185 topography causes a steep climatic gradient, with an average minimum
186 ground temperature below 0°C above 1500 m in August, above 1800 m from
187 June to October, and above 2300 m all year round. At the highest point, the
188 annual temperature variation ranges from -10°C to +26°C (Cadet, 1974; Rau-
189 net, 1991). The study area, located on the leeward side of the island, has a
190 slope of about 0.15 m per m and an annual rainfall ranging from 500 mm at
191 sea level to 2000 mm on the highest mountain slopes (Raunet, 1991). The
192 vegetation is organized in elevational belts arranged from sea level to moun-
193 tain tops. Partly orthogonal to this habitat gradient is a gradient of human
194 habitat conversion. The original ecosystems have been modified earlier and

195 more intensively at low elevations; patches of native tropical mountain for-
196 ests still remain at mid elevations (NATI in Table 1, the most important re-
197 maining native forest type in terms of surface and conservation). High eleva-
198 tions are still mostly uninvaded and covered by endemic vegetation (HIER and
199 ACFO in Table 1, Albert, Flores, Ah-Peng, et al., 2021; Cadet, 1980). The main
200 habitat belts sampled in this study can roughly be categorised into coastal ur-
201 banised plains (0 - 50 m), savannah (50 - 300 m), sugarcane monoculture (300
202 - 800 m), rural landscapes with crops (800 - 1200 m), primary forest mixed
203 with pastures and planted forests (1200 - 1800 m), heathlands dominated by
204 ericaceous plants (1800 - 2600 m) and bare soils with sparse herbaceous
205 vegetation (2600 - 3069 m).

206

207 **Bird sampling**

208

209 A total of 410 point counts were sampled during the breeding season of aus-
210 tral summer from December 1997 to April 1998. All points were visited once
211 by one of two trained ornithologists (GB and JT), between 5.30 a.m. and 10.30
212 a.m, under favourable weather (no rain or strong wind). On each point, the
213 observer recorded all birds heard or seen in a 150 m radius during 20 min. Fly-
214 ing birds were only recorded if they were obviously related to the point (*e.g.*
215 an individual hunting within the 150 m radius). Records are expressed in
216 abundance indices following Blondel et al (1970, 1981) : single bird = 1, terri-
217 torial singing male = 2 individuals if the female was not observable.

218

219 We discarded 38 points due to incomplete or incoherent environmental data
220 measurements, and thus performed our analyses on 372 points, arranged in
221 two geographical clusters for practical reasons (144 on the north-western
222 cluster and 228 on the south-western cluster, Fig.1). Sampling points were
223 evenly distributed all along the elevational gradient, with a mean elevational
224 distance of 8 m between two successive elevations and a horizontal distance
225 of at least 250 m between two successive point counts. All major extant vege-
226 tation types were covered within 100 m elevational bands, with a mean sam-
227 pling effort of 12.7 point counts per band. Wetlands and dry areas such as
228 depressions, ridges and mires were avoided, as well as places too close to
229 feeding troughs in grasslands, because they attract granivorous species.

230

231 **Habitat data**

232

233 Landscape composition within a 150 m radius around each point count was
234 characterized as the proportion of the total surface covered by 15 habitat
235 categories (Table 1), quantified through the interpretation of georeferenced
236 aerial photographs acquired in November 1996 at a native 1:5000 scale. We
237 summarized habitat and elevational variation by the two first axes of a princi-
238 pal component analysis (Fig. 2, 13 and 10% of total variance for the first and
239 second components, respectively; the third component, which accounted for
240 8% of total variance, was disregarded). The first principal component (PC1)

241 was dominated by elevation (higher altitudes in negative values) and ranged
242 from lowland cultivations (sugar cane, SUCA, and mixed crops, CULT) and sa-
243 vannah (SAHE, SASH) to a variety of mixed exotic and native habitats at mid-
244 elevations, replaced by endemic *Acacia heterophylla*-dominated forests
245 (ACFO), and ericoid shrublands (HIER) at the highest elevations. The second
246 principal component (PC2) reflected the spatial heterogeneity of local habi-
247 tats. It opposed a variety of homogeneous sites including native or exotic
248 habitats (negative values), to sites characterized by mosaic habitats with high
249 within-sites heterogeneity, mostly dominated by exotic vegetation (positive
250 values): fallows (HEFA, SHFA, ACFA), exotic thickets (EXTH), plantations
251 (CRYPT) and urban habitats (URBA).

252

253 **Species' status and ecological traits**

254

255 From the 23 species recorded at least once on the point counts, we discarded
256 three species observed less than three times, since we considered them to be
257 insufficiently represented to assess their habitat affinities (these species are
258 listed in Appendix S1).

259

260 We defined species' status based on Safford et al (2015) as either "native"
261 (nine species endemic to the island or having colonized it without human as-
262 sistance) or "exotic" (11 species introduced by humans, mostly in the 19th
263 century for ornament or hunting). For these 20 species, we compiled five eco-

264 logical traits that represent key phenotypical, behavioural and biogeographi-
265 cal characteristics, and may affect their habitat affinities: species' bio-
266 geographic origin (exotic species' zoogeographic region of origin, all native
267 species belong to the Madagascan biome), main diet and dietary specializa-
268 tion, main vegetation strata used for foraging and body mass (log-
269 transformed to limit the influence of a few large values). These traits are clas-
270 sical proxies of species' patterns of habitat selection, home range and re-
271 source use. Their distributions among species assemblages are therefore ex-
272 pected to change in response to habitat filtering and competitive exclusion
273 processes, allowing to investigate the role of niche-related processes in the
274 separation or co-occurrence of native and exotic species in habitats. Similar
275 traits were associated with the distinct habitat preferences of exotic and na-
276 tive birds in a previous study focused on New Zealand (Barnagaud et al.,
277 2022).

278
279 We used species-level trait averages synthesized from multiple sources and
280 published in the Handbook of the Birds of the World (Del Hoyo et al., 2013,
281 see Appendix S1 for trait values, their computation and references therein).
282 Intraspecific trait variance may be high especially in an insular context, even
283 for recently-established species which may diverge phenotypically from their
284 source populations in a few generations (Wiens et al., 2019). However, trait
285 data at the scale of local populations are currently lacking for most species in
286 La Réunion as in many other oceanic islands. We tempered this limitation by
287 considering a limited number of traits with rather coarse resolutions, thus en-

288 suring that they actually reflect ecological differences among species. Given
289 the low size of our species assemblage, using more traits would result in over-
290 splitting ecological variability among species, likely yielding uninterpretable
291 patterns.

292

293 **Statistical analyses**

294

295 We summarized the variation of these five traits among the 20 species in a
296 Hill & Smith analysis (an ordination method for tables mixing quantitative and
297 qualitative variables, Hill & Smith, 1976) in order to explore the ecological
298 overlaps and separations between native and exotic species. We then ex-
299 plored trait-habitat associations for the 20 species and 372 points in a three-
300 table ordination method known as the RLQ analysis (Doledec et al., 1996),
301 which links a matrix of environmental variation across sampling sites (table L,
302 based on the PCA described in the *Environmental variables* section) to an eco-
303 logical trait matrix (table Q, based on the Hill & Smith analysis described in
304 the “*Species’ status and ecological traits*” section), through a sites \times species
305 matrix (table R, here a correspondence analysis on species’ indices of abun-
306 dance per point, see “*Bird sampling*”).

307

308 We visually explored the RLQ space to search for trait-habitat associations
309 that may distinguish native from exotic species, and tested the robustness of
310 trait-habitat associations through two complementary permutation models

311 (Thioulouse et al., 2018, p.231). The first model tested the association be-
312 tween R and L (observed association vs 999 permutations under the null hy-
313 pothesis that species are distributed randomly across sites). The second
314 model tested the association between L and Q (permutations under the null
315 hypothesis that traits are randomly distributed across species assemblages).
316 The robustness of the association between R and Q corresponded to the
317 highest p-value between these two tests. We then tested phylogenetic signals
318 on axes scores of the Hill & Smith analysis and RLQ analysis with Pagel's λ and
319 Blomberg's K, as a sensitivity analysis to assess the role of species' evolution-
320 ary relatedness in the observed trait-environment associations (phylogenetic
321 tree, details on the method and results in Appendix S3).

322

323 To investigate variations in assemblage diversity, we computed point-level
324 species richness, Shannon's index, and functional dispersion (FDis : the aver-
325 age distance of species to the centroid of each assemblage in a multivariate
326 trait space formed by the five ecological traits described above, Laliberté &
327 Legendre, 2010). We discarded other functional diversity metrics to avoid an
328 inflation of statistical tests, especially because most of them are at least partly
329 redundant. In this respect, FDis is well suited to our study since it provides an
330 intuitive and integrative measure of functional diversity compared to the
331 mean functional assemblage (i.e., the spread of species forming a local as-
332 semblage in a multivariate trait space) while being computationally uncorre-
333 lated to species richness (Laliberté & Legendre, 2010).

