



Niche evolution reveals disparate signatures of speciation in the 'great speciator' (white-eyes, Aves: *Zosterops*)

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Abstract

Aim: Recent breakthroughs in environmental niche models (ENMs) have substantially improved our insights in niche evolution. Assuming that closely related taxa have similar niches (i.e. niche conservatism), the combination of ENMs with phylogenetic information allows the reconstruction of ancestral niches. This reconstruction helps to identify the underlying speciation processes leading to diversification (i.e. ecological speciation under niche divergence and mutation-order speciation under niche conservatism). Here, we studied the niche evolution in white-eyes (the so-called 'great speciator') to understand their extraordinarily fast diversification rate, wide distribution and rather conserved phenotypes. In a broader perspective, unravelling niche evolution in white-eyes can shed light on how different niche properties such as climate, habitat or trophic level may contribute to diversification.

Location: Asian-Pacific and Afrotropics.

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

Methods: We selected 10 wide-ranging taxa that are equally distributed across the genus' range and phylogeny. We studied niche evolution for a series of thermal and precipitation-related niche axes separately. We used a time-calibrated phylogeny encompassing the study taxa and estimated ancestral environmental niches in geographic and environmental niche spaces.

Results: We found that niche evolution in *Zosterops* is primarily driven by ecological speciation. Thermal niches, in particular, are characterized by a higher level of conservatism, as compared to precipitation-related niche axes. The fact that the youngest species diverged strongest stands in stark contrast to expectations stemming from niche conservatism.

Main conclusions: Contrasting evolutionary patterns in different niche axes suggest different underlying evolutionary pressures. Hence, future studies on niche evolution should take possible disparities between niche axes into account.

KEYWORDS

ecological niche modelling, ecological speciation, Eltonian niche, great speciator, Grinnellian niche, mutation-order speciation, niche evolution, species distribution modelling

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1 | INTRODUCTION

Over the past decade, conceptual and methodological breakthroughs in environmental niche models (ENMs) have substantially improved our insights in niche evolution (Engler et al., 2017; Pearman et al., 2008; Yesson & Culham, 2006). ENMs link information of observed species' occurrences with spatial environmental conditions into a correlative model to predict probabilities of occurrences (Guisan et al., 2017). Niche theory as formulated by Hutchinson (1957) forms the conceptual backbone of ENMs (Peterson et al., 2011; Soberón, 2007). Based on the underlying assumption that more closely related species will show higher niche similarities (i.e. niche conservatism *sensu* Wiens & Graham, 2005; Losos, 2008), ENMs can be used to reconstruct ancestral niches when integrated with phylogenetic data (Alvarado-Serrano & Knowles, 2014; Chan et al., 2011; Engler et al., 2017; Yesson & Culham, 2006). Combining ENMs with phylogenetic tools thus offers avenues to study the relative roles of different speciation processes (e.g. Mason & Taylor, 2015; Wiens & Graham, 2005), especially when different components of the environmental niche (i.e. climate, habitat and trophic niches) can be adequately quantified (Pearman et al., 2014).

Speciation theory generally assumes two main processes where evolutionary change can accumulate over space and time through natural selection: mutation-order speciation and ecological speciation. Mutation-order speciation assumes that populations independently fix different mutations under similar selection pressures (Nosil & Flaxman, 2011; Schluter & Conte, 2009). Here, evolutionary divergence between populations is primarily driven through isolation. Alternatively, ecological speciation assumes populations to fix beneficial mutations under ecologically divergent selection pressures (Rundle & Nosil, 2005; Schluter, 2009). Here, evolutionary divergence between populations primarily increases through adaptation. While both speciation processes are theoretically plausible, their relative frequency at which they are found in nature differs for two reasons (Schluter, 2009): first, because gene flow may prevent mutation-order speciation but not (necessarily) ecological speciation; and second, because ecological speciation is easier to detect as a consequence of environmental variation (Schluter, 2009), which imposes selective pressures on environmental niches that can lead to niche divergence. Yet, while the predominant speciation process remains unknown for most species (Schluter, 2009), linking phylogenetic with environmental information can shed light into the evolution of environmental niches, and hence, the underlying speciation processes (e.g. Ahmadzadeh et al., 2013; Rato et al., 2015). To this end, the key question is whether environmental niches remained more similar (i.e. niche conservatism) or not (i.e. niche divergence) in recently evolved taxa (Pyron et al., 2015).

Young and fast radiations pose ideal study systems in this context. Given their young age, their evolutionary trajectories have likely been less prone to potentially confounding extrinsic drivers compared with species with longer evolutionary histories. In the latter case, for instance, environmental changes that happened after the initial speciation event could mask mutation-order speciation as

initial cause for speciation as new mutations might be selected along with the changing environmental conditions (*sensu* Jeskova & Wiens, 2018). Signals of niche conservatism could, hence, diminish over time through subsequent adaptation to changing environments. For this reason, niche conservatism is predicted – and often found – to appear at higher frequencies in young sister lineages (Pearman et al., 2008; Peterson, 2011; Wiens et al., 2010; Wiens & Graham, 2005); yet, numerous counter-examples exist (Ahmadzadeh et al., 2013; Dormann et al., 2010; Engler et al., 2017). In particular, there is evidence for a disparity of how thermal and precipitation-related niche axes evolve (Lv et al., 2016; Miller et al., 2013). Such disparity can result when climatic predictors act at different components of a species' niche (Barnagaud et al., 2012; Engler et al., 2014; Pearman et al., 2014; Remeš & Harmáčková, 2018) and whether they represent proximal or distal predictors of species–environment relationships (Austin, 2002; Hawkins et al., 2003). In birds, thermal niche axes can be expected to be directly linked to physiological constraints, especially at the upper temperature limit (Engler et al., 2017). Thermal niche axes are, hence, proximal predictors of climatic niches. By contrast, precipitation is more likely to delimitate a bird's resource availability and to affect the type of vegetation (and by this the type of habitat) a species occupies (Both et al., 2006; Robinson et al., 2007; Tingley et al., 2009, 2012). Hence, precipitation-related niche axes are mostly distal predictors for depicting different components of environmental niches (such as trophic and habitat niches, *sensu* Pearman et al., 2014), as more processes get involved to describe a bird's species–environment relationship. Studying niche evolution in large yet young species radiations separately for thermal and precipitation-related niche axes could, hence, improve our understanding of the different evolutionary processes and at which niche component they act.

