



HAL
open science

Differences in phenotypic variance between old and young congeneric species on a small island

Guillaume Péron, Benjamin Vollot

► **To cite this version:**

Guillaume Péron, Benjamin Vollot. Differences in phenotypic variance between old and young congeneric species on a small island. *Journal of Biogeography*, 2024, 10.1111/jbi.14767 . hal-04315582

HAL Id: hal-04315582

<https://hal.science/hal-04315582v1>

Submitted on 30 Nov 2023

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Differences in phenotypic variance between old and young congeneric species on a small island

Running title: Phenotypic variance in island endemics

Guillaume Péron (1)*, Benjamin Vollot (2)

(1) Univ Lyon, Université Lyon 1, CNRS, Laboratoire de Biométrie et Biologie Évolutive UMR5558, F-69622 Villeurbanne, France.

(2) BV Nat, 195 chemin d'Aimargues 30670 Aigues-Vives, France

*corresponding author: guillaume.peron@univ-lyon1.fr

Acknowledgements: We are grateful to the Luecila, Qanono, and Wedrumel tribes and to the landowners who granted access for our work. The Environment Services of the province of the Loyalty Islands gave permit for the captures. Two reviewers provided insightful comments that greatly improved a previous version. This research received no external funding.

Abstract

Aim: Insular environments theoretically promote within-species phenotypic variance, in part but not only because insular species enjoy a lower number of trophic interactions than their mainland counterparts. However, environmental factors apparently confound empirical comparisons between insular and mainland systems. To address this issue, we studied sympatric, congeneric species from the same small island, but that stemmed from separate colonization events. We predicted that the time since the species had colonized the island would correlate positively with the within-species variance in morphometrics.

Location: Lifu island, New Caledonia, South Pacific

Taxa: *Zosterops inornatus*, *Z. minutus*, *Z. lateralis* (Passeriformes)

Methods: We measured 7 morphological traits and used principal component analysis to compute axes of variation.

Results: The within-species variance in bill size and in feet/tail ratio corrected for body size increased with the estimated time since the species had been on the island. A similar but nonsignificant trend existed for body size and bill width.

Main conclusions: The morphometrics of the three species of *Zosterops* birds from Lifu supported the hypothesis that insular environments promote within-species phenotypic variance, and cast a new light on the role of competition in the erosion of phenotypic variance.

Key-words: individual heterogeneity; biometry; island syndrome; taxon cycle; functional trait

Significance statement: Using the differences between congeneric species of a single island, we provide empirical support for the long-standing prediction that insular species should be more phenotypically diverse than mainland ones, and we cast a new light on the role of interspecific competition.

42 **Introduction**

43 Instead of consistently converging towards a locally optimal phenotype (Aubret & Shine, 2009;
44 Waddington, 1953), most populations exhibit significant within-species phenotypic variation, which
45 has been the topic of a rich literature (Barabás et al., 2022; Bolnick et al., 2011; Clegg et al., 2008;
46 Ibarra-Isassi et al., 2023; Violle et al., 2012). In this paper, we first conducted a review of the reasons
47 why island/mainland comparisons can provide insights into the maintenance of within-species
48 phenotypic variation, but also highlighted the issue of environmental confounding factors in
49 empirical island/mainland comparisons. We then described an approach to circumvent that
50 bottleneck by comparing the species inside single islands.

51 **Six reasons why insular populations should be more phenotypically diverse than mainland** 52 **ones**

53 *Decreased trophic degree*

54 In a species-rich system, the more variable a species is, the more it overlaps in niche with its
55 competitors (Fridley & Grime, 2010) and the more diverse are its potential predators (Schoener,
56 1969) and pathogens (Ganz & Ebert, 2010). By contrast, in species-poor island systems, the trophic
57 degree does not increase much with the phenotypic variance (Bolnick et al., 2011). In addition, the
58 more variable the phenotypes are, the more unique individuals are relative to conspecifics, and the
59 less they compete with conspecifics (Polis, 1984; Shine, 1989). In other words, within-species
60 variance is also a way to escape intra-specific density-dependence (Tinker et al., 2008), which is more
61 intense in island than mainland systems (MacArthur et al., 1972; Warren et al., 2015). These two
62 mechanisms are traditionally invoked to explain the greater variability in island than mainland
63 systems (MacArthur et al., 1972; Soule & Stewart, 1970). More recently, this theory was updated
64 with contributions from the niche variation hypothesis that species with broad niches are made of
65 variable individuals with narrow niches (Bolnick et al., 2007), and with the corollary that increased
66 phenotypic variation feeds back into increased resistance to invasion by new competitors (Barabás et
67 al., 2022).

68 *Jensen's inequality*

69 Considering a mathematical function f of a trait x , if the function is concave, then its value at the
70 population average \bar{x} is larger than the population average of the function value: $f(\bar{x}) > \overline{f(x)}$
71 (Jensen, 1906), and more importantly, the difference between $f(\bar{x})$ and $\overline{f(x)}$ increases with the
72 variance in x . Applying this rule to the strength of species interactions in trophic networks, one
73 reaches the theory that the odds of any two species coexisting increases with their within-species
74 phenotypic variance (Bolnick et al., 2011). Since island systems are extinction-filtered (Warren et al.,
75 2015), the species that survived on islands would then be more variable than those that went extinct.

76 *Portfolio effect*

77 Negative correlations between the demographic performance of different phenotypes in a
78 population, such as those caused by frequency-dependence and temporal fluctuations in the optimal
79 phenotype (Clegg et al., 2008; Schindler et al., 2010) can help different genotypes coexist in a
80 population, but also shelter variable species from extinction (Bolnick et al., 2011). This is especially
81 true in spatially-constrained systems, in which individuals cannot escape adverse conditions by
82 moving away. Therefore, under the portfolio effect, the species that survived on islands should be
83 more variable than those that went extinct.

84 *Additive genetic variance*

85 A high heritability makes it possible for species to evolve rapidly when environmental conditions
86 change, including when new competitors enter the stage, thereby stabilizing community equilibria
87 (Bolnick et al., 2011). By contrast, if heritability was low, ecological dynamics would dominate and
88 competitive exclusion would ensue irrespective of within-species variation (Warren et al., 2015). In
89 island systems, the species that survived the colonization of their home island by new competitors
90 should then be the ones with the most additive genetic variance.

91 *Demographic stochasticity*

92 In small populations, some phenotypes may contribute disproportionately to the next generation by
93 chance only, thereby helping maintain the phenotypic variance (trait sampling; Bolnick et al., 2011).
94 This demographic stochasticity plays a larger role in small than large populations (Gauthier et al.,

95 2016; Lande, 1993). Therefore, it would contribute more phenotypic variation in island than
 96 mainland populations.

