

Predictable evolution toward flightlessness in volant island birds

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Birds are prolific colonists of islands, where they readily evolve distinct forms. Identifying predictable, directional patterns of evolutionary change in island birds, however, has proved challenging. The “island rule” predicts that island species evolve toward intermediate sizes, but its general applicability to birds is questionable. However, convergent evolution has clearly occurred in the island bird lineages that have undergone transitions to secondary flightlessness, a process involving drastic reduction of the flight muscles and enlargement of the hindlimbs. Here, we investigated whether volant island bird populations tend to change shape in a way that converges subtly on the flightless form. We found that island bird species have evolved smaller flight muscles than their continental relatives. Furthermore, in 366 populations of Caribbean and Pacific birds, smaller flight muscles and longer legs evolved in response to increasing insularity and, strikingly, the scarcity of avian and mammalian predators. On smaller islands with fewer predators, birds exhibited shifts in investment from forelimbs to hindlimbs that were qualitatively similar to anatomical rearrangements observed in flightless birds. These findings suggest that island bird populations tend to evolve on a trajectory toward flightlessness, even if most remain volant. This pattern was consistent across nine families and four orders that vary in lifestyle, foraging behavior, flight style, and body size. These predictable shifts in avian morphology may reduce the physical capacity for escape via flight and diminish the potential for small-island taxa to diversify via dispersal.

birds | islands | morphology | flight | island rule

Birds on islands helped to inspire the theory of evolution by natural selection (1, 2), and they continue to illuminate its mechanisms (e.g., ref. 3). Some studies have reported that the bodies and bills of island birds systematically shift in size, reflecting evolution toward a generalist niche in species-poor communities (4–8). The tendency for island taxa to converge toward intermediate body size after colonizing islands is known as the island rule (4), but this ecogeographic rule has proven to be an inconsistent predictor of evolutionary trends in island bird populations (9–12). Detailed studies of island radiations have revealed idiosyncratic patterns of body size and bill size evolution among species, with morphological changes attributable to taxon-specific changes in foraging ecology (e.g., ref. 12). This inconsistency raises the question as to whether there are predictable evolutionary trends that apply generally to island birds.

The most striking evolutionary trend among island birds is the loss of flight. Transitions to flightlessness are rapid and irreversible (13, 14), with each instance involving the substantial reallocation of mass from the forelimbs to the hindlimbs and near elimination of costly flight muscles (15–18). More than 1,000 independent lineages of island birds have lost flight, including rails, parrots, pigeons, owls, waterfowl, and passerines (13–16). Although widespread, the evolution of island flightlessness requires extreme scarcity of predators and the ability to forage without flight (18–20). Thus, tens of thousands of island bird populations have remained volant, and many bird families that are prolific island colonists contain no flightless species (e.g., kingfishers, hummingbirds, whistlers, and white-eyes).

The dichotomous shift from flight to flightlessness may be subject to a tipping point associated with ecological release from

predators (18). Alternatively, flightlessness may represent an extreme state of a continuum of morphological variation that reflects locomotory requirements for survival and reproduction. Across a continuum of insularity, from continents to small islands, biotic communities exhibit gradients of species diversity (21) and corresponding ecological pressures (22). If flightlessness is illustrative of island bird evolution in general, reductions in predation pressure associated with increased insularity should trigger incremental shifts in energy allocation from the forelimbs to the hindlimbs. Accordingly, we hypothesize that volant island birds, even those unlikely to become flightless, reduce their investment in the flight apparatus. The amount of morphological change should be proportional to the degree of insularity, with more insular populations exhibiting greater reduction in flight morphology. Consistent with this hypothesis, our previous work showed that five species of birds evolved smaller flight muscles and longer legs on the small island of Tobago (23). In this study, we tested whether island size, landbird species richness, raptor species richness, and the presence of mammalian predators could predict shifts in the relative investment in forelimbs versus hindlimbs in 366 bird populations from 80 islands across the Pacific and Caribbean.