Here, we assess the relative contributions of mutation-order and ecological speciation in the explosive radiation of white-eyes (Aves: *Zosterops*) by studying niche evolution separately for thermal and precipitation-related niche axes. White-eyes constitute a highly appropriate study system given their wide geographic range, and their high diversification rate (one of the highest recorded in vertebrates *sensu* Moyle et al., 2009). The explosive radiation in these 'great speciators' (Diamond et al., 1976) originated around 2 million years ago in Southeast Asia from which a rapid expansion into the Palaeotropics and Oceania followed shortly after (Moyle et al., 2009; Warren et al., 2006). Previous studies (Cox et al., 2014; Moyle et al., 2009; Warren et al., 2006) proposed a complex radiation in white-eyes, covering diverse and dynamic environmental settings, in which both mutation-order and ecological speciation could locally dominate as evolutionary processes. Despite their – for birds – unprecedented diversification rate (Moyle et al., 2009), leading to almost 100 species and over 250 subspecies currently recognized, white-eyes are characterized by a rather conserved morphology (Moyle et al., 2009), which stands in stark contrast to other well-known avian radiations such as the Darwin finches (*Geospiza*) or Hawaiian honeycreepers (Drepanidini). Especially the conserved bill shape in white-eyes points towards stabilizing selection of resource use and

can, hence, be used to address the trophic niche – as one main niche component – likewise as very conserved. The fact that, of the three main niche components (*sensu* Pearman et al., 2014), one (i.e. the trophic niche) can be considered conserved while the two others (i.e. climatic and habitat niches) can be adequately assessed through bioclimatic information is an ideal prerequisite for the application of ENMs to study niche evolution in a holistic way (Engler et al., 2017). Furthermore, potential biases originating from incomplete niche characterization (Saupe et al., 2018) can be considered as minimal for white-eyes due to high dispersal capacities as well as an adaptation to predominantly warm environments – two conditions that minimize the effect of niche truncation (Saupe et al., 2018).

We quantified species–environment relationships for 10 wide-ranging white-eye lineages using bioclimatic information to reconstruct ancestral niches during diversification over the past 2 million years. In particular, we explored whether the radiation is associated with niche divergence or niche conservatism along thermal and precipitation-related niche axes at a macro-scale. Following up on prior research on linking climatic niche evolution to speciation processes (e.g. Ahmadzadeh et al., 2013; Jezkova & Wiens, 2018; Rato et al., 2015), our central aim was to identify whether (and where) mutation-order or ecological speciation was the predominant diversification process in this radiation at a macro-scale. To this end, we expect four possible speciation scenarios along respective climatic niche axes: (1) dominance of ecological speciation, where species show a high level of niche divergence; (2) dominance of mutation-order speciation, where species show a high level of niche conservatism; (3) early ecological speciation followed by late mutation-order speciation, where an initial high niche divergence is followed by niche conservatism or (4) early mutation-order speciation followed by late ecological speciation, where initial niche conservatism is followed by niche divergence (Figure 1).

2 | MATERIALS AND METHODS

2.1 | Species selection and phylogeny

For estimating ancestral niches, we focused on 10 white-eye taxa that are found across the phylogeny, cover large parts of the genus' distribution and environmental breadth, and having large ranges compared with most other white-eye congeners which occur either on remote oceanic islands or on isolated mountain massifs (Figure 2; Supplement S1). Note that including taxa that reside in intermediate environmental conditions would not change the position of the retained species in the environmental space and, thus, would not contribute to detect overall niche disparity of the entire clade. Hence, we selected *Zosterops atricapilla* (Salvadori, 1879), *Z. erythropleurus* (Swinhoe, 1863), *Z. japonicus* (Temminck & Schlegel, 1845), *Z. palpebrosus* (Temminck, 1824), *Z. lateralis* (Latham, 1801) and *Z. luteus* (Gould, 1843) distributed across the Asian-Pacific region and *Zosterops flavilateralis* (Reichenow, 1892), *Z. maderaspatanus* (Linnaeus, 1766), *Z. senegalensis* (Bonaparte, 1850) and

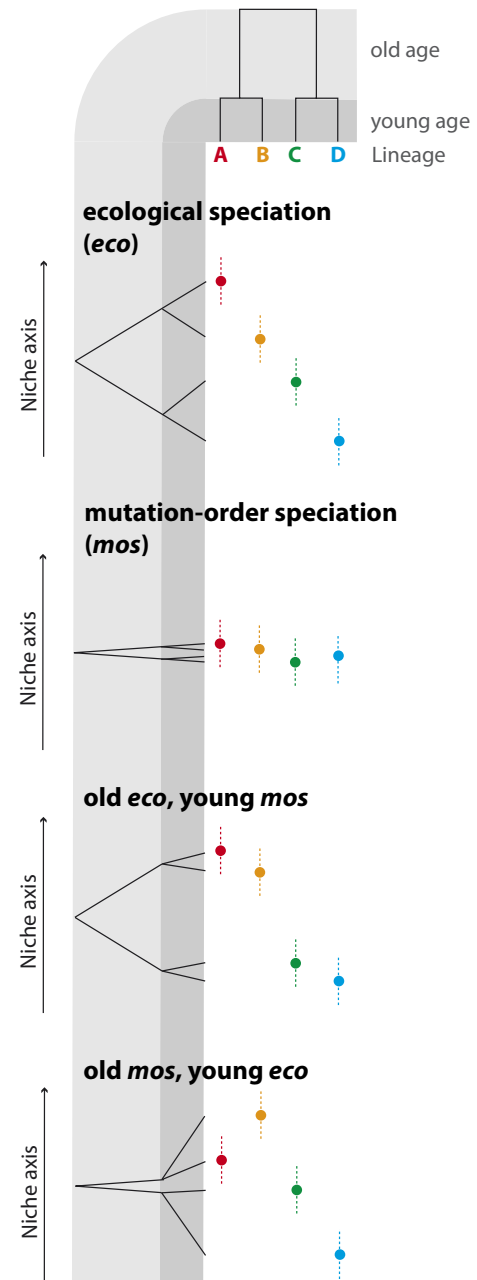


FIGURE 1 Four broad theoretical expectations of phylogenetic niche evolution. Considering a dated four-lineage tree (lineages A–D) with an ancestral origin (old age) and a recent diversification (young age), evolutionary processes may form different topologies related to a niche axis: (1) ecological speciation (*eco*) leads to prominent niche divergence in all lineages; (2) under mutation-order speciation (*mos*), niche conservatism is expected; (3) diversification might start by ancient *eco* followed by recent *mos* through subsequent colonization of isolated habitats (e.g. oceanic islands); (4) diversification might begin with *mos* by expanding into isolated areas followed by *eco* by colonizing contrasting niches such as elevational gradients or sky islands

Z. virens (Sundevall, 1850) distributed in the Afrotropical region. It is important to mention that most of the selected taxa consist of subspecies which are hard to distinguish geographically due to

