



# The Tortoise and the Finch: Testing for island effects on diversification using two iconic Galápagos radiations

Cristian Román-Palacios | John J. Wiens 

Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona

## Correspondence

John J. Wiens, Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ.  
Email: wiensj@email.arizona.edu

## Funding information

University of Arizona; NSF, Grant/Award Number: DEB 1655690

Editor: Brent Emerson

## Abstract

**Aims:** Islands are widely recognized as natural laboratories for evolutionary studies, but many questions about evolution on islands remain unresolved. Here we address two general questions from a macroevolutionary perspective. First, do lineages on islands have increased diversification rates relative to mainland lineages? Second, does the same geographical context (e.g., same archipelago) have similar effects on diversification in unrelated groups? We focused on Darwin's finches and Galápagos tortoises, two endemic radiations from the Galápagos Islands, and the larger families in which they are embedded.

**Location:** Global.

**Methods:** We estimated a new time-calibrated phylogeny for tortoises (Testudinidae). Then, we examined their macroevolutionary patterns and compared them to those of Darwin's finches and relatives (Thraupidae), using a published thraupid tree. Specifically, we estimated and compared diversification rates between islands and the mainland and between the Galapagos Islands and all other regions, using clade-based and species-based approaches.

**Results:** Contrary to expectations, occurrence on islands in general did not significantly increase diversification rates in tanagers or tortoises. However, occurrence in the Galápagos Islands in particular was associated with increased speciation and diversification rates, and explained ~28% of the variation in diversification rates for thraupids and ~46% for testudinids. Both Darwin's finches and Galápagos tortoises were unique within each family in exhibiting the highest diversification rates. The congruence of these macroevolutionary patterns between both radiations supports a strong "place-dependent" effect on diversification associated with the Galápagos. Finally, we found that Darwin's finches diversified ~2–8 times faster than Galápagos tortoises.

**Main conclusions:** Our results show that occurring on islands in general did not increase diversification rates in these clades, but occurrence in the Galápagos did. We also show that dramatic local-scale differences in diversification rates between clades in the Galápagos parallel global-scale differences in diversification rates between these families and between birds and turtles overall.

## KEYWORDS

diversification, islands, phylogeny, speciation, Testudinidae, Thraupidae



## 1 | INTRODUCTION

Islands and archipelagos are widely recognized as natural laboratories for evolutionary studies, and drivers of evolutionary radiations. Yet, it remains unclear whether occurring on islands in general, or on certain islands in particular, can significantly accelerate lineage diversification (relative to occurring on the mainland). By diversification, we mean the rate at which clades accumulate species (speciation minus extinction), such that clades with higher diversification rates have evolved many species in a relatively short period of time. More than 400 papers have been published on adaptive radiations from islands (Soulebeau et al., 2015). These studies suggest that diversification of island lineages is shaped by several factors, including geographical isolation, ecological opportunity, and island-specific environmental factors (e.g., Losos & Ricklefs, 2009; Warren et al., 2015). However, few studies have tested whether islands accelerate diversification by explicitly comparing rates between mainland and island lineages. Some previous studies suggested this pattern (e.g., Baldwin & Sanderson, 1998; Garcia-Porta & Ord, 2013; Grant, 1999; Morales-Hojas & Vieira, 2012), but did not provide a statistical test or a quantitative assessment of how much variation in diversification rates among clades is explained by the occurrence of some clades on islands. Similarly, to our knowledge, few studies have quantitatively evaluated the impact of occurring in particular island groups on diversification rates. This latter question is important for distinguishing whether islands have a general effect (or just particular islands) and for identifying factors that might make some islands better drivers of diversification than others (e.g., Valente, Etienne, & Phillimore, 2014).

Here we test whether occurring on islands in general (and certain islands in particular) accelerates diversification. Our analyses are based on two families that encompass Darwin's finches and Galápagos tortoises, two iconic radiations from the Galápagos Islands. Darwin's finches are classified within tanagers (Thraupidae), the second richest avian family (386 species; Burns, Hackett, & Klein, 2002; Burns et al., 2014; Clements et al., 2016). Tanagers include many island endemics (on many archipelagos) and many mainland species, making them an excellent model system for testing island effects on macroevolution. Darwin's finches include 14 species endemic to the Galápagos (forming a nonmonophyletic group called Galápagos finches; Burns et al., 2002) and one species endemic to nearby Cocos Island. There are also nine species on other Pacific Islands that also occur on the mainland (Lepage, Vaidya, & Guralnick, 2014). Nineteen thraupid species are island endemics in the West Indies, along with 31 species that each occur on both Caribbean islands and the mainland (Lepage et al., 2014). Additionally, four species (Gough finch and Tristan da Cunha finches) are endemic to islands in the southern Atlantic Ocean (Lefebvre, Ducatez, & Audet, 2016). Previous analyses in tanagers (Burns et al., 2014) suggested that there was accelerated speciation in both Darwin's finches (island) and a mainland clade (within Sporophilinae), but did not test whether speciation or diversification rates were significantly impacted by occurring on islands (or in the Galápagos) in this family.

Galápagos tortoises belong to Testudinidae, a family of 59 currently recognized modern species (Uetz & Hošek, 2016). Nineteen species (in three genera) occur on archipelagos and have been considered island-associated adaptive radiations (Austin & Arnold, 2001; Austin, Arnold, & Bour, 2003; Palkovacs, Marschner, Ciofi, Gerlach, & Caccone, 2003). These include: (a) *Chelonoidis* (Beheregaray et al., 2004), including 11 species from the Galápagos (Poulakakis, Russello, Geist, & Caccone, 2012; Poulakakis et al., 2015), (b) *Aldabrachelys*, with three species from Madagascar and the Seychelles (Austin et al., 2003), and (c) *Cylindraspis*, consisting of five recently extinct species from the Mascarene Islands (Austin & Arnold, 2001). Few studies have addressed macroevolutionary patterns in tortoises. In an analysis across turtles, Rodrigues and Diniz-Filho (2016) found that Galápagos tortoises had higher speciation rates than most other turtle clades in some results (using BAMM; Rabosky, 2014), but more frequently had an identical speciation rate to other turtle clades. They concluded that island invasions in general increased diversification rates. However, no studies have directly tested whether occurring on islands (or particular islands) significantly impacts diversification in tortoises.

Here, we test whether clades that diversified on islands (and the Galápagos) diversified at faster rates than their mainland relatives. Thus, we must include clades that occur on the mainland, in the Galápagos, and on other islands (to compare rates among these categories). We utilize extensive time-calibrated phylogenies for our two focal groups, including a new tree for testudinids and a published tree for thraupids. Within each family, we first estimate diversification rates for each genus-level clade. Then, using phylogenetic regression, we test if diversification rates are significantly related to occurring on islands in general, or occurring specifically on the Galápagos. Note that phylogenetic regression should be valid even if a trait occurs in a single clade, although this pattern can make it harder to obtain significant results. Next, using State-Dependent Speciation and Extinction models (SSE; FitzJohn, Maddison, & Otto, 2009), we test for overall differences in rates of speciation, extinction, and diversification between all islands and the mainland and between the Galápagos Islands and all other regions, without defining clades a priori. Contrary to expectations, our results show that occurring on islands in general does not have a significant impact on diversification rates in either tanagers or tortoises, even though both groups contain clades that diversified rapidly on the Galápagos.

## 2 | METHODS

### 2.1 | Tree for Thraupidae

We used the time-calibrated phylogeny for New World nine-primaried oscines (superfamily Emberizoidea) from Barker, Burns, Klicka, Lanyon, and Lovette (2015), which includes 353 of 386 described thraupid species (Clements et al., 2016). This tree was based on a concatenated analysis of several mitochondrial and



nuclear genes. We trimmed this tree to include only thraupids, using the R package *APE* version 3.5 (Paradis, Claude, & Strimmer, 2004).

