DIVERSIFICATION AND BIOGEOGRAPHIC PATTERNS IN FOUR ISLAND RADIATIONS OF PASSERINE BIRDS

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Declining diversification rates over time are a well-established evolutionary pattern, often interpreted as indicating initial rapid radiation with filling of ecological niche space. Here, we test the hypothesis that island radiations may show constant net diversification rates over time, due to continued expansion into new niche space in highly dispersive taxa. We investigate diversification patterns of four passerine bird families originating from the Indo-Pacific archipelagos, and link these to biogeographic patterns to provide independent indications of niche filling. We find a declining diversification rate for only one family, the Paradisaeidae (41 species). These are almost completely restricted to New Guinea, and have on average smaller species ranges and higher levels of species richness within grid cells than the other three families. In contrast, we cannot reject constant diversification rates for Campephagidae (93 species), Oriolidae (35 species), and Pachycephalidae (53 species), groups that have independently colonized neighboring archipelagos and continents. We propose that Paradisaeidae have reached the diversity limit imposed by their restricted distribution, whereas high dispersal and colonization success across the geologically dynamic Indo-Pacific archipelagos may have sustained high speciation rates for the other three families. Alternatively, increasing extinction rates may have obscured declining speciation rates in those three phylogenies.

KEY WORDS: Dispersal, diversity dependence, macroevolution, speciation, species richness.

The influence of ecological processes on the evolutionary trajectories of different clades has interested biologists for long (Willis 1922), starting with the observation that species richness differs markedly among taxa. Variation in clade size may be explained by differences in net diversification rates (i.e., speciation minus extinction) between clades or between areas of distribution, but also by differences in clade age if diversification rates through time are identical in different clades. Numerous recent studies have used molecular phylogenies of various vertebrate groups to demonstrate a pattern of declining diversification rates over time (e.g., Harmon et al. 2003; Kozak et al. 2006; Phillimore and Price 2008; Rabosky and Lovette 2008a). This pattern has been termed diversity dependence because it is argued to reflect the existence of upper limits to species richness of clades or regions

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(Nee et al. 1992; Rabosky 2009a). Recently, these limits have been called ecological limits because they are assumed to result from ecological processes, for example, competition for limited resources (Rabosky 2009a). Ecological limits imply that clade sizes should be independent of diversification rate and clade age after the initial radiation phase, a pattern that has now been reported for many taxa (Rabosky 2009b).

Diversity dependence of diversification is often explained in light of ecological opportunities following a geographic dispersal event or an adaptive shift into new niche space (Simpson 1953; Schluter 2000). For taxa in the early stages of diversification in a new niche space, resources are readily available, and potentially competing species are scarce, facilitating rapid speciation. As radiations progress, resources diminish and competition increases, thereby decreasing opportunities for speciation and/or increasing extinction rates (Gavrilets and Vose 2005). Species-rich groups whose diversification trajectories have been well studied include both adaptive and nonadaptive radiations, such as North American woodland salamanders (Kozak et al. 2006), different lizard groups, including *Anolis* in the Caribbean (Harmon et al. 2003; Rabosky and Glor 2010), and many bird groups (Nee et al. 1992; Weir 2006; Phillimore and Price 2008; Rabosky and Lovette 2008a; Moyle et al. 2009). The vast majority of these and other studies show patterns concordant with diversity dependence especially for species-rich taxa (see also McPeek 2008; Rabosky 2009a; Morlon et al. 2010), although constant diversification rates have recently been suggested for the large and ecologically diverse group of Neotropical furnariid birds (Derryberry et al. 2011).

However, many of these studies have focused on radiations either of continental origin or confined to a small geographic area. Radiations with an insular origin that have dispersed widely have rarely been studied (but see examples below). It is possible that net diversification rates are not diversity dependent for clades of highly dispersive organisms, which successfully expand their ranges within extensive archipelagos (possibly with initial "supertramp" strategies) or colonize other continents (Diamond 1974; Mayr and Diamond 2001; Bellemain and Ricklefs 2008). A pattern of roughly constant net diversification through time is expected under either constant speciation and extinction rates through time, or under low or declining speciation rates in connection with high or increasing extinction rates (Nee et al. 1994; Rabosky and Lovette 2008b; Quental and Marshall 2009). Both scenarios may be realistic in geologically dynamic archipelagos. So far, results for time-constant diversification rates in island taxa are inconclusive: the diversification patterns of Southeast Asian *Crocidura* shrews are consistent with constant diversification rates (Esselstyn et al. 2009), but *Anolis* lizards in the Caribbean and the passerine bird radiation of *Zosterops* and allies in Australasia and Africa appear to exhibit diversity dependence (Harmon et al.

2003; Moyle et al. 2009; Rabosky and Glor 2010). In *Phelsuma* day geckos, diversification appears to have declined for the clade endemic to Madagascar but not for the clades occurring in the Comoros, the Seychelles, and the Mascarene islands (Harmon et al. 2008). Although some more dated phylogenies of island-origin radiations exist, they have not been investigated in terms of diversification rates over time (e.g., Sato et al. 1999).

In the present study, we analyze and compare diversification patterns across four families of passerine birds. These families are part of the core Corvoidea radiation comprising approximately 750 species, which originated in the Indo-Pacific archipelagos (Jønsson et al. 2011). All four families are considered to be large clades in the diversification literature (Phillimore and Price 2008), and we analyze well-sampled molecular phylogenies: Oriolidae (orioles and figbirds, 31 of 35 species), Paradisaeidae (birds-of-paradise, 40 of 41 species), Pachycephalidae (whistlers, shrike-thrushes and allies, 36 of 53 species), and Campephagidae (cuckoo-shrikes, trillers, and minivets, 75 of 93 species). These families all originated in the same region, the Indo-Pacific archipelagos, with all the most basal species on New Guinea (Jønsson et al. 2011). As their area of origin has a complex history of geological terrane movements and sea-level fluctuations throughout the Cenozoic (Hall 1998; 2002), it may have provided exceptional opportunities for allopatric speciation (Mayr and Diamond 2001; Losos and Ricklefs 2009), but may also have caused increased extinction rates (Ricklefs 2010).