97 *Island syndrome*

98 In island systems, the low inter-specific density-dependence and high intra-specific density-
 99 dependence favor the evolution of “island syndromes”, which involve long lives and low fecundity
 100 rates (Covas, 2012; Terborgh, 2023). As part of this life history strategy, traits that are associated
 101 with longevity should be buffered against environmental and genetic variation (Péron et al., 2016)
 102 and therefore exhibit low phenotypic variance. By contrast, traits that are mostly associated with
 103 fecundity should remain individually variable and may actually increase in variance compared to
 104 shorter-lived species, as a result of life history tradeoffs that preserve longevity. This would
 105 contribute to phenotypic variance in islands, at least for fecundity-associated traits.

106 **Island/mainland comparisons can be confounded**

107 The average environment may differ between island and mainland systems, as well as across islands.
 108 Island systems may also exhibit less spatial and temporal heterogeneity in environmental conditions
 109 than mainland ones. These differences could inflate the variance in mainland populations, interfere
 110 with the above mechanisms, and explain why empirical island/mainland comparisons have so far
 111 yielded many negative results (Table 1).

112 **Table 1:** Overview of previous studies that compared the within-species phenotypic variance
 113 between island and mainland systems

Reference	Location	Taxa	Trait	Main result
(Kavanagh & Burns, 2015)	New Zealand /outlying islands	dioecious plants	Organ sizes	No predictable difference in the degree of sexual dimorphism
(Madeira, 2018)	African continent/ São Tomé	passerines	Body size and plumage	No predictable difference in the degree of sexual dimorphism
(Meiri et al., 2005)	Worldwide	carnivores	Cranial features	Mainland species are more variable on average
(Novosolov et al., 2018)	Worldwide	lizards	Niche breadth	Niche breadths are similar on average

(Scott et al., 2003)	Australia and New Zealand/outlying islands	<i>Zosterops lateralis</i>	Foraging substrate use	Substrate use is similar on average
(Aubret & Shine, 2009)	Australia/outlying islands	<i>Notechis scutatus</i>	Plasticity in cranial growth rate	Plasticity reverts back to mainland levels after 9000 years

114

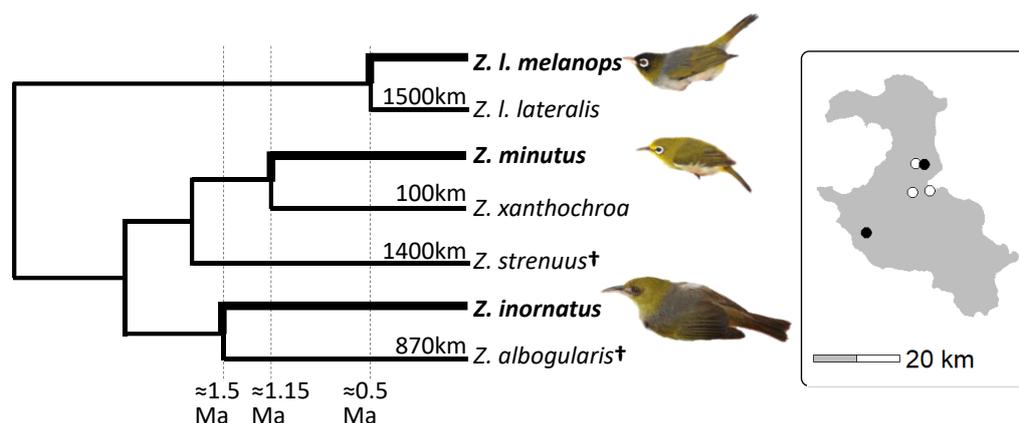
115 To control the influence of as many confounding factors as possible, we compared sympatric,
 116 congeneric species from the same small island. We especially looked for a set of species that
 117 exhibited a lot of spatial overlap even inside their home island. At first glance, the fact that all the
 118 species would be insular might seem counter-productive. Yet, in a given island system, there can be
 119 “young” and “old” species (*sensu* Fjeldså & Lovett, 1997), i.e., species that colonized the island at
 120 different points in time and have experienced the island environment for different amounts of time
 121 (Ricklefs & Cox, 1978). In some cases, this makes it possible to replace island/mainland comparisons
 122 with old/new comparisons, as described in the present study.

123 **Material and methods**

124 **The Lifu *Zosterops* and their morphometrics**

125 The *Zosterops* genus or white-eyes, known as the “great speciator” (Diamond, 1977; Moyle et al.,
 126 2009), has colonized the Old World in multiple waves, yielding complex patterns of secondary
 127 contacts that are just being deciphered (e.g., Cowles & Uy, 2019; Wickramasinghe et al., 2017).
 128 Lifu island (1200km²) is part of the Loyalty archipelago in New Caledonia (South Pacific) that was
 129 historically free of terrestrial mammals. It lies about 100km away from the main island of New
 130 Caledonia. It hosts three endemic species or subspecies of white-eyes that are found nowhere else:
 131 *Z. inornatus*, *Z. minutus*, and *Z. lateralis melanops*. These three species are not each other closest
 132 relatives (Cornetti et al., 2015) (Fig. 1). They did not diverge *in situ* and instead stem from three
 133 independent colonization events. Cornetti et al. estimated the colonization dates at 1.5Ma, 1.15Ma,
 134 and 0.5Ma respectively. This rare case of three-way insular sympatry after secondary contact raises
 135 the question of how the species coexisted and what were the consequences on their phenotypes.

136 **Fig. 1.** Simplified cladogram redrawn from Cornetti et al. (2015). Lifu species are indicated in bold
 137 font with a thick tree branch. The kilometric distances correspond to the oversea distances between
 138 Lifu and the ranges of the species. Based on the genetic divergence with *Zosterops albogularis*, the
 139 first species to colonize Lifu was *Z. inornatus*. *Z. minutus* colonized next based on the divergence with
 140 *Z. xanthochroa*. *Z. lateralis melanops* was clearly the last species to colonize given its shallow
 141 divergence with the subspecies *lateralis* from mainland Australia and paraphyly with other
 142 subspecies in the region (not shown here) (Cornetti et al., 2015). The cross symbols indicate recently
 143 extinct species. The inset represents the capture locations on Lifu (black for forest locations, white
 144 for edge locations).



145
 146 We focused on the morphometrics in this study. In passerines, measurements of the limbs, tail, and
 147 bill are often good indicators of the ecological niche, including adaptation to various habitats and
 148 foraging strategies (Marchetti et al., 1995; Miles et al., 1987; Pigot et al., 2016). *Zosterops* are mixed
 149 nectarivore-frugivore-insectivores, and when feeding on insects they exhibit a broad range of
 150 maneuvers including gleaning from branches and foliage, deaf-leaf probing, and aerial sallying
 151 (Winkler et al., 2020). In such generalist species, each individual could theoretically specialize on a
 152 few foraging maneuvers, or on a subset of the species' diet, depending on its individual morphology
 153 (Bolnick et al., 2007; Soule & Stewart, 1970).