## 2.2 | Tortoise phylogeny

For tortoises, we generated a new time-calibrated phylogeny (Figure 1), based on data in GenBank (Appendix S1, Table S1). To our knowledge, this is the most comprehensive time-calibrated tree for Testudinidae. Detailed methods are provided in Appendix S2. In short, we estimated relationships and divergence times simultaneously using *BEAST* 2.2.3 (Bouckaert et al., 2014). We analysed four mitochondrial genes and one nuclear gene. The data matrix is included as Supplementary File S1 (note: Supplementary Files S1–S8 will be available on Dryad). The estimated tree and divergence times (Figure 1) are described and compared to other recent estimates in Appendix S2. Overall, the topology and divergence times were broadly similar to those estimated in other recent studies.

## 2.3 | Clade-level diversification analyses

We first tested for a relationship between clade-level diversification rates and occurrence on islands (and the Galápagos specifically) using phylogenetic generalized-least squares regression (PGLS; Martins & Hansen, 1997). This allowed us to test how much variation in diversification rates is explained by occurrence on islands. Diversification rates for each tortoise and tanager genus were estimated using the method-of-moments estimator (ME; Magallón & Sanderson, 2001) implemented with the *bd.ms* function in the R package *GEIGER* version 2.0.6 (Pennell et al., 2014). Rates based on crown and stem-group ages were closely related (tortoises:  $r^2 = 0.7697$ ,  $p < 0.0001$ ; tanagers:  $r^2 = 0.9977$ ,  $p < 0.0001$ ; using PGLS as described below). However, the crown-group estimator cannot be used for monotypic genera (and these genera were excluded in the preceding analyses). Furthermore, the crown-group estimator is generally less accurate in simulations (Meyer & Wiens, 2018). Therefore, we emphasize results based on stem-group ages. Diversification rates were estimated based on richness data for each genus from the ReptileDatabase (Uetz & Hošek, 2016) and Avibase (Lepage et al., 2014). One tortoise genus (*Homopus*) and six thraupid genera were paraphyletic. In these cases, we combined paraphyletic and monophyletic genera into a single clade (e.g., *Chersina* is inside *Homopus*, and together these genera form a monophyletic group). Polyphyletic thraupid genera (12 of 94) were more difficult to deal with, and were simply excluded from these clade-based analyses. For brevity, we refer to all clades in these analyses as “genera” even though some contained more than one genus.

The ME estimator uses a correction for clades that are unsampled due to extinction, called the relative extinction fraction ( $\epsilon$ ). This value is usually assumed for the entire tree rather than estimated for individual clades. Following standard practice, we compared results utilizing low ( $\epsilon = 0$ ), medium ( $\epsilon = 0.5$ ), and high ( $\epsilon = 0.9$ ) epsilon values, corresponding to different levels of extinction relative to speciation. Results are shown using  $\epsilon = 0.5$ , but all three values were used

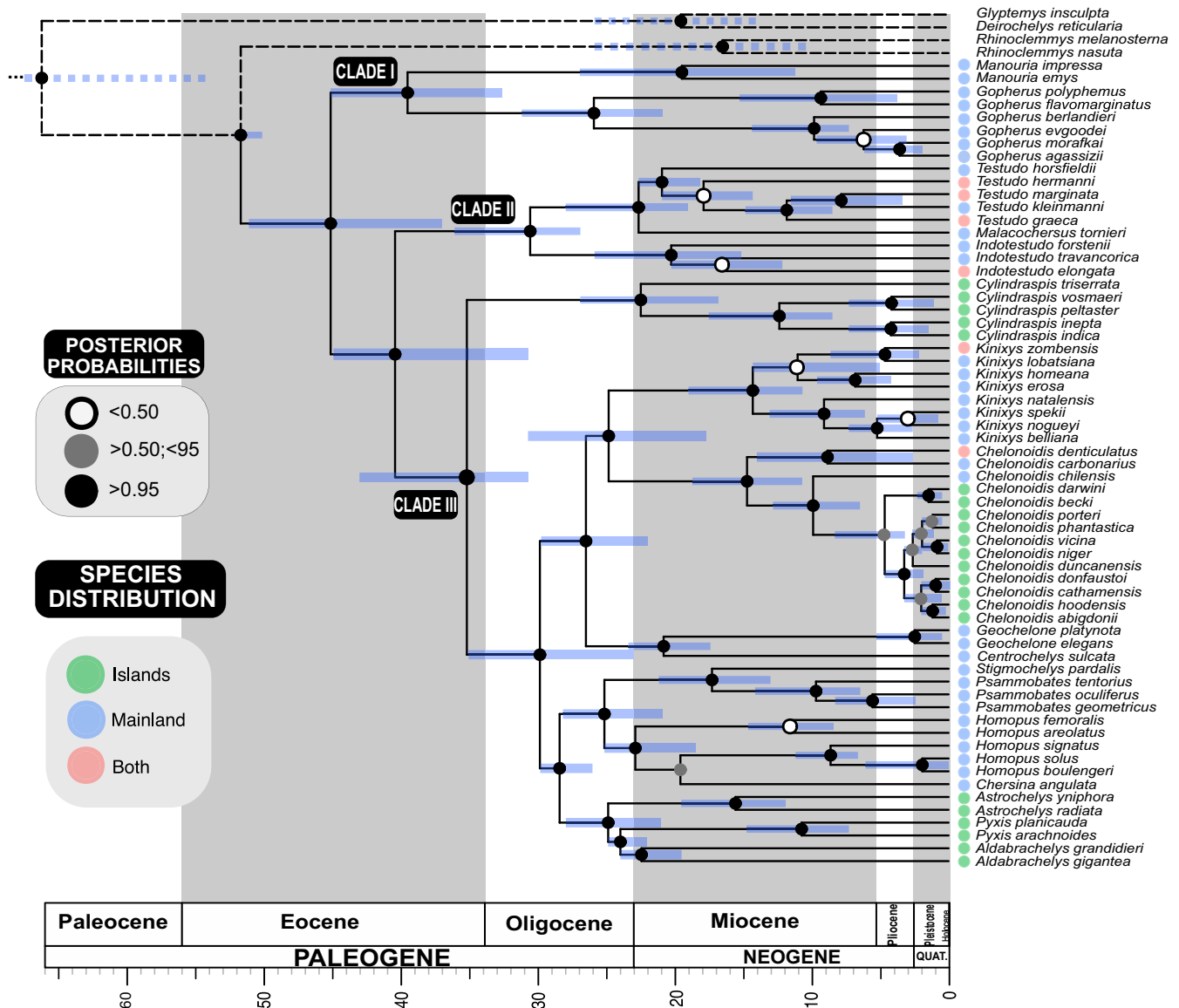
(Appendix S1, Tables S3 and S4 for tanagers and tortoises). Results were similar across different values, and simulations suggest that different values yield similar relationships between true and estimated stem-based rates (Meyer & Wiens, 2018).

Some studies have stated that the ME estimator will be inaccurate without a strong, positive correlation between clade ages and species richness (e.g., Rabosky, Slater, & Alfaro, 2012). However, these studies did not actually address the accuracy of the ME estimator. Instead, recent simulations show that the ME estimator is relatively accurate (i.e., strong relationships between true and estimated rates and relatively unbiased rate estimates) regardless of the relationship between clade ages and richness (Kozak & Wiens, 2016; Meyer & Wiens, 2018). Furthermore, the ME estimator depends only on the age and richness of clades (i.e., young clades with many species will have higher estimated net diversification rates than older clades with fewer species), regardless of changes in instantaneous rates within clades (among subclades or over time). Simulations have now explicitly shown that heterogeneity in rates within clades need not impact the accuracy of the ME estimators (Meyer & Wiens, 2018). Variation in diversification rates over time might decouple richness and diversification (e.g., Kozak & Wiens, 2016), but our focus here is only on diversification rates.

Genera are somewhat arbitrary taxonomic constructs. However, monophyletic genera (or groups of genera) offer a set of non-nested clades of similar age for comparison, and differences in ages are accounted for using diversification rates rather than raw richness values. We also performed similar analyses using SSE analyses (see below), which gave similar results (see Results), and do not depend on delimitation of genera.