Here, we investigate whether patterns of diversification for these four island-origin radiations are consistent with patterns of diversity dependence or those of rate constancy over time. We use two different statistical approaches, taking uncertainty of phylogenetic reconstruction and effects of missing species into account. Additionally, the link between decreasing diversification rates through time, diversity limits, and ecological niche differentiation has rarely been explicitly tested (but see Phillimore and Price 2009; Mahler et al. 2010) because measures of ecological niche filling across species within a clade are lacking. We use biogeographic information, that is, the properties of range-size frequency distributions and species richness within grid cells, as rough measures for the partitioning of ecological niche space across species at large spatial scales. Paradisaeidae are mostly restricted to the island of New Guinea, whereas the other three families have complex dispersal and diversification histories across Australia, Asia, Africa, and/or the Pacific islands (Frith and Beehler 1998; Jønsson et al. 2010a; Jønsson et al. 2010b; Jønsson et al. 2010d). Therefore, our a priori hypothesis was that Paradisaeidae may show signatures of both decreasing diversification rates through time and finer ecological niche partitioning, as suggested by smaller species ranges and higher overlap of these at large spatial grain sizes. Oriolidae, Campephagidae, and Pachycephalidae all seem to exhibit higher dispersal and colonization abilities, so they could

be expected to show overall constant diversification rates through time, and have both larger species ranges and less range overlap between species.

Materials and Methods

Dated phylogenies were obtained from published literature for the Paradisaeidae (Irestedt et al. 2009), the Pachycephalidae (Jønsson et al. 2010a), the Oriolidae (Jønsson et al. 2010b), and for the Campephagidae excluding the subclade *Pericrocotus* (hereafter called the *Coracina* tree, Jønsson et al. 2010c; all sequences on GenBank, see cited literature for accession numbers). To obtain absolute divergence times, different dating strategies have been chosen specifically for each family to reflect the most realistic time estimates (see also the reference for each phylogeny). The Paradisaeidae and *Coracina* trees have been calibrated using secondary calibration points from Barker et al. (2004), setting the origin of oscines at 76 million years ago (Mya; 95% confidence interval: 63.84–89.16 Mya). The phylogenies for Pachycephalidae and Oriolidae have been calibrated using a rate of mitochondrial DNA (mtDNA) evolution. Whereas the 2% rule (Weir and Schluter 2008) has been used for the Oriolidae, a faster rate reported for island groups (Drovetski et al. 2004) has been used in conjunction with island ages to calibrate the Pachycephalidae phylogeny.

A phylogeny for *Pericrocotus* (Campephagidae) was published without dates, and was based on one gene less than the *Coracina* tree (Jønsson et al. 2010d). We therefore decided to use the same dating procedure as for the *Coracina* tree on the *Pericrocotus* phylogeny, and then analyze the two parts of Campephagidae separately and in combination (see below). To obtain divergence time estimates for *Pericrocotus*, we used BEAST (Drummond et al. 2006; Drummond and Rambaut 2007), and assigned the best fitting model, as estimated by MRMODELTEST 2.0 (Nylander 2004) to each of the partitions. To calibrate the tree, we used an age estimate of approximately 15 Mya for the origin of *Pericrocotus*, based on Jønsson et al. (2010c,d). Thus, for the origin of *Pericrocotus* we used a normally distributed prior with a median at 15 Mya and a standard deviation of 1 (quintiles 2.5% = 13.04, 5% = 13.36, 95% = 16.64, 97.5% = 16.96). We assumed a Yule speciation process for the tree prior and an uncorrelated log-normal distribution for the molecular clock model (Ho 2007). For all other parameters, we used default prior distributions. Markov Chain Monte Carlo (MCMC) chains were run for 25 million generations.

To generate a dated phylogeny for all members of Campephagidae, we then inserted the *Pericrocotus* tree into the *Coracina* tree. The position was determined by two *Pericrocotus* species included in the original *Coracina* tree, which were subsequently deleted. The root age for the *Pericrocotus* clade was determined by the *Pericrocotus* tree, and the root age for the

Campephagidae by the more comprehensive *Coracina* tree. This procedure was followed for the combination of the maximum clade credibility trees, as well as for the combination of 1000 trees that were randomly sampled from the posterior distributions of the two dating analyses. To assess robustness of our results to this combination of two independently estimated phylogenies, we ran all analyses separately for the original *Pericrocotus* and *Coracina* trees as well.

We followed the taxonomy and family definitions in the IOC World Bird Names (Gill et al. 2009), with a few exceptions following previous phylogenetic studies as follows. The Pachycephalidae did not include *Aleadryas rufinucha*, *Oreoica gutturalis*, *Pitohui cristatus*, and *Rhagologus leucostigma* (Norman et al. 2009; Jønsson et al. 2010a). Also, *Pitohui kirhocephalus* and *Pitohui dichrous* were included within the Oriolidae, not the Pachycephalidae (Jønsson et al. 2008; Norman et al. 2009). To avoid polyphyletic species, *Coracina remota* (including the taxa *matthiae* and *heinrothi*) and *Coracina admiralitatis* were recognized as separate species (all previously part of *Coracina tenuirostris*, Jønsson et al. 2010c). *Pachycephala pectoralis* was separated into a western Australian species and a species occurring in eastern Australia, Australian islands, and New Guinea (Jønsson et al. 2010a). Finally, we split *Oriolus chinensis* into three species: one species in continental Asia represented by *Oriolus chinensis diffusus*, one species in the Sunda islands represented by *Oriolus chinensis maculatus*, and one species occurring in the Philippines and on Sulawesi represented by *Oriolus chinensis chinensis* and *Oriolus chinensis melanisticus* (Jønsson et al. 2010b). (The same study suggested splitting *Oriolus steerei*, which we decided against due to incomplete sampling of subspecies and the resulting difficulty of associating species range parts.) Following this revised taxonomy, we deleted tips from the phylogenies after dating, until each species was represented only once; outgroups were also deleted. Our trees represent the following proportions of sampled species: Pachycephalidae, 68%; Campephagidae, 81%; Oriolidae, 86%; and Paradisaeidae, 98%.