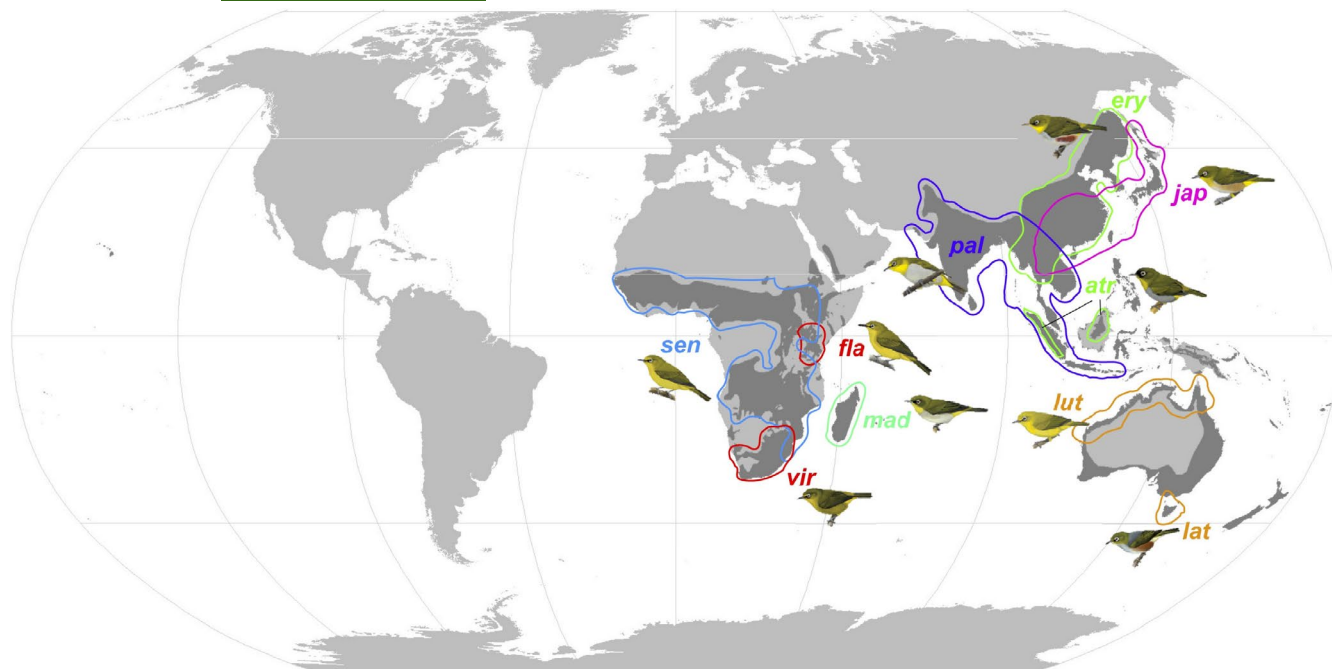


FIGURE 2 Global white-eye distribution (Genus: *Zosterops*, dark grey, modified from BirdLife.org) and the approximate ranges of the selected taxa. Taxon abbreviations correspond to the first three letters of the respective species epithet. Drawings courtesy of Del Hoyo et al. (1992)

overlapping regions or unclear taxonomic status (Cox et al., 2014; Lim et al., 2019). However, since the main goal of this study was to study the niche evolution across the entire white-eye radiation, we deemed the selected species fit for our purpose as they are distributed across the genus' phylogeny (Cai et al., 2019; Supplement S1). Nevertheless, where possible, we restricted the set of available occurrence records to areas known to be inhabited by the taxon where phylogenetic information was available (see below).

We extracted phylogenetic relationships for all selected taxa from a dated ultrametric tree consisting of 46 white-eye lineages based on *cyt b* and *ND3* sequences (Supplement S1). In particular, we loaded the dated tree in the newick format into R (v. 3.6.1) using the 'ape' package (v.5.0, Paradis & Schliep, 2019) and excluded all lineages not considered for this study using *ape's drop.tip* function. This way, we kept the dated phylogenetic distances for downstream analyses from a more coherent phylogeny which led to more reliable date estimates and reconstructed evolutionary rates (Ryberg & Matheny, 2011).

2.2 | Species distribution modelling

We ran a query on the Global Biodiversity Information Facility (GBIF) on Oct. 21st, 2016, to gather all available occurrence records ($n = 617,384$) at the genus level (see Data Availability Statement). From this raw dataset, we filtered the selected taxa (see above), resulting in an initial set of occurrence records ranging from 387 to over 325,000 single records per taxon (see Table S1 for initial and final occurrence numbers). We accounted for sampling biases that

are prevalent in this type of data (Fourcade et al., 2014). Particularly, we randomly selected one record per species at a 2.5 arc minute sized grid as this method has been previously shown to be robust under a wide range of circumstances (Fourcade et al., 2014). For the two migratory species of the genus (i.e. *Z. erythropleurus* and *Z. japonicus*), which were incorporated in the dataset, we decided to consider both breeding and winter ranges in the analyses. With this we keep comparability among species while implicitly integrating a behavioural aspect (i.e. migration) that is more related to ecological speciation. Accordingly, we selected occurrences from both seasonal ranges while excluding areas used only during migration.

For the bioclimatic information, we used WorldClim v2 (Fick & Hijmans, 2017) at a resolution of 2.5 min. To account for potential overfitting, we selected a subset of 5 predictors of the entire set of 19 bioclimatic variables in the WorldClim dataset, namely: *annual mean temperature* (bio1), *temperature seasonality* (bio4), *mean temperature of the warmest month* (bio10), *annual precipitation* (bio12) and *precipitation seasonality* (bio15). We focused on these bioclimatic predictors only as we deemed them most relevant for the group as the predictors depict amount and variation in annual temperature and precipitation (bio1, 4, 12 & 15) and point towards possible upper limits of the genus' thermal niches (bio10). We extracted the bioclimatic conditions from a background area covered by the whole genus. For this, we used the entire species-level range shapes (available through BirdLife) and merged them into a genus-specific range shape (Figure 2) in R.

To estimate the potential distribution of each lineage, we used the Bioclim algorithm (Busby, 1991) as implemented in the 'dismo' R package (v. 1.1–4; Hijmans et al., 2013). Our rationale for



choosing this relative simple ENM algorithm was that we wanted to assess the potential distribution of each species in the entire environmental space, regardless of the explanatory power of the variables or their interactions with each other (Hijmans & Graham, 2006). This notion fits closest to Hutchinson's original idea of a species' environmental niche which constitutes all environmental conditions under which a species may exist (Hutchinson, 1957). For assessing model fit, we used the AUC (area under the receiver operation characteristic Curve; Swets, 1988) as well as COR (point biserial correlation; Hijmans et al., 2013) metrics as implemented in the 'dismo' package.

