



RESEARCH PAPER

Journal of
Biogeography

WILEY

Contrasting trajectories of morphological diversification on continents and islands in the Afrotropical white-eye radiation

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Handling Editor: Richard Ladle

Abstract

Aim: Morphological and lineage evolution are predicted to follow different patterns in island and mainland radiations. However, the extent to which these geographical contexts influence evolutionary trajectories remains poorly understood, in part because few studies have focused on species-rich clades colonizing continents and archipelagos over comparable timeframes. Focusing on a diverse songbird clade radiating on the African continent and adjacent islands, we tested whether morphological evolution is best explained by adaptive or non-adaptive processes, and whether mainland and island lineages evolved to occupy different regions or volumes of morphological space (morphospace).

Location: Palaeotropics, with a particular focus on the Afrotropical region.

Taxon: White-eyes, *Zosterops* (Aves: Zosteropidae).

Methods: We generated principal component axes from novel trait data for 120 species and combined this information with a comprehensive dated phylogeny. We then analysed the dynamics of trait and lineage diversification using comparative evolutionary methods.

Results: An early burst and slowdown pattern of lineage accumulation is not mirrored by phenotypic evolution, which instead shows an apparent convergence on particular phenotypes. However, the overall signature of phenotypic convergence is strongly driven by mainland taxa, in which phenotypes appear to be highly constrained within elevational zones, while speciation events are often associated with phenotypic divergence from one body plan to the other after colonization of highland from lowland habitats, or vice versa. By contrast, island lineages have repeatedly explored novel areas of morphospace with patterns of phenotypic divergence generally not distinguishable from a random-walk model.

Main conclusions: Diversification of *Zosterops* highlights contrasting evolutionary trends and dynamics for continental versus island species. We suggest the different trajectory of evolution in insular lineages arises from reduced species competition leading to an increase in ecological opportunity, thereby providing a release to phenotypic constraints experienced by continental taxa.

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KEYWORDS

competition, cryptic species, disparity-through-time, diversification, islands, morphological evolution, niche divergence, white-eyes, *Zosterops*

1 | INTRODUCTION

Understanding evolutionary processes driving lineage and phenotypic diversification is a central concept in evolutionary biology, in which biologists have attempted to discern if there are commonalities across clades and regions (Harmon, Schulte, Larson, & Losos, 2003). In particular, recent evolutionary radiations containing a proliferation of taxa at lower taxonomic levels provide critical insight while avoiding complicated causal events of older radiations. A general feature attributed to insular (oceanic island, or lake) endemic radiations is that they are often characterized by adaptive radiation (Ford et al., 2016; Jönsson et al., 2012; Losos & Ricklefs, 2009; Lovette, Bermingham, & Ricklefs, 2001; Mahler, Revell, Glor, & Losos, 2011; Seehausen, 2006). Under an adaptive model, ecological opportunity (Schluter, 2000) is thought to drive the rapid increase in diversification during the early stages of the radiation, when there is less competition through fewer species and more available niches. As the radiation progresses, competition between species intensifies and there are fewer available resources, resulting in decreasing opportunities for speciation and/or greater extinction of species (Gavrilets & Vose, 2005). The scenario of an 'early-burst and slow-down' (density dependence) model for adaptive radiation has led to a prediction that lineage and morphological diversification are correlated (e.g. Rabosky et al., 2013). However, despite an early burst of lineage diversification being identified as a general pattern of adaptive radiations, this signal does not necessarily correlate with an early burst of morphological evolution. Instead, there is evidence to suggest that a constrained model of evolution (Ornstein–Uhlenbeck [OU] – a random walk, but with a selective optima) is more commonly supported, even for classic adaptive radiation examples such as Darwin's Finches and *Anolis* lizards (Harmon et al., 2010), although it has been shown that these models may incorrectly be favoured over simpler (Brownian motion) models (Cooper, Thomas, Venditti, Meade, & Freckleton, 2016). Irrespective of this, reasons for the absence of an early-burst model of trait evolution are unclear.

Studies of adaptive radiations have primarily focused on insular systems, whereas most biodiversity occurs on continents where land area is far larger and often far more complex in terms of geography or topology (May, 1994). The increased age and species richness of continental biota increases the potential for interspecific competition, leading to the prediction that mainland taxa should evolve more slowly and in a more constrained manner (Schluter, 1988; Tobias et al., 2014; Webb, Ackerly, McPeck, & Donoghue, 2002). Compared with island systems, continental radiations may be characterized by more allopatric diversification and reduced constraints on ecological niche divergence (Losos & Ricklefs, 2009), increasing the likelihood of non-adaptive or constrained models of diversification (Rundell & Price, 2009; Tobias et al., 2014). However, previous

studies provide conflicting evidence regarding the dynamics of diversification in mainland clades. On the one hand, adaptive radiation is clearly not limited to insular contexts because several continental radiations fit an adaptive model of lineage and morphological diversification, for example, mainland *Anolis* lizards (Pinto, Mahler, Harmon, & Losos, 2008) and cichlid fishes (López-Fernández, Arbour, Winemiller, & Honeycutt, 2013). On the other hand, while many continental clades are characterized by a density-dependent model of lineage diversification (Phillimore & Price, 2008; Rabosky & Lovette, 2008), it is possible that this pattern is generated by standard models of allopatric speciation (Pigot, Phillimore, Owens, & Orme, 2010). Moreover, several studies focusing on continental tropical clades have revealed a near-constant rate of diversification, suggesting that these radiations may either be too young to have reached their ecological limit or are less restricted by ecological opportunity (Day et al., 2013; Derryberry et al., 2011; Liedtke et al., 2016). Several studies of continental avian radiations have concluded that evolutionary processes underlying morphological disparity may be uncoupled from those driving species diversity (Derryberry et al., 2011; Schweizer, Hertwig, & Seehausen, 2014). For example, a constant rate of lineage diversification may be coupled with an adaptive signal of morphological diversification, although these contrasting signals may reflect the uncertainty of these models to infer correct processes.

Clades of highly dispersive organisms, such as those that can colonize multiple continents and can expand their ranges within extensive archipelagos, provide an opportunity to directly investigate evolutionary dynamics across landscapes of different spatial scales. However, there are limited studies investigating these trends within mainland and island settings (but see Schluter (1988), Pinto et al. (2008), Fritz, Jönsson, Fjeldså, and Rahbek (2012)), with few specifically investigating both lineage and phenotypic evolution. Focusing on a classic example of adaptive radiation, Pinto et al. (2008) found lineage diversification across Caribbean island and Central and South America mainland *Anolis* lizards were comparable, identifying an adaptive signal, yet island species occupied different parts of morphospace, suggestive that competition and/or predation between these regions differed. However, it is not clear if this is typical in radiations spanning mainland and islands, particularly in groups that exhibit limited morphological change over time.