334

335 We analysed diversity indices separately for three species groups: all species,
336 native species only or exotic species only (maps of the indices in Appendix S2).

337 We used generalized additive models (GAM, Wood, 2006) to express diversity
338 indices as a function of thin plate spline smoothers of the two first principal
339 component axes of the environmental PCA (PC1 and PC2), plus a covariate
340 separating the two geographical clusters of points (locations of the two clus-
341 ters in Fig.1 ; estimates of the cluster effect are provided in Appendix S4). We
342 fitted species richness as a Poisson distribution, and Shannon's index and
343 functional dispersion as Gaussian distributions. Residuals of all models were
344 slightly structured in space, but the magnitude of the spatial autocorrelation
345 in the first orders of neighbourhood was so low (Moran's I <0.05 within a few
346 kilometers) that we did not proceed with further correction.

347

348 We performed all analyses under the R 4.1.2 environment (R Core Team,
349 2021) with packages *ade4* (Thioulouse et al., 2018), *picante* (Kembel et al.,
350 2014) and *mgcv* (Wood, 2006).

351

352 **RESULTS**

353

354 **Trait overlap between native and exotic species**

355

356 The two first axes of the Hill & Smith analysis summarized 23 and 16% of the
357 total trait variation among the 20 species (third axis 14%, disregarded). The 20
358 species were evenly dispersed in the multivariate trait space, indicating rela-
359 tively low ecological redundancy and few extreme strategies with respect to
360 the traits used (Fig.3). The first axis (HS1) separated relatively large, ground-
361 foraging omnivorous species of oriental origin (*e.g.* Madagascar Buttonquail -
362 tuni, Common Myna – actr or Red-whiskered Bulbul - pyjo ; refer to Appendix
363 S1 for scientific names) from dietary specialists (mostly native insectivores or
364 nectarivores : Mascarene Swiftlet - aefr, Mascarene Martin - phbo, and Reun-
365 ion Stonechat - sate, and one ubiquitous exotic granivorous species, Common
366 Waxbill - esas). The second axis (HS2) separated introduced Palearctic and Af-
367 rican species with seed-based regimes (Common Waxbill - esas, Common
368 Quail - coco, Village Weaver - plcu) from frugivores and insectivores, such as
369 forest-prone native species (Reunion Bulbul – hybo, and Reunion White-Eye –
370 zool) or exotic forest species (Red-whiskered Bulbul - pyjo). Most of the over-
371 lap between native and exotic species was attributable to two species, Reun-
372 ion Harrier (cima, 8 occurrences in our data), the only extant endemic bird of
373 prey, and Malagasy Turtle Dove (stpi, 38 occurrences in our data). Species

374 scores along HS1 and HS2 did not depart from a Brownian evolution model
375 (tests of phylogenetic signal in Appendix S3).

376

377 **Native and exotic species' distributions along the elevation and habitat gra-**
378 **dients**

379

380 Native and exotic species were intertwined along the elevation gradient, but
381 natives tended to predominate at higher altitudes and were virtually absent
382 from coastal sites dominated by exotics (native species' mean elevation =
383 1395 m, sd = 478 m, range = 60 – 2880 m, Fig.4a). The Reunion Harrier (cima)
384 and the two aerial feeders (Mascarene Swiflet – aefr, and Mascarene Martin -
385 phbo) were present at lower altitudes than most native passerines. Exotic
386 species had similar elevation ranges, yet their altitudinal distribution was
387 skewed towards coastal plains (exotic species' mean elevation = 962 m, sd =
388 499 m, range = 20 – 2400 m, Fig. 4b).

389

390 Native species tended to avoid the most human-disturbed and fragmented
391 habitats (higher counts in the negative side of PC2, Fig.4c), with the excep-
392 tions of the Reunion Harrier (cima) and the two aerial feeders that showed a
393 larger habitat range on PC2 (Mascarene Martin - phbo, and Mascarene Swift-
394 let - aefr). Exotic species living in the lowlands (positive PC1 values) also
395 tended to avoid highly fragmented and urbanized areas (*i.e.*, exotics located
396 in positive PC1 values were more abundant in negative PC2 values).

397

398 **Trait-environment associations**

399

400 Species-habitat relationships were robust to permutations of tables R and L
401 (“Model 2” in Thioulouse et al., 2018, observed sum of eigenvalues = 1.6, $p =$
402 0.001 after 999 permutations), but not to permutations of Q and L (“Model 4”
403 in Thioulouse et al., 2018, observed sum of eigenvalues = 1.6, $p = 0.07$ after
404 999 permutations), indicating that ecological traits were overall not strongly
405 segregated along habitat gradients. This lack of power, in spite of clear-cut
406 patterns in Fig.5, may well have resulted from the relatively low species and
407 trait sample sizes, as from a low trait turnover along ecological gradients. For
408 instance, in the RLQ space, fruit- and nectar-eaters were strongly related with
409 native mid-elevation forests (NATI, Fig.5), but these two diets were repre-
410 sented by only one native species each (Reunion Bulbul - hybo, and Reunion
411 Olive White-eye – zool, left top corner of the RLQ space). On the opposite side
412 of the RLQ space, the only two palearctic species introduced on the island
413 (Common Quail – coco, and House Sparrow - pado) and, at higher elevations,
414 aerial feeders (Mascarene Swiftlet – aefr, and Mascarene Martin - phbo),
415 were associated with urbanized areas and *Cryptomeria* plantations (negative
416 coordinates along RLQ2, Fig.5). As for trait multivariate axes, the distribution
417 of species along RLQ1 and RLQ2 did not depart from a Brownian evolution
418 model (Appendix S3).

419

420 **Diversity-environment associations**

421

422 The GAMs showed that species richness, Shannon's index and functional dis-
423 persion varied non-linearly along PC1 (Fig.6) and to a lesser extent along PC2
424 (Fig.7). Species richness and Shannon's index exhibited hump-shaped rela-
425 tionships with PC1, with a maximum slightly shifted towards low-elevation ar-
426 eas (Fig.6a,d, positive scores), mainly due to the near-absence of native spe-
427 cies in coastal plains (Fig.6b). Inversely, exotic species richness and Shannon's
428 index decreased steadily from lower to higher elevations (Fig.6c,f, *i.e.* in-
429 creased along PC1). Total and exotic species' functional dispersion decreased
430 slightly from lower to higher elevations (Fig.6g,i), but peaked at mid-
431 elevations for native species (Fig.6h).

432

433 Total species richness was depleted, and Shannon's index was slightly lower,
434 in homogeneous sites with either native or exotic habitats (negative PC2 val-
435 ues, Fig.7a, d), in contrast to heterogeneous sites composed of interspersed
436 exotic habitats and urban areas (positive PC2 values). Exotic species richness
437 and Shannon's index peaked at intermediate levels of PC2 before plateauing
438 (Fig.7c,f). Inversely, the highest native species richness and diversity occurred
439 in homogeneous native habitats, then declined slightly to a lower plateau
440 with high variation (Fig. 7b,e). FDis varied little along PC2 overall (Fig.7g).
441 However, native species' FDis was slightly higher in homogeneous sites with
442 native habitats (negative PC2 values in Fig.7h). Conversely, it increased slowly

443 towards urban areas and exotic thickets up to a plateau for exotic species

444 (positive PC2 values in Fig.7i).

445

446

447 **DISCUSSION**

448

449 Most native species were tied to mid-and high altitude habitats dominated by
450 indigenous vegetation, while the abundance distributions of exotic species
451 spread along a wider gradient of habitats and elevations. Although insular avi-
452 faunas tend to be composed of ecologically flexible species (Prodon et al.,
453 2002; Reeve et al., 2018), native species clearly displayed narrow niche width
454 along the two gradients studied, contrasting with the flatter abundance dis-
455 tributions of many exotic species. The discrepancy between species' habitat
456 distributions among the two guilds was therefore not as obvious as expected
457 from other comparable studies on other oceanic islands (Acevedo & Restrepo,
458 2008; Barnagaud et al., 2014; Flaspohler et al., 2010; Hahn et al., 2011; van
459 Heezik et al., 2008).