We did not use BMM (Rabosky, 2014). Recent simulations show that BMM yields much weaker relationships between true and estimated diversification rates than ME estimators (Meyer & Wiens, 2018), given that it underestimates the number of distinct diversification rates present among subclades across a tree. Other simulations suggest that BMM does not accurately estimate diversification, speciation, and/or extinction rates (Moore, Höhna, May, Rannala, & Huelsenbeck, 2016; Rabosky, 2014). Moreover, Meyer and Wiens (2018) found that BMM can yield misleading results for empirical data, with no significant relationship between rates estimated from BMM for the same subclades in isolation and when estimated across a tree. We tested this prediction for tanagers and tortoises, using genera as subclades (see Appendix S3). Overall, the two sets of BMM estimates for the same clades were dissimilar and unrelated (tanagers:  $r^2 = 0.002$ ,  $p = 0.8127$ ; tortoises:  $r^2 = 0.2389$ ,  $p = 0.0901$ ). Importantly, analyses of genera in isolation inferred considerable variation in rates among genera, whereas family level analyses assigned very similar rates to almost all genera.

PGLS analyses were conducted in the R package *CAPER* version 0.5.2 (Orme et al., 2013). For PGLS analyses, branch lengths were transformed based on the estimated phylogenetic signal ( $\lambda$ ; Pagel, 1999), and the delta and kappa branch-length parameters were each fixed at one (following standard practice). The null hypothesis of independence between diversification rates for genera



**FIGURE 1** BEAST chronogram showing relationships among tortoises (Testudinidae). We found weak support for the position of *Cylindraspis* based on an unconstrained tree (Figure S1; Supplementary File S2). However, this is presumably caused by the limited gene sampling for this extinct genus, and its inclusion does not alter relationships among the other species (tree excluding *Cylindraspis* is provided in Figure S3; Supplementary File S4). We show here the support values for a tree in which the position of *Cylindraspis* was constrained to be the sister to all other members of Clade III, as found in the unconstrained topology (tree in Supplementary File S3). Support values across the tree increased when the position of *Cylindraspis* was constrained (Figure S2). The geographical distribution is indicated for each species

(dependent variable) and their proportion of insular species (independent variable) was tested. We estimated the proportion of insular species in each testudinid genus using Itescu, Karraker, Raia, Pritchard, and Meiri (2014). For tanagers, we used Schulenberg (2014), BirdLife International (2016), Avibase (Lepage et al., 2014), and Jiménez-Uzcátegui, Wiedenfeld, Vargas, and Snell (2017). Both families contain island-immigrant species (i.e., species having populations on both islands and the mainland: 2% of tanagers and ~12% of tortoise species). Therefore, we analysed the impact of insularity in each family based on two datasets. First, we considered only island-endemic species to be island species (the most relevant definition for evaluating island effects on diversification). Second, we also

considered immigrant species as island species. For PGLS analyses, genus-level phylogenies for tortoises and tanagers were constructed by pruning all but one species in each genus-level clade (the choice of species has no impact, since all give the same branch length on the pruned tree). For thraupid genera, diversification rates are in Appendix S1, Table S3, distributions are in Appendix S1, Table S5, and the tree is in Supplementary File S5. For testudinid genera, diversification rates are in Appendix S1, Table S4, distributional data in Table S6, and the tree is in Supplementary File S6.

For thraupids, excluding polyphyletic lineages removed 9 of 11 Caribbean endemic genera (Lepage et al., 2014). Therefore, the PGLS analysis may not give a fully accurate estimate of island effects on



diversification for tanagers. Nevertheless, the SSE analyses incorporated all Caribbean species, and gave similar results to the PGLS analyses (see Results).

We also tested if the same geographical context (Galápagos Islands) had a significant impact on diversification rates in tanagers and tortoises. For tanagers, all species from the same genus were either present or absent from the Galápagos (Appendix S1, Table S5). We therefore treated the occurrence of each thraupid clade in the Galápagos as the independent variable in the PGLS analyses. For tortoises, we used the proportion of species in each clade in the Galápagos as the independent variable in the PGLS analyses (Appendix S1, Table S6).

We recognize that each family contains only one invasion of the Galápagos, and thus only one data point each for statistical analyses. However, this paucity of Galápagos clades should make it more difficult to obtain significant results using PGLS, rather than easier. Nevertheless, we performed additional analyses to specifically test whether diversification rates in the single Galápagos clade in each family deviated significantly from the distribution of rates among the non-Galápagos clades. We used one-sample student *t* tests to address whether diversification rates of the non-Galápagos clades were significantly slower than the mean rate of the endemic Galápagos clades (i.e., one-tailed test). We used the three relative extinction fractions for both crown and stem-group ME estimators. Darwin's finches were considered the Galápagos clade for tanagers (i.e., *Geospiza*, *Camarhynchus*, *Certhidea*, *Pinaroloxias*). We subdivided *Chelonoidis* into three clades for estimating diversification rates, including the two mainland clades (*C. denticulatus* + *C. carbonarius*, and *C. chilensis*) and the Galápagos-endemic clade including the remaining species. This analysis was not phylogenetically corrected and was merely included as an alternative to the PGLS results, which were phylogenetically corrected.

## 2.4 | Species-level diversification analyses

We also used SSE to compare rates of speciation, extinction, and diversification between the mainland and all islands, and between the Galápagos and all other areas. These analyses allowed us to estimate additional rates (speciation, extinction), and without specifying clades a priori. For tanagers, we also compared diversification rates between Caribbean islands and all other areas, given the problem of polyphyletic genera mentioned above. Analyses were based on BiSSE (Binary State Speciation and Extinction; Maddison, Midford, Otto, & Oakley, 2007) and GeoSSE (Geographic State Speciation and Extinction; Goldberg, Lancaster, & Ree, 2011) models. GeoSSE allows species to be distributed simultaneously in two areas (e.g., immigrant species having populations on both islands and the mainland). However, BiSSE was used for estimating macroevolutionary parameters in tortoises and tanagers (for the Galápagos analyses), because no species occurs both on the mainland and in the Galápagos. We analysed GeoSSE and BiSSE models in the R package DIVERSITREE (FitzJohn et al., 2009) and compared parameters between (a) islands versus mainland (GeoSSE), and (b) Galápagos Islands versus all other areas (BiSSE). We also used GeoSSE to compare tanager diversification on Caribbean

islands versus all other areas. For each comparison, we first analysed an unconstrained model with speciation ( $\lambda_0, \lambda_1, \lambda_{01}$ ), extinction ( $\mu_0, \mu_1$ ), and dispersal ( $q_{01}, q_{10}$ ) varying freely between areas (where subscripts 0 and 1 indicate different areas). The second model constrained speciation rates to be similar between areas ( $\lambda_0 \sim \lambda_1$ ), with all other parameters free to vary. A third model was fitted with the same structure as the second model, but which also constrained speciation in species that occur in both areas to be zero ( $\lambda_{01} = 0$ ; see Goldberg et al., 2011). A fourth model constrained only extinction to be similar between areas ( $\mu_0 \sim \mu_1$ ). In the fifth model, only dispersal rates were constrained to be similar between areas ( $q_{01} \sim q_{10}$ ). Lastly, we tested if diversification rates were equivalent, and constrained both speciation ( $\lambda_0 \sim \lambda_1$ ;  $\lambda_{01} = 0$ ) and extinction ( $\mu_0 \sim \mu_1$ ) rates to be similar between areas. BiSSE models were equivalent to GeoSSE but estimated speciation only within each geographical category ( $\lambda_0, \lambda_1$ ), with no category for species in both areas ( $\lambda_{01}$ ; i.e., there is no model three in BiSSE).

These likelihood models were fitted through the `find.mle` function in DIVERSITREE, and were compared using the AIC (Akaike, 1974). The best-fitting model had the lowest AIC. For the best-fitting model for each clade, we also estimated the posterior distributions of parameters using the `mcmc` function in DIVERSITREE, using ten million generations each. The species-level trees used in these analyses are provided in Supplementary Files S7 and S8 (for testudinids and thraupids, respectively). Trait data are provided in Appendix S1, Tables S7 and S8 for thraupids and testudinids.

There has been some controversy about SSE estimators (e.g., Maddison & FitzJohn, 2015; Rabosky & Goldberg, 2015). Furthermore, tortoises may have limited power for SSE analyses (e.g., Davis, Midford, & Maddison, 2013), with only 58 species. However, our SSE results generally parallel those from the ME estimators, suggesting that our conclusions are not an artifact of potential problems associated with either approach.

