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

**Running title:** Phenotypic variance in island endemics

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## 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.,

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

#### *Island syndrome*

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

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

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

**Table 1:** Overview of previous studies that compared the within-species phenotypic variance 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

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

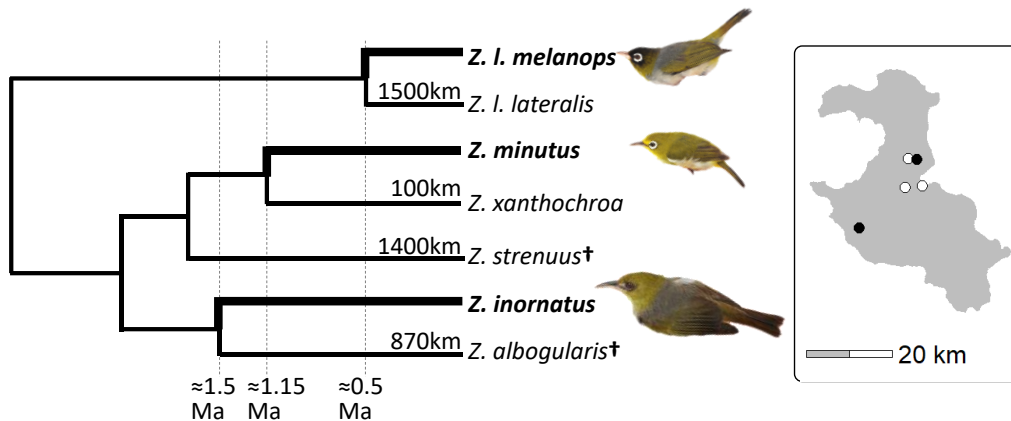
## Material and methods

### The Lifu *Zosterops* and their morphometrics

The *Zosterops* genus or white-eyes, known as the “great speciator” (Diamond, 1977; Moyle et al., 2009), has colonized the Old World in multiple waves, yielding complex patterns of secondary contacts that are just being deciphered (e.g., Cowles & Uy, 2019; Wickramasinghe et al., 2017).

Lifu island (1200km<sup>2</sup>) is part of the Loyalty archipelago in New Caledonia (South Pacific) that was historically free of terrestrial mammals. It lies about 100km away from the main island of New Caledonia. It hosts three endemic species or subspecies of white-eyes that are found nowhere else: *Z. inornatus*, *Z. minutus*, and *Z. lateralis melanops*. These three species are not each other closest relatives (Cornetti et al., 2015) (Fig. 1). They did not diverge *in situ* and instead stem from three independent colonization events. Cornetti et al. estimated the colonization dates at 1.5Ma, 1.15Ma, and 0.5Ma respectively. This rare case of three-way insular sympatry after secondary contact raises the question of how the species coexisted and what were the consequences on their phenotypes.

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



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

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

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

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

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

## Field work

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

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



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

## Statistical analysis

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

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

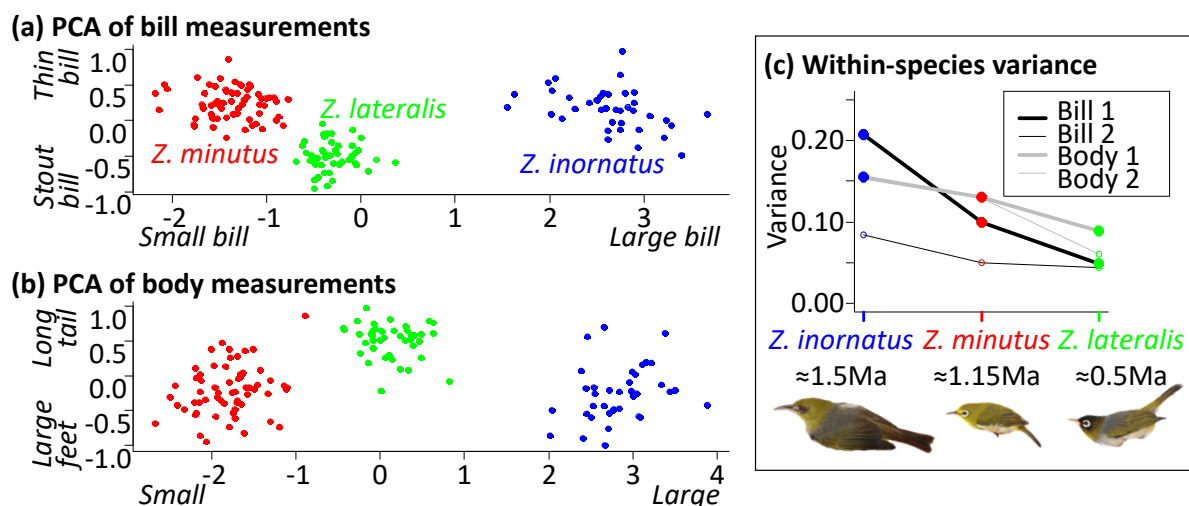
We applied the Fligner-Killeen nonparametric test of homogeneity of variances (Conover et al., 1981), on each of the 4 axes of variation (two for bill and two for body measurements) to determine whether the phenotypic variance differed between species. We also tested each of the 12 pairwise differences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

