



Reconciling supertramps, great speciators and relict species with the taxon cycle stages of a large island radiation (Aves: Campephagidae)

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Abstract

Aim: The taxon cycle concept provides a geographically explicit and testable set of hypotheses for exploring the evolutionary processes underlying the distribution of species in space and time. Here, we test taxon cycle predictions within a large avian island radiation, the core Campephagidae and explicitly integrate the concepts of 'supertramps', 'great speciators' and relictualization.

Location: The Indo-Pacific, Australia, Asia and Africa.

Taxon: Corvid passerine birds.

Methods: We constructed a new time-calibrated molecular phylogeny of the core Campephagidae (cuckooshrikes, cicadabirds and trillers) using Bayesian phylogenetic methods. Ancestral range estimation methods and diversification rate analyses were used to explore the dispersal and diversification history of the group. We used an extensive dataset on wing morphology and range distributions to test for correlations between evolutionary age of species and dispersal capacity, diversification and distribution, while accounting for phylogenetic non-independence.

Results: The core Campephagidae represents an ecologically homogeneous radiation distributed across the Indo-Pacific, Australia, Southeast Asia and Africa. Its members represent a continuum of dispersal abilities; some species are widespread and undifferentiated ('supertramps') or show strong differentiation of local populations ('great speciators'), and a few are endemic to single islands (relicts). We show that older species relative to younger species inhabit fewer and larger islands at higher elevations. The level of intraspecific variation measured as the number of subspecies also decreases with species age, and is highest in 'great speciators' with intermediate levels of dispersal abilities (as per hand-wing index).

Main conclusions: Based on trait correlations with species age, we infer phases of range expansion and contraction over millions of years (taxon cycles), within a single monophyletic group of birds. These observations demonstrate reconciliation of the concepts of 'supertramps', 'great speciators' and relictual palaeoendemics within the temporal stages of the taxon cycle.



KEYWORDS

great speciators, intermediate dispersal, islands, passerine birds, phylogeny, range size evolution, relict species, speciation, supertramps, taxon cycles

1 | INTRODUCTION

The idea that species pass through continuous phases of range expansion and contraction, known as taxon cycles (Wilson, 1959, 1961), has been suggested as an evolutionary framework for understanding contemporary geographical distributions of island faunas (Economo et al., 2015; Greenslade, 1969; Jönsson et al., 2017; Ricklefs & Cox, 1972). Phylogenetically young, expanding and widespread species experience an initial colonization stage (I), inhabiting coastal and disturbed habitats, whereas in later stages (II and III), intraspecific differentiation and incipient speciation take place associated with shifts in ecological distribution as island interiors are colonized (Ricklefs & Cox, 1978). Species in the 'final' stage IV are old, relictual palaeoendemics with niches restricted to montane habitats. As species progress through the taxon cycle stages, they are hypothesized to undergo a reduction in dispersal ability as early-stage generalist species become sedentary high-elevation specialists (Jönsson, Fabre, Ricklefs, & Fjeldsø, 2011; Jönsson et al., 2014; Ricklefs & Cox, 1972, 1978).

The phenomenon of species alternating between phases of range expansion and contraction (Brown, 1957; Darlington, 1957) has been referred to as 'colonization cycles' (Mayr, 1942), 'waxing and waning' of species (Simpson, 1953), 'taxon pulses' or 'Darlingtonian waves' (Erwin, 1981), and recently 'the hat pattern' (e.g. Žliobaitė, Fortelius, & Stenseth, 2017). Here, we reframe the taxon cycle concept of Wilson (1961), which predicts cyclical changes in species' geographical extent with a post-speciation increase in range size (e.g. Gaston, 1998) followed by a slow decline in range size towards extinction, as indicated in Figure 1. Rapid range expansion and high levels of gene flow between populations characterize taxa in taxon cycle stage I. Such taxa with high reproductive potential, broad habitat tolerance, but low competitive ability were considered supertramps by Diamond (1974, 1975). These species may be undifferentiated and continuously distributed across all small islands in a region, often including coastal and other marginal habitats on larger islands within their range. Diamond (1974, 1975) was not able to assess the temporal mode of supertramp evolution, but today we know, from molecular phylogenetic analyses, that the supertramp stage can extend over 700 kyr (Jönsson et al., 2014; Pedersen, Irestedt, Joseph, Rahbek, & Jönsson, 2018). Rapid sweepstake colonizations followed by a reduction in dispersal ability and subsequent population differentiation across the range of a widespread 'tramp' species (isolation by distance) may then result in a stage where the species is recognized as a 'great speciator' (stage II), which represents another 'extreme' diversification stage (Figure 2). Great speciators are widespread species that show an unusually high degree of intraspecific geographical variation (Mayr & Diamond, 2001) and were,

like supertramps, originally defined by Diamond, Gilpin, and Mayr (1976) relative to their geographical distribution in North Melanesia (species with ≥ 5 sub- or allospecies in this region). Many early-stage species do not occupy the maximum range size potential within a clade, and are characterized by rapid speciation and low persistence ('ephemeral species', for example, Harvey et al., 2017). Only some species, initially the nascent and temporary supertramps (stage I) and great speciators (stage II), may reach this maximum potential geographical range (Figure 2). The following stage III includes stasis, where a widespread distribution might be maintained as 'tramp' species experience shifts in habitat distributions. Incipient speciation and local extinction accompanied by a reduction in dispersal ability then fragment the range of the species, but the clade is now perceived as species rich. The transition from stage II to III is described in metapopulation models of speciation in the presence of gene flow between populations (e.g. Farrington, Lawson, Clark, & Petren, 2014). Such speciation events may lead to the onset of a new cycle of expansion (Matos-Maraví et al., 2018). In the last stage IV, relictualization is characterized by a gradual decline in range size and intraspecific diversity due to accumulated local extinctions, specialization (Raia et al., 2016, Figure 1) and confinement to higher elevations (Figure 2).