The songbird genus *Zosterops* (white-eyes) provides a useful model to examine trends of phenotypic and lineage diversification across different geographical contexts having radiated within various archipelagos (Warren, Bermingham, Prÿs-Jones, & Thébauds, 2006) and continents (Martins, Cox, Irestedt, Prÿs-Jones, & Day, 2020). Lauded by biologists as a 'great speciator' (Diamond, Gilpin, & Mayr, 1976; Moyle, Filardi, Smith, & Diamond, 2009), this genus contains ca. 100 species (van Balen, 2019),

including many exceptional colonizers (Melo, Warren, & Jones, 2011; Phillimore et al., 2008; Slikas, Jones, Derrickson, & Fleischer, 2000; Warren et al., 2006). Although a disproportionate number of species occur on islands (Moreau, 1957), recent studies have highlighted increased continental species diversity (Lim et al., 2019; Martins et al., 2020). Overall, the *Zosterops* clade has the highest net diversification rate of any bird lineage, and one of the highest among vertebrates (Jetz, Thomas, Joy, Hartmann, & Mooers, 2012; Moyle et al., 2009).

To address whether mainland and island lineages followed the same pattern of morphological and lineage evolution, we focus on the Afrotropics, which we define as continental Africa-Arabia, and associated island archipelagos including the western Indian Ocean, Madagascar and Gulf of Guinea. The advantage of this study region is the availability of a comprehensive species-level taxonomy of *Zosterops* (Martins et al., 2020) spanning a similar number of taxa distributed on the continent versus surrounding islands. Based on new measurements of nine morphological traits, we used evolutionary models to test if morphological diversity of Afrotropical *Zosterops* ($n = 46$ species and candidate species), and its constituent mainland and island radiations, is best explained by adaptive or non-adaptive processes. We also tested whether lineage diversification in these different geographical contexts followed a pattern of density dependence and mapped traits of all study species in multivariate morphological space (morphospace) to assess whether mainland and island lineages evolved to occupy different regions of morphospace. Finally, to place our findings in wider context, we compiled morphological data for the entire zosteropid clade, including both *Zosterops* and related genera, and compared how Afrotropical radiations have explored morphospace in relation to taxa from the rest of the Palaeotropics ($n = 75$ species).

2 | MATERIALS AND METHODS

2.1 | Study system

The white-eye family (Zosteropidae) is one of seven families in the diverse Old World babbler radiation (Cai et al., 2019). Members of Zosteropidae are small (ca. 10–12 cm) arboreal passerine birds, often gregarious, and regarded as ecological generalists, with reported diets consisting of a mixture of insects, fruits and nectar (van Balen, 2019). The geographical distribution of the clade extends across the Palaeotropics, which includes the Afrotropics and Austral-Asia (southern and eastern Asia, Australasia, and the eastern Indian Ocean islands) (van Balen, 2019). A few *Zosterops* species have colonized the temperate zone as far as South Africa, Japan and New Zealand. Within the Afrotropics, the division between island and continental forms is roughly equal (Martins et al., 2020), whereas outside the Afrotropics the majority of species are insular forms with another centre of diversification in continental South and East Asia. Despite exhibiting a signal of density dependence (Moyle et al., 2009), *Zosterops* are remarkably homogeneous in morphology and

plumage (Mayr 1963; Mees, 1953; Moreau, 1957), apart from some aberrant island forms (Melo et al., 2011).

2.2 | Molecular dated tree

We used the dated comprehensive phylogenetic tree from Martins et al. (2020) based on three mitochondrial markers (Cytb, ATP6 and ND3), five nuclear introns (TGF β 2, G3PDH, Fib 7, CHD1 and MUSK) and comprehensive sampling of all known Afrotropical species and subspecies (with the exception of *Z. maderaspatanus mennaiensis*). Overall, this timetree is based on results from phylogenetic inference and quantitative species delimitation methods for 46 Afrotropical taxa (described species, and possible candidate species [represented by trinomial nomenclature]), comprising 25 mainland and 21 island taxa, respectively (for locality data, see Martins et al., 2020, Appendix S1).

2.3 | Collection of trait data

We collected trait data from museum specimens of nearly all sampled *Zosterops* taxa ($n = 45$ species) included in the dated phylogenetic analysis of Martins et al. (2020), with only the extinct species *Z. semiflavus* missing. In addition, 59 *Zosterops* species and 16 species in other Zosteropidae genera were included from the remainder of the Palaeotropics, totalling 120 species (508 individuals) (see Appendix S1, Table S1 for biometric data). Where available, we selected approximately two males and two females per species collected from the same taxon. We selected ecomorphological traits linked to the ecological niche, with methods following Trisos, Petchey, and Tobias (2014) and Pigot et al. (2020): (i) culmen length from tip of the skull; (ii) bill width; (iii) bill depth from the anterior edge of nostril; (iv) tarsus length (from the notch of the knee to the third crease at the ankle); (v) unflattened wing length; (vi) tail length (from the tip of the longest rectrix to the 'point of insertion', where the two central rectrices protrude from the skin). In addition to these traits, we further measured (vii) culmen length from anterior edge of the nostril; (viii) gape width (bill width measuring from the meeting point of the upper and lower mandibles; (ix) Kipp's distance (measured from the tip of the first secondary to the tip of the longest primary). Digital callipers were used to measure all traits, apart from (v) and (vi), which were measured with a wing rule. The majority of Afrotropical *Zosterops* taxa were measured by FCM (136 individuals), with all other taxa measured by a team led by JAT (Pigot et al., 2020). To test for repeatability of measurements between recorders, FCM independently measured all traits from 12 specimens (across five species) originally measured in the JAT dataset to ensure congruence between observers. Additionally, a random sample of 11 specimens (different taxa) was remeasured by FCM in order to demonstrate intra-observer reliability. An ANOVA was applied to both datasets and showed that while measurements varied between traits (as expected), there was no evidence for any differences in the observers (i.e. FCM versus

JAT), and no interaction between observer and trait. Previous analyses on much larger samples of species found similar results, suggesting that measurement bias among observers is too low to influence results of macroecological studies across multiple species (McEntee, Tobias, Sheard, & Burleigh, 2018; Pigot et al., 2020).

2.4 | Morphometric analyses

Principal component analyses (PCA) were initially conducted using only those taxa included in the phylogeny (excluding *Z. semiflavus* and Austral-Asian outgroups), in which Africa-Arabia mainland taxa were based on species delimitation analysis and recommendations from Martins et al. (2020). Data were log-transformed, using the natural logarithm, to reduce variance between taxa (Ricklefs & Travis, 1980). For each trait, we calculated the mean for each taxon. Although sample size is fairly limited (*ca.* 4 individuals measured per taxon), potentially resulting in biases, small samples have been shown to provide relatively accurate estimates of mean size when comparing across species (see Cardini & Elton, 2007). To determine if these data needed to be phylogenetically corrected, the log-transformed data were analysed using a phylogenetic size correction via generalized least squares regression (Revell, 2009) in 'phytools' v0.6–99 (Revell, 2012), R 3.4.3 (R Development Core Team, 2018). As this was non-significant ($p > 0.5$), the PCA loadings of the non-phylogenetically corrected data were extracted using *PAST* 3.18 (Hammer, Harper, & Ryan, 2001) to obtain information on the proportion of the contribution of each parameter for each PC (see Appendix S1, Table S2 for PCA scores). Together, the first four PCs of the Afrotropical radiation explained 89.98% of the variance (52.94%, 20.72%, 10.84% and 5.49%, respectively) and these axes were used for subsequent comparative evolutionary analysis. To compare morphospace occupation of taxa comprising the Afrotropical radiation to Austral-Asian taxa, we included a further 59 *Zosterops* species from southern and eastern Asia, and 16 *Zosteropidae* from other genera using the methods previously described. Here, PC1–4 explained 93.07% of the variance (65.96%, 16.43%, 6.27%, 4.41%, respectively) based on the *PAST* analysis. A 95% confidence interval ellipsis was included for comparisons of identified groups for these axes.

