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Title

Niche shifts after island colonization spurred adaptive diversification and speciation in a cosmopolitan bird clade

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Abstract

Islands have long been recognized as key contributors to biodiversity because they facilitate geographic isolation and ecological divergence from mainland ancestors. However, island colonization has traditionally been considered an evolutionary dead-end process, and its consequences for continental biodiversity remain understudied. Here, we use the evolutionary radiation of Columbiformes (i.e., pigeons and doves) to examine if ecological niche shifts on islands shaped biological diversification and community composition on continents. We show that the colonization of islands by continental, terrestrial-foraging lineages led to exploitation of a new ecological niche (i.e., arboreal foraging). This transition towards arboreal foraging was associated with evolutionary adaptation towards a new morphological optimum. In addition, arboreal-foraging lineages of islands experienced an increase in speciation rates, which was associated with successful range expansions to other islands as well as back-colonization of continents. Our results provide empirical evidence that diversification on continents can only be fully understood when studying the diversification processes that took place on islands, challenging the view of islands as mere sinks of evolutionary diversity.

Introduction

A widely held view in evolutionary ecology is that island colonization promotes evolutionary diversification [1–8]. On islands, geographic isolation reduces gene flow from mainland ancestors [9], thereby facilitating allopatric speciation [10–12]. In vagile animals such as birds, allopatric speciation is considered to be a major driver of evolutionary diversification [10–12]. In addition, the usually depauperate biotas of islands, with fewer competitors and predators, offer ecological opportunities for colonizers to proliferate and modify their niches [13–15], facilitating evolutionary divergence and ecological speciation. For example, Alström et al. [16] found dramatic niche shifts and morphological changes in two bird species of the family Motacillidae after the colonization of islands. Thus, some of the most remarkable evolutionary radiations ever reported, like *Anolis* lizards [17], Darwin's finches [1], and Malagasy vangas [18] have occurred on islands.

For decades, it has been assumed that island colonization is generally a one-direction process [15] and, therefore, islands primarily represent sinks (rather than sources) of biological diversity [19,20]. This argument is based on two commonly held assumptions. The first is that continents are more difficult to invade than islands because the ecological space occupied by species is more densely packed [21]. The second assumption is that island colonizers tend to lose their ability to disperse, and hence rarely disperse to the continent. However, continents are large targets for dispersal and island lineages should be capable of back-colonizing continents [22,23] as long as they have conserved their ability to disperse [12]. Indeed, remarkable examples of successful back colonization of continents by island-dwelling lineages have been reported in a diverse array of life forms (reviewed by Bellemain & Ricklefs [23]), including plants [24], arthropods [25], amphibians [26], reptiles [27], birds [28–30] and bats [31,32]. Despite its important implications for evolutionary diversification and the assembly of biological communities in both islands and continents, the possibility that a mainland-island-mainland cycle promotes diversification remains understudied.

Here, we examine the hypothesis that evolutionary adaptation to new niches on islands might have allowed some lineages to successfully back-colonize continents, enhancing their evolutionary diversification. Unravelling the evolutionary importance of recolonization of continents from islands is challenging because it requires examining evolutionary diversification patterns in clades that have experienced several independent transitions between islands and continents [22]. Columbiformes (pigeons and doves) provide an excellent opportunity to address this because >50% of their 306 extant species [33] are island endemics [34]. In addition, the ecological niche of this clade can be primarily characterized by a single dimension, the terrestrial-arboreal foraging axis [35]. This axis is tightly associated with diet and predicts substantial variation in morphology, notably hindlimb morphology involved in locomotion and perching stability [35].

To conduct our study, we built a new phylogeny of Columbiformes, comprising 76% of all extant species. We coupled this new phylogenetic hypothesis with complete information on the geographic distribution, ecology, and ecologically relevant morphology of species. Using a variety of modelling approaches, we first inferred evolutionary transitions between islands and continents and between terrestrial and arboreal foraging along the evolutionary history of Columbiformes. Then, we examined whether these transitions played a major role in shaping both patterns of phenotypic evolution and rates of species diversification in this cosmopolitan bird clade.