The ultimate causes of taxon cycles are poorly explored, but possible density-dependent mechanisms include co-evolution with enemy populations or pathogens (through 'counter-adaptations', Ricklefs & Cox, 1978; Ricklefs & Bermingham, 2002; Žliobaitė et al., 2017) or competitive pressure from new colonizers (i.e. young species replacing older species as suggested by Wilson, 1959, 1961). We, therefore, expect that the signatures of taxon cycles are

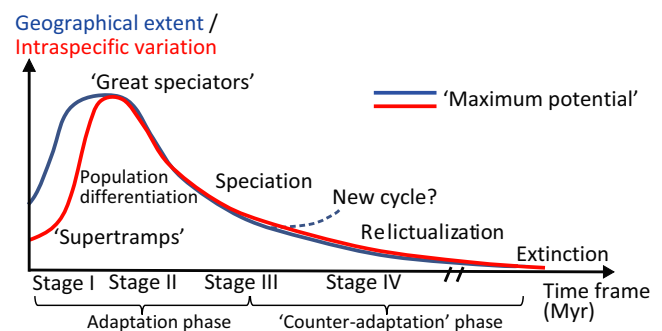


FIGURE 1 Conceptual depiction of the hypothesized evolution of geographical extent (blue, that is, range size, number or size of islands occupied etc.) and intraspecific variation (red, for example, number of subspecies or genetic variation) in the stages of the taxon cycle. The occurrence of 'supertramps' and 'great speciators' at evolutionary junctures are indicated along with some of the major evolutionary processes involved [Colour figure can be viewed at wileyonlinelibrary.com]

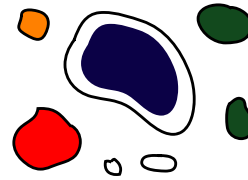
Stage I: Expansion to coastal lowlands, supertramps



Stage II: Population differentiation, great speciators



Stage III: Local extinctions, inland expansion, speciation



Stage IV: Relictualization at high elevations on large islands

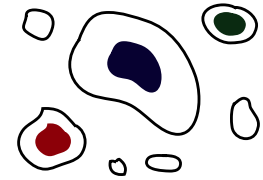


FIGURE 2 Conceptual sketch of geographical range evolution through the stages of the taxon cycle, see the introduction for a detailed description: Extreme stage I 'supertramp' (purple range) diversify into a stage II 'great speciator' (light colours), which is fragmented by extinctions and speciation in stage III (darker colours), followed by relictualization at high elevations (stage IV). Onsets of new expansion stages are omitted for clarity [Colour figure can be viewed at wileyonlinelibrary.com]

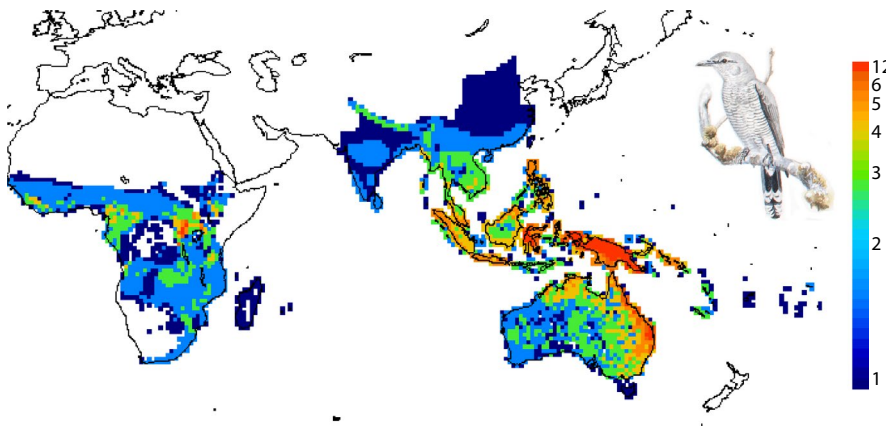


FIGURE 3 Species richness map of breeding ranges ($1^\circ \times 1^\circ$ grid cells) of all species within the core Campephagidae, adjusted to match the revised taxonomy of this study. The highest diversity per grid cell is found on the large and topographically complex islands of New Guinea and Sulawesi. Illustration by Jon Fjeldså: *Lalage fimbriata* (adult female) [Colour figure can be viewed at wileyonlinelibrary.com]

strongest in direct comparisons between closely related or ecologically similar sympatric species, which might interact competitively (e.g. Matos-Maraví et al., 2018). Alternatively, if older species do not show strong signatures of extinction (i.e. decrease in range size and within-species differentiation) as predicted by the taxon cycle model, older species, which have had more time to adapt to particular environments, might be assumed to be less prone to replacement by new colonizers (Pregill & Olson, 1981). However, although such 'priority effects' have been described among ecologically similar species (e.g. Fukami, 2015), the conditions and spatiotemporal scale at which they materialize in nature are not well understood (Rowsey, Heaney, & Jansa, 2018).

Although taxon cycles probably could occur on continents, especially in 'island-like' settings such as mountainous regions or habitat mosaics (Glazier, 1980), archipelagos provide well-defined geographical boundaries and dispersal barriers (water gaps) for terrestrial faunas, allowing us to clearly identify colonization and extinction in individual islands. The core Campephagidae (72 species, excluding *Pericrocotus*) is a large radiation within the Corvidae (*sensu* Cracraft, 2014), with a distribution across the Indo-Pacific, Southern Asia and Africa including remote islands in Polynesia, Micronesia and the Indian Ocean (Figure 3). We focus on the three most species-rich genera of the core Campephagidae *Coracina* (cuckoo-shrikes), *Edolisoma* (cicadabirds) and *Lalage* (trillers), which have overlapping distributions across the Indo-Pacific island region including Australia and South Asia. This group includes both single island endemics, widespread species with extreme

geographical variation (great speciators) and highly vagile tramp or supertramp species with large continuous distributions (Fuchs, Cruaud, Couloux, & Pasquet, 2007; Jönsson et al., 2010; Jönsson, Irestedt, et al., 2008; Pedersen et al., 2018).