2.3 | Estimating niche overlap

We compared multivariate niche overlap in both geographic and environmental space (referred to as g-space and e-space, respectively, Brown & Carnaval, 2019). Under e-space, we mention methods that are bonded on using the environmental information directly from the occurrence locations, while g-space-based methods extract environmental information from a projected realized niche as inferred by an ENM. For the g-space comparison, we applied the *maximum sum of sensitivity and specificity* (maxSS) threshold for each Bioclim ENM and set all values below the lineage-specific maxSS to zero. This was necessary because overlap metrics overestimate niche overlap when areas with very low probability values – and where species are most likely absent – are included in the calculation (Rödder & Engler, 2011). Using the nicheOverlap function in 'dismo', we calculated Schoener's *D* (Hijmans et al., 2013; Rödder & Engler, 2011) for each lineage pair. In addition, we calculated the average niche overlap for each metric within each major clade as well as between both clades. Schoener's *D* ranges from 0 (no overlap / separate potential distributions) to 1 (complete overlap / identical potential distributions) and is comparable to a percentage overlap (Rödder & Engler, 2011).

For e-space niche overlaps, we used the 'PCA-env' approach (Broennimann et al., 2012) as implemented in the 'ecospat' R package (Di Cola et al., 2017). In brief, this approach calculates niche overlap (using the Schoener's *D* metric) from the first two principal components drawn from a principal component analysis (PCA) spanning the environmental information from the respective species occurrence information and their joint background (distribution of the genus, see above). The PCA scores of the respective species were projected on a grid of 100 × 100 cells bounded by the extreme values of each principal component. Afterwards, a kernel density function estimated a smoothed occurrence density for each species across this grid which serves as basis for estimating the niche overlap. In addition, we used randomization tests to assess niche similarity and niche equivalency for each species pair (Di Cola et al., 2017). In particular, these tests assess statistical significance of niche differences against a set of null models drawn from the background area. Here, we tested the prediction

of niche divergence, i.e. whether the true niche overlap was less equivalent/similar than under random conditions based on 1000 replications.

2.4 | Ancestral niche reconstruction

We tested for phylogenetic signal across niche axes using the phylosignal R package (Keck et al., 2016) by using five different metrics (i.e. Abouheif's C_{mean} , Moran's *I*, Blombergs *K* and K^* , as well as Pagel's λ). We assessed their significance using a randomization test with 999 repetitions. We further simulated the behaviour of either phylogenetic signal metric given the underlying phylogenetic tree under varying amounts of Brownian motion with 1000 simulated solutions and 99 repetitions for p-value estimation. Finally, we calculated phylogenetic correlograms for each niche axis and tested the Local Indicator of Phylogenetic Association (LIPA, Anselin, 1995, see Supplement S2) for each tip of the tree using the 'two-sided' alternative hypothesis.

To assess niche evolution in white-eyes, we combined the phylogenetic information with the potential distributions from a) the Bioclim ENMs in g-space and b) the environmental conditions at the presence locations in e-space. For the g-space-based analyses, we computed predicted niche occupancy (PNO) profiles (Evans et al., 2009) in the 'phyloclim' R package (v. 0.9.5.; Heibl & Calenge, 2013). In particular, a PNO profile is generated by combining the species-specific occurrence probabilities from the ENM with the corresponding values of the bioclimatic variable into a binned vector (1000 intervals) of probabilities for each variable.

Using the PNO profiles, we calculated the ancestral climatic tolerances for each variable assuming Brownian-motion evolution for each node in the phylogenetic tree (Schluter et al., 1997) fitted by generalized least squares (Martins & Hansen, 1997). To assess uncertainty, we resampled the PNO profiles 1000 times.

For ancestral niche reconstruction in e-space, we chose an early-burst (EB) trait evolution model in the 'anc.ML' function in the phytools R package (Revell, 2012). The EB model fits an evolutionary rate that increases or decreases exponentially through time (Harmon et al., 2010) and we expect this to be realistic scenario in a 'great speciator' system. We further backed our choice based on the evolutionary history of the study system by comparing AICc values of the EB model with two other trait evolution models, namely Brownian Motion (BM) and single optimum Ornstein Uhlenbeck (OU, for a complete overview on model selection, see Supplement S2). For each species, we calculated the median of values of each environmental variable extracted from the occurrence locations. To assess uncertainty we randomly selected 30% of occurrence information of each species for a total of 100 repetitions that entered the analyses. We plotted results on a phenogram (Evans et al., 2009) representing the best-fit evolutionary model for each environmental variable and compared these against those generated in phyloclim for g-space-based analyses.

3 | RESULTS

3.1 | Environmental niche modelling

The bioclim ENMs showed good fits based on AUC values ranging from 0.653 in *Z. palpebrosus* to 0.996 in *Z. lateralis* (Table 1). Lowest AUC values were found in lineages with the largest ranges, namely *Z. palpebrosus* (0.653), *Z. senegalensis* (0.787) and *Z. erythropleurus* (0.793). All other lineages showed AUC values >0.9. COR values showed a similar pattern with highest values *Z. lateralis* (0.746) and *Z. virens* (0.647) and lowest values again in *Z. palpebrosus* (0.134), *Z. senegalensis* (0.235), and *Z. erythropleurus* (0.122, Table 1).

In general, most white-eyes preferred warm areas with annual mean temperatures of ca. 20°C. Remarkable extremes were represented by the young sister taxa *Z. luteus* (>25°C) and *Z. l. lateralis* (<15°C). This temperature regime became even more constrained when considering the average temperature during the warmest quarter (i.e. summer season temperatures). Along this niche axis, also the by-definition stronger deviating migratory species *Z. japonicus* and *Z. erythropleurus* showed little deviation from their non-migratory relatives. Considering humidity levels (as indicated by the annual precipitation), white-eyes showed a much higher amount of variability stretching from semi-arid (i.e. ca. 500 mm/a) to very humid (i.e. ~2500 mm/a) conditions. This characterizes *Zosterops* as a genus mostly confined to habitats in the tropical zone stretching from subtropical deserts or savannas to tropical rainforests but also more Mediterranean habitats and even temperate rainforests.

3.2 | Niche overlap

Niche overlap varied strongly among the lineages ranging from no (i.e. $D = 0-0.2$) to high (i.e. $D = 0.6-0.8$) overlap following the classification provided by Rödder and Engler (2011). In addition, there were differences whether niche overlap was measured in g-space

(D_{geo}) or e-space (D_{env}). Average D_{geo} values for each lineage could be separated into two groups: Lineages with D_{geo} overlaps <0.1 ($n = 5$ lineages) and with D_{geo} overlaps ranging between 0.2 and 0.3 ($n = 5$ lineages). This clear distinction vanished in average D_{env} values. The average niche overlap was higher among Afrotropic lineages ($D_{geo} = 0.283$, $D_{env} = 0.335$) than among Asian-Pacific lineages ($D_{geo} = 0.103$, $D_{env} = 0.101$). Pairwise differences between g- and e-space-based niche overlaps can be assessed in Table 1.

Randomization tests for niche similarity based on a PCA across all environmental predictors revealed one instance of niche divergence between *Z. erythropleurus* with *Z. atricapilla* ($p = 0.046$) and several cases of niche conservatism which were mostly confined to Afrotropical taxa but absent among Asian-Pacific taxa (Table S2). All other comparisons were not different from random conditions (Table S2). In contrast, randomization tests for niche equivalency revealed highly significant evidence for niche divergence (all $p < 0.003$) in all comparisons.

