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Behavioural changes and the adaptive diversification of pigeons and doves

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What factors determine the extent of evolutionary diversification remains a major question in evolutionary biology. Behavioural changes have long been suggested to be a major driver of phenotypic diversification by exposing animals to new selective pressures. Nevertheless, the role of behaviour in evolution remains controversial because behavioural changes can also retard evolutionary change by hiding genetic variation from selection. In the present study, we apply recently implemented Ornstein–Uhlenbeck evolutionary models to show that behavioural changes led to associated evolutionary responses in functionally relevant morphological traits of pigeons and doves (Columbiformes). Specifically, changes from terrestrial to arboreal foraging behaviour reconstructed in a set of phylogenies brought associated shorter tarsi and longer tails, consistent with functional predictions. Interestingly, the transition to arboreality accelerated the rates of evolutionary divergence, leading to an increased morphological specialization that seems to have subsequently constrained reversals to terrestrial foraging. Altogether, our results support the view that behaviour may drive evolutionary diversification, but they also highlight that its evolutionary consequences largely depend on the limits imposed by the functional demands of the adaptive zone.

1. Introduction

Much of current diversity across the tree of life is thought to have arisen from divergent selection leading to adaptation into a variety of ecological niches [1–3]. Thus, the extent of adaptive diversification is widely held to be enhanced by ecological opportunities [4,5], associated with either environmental changes or dispersal events that extended geographical ranges [6]. However, there are numerous situations where populations have failed to diversify despite inhabiting environments apparently conducive to adaptive radiation [7]. These situations highlight that divergent selection is not solely a function of the environment, but also depends on the way organisms interact with it [8,9]. Because changes in behaviour are necessary to take advantage of new ecological opportunities [10,11], behaviour has long been suggested to be a major driver of evolution in animals [9,12–24]. Mayr [15], for example, wrote: ‘A shift into a new niche or adaptive zone is, almost without exception, initiated by a change in behaviour. The other adaptations to the niche, particularly the structural ones, are acquired secondarily’ (p. 604). More than 50 years after Mayr’s quote, however, whether and how behaviours influence evolution are still the subject of intense debate [9].

Behaviour can act as a driver of evolutionary diversification by changing the way individuals interact with their environment, thereby placing divergent selection pressures on populations that promote adaptive divergence [9,19,22–24]. As suggested by Collar *et al.* [25], when there is a change in the way individuals interact with the environment, subsequent evolutionary changes can be promoted in two different ways. First, natural selection may pull the population’s phenotype towards a new adaptive optimum. Second, if the new environmental challenges may be dealt with in different ways, the

rates of phenotypic disparity within the new selective regime may also increase [25]. Although both mechanisms may act simultaneously to increase diversification, their consequences for the tree of life are different. The first mechanism results in an increased phenotypic disparity within the clade as a whole, but not among species experiencing the same selective regime. By contrast, the second mechanism predicts a higher disparity among species under the new selective regime [25].

While behaviour is classically viewed as an important driver of evolutionary change, the possibility that behaviour can sometimes also act to retard evolution has also been acknowledged [13,26,27]. On one hand, plastic changes in behaviour are an important way through which animals respond to new ecological pressures [28], which may hide genetic variation from natural selection, and hence inhibit evolutionary change (the so-called Bogert effect; reviewed in previous studies [22,23,26]). While some studies suggest that behavioural changes do not necessarily prevent natural selection from operating on other characters when individuals are exposed to new ecological pressures [27], this does not rule out the possibility that the Bogert effect plays a major role in retarding adaptive evolution on an evolutionary time-scale. On the other hand, if a behavioural change brings the population close to an adaptive peak that is functionally demanding, stabilizing selection will impose strong limits to subsequent phenotypic diversification, and hence favour evolutionary stasis and niche conservatism.

Current evidence about whether behaviour generally favours or inhibits evolutionary diversification is insufficient to draw firm conclusions. A few comparative studies in birds have revealed that lineages with a higher propensity for behavioural changes, as reflected by their larger brains, have generally experienced more extensive evolutionary diversifications in body size [29], subspecies richness [30] and species richness [31]. Nevertheless, it should be noted that behaviour may favour evolutionary change by mechanisms other than exposing animals to divergent selective pressures, such as by facilitating the establishment in a novel region or by reducing extinction risk [15,24,32–34]. In addition, Lynch [35] found no evidence that post-cranial morphological evolution has been faster in mammalian lineages with larger brains.

A more direct approach to study whether changes in behaviour drive or inhibit evolution would be to assess whether past behavioural changes can explain current patterns of phenotypic diversification. Recent progress in phylogenetic comparative methods provides a framework for such a retrospective approach [36–39]. With a well-supported phylogeny and information on contemporary phenotypic variation, it is possible to study the evolutionary trajectory of a phenotypic trait after a change in behaviour by fitting different evolutionary models of phenotypic evolution. The hypothesis that behavioural changes can retard phenotypic changes may be described with an Ornstein–Uhlenbeck (OU) model under stabilizing selection where phenotypic variation oscillates around a common phenotypic optimum for all species irrespective of their behavioural state. The alternative possibility, that behavioural shifts create novel selection pressures that lead to adaptations towards different phenotypic optima, can be approximated by fitting an OU process with different optima for each selective regime [36,37]. Using OU models, a few studies have yielded evidence of divergence towards different morphological optima associated with behavioural changes in

foraging strategy [40], habitat use [25,41] and locomotive strategy [42]. However, in-depth biological interpretations of these associations between behavioural shifts and evolutionary change under an OU process have been hindered by the restrictive assumption that both the strength of selection towards the new optima and its rate of stochastic variation away from the optima do not vary among selective regimes [43]. Recent OU model implementations now allow for the separate estimation of selective forces pulling species to different phenotypic optima and the range of variation around these optima [43]. This new framework allows researchers to move forward towards more mechanistic questions on the nature of the evolutionary consequences of changes in the selective regimes (e.g. do behavioural shifts accelerate or limit evolutionary change?).