154 Due to the earlier colonization date of *Z. inornatus*, the aforementioned mechanisms that promote
 155 within-species phenotypic variation operated for a longer period on *Z. inornatus* than the other two
 156 species. In addition, under the taxon cycling hypothesis (Ricklefs & Cox, 1978), *Z. inornatus*
 157 corresponds to a late-stage species (single island endemic), but it evolved to exploit most naturally-
 158 occurring landcovers on its home island, and it apparently escaped interspecific competition by

159 specializing on the lower strata of the vegetation and being the largest member of the genus
160 (Winkler et al., 2020). For these reasons, we expected *Z. inornatus* to be the most phenotypically
161 variable of our three study species.

162 By contrast, the newest species, *Z. lateralis*, would correspond to an early-stage species, i.e., a
163 species that specializes on early-successional, non-forest landcovers of many islands rather than
164 occupying all the landcovers of a single island (cf. results). Due to the need to fit in an already packed
165 community module, *Z. lateralis* likely experienced more constraints on phenotypic variance on Lifu
166 than anywhere else in its large geographic range. The mechanisms that promote within-species
167 phenotypic variation thereby operated not only for the least amount of time on *Z. lateralis*, but also
168 under the most constraints associated with inter-specific competition. For these reasons, we
169 expected *Z. lateralis* to be the least variable of the three species.

170 In a nutshell, based on the combination of the different colonization times and the different
171 ecological niches, we predicted that *Z. inornatus* should be more variable than *Z. minutus* which
172 should be more variable than *Z. lateralis*.

173 **Field work**

174 All the study individuals were free-flying birds that we captured over a period of 14 days in
175 November 2022, using mist-nets and playbacks of their vocalizations. We worked at 3 human-made
176 forest edge locations (around the coastal town of Wé) and 2 relatively untouched forest locations
177 (resp. near the settlement of Wedjumel and north of Wé) (Fig. 1). Within each location, we operated
178 3 to 8 mist-netting stations. The opening hours of the stations were not standardized in an attempt
179 to maximize the number of first captures as opposed to the number of recaptures.

180 The same experienced person (B.V.) measured individual morphology using the same devices. We
181 measured: tarsus length, tarsus width, wing length, tail length, bill length (the distance between the
182 distal extremity of the nostril and the bill tip), bill height (at the base of the bill, along the vertical

183 plane), and bill width (at the base of the bill, along the horizontal plane). We also determined the age
184 (juvenile or adult) using skull ossification in 95 individuals. Owing to the limited sexual dimorphism,
185 we did not document the sex of the study individuals, but we note that our prediction applies to all
186 the within-species variance, including that caused by sexual dimorphism if any, and that both sexes
187 incubate and display intraspecific aggression in this genus (Winkler et al., 2020), limiting the risk that
188 one of the sexes was over-represented in the sample.

189 **Statistical analysis**

190 We performed a principal component analysis (PCA) separately for the three bill measurements (bill
191 length, bill height, and bill width) and for the four body measurements (wing length, tail length,
192 tarsus length, and tarsus width). We obtained the three bill measurements for 149 individuals (39 *Z.*
193 *inornatus*, 65 *Z. minutus*, and 45 *Z. lateralis*) and the four body measurements for 144 individuals (38,
194 63, 42). The PCA for bill measurements yielded two independent axes of variation. The PCA for body
195 size yielded three axes, of which we selected the first two that captured most of the variance (cf.
196 results). We used the R-package FactoMineR (Husson et al., 2014).

197 We did not log-transform the measurements before analysis. When a dataset contains outliers, log-
198 transformation offset their disproportionate contribution to empirical moments and improves the fit
199 of the data to the normal distribution. Since there was no outlier in our dataset however, log-
200 transformation would hardly have improved the fit to the normal distribution, but would have
201 reduced the variance in some of the traits, eventually influencing the conclusions (not shown) (see
202 also Feng et al., 2014).

203 We applied the Fligner-Killeen nonparametric test of homogeneity of variances (Conover et al.,
204 1981), on each of the 4 axes of variation (two for bill and two for body measurements) to determine
205 whether the phenotypic variance differed between species. We also tested each of the 12 pairwise
206 differences individually, using variance F-tests with the usual statistical threshold ($P = 0.05$) and the
207 Bonferroni-adjusted threshold ($P = 0.004$, likely to be too conservative here).

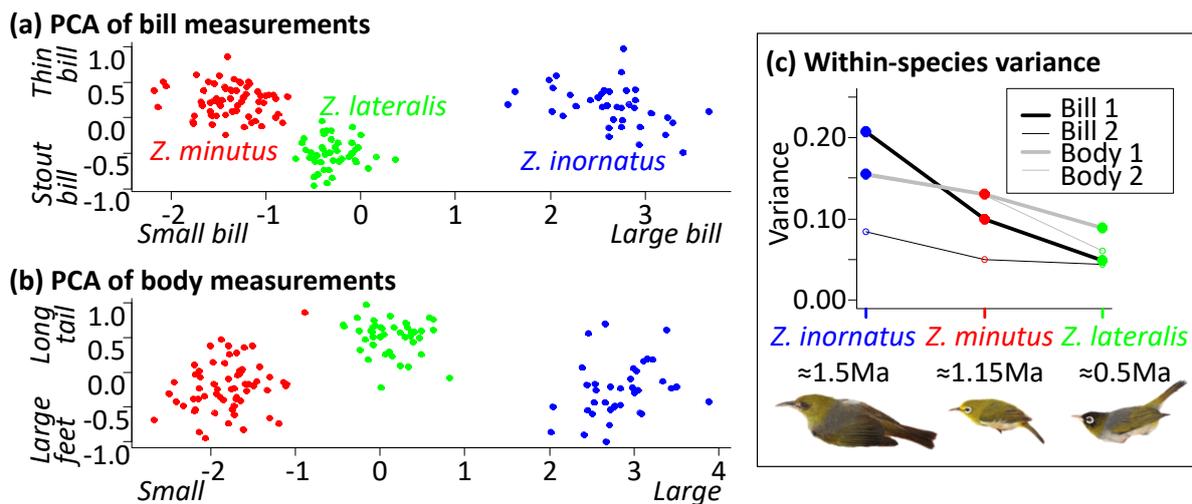
208 Finally, we investigated whether the prediction was better matched by the absolute values of the
209 traits, or by their values relative to the individuals' body sizes. To do that, we divided each trait by
210 the tarsus length (TL). A high trait/TL ratio indicates an individual that exhibits a larger trait than
211 expected from its body size. To also rescale relative to the species' average, we computed the
212 coefficient of variation of the trait/TL ratio: $RCV_s(trait) = \frac{Var_s(trait/TL)}{Mean_s(trait/TL)}$. We tested whether the
213 RCV decreased from *Z. inornatus* to *Z. minutus* to *Z. lateralis* using Feltz & Miller' (1996)
214 multipopulation asymptotic test of equality between coefficients of variation (R package cvequality:
215 Marwick & Krishnamoorthy, 2019).