By integrating an updated time-calibrated molecular phylogeny of the core Campephagidae with species distributions and a novel morphological dataset, we test how and if dispersal capacity, lineage-specific diversification rates (DR), evolutionary age and elevational segregation among co-distributed species on islands are correlated under the expectation that species pass through stages of expansions and contractions associated with shifts in ecological distribution. In line with taxon cycle predictions, we expect that older (relictual) species are confined to higher elevations in the interior of islands, have reduced dispersal ability and DR and that younger species representing recent colonizers, inhabiting lower elevational habitats, are good dispersers with larger ranges. We also investigate the relationship between dispersal ability and diversification in order to explain the intraspecific diversity of the great speciators, the supertramps and their relationship to the stages of the taxon cycle.

2 | MATERIALS AND METHODS

2.1 | Taxon sampling and ranges

Our sampling included 65 of the 72 (90%) currently recognized species (Dickinson & Christidis, 2014) within the core Campephagidae



(three of the unsampled species are found in Africa and the remaining in four Indo-Pacific locations; see Appendix S1 in Supporting Information). We compiled DNA sequences from GenBank (83 individuals) of the mitochondrial ND2 gene (80 out of a total of 85 individuals) and the nuclear genes GADPH (61 individuals), Myo (59 individuals) and ODC (58 individuals), see Table S1.1 in Appendix S1. We obtained new ND2 gene sequences from toe-pads of museum specimens of *Coracina personata floris* (NRM 554981), *C. javensis javensis* (NRM 572061) and *Edolisoma parvulum* (SNSD 4604). Laboratory procedures, primers, contig assembly and alignment information are detailed in Pedersen et al. (2018) and Appendix S1.

We compiled species breeding range sizes (in number of 1° latitude × 1° longitude grid cells) from Rahbek, Hansen, and Fjeldså (2012) (see supplementary material in Holt et al., 2013 for details). The number of core Campephagidae species occurring on 132 Indo-Pacific islands (>7 km²) were compiled from Taylor (2005) and Coates, Bishop, and Gardner (1997). Approximate island area and maximum elevations for these islands were compiled from the UNEP island directory (Dahl, 1991) or alternatively obtained from ArcGIS® Online basemaps by Esri (Table S1.2 in Appendix S1). Elevational ranges were obtained from Taylor (2005) and following Pedersen et al. (2018) we assigned all species into one of three elevational range classes: species usually inhabiting (a) coastal, (b) lowland or (c) montane areas (see Table S1.3 in Appendix S1).

2.2 | Phylogenetic analyses and calibration

We used Bayesian inference as implemented in BEAST 1.8.2 (Drummond, Suchard, Xie, & Rambaut, 2012) to reconstruct phylogenetic relationships assuming a birth–death speciation process (Gernhard, 2008) and an uncorrelated lognormal relaxed molecular clock model (Drummond, Ho, Phillips, & Rambaut, 2006) with nuclear genes linked. Convergence was determined in TRACER 1.6 (Rambaut, Suchard, Xie, & Drummond, 2014) ensuring all ESS values >200. TREEANNOTATOR 1.8.2 (Rambaut & Drummond, 2015) was used to summarize the distribution of trees in a single maximum clade credibility (MCC) tree after discarding 10% as burn-in. Following Jönsson et al. (2010), we used the island age of Réunion (c. 2 Myr) to calibrate the distal split between *L. newtoni* in Réunion and *L. typica* in Mauritius (assuming a normal prior with mean 1.5 Ma ± 0.25 SD, age within 95% confidence interval [CI]: 1.089–1.911 Ma). We used the split between the outgroup *Pericrocotus* and the core Campephagidae as a basal secondary calibration point (21.3 Ma ± 1.5 SD, CI: 18.83–23.77 Ma, consistent with the time when the Australian Plate margin converged with the Asian Plate in what would become Sulawesi [Hall, 2002], allowing *Pericrocotus* to disperse to mainland Asia) obtained from a supermatrix phylogeny of the Corvidae, which was calibrated using three Miocene corvid bird fossils (Jönsson et al., 2016). We adopted a temporal banding approach for species delimitation (Holt & Jönsson, 2014) by applying the species time threshold (c. 0.7 Ma) reported for *Edolisoma* in Pedersen et al. (2018), using a time-based molecular species delimitation test (GMYC).

2.3 | Ancestral range estimation

We estimated ancestral ranges using BioGEOBEARS (Matzke, 2014) as implemented in R (R Core Team, 2018). Several ancestral area reconstruction models are compared within a common likelihood framework (Table S2.1 in Appendix S2) including versions allowing for founder-event speciation in the form of a rare long-distance colonization event ('+J', Matzke, 2014). Akaike information criterion (AIC) and likelihood ratio tests were used to select the model with the highest probability of reproducing the data. The phylogeny was pruned to match our species-level revision of the taxonomy and we assigned each taxon to one or more of seven biogeographical areas according to contemporary distributions (Figure 4, maxareas = 3, corresponding to the most widespread species).

2.4 | Morphological data

The morphometric dataset consisted of 10 traits measured on 2–26 male specimens of each species (64 species after taxonomic revision, 386 specimens in total) according to a standardized protocol (Kennedy et al., 2016): bill length, bill width and bill depth; tarsometatarsus length; hallux length with and without the claw; length of the outer and the longest retrices; wing length measured from the carpal joint to the tip of the longest primary (WL), and wing breadth measured from the carpal joint to the tip of the most distal (first) secondary (SL). Following Claramunt, Derryberry, Remsen, and Brumfield (2012), two wing measurements were used to calculate a wing shape aspect ratio (hand-wing index [HWI]): $HWI = 100 \times \frac{WL - SL}{WL}$. HWI has been shown to be correlated with migratory behaviour (Lockwood, Swaddle, & Rayner, 1998, which is also found in our study, see Appendix S3) and natal dispersal distance (Dawideit, Phillimore, Laube, Leisler, & Bohning-Gaese, 2009) and appears to be a good proxy for dispersal capacity. Using the R package 'phytools' (Revell, 2012), we visualized the morphological diversification in a phylomorphospace plot of the first (PC1) and second (PC2) principal component axes with lines connecting species values according to phylogenetic relationships based on the MCC tree.