In the present study, we use the aforementioned flexible OU model to investigate the consequences of changes in foraging behaviour in the morphological diversification of pigeons and doves (order Columbiformes). Columbiformes experienced a worldwide radiation from the early Eocene, presumably facilitated by their high dispersal ability [44], which allowed them to diversify into a large number of species (greater than 310) and colonize an extremely diverse range of habitats in all continents except Antarctica [45]. During their geographical expansion, pigeons and doves probably encountered a myriad of different environments [45], which may have required behavioural adjustments that may or may not have led to subsequent evolutionary adjustments. Our focus here is on transitions from terrestrial to arboreal behaviour and vice versa, which represent a fundamental divergence in the way pigeons and doves exploit the resources. Almost all members of the lineage can be easily classified as either terrestrial or arboreal in their foraging behaviour, with only a few species combining both behaviours [45]. Tree-dwelling Columbiformes inhabit forested habitats and feed on fruit that they obtain by perching on tree branches, whereas terrestrial foraging species occur in both forested and open habitats, and primarily feed on seeds and grains, but also fruit [45].

With the aim of investigating whether and how such behavioural changes may have influenced morphological diversification, we built a molecular phylogeny of the Columbiformes encompassing over half of the extant species. Using this phylogeny as a framework, we reconstructed changes between arboreal, terrestrial and generalist foraging behaviours, and used these changes as the basis for fitting a variety of OU models to describe subsequent morphological evolution while taking into account uncertainties in phylogeny and ancestral state reconstructions. The OU models were contrasted with Brownian motion (BM) models, which assume that phenotypic variation accumulates at random over time without a defined trajectory [38,39]. As different morphological traits may follow different evolutionary trajectories under similar ecological scenarios, we used a variety of morphological traits predicted to have functional consequences for pigeons' foraging performance, and integrated them in a few multivariate axes explaining the vast majority of variation in morphology. However, we predict that the evolutionary consequences of changes in foraging behaviour should be primarily reflected in the hindlimb and the tail. This is because shorter hindlimbs and a longer tail are expected to increase stability in birds perching on slender and unstable branches by keeping the centre of mass close to the perch, whereas a

long hindlimb increases stride length, and hence enhances speed during terrestrial locomotion [46,47]

2. Material and methods

(a) Taxon sampling and phylogenetic analyses

We constructed our phylogenetic hypothesis for Columbiformes with both maximum-likelihood (RAxML) and Bayesian methods (BEAST) using six mitochondrial and three nuclear genes (for the detailed information regarding the construction of the phylogenies, see the electronic supplementary material, appendix S1) from the GenBank database. We obtained enough information for 156 species of pigeons and doves (about half of the whole order) plus eight outgroups to root the tree. A list of all the specimens included in the phylogenetic analyses with the GenBank accession numbers can be found in the electronic supplementary material, appendix S2. The alignment is available from TreeBASE (study ID 13646).

(b) Foraging behaviour

We obtained information on each species's biology from published literature sources, mainly from Gibbs *et al.* [45]. We considered as terrestrial those species that primarily obtain their food (usually seeds and grain, but also fruits) by searching on the ground, and as arboreal those that primarily forage on fruits found on trees and rarely descend to the ground. Almost all species could be easily classified to have either a terrestrial or arboreal foraging mode (see the electronic supplementary material, table S4). However, 12 species with a mixed strategy (i.e. those species regularly using both foraging modes) were classified into an intermediate category (i.e. generalists). A simplified alternative analysis with species classified into only two main foraging categories (i.e. terrestrial and arboreal) yielded similar results.

(c) Ancestral state reconstructions

To reconstruct the history of foraging behaviour in Columbiformes, we used stochastic character mapping [48,49]. This is a Bayesian method that, given a phylogeny and discrete character states for extant species, 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 [48,49]. The R package *phytools* [50] was used to build stochastic character-mapped reconstructions for each of the 500 trees sampled from the posterior distribution of the BEAST. The resulting 500 reconstructions of behavioural states and phylogeny represent a set of phylogenetic topologies, branch lengths and habitat histories sampled in proportion to their posterior probabilities. All these trees were used in subsequent analyses as a way of integrating over uncertainty in phylogeny and ancestral states.

(d) Morphology

Information on five ecologically relevant morphological characters (length of the tarsus, tail, wing and beak, and body mass) was obtained for the 156 species from the literature [45,51] (electronic supplementary material, table S4). Although the size of the hindlimb was described with a single trait (the length of the tarsus), previous work has shown that the tarsus length is correlated with the length of the other hindlimb bones across flying animal groups (R^2 of 0.68 and 0.85 with femur and tibia lengths, respectively [52]). For twelve species we could not find information on body mass, and these were estimated with imputation techniques based on multiple regressions [53].

Morphological evolution may be tightly correlated with changes in overall body size, and this allometric relationship can lead to equivocal positive results if the function of the character is confounded with that of body size. To tackle this difficulty, we conducted a phylogenetic size correction following Revell [54] to obtain morphological measurements independent from body size (body mass, in our case). All measurements were log-transformed and body mass was also first cubic root-transformed. The procedure uses the residuals from a log–log least-squares regression analysis, while controlling for non-independence owing to phylogenetic history. Once these corrected scores were obtained, we conducted a phylogenetic principal components analysis (PCA) again following Revell [54]. The resulting PCA scores for each axis were used as the input to investigate the most likely evolutionary scenarios of morphological evolution. As phylogenetic principal components provide estimates of the eigenstructure with lower variance relative to non-phylogenetic procedures when residual error is autocorrelated among species, this should reduce type I errors when they are used in subsequent analyses [54].

To illustrate the amount of unique morphospace occupied by each foraging behaviour category, we used a bivariate plot of the first two components from the phylogenetically corrected PCA. This plot shows a projection of the tree into morphospace (phylogenetic morphospace plot), in which lines connect hypothetical ancestral phenotypes to the known or estimated phenotypes of their descendants (i.e. a representation of the phylogenetic morphospace [50]).

We also obtained similar information for 150 additional species not present in the phylogeny to test whether our subset of 156 species accurately represents the morphospace of the entire clade. With these additional data, we confirmed that the species sampled in the study were not a biased sample of the complete Columbiformes order (see the electronic supplementary material, table S5). We quantified the disparity of the raw values of all morphological traits by computing the average-squared Euclidean distance among all pairs of points within the dataset using the 'disp.calc' function in the *GEIGER* package written for R [55]. This allowed us to investigate whether disparity differs across lineages showing diverging foraging behaviours, and whether it is different between different morphological traits that may be under different selective regimes.