216 **Comparison with published data**

217 We were aware of another set of morphometric data, that was collected in Oct-Nov 2011 and
218 available in the form of data summaries (PCA results) (Cornetti et al., 2015, Fig. 2a). There were some
219 technical differences: Cornetti et al. included the body mass in the PCA, measured the bill at different
220 cross sections than we did, and did not measure the tarsus width. In addition, several different field
221 workers contributed to that dataset. Observer bias and differences between measuring devices can
222 contribute significant amounts of artefactual variance in the morphometrics of small passerines. For
223 these reasons, we did not pool the two datasets together, but instead analyzed them separately
224 using the same procedure.

225

226 **Fig. 2.** (a) Individual ordinations in the PCA of the bill measurements. (b) Same for body
227 measurements. (c) Within-species variance in the resulting four axes of variation.



228

229 Results

230 The proportion of *Z. lateralis* in the captures increased from 0-4% at forest locations to 36-46% at
 231 edge locations, while the ratio between *Z. inornatus* and *Z. minutus* decreased from 6:5 to 1:5. These
 232 data indicated that *Z. lateralis* specialized on edge locations. There was no evidence of a difference in
 233 morphology between edge and forest locations in either species (all t-tests $P > 0.25$). The proportion
 234 of juveniles was 61%, 67% and 41% juveniles in *Z. inornatus*, *Z. minutus* and *Z. lateralis* respectively.
 235 These data suggested a possible difference in breeding phenology between *Z. lateralis* and the
 236 others. There was no evidence of a difference in morphology between adults and (fledged) juveniles
 237 in either species (all ANOVA $P > 0.20$).

238 Four axes of variation among morphological features

239 In the PCA of the bill measurements, the first axis of variation, which we interpreted as an index of
 240 individual bill size, accounted for 95% of the variance in three measurements. The second axis
 241 accounting for the remaining 5% captured variation in bill width not explained by bill size.
 242 In the PCA of the body measurements, the first axis of variation, which we interpreted as an index of
 243 individual body size, accounted for 92% of the variance in four measurements. The second axis
 244 accounted for 6% of the variance and captured a negative correlation between the remaining
 245 variation in feet size and tail length.

246 Comparing the within-species variance across species

247 The data contained very strong evidence that the variance in bill size decreased from *Z. inornatus* to
 248 *Z. minutus* to *Z. lateralis* (Fig. 2 and Table 2: “Bill 1”; Fligner-Killeen test: $\chi^2(2) = 9.76$, $P = 0.008$), and
 249 moderate evidence regarding the feet/tail ratio (Fig. 2 and Table 2: “Body 2”; $\chi^2(2) = 6.84$, $P = 0.03$).
 250 These results supported our prediction. Bill width (Fig. 2 and Table 2: “Bill 2”) and overall body size
 251 (Fig. 2 and Table 2: “Body 1”) on the contrary provided little support for the prediction (Fligner-
 252 Killeen tests: both $P > 0.2$).

253 **Table 2:** Pairwise F-tests of differences between variances in the four axes of variation and between
 254 the 3 pairs of species. Statistically significant differences (P -value < 0.05) are highlighted in bold font,
 255 and those that remain significant after Bonferroni adjustment (P -value < 0.004) are underlined. (a)
 256 Variance in the bill measurements. (b) Variance in the body measurements. In both cases, the upper
 257 triangle is for the first axis of the PCA and the lower triangle is for the second axis of the PCA.

(a) Bill measurements

	<i>Z. inornatus</i>	<i>Z. minutus</i>	<i>Z. lateralis</i>
<i>Z. inornatus</i>		F(38, 64) = 2.09; P = 0.009	<u>F(38, 44) = 4.28; P < 0.001</u>
<i>Z. minutus</i>	F(38, 64) = 1.7; P = 0.06		F(44, 64) = 0.49; P = 0.013
<i>Z. lateralis</i>	F(38, 44) = 1.9; P = 0.04	F(44, 64) = 0.9; P = 0.71	

(b) Body measurements

	<i>Z. inornatus</i>	<i>Z. minutus</i>	<i>Z. lateralis</i>
<i>Z. inornatus</i>		F(37, 62) = 1.19; P = 0.54	F(37, 42) = 1.75; P = 0.08
<i>Z. minutus</i>	F(37, 62) = 1.18; P = 0.57		F(42, 62) = 0.68; P = 0.19
<i>Z. lateralis</i>	<u>F(37, 42) = 2.54; P = 0.004</u>	F(42, 62) = 0.46; P = 0.009	