2.5 | Phylogenetic comparative analyses of diversification and dispersal

We used the R package 'ape' (Paradis, Claude, & Strimmer, 2004) to construct lineage-through-time (LTT) plots of the MCC tree and 100 randomly sampled trees from the posterior distribution to reflect topological uncertainty. The 'laser' package (Rabosky & Schliep, 2013) was then used to compare constant and variable DR models using the AIC and maximum likelihood methods. We also ran a speciation–extinction simulation to search for significant DR shifts and modelled trait evolution using the first principal component value (PC1, corresponding to body size) in BAMM (Rabosky, 2014, see Appendix S1).

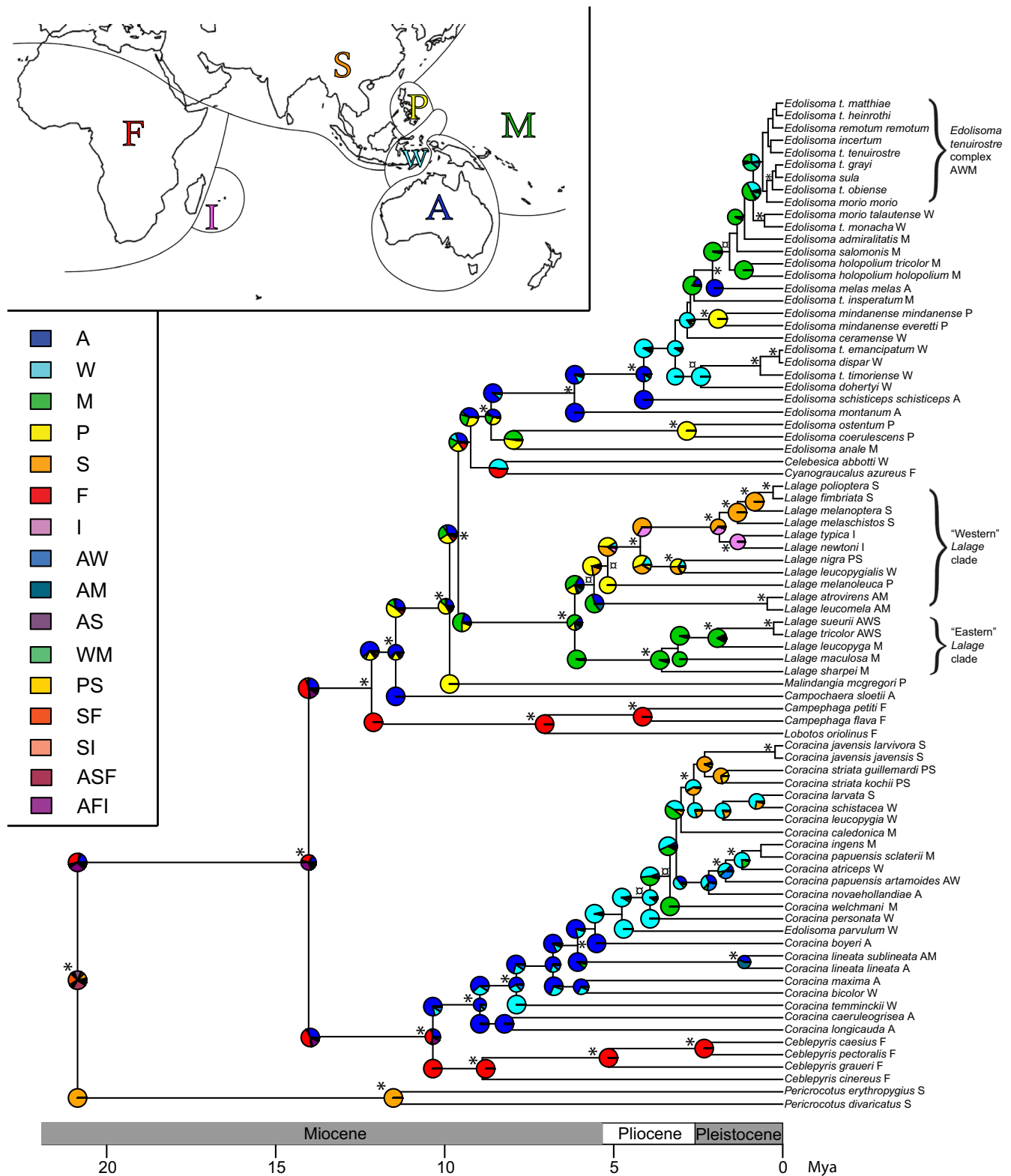


FIGURE 4 Time-calibrated maximum clade credibility tree of the core Campephagidae with ancestral areas (DEC+J). Subspecies of *Edolisoma tenuirostre* are abbreviated *Edolisoma t.* Asterisks indicate posterior probabilities ≥ 0.99 and ≥ 0.97 . Letters refer to the geographical area assignment: (A) Australo-Papua, (W) Wallacea incl. Sangihe, Talud and Palau in the Pacific Ocean, (M) Pacific Islands in Melanesia, Micronesia and Polynesia, (P) Philippines, (S) Southeast Asia, (F) Africa and (I) Mauritius and Réunion in the Indian Ocean. Not all ancestral states are shown for clarity [Colour figure can be viewed at wileyonlinelibrary.com]



We calculated the DR statistic (Jetz, Thomas, Joy, Hartmann, & Mooers, 2012, see Appendix S1) for all species: DR reflects the splitting rate of a lineage from the root to the tip, thus, the rapidly diversifying clades have high DR values and the isolated lineages have low values. DR values were log-transformed for normalization before we tested for correlations with HWI. We also used the number of subspecies (using our temporally consistent species-level taxonomy, based on subspecies recognized by Dickinson & Christidis, 2014) as a simple index of differentiation of geographical populations within recognized species (Mayr & Diamond, 2001; Phillimore et al., 2007) and compared it with the average species HWI and MCC tree node ages (species age). We define 'species age' as the time since the most recent divergence of extant species, which is a proxy for evolutionary persistence and distinctiveness of a taxon, but can be biased by taxonomic delimitations and incomplete phylogenies (e.g. Warren et al., 2018). We used the phylogenetic generalized least-squares regression method in the R package 'caper' (Orme et al., 2013) to account for phylogenetic non-independence between species. Branch length transformations (λ) were optimized numerically using maximum likelihood with default bounds and we compared model fits (linear, quadratic and cubic) using AIC and ANOVA *F*-test comparisons.