3.3 | Ancestral niches

We identified the Early Burst (EB) model as best-fit evolutionary model for *annual mean temperature* (bio1; AICc = 54.673), *mean temperature of the warmest quarter* (bio10; AICc = 53.109) and *precipitation seasonality* (bio15; AICc = 102.265), for whose the Δ AICc to the next best model was above 49 (Supplement S2). By contrast, the Brownian Motion (BM) model was the best fit for *temperature seasonality* (bio4; AICc = 213.59) and *annual precipitation* (bio12; AICc = 255.819), with Δ AICc values above 11 for each environmental variable (see Supplement S2 for further details).

We did not detect a statistically significant phylogenetic signal irrespective of the metric and niche axis in focus. Not only did our simulations reveal that the underlying tree topology hardly generates significant phylogenetic signals, even under strong influence of Brownian Motion, but we also detected negative correlations in

TABLE 1 Niche overlap among white-eye (*Zosterops*) species. D_{geo} below and D_{env} above diagonal. Warmer cell colours correspond to higher overlap values. AUC and COR values show the fit of the respective ENM, and maxSS defines the threshold below which absence is assumed (equals zero to not inflate overlap metrics). Tree topologies highlight the phylogenetic relationships for better orientation along columns and rows respectively

	AUC	COR	maxSS	<i>jap</i>	<i>ery</i>	<i>atr</i>	<i>lut</i>	<i>lat</i>	<i>pal</i>	<i>sen</i>	<i>mad</i>	<i>vir</i>	<i>fla</i>
<i>Zosterops japonicus</i>	0.905	0.438	0.0235		0.181	0.298	0.029	0.061	0.321	0.544	0.290	0.285	0.205
<i>Zosterops erythropleurus</i>	0.793	0.122	0.0466	0.393		0.004	0.026	0.004	0.172	0.126	0.061	0.081	0.061
<i>Zosterops atricapilla</i>	0.992	0.409	0.0255	0.000	0.000		0.000	0.097	0.210	0.292	0.076	0.000	0.000
<i>Zosterops luteus</i>	0.908	0.344	0.0065	0.025	0.166	0.000		0.000	0.108	0.099	0.070	0.014	0.080
<i>Zosterops l. lateralis</i>	0.996	0.746	0.0009	0.002	0.000	0.000		0.000	0.008	0.096	0.000	0.035	0.035
<i>Zosterops palpebrosus</i>	0.653	0.134	0.0142	0.230	0.492	0.006	0.228	0.000		0.375	0.193	0.060	0.123
<i>Zosterops senegalensis</i>	0.787	0.235	0.0062	0.098	0.428	0.006	0.114	0.001	0.549		0.361	0.182	0.243
<i>Zosterops maderaspatanus</i>	0.949	0.375	0.0075	0.081	0.356	0.000	0.050	0.000	0.590	0.697		0.310	0.470
<i>Zosterops virens</i>	0.966	0.647	0.0048	0.035	0.081	0.000	0.000	0.005	0.033	0.027	0.017		0.444
<i>Zosterops flavilateralis</i>	0.964	0.468	0.0098	0.002	0.278	0.000	0.128	0.000	0.484	0.651	0.308	0.000	

Dgeo below, *Denv* above diagonal



three of the five niche axes when phylogenetic distances were small (see Supplement S2 for a closer inspection also in relation to the underlying evolutionary model). The LIPA revealed a significant negative association between phylogenetic distance and environmental similarity in *Zosterops lateralis* and *Z. luteus* for the *annual mean temperature*, *mean temperature of the warmest quarter* and *precipitation seasonality*, as well as for *Z. atricapilla* for *temperature seasonality* (see Supplement S2 for further details).

We detected no niche divergence between the two main clades of the white-eye radiation (Figure 3). However, we detected signals of niche divergence among younger taxon pairs. We found that thermal niche axes evolved differently than precipitation-related niche axes. In particular, considering *annual mean temperature* and even more so *mean temperature of the warmest quarter*, lineages show a high amount of initial niche conservatism with similar internal nodes (Figures 3 and 4). A remarkable exception is the extreme divergent evolution in the young sister taxa *Z. luteus/lateralis* exceeding the thermal limits beyond that of all other lineages at the upper (*luteus*) and lower (*lateralis*) thermal bounds. Variation along the *temperature seasonality* niche axis was very limited in most lineages except the two migratory taxa *Z. erythropleurus* and *Z. japonicus* which were characterized by very wide density variations. This variation was also very pronounced in the *annual mean temperature* for those two species, while for the *mean temperature of the warmest quarter* the variation equalled that of most other lineages.

In contrast to thermal niche axes, precipitation-related niche axes are characterized by a wider initial split (Figures 3 and 4). This became most pronounced in *annual precipitation*, where lineages diversified early on into precipitation regimes ranging between approximately 800 and 2000 mm of rain per year. Exceptions were *Z. atricapilla* and *Z. virens* which diverged from their ancestry into very humid (i.e. >2000 mm/a) and dry (i.e. <800 mm/a) conditions, respectively. As for the thermal niche axes, the lineage pair *Z. luteus/lateralis* shows the highest divergence in *precipitation seasonality*, again surpassing all other lineages along with the upper and lower bounds of this predictor. As with the annual precipitation, *Z. atricapilla* also diverges from most other lineages (except *Z. lateralis*) in *precipitation seasonality*.

4 | DISCUSSION

Mutation-order and ecological speciation are recognized as the predominant processes underlying diversification patterns (e.g. Schluter, 2009). Yet, their relative contributions are often unknown even though the dominant speciation mode should be reflected in whether species' climate niche axes are conservative (pointing to mutation-order speciation) or divergent (pointing to ecological speciation; e.g. Ahmadzadeh et al., 2013; Pyron et al., 2015; Rato et al., 2015). High divergences in both e- and g-space in at least one niche axes indicate that climatic niche evolution in the great speciator genus *Zosterops* is primarily driven by ecological speciation at a macro-scale. Yet, we found both niche conservatism and niche

divergence to act at different niche components (Figures 3 and 4). Thermal niche evolution in *Zosterops* conforms our assumption of early niche conservatism and young niche divergence (scenario 4 in Figure 1), while the precipitation-related niche axes show a reversed pattern of either early niche divergence and young niche conservatism (scenario 3), or continuous niche divergence (scenario 1). The disparity between predominantly conserved thermal and divergent precipitation-related niche axes reveals a complex interplay of selective pressures acting at different spatiotemporal scales across the white-eye radiation. In the following, we discuss this pattern in the general context of avian niche evolution and take special emphasis on the importance of focusing on different components of the environmental niche.