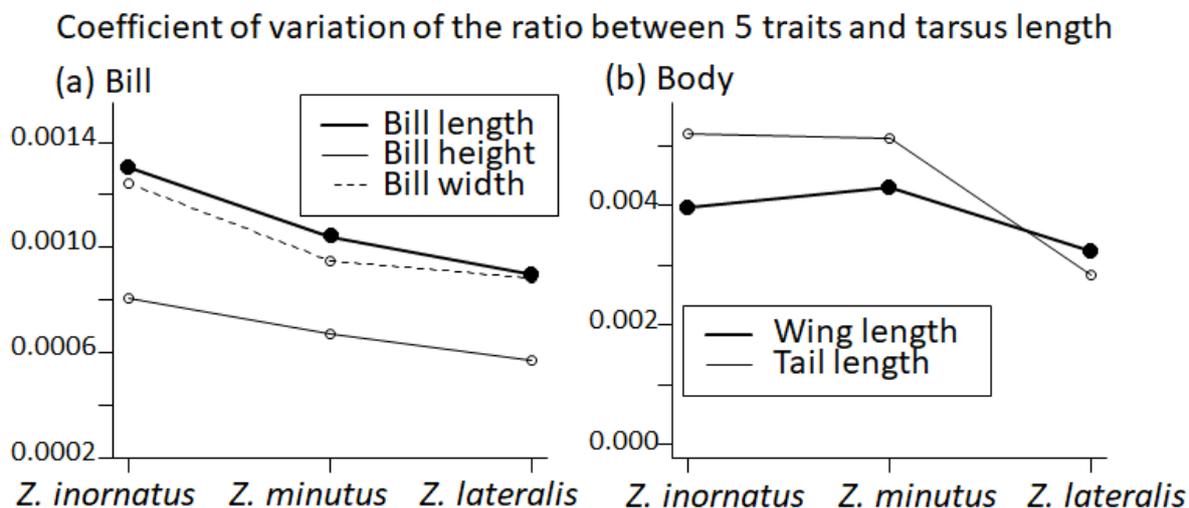
258

259 Validations

260 The Cornetti et al. data contained moderate support for the prediction in their second axis of
 261 variation (Fig. S1: “PCA2”; $\chi^2(2) = 3.77$, $P = 0.05$) and none in their first axis of variation ($P = 0.53$).
 262 Thus the conclusions from the two datasets were similar: some aspects of the morphology supported
 263 the prediction and the aspects that did not support the prediction did not contradict it either.
 264 After the rescaling procedure (Eq. 1), the trends hold (Fig. 3) but the statistical support disappeared
 265 (Feltz-Miller CV tests: $P > 0.25$) except for tail length ($P = 0.02$; Fig. 3b: thin line). In other words, our
 266 prediction was better matched by the absolute values of the traits than by their values relative to
 267 individual body sizes.

268

269 **Fig. 3:** Relative coefficient of variation (RCV) for 5 morphometric measurements. The ratio between
 270 tarsus width and tarsus length was almost invariant in all three species (RCV=0; not shown).



271

272 Discussion

273 After reviewing the mechanisms that lead to the prediction that insular populations should be more
 274 phenotypically diverse than mainland ones, and after highlighting that empirical island/mainland
 275 comparisons seem to be confounded by environmental factors, we set out to Lifu island. The Lifu
 276 *Zosterops* birds provided an opportunity to test the prediction while controlling the influence of
 277 many potentially confounding environmental factors. We predicted that *Zosterops inornatus* should
 278 be more morphologically variable than *Z. minutus* which should be more variable than *Z. lateralis*, at
 279 least for those traits that indicate the individual ecological niche or niche breadth. The
 280 morphometrics of ~140 individuals supported that prediction in two out of four axes of variation,
 281 with nonsignificant trends in the other two, prompting us to call for continued research into the
 282 morphological variance inside insular guilds rather than between insular and mainland systems.

283 Ecological function of the four axes of variation in morphology

284 Bill PCA1 corresponded to the bill size, which across insectivorous passerine species correlates
 285 positively with the frequency of probing maneuvers (for nectar, fruit pulp, in the leaf litter, etc.) and
 286 negatively with the frequency of gleaning from branches and foliage (Marchetti et al., 1995; Miles et

287 al., 1987; Pigot et al., 2016). Thus, we might speculate that the variance we observed in bill size may
288 correspond to varying levels of individual specialization into probing vs. gleaning.

289 Body PCA2 corresponded to a negative correlation between feet size and tail length after correcting
290 for body size. This covariation between traits might have to do with the birds' agility when foraging
291 for fruit and insects (Marchetti et al., 1995) or when escaping avian predators (Adriaensen et al.,
292 1998). Predators of forest-dwelling passerines are indeed relatively numerous on Lifu, (*Accipiter*
293 *fasciatus*, *Circus approximans*). If the feet/tail ratio provided anti-predator benefits, we would have
294 expected the most typically insular species and therefore the species with the most buffering against
295 lifespan-reducing threats, *Z. inornatus*, to exhibit the least variance the feet/tail ratio. This is not
296 what we observed. Therefore, we might speculate that the feet/tail ratio mostly helped with foraging
297 efficiency.

298 Body PCA1 corresponded to body size, which is highly diverged in our three species. Indeed, *Z.*
299 *inornatus* and *Z. minutus* are respectively the largest and smallest members of a 105+ species-strong
300 genus (Winkler et al., 2020), which suggests that these two species underwent an episode of
301 character displacement. Since traits that are under strong directional selection are more buffered
302 against environmental and genetic variation than traits under weak selection (Waddington, 1953), it
303 is maybe not surprising that the variation in body size was more constrained than other aspects of
304 the morphology. Our data suggested that individual variation in body size within species did not
305 reflect individual variation in ecological niche.

306 Bill PCA2 corresponded to bill width corrected for bill size, which, among passerines and near
307 passerines, often indicates the diet. Very thin bills can indicate a nectarivore diet whereby the bird
308 probe flowers for nectar, whereas very broad bills usually indicate a sallying insectivore (Pigot et al.,
309 2016). The Lifu *Zosterops* do exhibit these two foraging maneuvers, but infrequently only (pers. obs.).
310 The infrequent use of foraging maneuvers that require a particularly thin or broad bill could have
311 contributed to the relative lack of variance in bill width.

312 **A caveat regarding the focus on morphology as opposed to directly quantifying the**
313 **ecological niche**

314 In this study we assumed but did not demonstrate that the individual morphology conditioned the
315 individual behavior (e.g., the preferred foraging maneuver, preferred foraging strata, or the
316 preferred diet) and in turn the individual ecological niche. However, individuals may conceivably
317 buffer the effect of their traits on their fitness. For example individuals may buffer the effect of their
318 morphology on their survival rate by adopting risk-minimizing behaviors (Péron et al., 2016).
319 Alternatively, individual behaviors and individual morphologies may be uncorrelated, in which case
320 behavioral traits if ever documented would offer the opportunity for an independent test of the
321 prediction we made in this study. In any case, we note that the use of morphological traits as
322 functional traits is traditional and well substantiated in avian ecology (e.g., Luck et al., 2012; Pigot et
323 al., 2016).

324 **Character displacement in *Z. lateralis***

325 Our data indicated that *Z. lateralis melanops* was an edge specialist on Lifu, whereas *Z. inornatus* and
326 *Z. minutus* occurred in both edge and interior forest but were more frequent in the interior,
327 especially the former species. *Z. inornatus* and *Z. minutus* were thus single-island endemics that used
328 all the naturally-occurring landcovers on their home island, which corresponded to a late-stage
329 species under the taxon cycling hypothesis (Ricklefs & Bermingham, 2002; Ricklefs & Cox, 1978). By
330 contrast, we would interpret *Z. lateralis* as an early-stage species, because it is widespread and
331 expanding (e.g., reaching New Zealand in historical time), but on Lifu it was specialized on early-
332 successional landcovers. Another perspective on the same pattern is that *Z. lateralis* was relegated to
333 early-successional landcovers by competition with the older species. In any case, the result that *Z.*
334 *lateralis* was the least morphologically diverse helped explain its ability to coexist with two older
335 congeneric species on a single small island, in line with broader theories of character displacement
336 and coexistence (Taper & Case, 1992).