Material and methods

Geographic, ecological and morphological information

We compiled information on species geographic distribution and ecology of pigeons from published literature sources [34,36]. We used this information to classify species as either: 1) island (including both continental and oceanic islands) or mainland dwellers; 2) terrestrial or arboreal foragers, based on whether they primarily forage on the ground or in the canopy; 3) open or forest habitat dwellers, depending on whether the species was primary associated with open habitats (e.g., savanna, shrublands and grasslands) or forested habitats. Based on Lapiedra *et al*. [35], we then combined the above geographic and ecological features to define five main eco-geographic groups: 1) Terrestrial-foraging species inhabiting open habitats in continents (TOC, n=40). 2) Terrestrial-foraging, forest-dwelling species inhabiting continents (TFC, n=37); 3) Terrestrial-foraging, forest-dwelling species inhabiting islands (TFI, n=28); 4) Arboreal-foraging, forest-dwelling species inhabiting continents (AFC, n=27); and 5) Arboreal-foraging, forest-dwelling species inhabiting islands (AFI, n=82). Only two species from open areas were endemic on islands, and hence this category was excluded from the analyses. We also excluded five species for which we did not have complete habitat use or foraging ecology information. Finally, species reported to commonly forage both on the ground and on tree branches were excluded from the analysis (n=13).

Morphometric information was primarily obtained from Gibbs et al. [34] and Dunning [37]. The morphological traits assembled for the analysis included the length of the wing, tail, tarsus and beak (in mm). Morphological values were log-transformed and converted to two main Phylogenetic Principal Component axes using the “phylo.pca” function in the R-package *phytools* [38]. Whereas the first axis was related to variation in body size, the second axis was mostly related to variation in tarsus (i.e., hindlimb) length independent of body size (i.e., relative tarsus length) (**Supplementary Table S1**). The ecological relevance of relative tarsus length in Columbiformes is backed up by eco-morphological predictions [39], comparative evidence of evolutionary patterns in island birds [40], and previous results showing that this axis is associated with foraging niche in pigeons and doves [35,41]. Therefore, we focused our further analyses of evolution on tarsus length, relative to body size. To do so, we removed the allometric effects of tarsus length by fitting a log-log regression between body size and tarsus length and used the residuals as a measure of relative tarsus length.

Taxon sampling and phylogenetic hypotheses

To infer the phylogenetic relationships of Columbiformes, we searched for all genetic markers available for extant Columbiformes in GenBank (accessed 27/10/2020, [42]). We selected the combination of markers that allowed the maximum taxonomic coverage as well as the maximum phylogenetic resolution according to previous published phylogenies of the group [43–45]. Our final molecular dataset (**Supplementary Table S2**) included the nuclear recombination activating protein (RAG-1) and six mitochondrial fragments of the following eight genes: 12S ribosomal RNA, ATP synthase F0 subunit 8 (ATPase 8), synthase F0 subunit 6 (ATPase 6), cytochrome oxidase subunit III (COIII), cytochrome oxidase subunit 1 (COI), cytochrome b (cytb), NADH dehydrogenase subunit 2 (ND2) and NADH dehydrogenase subunit 3 (ND3). Sequences of these markers were available for 234 species of Columbiformes, plus eight species of Pterocliformes (the most likely sister group of Columbiformes [46]) that were used as outgroups. All genes were aligned using the software MAFFT [47] (available in https://www.ebi.ac.uk/Tools/msa/mafft/), assigning a gap penalty of 1.53, a gap extension penalty of 0.123 and a maximum of 80 iterations. All alignments were concatenated producing a final molecular dataset of a maximum of 7,752 base pairs. We used BEAST v2.5.2 [48] to conduct phylogenetic analyses. We used a Yule process as tree prior and an uncorrelated relaxed molecular clock that sampled rates from a lognormal distribution. The best nucleotide substitution model and partition strategy was estimated through a reversible-jump algorithm [49], as implemented in the plugin RB in the package BEAST. To obtain a phylogeny of Columbiformes in units of time, we calibrated the root node (the split that separates Columbiformes and Pterocliformes) at an age of 82 Ma (with an interval of confidence of 72 to 91 Ma), based on the estimates produced in 18 previous phylogenetic studies [50]. Final analyses consisted of two independent runs of 10^8 generations each with a thinning interval of 16,000 generations. The mixing of the traces and the effective sample sizes (ESS) of all parameters sampled in the MCMC chains were assessed using the software Tracer [51]. Parameters and trees of both runs were combined using the software LogCombiner (included in the BEAST package), excluding the initial 10% of trees and parameter estimates as “burn in”. We then randomly sampled 100 trees from the posterior distribution of our BEAST analysis and used this sample to integrate phylogenetic uncertainty in all the comparative analyses. Finally, we also computed a “summary tree” by means of the program TreeAnnotator (included in the BEAST package), as the maximum clade credibility tree estimated with common ancestor heights (**Supplementary Fig. S1)**.