460

461 In spite of these abundance patterns, field observations show that native spe-
462 cies in La Réunion frequent a relatively wide range of native habitats (*e.g.* Re-
463 union Stonechat or Reunion Grey White-eye, which occur from mid-elevation
464 forests to open scrubs at mountain tops), while the vast majority of exotic
465 species do not divert from anthropogenic settlements and exotic habitats for
466 more than a few hundred meters, irrespective of altitude (authors' personal
467 observations). These observations conform to patterns observed on other is-
468 lands (Acevedo & Restrepo, 2008; Barbaro et al., 2012; Barnagaud et al.,
469 2014; Hahn et al., 2011; Thibault et al., 2018; van Heezik et al., 2008). Nar-

470 lower abundance distributions in native species thus likely reflect the reduced
471 availability of native habitat and resources within landscapes, while the de-
472 velopment of agriculture on mid-altitude plateaus have provided exotic spe-
473 cies adequate conditions for their expansion along the elevation gradient.

474

475 Converging with this niche-based interpretation, native and exotic species
476 showed distinct ecological trait syndromes and were well separated in the
477 RLQ space. We did not detect any phylogenetic signal contributing to shape
478 these trait-environment relationships, which may be due to lack of statistical
479 power, but more likely suggests that native and exotic species' distributions
480 along the island environmental gradients do not stem from niche conserva-
481 tism alone. This pattern aligns with results obtained in New Zealand, where
482 exotic and native species also bear distinct trait syndromes and habitat pref-
483 erences at a landscape scale (Barnagaud et al., 2022). In the case of La Réun-
484 ion, trait-environment relationships were predominantly explained by the dis-
485 tribution of species along environmental gradients rather by than traits them-
486 selves, suggesting that habitat barriers are independent from the traits we
487 considered.

488

489 Still, we found that most frugivorous, insectivorous and nectarivorous native
490 species were associated with high elevation and native forests, and did not
491 come in contact with ground-dwelling omnivorous and granivorous exotic
492 species, which are limited to man-modified habitats. Irrespective to whether

493 or not ecological traits trigger an ecological filter, these results conform to the
494 hypothesis that exotic species opportunistically remained confined to their
495 historical habitats of introduction (Blackburn et al., 2013; Duncan et al.,
496 2003), even though successfully introduced species usually exhibit traits ena-
497 bling them to cope with novel environments (Blackburn et al., 2009). Con-
498 versely, native species may not be excluded from modified landscapes be-
499 cause their ecological traits prevent them from using man-related resources,
500 but more likely due to other processes such as predation, competitive exclu-
501 sion by exotic species, fine-grained ecological specialization, or preference for
502 large extents of undisturbed habitats (Parlato et al., 2015).

503

504 Native aerial feeders such as Reunion Harrier, Mascarene Swiflet and Mas-
505 carene Martin had wider abundance distributions along the axis of habitat
506 heterogeneity and were closer to exotic species than other native species in
507 the RLQ space. These species cover large distances for foraging and thus de-
508 pend less on the composition of local habitats where they were detected.
509 Conversely, the frugivorous Red-Whiskered Bulbul was closer to native forest
510 species than most other exotic species in the RLQ space. This recently-
511 introduced bulbul is currently restricted to ecotone areas and infrequently en-
512 ters native forests, but it has a high propensity to fast colonization after intro-
513 duction and naturalisation (Clergeau & Mangon-Dalger, 2001), enabling it to
514 rapidly adapt to novel environments (Amiot et al., 2007). It is also well known
515 for spreading invasive exotic plant species through zoochory (Mandon-Dalger
516 et al., 1999). Hence, its possible expansion into uninvaded habitats needs to

517 be cautiously monitored since it may pose serious conservation issues for na-
518 tive plant assemblages, which can moreover be affected by a reduction of
519 their dispersal by local functional extinctions of native birds (Anderson et al.,
520 2021).

521

522 Diversity patterns were in line with species-level analyses. Native species re-
523 veal hump-shaped curves of diversity along the mixed elevation / habitat type
524 gradient (PC1), reflecting the higher availability of native habitats at mid-
525 elevations. Meanwhile, monotonous variation in all forms of exotic species'
526 diversity was coherent with their reluctance to enter native habitats and gen-
527 erally to disperse out of human settlements (Duncan et al., 2003; Sol et al.,
528 2017). Interestingly, the role of habitat heterogeneity (PC2) was low for native
529 species, although they were more diverse in non-fragmented native habitats.
530 By contrast, and as expected, exotic species were clearly more diverse in habi-
531 tat mosaics, corresponding to former forest areas converted to agriculture
532 and urban settlements. Functional dispersion also matched these patterns,
533 suggesting that traits are sampled in local assemblages according to species
534 richness rather than under the influence of strong ecological filters, in coher-
535 ence with the permutation tests performed on the RLQ analysis.

536

537 These habitat-related patterns of assemblage composition may change in the
538 future due to continuing anthropogenic pressure on habitats, selective habi-
539 tat restoration and species protection or control. At a landscape scale, modifi-
540 cations of interaction networks and the emergence of new eco-evolutionary

541 processes may arise if individuals of trophically-similar species come increas-
542 ingly into direct contact in the future (Lugo et al., 2012). Given our results,
543 this threat is however unlikely in the current avifauna of La Réunion, unless
544 recently-introduced species, such as the frugivorous Ring-necked Parakeet
545 *Psittacula krameri* in 1972 (currently subjected to eradication campaigns, Ca-
546 ceras et al., 2022) or the Red-billed Leiothrix (*Leiothrix lutea*, Tassin & Rivière,
547 2001), manage to establish feral populations in native habitats. Once estab-
548 lished, these novel colonisers might unpredictably create novel species-
549 resource interactions through *e.g.* zoochorous seed dispersal (Anderson et al.,
550 2021), as is currently the case for the red-whiskered bulbul in La Réunion. Fur-
551 thermore, elevational shifts in bird ranges could ultimately cause thermal
552 squeezes in response to climate change (Freeman et al., 2018; Walker et al.,
553 2019). However, historical records on species distributions are still insufficient
554 to document such long-term dynamics and the resulting assemblage-level
555 modifications that would reflect potential thermal squeezes. In the case of La
556 Réunion, our study was based on the oldest protocolled survey of bird com-
557 munities with sufficient sample size and spatial coverage, making it a poten-
558 tial point of reference for future diachronic studies focused on the effects of
559 habitat or climate changes (McNellie et al., 2020).

560

561 **Conclusion**

562

563 As on other islands, the avifauna of La Réunion is not a single “novel” species
564 assemblage (Lugo et al., 2012), but consists of two distinct species assem-
565 blages separated by local habitat, which merge together at the landscape
566 scale mostly around mid-elevations where sufficient amounts of native habi-
567 tats persist within an otherwise man-modified matrix. Apart from the specific
568 case of the Red-whiskered Bulbul, which could still be undergoing a positive
569 colonization dynamic, recent field observations did not suggest substantial
570 changes in this segregation pattern. However, La Réunion habitats and land-
571 scapes have changed in the 25 years since our data collection, due to the con-
572 flicting effects of increasing anthropogenic pressures and efforts to preserve
573 wide expands of native habitats in the National Park. Replicating our field pro-
574 tocol may allow a quantitative, landscape-level overview of the consequences
575 of these changes for the composition of bird assemblages. Given the high
576 pace of ecosystem-level changes experienced on oceanic islands and its con-
577 sequences for endemic insular biodiversity, we suggest that long-term studies
578 and surveys become a priority for local conservationists and stakeholders. We
579 also advocate in favour of further analysis of historical datasets on other is-
580 lands, including still unpublished data wherever they exist, to increase the
581 availability of reference points enabling the evaluation of conservation-
582 oriented policies in protected areas, especially when established on insular
583 ecosystems.

584

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806

807

808 **TABLES**

809

810 **Table 1.** Habitat types used in the study and acronyms. Native habitats were mostly
 811 composed of NATI, HIER, ACFA, and to a lesser degree ACMI. The Elevation column indicates
 812 the elevational barycenter of each habitat, weighted proportionally to the surface covered
 813 by this habitat on each site. Figures in brackets give the altitudinal range of each habitat.