2.5 | Comparative evolutionary methods

To test if morphological evolution shows a departure from the null model of Brownian motion, we used Disparity-through-time (DTT) analyses (Harmon et al., 2003). We employed the recently developed rank envelope method to compare the empirical data to the null model simulations, following Murrell (2018). Here, the DTT curves from the null model simulations are ordered according to their most extreme relative disparity value, and the empirical DTT curve is then ranked to see if it falls within the most extreme 5% of curves in which case the null hypothesis of Brownian evolution

is rejected. This method has been shown to generally have higher power to detect non-Brownian evolution than other popular DTT methods, and it is straightforward to visually inspect the time points where the null model is rejected (Murrell, 2018). Since the method gives a rank to each simulation and empirical DTT curve based upon their most extreme relative disparity value, ties in ranking between empirical and simulation curves are almost certain to occur. Rather than break ties, we report a *p* value interval, within which the true *p* value is estimated to be found, and large numbers of simulations ensure this interval is small. We ran all models with 5,000 simulations. The scores from the PCA were extracted for each taxon for principal component axes 1–4 and combined with the timetree. DTT plots that show high subclade disparity, in which there is greater disparity within subclades, have been described as evidence of convergent evolution. However, caution in interpretation is required since, assuming the phylogenetic tree is ultrametric, high subclade disparity (i.e. disparity >1) can also be caused by an accelerating rate of trait evolution, and it is not possible to distinguish between this model and the OU model with a single optimum using DTT analysis (Uyeda, Caetano, & Pennell, 2015). Conversely, plots that have low subclade disparity (i.e. disparity <1), where there is greater disparity between subclades, might indicate a signal of adaptive radiation (Harmon et al., 2003). Building on Murrell (2018), we analysed all PC axes separately but within one test (i.e. one *p* value interval is returned), with visual inspection of the curves against the null model confidence interval showing which PCs are responsible for rejecting the null model.

In addition to the null model tests, we also compared the fit of the three models – Brownian motion (BM), Ornstein–Uhlenbeck (OU) and Early-Burst (EB) – regarding continuous character evolution, to PC axes 1–4 using the fitcontinuous function in 'geiger' v2.0.6 (Harmon, Weir, Brock, Glor, & Challenger, 2008) in R. Models were compared using the Akaike Information Criterion (AIC) in which a lower AIC score indicates the model that is best fitted by the data. To account for sample size, we also calculated the AICc, which was used to obtain the deltaAICc and Akaike weights (Aw). All analyses were conducted in R 3.4.3 (R Development Core Team, 2018).

2.6 | Diversification rate analyses

We used several methods to investigate lineage diversification. To detect if there was an early burst followed by a slowdown in diversification rate over time, we calculated the Υ statistic of Pybus and Harvey (2000), and generated a lineage-through-time (LTT) plot using 'ape' software (Paradis et al. 2004). We also applied a likelihood approach (Morlon, 2014) and compared two constant rate models – (1) pure birth (PB) and (2) birth–death (BD) – to four variable rate models: (1) PB with an exponential speciation rate; (2) BD with a constant speciation rate and exponential extinction rate; (3) BD with an exponential speciation rate and constant extinction rate and (4) BD with both exponential speciation and extinction

rates, where rates are changing over time, in *RPANDA* package v1.3 (Morlon, 2014). Model fit was compared using AIC and adjusted for small sample sizes (AICc), which was used to obtain *Aw*. These analyses were conducted in R 3.4.3 (R Development Core Team, 2018). To test if subclades of the Afrotropical radiation diversified under distinct rate regimes, we also implemented *BAMM* 2.5.0 (Bayesian Analysis of Macroevolutionary Mixtures, Rabosky (2014)) and used *BAMM* tools version 2.1.6 (Rabosky et al., 2014) to investigate rate dynamics. The following priors placed on the evolutionary rate parameters, which are critical to the performance of *BAMM*, were generated for our dataset using *BAMM* tools (expected number of shifts = 1; λ Init.Prior = 0.126; λ ShiftPrior = 0.578; μ Init.Prior = 0.126; λ TimeVariablePrior = 1) and applied to downstream analysis. We ran three independent MCMC runs for five million generations each sampling every 1,000th, and used *TRACER* 1.7 (Rambaut, Drummond, Xie, Baele, & Suchard, 2018) to assess convergence. Models were compared in *BAMM* tools using Bayes factors (BF).

3 | RESULTS

3.1 | Dynamics of lineage diversification

Visual inspection of the LTT plot reveals a pattern of rapid cladogenesis followed by declining diversification rates for the Afrotropical radiation (Appendix S1, Figure S1.1), which is supported by a gamma (Υ) statistic that is a strongly negative (-4.43 , $p \leq .001$ [two-tailed p value]). The variable rate model, pure birth model, with an exponential speciation rate was by far the best fit to our data (Table 1). Strongly declining net diversification rates were also recovered from the *BAMM* analysis (Figure 1) in which a mean speciation rate (λ) was 1.82 (1.32–2.48 upper/lower 95% highest probability density [HPD]), and the mean extinction rate (μ) was 0.54 (0.03–1.56 upper/lower 95% highest probability density [HPD]). We found no strong evidence for any rate shift (BF = 0.86) among subclades (i.e. no rate

heterogeneity), indicating that neither island nor mainland clades exhibited faster rates with respect to one another.

3.2 | Dynamics of trait evolution

The DTT analyses showed that when Afrotropical taxa are analysed together across PC1–4 disparity is predominately partitioned within subclades throughout the entire radiation (Figure 2a). Closer inspection reveals, PC1, PC3 and PC4 to all be significantly different from Brownian evolution ($0.001 < p < 0.006$), with evidence of greater disparity within clades than expected under the null model, although only during the most recent third of the radiation. When the island ($n = 21$) and mainland ($n = 25$) taxa from the Afrotropical radiation are analysed separately (Figure 2 B and C, respectively), we again find significant departures from the null model ($0.007 < p < 0.011$, and $0.005 < p < 0.009$, respectively). However, the null model of Brownian evolution is now only rejected for PC3, and we can see that the pattern of greater within-clade disparity for PC3 across all species (Figure 2a) is largely driven by the extreme peak in relative disparity found in the mainland species (Figure 2c). When the proportion of each trait is examined for each axis (Table 2), Kipp's distance (distance between the first secondary feather and wingtip) influences the greatest proportion of PC1 (0.175) and PC2 (0.267), while for PC3, tail length contributes the greatest proportion of each trait (0.245), followed by Kipp's distance (0.151), and for PC4, bill depth contributes the greatest proportion of each trait (0.202).