Evolutionary transitions

We used the phylogenies to reconstruct evolutionary transitions between each of the five eco-geographic groups. We used a stochastic character mapping approach that applies a Monte Carlo algorithm to sample the posterior probability distribution of ancestral states and timings of transitions on phylogenetic branches under a Markov process of evolution [52]. In our reconstructions, we considered phylogenetic uncertainty by integrating results from the 100 randomly sampled trees of the posterior distribution of our BEAST analysis (see above), running 10 reconstructions for each phylogenetic tree. Thus, we obtained 1000 reconstructed ancestral character stages. We allowed the transitions to be asymmetrical between character stages. To do so, we used the “*make.simmap*” function in R-package *phytools* [38] to build the stochastic character-mapped reconstructions with model “ARD”, and then applied the “*describe.simmap*” function in *phytools* [38] to summarize the results.

Morphological evolution

We used the R-package *OUwie [53]* to fit Ornstein-Uhlenbeck models (OU, hereafter) of character evolution to assess whether and how hindlimb morphology (i.e. relative tarsus length) evolved toward different phenotypic optima according to our five eco-geographic groups. We tested two OU models, one with a single optimum for the entire clade and another where the phenotypic optimum was allowed to vary across eco-geographic groups [53]. The fit of these OU models was contrasted with two Brownian motion models (BM hereafter). BM models do not assume the existence of any phenotypic optima, but model the phenotype as a random walk where each group can have a different rate of evolution. To compare the fit of the models, we used the second-order Akaike information criteria (AICc). The models were run a sample of 100 random reconstructions (see previous section) and for the best model, we then computed the mean, median, SD and 95% confidence intervals of each parameter among the 100 reconstructions. In addition, we compared estimated parameters between pairs of trait categories by computing the percentage of trees where the value for one category was greater than for the other category.

To further confirm these results, we modelled hindlimb morphology by means of a Phylogenetic Generalized Least Squares approach (PGLS), as implemented in the R-package *caper* (Orme et al. [54]). We modelled changes in hindlimb morphology as a function of foraging behavior, habitat type, and island vs. continental dwelling. These ecological and geographic predictors were included in the models as binary traits together with body mass as a covariate.