337 To further support this view that interspecific competition played a role in the erosion of phenotypic
338 variation in *Z. lateralis*, and that this role was additive to the effect of the short time that *Z. lateralis*
339 spent on Lifu, we turned to the long term study of *Z. lateralis chlorocephalus* on Heron island (off
340 eastern Australia) (Clegg et al., 2008). The Heron island population has been exposed to the island
341 environment for a shorter period of time than the Lifu population (4000 years: Clegg et al., 2008). But
342 on the other hand, *Z. lateralis* is the only representative of the *Zosterops* genus on Heron island and
343 does not have to compete with two congeneric species as is the case on Lifu. If only the time since
344 the populations had colonized their respective islands played a role, then the Heron island
345 population should have been unambiguously less variable than the Lifu one. Although differences in
346 methodology prevented direct comparisons between our results and Clegg et al.'s, that prediction
347 did not seem to be met, especially by the bill and tarsus lengths. One of the reasons for the rapid
348 emergence of large within-species variation on Heron island was reported to be the displacement of
349 the optimal phenotype from one year to the next, owing to environmental stochasticity (Clegg et al.,
350 2008) (termed the portfolio effect in our introduction, following Bolnick et al., 2011). On Lifu, we can
351 speculate that the competition with conspecifics stabilized the optimal phenotype of *Z. lateralis*.

352 **Comparing old and young insular taxa instead of mainland and insular taxa**

353 Island/mainland comparisons have so far yielded many negative results regarding the predictions
354 that insular taxa should be more phenotypically diverse than mainland taxa (Table 1). Our study
355 helped contextualize some of these previous results by highlighting not only the role of
356 environmental confounding factors, but also the consequences of the colonization sequence. We
357 demonstrated that different species from the same small island may exhibit different amounts of
358 phenotypic variance. Therefore, island/mainland comparison studies should strive to include all the
359 species from insular guilds, and to factor in the colonization sequences, which might be achieved by
360 treating the different stages of the taxon cycles separately in meta-analyses. In extreme cases, the
361 island systems may actually have operated as a source for the mainland systems (Moysi et al., 2023;
362 Vinciguerra et al., 2023), rather than the opposite which is the default working hypothesis. Such a

363 situation would lead to completely opposite predictions regarding phenotypic variance. Lastly, we
364 speculated a role for the shape of the selection gradient. In our study, body size did not verify our
365 prediction and seemed likely to be, or at least have been, under strong directional selection. By
366 contrast, the feet/tail ratio and bill size verified our prediction and seemed likely to be under
367 stabilizing selection

368 **Conclusion**

369 This study advanced our understanding of the role of the insular environment in the maintenance of
370 phenotypic variance, and specifically the lack of interspecific competition. We did that both
371 theoretically through our review of the mechanisms and empirically in a non-model system that we
372 explored for the first time. Our results based on a moderate sample size were encouraging but also
373 illustrated the challenges of working with empirical variances, and the fact that our working
374 hypothesis rested on the assumption that the morphological traits indicated the individual ecological
375 niche, making it critical to select appropriate traits. We recommend publishing the raw phenotypic
376 variances in addition to the population means in all studies of insular populations, and also envision
377 insights from longer-term or more in-depth studies into the behavioral, demographic, and genetic
378 basis of phenotypic variance.

379

380 **Data availability:** The source data will be deposited onto Dryad or similar upon acceptance

381 **Biosketch:** The Lifu Zosterops project aims at leveraging the configuration of the avian community of
382 Lifu island to test hypotheses about mutation accumulation, Allee effects, and species coexistence.

383 **Author contributions:** G.P. conceived the ideas; B.V. and G.P. collected the data; G.P. analyzed the
384 data; and G.P. led the writing.

385

386 **Supplementary material**

387 Fig. S1 and Table S1: reanalysis of Cornetti et al. (2015) morphometric datasets using the same
388 procedure as the present study.

389

390 **References**

391 Adriaensen, F., Dhondt, A. A., Van Dongen, S., Lens, L., & Matthysen, E. (1998). Stabilizing selection
392 on blue tit fledgling mass in the presence of sparrowhawks. *Proceedings of the Royal Society*
393 *of London. Series B: Biological Sciences*, 265(1400), 1011–1016.

394 <https://doi.org/10.1098/rspb.1998.0392>

395 Aubret, F., & Shine, R. (2009). Genetic Assimilation and the Postcolonization Erosion of Phenotypic
396 Plasticity in Island Tiger Snakes. *Current Biology*, 19(22), 1932–1936.

397 <https://doi.org/10.1016/j.cub.2009.09.061>

398 Barabás, G., Parent, C., Kraemer, A., Van de Perre, F., & De Laender, F. (2022). The evolution of trait
399 variance creates a tension between species diversity and functional diversity. *Nature*
400 *Communications*, 13(1), 2521. <https://doi.org/10.1038/s41467-022-30090-4>

401 Bolnick, D. I., Amarasekare, P., Araújo, M. S., Bürger, R., Levine, J. M., Novak, M., Rudolf, V. H. W.,
402 Schreiber, S. J., Urban, M. C., & Vasseur, D. A. (2011). Why intraspecific trait variation
403 matters in community ecology. *Trends in Ecology & Evolution*, 26(4), 183–192.

404 <https://doi.org/10.1016/j.tree.2011.01.009>

405 Bolnick, D. I., Svanbäck, R., Araújo, M. S., & Persson, L. (2007). Comparative support for the niche
406 variation hypothesis that more generalized populations also are more heterogeneous.

407 *Proceedings of the National Academy of Sciences of the United States of America*, 104(24),
408 10075–10079. <https://doi.org/10.1073/pnas.0703743104>