Results

To test the hypothesis that island species had evolved smaller flight muscles than their continental relatives, we weighed the two main flight muscles, the *pectoralis major* and the *supracoracoideus*, from more than 8,000 bird carcasses, representing 868 landbird species, 38 of which are restricted to islands (23, 24). With all taxa combined, island-restricted species had smaller flight muscles, relative to body

Significance

Predictable evolutionary trends illuminate mechanisms that affect the diversity of traits and species on the tree of life. We show that when birds colonize islands, they undergo predictable changes in body shape. Small-island bird populations evolve smaller flight muscles and longer legs. These shifts in investment from wings to legs, although often subtle, are qualitatively similar to changes that have occurred in flightless bird lineages. Islands with fewer predator species were associated with more dramatic shifts toward flightlessness, implicating reduced predation pressure as the most likely cause of this trend. These predictable evolutionary changes likely exacerbate the vulnerability of flighted island birds to introduced predators and reduce the potential for small-island species to give rise to subsequent radiations.

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Data deposition: The data are included in *SI Appendix*, have been deposited in figshare (<https://dx.doi.org/10.6084/m9.figshare.3123148.v1>), and are available, along with all code needed to replicate all results and figures, at <https://github.com/coereba/islands>.

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mass, than their continental relatives [phylogenetic generalized linear model (PGLS): $P < 0.001$, df: 2 and 866].

To understand the causes of this difference between continents and islands, we examined forelimb and hindlimb investment in bird populations on islands of varying size and ecological characteristics. To achieve this goal, we measured museum skeletal specimens from island taxa in nine families, including taxa that require flight to forage, such as fruit-doves, kingfishers, hummingbirds, monarch flycatchers, and other songbirds. Here, we focus on two measurements: the lengths of the sternal keel (an index of pectoral muscle mass; ref. 23) and the tarsometatarsus, the distal-most long bone in the avian leg. In birds, hindlimb and forelimb size are negatively correlated due to tradeoffs in energetic investment and locomotor function (25). In our dataset, the lengths of the keel and tarsometatarsus were negatively correlated (PGLS: $P < 0.001$, df: 2 and 364; *SI Appendix*, Fig. S1), and this correlation persisted in 13 of 15 focal taxa when analyzed individually (*SI Appendix*, Table S1). We developed an index of hindlimb vs. forelimb investment from a principal component analysis of keel and tarsometatarsus lengths. Larger values of this “forelimb-hindlimb index” indicate larger flight muscles and shorter legs. We used island area, landbird species richness, raptor species richness, and the presence or absence of native mammalian predators as metrics of insularity, because each

should be mechanistically related to the intensity of ecological pressures such as competition, predation, and resource diversity (16, 21). Our dataset included islands ranging from 786,000 km² and >620 resident landbird species, to atolls of 19 km² that support as few as three species. We used PGLS, with island populations as the units of analysis, to test the hypothesis that locomotor morphology evolved predictably with island characteristics.

Smaller flight muscles and longer legs have evolved repeatedly on islands of low species richness and with no mammalian predators (Fig. 1, Table 1, and *SI Appendix*, Figs. S2–S10). Forelimb-hindlimb index was positively correlated with raptor species richness, landbird species richness, and island area across 366 island populations in PGLS analyses (Table 1 and Fig. 1). Raptor species richness and the presence of native mammalian predators provided the greatest explanatory power, whereas island area was the least informative predictor of morphological shifts (Table 1). The correlation between the forelimb-hindlimb index and insularity was evident within 15 focal families and genera in nonphylogenetic analyses (Fig. 2 and *SI Appendix*, Tables S2 and S4) and was statistically significant at $P < 0.01$ for 14 of 15 focal taxa (*SI Appendix*, Table S4). Strikingly, island species richness explained as much as 60% of the variation in forelimb-hindlimb index among individual *Todiramphus* kingfishers on 27 Pacific islands representing 32