To compare diversification patterns through time with biogeographic patterns, we matched information on the breeding range for species of these groups to the same taxonomy. Distribution data were extracted from a comprehensive global geographic range database for all land and freshwater birds (version 30 June 2009). The geographic range of each species was mapped at a resolution of $1°$ latitude $\times$ $1°$ longitude following the approach outlined by Rahbek and Graves (2000; 2001; see also Brooks et al. 2001; Jetz and Rahbek 2002). Maps represent a conservative extent-of-occurrence of the breeding ranges based on museum specimens, published sight records, and spatial distribution of habitats between documented records, which have subsequently been validated by ornithological experts. Over 1000 references have been used to map avian distributions in the region of the

world covered by the current article (reference list and additional information is available upon request from C. Rahbek). We modified distributions from this dataset to match the taxonomy (described above) based on information from Taylor (2005), Boles (2007), Walther and Jones (2008), and Frith and Frith (2009).

Frequency distributions of species richness within grid cells were generated from this dataset for each family. We generated species range-size frequency distributions by calculating the land area contained within each cell using a Behrmann global equal-area projection, and then summing these land values for each species. This approach attempts to take the effects of coastlines into account, as our study area contains many islands, while assuming that a species occupies all land area in each grid cell it is recorded for. Simply counting the number of grid cells for each species provided similar results (not shown). To describe statistical properties of these frequency distributions, we calculated skew and kurtosis and compared these to the normal distribution (Graves and Rahbek 2005).

We used R version 2.10.1 (R Development Core Team 2009) and the LASER package for R (Rabosky 2006). All analyses were run on each maximum clade credibility tree as well as on 1000 phylogenies randomly sampled from the posterior distributions of trees (excluding the burn-in) for each of the four families, to take uncertainty in phylogenetic reconstruction into account. We tested for constant diversification rates over time using both the γ statistic (Pybus and Harvey 2000) and ΔAIC_{RC}, which uses a maximum-likelihood framework (Rabosky 2006). Null distributions for both measures were obtained from 5000 phylogenies simulated for each group, which were of the same size as the group of interest and grown under a Yule model (constant speciation rate, no extinction).

We accounted for missing species when simulating the phylogenies from which we obtained the null distributions for our test statistics (Pybus and Harvey 2000; Rabosky and Lovette 2008a). Trees were simulated to grow from the root until the total number of species for a given family was reached. Subsequently, tips and the internal branches leading to them were deleted at random until the tip number equaled that of our phylogenetic sampling for the family. This approach assumed that all species in the family are known, thus only accounting for species not sampled in our phylogenies. Additionally, we used three further levels of total species richness, assuming that the known species numbers represent 75%, 50%, and 25% of the true species number, and therefore testing the effects of undetected or extinct species. In these cases, trees were simulated to the assumed total species number, and tips were reduced to the number sampled in our phylogenies as before. All our simulations assumed that species were missing at random from the phylogeny. Our actual species sampling was above the recommended 80% of known species (Cusimano and Renner 2010) in

all families except one: for Pachycephalidae, our relatively low proportion of sampled species may introduce increased type I error rates, as it is possible that many missing species are recent (but see "Discussion").

The interpretation of the γ measure is that strongly negative values indicate a decrease in diversification rate over time, whereas positive values can arise under constant or increasing diversification. Therefore, we used a one-tailed test to detect significantly negative γ values, which is seen as conservative if extinction is nonzero (Pybus and Harvey 2000). We fitted five maximum-likelihood models of diversification to each phylogeny: the Yule model and a birth–death model (constant speciation rate and constant, nonzero extinction rate) represented constant-rate models, and models with rates that vary through time were represented by a diversity-dependent diversification model with linearly decreasing speciation and zero extinction rates, a diversity-dependent diversification model with exponentially decreasing speciation and zero extinction rates, and a modified Yule model allowing for two different speciation rates with a breakpoint (Rabosky 2006). The ΔAIC_{RC} measure is defined as the difference in AIC values between the best rate-variable model and the best rate-constant model, that is, it is positive if the best model is rate variable. Therefore, significantly positive ΔAIC_{RC} values were tested for with a one-tailed test against the simulated null distributions (Rabosky 2006).