The results of the DTT analyses are supported by models investigating continuous character evolution (Table 3) in which the Afrotropical radiation, and its constituent mainland taxa when analysed separately, do not show an adaptive signal, but instead are strongly supported by an Ornstein–Uhlenbeck (OU) model, indicating bounded evolution around a phenotypic optimum, across all PC axes retained ($Aw = >0.92$). In contrast, there is weak support for either the OU or Brownian motion (BM) across all axes for the island taxa.

TABLE 1 Testing models of diversification for the Afrotropical *Zosterops* radiation (comprising 46 taxa). Models include pure-birth (PB); birth–death (BD); PB with an exponential rate (PB λ exp); BD with a constant speciation rate and exponential extinction rate (BD λ cst- μ exp); BD with an exponential speciation rate and constant extinction rate (BD λ exp- μ cst); BD in which speciation and extinction rates are both exponential (BD λ exp- μ exp). Log-likelihood, AICc, Δ AIC (the difference in AICc with the best model) and Akaike Weights (AW) are shown. Bold text denotes the best model

Model	λ parameter	μ parameter	Log L	AICc	Δ AICc	Aw
Constant rate models						
Pure birth (PB)	1.10		-40.68	83.44	12.34	0.0015
Birth-death (BD)	1.10	<0.001	-40.68	85.63	14.53	0.0005
Variable rate models						
PBλexp	0.50–1.16		-33.41	71.10	0	0.7054
BD λ cst- μ exp	1.10	<0.001; -1.16	-40.68	87.91	16.81	0.0002
BD λ exp- μ cst	0.49–1.19	<0.001	-33.42	73.39	2.29	0.2245
BD λ exp- μ exp	0.50; 1.17	<0.001; -0.90	-33.41	75.78	4.68	0.0680