(e) Model selection for morphological evolution

We fitted five different OU models of character evolution to morphological data to test whether behavioural changes have been associated with selective constraints on the evolution of several morphological trait axes. The simplest model was an OU model with a single optimum (θ) applied to all branches regardless of the behavioural state ('OU1' model). The remaining four OU models differed in how the rate parameters were allowed to vary in the model. The first was an OU model with different phenotypic optima means (θ_x), and both identical strengths of selection (α_x) and rate of stochastic motion around the optima (σ_x^2) acting on all selective regimes ('OUM' model). This model is equivalent to that implemented by Butler & King [37]. We also fitted a model that only allowed strengths of selection to vary among selective regimes ($\alpha_1, \alpha_2, \dots$; 'OUMA' model), as well as one that only allowed the rates of stochastic evolution away from the optimum to vary ($\sigma_A^2, \sigma_B^2, \dots$; 'OUMV' model). Finally, we fitted a model that allowed all three parameters (θ, α, σ) to vary among different selective regimes ('OUMVA' model). All models were fitted using the R package *OUwie* [43]. We used a model-averaging approach, where we calculated the Akaike weights for each model (i.e. the relative likelihood of each model) by means of the second-order Akaike information criteria (AICc), which includes a correction for reduced sample

sizes [56]. The parameter estimates for each model were then averaged together, using their corresponding Akaike weight (AICw) as the weights.

An alternative possibility would be that morphology varies at random following a BM process, where phenotypic variation accumulates with time. Although BM does not necessarily represent a model of random variation (it can be also consistent, for example, with neutral genetic drift, selection towards a moving optimum or drift–mutation balance [43]), rejecting this as the best model implies that phenotypic evolution has not followed a random evolutionary trajectory. We also tested the possibility that the BM process has a different rate of evolution among different selective regimes (terrestrial, generalist, arboreal, BMS model).

Finally, we estimated the phylogenetic half-life ($t_{1/2} = \ln(2)/\alpha$) for each PC axis in each selective regime. This parameter is defined as the time required for the expected phenotype, starting in an ancestral state and evolving under a new selective regime, to traverse half the morphological distance from the ancestral state to the optimum [36], and was estimated in relative time units for comparative purposes among selective regimes only.

3. Results

(a) Phylogenetic analyses

The results of the ML and Bayesian analyses were congruent (see figure 1 and electronic supplementary material, figure S1), and corroborate the main phylogenetic relationships among Columbiformes found in a previous analysis by Pereira *et al.* [44]. The main difference is that in our ML and Bayesian trees the clade B (*sensu* [44]) is considered sister to clades A and C instead of being sister to only clade C. However, in both the present analysis and that of Pereira *et al.* [44], the bootstrap support and posterior probabilities for the relationships among clades A, B and C are low (see the electronic supplementary material, figure S1 of the present paper, and figures 1 and 2 from Pereira *et al.* [44]).

(b) Character reconstructions and evolutionary transitions

Figure 1 shows one of the 500 sampled trees from the stochastic character mapping reconstruction of changes in foraging behaviour derived from the ultrametric Bayesian analysis in BEAST. Two species for which no morphological information was available (*Raphus cucullatus* and *Pezophaps solitaria*) were pruned from the trees.

Table S6 in the electronic supplementary material indicates the mean, median, s.d., modal number, and maximum and minimum number of transitions estimated for each sampled tree from/to all foraging strategies. The modal number of transitions computed from the sample of 500 trees was 20. According to the reconstructions, terrestrial pigeons and doves were inferred to have changed their foraging behaviour 12 times (seven to generalist and five to arboreal foraging, modal values). The modal number of transitions from generalist lineages was eight (six times to arboreal and twice to terrestrial foraging). Finally, arboreal lineages did not show any transition to other foraging strategies (modal number = 0 for both transitions to terrestrial and generalist foraging strategies), suggesting that specialization in arboreal foraging may be an evolutionary dead-end (figure 1; see also electronic

supplementary material, appendix S7 for a formal analyses of evolutionary transitions rates with BAYESTRAITS).

(c) Defining the morphospace

To investigate whether behavioural changes have led to morphological changes, we started by defining the morphospace of Columbiformes with a size-corrected phylogenetic PCA. We restricted our analyses to the first three axes, which together accounted for 90.79 per cent of the morphological variation of the lineage (see the electronic supplementary material, table S8). The first axis correlated mostly with the length of the tail and less strongly with tarsus length; the second axis primarily correlated positively with tarsus length and negatively with tail length. Finally, the third axis correlated with both wing length and beak length.

The phylomorphospace defined by the PC axes showed that terrestrial species occupy a broader space than arboreal and generalist lineages, which instead showed a more clumped phenotypic distribution pattern (see figure 2; see also electronic supplementary material, figures S2 and S3). This result was further confirmed when comparing morphological disparity metrics, which were higher for terrestrial species than for arboreal and generalist species for all morphological traits (see the electronic supplementary material, table S5). The extent of increased morphological diversity in terrestrial lineages was particularly pronounced in the case of tarsus length, for which disparity in terrestrial species was more than three times higher than in arboreal-dwelling species. The phylogenetic morphospace representation showed that a significant part of the variation in PC1 corresponded to the effect of a single phylogenetic clade (i.e. species in the bottom right morphospace representation correspond to clade B, defined above), which could affect the interpretation of the model results. This pattern of phylogenetic clustering was not found for PC2 (figure 2) nor for PC3 (see the electronic supplementary material, figures S1 and S2).

(d) Evolutionary model fitting

All BM models received less support than any of the OU models for all PC axes and body size evolution (table 1), suggesting that the evolution of these traits oscillates at least in part around one or more phenotypic optima. In the OU models, the estimated optima were found within the values realized for extant species in all cases (table 2), suggesting that the models were a realistic description of current morphological patterns.