Results

The lineage-through-time plot for Paradisaeidae leveled off after an initially fast diversification, generating an apparently diversity-dependent pattern, whereas the lineage-through-time plots for the three other families appeared straight (Fig. 1A–D). Both the γ statistic and ΔAIC_{RC} confirmed this visual impression: the observed γ of the maximum clade credibility tree for the Paradisaeidae was significantly lower than expected if diversification was constant through time, whereas γ values did not reject constant rates for the Campephagidae, Oriolidae, and Pachycephalidae (Table 1). Similarly, ΔAIC_{RC} for the Paradisaeidae was significantly higher than expected when assuming constant diversification rates, but ΔAIC_{RC} for the other families was not (Table 1; Fig. 2). Although the best diversification model for the Paradisaeidae was rate variable (Table 1), the differences in AIC values of the best model (diversity-dependent diversification with linearly decreasing speciation rate) to the other two rate-variable models (diversity-dependent diversification with exponentially decreasing speciation rate and modified Yule model with a shift in speciation rate) were small (4.4 and 2.4, respectively). Pachycephalidae fitted the Yule model best, and Oriolidae and Campephagidae the Yule model with one rate shift, but discriminatory power for these families was low: differences in AIC values between the best and
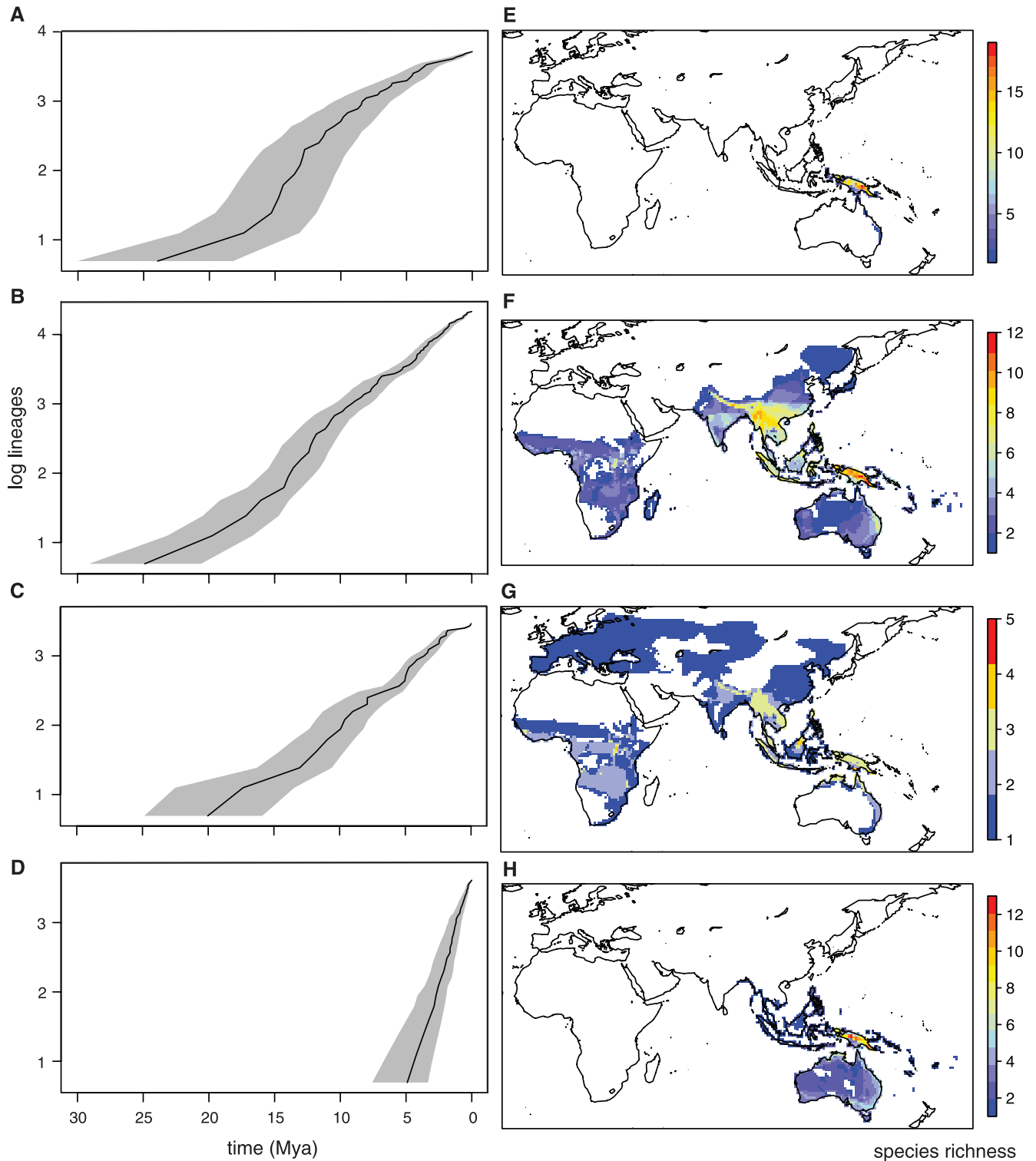
Figure 1. Lineage-through-time plots (A–D) and species richness maps (E–H) for the four families. (A and E) Paradisaeidae; (B and F) Campephagidae; (C and G) Oriolidae; (D and H) Pachycephalidae. In (A–D), solid lines represent the maximum clade credibility trees, and gray areas are the 95% confidence interval for phylogenetic uncertainty generated by randomly sampling 1000 trees from the posterior distribution. Axes were scaled equally in (A–D) to facilitate comparison.

Table 1. Testing for constant diversification rates using the γ and ΔAIC_{RC} statistics. Observed statistics are for the maximum clade credibility (MCC) trees; *P*-values are shown for the MCC tree and the 95th percentile of a random sample (1000 trees) from the posterior distribution of trees. The *P*-values were generated from simulated null distributions of 5000 trees for each family and each of the assumed total species numbers. Simulations all accounted for the number of species not sampled in our phylogenies, and assumed that all species were known (100%), or that only 75%, 50%, and 25% were known, respectively.