3 | RESULTS

3.1 | Phylogenetic relationships and taxonomy

A deep split (14.0 Ma, HPD: 11.4–17.0 Ma) is evident between *Coracina/ceblepyris* and the remaining genera, however, the three species-rich clades, *Coracina*, *Edolisoma* and *Lalage*, are of similar age (c. 9.2–10.4 Ma, HPD: 7.4–12.8 Ma). In addition to the taxonomical changes for *Edolisoma* reported in Pedersen et al. (2018), our temporal banding approach results in tentative lumping of the following allopatrically occurring species pairs: (a) *L. polioptera* and *L. fimbriata*, (b) *L. atrovirens* and *L. leucomela*, (c) *L. sueurii* and *L. tricolor*, (d) *C. ingens* and *C. papuensis sclaterii*, while *C. papuensis artamoides* (including Australian subspecies) is separated from the latter. All of the species pairs above have at times been considered conspecific (Taylor, 2005). *Edolisoma parvulum* placed within *Coracina*. *C. lineata lineata* (Australia) is separated from the *C. lineata (sublineata)* complex, and *C. striata guillemardi* (Sula Archipelago) from the *C. striata (kochii)* complex, suggesting the need to further revise these large and widespread species. The youngest sympatric species pairs diverged 1.2–1.6 Ma (*C. atriceps* and *C. papuensis*, 1.2 Ma; *L. melaschistos* and *L. polioptera*, 1.3 Ma; *E. holopolium* and *E. tenuirostre/remotum*, 1.6 Ma).

3.2 | Biogeographical analyses

The ancestral area reconstruction model DEC+J (Figure 4) performed only marginally better than other models, but the '+J' model was consistently favoured over the simpler alternatives (Table S2.1 in Appendix S2). This might reflect the general importance

of founder-event speciation (Matzke, 2014) within this family. Transoceanic dispersal directly from Australo-Papua to Africa probably occurred at least twice during the history of the Campephagidae (Fuchs et al., 2007; Jönsson et al., 2010). The origin of both the core Campephagidae and the Corvidae in general has been shown to be in the Australo-Papuan area (Jönsson et al., 2010, 2011, 2016). While some old campephagid lineages add a significant African influence (F in Figure 4) on the ancestral states of the core Campephagidae, we reconfirm the importance of the Australo-Papuan area (A) as the origin of the *Coracina* and *Edolisoma* radiations, with subsequent dispersal to and diversification within the surrounding archipelagos (W: Wallacea, M: West Pacific). *Lalage* expanded west into the Philippines (P) and Southeast Asia (S) in the late Miocene, from where the Indian ocean was crossed again to Mauritius and Réunion (I) 1.9 Ma (HPD: 1.4–2.4 Ma). Within *Lalage* a deep split is recognized (6.2 Ma, HPD: 4.8–7.6 Ma) separating an 'eastern' and a 'western' clade. *Lalage* has been suggested to represent a 'ring species' complex with sympatric terminal ends in Sulawesi (Mayr, 1942), but the strong molecular divergence between the two clades does not support this (Appendix S3).

3.3 | Diversification analyses

The phylorate plot from the speciation–extinction analyses in BAMM (Figure S2.1a in Appendix S2) indicates an overall temporal deceleration in molecular speciation rates (and trait diversification, Figure S2.1b in Appendix S2), with no clades showing any significant rate shifts. The LTT plot confirms this trend (Figure 5a): The variable DR models outperformed the constant models (Table S2.2 in Appendix S2) and when excluding the most recent 0.8 Myr (corresponding to the youngest species split), for which our taxonomic delimitations most strongly affect the apparent lineage accumulation, the best model (AIC) was an exponentially decreasing density-dependent diversification rate model (DDX, Rabosky & Schliep, 2013). Although we do not recover any rate shifts, we find that highly sexually dichromatic species, especially the terminal radiations in *Lalage* and *Edolisoma*, have higher DR than species for which the sexes are more alike ($p < 0.005$, Appendix S3).

The three genera *Coracina*, *Edolisoma* and *Lalage* are clearly segregated along PC1 (loaded equally between the morphological traits indicating body size), which explains 92% of the morphological variance (Figure 5b). The genera overlap along PC2 (indicating a ratio of bill dimensions to tarsus length, that is, body shape, explaining 4% of the variance). Overall, *Coracina* species are comparatively large with heavier bills (orange in Figure 5b), *Edolisoma* species medium-sized (pink) and *Lalage* species comparatively small and slender (purple).

3.4 | Correlations of HWI, elevational range and diversification rates

Within the Indo-Pacific islands, the number of Campephagidae species per island is positively correlated with island area ($R^2 = 0.4673$,

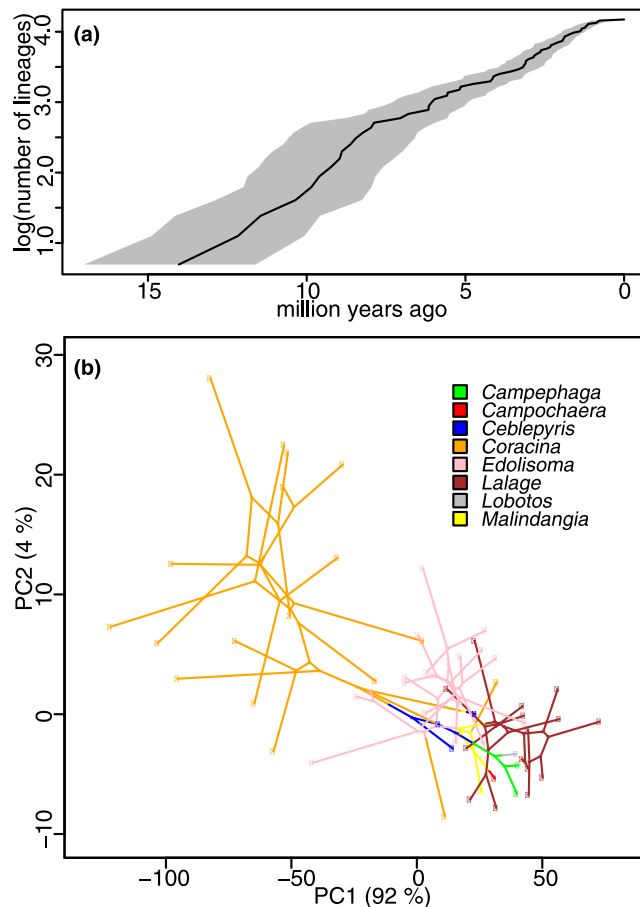


FIGURE 5 (a) Lineage-through-time plot of the number of lineages (log-transformed) as a function of time before present. The black line represents the maximum clade credibility tree lineage accumulation and the grey area is the 95% confidence interval for topological uncertainty from randomly sampling 100 trees of the posterior distribution. (b) Phylomorphospace plot of PC1 (body size) and PC2 (body shape) of the core Campephagidae species coloured according to currently recognized genera [Colour figure can be viewed at wileyonlinelibrary.com]