Speciation rates

To investigate whether and how island-mainland colonization events and foraging niche shifts influenced rates of species diversification, we compared different models of diversification using the “hisse” framework, implemented in the R-package SeqSSE [55]. This framework allows one to assess whether the acquisition of a character by a lineage either accelerates or slows down speciation rates, taking into account possible “hidden” factors that could inflate or obscure this effect [56]. In our case, we tested the hypothesis that speciation rates could differ among the five eco-geographic groups (AFC, AFI, TFC, TFI, TOC). To do this, we used a character-dependent diversification model (CDD-0), where speciation rates vary among the five-character states. It has been shown that these speciation models may find spurious associations between character states and diversification rates (‘false positives’, *sensu* [57]) due to the existence of ‘hidden traits’ that could explain variation in diversification rates better that the traits being investigated [58]. We examined for the potential existence of these ‘hidden traits’ by modelling an alternative character-dependent diversification model that included a hidden trait (CDD-1) with two states (A/B) that allow speciation rates to vary between all character states combinations of eco-geographic and hidden characters. In all cases, we fixed extinction rates to 0.0001 (i.e. assumed that speciation was the main driver of evolutionary diversification), while speciation rates were estimated for each character state. In all models, we also estimated transition rates among character states, and restricted dual transitions to 0. In addition, SecSSE models allows to account for the potential effect of differences in species sampling among character states. To do this, we also specified to the model the proportion of species included in the phylogeny for each of the eco-geographic groups (AFC=0.794, AFI=0.689, TFC=0.804, TFI=0.718, TOC=0.930). For each of the 100 phylogenetic trees we ran the analysis for 250,000 generations. The performance of the two models was assessed using the second-order Akaike information criteria (AICc).

Results

Evolutionary transitions among major eco-geographic groups

Our phylogenetic reconstructions suggest that Columbiformes evolved from a continental, terrestrial-foraging ancestor that inhabited either open areas or forests (**Fig. 1**). The analysis of evolutionary transitions indicates that most of the present-day arboreal-foraging species derive from terrestrial lineages that evolved arboreality on islands (**Fig. 1**). For example, the lineage including very speciose arboreal-foraging genera such as *Ducula, Ptilinopus, and Treron* emerged from a well-defined lineage of ground-foraging island-dwelling species that includes genera like *Goura* and *Gallicolumba*. Within this Indo-Pacific clade, the same pattern of arboreal foraging emerging on island-dwelling lineages is replicated in the lineage leading to present-day *Phapitreron*.

The evolution of arboreal forms on islands enabled multiple back-colonizations of continents. On average, 40.3% of all the transitions among major eco-geographic groups involved arboreal species that moved from islands to continents (**Fig. 1b**), which largely explains the presence of arboreal-foraging species in continents (33 species at present, **Fig. 1**). Within all the major arboreal lineages, like genus *Ducula*, *Ptilinopus* and *Macropygia*, there are indeed examples of arboreal species that back-colonized the continent. Likewise, species of the arboreal-foraging genus *Treron* that inhabit continents are embedded within a major island-dwelling clade, again suggesting that they evolved from an island-ancestor that back-colonized the continent (**Fig. 1**). The only case where arboreal species could have evolved within the continent are in genus *Patagioenas*, although there is some uncertainty in the phylogenetic reconstruction of this transition. With the exception of *Macropygia* species, which derive from island-dwelling arboreal species according to our data (**Fig. 1**), the evolutionary transition to arboreality in Holarctic/New World clades (e.g., *Reinwardtoena* and *Turacoena)* also remain unclear.

In contrast, back-colonizations of continents by terrestrial-foraging island lineages occurred less frequently (only in 4,2% of the transitions) as compared with back-colonizations by arboreal-foraging island lineages. These contrasting patterns can in part reflect that most island Columbiformes (82 out of 110 species) are arboreal. Thus, enhanced speciation rates in arboreal-foraging lineages could largely explain the increased number of continental back-colonizations by these clades.

Morphological evolution in association with island colonization and foraging niche shifts

Our results show that island colonizations and the subsequent shift to arboreal foraging favored changes in hindlimb morphology. Our evolutionary models indicate that these morphological differences among major eco-geographic groups (i.e. island vs. continental, arboreal- vs. terrestrial-foraging, forest vs. open areas) arose from directional selection toward different phenotypic optima. The best-fitting model for hindlimb evolution was an OU model in which different eco-geographic groups had different phenotypic optima (OUM) (**Supplementary Table S3**). Shifts to arboreal foraging were associated with the evolution of shorter hindlimbs relative to body size (**Fig. 1c**; **Table 1, Supplementary Table S4**). On islands, both terrestrial- and arboreal-foraging species inhabiting forested areas had longer tarsi than their mainland counterparts (**Fig. 1c**; **Table 1, Supplementary Table S4**). We obtained similar results when we repeated the models using PCs scores instead of raw measurements of morphological traits (**Supplementary Fig. S2**). The results were also consistent with those obtained from a PGLS analysis modelling hindlimb evolution as a function of geographic isolation, arboreality and habitat type (**Supplementary Table S5**).