| | Observed Statistic | *P*-values | | | | | | | |
| | | 100% known | | 75% known | | 50% known | | 25% known | |
		MCC	95th	MCC	95th	MCC	95th	MCC	95th
γ									
Paradisaeidae	−2.629	0.001**	0.005**	<0.001***	0.004**	0.004**	0.016*	0.209	0.412
Campephagidae	−0.988	0.121	0.320	0.472	0.747	0.702	0.899	0.998	>0.999
Oriolidae	−0.869	0.065	0.181	0.201	0.459	0.121	0.349	0.997	>0.999
Pachycephalidae	−1.074	0.269	0.583	0.341	0.687	0.739	0.930	0.978	0.998
ΔAIC_{RC}									
Paradisaeidae	6.672	0.015*	0.055	0.013*	0.052	0.030*	0.090	0.281	0.507
Campephagidae	0.074	0.491	0.883	0.647	0.906	0.871	0.974	0.997	>0.999
Oriolidae	2.947	0.062	0.518	0.165	0.730	0.142	0.742	0.927	0.999
Pachycephalidae	−0.040	0.484	0.773	0.747	0.918	0.826	0.945	0.986	0.999

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

second best models (Yule model with one rate shift or Yule model in all cases) were below 3 for the Oriolidae and below 0.1 for the Pachycephalidae and Campephagidae.

 Significance of γ results for the 95th percentile of the posterior trees was very similar to results for the maximum clade credi-

bility tree in all families (Table 1). Equally, significance was only affected by our proportion of species sampled for the phylogenies if as little as 25% of the true number of Paradisaeidae species were known (the statistics for the 50% level were still significant). Using ΔAIC_{RC}, constant diversification rates for the Paradisaeidae

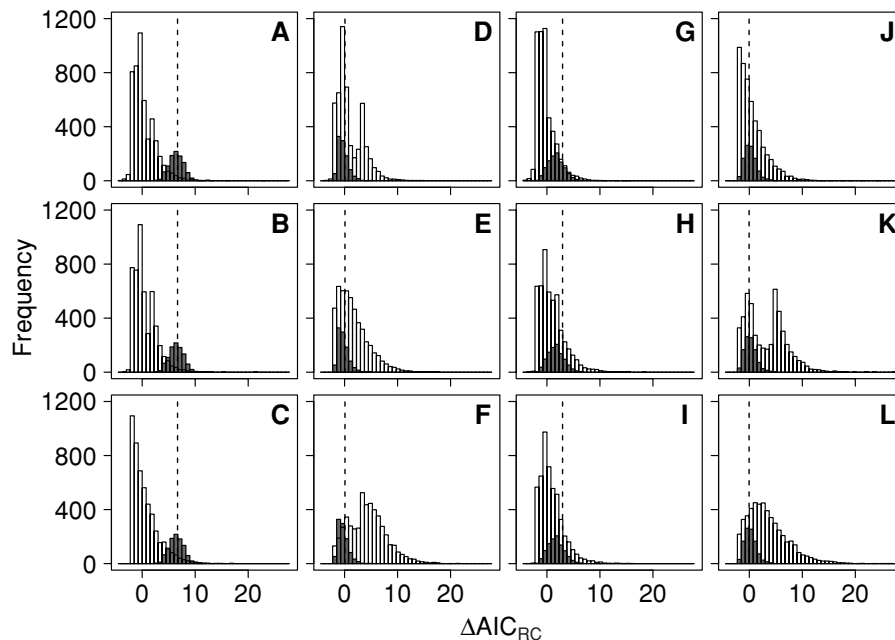**Figure 2.** Observed and simulated frequency distributions for the ΔAIC_{RC} statistic. (A–C) Paradisaeidae; (D–F) Campephagidae; (G–I) Oriolidae; (J–L) Pachycephalidae. Gray distributions are the observed frequency distributions of ΔAIC_{RC} from 1000 phylogenies randomly sampled from each posterior distribution; the corresponding value for the maximum clade credibility tree is shown by the dashed line. Transparent distributions are the simulated null distributions (5000 trees) when assuming different total species numbers: top row, 100% of species known; middle row, 75% known; bottom row, 50% known.

could not be rejected for the 95th percentile of the posterior trees (Table 1). However, *P*-values were only just above significance if 100% or 75% of species were assumed to be known, and there was very little overlap between the observed distribution of the ΔAIC_{RC} statistic for the posterior trees and the different null distributions simulated for the Paradisaeidae (Fig. 2). All results for the other three families were qualitatively the same for the maximum clade credibility tree and the 95th percentile of the posterior trees, as well as for all simulations taking different proportions of sampled species into account. Results for the Campephagidae did not change when the *Pericrocotus* and *Coracina* trees were analyzed separately (Supporting information).

The distribution of Paradisaeidae is relatively restricted, with most species in New Guinea and very few in northeastern Australia and Wallacea (Fig. 1E). The Campephagidae and the Oriolidae have spread throughout Australasia, continental Asia, Africa, and Europe, and the Pachycephalidae occur throughout the Indo-Pacific archipelagos, with one species on the Asian mainland (Fig. 1F–H). Paradisaeidae had the smallest species range sizes and highest species richness within grid cells at our study scale (Fig. 3). Species range-size frequency distributions had a much longer tail for Campephagidae, Oriolidae, and Pachycephalidae than for Paradisaeidae (Fig. 3A–D). The frequency distribution of species richness within grid cells was less steep for Paradisaeidae than for the other groups, that is, comparatively few grid cells contained low levels of species richness for Paradisaeidae (Fig. 3E–H). Skew and kurtosis of both frequency distributions were relatively lower for Paradisaeidae than for the other three families (Table 2). All skew and kurtosis statistics significantly deviated from a normal distribution, except for kurtosis values for both frequency distributions in Paradisaeidae.