$p < 0.001$, Figure S2.2a in Appendix S2) and maximum island elevation ($R^2 = 0.2422$, $p < 0.001$, Figure S2.2b). Island area and maximum elevation are positively correlated (Figure S2.2c in Appendix S2). Plots of species ages and the area of each island they occupy ($R^2 = 0.0583$, $p < 0.001$, Figure 6a) and the total number of islands each species occupies ($R^2 = 0.1444$, $p < 0.05$, Figure 6b) show that older species are found on fewer and larger islands compared to younger species. This pattern of decreasing maximum geographical extent with species age is also recovered when comparing all species ages and ranges on continents and islands (Figure 6c).

Species in elevational range class 3 are significantly older ($n = 6$, $\text{mean}_{\text{class 3}} = 7.64$ Myr, ANOVA, $p < 0.001$, Figure 6d, even when correcting for range size, see model summary in Table S2.4a) than species in class 1 ($n = 41$, $\text{mean}_{\text{class 1}} = 3.01$ Myr) and class 2 ($n = 17$, $\text{mean}_{\text{class 2}} = 3.42$ Myr), but species ages in classes 1 and 2 are not significantly different. Similarly, species-specific DR values are

significantly lower in the high elevational range class 3 (ANOVA, $p < 0.001$, Figure S2.3a in Appendix S2). HWI is positively correlated with range size (Table S2.3) and there is a marginally significant tendency for species in elevational range class 3 to have lower HWI ($p < 0.07$, not shown).

The best-fitting model of the number of subspecies per species plotted against HWI (corrected for phylogenetic non-independence) was a quadratic function (AIC = 349.3, $R^2 = 0.0764$, $p < 0.04$) peaking at intermediate values of HWI (Figure 6e, model summary in Table S2.4b including HWI, range size and age as predictors). This model was significantly different from a linear model (AIC = 352.5, ANOVA, $p < 0.03$). We found no significant correlation between HWI and log(DR) (Figure S2.3b in Appendix S2). We detected a strong phylogenetic signal in HWI ($\lambda = 0.8$) and DR ($\lambda = 1.0$), a weak signal in (log-transformed) range size ($\lambda = 0.1$) and no signal in the number of subspecies ($\lambda = 0.0$). See Figure S2.4 in Appendix S2 for models without the high HWI outliers (*C. maxima* and *C. novaehollandiae*). There are tendencies for older species to have lower HWI values (Figure S2.5, not significant after phylogenetic correction) and fewer subspecies (when excluding the lumped *L. leucomela/atrovirens* complex, $p < 0.06$, Figure 6f, not significant when accounting for range size, which is positively correlated with the number of subspecies, Table S2.4b).

4 | DISCUSSION

We find that species ages, elevational ranges, distributions, intraspecific diversity and dispersal capacity of species within the core Campephagidae follow trends predicted by the taxon cycle concept (Ricklefs & Bermingham, 2002). These observations suggest a reconciliation of 'supertramps', 'great speciators' and range-restricted endemics with the idea of evolutionary pulses of expansion, diversification and contraction (i.e. taxon cycles).

4.1 | Geographical and ecological limits to diversification

The BAMM analysis groups all core Campephagidae species within a single cohort, but the overall decrease in speciation rate and DR (Figure 5a and S2.1 in Appendix S2) is consistent with a diversity-dependent interpretation suggesting upper limits to species richness within this clade at both regional (Fritz, Jönsson, Fjeldsø, & Rahbek, 2012) and local levels (island specific). We find that island area (and associated maximum elevation) is correlated with the number of Campephagidae species within the Indo-Pacific. Such species–area relationships are well known (e.g. Arrhenius, 1923) and suggest geographical limits to within-island Campephagidae diversity. Combined, this might indicate a limiting range expansion as the Indo-Pacific was colonized and islands reached their species limit (Price, 2008). However, despite several independent dispersal events to a large land mass that could provide novel geographical and ecological opportunities for diversification, only 11 African