## 3 | RESULTS

### 3.1 | Clade-level diversification analyses

Clade-level analyses (using PGLS) did not support islands in general as significant drivers of diversification in tanagers or tortoises, but showed that occurrence in the Galápagos was important for diversification in both clades. For tanagers, the mean diversification rate for genera containing island-endemic species was 0.0558 events/Myr, and the mean rate for mainland genera was very similar (0.0529 events/Myr; all results based on stem-group ages and  $\epsilon = 0.5$ ; full results in Appendix S1, Table S3). Insularity had no significant impact on diversification in tanagers (Table 1), regardless of whether island species included only endemics or also included immigrant species.

In tortoises, the average diversification rate of mainland clades was 0.0248 events/Myr, which was very similar to the mean rate for genera containing island endemics (0.0240 events/Myr) and for all genera containing island species (both endemic and immigrant; 0.0257 events/Myr; Appendix S1, Table S4). Insularity showed no significant relationships with diversification (Table 1; island



endemics:  $r^2 = 0.0177$ ,  $p = 0.6799$ ; island endemics and immigrants:  $r^2 = 0.0182$ ,  $p = 0.6754$ ).

In contrast, occurrence in the Galápagos explained 28% of the variation in diversification rates for tanagers ( $r^2 = 0.2759$ ,  $p < 0.0001$ ) and 46% for tortoises ( $r^2 = 0.4557$ ,  $p = 0.0160$ ; Table 1). These results were highly significant despite the limited power associated with a single invasion of the Galápagos in each family. The net diversification rate for Darwin's finches was 26 times higher than the mean rate among other tanager clades (see Table 2 for Darwin's finches and Appendix S1, Table S3 for all other thraupid clades). The rate for Galápagos tortoises was seven times higher than that for non-Galápagos clades (Table 2). The other island-endemic genera, *Aldabrachelys* and *Cylindraspis*, had rates similar to the mean rate (Appendix S1, Table S4). The net rate for Galápagos tortoises was 0.1830 events/Myr and 1.3772 events/Myr for Darwin's finches (Table 2). Thus, Darwin's finches diversified ~7.5 times faster than Galápagos tortoises in the same archipelago.

We also compared estimated diversification rates for the non-Galápagos clades to the mean rate of diversification in the Galápagos using one-sample student t-tests (Appendix S1, Table S9). These results corroborated those from PGLS (see above). Diversification rates for non-Galápagos tanagers and tortoises were significantly lower than for the Galápagos endemics (e.g., tanagers:  $t = -24.9594$ ,  $p < 0.0001$ ; tortoises:  $t = -11.9528$ ,  $p < 0.0001$ ).

### 3.2 | Species-level diversification analyses

The results from SSE analyses also failed to support a positive effect of islands on diversification, but confirmed the significant impact of the Galápagos on diversification and speciation in both groups. When comparing islands and mainland for testudinids (Appendix S1, Table S10), the best-fitting GeoSSE model had speciation and extinction rates constrained to be similar between the mainland and islands. Alternative models with similar fit (AIC differences <2) had different

speciation and extinction rates but actually showed faster diversification rates on the mainland than on islands (Appendix S1, Table S11).

For tanagers, the best-fitting model had similar speciation and extinction rates between mainland and islands (and therefore equal diversification rates), with all other models having much poorer fit (AIC differences >12; Appendix S1, Table S10). Comparing Caribbean tanagers to those in all other areas, the best-fitting model had different speciation rates between regions but constrained extinction rates to be similar (Table S12), with slower speciation and diversification rates in Caribbean tanagers (Appendix S1, Table S13).

Lastly, we compared rates (from SSE) between the Galápagos and all other regions (both mainland and other islands). For tortoises, the best-fitting model had similar dispersal rates between regions, with speciation and extinction rates significantly different (Figure 2; Appendix S1, Table S14). For tanagers, the best-fitting model had different rates for all parameters (Figure 2; Table S14). Speciation rates for Galápagos tortoises were >5 times higher than for other regions (0.3583 vs. 0.0641 events/Myr; Appendix S1, Table S15). Speciation rates for Galápagos tanagers were six times higher than for other regions (1.1169 vs. 0.1887 events/Myr; Appendix S1, Table S15). Diversification rates (speciation minus extinction; Table S15) were also much higher in the Galápagos than in other regions (Galápagos tortoises: 0.2656 vs. 0.0553 events/Myr; Darwin's finches: 0.5038 vs. 0.1737 events/Myr). For tanagers, the difference in diversification rates between the Galápagos and other regions was dampened somewhat by the inference of relatively high extinction rates in the Galápagos.

## 4 | DISCUSSION

### 4.1 | Overview

In this paper, we ask a fundamental but somewhat neglected question in evolutionary biology: do islands in general (and certain islands

**TABLE 1** Summary of PGLS results for tortoises and tanagers testing the relationship between two traits (insularity, Galápagos) and diversification rates. Results are shown for stem-group ages using three relative extinction fractions ( $\epsilon$ ). Analyses were conducted either treating only island endemics as island species or else treating both island endemics and immigrant species (occurring on both islands and mainland) as island species. For both tanagers and tortoises, the only species that occur in the Galápagos are endemic to the archipelago. Diversification rates and geographical data are given in Appendix S1, Tables S3 and S5 (tanagers), and Tables S4 and S6 (tortoises). The genus-level trees used are in Supplementary Files S5 (tanagers) and S6 (tortoises). Full results, including those for crown-group estimators, are given in Appendix S1, Table S9. For tanagers, results using the crown-group estimator sometimes conflict with those from the stem-group estimator. This seems to occur because of the large number of monotypic tanager genera, which were included in the stem-group analyses but excluded for the crown-group analyses

Group	Clade age	Relative extinction fraction ( $\epsilon$ )	Island: endemics		Island: endemics + immigrants		Galápagos Islands: endemics	
			$r^2$	$p$	$r^2$	$p$	$r^2$	$p$
Tanagers	Stem	Low (0)	0.0302	0.1229	0.0121	0.3308	0.2879	<0.0001
		Medium (0.5)	0.0278	0.1388	0.0118	0.3367	0.2759	<0.0001
		High (0.9)	0.0157	0.2667	0.0076	0.4416	0.1959	<0.0001
Tortoises	Stem	Low (0)	0.0129	0.7250	0.0110	0.7462	0.4007	0.0272
		Medium (0.5)	0.0177	0.6799	0.0183	0.6754	0.4557	0.0160
		High (0.9)	0.0302	0.5885	0.0394	0.5366	0.5854	0.0037



**TABLE 2** Diversification rates for Darwin's finches and Galápagos tortoises estimated using three values of  $\epsilon$  and stem-group ages, along with results of PGLS regression between diversification rates and the proportion of species in the Galápagos. Two different phylogenetic regressions were performed for Darwin's finches. In the first one, the relationship between diversification rates and occurrence in the Galapagos was tested by considering *Geospiza* and *Certhidea* as independent clades ("Multiple genera" column, as in Appendix S1, Table S3). For the second, we considered Darwin's finches as a single clade ("Single clade"). Note that  $n$  is the number of included genera

Analysis	Relative extinction fraction ( $\epsilon$ )	Darwin's finches		Galápagos tortoises
		Multiple genera ( $n = 2$ )	Single clade ( $n = 4$ )	
Rate of diversification	Low (0)	—	1.5632	0.2449
	Medium (0.5)	—	1.3772	0.1830
	High (0.9)	—	0.6138	0.0708
PGLS	Low (0)	$r^2 = 0.2879$ ; $p < 0.0001$	$r^2 = 0.7151$ ; $p < 0.0001$	$r^2 = 0.4007$ ; $p = 0.0272$
	Medium (0.5)	$r^2 = 0.2759$ ; $p < 0.0001$	$r^2 = 0.8040$ ; $p < 0.0001$	$r^2 = 0.4557$ ; $p = 0.0160$
	High (0.9)	$r^2 = 0.1959$ ; $p < 0.0001$	$r^2 = 0.8375$ ; $p < 0.0001$	$r^2 = 0.5854$ ; $p = 0.0037$