Discussion

The differences in diversification trajectory and biogeographic patterns between the Paradisaeidae and each of the other families are striking. Whereas our results were concordant with a diversity-dependent pattern of diversification for the Paradisaeidae, we detected no apparent slowdown in diversification rates for the other families. Correspondingly, biogeographic patterns for the Paradisaeidae clearly differed from those of the other three families: species ranges were smaller on average and overlapped more at the spatial scale of our study. Both diversification and biogeographic patterns therefore offer some support for our hypothesis that island radiations with high dispersal and colonization abilities may show constant diversification rates through time, and less fine partitioning of niches. Our results are unusual when compared to most previous studies of avian taxa with similar numbers of species (e.g., Weir 2006; Phillimore and Price 2008; Rabosky and Lovette 2008a), presumably because the four
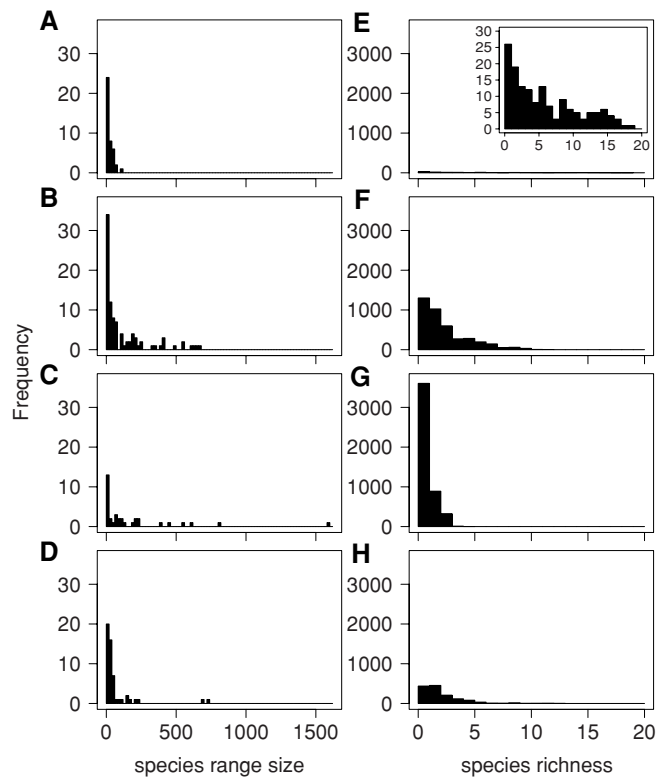

Figure 3. Species range-size frequency distributions (A–D) and frequency distributions of species richness within grid cells (E–H) for the four families. (A and E) Paradisaeidae; (B and F) Campephagidae; (C and G) Oriolidae; (D and H) Pachycephalidae. Species range size (in million km²) was measured as the total land area of occupied grid cells.

Table 2. Testing species range-size frequency distributions and frequency distributions of species richness within grid cells against the normal distribution. Species range size was measured as the total land area of occupied grid cells.

	Species range size		Species richness	
	Skew	Kurtosis	Skew	Kurtosis
Paradisaeidae	0.92*	0.38	0.73***	−0.66
Campephagidae	1.93***	2.81***	1.42***	1.67***
Oriolidae	2.06***	3.76***	1.77***	2.29***
Pachycephalidae	4.19***	17.27***	2.26***	6.82***

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

families analyzed in this study originated in a geologically dynamic insular setting. Notably, the large continental radiation of Furnariidae (Neotropical ovenbirds and woodcreepers) seems to have maintained constant diversification rates through time, possibly because furnariid birds span a geologically and climatically highly dynamic continent (Derryberry et al. 2011). Below, we first interpret our results in light of general diversity dependence of

diversification rates, assuming the existence of upper limits on the species richness of clades or regions ultimately arising from ecological processes (Rabosky 2009a). Then, we discuss alternative interpretations that do not assume existence of these ecological limits to diversity, and we conclude with discussing the statistical robustness of our results.

ECOLOGICAL LIMITS TO DIVERSITY

The diversification pattern and biogeographic patterns for Paradisaeidae are concordant with the idea of increased filling of ecological niches over time (Nee et al. 1992; Ricklefs 2006; Phillimore and Price 2009). In Paradisaeidae, diversification rates have apparently slowed down over time, and our biogeographic analyses indicated relatively high species richness within grid cells and a relatively high amount of small-ranged species. Progressively finer niche partitioning, for example during adaptive radiation, should lead to higher proportions of species with small geographic ranges, and to higher overlap of these species ranges on coarse spatial scales (Nee et al. 1992; Schluter 2000; Gavrilets and Vose 2005; McPeek 2008). This process is thought to eventually cause a slowdown in diversification rates as clade size reaches its so-called ecological limit (Rabosky 2009a). Our combination of diversification analyses and biogeographic patterns links these two hypotheses: the kurtosis and skew of range-size frequency distributions and of frequency distributions of species richness within grid cells clearly differentiated Paradisaeidae from the other three groups, in parallel to the difference in diversification statistics for phylogenetic branching patterns. These measures may therefore be a promising avenue for future research on describing niche partitioning across species within clades at the macroecological scale, compared to previously used measures such as the total geographic area occupied by the clade or the median number of co-occurring species (Phillimore and Price 2009). However, none of these measures are able to distinguish between the processes underlying limits to diversity, such as competition, low dispersal probability, or lack of geographic opportunities for speciation.

The diversification pattern of Paradisaeidae seems similar to the diversity-dependent patterns reported for a large number of other taxa (see Rabosky 2009a for a recent review). Why, then, do the patterns for Oriolidae, Pachycephalidae, and Campephagidae not conform to this apparently general pattern? Assuming that diversity dependence is universal, the three radiations may be too young to have reached their ecological limits yet. Especially, the Pachycephalidae are a clade much younger than the Paradisaeidae, which seem to have reached their diversity limit. Compared to the Paradisaeidae, our frequency distributions of species richness within grid cells for the other three families show that geographic ranges overlap much less at our coarse spatial scale, perhaps reflecting a potential for further ecological niche differentiation.