Label	Variable	Type	Mean \pm sd [range]	Elevation (m)
ELEV	Elevation (m)	Quantitative	1202.3 \pm 649.2 [20, 2880]	
ACFA	<i>Acacia mearnsii</i> -dominated fallows		12.4 \pm 29.2 [0, 100]	1263 [640, 2070]
ACMI	Degraded native forest mixed with <i>Acacia mearnsii</i>		0.4 \pm 4.2 [0, 70]	1746 [1510, 2880]
NATI	Native mid-elevation forest (« Bois de couleurs »)		12.9 \pm 31.9 [0, 100]	1398 [620, 2540]
HIER	High-elevation ericoid thickets		9.3 \pm 28.9 [0, 100]	2377 [1620, 2880]
SUCA	Sugar cane fields		14.7 \pm 34.2 [0, 100]	593 [250, 1010]
CRYPT	Plantations of <i>Cryptomeria japonica</i> (conifer)	Proportion in 150 m around each sampling Point (expressed in %)	4.9 \pm 15.8 [0, 94]	1025 [320, 1680]
CULT	Cultivated land		4.6 \pm 20.6 [0, 100]	189 [60, 320]
EXTH	Thicket of exotic species		5.8 \pm 13.4 [0, 72]	1239 [350, 2010]
HEFA	Herbs-dominated fallow		0.3 \pm 2.7 [0, 39]	1415 [770, 2010]
SHFA	Shrubs-dominated fallow		10.7 \pm 25.1 [0, 100]	1120 [320, 1505]
PAST	Pasture		5.9 \pm 21.6 [0, 100]	1583 [630, 1960]
SASH	Mixed savanna-shruland		3.7 \pm 18.6 [0, 100]	125 [20, 230]
SAHE	Savannah (herbs)		3.8 \pm 19.6 [0, 100]	64 [20, 170]
ACFO	Monodominant forests of <i>Acacia heterophylla</i>		9.3 \pm 28.4 [0, 100]	1637 [1400, 2560]
URBA	Urbanized area		1.4 \pm 5.7 [0, 46]	1118 [320, 1670]

814

815

816 **FIGURE LEGENDS**

817

818 **Figure 1.** Location of La Réunion island (a) and sampling design (b). The 38 red crosses depict
819 points removed from the analysis due to missing data. Background layer: elevation raster
820 (Jarvis et al., 2008)

821

822 **Figure 2.** Projection of the 372 bird point counts on the first two axes of a principal
823 component summarizing habitat and elevational variation on the study area (a) ; maps of
824 principal components values : PC1 (b), PC2 (c). See acronyms for habitat types in Table 1.
825 Background layer: elevation raster (Jarvis et al., 2008)

826

827 **Figure 3.** The ecological trait space of 22 bird species based on five ecological traits
828 (biogeographic origin, main diet, dietary specialization, foraging vegetation strata and log-
829 transformed body mass), with convex hulls separating native (N) and exotic (E) species.
830 Species' acronyms are defined in Appendix S1.

831

832 **Figure 4.** Count density of the 22 native and exotic species recorded in the survey along the
833 elevation gradient (a) and the two first axes of the principal component analysis on habitat
834 variables (b,c) (no density curve for Blue-breasted Quail *Synoicus chinensis* since it occurred
835 only once in the dataset).

836

837 **Figure 5.** Trait-environment associations in a RLQ space (projection of habitat variables in (a),
838 traits in (b), with exotic and native species' convex hulls). See acronyms for habitat types in
839 Table 1.

840

841 **Figure 6.** Variation of species richness (SR), Shannon's index (Shannon) and functional
842 dispersion (FDis) along a principal component axis synthesizing an elevational gradient
843 associated with spatial turnover in vegetation types (PC1, native vegetation at higher
844 elevations in negative values, exotic vegetation in lowlands in positive values). From left to
845 right: all species, native species, exotic species.

846

847 **Figure 7.** Variation of species richness (SR), Shannon's index (Shannon) and functional
848 dispersion (FDis) along a principal component axis synthesizing habitat heterogeneity within
849 sampling sites (PC2, homogeneous sites in negative values, heterogeneous sites showing
850 mosaics of native and anthropogenic habitats in positive values). From left to right: all
851 species, native species, exotic species.

852

853

854 **Plate 1.** The diversity and spatial structure of habitats in La Réunion island. (a) Background:
855 exotic savannas, and sugar cane crops at low elevation, middle ground: mosaics of exotic
856 thickets, woodlands along cliffs, foreground: mid-elevation mosaics of pastures and fallows.
857 Sub-urban and urban habitats are present at all elevation levels. (b) Background: slopes of
858 the Piton des Neiges massif (3070 masl) covered with high elevation ericoid thickets, mid-
859 ground: pastures in the central mid-elevation plain and mosaic of exotic plantations and
860 native forests on higher ancient craters, foreground: native ericoid thickets on the lower
861 slopes of the Piton de la Fournaise massif (2646 masl). (c) View of a steep high cliff in the
862 center of the island with native forest of variable stature depending on local slope. All
863 photographic credits (c) Jean-Yves Barnagaud

864

865 **Plate 2.** Some common native and exotic species represented in our data : (a) Reunion
866 Harrier (cima, native), (b) Reunion Bulbul (hybo, native), (c) Reunion White-Eye (zool,
867 native), (d) Reunion Stonechat (sate, native), (e) Mascarene Paradise Flycatcher (tebo,
868 native), (f) Common Myna (actr, exotic), (g) Zebra Dove (gest, exotic), (h) Red-whiskered
869 Bulbul (pyjo, exotic), (i) Village Weaver (plcu, exotic). All photographic credits (c) Paul-
870 Alexandre Leclerc.

871

872 **DATA ACCESSIBILITY STATEMENT**

873

874 The data and R scripts related to this study are archived on Recherche Data Gouv

875 (<https://entrepot.recherche.data.gouv.fr/>) : doi:10.57745/BFEXCE

876

877 **COMPETING INTERESTS STATEMENT**

878

879 The authors declare no competing interests.

880

881 **AUTHOR CONTRIBUTIONS**

882

883 JYB* : contributed to the conceptual development, designed the methodological framework,

884 performed the analyses, co-led the writing.

885 OF* : contributed to the conceptual development, compiled the data and performed data

886 exploration and initial analyses, co-led the writing.

887 GB – YT : conceived the original idea, designed the protocol and performed the fieldwork, led

888 exploratory analyses, contributed to the writing.

889 LB* : compiled the data, contributed to the conceptual and methodological development, co-led the

890 writing.

891 * *contributions considered as equal.*

892

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894

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898 RLQ analysis and Paul Dufour for the compilation of the phylogenetic tree. Further thanks

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900 sampling and analysis of aerial photographs for site characterization using geographic

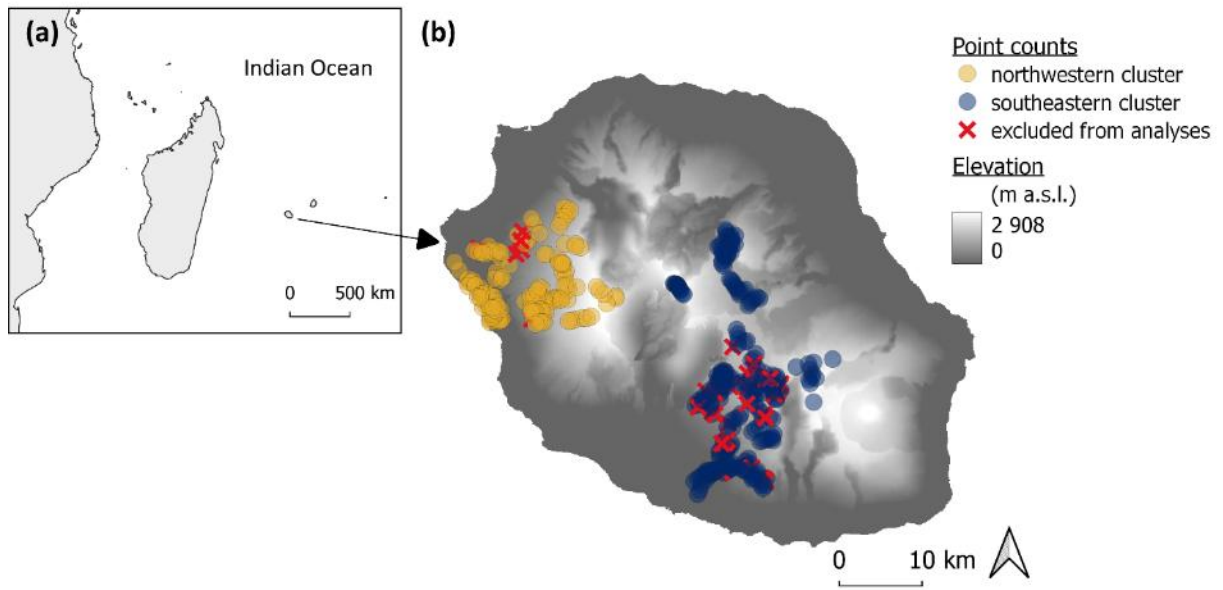
901 information systems. A linguistic proofreading was performed by Gayle & Ralph Padgett.