- 409 Clegg, S. M., Frentiu, F. D., Kikkawa, J., Tavecchia, G., & Owens, I. P. F. (2008). 4000 Years of
410 phenotypic change in an island bird: Heterogeneity of selection over three microevolutionary
411 timescales. *Evolution*, *62*(9), 2393–2410. <https://doi.org/10.1111/j.1558-5646.2008.00437.x>
- 412 Conover, W. J., Johnson, M. E., & Johnson, M. M. (1981). A Comparative Study of Tests for
413 Homogeneity of Variances, with Applications to the Outer Continental Shelf Bidding Data.
414 *Technometrics*, *23*(4), 351–361. <https://doi.org/10.1080/00401706.1981.10487680>
- 415 Cornetti, L., Valente, L. M., Dunning, L. T., Quan, X., Black, R. A., Hébert, O. H., & Savolainen, V.
416 (2015). The genome of the “great speciator” provides insights into bird diversification.
417 *Genome Biology and Evolution*, *7*(9), 2680–2691. <https://doi.org/10.1093/gbe/evv168>
- 418 Covas, R. (2012). Evolution of reproductive life histories in island birds worldwide. *Proceedings of the*
419 *Royal Society B: Biological Sciences*, *279*(1733), 1531–1537.
420 <https://doi.org/10.1098/rspb.2011.1785>
- 421 Cowles, S. A., & Uy, J. A. C. (2019). Rapid, complete reproductive isolation in two closely related
422 *Zosterops* White-eye bird species despite broadly overlapping ranges. *Evolution*, *73*(8), 1647–
423 1662. <https://doi.org/10.1111/EVO.13797>
- 424 Diamond, J. M. (1977). Continental and Insular Speciation in Pacific Land Birds. *Systematic Zoology*,
425 *26*(3), 263–268. <https://doi.org/10.2307/2412673>
- 426 Feltz, C. J., & Miller, G. E. (1996). An asymptotic test for the equality of coefficients of variation from
427 *k* populations. *Statistics in Medicine*, *15*(6), 646–658. [https://doi.org/10.1002/\(sici\)1097-0258\(19960330\)15:6<647::aid-sim184>3.0.co;2-p](https://doi.org/10.1002/(sici)1097-0258(19960330)15:6<647::aid-sim184>3.0.co;2-p)
- 429 Feng, C., Wang, H., Lu, N., Chen, T., He, H., Lu, Y., & Tu, X. M. (2014). Log-transformation and its
430 implications for data analysis. *Shanghai Archives of Psychiatry*, *26*(2), 105–109.
431 <https://doi.org/10.3969/j.issn.1002-0829.2014.02.009>
- 432 Fjeldså, J., & Lovett, J. C. (1997). Geographical patterns of old and young species in African forest
433 biota: The significance of specific montane areas as evolutionary centres. *Biodiversity and*
434 *Conservation*, *6*, 325–346.

- 435 Fridley, J. D., & Grime, J. P. (2010). Community and ecosystem effects of intraspecific genetic
436 diversity in grassland microcosms of varying species diversity. *Ecology*, *91*(8), 2272–2283.
437 <https://doi.org/10.1890/09-1240.1>
- 438 Ganz, H. H., & Ebert, D. (2010). Benefits of host genetic diversity for resistance to infection depend
439 on parasite diversity. *Ecology*, *91*(5), 1263–1268. <https://doi.org/10.1890/09-1243.1>
- 440 Gauthier, G., Péron, G., Lebreton, J., Grenier, P., & Oudenhove, L. V. (2016). Partitioning prediction
441 uncertainty in climate-dependent population models. *Proceedings of the Royal Society B*,
442 *283*(1845), 20162353.
- 443 Husson, F., Josse, J., Le, S., & Mazet, J. (2014). *FactoMineR: Multivariate Exploratory Data Analysis*
444 *and Data Mining with R*. [Computer software]. [http://cran.r-](http://cran.r-project.org/package=FactoMineR)
445 [project.org/package=FactoMineR](http://cran.r-project.org/package=FactoMineR)
- 446 Ibarra-Isassi, J., Handa, I. T., & Lessard, J.-P. (2023). Community-wide trait adaptation, but not
447 plasticity, explains ant community structure in extreme environments. *Functional Ecology*,
448 *37*(1), 139–149. <https://doi.org/10.1111/1365-2435.14185>
- 449 Jensen, J. L. W. V. (1906). Sur les fonctions convexes et les inégalités entre les valeurs moyennes.
450 *Acta Mathematica*, *30*(0), 175–193. <https://doi.org/10.1007/BF02418571>
- 451 Kavanagh, P. H., & Burns, K. C. (2015). Sexual size dimorphism in island plants: The niche variation
452 hypothesis and insular size changes. *Oikos*, *124*(6), 717–723.
453 <https://doi.org/10.1111/oik.01753>
- 454 Lande, R. (1993). Risks of population extinction from demographic and environmental stochasticity
455 and random catastrophes. *The American Naturalist*, *142*(6), 911.
456 <https://doi.org/10.1086/285580>
- 457 Luck, G. W., Lavorel, S., McIntyre, S., & Lumb, K. (2012). Improving the application of vertebrate trait-
458 based frameworks to the study of ecosystem services. *Journal of Animal Ecology*, *81*(5),
459 1065–1076. <https://doi.org/10.1111/j.1365-2656.2012.01974.x>

- 460 MacArthur, R. H., Diamond, J. M., & Karr, J. R. (1972). Density Compensation in Island Faunas.
461 *Ecology*, 53(2), 330–342. <https://doi.org/10.2307/1934090>
- 462 Madeira, B. de C. M. A. (2018). *Sexual dimorphism and reproductive phenology of common birds in*
463 *São Tomé island: Conservation implications* [masterThesis].
464 <https://repositorio.ul.pt/handle/10451/33859>
- 465 Marchetti, K., Price, T., & Richman, A. (1995). Correlates of wing morphology with foraging behaviour
466 and migration distance in the genus *Phylloscopus*. *Journal of Avian Biology*, 26(3), 177–181.
467 <https://doi.org/10.2307/3677316>
- 468 Marwick, B., & Krishnamoorthy, K. (2019). *Cvequality: Tests for the Equality of Coefficients of*
469 *Variation from Multiple Groups. R software package version 0.1.3.*
470 <https://github.com/benmarwick/cvequality>,
- 471 Meiri, S., Dayan, T., & Simberloff, D. (2005). Variability and Sexual Size Dimorphism in Carnivores:
472 Testing the Niche Variation Hypothesis. *Ecology*, 86(6), 1432–1440.
473 <https://doi.org/10.1890/04-1503>
- 474 Miles, D. B., Ricklefs, R. E., & Travis, J. (1987). Concordance of Ecomorphological Relationships in
475 Three Assemblages of Passerine Birds. *The American Naturalist*, 129(3), 347–364.
476 <https://doi.org/10.1086/284641>
- 477 Moyle, R. G., Filardi, C. E., Smith, C. E., & Diamond, J. (2009). Explosive Pleistocene diversification and
478 hemispheric expansion of a “great speciator.” *Proceedings of the National Academy of*
479 *Sciences of the United States of America*, 106(6), 1863–1868.
480 <https://doi.org/10.1073/pnas.0809861105>
- 481 Moysi, M., Ogolowa, B. O., Nikiforou, C., Dretakis, M., Purcell, J., Brelsford, A., & Kirschel, A. N. G.
482 (2023). Genomic data reveal contrasting patterns of divergence among island and mainland
483 birds of the Eastern Mediterranean. *Ibis*. <https://doi.org/10.1111/ibi.13178>