Assuming that diversity limits exist and have not been reached by our three families exhibiting patterns of constant diversification rates, our results suggest that these ecological limits differ between clades and regions. First, even clades originating in the same region at roughly the same time can have very different upper limits to their size, as suggested by our diversification patterns for Campephagidae and Paradisaeidae. Second, the species numbers in each of our three families are unusually large compared to the other bird clades for which patterns consistent with constant net diversification rates have been shown previously (Phillimore and Price 2008, 2009), and compared to the species number at which the species richness–age relationship across clades typically levels off (Ricklefs 2006). One exception from this general pattern of diversity dependence in large (avian) taxa is the Neotropical Furnariidae radiation, but these birds show unusual ecological divergence between subclades and species groups, and they span an entire, geologically highly dynamic continent (Derryberry et al. 2011). As our three families originated in island areas, unlike most previously studied avian clades, we suggest that geologically dynamic regions such as the Indo-Pacific archipelagos may allow higher ecological limits to clade size than continental regions usually do, by providing numerous opportunities for speciation (Mayr and Diamond 2001; Losos and Ricklefs 2009). In geologically dynamic archipelagos, new ecological opportunities open up frequently, or areas are repeatedly geographically isolated, which should lead to high speciation rates in successfully colonizing lineages (Bellemain and Ricklefs 2008). In concordance with our results for Campephagidae, Oriolidae, and Pachycephalidae, previous studies have suggested elevated or constant net diversification rates for shrews in the Philippines and day geckos in Indian Ocean archipelagos (Harmon et al. 2008; Esselstyn et al. 2009).

If ecological limits to diversity differ between clades, then presumably these limits are influenced not only by the region in which a clade diversified, but also by a clade's ability to disperse and colonize, and so ultimately by its ecological traits (Rabosky 2009a; Vamosi and Vamosi 2010). The geographical distribution of Paradisaeidae as a family, which seems to have reached their diversity limit, is much more restricted than that of each of the other three families. Similarly, decreasing diversification rates have been shown for the day gecko clade endemic to Madagascar, but not for the related clades in Indian Ocean archipelagos (Harmon et al. 2008). These findings suggest a link between geographic area occupied and ecological limits on clade size, and might relate to large-scale species–area relationships (Ricklefs 2006; Kisel et al. 2011). Restricted geographic ranges, both for the Paradisaeidae as a whole and for most of its species, may reflect low dispersal and colonization abilities. In contrast, our other three families have large geographical distributions and complex colonization histories from centers of

diversification in New Guinea across the Indo-Pacific archipelagos (Jønsson et al. 2010a,b,c). Likewise, a measure of annual dispersal correlated strongly with net diversification rates across bird families (Phillimore et al. 2006), and unusually species-rich radiations of mammals have been linked to colonization of new geographic areas (Kisel et al. 2011; Purvis et al. 2011) We further speculate that dispersal and colonization abilities within the families are determined by ecological traits. For example, most species of Paradisaeidae are promiscuous and use male display areas (Frith and Beehler 1998), which may restrict individuals' capacity for long-distance dispersal and thus limit the chances of establishing breeding populations in new areas (Irestedt et al. 2009).

ALTERNATIVE INTERPRETATIONS OF DIVERSIFICATION PATTERNS

The interpretation that our analyses show patterns of constant net diversification rates should be taken cautiously because our failure to reject the null hypothesis does not prove its validity. Also, the conclusion that sustained high speciation rates through time have generated the observed patterns is hypothetical, because only net diversification rates are inferred from molecular phylogenies, and the estimation of speciation and extinction rates from these is problematic. Hence, an alternative explanation for the diversification patterns in our three families could be that these families have already reached a diversity limit, but the signature of diversity dependence in their lineage-through-time plots has been erased by increasing or high extinction rates (Rabosky and Lovette 2008b; Quental and Marshall 2009; McInnes et al. 2011). Two observations support this hypothesis: first, it is generally assumed that extinction rates are high in island settings (e.g., Ricklefs 2010). Second, our lineage-through-time plots for Campephagidae, Oriolidae, and Pachycephalidae do not show the "pull of the present," that is, an upturn in net diversification rate toward the present that is expected under a birth–death model with constant, high death rates (Nee et al. 1994). Indeed, all our best models assumed no extinction at all, which seems unlikely but is a surprisingly common occurrence in analyses of lineage-through-time plots (Rabosky and Lovette 2008b; Quental and Marshall 2009). Recently introduced coalescent approaches, or the combination of molecular data with the fossil record if available, may prove superior in detecting extinction signatures (Liow et al. 2010; Morlon et al. 2010).

So far, we have assumed that diversity dependence of diversification rates is a general pattern, and that ecological processes limit the species richness of clades. However, other explanations exist for observed slowdowns in diversification rates. For example, a recent simulation study criticized the use of the birth–death model as a null hypothesis in phylogenetics for its lack of geographic context (Pigot et al. 2010). Pigot and colleagues simulated

ecologically neutral cladogenesis under geographic speciation, either through vicariance or peripatry, and found that several properties of the simulated phylogenies and species ranges approximated those of real avian clades. In their models, clades with rapid initial diversification experienced slowdowns because the geographic ranges of their species became smaller over time, making speciation less likely. The resulting patterns of diversification and geographic ranges are comparable to our patterns for Paradisaeidae, and to previous studies showing apparent diversity dependence. A pattern of constant net diversification arose when simulating peripatric speciation with moderate rates of range growth and high volatility of ranges over time (Pigot et al. 2010). This model seems quite reasonable for our three other families, given their origin in the Indo-Pacific and successful colonization of neighboring archipelagos and continents. Further development endeavoring to fit such geographically explicit, ecologically neutral diversification models to real clades seems a promising approach.