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

### Comparison with published data

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

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



## Results

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

### Four axes of variation among morphological features

In the PCA of the bill measurements, the first axis of variation, which we interpreted as an index of individual bill size, accounted for 95% of the variance in three measurements. The second axis accounting for the remaining 5% captured variation in bill width not explained by bill size.

In the PCA of the body measurements, the first axis of variation, which we interpreted as an index of individual body size, accounted for 92% of the variance in four measurements. The second axis accounted for 6% of the variance and captured a negative correlation between the remaining variation in feet size and tail length.

## Comparing the within-species variance across species

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

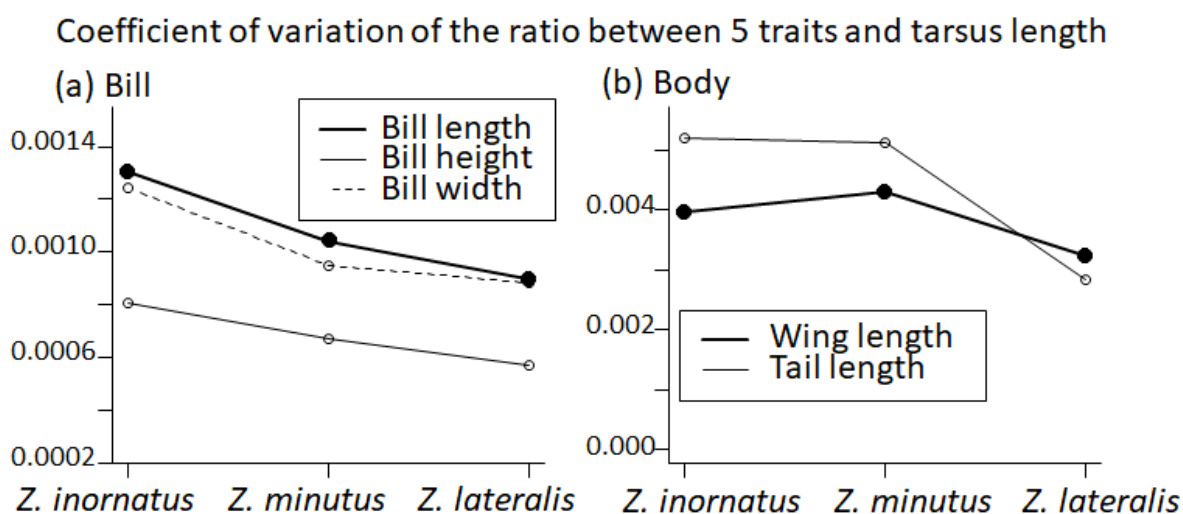
**Table 2:** Pairwise F-tests of differences between variances in the four axes of variation and between the 3 pairs of species. Statistically significant differences ( $P$ -value  $< 0.05$ ) are highlighted in bold font, and those that remain significant after Bonferroni adjustment ( $P$ -value  $< 0.004$ ) are underlined. (a) Variance in the bill measurements. (b) Variance in the body measurements. In both cases, the upper 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>		<b><math>F(38, 64) = 2.09</math>; <math>P = 0.009</math></b>	<b><u><math>F(38, 44) = 4.28</math>; <math>P &lt; 0.001</math></u></b>
<i>Z. minutus</i>	$F(38, 64) = 1.7$ ; $P = 0.06$		<b><u><math>F(44, 64) = 0.49</math>; <math>P = 0.013</math></u></b>
<i>Z. lateralis</i>	<b><u><math>F(38, 44) = 1.9</math>; <math>P = 0.04</math></u></b>	$F(44, 64) = 0.9$ ; $P = 0.71$	
(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>	<b><u><math>F(37, 42) = 2.54</math>; <math>P = 0.004</math></u></b>	<b><u><math>F(42, 62) = 0.46</math>; <math>P = 0.009</math></u></b>	

## Validations

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

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



## Discussion

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

## Ecological function of the four axes of variation in morphology

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

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

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

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

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

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

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

### **Character displacement in *Z. lateralis***

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

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

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

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



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

## **Conclusion**

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

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

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

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

## Supplementary material

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

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