Speciation rates in association with island colonization and foraging niche shifts

Our models show that arboreal foraging species from islands had the highest rates of speciation (**Fig. 2, Supplementary Fig. S3**), suggesting that shifts to arboreal foraging in island dwelling Columbiformes spurred diversification rates. In contrast, arboreal lineages colonizing continents did not show equally high rates of diversification (**Fig. 2, Supplementary Fig. S3**). Terrestrial species had lower rates of diversification irrespective of their geographic location. Together, these findings suggest that increased diversification rates within Columbiformes result from the combination of arboreal foraging and island dwelling rather than by each of these factors alone. These results hold when testing for the potential effect of hidden character states on diversification rates. Specifically, a state-dependent model including the five combinations of foraging behavior and geographical factors was better supported than an alternative, more complex model that took into account the possibility that spurious associations between traits and speciation rates (i.e. hidden traits) were affecting these diversification rates in Columbiformes (**Supplementary Table S6**).

Discussion

The widely-held view of islands as sinks of evolutionary diversity derives from the assumption that range expansions between continents and islands mostly take place in a single direction, that is, from continents to islands [4,19]. The evolutionary history of Columbiformes challenges this view, providing an empirical example where diversification on continents cannot be understood without understanding diversification processes that took place on islands.

Evolving from terrestrial-dwelling ancestors [36,59], continental lineages of Columbiformes colonized islands in several, independent occasions. In some of these cases, island colonization paved the way for forest-dwelling terrestrial species to shift to an arboreal foraging niche. These independent changes in foraging niche likely reflect behavioral innovations (*sensu* Lefebvre et al. [60]) and have spurred evolutionary diversification of the clade in two ways. First, the acquisition of an arboreal foraging niche on islands brought dramatic adaptive changes in morphology. Second, arboreal foraging spurred rates of taxonomic diversification, allowing the colonization of arboreal niches in other islands and the back colonization of continents.

Like two sides of the same coin, we found that island colonization by terrestrial-foraging lineages led to opposed evolutionary trajectories. After colonizing an island, some terrestrial clades tended to conserve their niche and evolved relatively longer tarsi (e.g. genera *Gallicolumba, Goura, Trugon,* or *Caloenas*). In some of these cases, terrestrial habits led to the evolution of flightlessness, the most famous cases being the Dodo (*Raphus cucullatus*) and the Rodriguez solitaire (*Pezophaps solitaria*). By preventing further cladogenesis, due to dispersal limitations, this evolutionary trajectory represents the end of an evolutionary road. In other side of the coin, a shift to arboreal foraging apparently opened an entire new ecological space that allowed Columbiformes to widely expand their ranges, and even successfully exploit niches that continental terrestrial pigeons had been unable to invade. The increased likelihood of niche shifts observed on islands as compared with continents is consistent with previous suggestions that an impoverished species richness on islands favors niche shifts associated with increased intra-specific competition driven by a relaxation of inter-specific competition and enemies pressure [3,14,61–64]. The invasion of previously unexploited ecological niches is a phenomenon commonly reported on islands [16,18,61], and has also been described in Columbiformes [64]. With the invasion of arboreal niches, the hindlimbs of Columbiformes evolved towards a new adaptive phenotypic optimum. Specifically, we found that arboreal-foraging Columbiformes evolved remarkably shorter hindlimbs as compared with their terrestrial-dwelling ancestors. Differences for similarly sized arboreal vs. terrestrial closely related species from islands were remarkable. For example, arboreal *Ptilinopus* of ~100 grams had tarsus commonly 7-11mm shorter as compared with their closest terrestrial-dwelling ancestors in the *Gallicolumba* genus. In most cases, this difference represents a decrease of 30-40% in tarsus length in arboreal-foraging, island dwelling Columbiformes as compared with their closest terrestrial-foraging, island dwelling ancestors. Despite being more pronounced across the Indo-Pacific clade (*sensu* Soares et al. [65]), which encompasses most of the extant arboreal species, this remarkable change in hindlimb morphology is paralleled within the Holarctic clade that includes several New World arboreal species in the genus *Columba* and Patagioenas. Differences in hindlimb optima are robust when independently comparing arboreal vs.