Finally, it has been argued recently that the common finding of diversification patterns with a slowdown does not mean that these slowdowns are in fact common, because the patterns may actually arise from researcher selection of study groups or low proportions of sampled species (Phillimore and Price 2008; Cusimano and Renner 2010). The focus on taxa with continental origin in previous studies may have led to the common finding of diversity-dependent patterns, with an overlooked predominance of patterns concordant with constant diversification rates through time in archipelagos (Harmon et al. 2008; Esselstyn et al. 2009). Even though Moyle et al. (2009) found a slowdown in diversification rates for *Zosterops* in Southeast Asia and Africa, that result may have been caused by the rather low proportion of sampled taxa. The literature so far may be biased against island-origin taxa because researchers generally choose to study well-defined clades with a large but manageable number of species, which are less likely to be from archipelagos given the sampling difficulties and taxonomic issues involved. Due to the preference for species-rich groups, researchers are also more likely to work on clades that have reached saturation, or clades that show apparent diversity dependence by chance (Phillimore and Price 2008).

STATISTICAL ROBUSTNESS OF OUR RESULTS

Our results appear robust to uncertainty of phylogenetic reconstruction, because results for a random sample of 1000 posterior trees from the Bayesian phylogenetic reconstruction were consistent with those for the maximum clade credibility tree. However, we acknowledge that the two different procedures used to obtain absolute divergence times for the four phylogenies may affect direct comparisons between taxa. Although the different dating strategies were chosen to reflect most realistic time estimates for each family, particularly the Pachycephalidae would be estimated as older if dated within the standard

2% mtDNA rate framework (Weir and Schluter 2008). Because the dating procedure should affect all time estimates within a phylogeny, we think that the comparison of diversification trajectories is still valid.

Our simulations of expected distributions for the statistic measures of diversification rates through time accounted for the effects of unsampled or unknown species, if these were missing from the phylogenies at random. Although this assumption of random phylogenetic sampling may have been violated, the high proportions of species sampled in our phylogenies should limit the inflation of type I error rates, that is, the probability of incorrectly rejecting the null hypothesis of constant diversification rates when it is in fact true (Cusimano and Renner 2010). The phylogeny for the Paradisaeidae included all but one known species, which makes it unlikely that the observed slowdown in diversification rates was caused by low sampling. Likewise, it is improbable that only 25% of the species of Paradisaeidae are known to science or have survived to the present (Frith and Beehler 1998), the only case for which we could not reject constant diversification rates. The only family for which we sampled less than 80% of known species (the minimum recommended by Cusimano and Renner 2010) was the Pachycephalidae, but because we could not reject the null hypothesis for this family, our sampling did not cause inflation of type I error.

Another bias, which we (and comparative studies in general) have been unable to address adequately, may arise because of differences in species concepts. For objectivity, we used a recognized global taxonomy, but we recognize that different taxonomists have followed different practices in their treatment of island forms, some authorities defining all isolated and diagnosable populations as separate species, others trying to combine them as polytypic superspecies (see Mayr and Diamond 2001). Our study, as well as any other study investigating multiple species groups across large regions, will be subject to such taxonomic biases.

Finally, we investigate diversification patterns through time for whole families, whereas previous studies have focused mainly on genera (Weir 2006; McPeek 2008; Phillimore and Price 2008). A meaningful rationale for studying diversification should be the analysis of monophyletic clades consisting of closely related species, that is, of single but separate radiations, whether they are at genus or family level. This condition is true for our families: the phylogenies for Pachycephalidae and Oriolidae are dominated by their nominate genera (*Pachycephala*, 27 of 36 species; *Oriolus*, 28 of 31 species), for which we expect family-level diversification patterns to hold. The two separate phylogenies of Campephagidae conform to our condition of single radiations, and they show qualitatively similar patterns to the family level when analyzed separately (Supporting information; one tree for *Pericrocotus* and the other dominated by *Coracina*). Finally, the Paradisaeidae con-

sist of 41 species in 16 genera, with generic splitting mainly based on sexually selected traits. Therefore, we may argue that the family comprises two radiations only, corresponding to the two main clades on the phylogeny (Irestedt et al. 2009). These two clades have approximate crown ages of 18 and 16 Mya (cf. the upturn around that time in Fig. 1A), and most nodes are clustered in the early history for both. In conclusion, all family patterns we show should hold at meaningful lower levels of clade definition, although we also believe that the question of taxonomic scale and its consequences for diversification rate analyses would be an interesting opportunity for more comprehensive comparative studies.

Conclusion

There are several possible mechanisms producing the patterns of diversification rates and species ranges we found for our four island-origin radiations. We suggest that the dynamics of extensive island systems may allow for sustained high net diversification rates, at least for a surprisingly long time, through several possible mechanisms. These processes depend on dispersal ability and colonization success of the clades involved, and our suggestions assume that diversity dependence of diversification rates is a general pattern, with most likely ecological processes setting upper limits to species richness in clades or regions. As illustrated by our study, a general understanding of diversification dynamics and the resulting biogeographic patterns depends on obtaining results from a broader array of cases, for example, from species-poor and species-rich taxa, and those originating within continents and archipelagos. Interpretations of the underlying processes will benefit from linking these patterns to additional biogeographic and ecological data on species-richness patterns, species range-size frequency distributions, dispersal and colonization ability, ecological traits, and not least to ecological processes at smaller scales influencing species assembly processes.

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Supporting Information

The following supporting information is available for this article:

Table S1. Testing for constant diversification rates using the γ and ΔAIC_{RC} statistics.
Figure S1. Lineage-through-time plots (A–B) and species richness maps (C–D) for the two campephagid phylogenies.
Figure S2. Observed and simulated frequency distributions for the ΔAIC_{RC} statistic for the two campephagid phylogenies.

Supporting Information may be found in the online version of this article.

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