There was substantial support for the OUMVA model of evolution (AICw ranging from 0.612 to 0.699; table 1) for PC1, PC2 and body size, and with the exception of OU1 for PC1, all alternative models received low support (AICw < 0.09). Indeed, the model-averaged parameter estimates from all five OU models suggest that the adaptive optima differed among behavioural strategies (see mean phenotypic optimum scores in table 2), although phenotypic optima were much more similar between arboreal and generalist lineages compared with terrestrial-dwelling lineages. Tail length was the morphological trait most strongly loading in PC1, whereas tarsus length was the trait most strongly loading in PC2. Taken together, the values of phenotypic optima suggest that species evolved towards shorter tarsi and longer tails when changing from terrestrial to either arboreal or generalist behaviour (table 2). The evolution of PC3

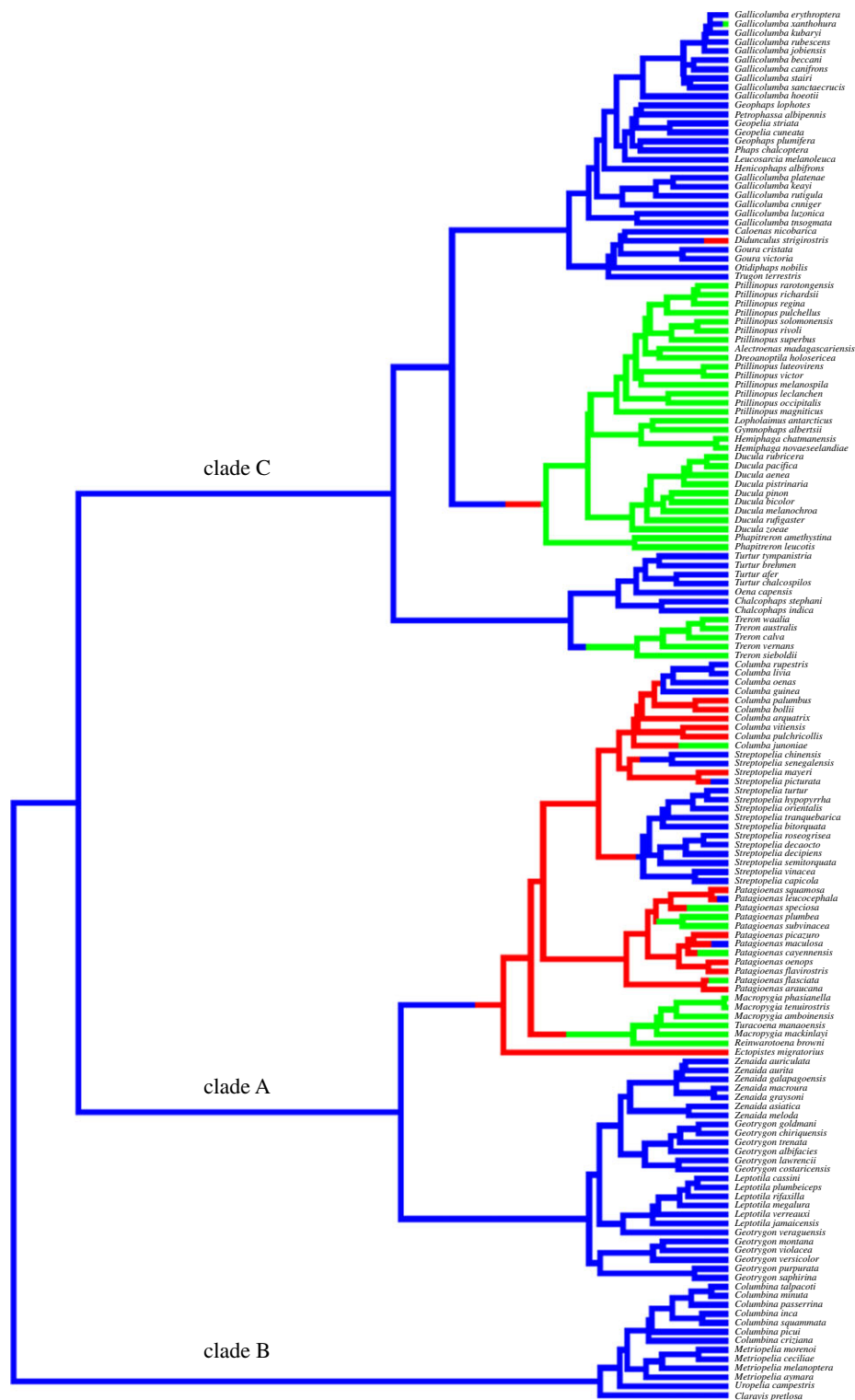


Figure 1. Sample tree of one of the 500 foraging behaviour reconstructions generated through stochastic character mapping. Coloured branches illustrate foraging behaviour estimated at each branch: terrestrial lineages (in blue), generalist (in red) and arboreal (in green). Changes may occur within branches because reconstructions depict not only the states at the nodes but also the states at all points along a branch between nodes.

(described mainly by wing length and secondarily by beak length) was best fitted by an OUMA model, although alternative models, such as OU1, also received some statistical support (table 1). It should be noted, however, that differences between the phenotypic optima of each selective regime were comparatively much smaller for PC3 than those inferred for both PC1 and PC2 (table 2), consistent with its lower functional relevance in the context of foraging substrate. Finally, although the optimum for body mass was estimated to be larger for arboreal and generalist lineages

(table 2), this could simply be the consequence of the pulling effect of some very small terrestrial-dwelling Neotropical species belonging to clade B (*sensu* [44]; figure 1).

Interestingly, we found striking differences in the parameters describing the evolution of morphological traits between different selective regimes. Although individual estimates varied considerably from tree to tree, the strength of selection (α) towards the phenotypic optimum was consistently higher in PC1, PC2 and body mass, and consistently lower in PC3, after a change towards arboreal or generalist

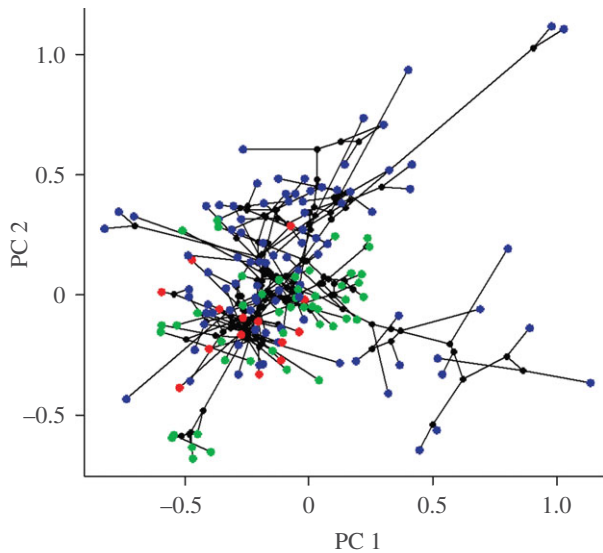


Figure 2. A phylogenetic morphospace representation of all 154 Columbigormes that superimposes the branching patterns of the phylogeny (black lines) on the plot of the two first PC axes from the phylogenetic PCA. Species are coloured with respect to their foraging behaviour category: terrestrial (blue), generalist (red) and arboreal (green).

foraging strategy than when the lineage used a terrestrial strategy (table 2). Similarly, the rate of stochastic motion away from the optimum (σ^2) was consistently higher in terrestrial lineages than in the other two strategies, despite a range of estimates across our tree set (table 2). Finally, phylogenetic half-life for PC1, PC2 or body size is markedly lower in arboreal and generalist lineages (see the electronic supplementary material, table S9). In particular, the phylogenetic half-life estimated for body size is about four times faster when governed by either the arboreal or generalist selective regimes (see the electronic supplementary material, table S9).