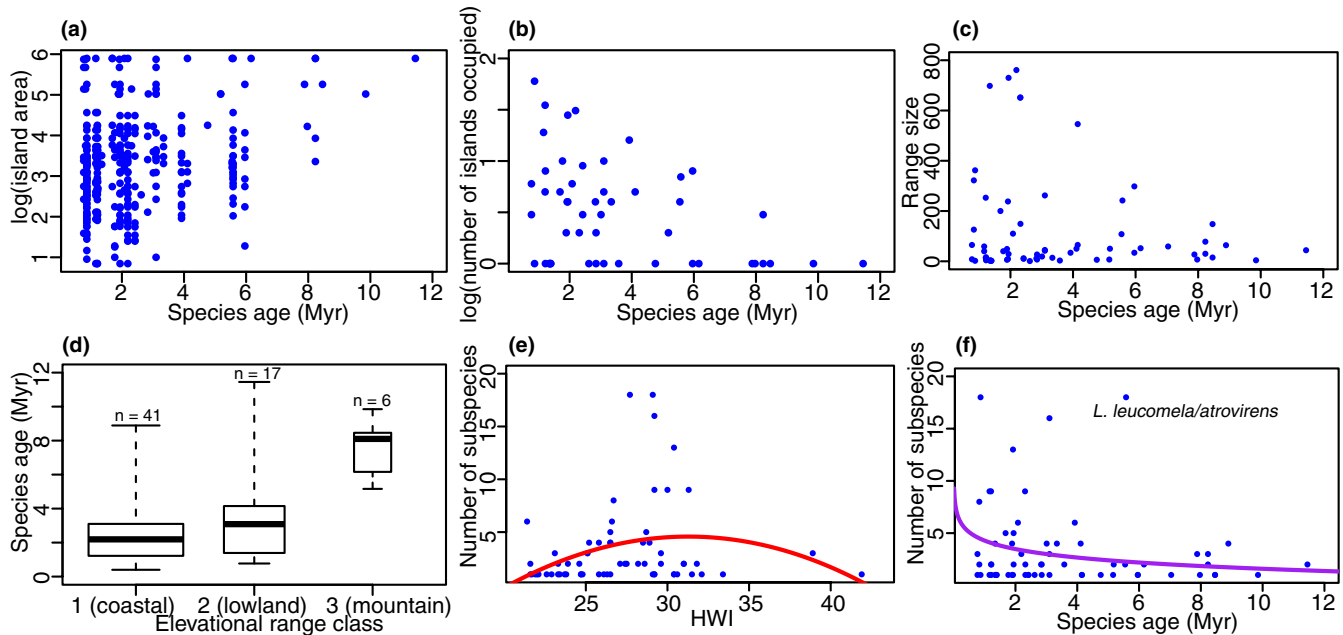


FIGURE 6 (a) Correlation between island area and age of each species (Myr) occurring on the island, and (b) between species age and the number of islands occupied by the species. Old species occur on few, large islands. (c) Correlation between range size (number of $1^\circ \times 1^\circ$ grid cells) and species age for all core Campephagidae species (i.e. both insular and continental species). (d) Boxplot showing species ages in elevational range class 1 (coastal areas), 2 (lowlands) and 3 (montane areas). The width of the boxes is proportional to the number of species in the range class. (e) Hand-wing index (HWI) plotted against the number of subspecies per species showing the best-fitting quadratic model (red, $p < 0.04$). (f) Correlation between the number of subspecies and species age; the exponentially decreasing function (purple) is marginally significant when excluding the outlier ($p < 0.06$) [Colour figure can be viewed at wileyonlinelibrary.com]

Campephagidae species exist today and 7 of these have fragmented or small ranges (Taylor, 2005, Figure 3), suggesting past extinctions. Prior to the African dispersal events in the middle Miocene, closely related families within the Corvidae (e.g. Malaconotidae and Vangidae) had already arrived and radiated extensively in Africa and Madagascar (Jönsson et al., 2016), potentially competing with campephagid species resulting in priority effects. The same might be true of *Pericrocotus* in the Asian continent.

In several (>20) large islands, triplets of one large *Coracina*, one medium-sized *Edolisoma* and one small *Lalage* coexist (some including the non-breeding migrant *C. novaehollandiae*). In the main Solomon Island chain, where *Lalage* is notably absent, a high number of sympatric (congeneric) *Coracina* (3) and *Edolisoma* (2) species is found instead. While early ecological divergence in sympatry might underlie the intergeneric segregation in body size (c. 10 Ma, Figure 5b and Figure S2.1), subsequent non-adaptive (geographical) radiation within each genus could have produced the pattern of size-based coexistence observed across the Indo-Pacific islands (Rundell & Price, 2009). Although this suggests direct competition between species, young sympatric species pairs occurred within 1.6 Myr in each genus indicating rapid stages of differentiation and colonization (Weir & Price, 2011). Competition with species outside of the Campephagidae, in particular with other members of the Corvidae (see Jönsson et al., 2017), might also have affected distributions (as suggested for the African clades) and morphological adaptations.

4.2 | Intermediate dispersal and the 'great speciators'

Within the core Campephagidae, intraspecific diversification peaks at intermediate values of dispersal ability relative to the range of HWI values (Figure 6e). This may support the intermediate dispersal hypothesis (Diamond et al., 1976; Mayr & Diamond, 2001): Taxa with intermediate levels of dispersal can overcome barriers but still diversify in geographical isolation, while continuous gene flow across such barriers in species with high dispersal capacity will prevent differentiation of populations (White, 2016). However, wing morphology is a complex ecological trait and other studies have reported both negative correlations between dispersal capacity and DR in island regions (across genera, Weeks & Claramunt, 2014) and continents (across species, Claramunt et al., 2012; Smith et al., 2014), positive global correlations (across families, Phillimore, Freckleton, Orme, & Owens, 2006) and no global correlations (across species, Kennedy et al., 2016). These studies used different proxies for DR and dispersal capacity, and at different taxonomic, ecological and geographical scales, clade-specific patterns could be averaged out. In contrast, the core Campephagidae represents a monophyletic and ecologically homogeneous clade (consisting of mainly arboreal canopy-feeding insectivores, Taylor, 2005).

Intermediate levels of dispersal ability has been suggested to explain high rates of diversification of apparently good dispersers

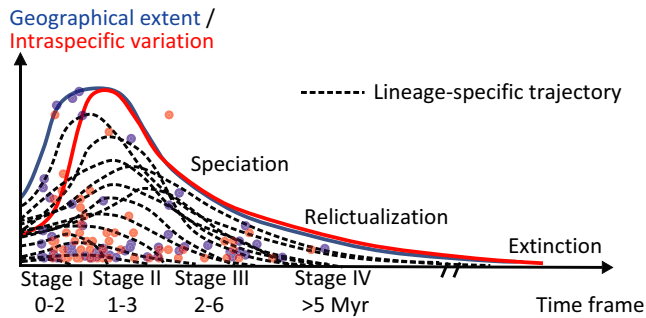


FIGURE 7 The integral of the 'maximum potential' outlines (Figure 1) are filled out by lineage-specific trajectories (dotted lines). Range sizes (blue dots, Figure 5c) and the number of subspecies (red dots, Figure 5f) of the core Campephagidae are shown (not to scale) [Colour figure can be viewed at wileyonlinelibrary.com]