Temperature is deemed a key factor describing a species environmental niche, given its causal links to physiological constraints in most animals (Porter & Kearney, 2009). In particular, the upper critical temperature in endotherms (such as birds) only has a limited potential for adaptation, which limits evolutionary responses to climate change (Engler et al., 2017; Huey et al., 2012). We confirm this general constraint, as thermal niche evolution at the upper temperature limit narrowly scatters at around 23 to 24 degrees Celsius on average (Figure 3). Yet, the youngest species pair in our dataset, *Z. luteus/lateralis*, breaks out of this clear pattern of niche conservatism by forming the upper and lower ends on several niche axes (Figures 3 and 4), which conflicts with our expectations of niche conservatism but supports the Early Burst evolution model (Supplement S2). Considering the annual mean temperature alone, there is also a second species pair, *Z. flavilateralis/virens*, which strongly diverges from each other (Figure 3). Yet, this pattern diminishes in this species pair when taking the temperature of the warmest quarter into account (Figure 3). Considering temperature seasonality, there is a much higher lineage-specific variability stretching from very low to moderate seasonalities that follows the expectations under Brownian motion evolution (Supplement S2). The two migratory lineages in the dataset (and the only ones for the entire genus, *Z. erythropleurus* and *japonicus*) show the highest seasonalities and variations in both, g- and e-space, comparisons. Our analysis incorporated both seasonal ranges using the original predictors which are based on year-round monthly averages. This was necessary to achieve comparability of the results among lineages, while this approach certainly adds spurious outcomes for migratory species. However, when taking into account, *temperature of the warmest quarter*, the results become more reliable as this information fits closer to the actual breeding season, especially in temperate environments. Focusing on this predictor instead of the *annual mean temperature* or *temperature seasonality*, averages as well as the variation in both g- and e-space analyses were similar for the two migratory species compared to other white-eye lineages (Figure 3). While more refined analyses need to be done to understand seasonal range dynamics in these migratory species, the results point to a pattern of niche tracking (i.e. where migratory species follow similar niche conditions in their respective seasonal ranges) when compared to its nearest non-migrating relative *Z. atricapilla*.

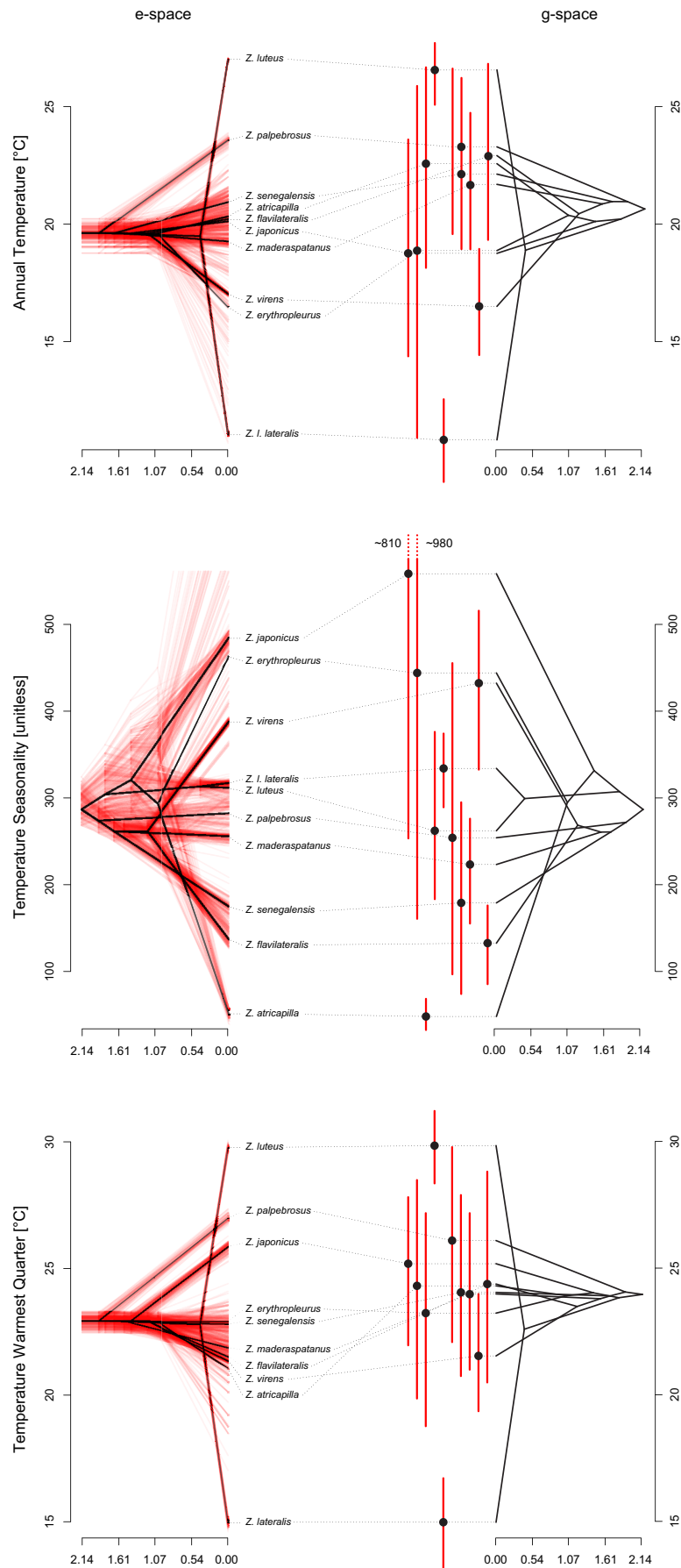
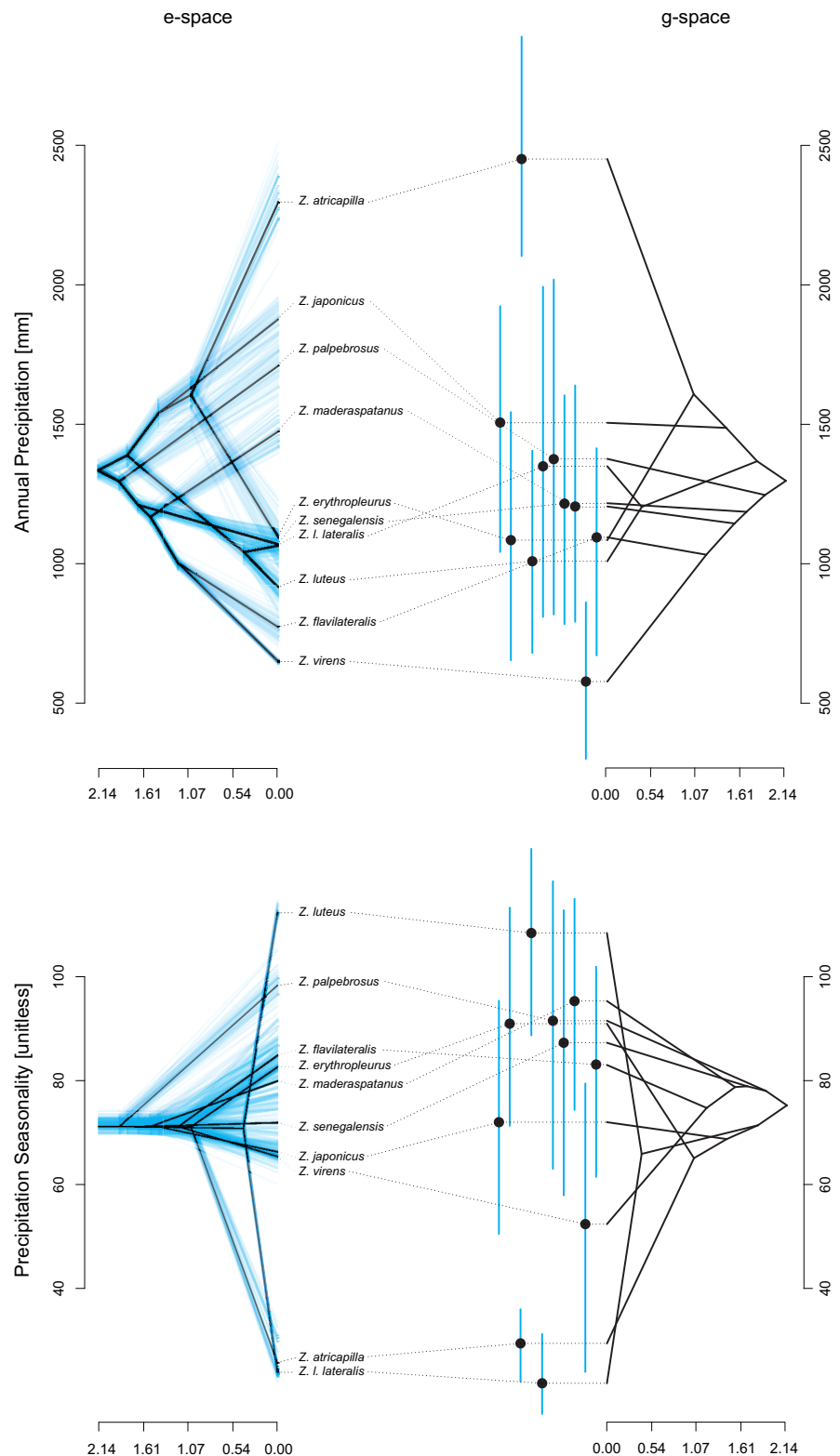