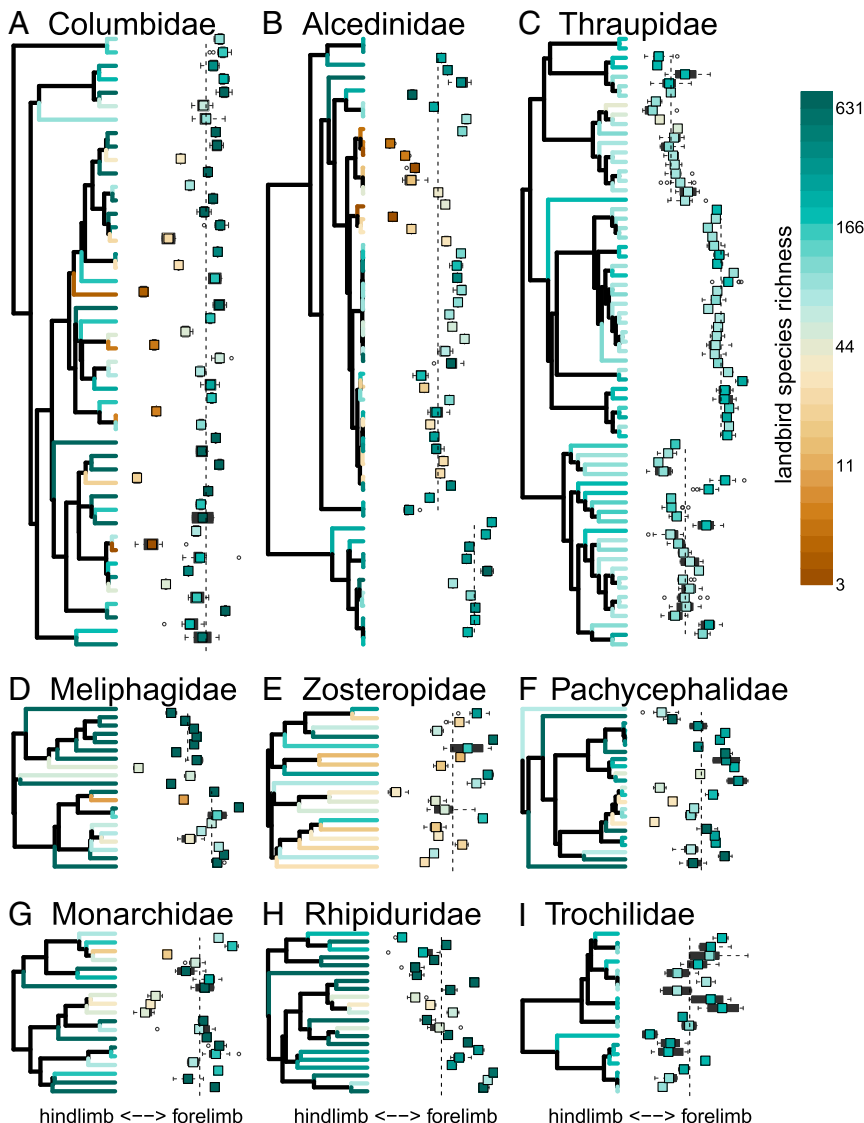


Fig. 1. Avian populations on islands of low species richness have repeatedly evolved smaller flight muscles and longer legs (Table 1 and *SI Appendix*, Table S2). Colors of tree tips and boxes represent island landbird species richness. The positions of colored squares represent population means of the forelimb-hindlimb index, with values further to the right indicating larger flight muscles and shorter legs. Dashed vertical lines represent clade means of the forelimb-hindlimb index. Gray box-and-whisker plots behind the colored squares show the first and third quartiles, with whiskers extending to 1.5 times the inner quartile range or the outermost data point within that range. Tree tips are species (trees A, D, E, G, and H), where differences among species encompass the majority of the variation among islands, or island populations (trees B, C, F, and I). *SI Appendix*, Figs. S2–S10 contain additional details, including island population names and individual keel and tarsometatarsus lengths.

distinct populations (*SI Appendix, Table S4*). Two-thirds of taxa (10 of 15) exhibited sexual dimorphism in forelimb-hindlimb index; thus, models that included sex as a predictor tended to explain significantly more variation (*SI Appendix, Table S4*). There was no interaction between sex and other predictor variables. Analyses with keel length or leg length as the dependent variable, respectively, followed the same general pattern: Keels became smaller and legs longer on islands of low raptor and landbird species richness (Table 1 and *SI Appendix, Figs. S2–S10 and Tables S3 and S5*).

To test the island rule, we examined whether island birds evolved toward intermediate body size as they became more hindlimb-dominant. Most of our study taxa were small-bodied birds (median body size: 14.5 g; range: 2.6–915 g). The island rule predicts that small taxa should become larger on smaller, more insular islands. Following this prediction, in PGLS analysis including all taxa with island population as the unit of analysis, body size was negatively correlated with island species richness and island area, albeit weakly (Table 1). Individual lineages, however, showed no consistent patterns of directional body size change. Body size correlated negatively with island species richness in 5 of 15 focal taxa and positively in another five taxa in nonphylogenetic analyses (*SI Appendix, Tables S3 and S5*). We tested whether body size predicted the direction of body-size evolution on islands by examining how the slope of the regression of body size vs. island species richness within each focal taxon correlated with its mean body size. The island rule predicts a positive relationship, with larger taxa evolving smaller body sizes on small islands and small taxa evolving in the opposite direction (*SI Appendix, Fig. S11*). We found no significant relationship between the magnitude or direction of

body size changes on islands and mean body size (*SI Appendix, Figs. S12–S14*).