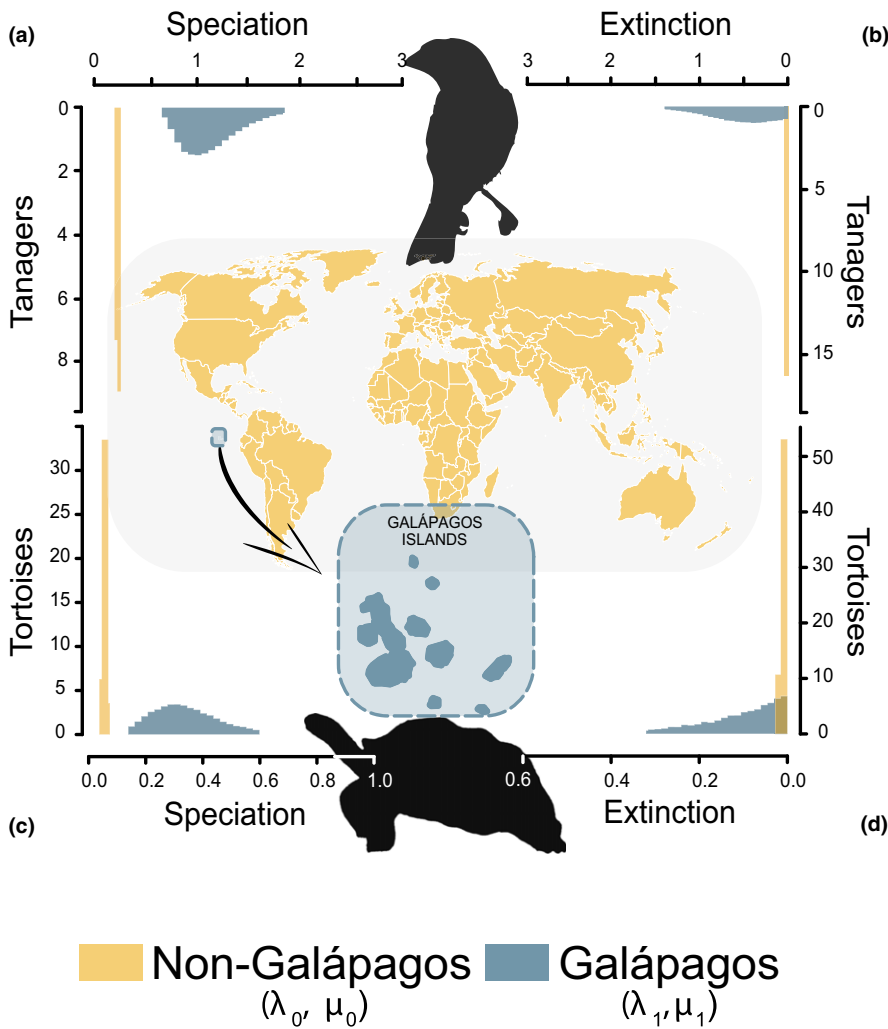
in particular) accelerate diversification? We address this question using two clades (tanagers and tortoises) that encompass two classic systems in evolutionary research (Darwin's finches and Galápagos tortoises). Our results suggest that islands in general do not necessarily increase diversification rates. However, the Galápagos Islands in particular have strongly accelerated diversification rates in both tanagers and tortoises, including diversification and speciation rates that are both at least three times higher than in other lineages in these groups. Specifically, both Galápagos clades evolved a substantial number of species in a very short period of time. In the sections below, we address how islands might impact diversification and the differences in diversification rates between tanagers and tortoises.

## 4.2 | Impacts of islands on diversification

Islands are often considered drivers of rapid diversification and adaptive radiation (e.g., Losos, 2010; Rodrigues & Diniz-Filho, 2016). In contrast to this expectation, our results show that islands did not have a significant, positive impact on diversification in tanagers or tortoises. However, we show that occurrence in the Galápagos Islands in particular strongly impacted diversification in both groups. Thus, in both families, the strong signal of increased island diversification from the Galápagos clades is drowned out by clades on other islands where accelerated diversification has failed to occur. The results for both groups raise the obvious question: what is special about the Galápagos, relative to other islands where tanagers and tortoises occur? We address this first for tanagers and then tortoises. Overall, our results suggest that only the Galápagos Islands drive rapid island diversification in tanagers. This result is somewhat surprising, given that tanagers also occur in the West Indies, but do not appear to have rapidly diversified there. Although ~50 tanager species occur in the West Indies (with 19 endemics), our SSE analyses show no positive impact of occurring in the West Indies on tanager diversification. Instead, we found slower diversification rates in Caribbean tanagers relative to those in other areas (Appendix S1, Tables S12–S13). It remains unclear why tanagers did not radiate rapidly in the West Indies. With few exceptions, Caribbean tanagers are endemic to one (or two) of the four large islands (Cuba, Hispaniola,

Jamaica, Puerto Rico; Lepage et al., 2014). These large islands have had impressive within-island speciation in other lineages, such as *Anolis* lizards (Losos, 2009) and *Eleutherodactylus* frogs (Heinicke, Duellman, & Hedges, 2007). However, only sister pairs in two genera, *Phaenicophilus* (*P. palmarum*, *P. poliocephalus*) and *Calyptophilus* (*C. tertius*, *C. frugivorus*), are known to occur in the same island (Hispaniola), and apparently without within-island speciation (Sly et al., 2010). Possible explanations for this lack of Caribbean radiation include: (a) extrinsic factors, such as competition with other avian lineages, and (b) intrinsic factors, such as a lack of variability in traits that would promote rapid radiation (e.g., bill morphology). Apart from the Galápagos, Cocos Island, and West Indies, the remaining island-endemic tanagers are restricted to the Southern Atlantic and classified in two genera (Ryan, Klicka, Barker, & Burns, 2013). *Rowettia* is monotypic. *Nesospiza* contains only three species, and has a diversification rate similar to the families' mean rate (1.17 times higher). Finally, the rapid radiation of thraupids in the Andes mountains of South America (i.e., Fjeldså & Rahbek, 2006; Sedano & Burns, 2010) may also help equalize diversification rates between islands and mainlands.

In contrast to thraupids in the West Indies, non-Galápagos endemic insular tortoises inhabit two tiny archipelagos that each consists of a few small islands (i.e., Mascarene Islands, Seychelles), and have very few tortoise species (Table 3; Austin et al., 2003). These two island groups contrast with the Galápagos, with 13 relatively large islands (Table 3). With few exceptions, every large island in these three archipelagos (Galápagos, Mascarene, Seychelles) has one endemic tortoise species (Table 3). Specifically, the Galápagos have 11 extant species, and almost all species are endemic to one island, and almost all islands have only one species (Poulakakis et al., 2012, 2015). Only *Chelonoidis becki* and *C. vicina* inhabit the same island (Isabela Island). Given this, if these other two archipelagos had 13 islands of adequate size, we speculate that they might have a similar number of endemic species to the Galápagos. The Galápagos have also been the home to other endemic radiations (review in Parent, Caccione, & Petren, 2008), but it is unclear whether these are rapid radiations relative to mainland members of these clades. In contrast, we are unaware of rapid or large radiations on either of the smaller archipelagos where tortoises occur (Mascarene, Seychelles).



**FIGURE 2** Posterior probability distribution for the best-fitting BiSSE models comparing diversification in the Galápagos Islands versus all other areas in tanagers (a–b) and tortoises (c–d; details in Appendix S1, Table S15). For both families, model selection for BiSSE is shown in Appendix S1, Table S14. Speciation (a, c) and extinction (b, d) rates are shown for non-Galápagos areas in yellow ( $\lambda_0$  and  $\mu_0$ , respectively) and Galápagos Islands in blue ( $\lambda_1$  and  $\mu_1$ , respectively)

Intriguingly, they do have endemic species and radiations, but these radiations have very few species, as do the tortoises (e.g., sooglossid frogs in the Seychelles with four species; AmphibiaWeb, 2016). The low richness of sooglossid frogs is particularly intriguing, since this lineage is relatively old (stem age >100 Ma; crown age ~24 Ma; Frazão, Silva, & Russo, 2015).