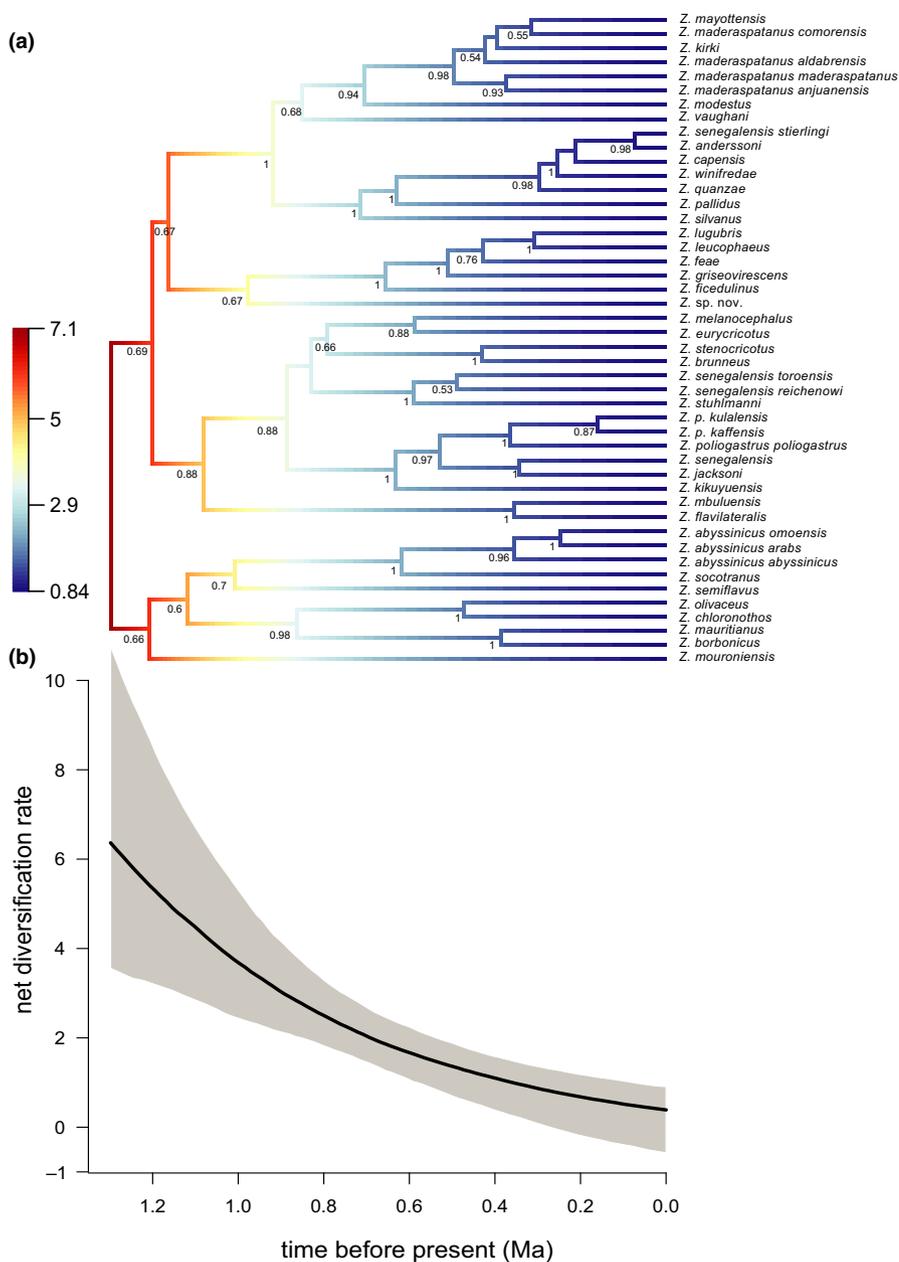


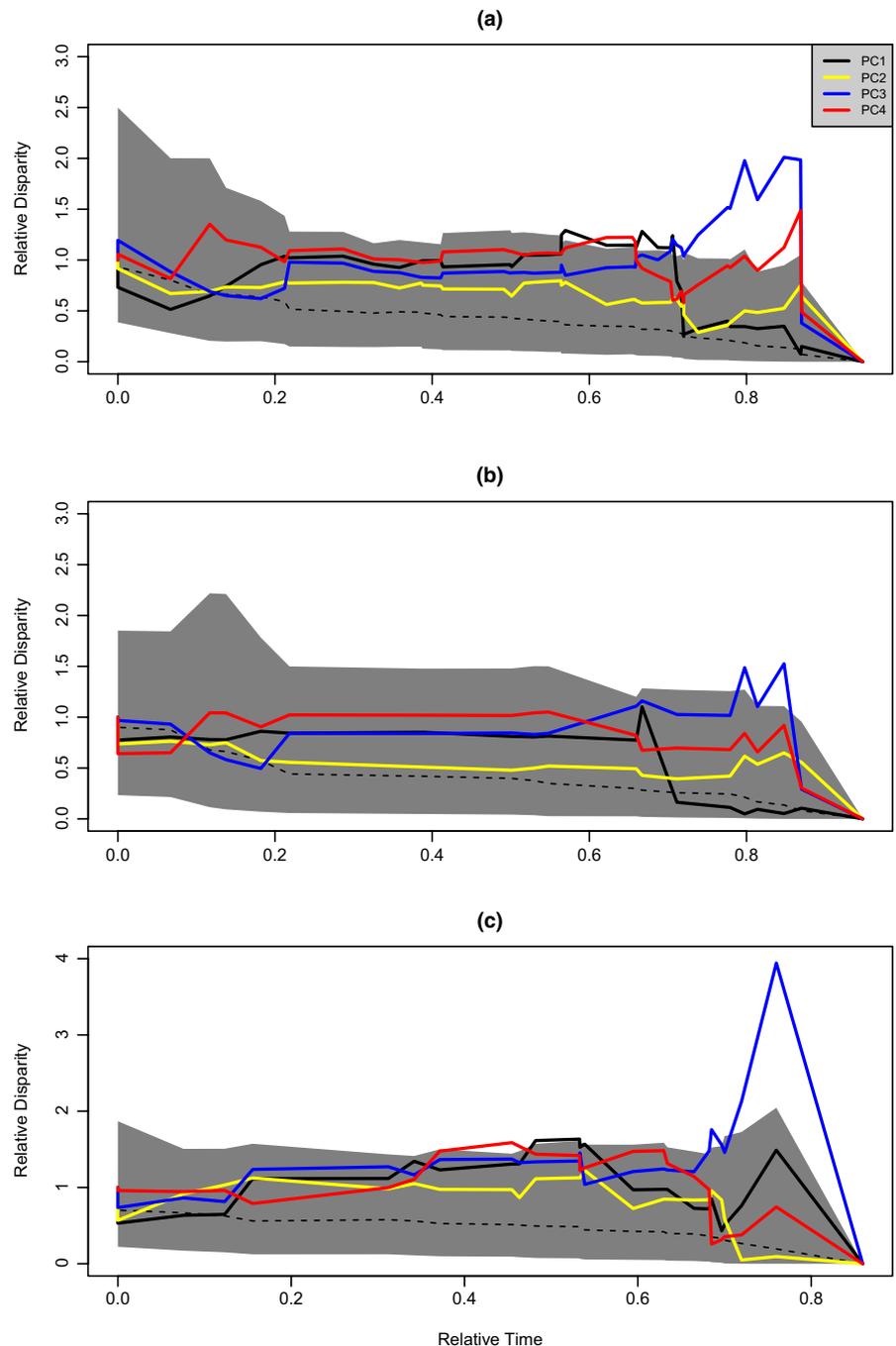
FIGURE 1 Diversification dynamics for the Afrotropical *Zosterops* radiation generated using BAMM software. (a) Phylorate plot denoting speciation rate along each branch, with warmer colours representing faster rates; and (b) Net diversification rate through time plot. Shading represents confidence on rate reconstructions at any point in time

3.3 | Distribution of mainland and island taxa in morphospace

Mainland Afrotropical taxa are tightly clustered in morphospace compared to their island counterparts (Figure 3) and are nested within the broader morphospace occupied by Afrotropical island taxa, irrespective of the axis of variation considered. The expansion of morphospace occupied by island taxa is largely the result of several peripheral clusters of taxa, which include the highly aberrant Gulf of Guinea species (Melo et al., 2011). The Afrotropical radiation is in turn nested within the larger region of morphospace occupied by the extra-Afrotropical (Austral-Asian) *Zosteropidae* (Figure 3). This expansion into unique areas of morphospace by Austral-Asian *Zosteropidae* is observed across all axes (data for other PC axes not shown), in which taxa again tend to be positively clustered. Closer

examination of the mainland Afrotropical taxa revealed some disjunction between highland and lowland ecotypes, with highland lineages more positively clustered in morphospace (Figure 4a). This finding is, however, only apparent when PC1 is compared to the other axis (data shown for PC1 vs. 2), as comparisons of PC2-4 conversely revealed considerable overlap of these ecotypes (Figure 4b, data shown for PC2 versus 3). Examination of Afrotropical island clades (Figure 4c,d) revealed divergence in the regions of morphospace occupied by the two Western Indian Ocean island radiations: 'Ancient Indian ocean', and 'Indian Ocean *maderaspatanus*' sensu Warren et al. (2006). A third group of island taxa - the Gulf of Guinea clade sensu Melo et al. (2011) - is distinct from both the Indian Ocean radiations when plotting PC1 versus 2 (Figure 4c), but overlaps somewhat in morphospace with the 'Indian Ocean *maderaspatanus*' radiation when comparing other axes (Figure 4d).

FIGURE 2 Disparity-Through-Time (DDT) plots for the Afrotropical zosteropid radiation generated using the rank envelope method. (a) including all mainland and island Afrotropical taxa; (b) island Afrotropical taxa only; (c) mainland Afrotropical taxa only, depicting the first four principal component axes. Disparity profiles are indicated by lines (PC1–4), average Brownian motion simulation by the dashed lines, and 95% confidence intervals from 5,000 simulations by the grey polygons. The x-axis is relative time in which zero is the start of the radiation



4 | DISCUSSION

4.1 | Contrasting patterns of morphological evolution between mainland and island white-eyes

Our analyses show that morphological evolution of Afrotropical zosteropids is best explained by convergence, and that constrained as opposed to adaptive evolutionary processes have occurred during their radiation. This finding contrasts with adaptive bursts of trait diversification found in classic avian adaptive radiations (see Grant & Grant, 2006; Price, 2008), as well as early adaptive signals shown in other spatially extensive radiations in birds occurring on continents (Derryberry et al., 2011; Schweizer et al., 2014). However, it

supports previous studies showing a pattern of rapid evolution followed by stasis may be rarer than one of constraint on phenotypic evolution (Harmon et al., 2010), although see Cooper et al. (2016).

The absence of an adaptive signal of phenotypic evolution in *Zosterops* is not unsurprising given that taxonomists (Mees, 1953; Moreau, 1957) have struggled to differentiate taxa, particularly those from the Africa-Arabian mainland, due to their overall remarkably cryptic phenotypes. In island *Zosterops*, the lack of an early adaptive signal perhaps reflects constraints on trophic specialization associated with their generalized diets, or else may suggest that this clade lacks the inherent developmental plasticity (i.e. 'evolvability') of beaks and foraging behaviours associated with other avian clades that underwent adaptive radiation on islands. In line with trophic

traits, the diversification of plumage colouration in zosteropids is also subtle, although further study is warranted to investigate evolutionary patterns in some of the clade's more variable plumage features, including eye-ring size and belly colouration (Milá, Warren, Heeb, & Thébaud, 2010; Oatley, Voelker, Crowe, & Bowie, 2012). Overall, since our study focuses on the exceptionally short timescale of the Afrotropical radiation, future analyses should consider the entire zosteropid clade, particularly as Austral-Asian lineages have diversified across a considerably larger volume of morphospace.