terrestrial-dwelling species from islands and from continents. This suggests that, once the arboreal foraging niche was colonized, selective pressures experienced by arboreal-dwellers in continents were similar to those on islands. Morphological divergence may explain the absence of evolutionary transitions from arboreal lineages back to terrestrial-foraging ones, a pattern already observed using a less comprehensive phylogeny of the group [35].

According to our models, speciation rates also increased after Columbiformes shifted from terrestrial to arboreal foraging on islands. In fact, more than half of the extant species of Columbiformes are arboreal foragers derived from these evolutionary transitions. The enormous diversification of arboreal-dwellers seems to be primarily the consequence of the mainland-island-mainland colonization loop, which was more frequent than any other transition (representing about 40% of all transitions). Unlike terrestrial-dwelling species, which have often reduced their dispersal ability on islands [34,66], arboreal lineages have maintained a high ability for dispersal [34,66]. Indeed, numerous tropical and subtropical arboreal-dwelling species of Columbiformes show highly nomadic ranging patterns when searching for fruiting trees [36,67,68] and are frequently observed flying over the ocean and reaching islands where they do not breed [34,66,69]. A high tendency to disperse could hinder diversification in the mainland by promoting gene flow, but range expansions may still facilitate allopatric diversification when occurring over long distances [10,12].

The alternative that higher diversification rates in arboreal-dwelling clades reflects lower extinction rates is little supported by evidence. Although a number of terrestrial species of Columbiformes—including the flightless Dodo and the Rodriguez solitaire— became extinct from Pacific islands in modern times [70], there is no evidence that the number of recently extinct lineages is higher for terrestrial-foraging lineages as compared with arboreal-foraging ones. Using an assembled extensive database of recently extinct species of birds [71], we indeed found similar numbers of extinct species in arboreal and terrestrial Columbiformes from islands (18 and 21, respectively), even when arboreal forms exhibit higher species richness.

Our findings support the notion that islands should not only be seen as sinks of biological diversity [22–24,27]. Instead, islands can represent sources of biological diversity that can spread beyond island ecosystems and even represent an important proportion of biodiversity on continents. The evolution of Columbiformes shows that successful range expansions onto islands were in fact necessary to enable behavioral innovations that spurred their evolutionary diversification [35,72–76]. The numerous back-colonizations of continents by island-dwelling, arboreal-foraging Columbiformes underscores that the evolutionary particularities of islands can be crucial to understand patterns of biological diversity on continents.

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Competing interests

The authors declare no competing interests.

Data availability

The data generated in this study can be accessed on: https://doi.org/10.5061/dryad.rjdfn2zbc.

Author contributions

OL, FS and DS conceived and designed the study. OL and FS collected the data and OL, FS, JGP ran the analyses. OL wrote the first draft of the paper, with later input from FS, JGP, and DS.

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Table 1. Phenotypic optima for tarsus length, estimated for the OUM model showing the mean, median, standard deviation (SD) and 95% confidence intervals (C.I.) in 100 phylogenetic trees. Abbreviations correspond to: AFC (Arboreal, Forest-dwelling, Continental), AFI (Arboreal, Forest, Island), TFC (Terrestrial, Forest, Continental), TFI (Terrestrial, Forest, Island), TOC (Terrestrial, Open habitat, Continental).