902 Photographic credits: Jean-Yves Barnagaud (Plate 1) and Paul-Alexandre Leclerc (Plate 2).

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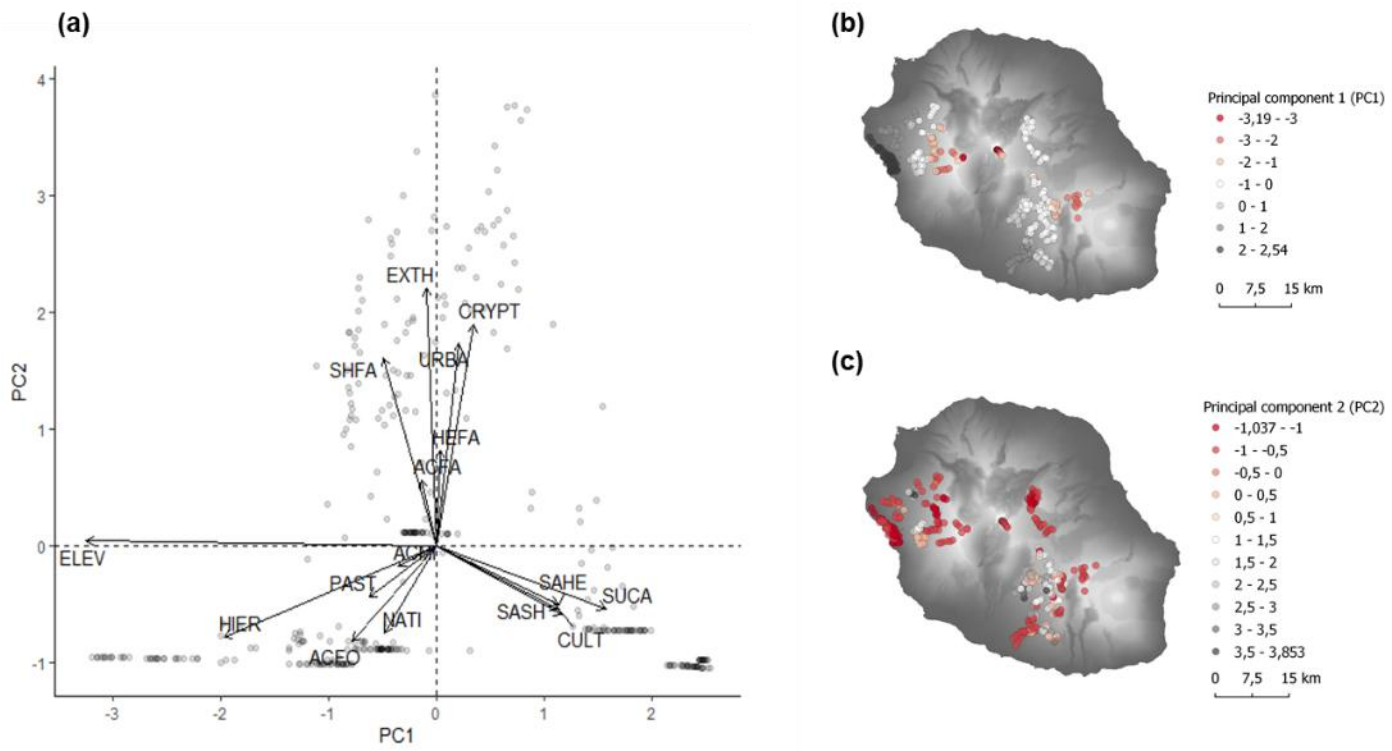
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907 **Figure 1.**

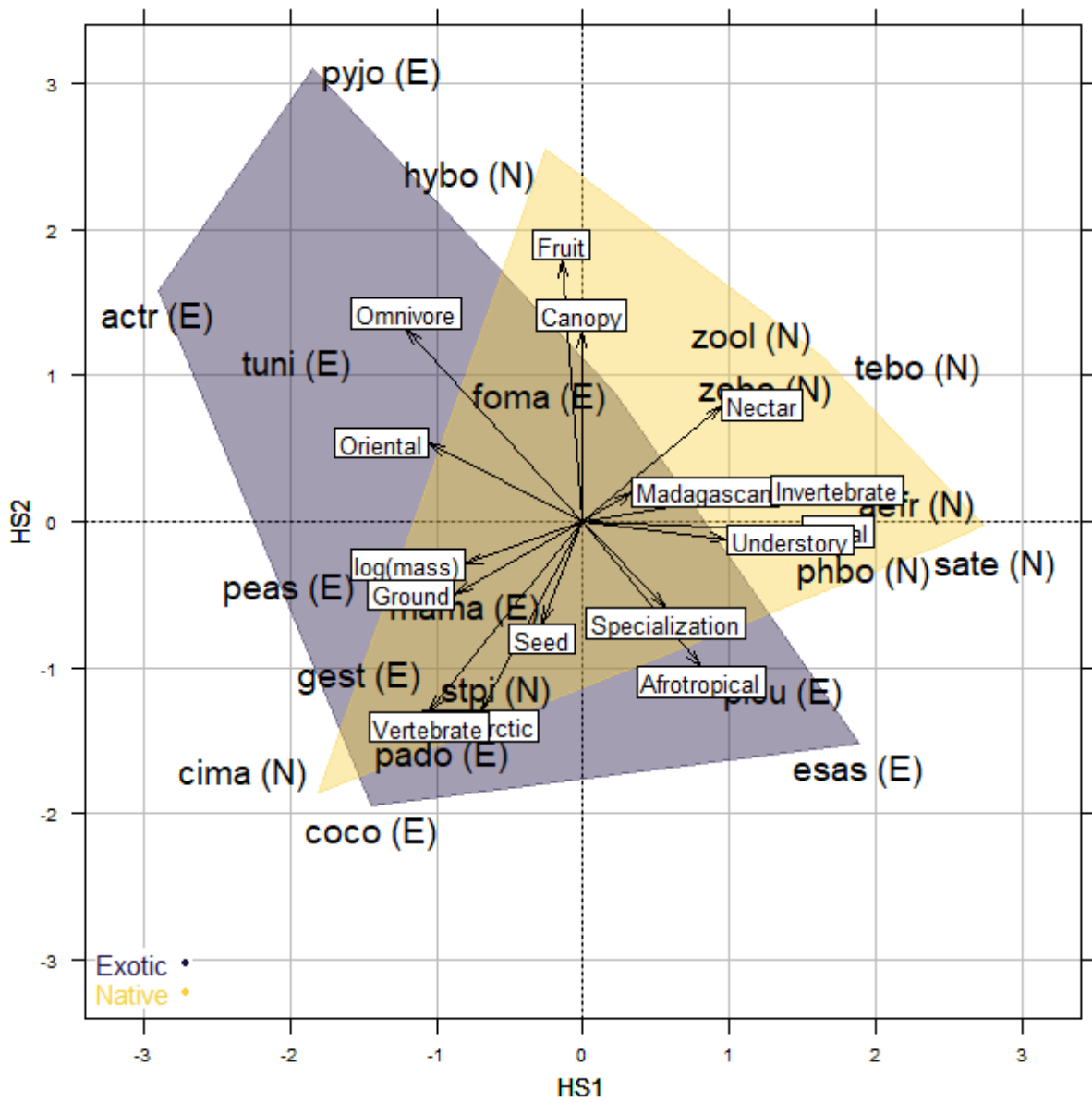
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911 **Figure 2.**