4. Discussion

Evolutionary models always represent an over-simplification of the evolutionary processes that have shaped adaptive diversification within a lineage, as incorporating all factors that may affect evolutionary change is virtually impossible [57]. At present, however, the implementation of models that allow for both the strength of selection and the rate of stochastic motion around the phenotypic optima to vary between presumed selective regimes [43] makes it possible to fit more mechanistic evolutionary models. The success of such a model selection approach is nonetheless contingent on the existence of a robust phylogenetic hypothesis and of several independent behavioural transitions that allow the assessment of convergent evolution for lineages under similar selective regimes (e.g. all lineages that adopted an arboreal foraging behaviour). When these conditions are met, as they are here, the comparison of different models may provide important insights into the factors influencing evolutionary diversification [25,40–42,58–62].

Our results shed new light on the unresolved controversy of whether behavioural shifts accelerate or inhibit evolutionary change [23,26]. On the one hand, we find that past changes in foraging behaviour of Columbigormes have brought associated changes in functionally relevant

morphological traits in the direction predicted by eco-morphological theory. On the other hand, by applying recently implemented evolutionary models, we provide evidence that changes in the way Columbigormes obtain their foraging resources are associated with accelerated rates of evolutionary change in some morphological characters. Nevertheless, the results also highlight scenarios where a behavioural change may limit subsequent evolutionary diversification. Thus, the functional demands of arboreality seem to limit further diversification of arboreal-dwelling lineages, perhaps representing a form of evolutionary dead end.

Our analyses suggest that the evolutionary trajectories of morphological traits have changed in a predictable manner associated with a change in foraging behaviour, mostly in the PCAs related to tail length (PC1, but also PC2) and hindlimb (PC2) morphology, as well as overall body size, but not for the evolution of wing and beak lengths (PC3). The best evolutionary models for PC1, PC2 and body size were multiple-peak OU models, with a divergent optimum for terrestrial specialists compared with both generalists and arboreal specialists. With the exception of body size, where functional implications of different optima are unclear, the existence of different phenotypic optima is in agreement with biomechanical predictions [47,63–65]. Long hindlimbs are thought to increase stride length and enhance speed in terrestrial locomotion, whereas short hindlimbs and longer tails should increase stability in birds perching on slender and unstable branches by keeping the centre of mass close to the perch [47]. Our results fit these expectations well, with changes to arboreal behaviour associated with evolutionary trajectories towards shorter tarsi and longer tails, and changes to terrestrial behaviour leading to opposed trajectories. While with a retrospective analysis it is not possible to demonstrate that behaviour is the driving force behind morphological evolution, the stronger support for OU models relative to BM models is incompatible with a scenario where morphological evolution occurs at random with a correlated effect on behaviour. Moreover, although morphology can influence behavioural decisions, for example by affecting motor performance in different substrates, the existence of stabilizing selection pulling lineages with different foraging behaviours towards different phenotypic optimum zones is difficult to understand, unless each foraging behavioural type imposes a different selective regime.

Behavioural changes can promote phenotypic evolution not only by imposing selection towards different adaptive peaks, but also by facilitating the use of available resources in different ways within a selective regime [25]. By investigating the variation in the strength of selection (α) and the stochastic motion (σ^2) parameters [43], we show that terrestrial lineages indeed exhibited a more relaxed effect of stabilizing selection and a higher rate of stochastic variation in the size of the tarsus, tail and body than the other lineages, which may explain their higher morphological disparity. On the contrary, foraging on trees may require higher levels of morphological specialization, as shown by the reduced variation in the morphospace, which may subsequently limit the performance of individuals in other foraging contexts. This may explain why transitions from arboreal foraging behaviour to any of the other behavioural strategies have rarely occurred in the evolutionary history of Columbigormes. Thus, it may very well be that a change in behaviour increases phenotypic disparity within the clade as a whole

Table 1. Average AIC weights (AICw) representing the relative likelihood of each of the seven evolutionary models investigated to morphological data for PC1, PC2 and PC3 axes, and body size computed after fitting all evolutionary models on 500 reconstructions of the foraging strategy obtained from the trees after stochastic character mapping.

| | BM1 | BMS | OU1 | OUM | OUMV | OUMA | OUMVA |
|-----------|--------|--------|--------|-------|-------|-------|-------|
| PC1 | <0.001 | <0.001 | 0.255 | 0.035 | 0.012 | 0.060 | 0.638 |
| PC2 | <0.001 | <0.001 | <0.001 | 0.019 | 0.313 | 0.009 | 0.612 |
| PC3 | <0.001 | 0.002 | 0.322 | 0.130 | 0.085 | 0.388 | 0.073 |
| body size | 0.061 | 0.017 | 0.045 | 0.057 | 0.088 | 0.034 | 0.699 |

Table 2. Model-averaged parameters for every PC axis and body mass. The means and both 2.5 and 97.5% quantiles around the average (in parentheses) are shown for each selective regime for the mean phenotypic optimum (θ), the strength of selection (α) and the rate of stochastic motion (σ^2). The proportion of trees where mean adaptive optima or parameter estimates significantly differ between terrestrial and arboreal/generalist selective regimes is indicated in all cases.