On closer inspection of the Afrotropical radiation, which included near even taxonomic richness of mainland versus island members, the signal of evolutionary convergence appears to have been largely

TABLE 2 Proportion of contribution from each trait for principal component (PC) axes 1–4 (see Methods, Collection of trait data, for a more detailed description of traits measured). Bold text denotes the trait that contributes the greatest proportion across PCs

Trait	PC1	PC2	PC3	PC4
i Bill length	0.120	0.078	0.097	0.132
ii Bill width	0.113	0.137	0.017	0.028
ii Bill depth	0.090	0.145	0.109	0.202
iv Tarsus length	0.102	0.016	0.100	0.185
v Wing chord	0.087	0.054	0.106	0.012
vi Tail length	0.106	0.083	0.245	0.079
vii Bill from nostril	0.121	0.144	0.146	0.099
viii Gape width	0.087	0.077	0.029	0.154
ix Kipp's Distance	0.175	0.267	0.151	0.110

TABLE 3 Comparison of three models of evolution based on principal component (PC) data. Models assessed using Akaike Information Criterion (AIC) values and Akaike Weights (AW), with best models highlighted. Brownian motion (BM), Ornstein–Uhlenbeck (OU), Early Burst (EB). Bold text denotes best model

Afrotropical radiation	BM		OU		EB	
	AIC	AW	AIC	AW	AIC	AW
PC1-4						
PC1	12.485	0.006	1.898	0.992	14.485	0.002
PC2	–45.994	0.063	–51.642	0.917	–43.994	0.020
PC3	–66.533	0.013	–75.533	0.983	–64.533	0.004
PC4	–104.168	0.051	–110.300	0.933	–102.168	0.016
Mainland						
PC1-4						
PC1	–0.595	0.033	–7.903	0.957	1.405	0.009
PC2	–24.906	0.050	–31.354	0.936	–22.906	0.014
PC3	–42.531	0.005	–53.801	0.994	–40.531	0.001
PC4	–67.723	0.036	–74.860	0.954	–65.723	0.010
Islands						
PC1-4						
PC1	11.465	0.258	8.739	0.678	13.465	0.064
PC2	–18.045	0.484	18.440	0.396	–16.045	0.120
PC3	–22.812	0.256	–25.556	0.680	–20.812	0.063
PC4	–36.922	0.414	–38.031	0.484	–34.922	0.102

driven by mainland taxa. Morphological diversification in this group of taxa strongly favoured an Ornstein–Uhlenbeck model, indicating bounded evolution around a phenotypic optimum. Constrained phenotypic evolution in cryptic continental species has also been shown in agamid lizards (Smith, Harmon, Shoo, & Melville, 2011). The significant recent increase in trait disparity of mainland *Zosterops* taxa is potentially explained by repeated patterns of niche divergence driven by Plio-Pleistocene climatic fluctuations (Cox, Prÿs-Jones, Habel, Amakobe, & Day, 2014). These authors investigated East African montane *Zosterops* taxa using phylogenetic inference and showed a general trend for sister species to comprise highland and lowland members. The highland birds, which tend to have more restricted ranges on mountain tops, are larger and heavier, whereas lowland birds are smaller with larger ranges (Habel et al., 2015). Although mainland species are similar and only show small phenotypic differences, adhering to the typical *Zosterops* phenotype, there is some evidence from our study that highland and lowland bauplans, which show some separation (Figure 4a), may have evolved rapidly based on the timetree (Figure 1). Such rapid phenotypic disparity has also been found in highland and lowland island *Z. borbonicus* populations from Réunion (Cornuault et al., 2015), as well as in island populations of *Z. lateralis* which show phenotypic differentiation from mainland source populations (Australia) even in populations founded in the southwestern Pacific over the last 200 years (Clegg et al., 2002).

When comparing PC1 of traits (Table 2), it is clear that highland and lowland Africa-Arabian mainland species occupy highly divergent regions of morphospace, although there is some overlap

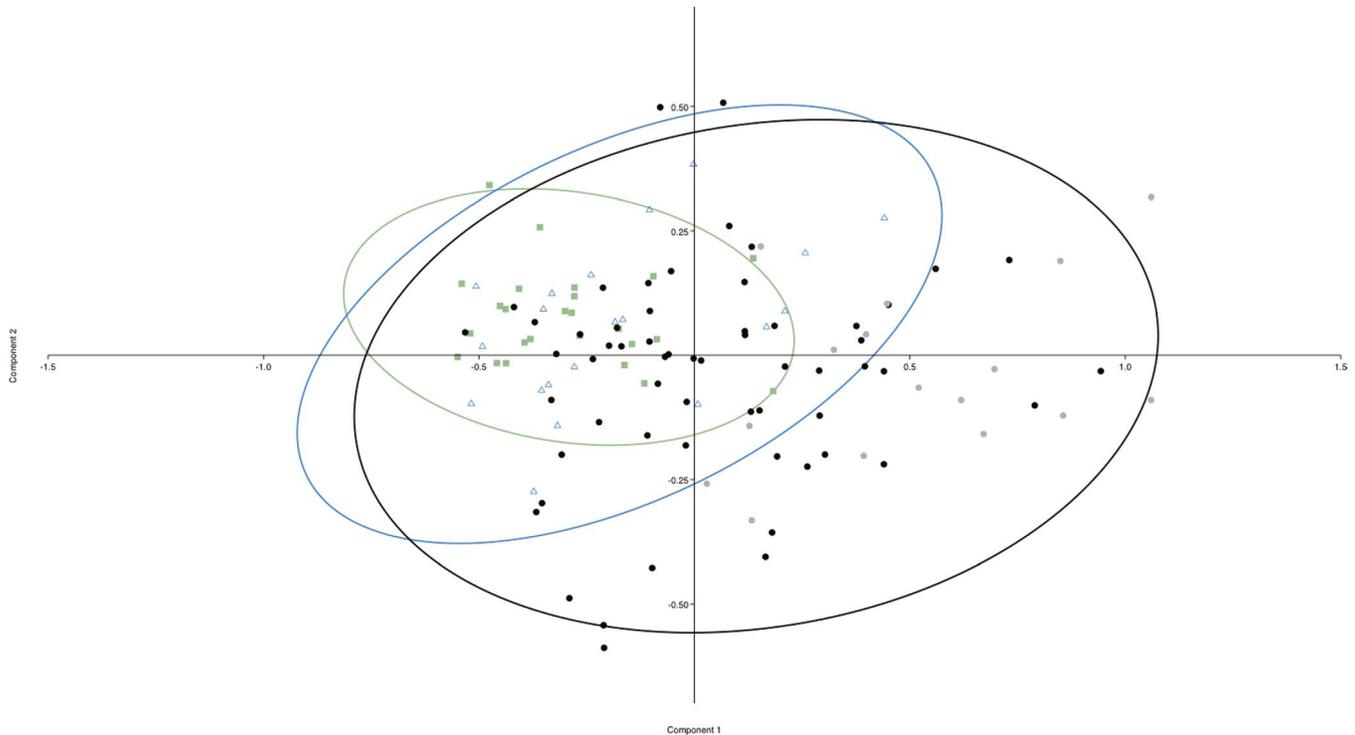


FIGURE 3 Morphospace occupation depicting the first two principal component axes of the Afrotropical radiation, with 95% confidence interval ellipsis for constituent mainland (green squares filled) and island (i.e. western Indian Ocean, Gulf of Guinea, Madagascar, Pemba Island, Socotra Island) (blue triangles) species. Remaining Palaeotropical zosteropid species: black circles, *Zosterops*; grey circles, other *Zosteropidae* genera