FIGURE 3 Reconstruction of ancestral niches in 10 major white-eye lineages across the radiation for thermal niches in environmental space (e-space, left panel) and geographic space (g-space, right panel). Ancestral niche reconstruction in e-space was performed under the best-fit trait evolution model (see Supplement S2 and main text for details) with uncertainty assessed using 100 random subsets (red-shaded phenograms) incorporating 30% of the occurrence records. The black phenogram represents the full data model with median node locations. For ancestral niche reconstruction in g-space, internal nodes reflect average climate tolerances inferred from the tip lineages deriving from that node using a Brownian motion trait model as implemented in the R package *phyloclim*. Eighty per cent central densities are shown as vertical red lines



FIGURE 4 Reconstruction of ancestral niches in 10 major white-eye lineages across the radiation for precipitation-related niches in environmental space (e-space, left panel) and geographic space (g-space, right panel). Ancestral niche reconstruction in e-space was performed under the best-fit trait evolution model (see Supplement S2 and main text for details) with uncertainty assessed using 100 random subsets (blue-shaded phenograms) incorporating 30% of the occurrence records. The black phenogram represents the full data model with median node locations. For ancestral niche reconstruction in g-space, internal nodes reflect average climate tolerances inferred from the tip lineages deriving from that node using a Brownian motion trait model as implemented in the R package phyloclim. Eighty per cent central densities are shown as vertical blue lines



The studied white-eye species spread across a wide range of annual precipitation, ranging from arid to very humid environments. Both, g- and e-space-focused analyses indicate a higher variability that might be explained by gradual ecological speciation (Figure 4) and follow a Brownian motion pattern (Supplement S2). Continued ecological speciation is pronounced in *Z. atricapilla* which occupies

by far a much wetter range with low seasonality, and *Z. virens* which inhabits exceptionally dry environments. Strong divergence also remains for *precipitation seasonality*, as for the youngest species pair *Z. lateralis/luteus* which, again, form upper and lower bounds across the seasonality range of the genus while keeping a similar amount of rainfall. This shows that under short evolutionary time-scales



(i.e. in the range of 200 ka) white-eyes have been able to adapt to strongly seasonal (*Z. luteus*) and very continuous (*Z. l. lateralis*) humid environments and, hence, strongly contrasting ecosystems, which are reflected under an Early Burst evolution model (Supplement S2). Most other lineages face intermediate to high seasonality in precipitation regimes. In contrast to proximal thermal niche axes, precipitation-related niche axes act more distal on birds. Above a minimum amount necessary for hydration and transpiration, amount and seasonality of precipitation rather link to the availability of food and habitat in birds (Hawkins et al., 2003; Remeš & Harmáčková, 2018). The higher variability along precipitation-related niche axes, paired with the indication of early ecological speciation, might be explained by white-eyes exploiting a broad set of similar resources in different environments (i.e. small fruits, invertebrates and nectar; Kopij, 2004; Moeed, 1979). The morphology of the entire genus is very constrained, including size and shape of the bill (even though evidence for minor divergences in bill shape exist in sympatric white-eye species; Grant, 1972; Wijesundara & Freed, 2018). For birds, bill shape can be used as a proxy for dietary information and, hence, allows the approximation of trophic niches (Cooper et al., 2010). While prominent examples of rapid radiations exist that show strong diversification in trophic niches alongside conserved climate niches and restricted geographic ranges (e.g. Darwin Finches or Hawaiian Honeycreepers), white-eyes seem to reflect a reverse pattern of rather constrained trophic niches and divergent habitat/climate niches and an overall large geographic range.

Despite these variations, most white-eye lineages studied here are confined by tropical or subtropical conditions, with a low seasonality in temperature and a medium-to-high seasonality in precipitation. Yet, three of the ten studied species diverged into different directions across the climatic niche space. *Z. atricapilla* is the only moist tropical species with the highest precipitation sum and lowest precipitation seasonality. Likewise, the niche of *Z. l. lateralis* is characterized by a low precipitation seasonality and annual precipitation levels comparable to most other white-eye lineages, while it is the only species that occurs in year-round temperate climates. Finally, *Z. virens* also occurs in cooler, but more Mediterranean climates with a much drier and less seasonal environment than in the other white-eye lineages studied here. Interestingly, all three cases mark the youngest species splits in the entire dataset, which is in stark contrast to the expectations of niche conservatism (i.e. an increase in niche differences with lineage age). This result also explains the absence of phylogenetic signals across metrics and niche axes (Supplement S2). For instance, an extensive simulation study done by Revell et al. (2008) covering a wide range of scenarios found that phylogenetic signal was consistently low under conditions of divergent selection. In particular, niche shifts resulting from fast divergent selection can cause lower than expected phylogenetic signals in a phylogeny (Revell et al., 2008), which is what we have found in the species pair *Zosterops lateralis/luteus* and which may have driven the high support in EB models for those niche axes (Supplement S2). Despite these findings we want to stress that a larger set of species included in such analyses may diminish the effect of lower than

expected phylogenetic signal as long as *Z. lateralis/luteus* remains as the only pair showing such a high degree of niche divergence.