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915 **Figure 3.**

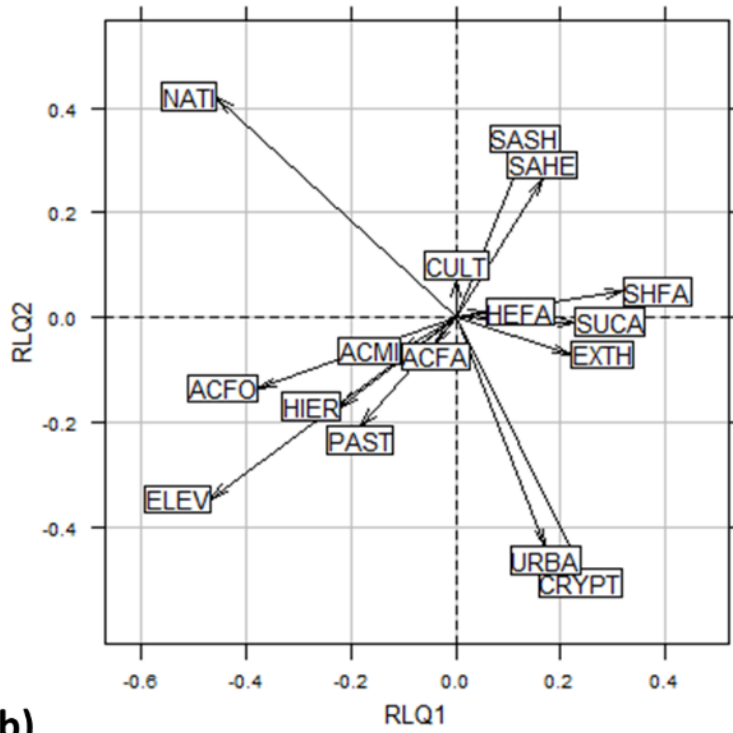
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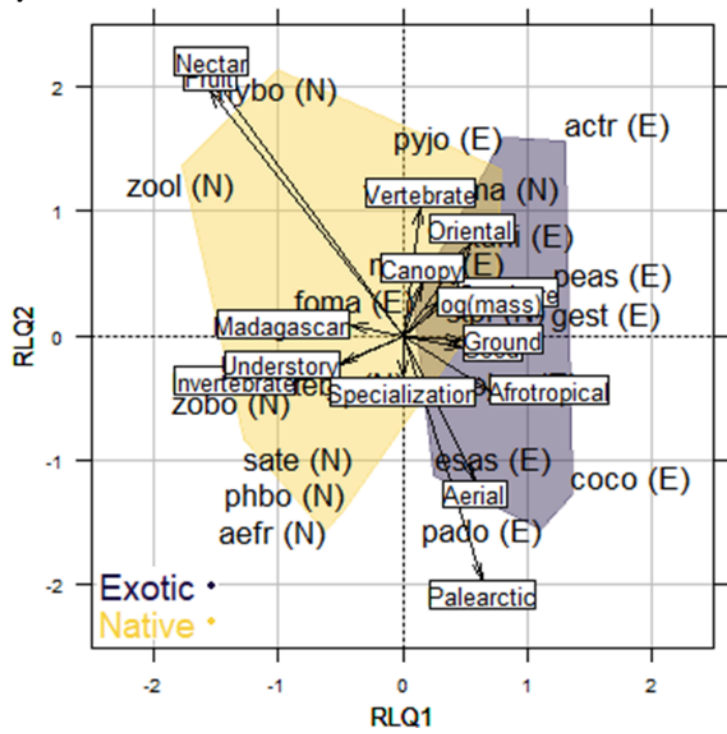
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918 **Figure 4.**

(a)



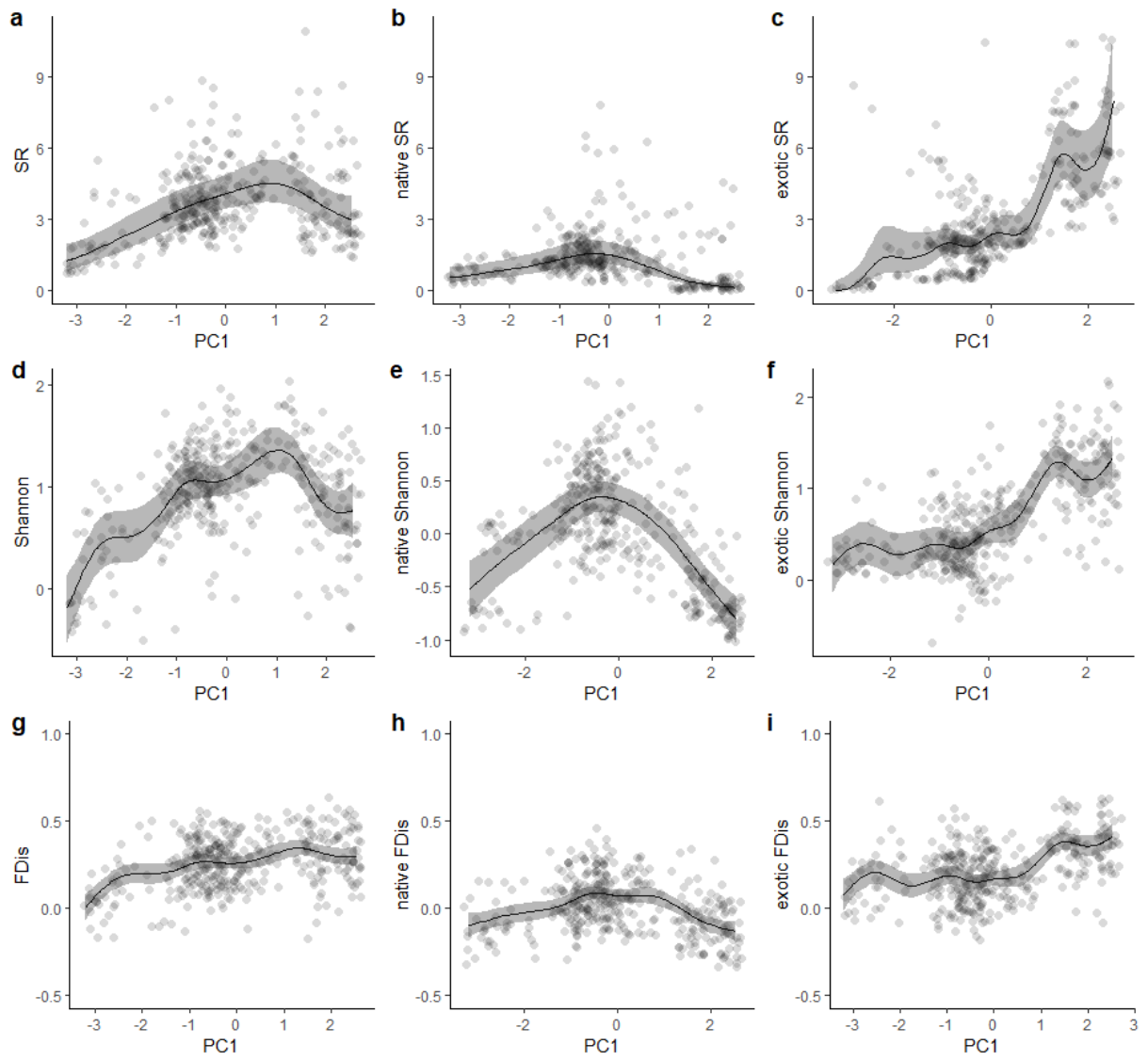
(b)



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920 **Figure 5.**

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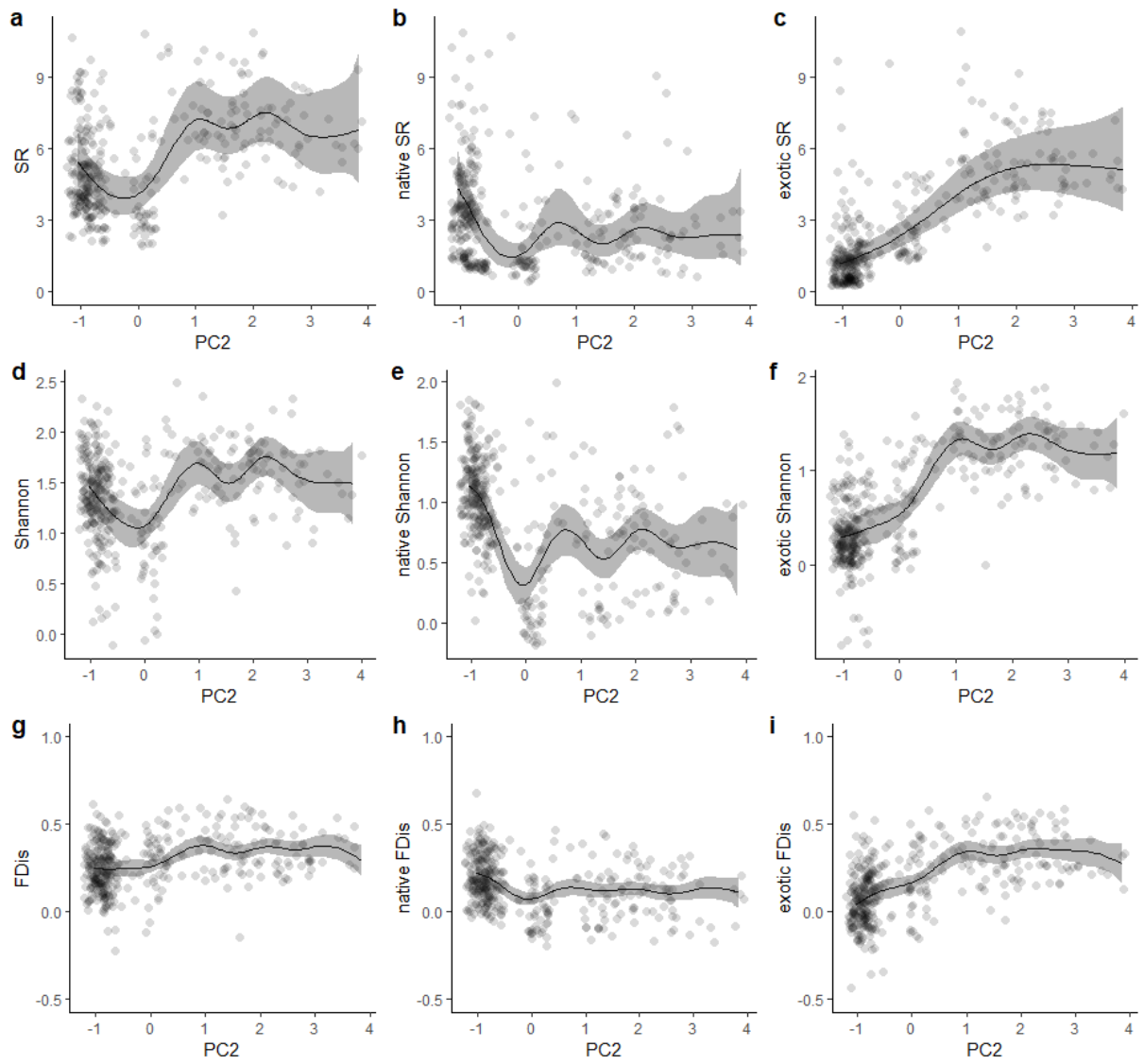