| | terrestrial | generalist | arboreal | |
|-----------|--------------------|----------------------|----------------------|---|
| | θ_1 | θ_2 | θ_3 | prop $\theta_1 \neq \theta_2, \theta_3$ |
| PC1 | -0.05 (-0.09/0.01) | -0.14 (-0.26/ -0.07) | -0.13 (-0.26/ -0.07) | 98.9% (>) |
| PC2 | 0.19 (0.16/0.23) | -0.10 (-0.25/0.04) | -0.10 (-0.25/0.04) | 99.7% (>) |
| PC3 | 0.03 (0.02/0.05) | 0.02 (-0.03/0.10) | 0.01 (-0.03/0.08) | 80% (>) |
| body size | 1.66 (1.60/1.81) | 1.88 (1.71/2.00) | 1.85 (1.69/2.00) | 97.1% (<) |
| | α_1 | α_2 | α_3 | prop $\alpha_1 \neq \alpha_2, \alpha_3$ |
| PC1 | 8.86 (2.06/15.13) | 20.9 (3.26/43.6) | 21.4 (3.27/48.0) | 98.8% (<) |
| PC2 | 7.16 (1.83/10.2) | 13.4 (3.68/34.1) | 14.7 (6.19/35.2) | 94.1% (<) |
| PC3 | 19.6 (11.6/27.9) | 16.2 (10.8/23.9) | 17.4 (11.0/25.6) | 90.9% (>) |
| body size | 3.79 (<0.01/9.68) | 16.0 (1.06/61.3) | 15.0 (0.99/60.5) | 96.3% (<) |
| | σ^2_1 | σ^2_2 | σ^2_3 | prop $\sigma^2_1 \neq \sigma^2_2, \sigma^2_3$ |
| PC1 | 2.66 (0.79/4.83) | 0.99 (0.02/2.42) | 1.14 (0.04/2.31) | 99.2% (>) |
| PC2 | 1.82 (1.42/2.25) | 1.36 (0.11/3.44) | 1.02 (0.06/3.27) | 81.9% (>) |
| PC3 | 0.86 (0.53/1.21) | 0.81 (0.48/1.17) | 0.81 (0.49/1.17) | 76.3% (>) |
| body size | 0.90 (0.52/1.51) | 0.37 (<0.01/0.93) | 0.45 (<0.01/0.91) | 98.3% (>) |

and, at the same time, either increases or reduces rates of evolutionary diversification within the clade depending on the intensity of stabilizing selection.

Although the factors that have triggered changes in foraging behaviour in Columbiformes are unknown, there are two obvious possibilities. The first is the colonization of areas where the distribution of resources forces individuals to change their behavioural strategy [57]. Dispersal ability is held to be one of the most important factors related to diversification in birds [24,66], and may have also played a major role in the evolutionary history of Columbiformes. Pereira *et al.* [44] identified at least fifteen independent inter-continental colonization events along the evolutionary history of Columbiformes, apart from many colonization events of remote islands. It is quite conceivable that the high dispersal ability of pigeons and doves [44,45] may have contributed to the adaptive diversification of the group by facilitating the colonization of distant regions offering novel ecological opportunities. Moreover, the reproductive isolation and small population numbers associated with allopatric (and peripatric) events of colonization may have facilitated rapid evolutionary shifts in isolated populations of Columbiformes. The second factor that may have

triggered changes in foraging behaviour in Columbiformes is competition [4], which may also be related (although not necessarily) to the invasion of remote areas. On the West Indian island of Barbados, for example, Zenaida doves (*Zenaida aurita*) aggressively defend feeding territories from conspecifics, but in some areas individuals have recently started feeding in large unaggressive groups with conspecifics. This behavioural shift, facilitated by the availability of a novel resource opportunity, has been suggested to be the consequence of competition for territory, which forced less competitive individuals to use alternative resources [67]. The finding that body size notably varies among closely related arboreal species could indeed be a consequence of competition if, as suggested by Diamond [68,69], differences in body size allow coexistence among species that consume fruits of different sizes on branches of different diameters.

Once a novel behaviour has established in the population, evolution may proceed remarkably rapidly [24]. Our results estimate that substantial changes in morphology can occur in short periods of time, particularly after a behavioural change to arboreality. Such relatively short periods needed to produce important divergence in morphological traits contrast with the long evolutionary period since

Columbiformes diverged from their ancestor (between 83 and 107 Mya, as estimated by Pereira *et al.* [44]), and agrees with empirical evidence that changes in locomotive demands may exert strong selection on pigeons' morphology [46]. Thus, our study adds to the extensive comparative and experimental evidence supporting the importance of locomotion in the evolutionary diversification of animals, as exemplified in the classical adaptive radiation of *Anolis* lizards (reviewed by Losos [57]; and see also [70]).

Overall, our results support the widely held yet rarely tested hypothesis that modifications in behaviour can promote adaptive diversification of a whole clade by exposing individuals with different behavioural traits to divergent selective pressures. At the same time, the results also highlight that changes in behaviour may either increase or reduce rates of evolutionary diversification within each selective regime depending on the force of stabilizing selection. Coupled with other mechanisms, such as a high dispersal ability and competition, behaviour may thus be a powerful force in the evolutionary diversification

of animals. To better integrate behaviour into the ecological theory of evolution, however, we need further studies specifically examining the interplay between colonization, competition and behavioural shifts in determining the adoption of novel ecological opportunities and subsequent phenotypic divergence. These studies are likely to provide important insight into the causes underlying the enormous adaptive diversification experienced by some lineages.