While white-eyes fulfil a lot of prerequisites for studying niche evolution, niche truncation (i.e. an incomplete characterization of the fundamental climatic niche, Saupe et al., 2018) could still have affected our inferences. In particular, we would expect that single species might not be able to access their entire potential distribution because of competitive exclusion with other members of the genus forming the radiation. Yet, the result would be to detect an overestimation of niche divergence, whereas the opposite was true in the simulations performed by Saupe et al. (2018), for which an underestimation of divergence rates was the main outcome. Given the young age and fast spread of the white-eye radiation, we still deem the effect of niche truncation to be minimal. Nevertheless, an interesting research avenue would be to systematically assess the effect of niche truncation depending on e- and g-space-based estimates since the approach by Saupe et al. (2018) was g-space focused. In particular, such an assessment could reveal changes in the adaptive landscape in the realized parts of the fundamental niche depending on the degree of niche truncation, how these changes affect niche evolution and ultimately how available methods for reconstructing ancestral niches will be able to quantify these changes. Next to studying whether the effect of niche truncation will be more pronounced in g- or e-space-based methods, another interesting aspect would be to study the effect on more niche axes different from thermal ones. As outlined throughout this study, the niche axes chosen to represent different facets of the environmental niche in white-eyes, some (i.e. thermal) being more proximal/scenopoetic and some (i.e. precipitation) being more distal/bionomic. If a set of niche axes cover more bionomic parts of the niche (trophic, habitat) than scenopoetic (i.e. physiologic) parts, it would be interesting to understand whether the effect of niche truncation is increased or minimized in parts of the niche other than the thermal. The question whether the effect of niche truncation would vary depending on which part of the niche is assessed would be cornerstone to our understanding of niche evolution. The focus on thermal niche axes in Saupe et al. (2018) already gives hints in that direction, where the impact of niche truncation was weak in axes facing stronger physiological bounding.

Taken together we were able to identify ecological speciation as a key driver of speciation across the genus in both g- and e-space-based analyses. Nevertheless, our comparative analyses revealed some interesting differences between g- and e-space. An increasing amount of researchers favour e-space-based approaches over g-space-based ones, as g-space-based approaches often suffer from flawed and simplistic assumptions that are rarely met in real-world systems leading to artificially high niche similarities (see Brown & Carnaval, 2019 for a recent summary on that topic). We could confirm this in our comparison, where the 80% central densities from the PNO profiles (g-space) were much wider compared to the variation depicted in the bootstrapping of species-specific environmental information that entered the EB trait evolution model (e-space). The g-space-based analyses lead to the impression that many white-eye



species share high amounts of niche space, where in e-space-based analyses differences are much more nuanced. However, in e-space we often found a surprisingly low variation along many niche axes for some species that might point to an overprediction of species–environment relationships. Hence, while under the assumption of niche conservatism, a g-space-based approach might lead to a higher commission (false positive) error (i.e. confirming niche conservatism where there is none), an e-space approach may risk omission (false negative) errors (i.e. rejecting niche conservatism where there is). To that end we recommend a complementary approach that looks at both g- and e-space to detect potential inconsistencies in niche similarities and ancestral niche evolution.

5 | CONCLUSION

The hypothesis of phylogenetic niche conservatism is frequently conflicted in birds and other taxonomic groups (Engler et al., 2017; Peterson, 2011). In particular, differences of precipitation-related versus thermal niche axes have been found in Australian honeyeaters (Miller et al., 2013) as well as in Scimitar babblers (Nyári & Reddy, 2013). In line with those findings, we were able to show that thermal niche axes show a higher level of conservatism than precipitation-related niche axes in most of the 10 white-eye taxa. In the diversification process, selective pressures might be stronger for maintaining the exploitation of familiar resources in dissimilar habitats, than for exploiting novel resources in the same habitat (Price, 2008; Richman & Price, 1992). At the same time, adaptation to novel thermal conditions might pose stronger barriers to selection than adaptation to a different habitat/resource because of the complexity in physiological changes to cope with higher upper thermal maxima (see, e.g. Somero, 2010) relative to behavioural adaptations to stay within thermal means (Huey et al., 2012). The disparity, albeit not fully independent, between more conserved thermal and more divergent precipitation-related niche axes would, thus, reflect a line of least resistance in the early stage of diversification (Price, 2008): Neither major physiological changes to cope with hotter – or cooler – climates nor morphological changes to exploit novel resources are necessary to diversify, as long as suitable, yet distinct, habitats can be occupied followed by reproductive isolation. A logical next step would be to focus analyses on fine-scale niche partitioning across the genus alongside the evolution of migration in the predominant non-migratory genus that could further specify ecological speciation and the different evolutionary trajectories to which certain white-eye lineages are heading. In more general terms, future studies on niche evolution also need to take possible disparities between thermal and precipitation-related niche axes into account, as, for instance, the rejection of niche conservatism only along precipitation-related niche axes might have different implications than if niche conservatism is conflicted along thermal niche axes (or in both axes). Finally, this disparity also has important implications for the use of multivariate methods to reduce the dimensionality in the climatic predictors (such as principal component analysis, see e.g. Ahmadzadeh et al., 2013): Mixing up temperature

and precipitation variables – even if correlated – might lead to misinterpretations of the causal links between the variables and the evolutionary drivers of the diversification process when different facets of the niche are depicted along these axes.

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DATA AVAILABILITY STATEMENT

All data are available from open source platforms. Raw GBIF.org occurrence data used for this work (as accessed on 21st October 2016) can be accessed through GBIF Occurrence Download <http://doi.org/10.15468/dl.erwqs6>. We have deposited the prepared data used for this work on FigShare accessible through <https://doi.org/10.6084/m9.figshare.13042031.v1> as well as R scripts for data analysis in a GitHub repository accessible through <https://github.com/JOEngler/ZostiNicheEvol>.

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BIOSKETCH

Jan O. Engler works on how species cope with a changing world, combining molecular and niche modelling tools. The entire research team uses white-eyes as a model system to understand the eco-evolutionary dynamics of birds in the wake of sudden environmental changes.

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SUPPORTING INFORMATION

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

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