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923 **Figure 6.**

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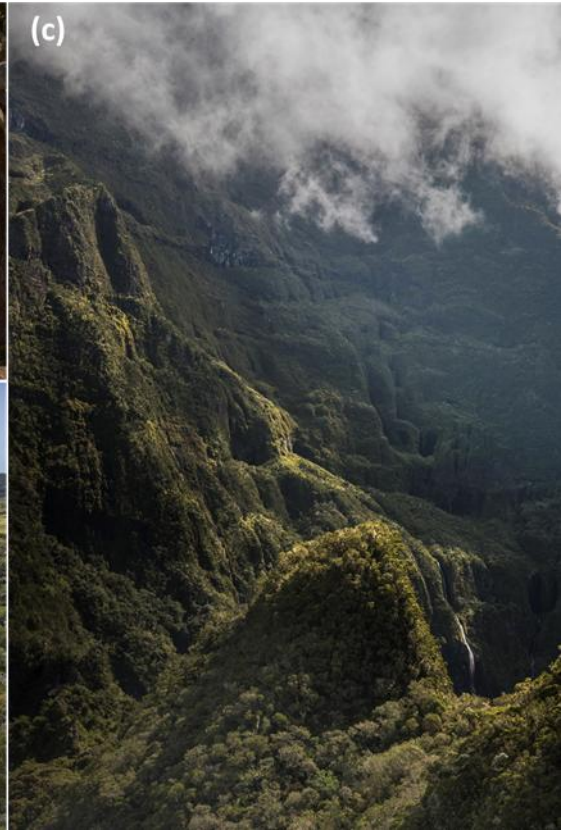
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927 **Figure 7.**

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Plate 1.



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Plate 2.

934 **SUPPLEMENTARY MATERIALS**

935

936 APPENDIX S1 : Species list and ecological traits

937 APPENDIX S2 : Maps of bird diversity

938 APPENDIX S3 : phylogenetic tree and tests of phylogenetic signal

939 APPENDIX S4 : Complements to models

APPENDIX S1 : Species list and ecological traits

Acronym	Species	Common names	Status	Biogeographic origin	Main diet	Foraging vegetation strata	Body mass (g)	Dietary specialization
actr	<i>Acridotheres tristis</i>	Common Myna	Exotic	Oriental	Omnivore	ground	117.9	1.581
aefr	<i>Aerodramus francicus</i>	Mascarene Swiftlet	Native	Madagascan	Invertebrate	aerial	9.7	3.536
cima	<i>Circus maillardi</i>	Reunion Harrier	Native	Madagascan	Vertebrate	ground	638.5	3.151
coco	<i>Coturnix coturnix</i>	Common Quail	Exotic	Palaearctic	Seed	ground	104.4	2.816
esas	<i>Estrilda astrild</i>	Common Waxbill	Exotic	Afrotropical	Seed	understory	7.8	3.536
foma	<i>Foudia madagascariensis</i>	Red Fody	Exotic	Madagascan	Seed	canopy	16.3	2.550

	sis							
frpo	<i>Fringilla</i> <i>pondicerianus</i> <i>* removed</i> <i>from analyses</i> <i>(only 2</i> <i>occurrences)</i>	Grey Francolin	Exotic	Oriental	Omnivore	ground	291.4	1.389
gest	<i>Geopelia</i> <i>striata</i>	Zebra Dove	Exotic	Oriental	Seed	ground	55.8	3.536
hybo	<i>Hypsipetes</i> <i>borbonicus</i>	Reunion Bulbul	Native	Madagascan	Fruit	canopy	54.4	2.375
lopu	<i>Hypsipetes</i> <i>borbonicus</i> <i>* removed</i> <i>from analyses</i> <i>(only one</i> <i>occurrence)</i>	Scaly-breasted Munia	Exotic	Oriental	Seed	understory	14.2	2.816

mama	<i>Margaroperdix madagarensis</i>	Madagascar Partridge	Exotic	Madagascan	Seed	ground	235.0	2.375
pado	<i>Passer domesticus</i>	House Sparrow	Exotic	Palaearctic	Seed	ground	28.6	2.816
peas	<i>Perdica asiatica</i>	Jungle Bush Quail	Exotic	Oriental	Seed	ground	69.5	2.816
phbo	<i>Phedina borbonica</i>	Mascarene Martin	Native	Madagascan	Invertebrate	aerial	21.0	3.536
plcu	<i>Ploceus cucullatus</i>	Village Weaver	Exotic	Afrotropical	Seed	understory	37.7	2.816
pyjo	<i>Pycnonotus jocosus</i>	Red-whiskered Bulbul	Exotic	Oriental	Omnivore	canopy	28.3	1.581
sate	<i>Saxicola tectes</i>	Reunion Stonechat	Native	Madagascan	Invertebrate	understory	12.7	3.536

stpi	<i>Nesoenas picturatus</i>	Malagasy Turtle Dove	Native	Madagascan	Seed	ground	173.5	2.816
sych	<i>Synoicus chinensis</i> <i>* removed from analyses (only one occurrence)</i>	Blue-breasted Quail	Exotic	Oriental	Omnivore	ground	39.6	1.753
tebo	<i>Terpsiphone bourbonnensis</i>	Mascarene Paradise Flycatcher	Native	Madagascan	Invertebrate	canopy	11.1	3.536
tuni	<i>Turnix nigricollis</i>	Madagascar Buttonquail	Exotic	Madagascan	Omnivore	ground	68.8	2.315
zobo	<i>Zosterops borbonicus</i>	Reunion Grey White-Eye	Native	Madagascan	Invertebrate	understory	8.1	2.121
zool	<i>Zosterops olivaceus</i>	Reunion White-Eye	Native	Madagascan	Nectar	understory	9.4	2.375

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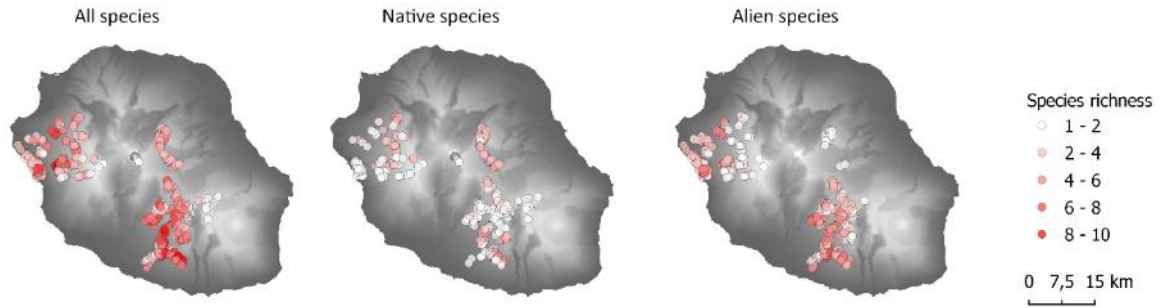
941 **Sources:** Status, biogeographic origin : Safford et al., 2015 ; Main diet and dietary specialization : Barnagaud et al., 2019 (main diet based on the maximum
942 score over 10 dietary items scored from 0 to 10 ; specialization is the standard deviation of these scores ; raw scores from Del Hoyo et al. 2013, available
943 upon request ; not displayed by the data owner's request); Foraging vegetation strata and body mass from Del Hoyo et al. 2013.