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References

- Darwin C. 1859 *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. London, UK: John Murray.
- Simpson GG. 1953 *The major features of evolution*. New York, NY: Columbia University Press.
- Schluter D. 2001 Ecology and the origin of species. *Trends Ecol. Evol.* **16**, 372–380. (doi:10.1016/S0169-5347(01)02198-X)
- Schluter D. 2000 *The ecology of adaptive radiation*. Oxford, UK: Oxford University Press.
- Yoder JB *et al.* 2010 Ecological opportunity and the origin of adaptive radiations. *J. Evol. Biol.* **23**, 1581–1596. (doi:10.1111/j.1420-9101.2010.02029.x)
- Ricklefs RE. 2006 Global variation in the diversification rate of passerine birds. *Ecology* **87**, 2468–2478. (doi:10.1890/0012-9658(2006)87[2468:GVITDR]2.0.CO;2)
- Seehausen O. 2006 African cichlid fish: a model system in adaptive radiation research. *Proc. R. Soc. B* **273**, 1987–1998. (doi:10.1098/rspb.2006.03539)
- Odling-Smee FJ, Laland KN, Feldman MW. 2003 *Niche construction: the neglected process in evolution*. Princeton, NJ: Princeton University Press.
- Duckworth RA. 2008 The role of behavior in evolution: a search for mechanism. *Evol. Ecol.* **23**, 513–531. (doi:10.1007/s10682-008-9252-6)
- Lefebvre L, Whittle P, Lascaris E, Finkelstein A. 1997 Feeding innovations and forebrain size in birds. *Anim. Behav.* **53**, 549–560. (doi:10.1006/anbe.1996.0330)
- Lefebvre L, Reader SM, Sol D. 2004 Brains, innovations and evolution in birds and primates. *Brain Behav. Evol.* **63**, 233–46. (doi:10.1159/000076784)
- Baldwin MJ. 1896 A new factor in evolution. *Am. Nat.* **30**, 441–451. (doi:10.1086/276408)
- Bogert CM. 1949 Thermoregulation in reptiles, a factor in evolution. *Evolution* **3**, 195–211. (doi:10.2307/2405558)
- Miller AH. 1956 Ecological factors that accelerate formation of races and species of terrestrial vertebrates. *Evolution* **10**, 262–277. (doi:10.2307/2406011)
- Mayr E. 1963 *Animal species and evolution*. Cambridge, MA: Harvard University press.
- Wyles JS, Kunkel JG, Wilson AC. 1983 Birds, behavior and anatomical evolution. *Proc. Natl. Acad. Sci. USA* **80**, 4394–4397. (doi:10.1073/pnas.80.14.4394)
- Bateson P. 1988 The active role of behaviour in evolution. In *Evolutionary processes and metaphors* (eds M-W Ho, SW Fox), pp. 191–207. New York, NY: Wiley.
- Plotkin HC. 1988 *The role of behaviour in evolution*. Cambridge, MA: MIT Press.
- Wcislo WT. 1989 Behavioral environments and evolutionary change. *Annu. Rev. Ecol. Syst.* **20**, 137–169.
- West-Eberhard MJ. 1989 Phenotypic plasticity and the origins of diversity. *Annu. Rev. Ecol. Syst.* **20**, 249–278. (doi:10.1146/annurev.es.20.110189.001341)
- Futuyma DJ. 1998 *Evolutionary biology*. Sunderland, MA: Sinauer Associates.
- Robinson BW, Dukas R. 1999 The influence of phenotypic modifications on evolution: the Baldwin effect and modern perspectives. *Oikos* **85**, 582–589. (doi:10.2307/3546709)
- Huey RB, Hertz PE, Sinervo B. 2003 Behavioral drive versus behavioral inertia in evolution: a null model approach. *Am. Nat.* **161**, 357–366. (doi:10.1086/346135)
- Price TD. 2008 *Speciation in birds*. Greenwood Village, CO: Roberts and Company Publishers.
- Collar DC, Schulte II JA, Losos JB. 2011 Evolution of extreme body size disparity in monitor lizards (*Varanus*). *Evolution* **65**, 2664–2680. (doi:10.1111/j.1558-5646.2011.01335.x)
- Price TD, Qvarnstrom A, Irwin DE. 2003 The role of phenotypic plasticity in driving genetic evolution. *Proc. R. Soc. Lond. B* **270**, 1433–1440. (doi:10.1098/rspb.2003.2372)
- Losos JB, Schoener TW, Spiller DA. 2004 Predator-induced behaviour shifts and natural selection in field-experimental lizard populations. *Nature* **432**, 505–508. (doi:10.1038/nature03039)
- Sih A, Ferrari MCO, Harris DJ. 2011 Evolution and behavioural responses to human-induced rapid environmental change. *Evol. Appl.* **4**, 367–387. (doi:10.1111/j.1752-4571.2010.00166.x)
- Sol D, Price TD. 2008 Brain size and the diversification of body size in birds. *Am. Nat.* **172**, 170–177. (doi:10.1086/589461)
- Sol D, Stirling DG, Lefebvre L. 2005 Behavioral drive or behavioral inhibition in evolution: subspecific diversification in holarctic passerines. *Evolution* **59**, 2669–2677. (doi:10.1111/j.0014-3820.2005.tb00978.x)
- Nicolakakis N, Sol D, Lefebvre L. 2003 Behavioural flexibility predicts species richness in birds, but not extinction risk. *Anim. Behav.* **65**, 445–452. (doi:10.1006/anbe.2003.2085)
- Sol D, Duncan RP, Blackburn TM, Cassey P, Lefebvre L. 2005 Big brains, enhanced cognition, and response of birds to novel environments. *Proc. Nat. Acad. Sci. USA* **102**, 5460–5465. (doi:10.1073/pnas.0408145102)
- Mayr E. 1969 *Principles of systematic zoology*. New York, NY: McGraw-Hill.
- Mayr E. 1965 The nature of colonising birds. In *The genetics of colonizing species* (eds HG Bakker, GL Stebbins), pp. 29–43. New York, NY: Academic Press.
- Lynch M. 1990 The rate of morphological evolution in mammals from the standpoint of the neutral expectation. *Am. Nat.* **136**, 727–741. (doi:10.1086/285128)
- Hansen TF. 1997 Stabilizing selection and the comparative analysis of adaptation. *Evolution* **51**, 1341–1351. (doi:10.2307/2411186)