Overall, our results for tanagers and tortoises suggest that occurring on archipelagos with many large islands was necessary but not sufficient for driving rapid diversification. Thus, archipelagos with very few large islands may be insufficient to drive rapid diversification (e.g., in tortoises), whereas occurring in island groups with many large islands can drive diversification (e.g., in Galápagos tortoises and finches) but not always (Caribbean tanagers). Our results suggest that rapid island radiations require both the right geographical setting and the right lineage.

Along these lines, we note that not every clade in the Galápagos has radiated there (i.e., not the right lineage). Nevertheless, Parent et al. (2008) estimated that most animal groups present there are dominated by species from within-Galápagos radiations (mammals: 83%; land birds: 60%; nonavian reptiles: 88%; beetles: 43%; land snails: 94%). Thus, the Galápagos fauna appears to be dominated by

endemic radiations. Future studies should also test whether other endemic radiations have accelerated diversification rates relative to mainland lineages and other island systems. However, our point here is not that the Galápagos had an equal impact on diversification in every clade (indeed, our results strongly counter this). Instead, we demonstrate that occurring on particular islands can have a strong effect on diversification in some clades, more so than occurring on islands in general.

Finally, we acknowledge that some readers may be concerned that our analyses focused on two groups that were already known to have radiated on the Galápagos. However, previous studies of these groups did not explicitly test and quantify the impact of occurring on islands relative to the mainland on diversification rates, nor the effect of the Galápagos relative to other regions.

### 4.3 | Comparing radiations of tortoises and finches

A striking result of our study is that Darwin's finches diversified ~2–8 times faster than Galápagos tortoises. The range of rates comes from the two different methods (BiSSE, ME estimator), and the lower estimate (~2) reflects the estimate of high extinction rates in the





Galápagos from BiSSE, which may be inaccurate. Although finches began diversifying in the Galápagos later than tortoises (age of the first split for Darwin's finches: 1.5 Ma; age of the first split for Galápagos tortoises: 3.2 Ma), Darwin's finches have more species than Galápagos tortoises ( $n = 15$  vs. 11). In both tortoises and finches, the number of Galápagos species is similar to the overall number of islands  $>10$  km<sup>2</sup> ( $n = 13$ ). However, in finches, that number was achieved more quickly (Figure 3). In tortoises, lineage accumulation seems to be linked to the appearance of islands over time (Figure 3).

**TABLE 3** Summary of the main characteristics of the archipelagos where insular tortoises are distributed. *Chelonoidis* are from the Galápagos Islands, *Cylindraspis* from the Mascarene Islands, and *Aldabrachelys* from Seychelles and Madagascar (Aldabra atoll). This information was summarized from Parent et al. (2008) and Gillespie and Clague (2009)

Characteristic	Galápagos Islands	Mascarene Islands	Seychelles and Madagascar (Aldabra atoll)
Major islands ( $>10$ km <sup>2</sup> )	13	3	3
Combined area of all major islands (km <sup>2</sup> )	7,863.82	4,659	152.3
Number of volcanoes	12	4	0
Geological clustering	Nonlinear and linear*	Linear	Nonlinear
Distance to mainland (km)	960	1700 <sup>†</sup> ; 690 <sup>‡</sup>	634 <sup>†</sup> ; 421 <sup>‡</sup>
Endemic tortoise species	11	5	3

\*Groups of islands with similar age are clustered together (nonlinear). However, the overall distribution of these groups of islands across the archipelago follows a linear pattern.

<sup>†</sup>Distance from mainland.

<sup>‡</sup>Distance from Madagascar.

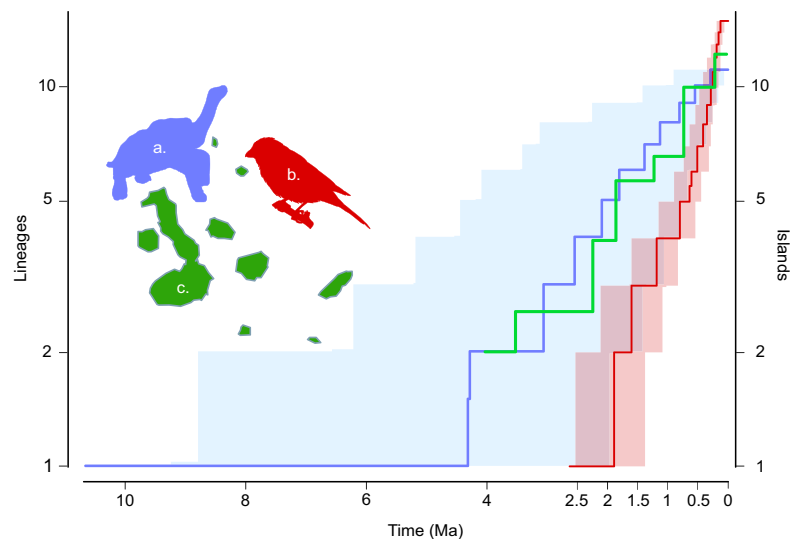
The different diversification rates between Galápagos finches and tortoises parallel large-scale differences in diversification rates between these families and higher clades. Birds have higher net diversification rates than turtles ( $\sim 0.028\text{--}0.037$  vs.  $\sim 0.014\text{--}0.022$ ; based on stem-group ages and three epsilon values; Wiens, 2015). Thus, despite their similar stem-group ages, birds have many more species than turtles, with  $\sim 10,000$  birds (Lepage et al., 2014) and  $\sim 350$  turtles (Turtle Taxonomy Working Group, 2014). Similarly, thraupids are far more diverse than testudinids ( $\sim 386$  species vs. 59). Yet testudinids are roughly four times older (stem ages = 4.01; crown ages = 3.64 times) and distributed almost globally, whereas thraupids are confined to the New World. One obvious mechanism that might drive the more rapid evolution of Darwin's finches (relative to tortoises) is their ecological radiation, especially to utilize diverse food resources (Grant, 1999). In contrast, despite interesting variation in shell morphology associated with habitats on different islands (Caccone et al., 2002), Galápagos tortoises are relatively similar (e.g., large, terrestrial herbivores). Intriguingly, finches are the only birds to radiate extensively (in ecology and species numbers) in the Galápagos (Parent et al., 2008). Shorter finch/bird generation times relative to turtles might also be important.

Overall, these results show that small-scale patterns of diversification of different clades in the same location can parallel large-scale patterns of diversification over much broader spatial and temporal scales (e.g., differences between turtles and birds). We are unaware of previous studies that have shown such a pattern. It could be interesting to test the generality of this pattern in future studies, as applied to other regions and clades.

## 5 | CONCLUSIONS

In this study, we test the hypothesis that occurrence on islands in general (and certain islands in particular) accelerates diversification, focusing on two clades that include iconic radiations on the

**FIGURE 3** Lineage-through-time (LTT) plots for Galápagos tortoises (a) and Darwin's finches (b). The number of Galápagos Islands over time (c) is indicated in an independent axis (right). Both y-axes are ln-transformed. Shaded areas correspond to 95% confidence interval after discarding 25% as burnin from the BEAST posterior sample for each lineage. Methods are detailed in Appendix S4. Note that we are not assuming any trend in the number of islands before 4 Ma



Galápagos Islands. Our results do not support the idea that islands generally promote diversification overall, but strongly support the hypothesis that occurring in the Galápagos specifically drives faster speciation and diversification rates. Our results also suggest that finches diversified far more rapidly in the Galápagos than did tortoises, a small-scale pattern that parallels larger ones across these families and across birds and turtles globally.

## ACKNOWLEDGEMENTS

For financial support during the preparation of this manuscript we thank the University of Arizona and NSF grant DEB 1655690.

## DATA AVAILABILITY

All data are available as Supporting Information and on Dryad.