between these highland and lowland mainland species (Figure 4a). However, when mainland birds are compared to island taxa, we find that the volume of morphospace occupied by mainland birds is relatively restricted (Figure 3). It appears that repeated diversification into highland and lowland continental habitats has been followed by phenotypic convergence towards particular optimal trait combinations. In addition, some speciation events appear to be driven by vicariance rather than colonization of different habitats since some sister species of continental *Zosterops* are comprised of both lowland or both highland forms (Martins et al., 2020). Moreover, we only found small variations within species from each of these habitats, suggesting that morphological novelty is constrained in continental birds. This may ultimately be due to fewer ecological opportunities since continental communities are probably closer to carrying capacity and the available niches more highly saturated with potential competitors (Losos & Ricklefs, 2009; Tobias et al., 2014).

In contrast to the mainland taxa, island *Zosterops* show a relatively weak signal of morphological convergence, in which phenotypic diversification is typically not distinguishable from a random-walk pattern (Brownian motion, BM). Although a BM model of character evolution may occur when evolutionary change is neutral, in which traits change only as a result of genetic drift (Lande, 1976), it can also occur from natural selection (Harmon, 2018). Certainly, island evolution has been shown to result from neutral processes, such as genetic drift and founder events (González-Quevedo, Spurgin, Illera, & Richardson, 2015; Spurgin, Illera, Jorgensen, Dawson, & Richardson, 2014), and divergent natural selection (Clegg, Frentiu,

Kikkawa, Tavecchia, & Owens, 2008; Grant & Grant, 2006; Losos & Ricklefs, 2009; Milá et al., 2010; Ryan, Bloomer, Moloney, Grant, & Delport, 2007). As these mechanisms are not mutually exclusive, it is likely that both neutral and selective factors underlie the evolutionary history of island zosteropids, as has been shown in island populations of *Z. borbonicus* (Milá et al., 2010).

One reason why island *Zosterops* lineages may show less evidence of evolutionary constraints is that they experience reduced levels of interspecific competition. Most islands are occupied by single endemic taxa, and those occupied by two (e.g. Réunion, Mauritius), are the result of independent invasions (van Balen, 2019). Single colonization events have often led to *Zosterops* radiations across archipelagos, for example, the 'Indian Ocean *maderaspatanus*' and 'Ancient Indian Ocean' clades diversified in the western Indian Ocean islands, but in general they involve a single species per island (Warren et al., 2006). Interspecific competition may therefore be reduced in island *Zosterops*, not only because they co-occur with no or few close relatives but also because the total number of sympatric passerine bird species on islands is also much lower than on the mainland. Thus, an ecological release may have allowed for greater evolutionary novelty in these island radiations, as implied by their exploration of a greater volume of morphospace compared to mainland birds (Figure 3).

The situation is reversed for mainland birds, which coexist with higher diversity of phylogenetically and ecologically similar species, implying much higher competition and constraints on morphological evolution. A pattern of limited phenotypic evolution on mainlands compared to a more explosive radiation on islands has previously

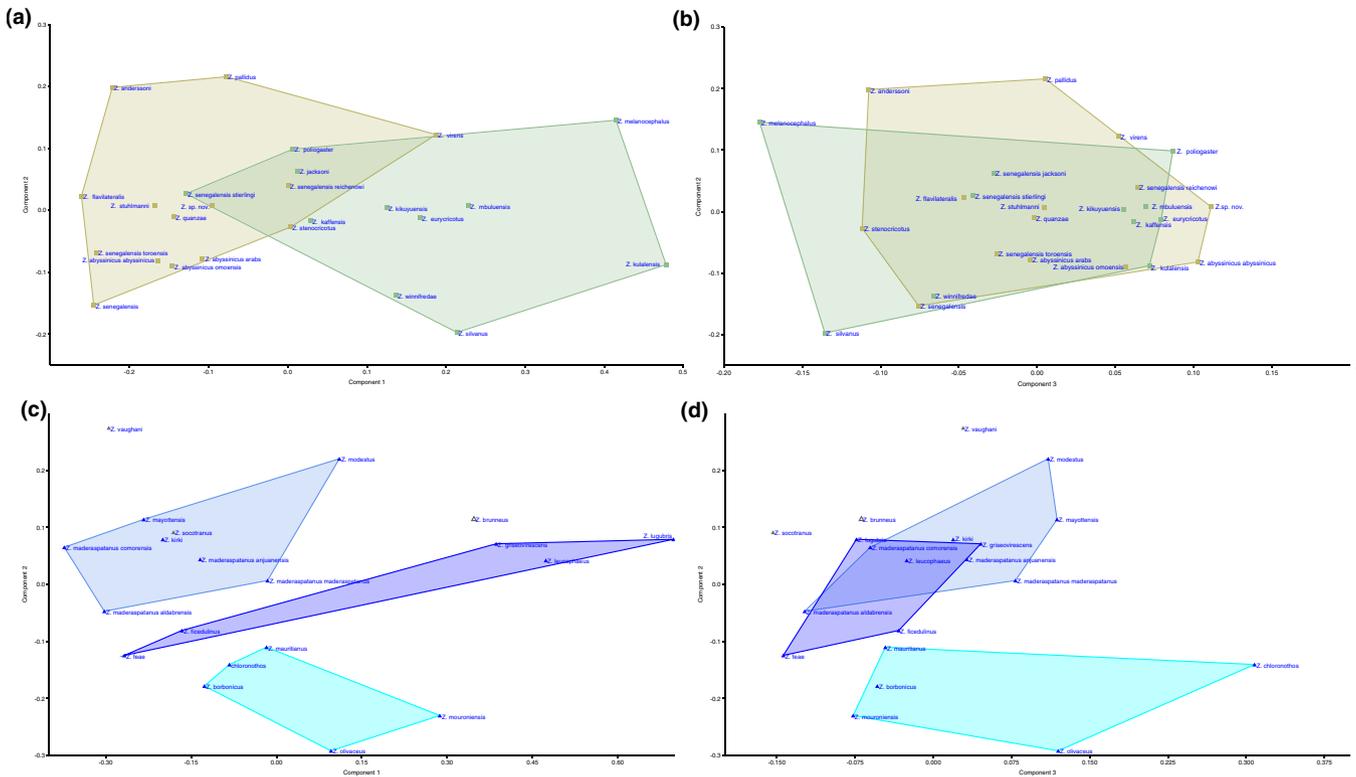


FIGURE 4 Morphospace occupation of Africa-Arabian mainland highland (green) and lowland (khaki) taxa for (a) PC1 versus PC2, and (b) PC2 versus PC3; and morphospace occupation of island radiations: western Indian Ocean 'maderspatanus' (light blue); Gulf of Guinea 'oceanic' (dark blue); Ancient Indian Ocean (aqua) for (c) PC1 versus PC2, and (d) PC2 versus PC3 applying convex hulls. Additional island taxa within the Afrotropical radiation are also included (grey filled triangles): *Z. vaughani* (Pemba Island); *Z. socotranus* (Is. Socotra) from the Western Indian Ocean and (grey outline only) *Z. brunneus* (Bioko Island) from the Gulf of Guinea. The taxonomy follows van Balen (2019) and Martins et al. (2020)