	Mean	Median	SD	Lower 95% C.I.	Upper 95% C.I.
AFC	-0.20	-0.19	0.05	-0.29	-0.10
AFI	-0.12	-0.13	0.04	-0.19	-0.01
TFC	0.16	0.15	0.04	0.10	0.28
TFI	0.30	0.30	0.04	0.20	0.34
TOC	-0.25	-0.26	0.08	-0.44	-0.10

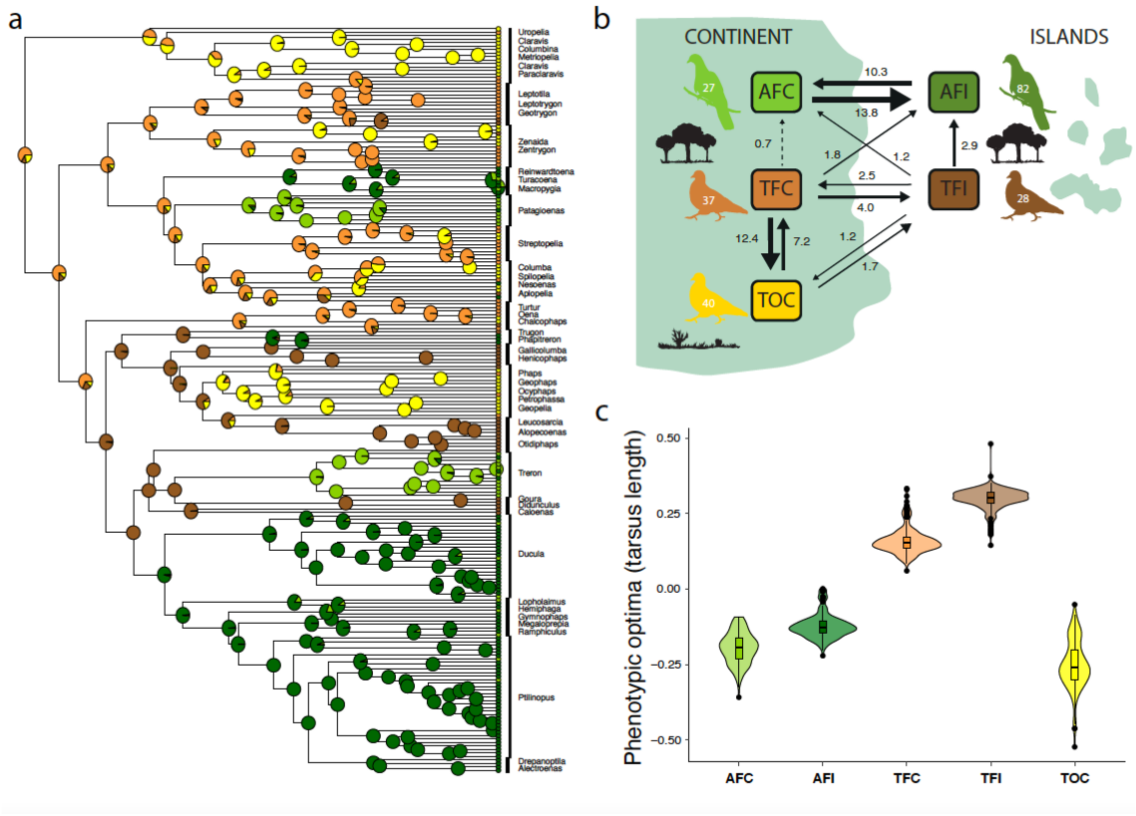

Figure 1. Evolutionary reconstructions of the niche in Columbiformes and its relation with tarsus length. **a.** Reconstruction of each of the major five eco-geographic groups throughout the evolutionary history of Columbiformes. Each category results from the combination the foraging niche (A: Arboreal, T: Terrestrial), habitat type (F: forests, O: open areas) and geographic origin (C: Continent, I: Island). The plotted tree corresponds to the integration of 1000 different tree reconstructions. **b.** Transitions between eco-geographic categories, with numbers next to rows indicating the mean number of transitions estimated from 1000 simmap-formatted trees and numbers within each silhouette correspond to number of species of each category. **c.** Phenotypic optima for tarsus length for each of the eco-geographic groups, showing the distribution of values for 100 phylogenetic trees by boxplots and density plots.