## ORCID

John J. Wiens  <http://orcid.org/0000-0003-4243-1127>

## REFERENCES

- Akaike, H. (1974). A new look at the statistical model identification. *IEEE Transactions on Automatic Control*, *19*, 716–723. <https://doi.org/10.1109/TAC.1974.1100705>
- AmphibiaWeb (2016). *AmphibiaWeb: Information on amphibian biology and conservation*. Berkeley, CA: University of California. Retrieved from <http://amphibiaweb.org/>.
- Austin, J. J., & Arnold, E. N. (2001). Ancient mitochondrial DNA and morphology elucidate an extinct island radiation of Indian Ocean giant tortoises (*Cylindraspis*). *Proceedings of the Royal Society B: Biological Sciences*, *268*, 2515–2523. <https://doi.org/10.1098/rspb.2001.1825>
- Austin, J. J., Arnold, E. N., & Bour, R. (2003). Was there a second adaptive radiation of giant tortoises in the Indian Ocean? Using mitochondrial DNA to investigate speciation and biogeography of *Aldabrachelys* (Reptilia, Testudinidae). *Molecular Ecology*, *12*, 1415–1424. <https://doi.org/10.1046/j.1365-294X.2003.01842.x>
- Baldwin, B. G., & Sanderson, M. J. (1998). Age and rate of diversification of the Hawaiian silversword alliance (Compositae). *Proceedings of the National Academy of Sciences of the USA*, *95*, 9402–9406. <https://doi.org/10.1073/pnas.95.16.9402>
- Barker, F. K., Burns, K. J., Klicka, J., Lanyon, S. M., & Lovette, I. J. (2015). New insights into New World biogeography: An integrated view from the phylogeny of blackbirds, cardinals, sparrows, tanagers, warblers, and allies. *The Auk*, *132*, 333–348. <https://doi.org/10.1642/AUK-14-110.1>
- Beheregaray, L. B., Gibbs, J. P., Havill, N., Fritts, T. H., Powell, J. R., & Caccione, A. (2004). Giant tortoises are not so slow: Rapid diversification and biogeographic consensus in the Galápagos. *Proceedings of the National Academy of Sciences of the USA*, *101*, 6514–6519. <https://doi.org/10.1073/pnas.0400393101>
- BirdLife International (2016). IUCN Red List for birds. Retrieved from <http://www.birdlife.org>.
- Bouckaert, R., Heled, J., Kühnert, D., Vaughan, T., Wu, C.-H., Xie, D., ... Drummond, A. J. (2014). BEAST 2: A software platform for Bayesian evolutionary analysis. *PLoS Computational Biology*, *10*, e1003537. <https://doi.org/10.1371/journal.pcbi.1003537>
- Burns, K. J., Hackett, S. J., & Klein, N. K. (2002). Phylogenetic relationships and morphological diversity in Darwin's finches and their relatives. *Evolution*, *56*, 1240–1252. <https://doi.org/10.1111/j.0014-3820.2002.tb01435.x>
- Burns, K. J., Shultz, A. J., Tittle, P. O., Mason, N. A., Barker, F. K., Klicka, J., ... Lovette, I. J. (2014). Phylogenetics and diversification of tanagers (Passeriformes: Thraupidae), the largest radiation of Neotropical songbirds. *Molecular Phylogenetics and Evolution*, *75*, 41–77. <https://doi.org/10.1016/j.ympev.2014.02.006>
- Caccione, A., Gentile, G., Gibbs, J. P., Fritts, T. H., Snell, H. L., Betts, J., Powell, J. R. (2002). Phylogeography and history of giant Galápagos tortoises. *Evolution*, *56*, 2052–2066.
- Clements, J. F., Schulenberg, T. S., Roberson, D., Fredericks, B. L., Sullivan, B. L., & Wood, C. L. (2016). The eBird/Clements checklist of birds of the world: Version 6.8. Retrieved from <http://www.birds.cornell.edu/clementschecklist/download/>.
- Davis, M. P., Midford, P. E., & Maddison, W. (2013). Exploring power and parameter estimation of the BiSSE method for analyzing species diversification. *BMC Evolutionary Biology*, *13*, 38. <https://doi.org/10.1186/1471-2148-13-38>
- Fjeldså, J., & Rahbek, C. (2006). Diversification of tanagers, a species rich bird group, from lowlands to montane regions of South America. *Integrative and Comparative Biology*, *46*, 72–81. <https://doi.org/10.1093/icb/icj009>
- FitzJohn, R. G., Maddison, W. P., & Otto, S. P. (2009). Estimating trait-dependent speciation and extinction rates from incompletely resolved phylogenies. *Systematic Biology*, *58*, 595–611. <https://doi.org/10.1093/sysbio/syp067>
- Frazão, A., Silva, H. R. D., & Russo, C. A. D. M. (2015). The Gondwana breakup and the history of the Atlantic and Indian Oceans unveils two new clades for early neobatrachian diversification. *PLoS ONE*, *10*, 1–18.
- García-Porta, J., & Ord, T. J. (2013). Key innovations and island colonization as engines of evolutionary diversification: A comparative test with the Australasian dipodactyloid geckos. *Journal of Evolutionary Biology*, *26*, 2662–2680. <https://doi.org/10.1111/jeb.12261>
- Gillespie, R. G., & Clague, D. A. (Eds.) (2009). *Encyclopedia of islands*. Berkeley, CA: University of California Press.
- Goldberg, E. E., Lancaster, L. T., & Ree, R. H. (2011). Phylogenetic inference of reciprocal effects between geographic range evolution and diversification. *Systematic Biology*, *60*, 451–465. <https://doi.org/10.1093/sysbio/syr046>
- Grant, P. R. (1999). *Ecology and evolution of Darwin's finches*. Princeton, NJ: Princeton University Press.
- Heinicke, M. P., Duellman, W. E., & Hedges, S. B. (2007). Major Caribbean and Central American frog faunas originated by ancient oceanic dispersal. *Proceedings of the National Academy of Sciences of the USA*, *104*, 10092–10097. <https://doi.org/10.1073/pnas.0611051104>
- Itescu, Y., Karraker, N. E., Raia, P., Pritchard, P. C. H., & Meiri, S. (2014). Is the island rule general? Turtles disagree. *Global Ecology and Biogeography*, *23*, 689–700. <https://doi.org/10.1111/geb.12149>
- Jiménez-Uzcátegui, G., Wiedenfeld, D. A., Vargas, F. H., & Snell, H. L. (2017). CDF checklist of Galápagos birds. In F. Bungartz, H. Herrera, P. Jaramillo, N. Tirado, G. Jiménez-Uzcátegui, D. Ruiz, A. Guézou & F. Ziemmeck (Eds), *Charles Darwin Foundation Galapagos Species Checklist - Lista de Especies de Galápagos de la Fundación Charles Darwin*. Puerto Ayora, Galapagos: Charles Darwin Foundation. Retrieved from <http://www.darwinfoundation.org/datazone/checklists/vertebrates/aves>.
- Kozak, K. H., & Wiens, J. J. (2016). Testing the relationships between diversification, species richness, and trait evolution. *Systematic Biology*, *65*, 975–988. <https://doi.org/10.1093/sysbio/syw029>