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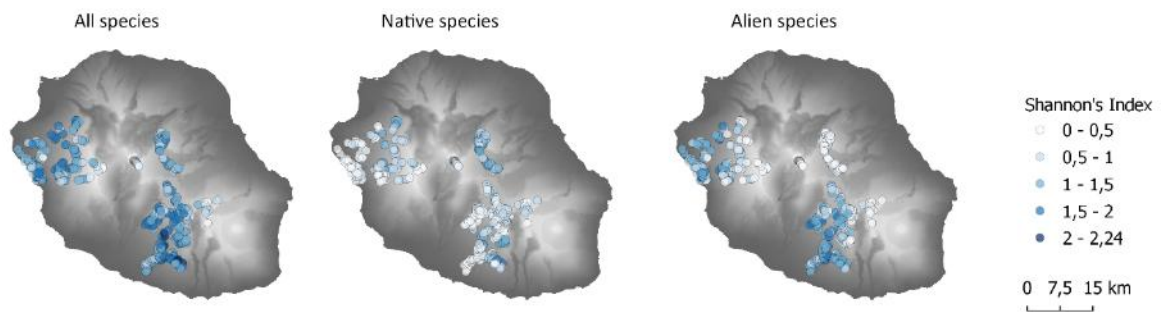
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APPENDIX S2 : Maps of bird diversity

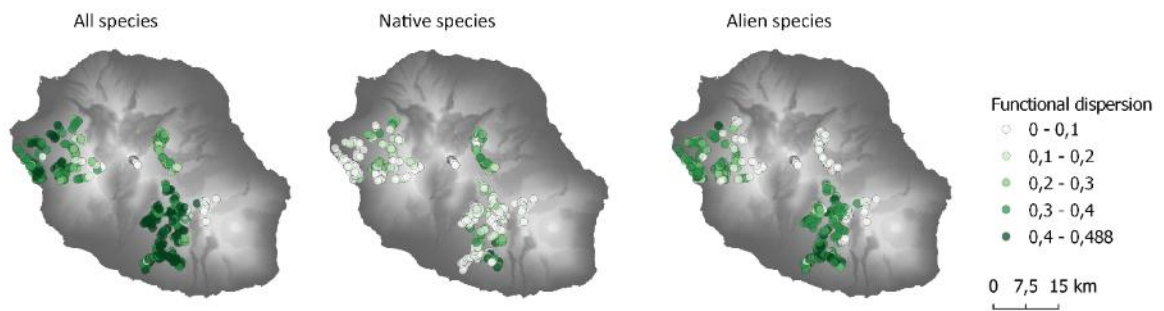
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953

954 *See main text for the traits underlying functional dispersion. Total species pool : eight native*

955 *species, 14 exotic species (22 species).Background layer : elevation raster (Jarvis et al., 2008).*

956

957

APPENDIX S3 : Phylogenetic tree and tests of phylogenetic signal958 **Methods**

959 We constructed a phylogeny of the 20 species with a composite of bird phylogeny established by
 960 Prum et al. (2015) and a maximum clade credibility tree computed from 10,000 iterations of the
 961 Hackett backbone (Jetz et al., 2012, downloadable at www.birdtree.org, “Stage 2 Hackett
 962 Backbone”), following the method of Cooney et al. (2017) also used in Barnagaud et al. (2022). We
 963 then tested for phylogenetic signal on species’ scores on the axes of the Hill & Smith and RLQ
 964 analyses using Pagel’s λ and Blomberg’s K , assuming a Brownian evolution model (Phylocom R
 965 package, Revell 2012).

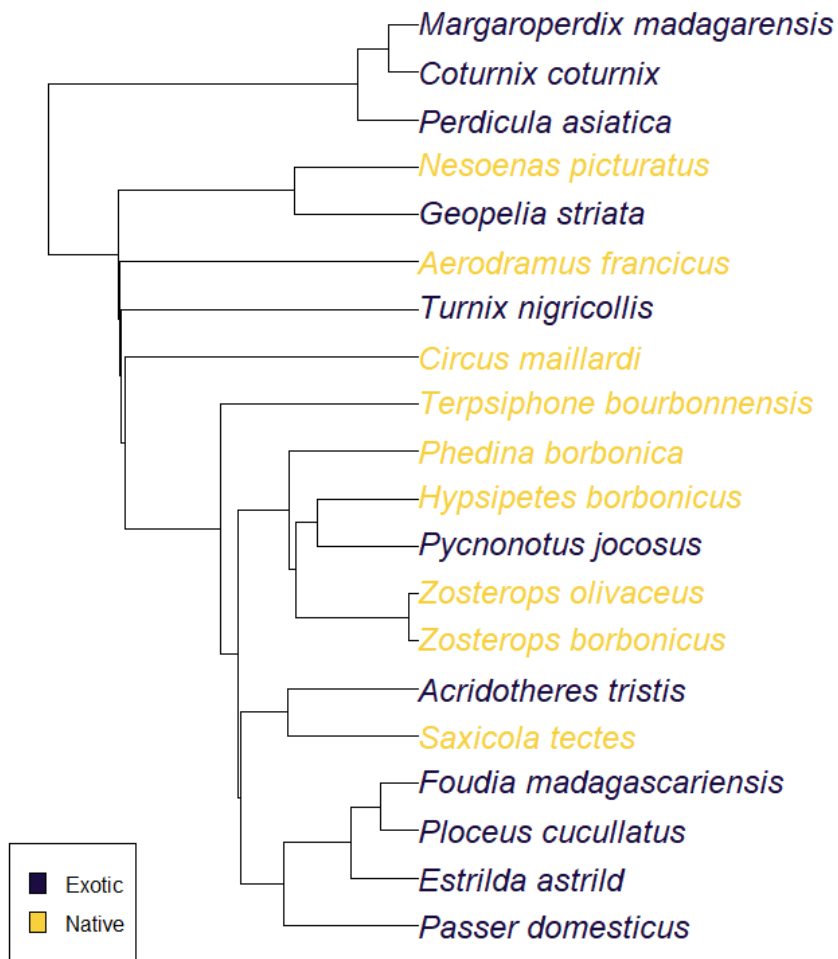
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967 **Results**

968 Table S3.1. Phylogenetic signals on the axes of the Hill & Smith analysis (HS1, HS2) and RLQ analysis
 969 (RLQ1, RLQ2).

<i>Variable</i>	Pagel’s λ			Blomberg’s K	
	λ	$LR(\lambda = 0)$	<i>p-value</i>	K	<i>p-value</i>
HS1	0.28	0.35	0.55	0.68	0.03
HS2	0.64	1.84	0.17	0.62	0.04
RLQ1	0.97	3.73	0.05	0.71	0.01
RLQ2	6.77×10^{-5}	-0.0006	1	0.23	0.07

970 *Phylogenetic indices are computed with the function phylosig in the phylocom R package*
 971 *(Revell 2012). We assumed a Brownian motion evolutionary model. LR = likelihood ratio test.*
 972 *The p-value associated with Blomberg’s K is based on 1000 permutations.*
 973



974
 975 Figure S3.1. Phylogenetic tree of the 20 species.

976
 977
 978
 979 **References**

980
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995

APPENDIX S4 : Complements to generalized additive models

996 Table S4.1. Estimated differences in bird diversity between the two geographical clusters (see Fig.1 in the main text for the locations and spread of the two
 997 clusters). The table displays estimated marginal species richness for the two clusters with 95% confidence intervals for the three response variables (SR =
 998 species richness, H' = Shannon's Index, FDis = functional dispersion) and the three species guilds. Model details are provided in the main text.

<i>Response</i>	<i>Guild</i>	North-Western cluster			South-Eastern cluster		
		<i>Estimate</i>	<i>lower bound</i>	<i>upper bound</i>	<i>Estimate</i>	<i>lower bound</i>	<i>upper bound</i>
SR	All species	4.09	3.44	4.87	3.64	3.1	4.28
SR	Native species	1.52	1.13	2.05	1.32	0.99	1.76
SR	Exotic species	2.36	1.9	2.95	2.07	1.69	2.54
H'	All species	1.08	0.92	1.23	0.97	0.82	1.12
H'	Native species	0.32	0.18	0.46	0.23	0.1	0.37
H'	Exotic species	0.54	0.4	0.68	0.5	0.37	0.63
FDis	All species	0.26	0.23	0.3	0.24	0.21	0.27
FDis	Native species	0.07	0.04	0.11	0.05	0.02	0.08
FDis	Exotic species	0.17	0.13	0.21	0.15	0.11	0.18

999

1000