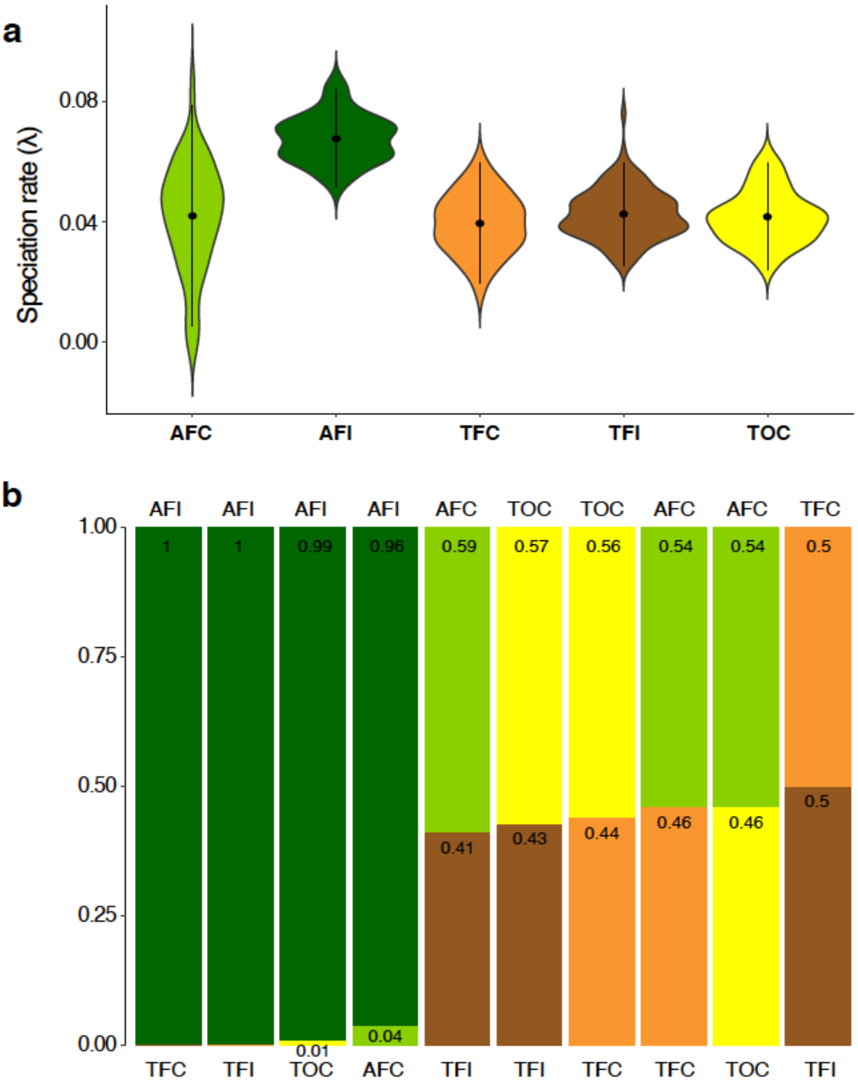

Figure 2: Speciation rates obtained from the best supported diversification model (CDD-0). **a.** Distribution of speciation rates (ʎ) obtained for each ecological group over 100 phylogenetic trees. The dots and bars represent means and 95% confidence intervals **b.** Proportion of samples in which the speciation rate is higher (or lower) for each pair-wise comparison between different combinations of behavioral, ecological and geographical factors. For example, the first bar indicates that in all trees, the diversification rate of arboreal, forest-dwelling, island species (AFI) was higher than that of terrestrial, forest-dwelling, island species (TFC).