- Lefebvre, L., Ducatez, S., & Audet, J. N. (2016). Feeding innovations in a nested phylogeny of Neotropical passerines. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 371, 20150188. <https://doi.org/10.1098/rstb.2015.0188>
- Lepage, D., Vaidya, G., & Guralnick, R. (2014). Avibase—A database system for managing and organizing taxonomic concepts. *ZooKeys*, 420, 117–135. <https://doi.org/10.3897/zookeys.420.7089>
- Losos, J. B. (2009). *Lizards in an evolutionary tree: Ecology and adaptive radiation of anoles*. Berkeley, CA: University of California Press.
- Losos, J. B. (2010). Adaptive radiation, ecological opportunity, and evolutionary determinism. *The American Naturalist*, 175, 623–639. <https://doi.org/10.1086/652433>
- Losos, J. B., & Ricklefs, R. E. (2009). Adaptation and diversification on islands. *Nature*, 457, 830–836. <https://doi.org/10.1038/nature07893>
- Maddison, W. P., & FitzJohn, R. G. (2015). The unsolved challenge to phylogenetic correlation tests for categorical characters. *Systematic Biology*, 64, 127–136. <https://doi.org/10.1093/sysbio/syu070>
- Maddison, W. P., Midford, P. E., Otto, S. P., & Oakley, T. (2007). Estimating a binary character's effect on speciation and extinction. *Systematic Biology*, 56, 701–710. <https://doi.org/10.1080/10635150701607033>
- Magallón, S., & Sanderson, M. J. (2001). Absolute diversification rates in angiosperm clades. *Evolution*, 55, 1762. <https://doi.org/10.1111/j.0014-3820.2001.tb00826.x>
- Martins, E. P., & Hansen, T. F. (1997). Phylogenies and the comparative method: A general approach to incorporating phylogenetic information into the analysis of interspecific data. *The American Naturalist*, 149, 646–667. <https://doi.org/10.1086/286013>
- Meyer, A. L. S., & Wiens, J. J. (2018). Estimating diversification rates for higher taxa: BAMM can give problematic estimates of rates and rate shifts. *Evolution*, 72, 39–53. <https://doi.org/10.1111/evo.13378>
- Moore, B. R., Höhna, S., May, M. R., Rannala, B., & Huelsenbeck, J. P. (2016). Critically evaluating the theory and performance of Bayesian analysis of macroevolutionary mixtures. *Proceedings of the National Academy of Sciences of the USA*, 113, 9569–9574. <https://doi.org/10.1073/pnas.1518659113>
- Morales-Hojas, R., & Vieira, J. (2012). Phylogenetic patterns of geographical and ecological diversification in the subgenus *Drosophila*. *PLoS ONE*, 7, e49552. <https://doi.org/10.1371/journal.pone.0049552>
- Orme, D., Freckleton, R., Thomas, G., Petzoldt, T., Fritz, S., Isaac, N., & Pearse, W. (2013). caper: comparative analyses of phylogenetics and evolution in R. Retrieved from <http://CRAN.R-project.org/package=caper>.
- Pagel, M. (1999). Inferring the historical patterns of biological evolution. *Nature*, 401, 877–884. <https://doi.org/10.1038/44766>
- Palkovacs, E. P., Marschner, M., Ciofi, C., Gerlach, J., & Caccione, A. (2003). Are the native giant tortoises from the Seychelles really extinct? A genetic perspective based on mtDNA and microsatellite data. *Molecular Ecology*, 12, 1403–1413. <https://doi.org/10.1046/j.1365-294X.2003.01834.x>
- Paradis, E., Claude, J., & Strimmer, K. (2004). APE: Analyses of Phylogenetics and Evolution in R language. *Bioinformatics*, 20, 289–290. <https://doi.org/10.1093/bioinformatics/btg412>
- Parent, C. E., Caccione, A., & Petren, K. (2008). Colonization and diversification of Galápagos terrestrial fauna: A phylogenetic and biogeographical synthesis. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363, 3347–3361. <https://doi.org/10.1098/rstb.2008.0118>
- Pennell, M. W., Eastman, J. M., Slater, G. J., Brown, J. W., FitzJohn, R. G., Alfaro, M. E., & Harmon, L. J. (2014). geiger v2.0: An expanded suite of methods for fitting macroevolutionary models to phylogenetic trees. *Bioinformatics*, 30, 2216–2218. <https://doi.org/10.1093/bioinformatics/btu181>
- Poulakakis, N., Edwards, D. L., Chiari, Y., Garrick, R. C., Russello, M. A., Benavides, E., ... Caccione, A. (2015). Description of a new Galapagos giant tortoise species (*Chelonoidis*; Testudines: Testudinidae) from Cerro Fatal on Santa Cruz Island. *PLoS ONE*, 10, e0138779. <https://doi.org/10.1371/journal.pone.0138779>
- Poulakakis, N., Russello, M., Geist, D., & Caccione, A. (2012). Unravelling the peculiarities of island life: Vicariance, dispersal and the diversification of the extinct and extant giant Galápagos tortoises. *Molecular Ecology*, 21, 160–173. <https://doi.org/10.1111/j.1365-294X.2011.05370.x>
- Rabosky, D. L. (2014). Automatic detection of key innovations, rate shifts, and diversity-dependence on phylogenetic trees. *PLoS ONE*, 9, e89543. <https://doi.org/10.1371/journal.pone.0089543>
- Rabosky, D. L., & Goldberg, E. E. (2015). Model inadequacy and mistaken inferences of trait-dependent speciation. *Systematic Biology*, 64, 340–355. <https://doi.org/10.1093/sysbio/syu131>
- Rabosky, D. L., Slater, G. J., & Alfaro, M. E. (2012). Clade age and species richness are decoupled across the eukaryotic Tree of Life. *PLoS Biology*, 10, e1001381. <https://doi.org/10.1371/journal.pbio.1001381>
- Rodrigues, J. F. M., & Diniz-Filho, J. A. F. (2016). Ecological opportunities, habitat, and past climatic fluctuations influenced the diversification of modern turtles. *Molecular Phylogenetics and Evolution*, 101, 352–358. <https://doi.org/10.1016/j.ympev.2016.05.025>
- Ryan, P. G., Klicka, L. B., Barker, K. F., & Burns, K. J. (2013). The origin of finches on Tristan da Cunha and Gough Island, central South Atlantic Ocean. *Molecular Phylogenetics and Evolution*, 69, 299–305. <https://doi.org/10.1016/j.ympev.2013.05.026>
- Schulenberg, T. S. (2014). Neotropical Birds Online. Retrieved from <http://neotropical.birds.cornell.edu/>
- Sedano, R. E., & Burns, K. J. (2010). Are the Northern Andes a species pump for Neotropical birds? Phylogenetics and biogeography of a clade of Neotropical tanagers (Aves: Thraupini). *Journal of Biogeography*, 37, 325–343. <https://doi.org/10.1111/j.1365-2699.2009.02200.x>
- Sly, N. D., Townsend, A. K., Rimmer, C. C., Townsend, J. M., Latta, S. C., & Lovette, I. J. (2010). Phylogeography and conservation of the endemic Hispaniolan Palm-Tanagers (Aves: *Phaenicophilus*). *Conservation Genetics*, 11, 2121–2129. <https://doi.org/10.1007/s10592-010-0098-4>
- Soulebeau, A., Aubriot, X., Gaudeul, M., Rouhan, G., Hennequin, S., Haevermans, T., ... Jabbour, F. (2015). The hypothesis of adaptive radiation in evolutionary biology: Hard facts about a hazy concept. *Organisms Diversity & Evolution*, 15, 747–761. <https://doi.org/10.1007/s13127-015-0220-z>
- Turtle Taxonomy Working Group [van Dijk, P. P., Iverson, J., Rhodin, A., Shaffer, H. B., & Bour, R.] (2014). *Turtles of the World, 7th Edition: Annotated Checklist of Taxonomy, Synonymy, Distribution with Maps, and Conservation Status*. *Chelonian Research Monographs* pp. 329–479.
- Uetz, P., & Hošek, J. (2016). The Reptile Database. Retrieved from <http://www.reptile-database.org/>.
- Valente, L. M., Etienne, R. S., & Phillimore, A. B. (2014). The effects of island ontogeny on species diversity and phylogeny. *Proceedings of the Royal Society B: Biological Sciences*, 281, 20133227. <https://doi.org/10.1098/rspb.2013.3227>
- Warren, B. H., Simberloff, D., Ricklefs, R. E., Aguilée, R., Condamine, F. L., Gravel, D., ... Thebaud, C. (2015). Islands as model systems in ecology and evolution: Prospects fifty years after MacArthur-Wilson. *Ecology Letters*, 18, 200–217. <https://doi.org/10.1111/ele.12398>
- Wiens, J. J. (2015). Explaining large-scale patterns of vertebrate diversity. *Biology Letters*, 11, 20150506. <https://doi.org/10.1098/rsbl.2015.0506>



## BIOSKETCHES

**Cristian Román-Palacios** is a doctoral student at the Department of Ecology and Evolutionary Biology at the University of Arizona. His main interest is in understanding large-scale patterns of biodiversity from an ecological and evolutionary perspective. He is also widely interested in the systematics of different animal groups and the effects of climate change on local populations.

**John J. Wiens** is a professor in the Department of Ecology and Evolutionary Biology at the University of Arizona. His main interest is in using integrative phylogenetic approaches to address conceptual questions at the interface of ecology and evolutionary biology, including species richness, speciation, niche evolution, and species responses to climate change.

## SUPPORTING INFORMATION

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

**How to cite this article:** Román-Palacios C, Wiens JJ. The Tortoise and the Finch: Testing for island effects on diversification using two iconic Galápagos radiations. *J Biogeogr.* 2018;45:1701–1712. <https://doi.org/10.1111/jbi.13366>