- 484 Novosolov, M., Rodda, G. H., Gainsbury, A. M., & Meiri, S. (2018). Dietary niche variation and its
485 relationship to lizard population density. *Journal of Animal Ecology*, *87*(1), 285–292.
486 <https://doi.org/10.1111/1365-2656.12762>
- 487 Péron, G., Gaillard, J. M., Barbraud, C., Bonenfant, C., Charmantier, A., Choquet, R., Coulson, T.,
488 Grosbois, V., Loison, A., Marzolin, G., Owen-Smith, N., Pardo, D., Plard, F., Pradel, R., Toïgo,
489 C., & Gimenez, O. (2016). Evidence of reduced individual heterogeneity in adult survival of
490 long-lived species. *Evolution*, *70*(12), 2909–2914. <https://doi.org/10.1111/evo.13098>
- 491 Pigot, A. L., Trisos, C. H., & Tobias, J. A. (2016). Functional traits reveal the expansion and packing of
492 ecological niche space underlying an elevational diversity gradient in passerine birds.
493 *Proceedings of the Royal Society B: Biological Sciences*, *283*(1822), 20152013.
494 <https://doi.org/10.1098/rspb.2015.2013>
- 495 Polis, G. A. (1984). Age structure component of niche width and intraspecific resource partitioning—
496 Can age-groups function as ecological species? *American Naturalist*, *123*(4), 541–564.
497 <https://doi.org/10.1086/284221>
- 498 Ricklefs, R. E., & Bermingham, E. (2002). The concept of the taxon cycle in biogeography. *Global*
499 *Ecology and Biogeography*, *11*(5), 353–361. [https://doi.org/10.1046/j.1466-](https://doi.org/10.1046/j.1466-822x.2002.00300.x)
500 [822x.2002.00300.x](https://doi.org/10.1046/j.1466-822x.2002.00300.x)
- 501 Ricklefs, R. E., & Cox, G. W. (1978). Stage of Taxon Cycle, Habitat Distribution, and Population Density
502 in the Avifauna of the West Indies. *The American Naturalist*, *112*(987), 875–895.
503 <https://doi.org/10.1086/283329>
- 504 Schindler, D. E., Hilborn, R., Chasco, B., Boatright, C. P., Quinn, T. P., Rogers, L. A., & Webster, M. S.
505 (2010). Population diversity and the portfolio effect in an exploited species. *Nature*,
506 *465*(7298), Article 7298. <https://doi.org/10.1038/nature09060>
- 507 Schoener, T. W. (1969). Models of Optimal Size for Solitary Predators. *The American Naturalist*,
508 *103*(931), 277–313. <https://doi.org/10.1086/282602>

- 509 Scott, S. N., Clegg, S. M., Blomberg, S. P., Kikkawa, J., & Owens, I. P. F. (2003). Morphological shifts in
510 island-dwelling birds: The roles of generalist foraging and niche expansion. *Evolution*, *57*(9),
511 2147–2156. <https://doi.org/10.1111/j.0014-3820.2003.tb00392.x>
- 512 Shine, R. (1989). Ecological Causes for the Evolution of Sexual Dimorphism: A Review of the Evidence.
513 *The Quarterly Review of Biology*, *64*(4), 419–461. <https://doi.org/10.1086/416458>
- 514 Soule, M., & Stewart, B. R. (1970). The “Niche-Variation” Hypothesis: A Test and Alternatives. *The*
515 *American Naturalist*, *104*(935), 85–97. <https://doi.org/10.1086/282642>
- 516 Taper, M. L., & Case, T. J. (1992). Models of Character Displacement and the Theoretical Robustness
517 of Taxon Cycles. *Evolution*, *46*(2), 317–333. [https://doi.org/10.1111/j.1558-](https://doi.org/10.1111/j.1558-5646.1992.tb02040.x)
518 [5646.1992.tb02040.x](https://doi.org/10.1111/j.1558-5646.1992.tb02040.x)
- 519 Terborgh, J. (2023). The ‘island syndrome’ is an alternative state. *Journal of Biogeography*, *50*(3),
520 467–475. <https://doi.org/10.1111/jbi.14530>
- 521 Tinker, M. T., Bentall, G., & Estes, J. A. (2008). Food limitation leads to behavioral diversification and
522 dietary specialization in sea otters. *Proceedings of the National Academy of Sciences*, *105*(2),
523 560–565. <https://doi.org/10.1073/pnas.0709263105>
- 524 Vinciguerra, N. T., Oliveros, C. H., Moyle, R. G., & Andersen, M. J. (2023). Island life accelerates
525 geographical radiation in the white-eyes (Zosteropidae). *Ibis*, *ibi.13177*.
526 <https://doi.org/10.1111/ibi.13177>
- 527 Violle, C., Enquist, B. J., McGill, B. J., Jiang, L., Albert, C. H., Hulshof, C., Jung, V., & Messier, J. (2012).
528 The return of the variance: Intraspecific variability in community ecology. *Trends in Ecology &*
529 *Evolution*, *27*(4), 244–252. <https://doi.org/10.1016/j.tree.2011.11.014>
- 530 Waddington, C. (1953). Genetic Assimilation of an Acquired Character. *Evolution*, *7*(2), 118–126.
531 <https://doi.org/10.2307/2405747>
- 532 Warren, B. H., Simberloff, D., Ricklefs, R. E., Aguilée, R., Condamine, F. L., Gravel, D., Morlon, H.,
533 Mouquet, N., Rosindell, J., Casquet, J., Conti, E., Cornuault, J., Fernández-Palacios, J. M.,
534 Hengl, T., Norder, S. J., Rijdsdijk, K. F., Sanmartín, I., Strasberg, D., Triantis, K. A., ... Thébaud, C.

- 535 (2015). Islands as model systems in ecology and evolution: Prospects fifty years after
536 MacArthur-Wilson. *Ecology Letters*, 18(2), 200–217. <https://doi.org/10.1111/ele.12398>
- 537 Wickramasinghe, N., Robin, V. V., Ramakrishnan, U., Reddy, S., & Seneviratne, S. S. (2017). Non-sister
538 Sri Lankan white-eyes (genus *Zosterops*) are a result of independent colonizations. *PLOS ONE*,
539 12(8), e0181441. <https://doi.org/10.1371/journal.pone.0181441>
- 540 Winkler, D. W., Billerman, S. M., & Lovette, I. J. (2020). White-eyes, Yuhinas, and Allies
541 (*Zosteropidae*). In S. M. Billerman, B. K. Keeney, P. G. Rodewald, & T. S. Schulenberg (Eds.),
542 *Birds of the World*. Cornell Lab of Ornithology. <https://doi.org/10.2173/bow.zoster2.01>
- 543