been reported in a number of passerine lineages, including Darwin's finches (Lovette et al., 2001), Hawaiian honeycreepers (Lerner, Meyer, James, Hofreiter, & Fleischer, 2011) and Madagascan vangas (Reddy, Driskell, Rabosky, Hackett, & Schulenberg, 2012). However, island forms often occupy different areas of morphospace from their mainland relatives, as shown in Hawaiian honeycreepers (Gavrilets & Losos, 2009) and Caribbean anoles (Pinto et al., 2008), indicating that these different landscapes can promote different evolutionary trajectories. In contrast, island *Zosterops* have expanded the volume of morphospace occupied by their mainland relatives (Figure 3) and appear to have evolved novel phenotypes around the generalized bauplan of the 'typical' *Zosterops*. This morphospace expansion is further amplified with the inclusion of Austral-Asian taxa, which are dominated by island forms, again highlighting the constrained morphological evolution of continental taxa.

4.2 | Evidence for density-dependent lineage diversification

The pattern of phenotypic evolution contrasts with the early burst and subsequent slow-down pattern of lineage diversification identified by our analyses, in line with a previous study (Moyle et al., 2009). These authors investigated a subset of *Zosterops* species

from across the radiation (ca. 30 species) and also showed exceptional rates of lineage accumulation relative to *Zosteropidae* as a whole, suggesting dispersal ability, generalist ecology, short generation time, sociality and capacity for phenotypic evolution as possible influencing factors. Although the early burst pattern of lineage accumulation has been suggested to indicate adaptive radiation (Gavrilets & Vose, 2005; Rabosky & Lovette, 2008), this pattern can also be recovered from simple geographical speciation in the absence of niche filling mechanisms (Pigot et al., 2010). Given the apparent lack of ecological diversification, and limited insular diversification in *Zosterops*, the general pattern observed in this group may be explained by geographical speciation involving non-adaptive radiation (Czekanski-Moir & Rundell, 2019; Rundell & Price, 2009). Notably, for some other passerine radiations that display high dispersal and colonization success, such as the Indo-Pacific Campephagidae (cuckooshrikes), Oriolidae (orioles) and Pachycephalidae (whistlers), a pattern of constant diversification has conversely been suggested (Fritz et al., 2012), although the Paradisaeidae (birds-of-paradise), with their more restricted distribution and low dispersal, showed density dependence. The former systems may have maintained the high speciation rates because they have not reached their ecological limit and/or are not as limited by ecological opportunity, although an alternative explanation is that increasing extinction rates have masked a density-dependant pattern (Fritz et al., 2012).

It has been suggested that island clades diversify more rapidly than mainland clades owing to reduced gene flow and the availability of new niches (e.g. Grant & Grant, 2006; Price, 2008). However, we found no evidence for this in Afrotropical zosteropids since rate shifts were not identified from our analyses (Figure 1a), perhaps due to relatively small sample size. In general, the comparable rates across island and mainland clades that we identify in zosteropids supports the findings of Pinto et al. (2008) who suggested that recent, rapid diversification of anoles proceeded in similar ways in insular and continental landscapes. This is contrary to a global avian study that showed bird species with more than half of their range on islands have higher diversification rates than mainland bird species (Jetz et al., 2012). Clearly, further investigation is needed as to why these different patterns have emerged in clades of highly dispersive organisms that have colonized multiple continents and archipelagos.

5 | CONCLUSION

Our results suggest that continental lineages in the Afrotropical *Zosterops* radiation follow different evolutionary trajectories to island lineages. Unlike some widespread continental avian clades that show an early burst of phenotypic evolution (Derryberry et al., 2011; Schweizer et al., 2014), mainland zosteropids show constrained evolution, with apparent convergence on particular morphological phenotypes. The lack of density dependence of morphological traits in mainland forms is perhaps not surprising given their remarkably conserved phenotypes. More surprising, however, is the contrasting pattern of morphological evolution in island zosteropids. These birds have explored more novel regions of morphospace, although their phenotypic divergence is again not characterized by an early burst and instead generally not distinguishable from a random-walk model. This pattern may be the result of island clades evolving into a larger morphospace around the generalized bauplan of the 'typical' *Zosterops*, as opposed to evolving truly novel phenotypic trajectories as observed in some island lineages of birds (Jönsson et al., 2012; Lerner et al., 2011; Lovette et al., 2001; Reddy et al., 2012) and lizards (Pinto et al., 2008). We suggest the expanded scope of morphological evolution in insular *Zosterops* arises from reduced interspecific competition with passerine species in general, as well as with congeners, leading to a relaxation of the evolutionary constraints experienced by continental taxa. Unlike previous studies making broadly similar claims (e.g. Clegg & Owens, 2002), however, we find no evidence for a consistent tendency towards enlarged body sizes predicted by the 'island rule'. Overall, our results suggest that divergent evolutionary pathways on continents and islands are not limited to famed adaptive radiations or 'island rule' effects, but can help to explain more subtle patterns of diversification in the world's 'great speciators'.

ACKNOWLEDGEMENTS

We are grateful to Robert Prÿs-Jones, Mark Adams and Hein Van Grouw for facilitating collection visits to the Natural History Museum at Tring. We also thank Adam Devenish and Catherine Sheard for

help with data curation and collection, and Ally Phillimore, Sushma Reddy and two anonymous reviewers for providing helpful comments on an earlier version of this work.

DATA AVAILABILITY STATEMENT

Biometric data are available from the DRYAD Digital Repository <https://doi.org/10.5061/dryad.x3ffbg7g3>.

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BIOSKETCH

Julia J. Day is an Associate Professor at UCL. She is interested in phylogenetics, diversification and biogeography, particularly of Afrotropical biotas. She and the other authors on this paper are interested in questions pertaining to the generation and maintenance of biodiversity.

Authorship contributions: JJD lead the study design, with contributions from all authors. FCM and JT collected trait data; JJD and FCM analysed these data; DJM provided new DDT code. JJD wrote the article and all authors provided comments.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: DayJJ, Martins FC, Tobias JA, Murrell DJ. Contrasting trajectories of morphological diversification on continents and islands in the Afrotropical white-eye radiation. *J Biogeogr.* 2020;00:1–13. <https://doi.org/10.1111/jbi.13917>