37. Butler MA, King AA. 2004 Phylogenetic comparative analysis: a modeling approach for adaptive evolution. *Am. Nat.* **164**, 683–695. (doi:10.1086/426002)
38. O'Meara BC, Ane C, Sanderson MJ, Wainwright PC. 2006 Testing for different rates of continuous trait evolution using likelihood. *Evolution* **60**, 922–933. (doi:10.1554/05-130.1)
39. Thomas GH, Freckleton RP, Szekely T. 2006 Comparative analyses of the influence of developmental mode on phenotypic diversification rates in shorebirds. *Proc. R. Soc. B* **273**, 1619–1624. (doi:10.1098/rspb.2006.3488)
40. Collar DC, O'Meara BC, Wainwright PC, Near TJ. 2009 Piscivory limits diversification of feeding morphology in Centrarchid fishes. *Evolution* **63**, 1557–1573. (doi:10.1111/j.1558-5646.2009.00626.x)
41. Collar DC, Schulte JA, O'Meara BC, Losos JB. 2010 Habitat use affects morphological diversification in dragon lizards. *J. Evol. Biol.* **23**, 1033–1049. (doi:10.1111/j.1420-9101.2010.01971.x)
42. Dornburg A, Sidlauskas B, Santini F, Sorenson L, Near TJ, Alfaro ME. 2011 The influence of an innovative locomotor strategy on the phenotypic diversification of Triggerfish (Family: Balistidae). *Evolution* **65**, 1912–1926. (doi:10.1111/j.1558-5646.2011.01275.x)
43. Beaulieu JM, Jhueng D-C, Boettiger C, O'Meara BC. 2012 Modeling stabilizing selection: expanding the Ornstein–Uhlenbeck model of adaptive evolution. *Evolution* **66**, 2369–2383. (doi:10.1111/j.1558-5646.2012.01619.x)
44. Pereira SL, Johnson KP, Clayton DH, Baker AJ. 2007 Mitochondrial and nuclear DNA sequences support a cretaceous origin of columbiformes and a dispersal-driven radiation in the paleogene. *Syst. Biol.* **56**, 656–672. (doi:10.1080/10635150701549672)
45. Gibbs D, Barnes E, Cox JD. 2001 *Pigeons and doves: A guide to the pigeons and doves of the world*. Mountfield, UK: Pica Press.
46. Sol D. 2008 Artificial selection, naturalization, and fitness: Darwin's pigeons revisited. *Biol. J. Linn. Soc.* **93**, 657–665. (doi:10.1111/j.1095-8312.2008.00957.x)
47. Zeffler A, Johansson LC, Marmebro A. 2003 Functional correlation between habitat use and leg morphology in birds (Aves). *Biol. J. Linn. Soc.* **79**, 461–484. (doi:10.1046/j.1095-8312.2003.00200.x)
48. Nielsen R. 2002 Mapping mutations on phylogenies. *Syst. Biol.* **51**, 729–739. (doi:10.1080/10635150290102393)
49. Huelsenbeck JP, Nielsen R, Bollback JP. 2003 Stochastic mapping of morphological characters. *Syst. Biol.* **52**, 131–158. (doi:10.1080/10635150390192780)
50. Revell LJ. 2012 Phytools: an R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.* **3**, 217–223. (doi:10.1111/j.2041-210X.2011.00169.x)
51. Dunning J. 2008 *CRC handbook of avian body masses*, 2nd edn. Boca Raton, FL: CRC Press.
52. McGowan AJ, Dyke GJ. 2007 A morphospace-based test for competitive exclusion among flying vertebrates: did birds, bats and pterosaurs get in each other's space? *J. Evol. Biol.* **20**, 1230–1236. (doi:10.1111/j.1420-9101.2006.01285.x)
53. Gelman Hill JA. 2007 *Data analysis using regression and multilevel/hierarchical models*. Cambridge, UK: Cambridge University Press.
54. Revell LJ. 2009 Size-correction and principal components for interspecific comparative studies. *Evolution* **63**, 3258–3268. (doi:10.1111/j.1558-5646.2009.00804.x)
55. Harmon LJ, Weir JT, Brock CD, Glor RE, Challenger W. 2008 GEIGER: investigating evolutionary radiations. *Bioinformatics* **24**, 129–131. (doi:10.1093/bioinformatics/btm538)
56. Burnham KP, Anderson DR. 2002 *Model selection and mixed model inference: a practical information-theoretic approach*. New York, NY: Springer.
57. Losos JB. 2009 *Lizards in an evolutionary tree: ecology and adaptive radiation of anoles*. Berkeley, CA: University of California Press.
58. Pinto G, Mahler DL, Harmon LJ, Losos JB. 2008 Testing the island effect in adaptive radiation: rates and patterns of morphological diversification in Caribbean and mainland *Anolis* lizards. *Proc. R. Soc. B* **275**, 2749–2757. (doi:10.1098/rspb.2008.0686)
59. Price SA, Wainwright PC, Bellwood DR, Kazancioglu E, Collar DC, Near TJ. 2010 Functional innovations and morphological diversification in parrotfish. *Evolution* **64**, 3057–3068. (doi:10.1111/j.1558-5646.2010.01036.x)
60. Price SA, Holzman R, Near TJ, Wainwright PC. 2011 Coral reefs promote the evolution of morphological diversity and ecological novelty in labrid fishes. *Ecol. Lett.* **14**, 462–469. (doi:10.1111/j.1461-0248.2011.01607.x)
61. Derryberry EP, Claramunt S, Derryberry G, Chesser RT, Cracraft J, Aleixo A, Perez-Eman J, Remsen Jr JV, Brumfield RT. 2011 Lineage diversification and morphological evolution in a large-scale continental radiation: the neotropical ovenbirds and woodcreepers (Aves: Furnariidae). *Evolution* **65**, 2973–2986. (doi:10.1111/j.1558-5646.2011.01374.x)
62. Raia P, Meiri S. 2011 The tempo and mode of evolution: body size of island mammals. *Evolution* **65**, 1927–1934. (doi:10.1111/j.1558-5646.2011.01263.x)
63. Fitzpatrick JW. 1985 Form, foraging behavior, and adaptive radiation in the tyrannidae. *Ornithol. Monogr.* **36**, 447–470. (doi:10.2307/40168298)
64. Barbosa A, Moreno E. 1999 Evolution of foraging strategies in shorebirds: an ecomorphological approach. *Auk* **116**, 712–725. (doi:10.2307/4089332)
65. Miles DB, Ricklefs RE. 1984 The correlation between ecology and morphology in deciduous forest passerine birds. *Ecology* **65**, 1629–1640. (doi:10.2307/1939141)
66. Phillimore AB, Freckleton RP, Orme CDL, Owens IPF. 2006 Ecology predicts large-scale patterns of phylogenetic diversification in birds. *Am. Nat.* **168**, 220–229. (doi:10.1086/505763)
67. Sol D, Elie M, Marcoux M, Chrostovsky E, Porcher C, Lefebvre L. 2005 Ecological mechanisms of a resource polymorphism in *Zenaidura* doves of Barbados. *Ecology* **86**, 2397–2407. (doi:10.1890/04-1136)
68. Diamond JM. 1975 Assembly of species communities. In *Ecology and evolution of communities* (eds ML Cody, JM Diamond), pp. 342–444. Cambridge, MA: Harvard University Press.
69. Diamond JM. 1973 Distributional ecology of New Guinean birds. *Science* **179**, 759–769. (doi:10.1126/science.179.4075.759)
70. Kolbe JJ, Leal M, Schoener TW, Spiller DA, Losos JB. 2012 Founder effects persist despite adaptive differentiation: a field experiment with lizards. *Science* **335**, 1086–1089. (doi:10.1126/science.1209566)