('great speciators') faced with the homogenizing effects of gene flow (i.e. the 'paradox of the great speciators', Diamond et al., 1976). Within northern Melanesia Mayr and Diamond (2001, see Appendix S3) described *E. tenuirostre*, *C. lineata* and *L. leucomela* (lumped with *L. atrovirens* herein) as great speciators: These have intermediate HWI values, a high number of subspecies and large geographical distributions across the Indo-Pacific. Outside northern Melanesia, these characteristics are shared by *C. papuensis* and *C. striata* and all the great speciators are young species (<2 Myr, except *L. leucomela/atrovirens*). Another widespread non-passerine great speciator *Gallirallus philippensis* (HWI~27, 21 subspecies) belongs to a genus with generally low HWI (~17), including several flightless endemics (Weeks & Claramunt, 2014). This large within genus variation would not be evident from comparisons across genera (e.g. Weeks & Claramunt, 2014). *Pitta erythrogastrer* (26 subspecies, Dickinson & Christidis, 2014) is a highly sedentary species with a low dispersal capacity (average *Pitta* HWI~19, Weeks & Claramunt, 2014), but was also classified as a great speciator by Mayr and Diamond (2001). However, Irestedt et al. (2013) suggested that *P. erythrogastrer* should be divided into 17 terminal species. Evolutionary shifts in dispersal ability can occur rapidly (Slikas, Olson, & Fleischer, 2002) and *P. erythrogastrer* dispersed and diversified rapidly within the Pleistocene (Irestedt et al., 2013), likely taking advantage of the greater connectivity of islands during much of the Pleistocene (Voris, 2000), but subsequently lost its ancestrally high dispersal ability and did not obtain secondary sympatry. This is reminiscent of the dispersal cycle described in, for example, *Coturnix* species (Hosner, Tobias, Braun, & Kimball, 2017). The high phylogenetic signal in HWI found in our study, does however, suggest that wing morphology is relatively conserved across species within the core Campephagidae. Thus, if we define a great speciator under the condition that differentiation in isolation is balanced by gene flow to maximize geographical intraspecific variation (see White, 2016), then the *P. erythrogastrer* species complex is better considered a species-rich clade consisting of fragmented taxon cycle stage III species.

4.3 | Taxon cycles within the core Campephagidae

We find that older species occupy fewer, larger islands compared to younger species, which indicates historical range contraction (Jönsson et al., 2014, 2017). Furthermore, the elevational range of a species is positively correlated with its age, suggesting that older (later stage) taxa gradually shift distribution towards higher elevations (Economio & Sarnat, 2012). The oldest species are relictual montane species. Intraspecific variation also decreases with age (Figure 6f), suggesting that late-stage species have experienced local extinctions (on small islands) and are now only found on islands with higher elevations acting as refugia (centrifugal speciation *sensu* Brown, 1957). The distribution of the correlates between range size and age (Figure 6c) outlines a 'maximum potential' for the geographical extent of a species given its age (Figure 7), suggesting that we observe both supertramps (see Appendix S3) and great speciators at evolutionary junctures. However, extrinsic geographical and ecological factors (changing water barriers and evolutionary shifts in dispersal ability in relation to geography, Pedersen et al., 2018) and intrinsic factors (e.g. sociability and short generation times, Moyle, Filardi, Smith, & Diamond, 2009) have contributed to the emergence of the great speciators. The dramatic changes in geographical connectivity during low Pleistocene sea levels, when large areas of lowland habitat were available across the Indo-Pacific (Voris, 2000), might have provided very different opportunities for early expansion stages compared to the Pliocene and Miocene epochs. However, the geographical clustering of closely related species (especially within *Lalage* and *Edolisoma*, Figure 4) suggests ancestral stages of supertramps and great speciators across the archipelagos. Several studies have demonstrated how turnover within such stage I supertramps may generate stage II great speciators (Jönsson, Bowie, et al., 2008; Linck, Schaack, & Dumbacher, 2016; Pedersen et al., 2018).

The difference in mean age of species in elevational range classes 1 and 3 is 4.7 Myr and this provides a lower estimate of the period of potential taxon cycles within Campephagidae (Figure 2). Ricklefs and Bermingham (2002) estimated taxon cycle periods of 0.1–10 Myr in various avian groups in the Lesser Antilles. At the temporal scale observed in this study, taxon cycles are not likely to be driven by Pleistocene climatic cycles (Pregill & Olson, 1981), which occur with periodicities of 0.02–0.1 Myr (Hays, Imbrie, & Shackleton, 1976). However, recent climatic oscillations could drive episodic population differentiation (Harvey et al., 2017) leading to delayed cycles of incipient speciation. We further believe that geological processes (e.g. orogenesis) could influence the transition from one taxon cycle stage to the next, as habitat changes: for example, the collision of the Australian and Pacific geological plates, which gave rise to a major uplift of the Central Ranges of New Guinea and across Sulawesi during the last 5 Myr (Hall, 2002), could have allowed for opportunities for speciation by elevation. On these topographically complex islands, the segregation of old and young species according to elevational range is particularly clear (Appendix S3).

Species ages on the x-axes in Figures 1, 6 and 7 thereby illustrate relative timelines of species evolution, but do not imply causal



relationships. The correlates of species age thus form parts of a predictable 'taxon senescence' (Žliobaitė et al., 2017) or 'taxon ageing' (Warren et al., 2018) syndrome. Ricklefs and Cox (1978) speculated that dynamic co-evolutionary interactions between pathogens and their hosts could be a potential underlying frequency-dependent driver for population expansions and contractions through ecological release and the apparent competition in species abilities to escape pathogens, thereby reflecting a Janzen–Connell effect (Connell, 1978; Janzen, 1970), but at large evolutionary (temporal) and biogeographical (spatial) scales (Ricklefs, 2015). However, it is also possible that the ontogeny of the islands themselves (Whittaker, Triantis, & Ladle, 2008) shape the species ontogeny outlined here, providing a line of thought for future hypothesis development on taxon cycles and the co-evolution of islands and species.

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DATA AVAILABILITY

All sequence data have been deposited on GenBank (Table S1.1 in Appendix S1) and alignment is available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.1m7n014> (Pepke, Irestedt, Fjeldsø, Rahbek, & Jønsson, 2019). All other data are available in Appendix S1 in the Supporting Information.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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