Discussion

These results suggest an ecogeographic rule for birds that relates to shape rather than size: Island birds evolve reduced flight muscles and larger legs in response to the ecological pressures associated with small, species-poor islands. This trend toward reallocation of energy from the forelimbs to the hindlimbs is evident in separate analyses of nine avian families and four orders, representing a range of lifestyles, diets, foraging behaviors, flight styles, and body plans. The pattern holds regardless of whether we focus on differences among individuals, populations, or species, with or without accounting for phylogenetic relationships. It is consistently supported for birds on continental or oceanic islands, and in Caribbean or Pacific archipelagoes.

Island raptor species richness and the presence of mammalian predators were the best predictors of forelimb-hindlimb index, keel length, and tarsometatarsus length (Table 1). Landbird species richness was slightly less informative than raptor richness, whereas island area explained substantially less variation (Table 1 and *SI Appendix, Tables S3–S5*). Although species richness and island area were correlated ($P < 0.001$, adjusted $R^2 = 0.42$, df: 1 and 78) and are expected to be mechanistically linked (21), the islands in this study vary in remoteness, archipelago size, geologic history, and topography. These size-independent factors affect the complexity of ecological communities, including species richness of landbirds and raptors (16, 21, 26). Accordingly, the repeated evolution of reduced flight muscles and longer legs

Table 1. PGLS comparisons for island population means ($n = 366$) of forelimb-hindlimb index, keel length, tarsometatarsus length, and body size

Dependent variable	Predictor variable(s)	AIC	<i>P</i> value	R^2
Forelimb-hindlimb index	Raptor richness + mammal predators	76	<0.001	0.50
Forelimb-hindlimb index	Raptor richness	82	<0.001	0.49
Forelimb-hindlimb index	Landbird richness + mammal predators	83	<0.001	0.46
Forelimb-hindlimb index	Landbird richness	86	<0.001	0.45
Forelimb-hindlimb index	Mammal predators + area	100	<0.001	0.39
Forelimb-hindlimb index	Mammal predators	122	<0.001	0.29
Forelimb-hindlimb index	Area	128	<0.001	0.28
Keel length	Raptor richness + mammal predators	1,899	<0.001	0.45
Keel length	Raptor richness + landbird richness	1,900	<0.001	0.45
Keel length	Raptor richness	1,901	<0.001	0.46
Keel length	Landbird richness + mammal predators	1,906	<0.001	0.41
Keel length	Landbird richness	1,908	<0.001	0.41
Keel length	Area + mammal predators	1,921	<0.001	0.33
Keel length	Area	1,938	<0.001	0.27
Keel length	Mammal predators	1,943	<0.001	0.23
Tarsometatarsus length	Raptor richness + mammal predators	1,024	<0.001	0.37
Tarsometatarsus length	Landbird richness + mammal predators	1,026	<0.001	0.34
Tarsometatarsus length	Raptor richness + landbird richness	1,035	<0.001	0.34
Tarsometatarsus length	Landbird richness	1,036	<0.001	0.32
Tarsometatarsus length	Raptor richness	1,038	<0.001	0.34
Tarsometatarsus length	Area + mammal predators	1,040	<0.001	0.30
Tarsometatarsus length	Mammal predators	1,059	<0.001	0.24
Tarsometatarsus length	Area	1,073	<0.001	0.18
Body size	Landbird richness	530	0.004	0.03
Body size	Mammal predators	533	0.027	0.01
Body size	Raptor richness	533	0.023	0.02
Body size	Area	535	0.02	0.0

Forelimb-hindlimb index indicates the size of the flight muscles relative to the legs. We tested all possible combinations of the four predictor variables and eliminated models that contained uninformative variables (55). R^2 values are for the models after phylogenetic signal has been taken into account. "Mammal predators" refers to the presence or absence of native mammalian predators of landbirds on the island. Body size variable is the first principal component from a PCA of skeletal measurements (coracoid, humerus, femur, and tarsometatarsus).

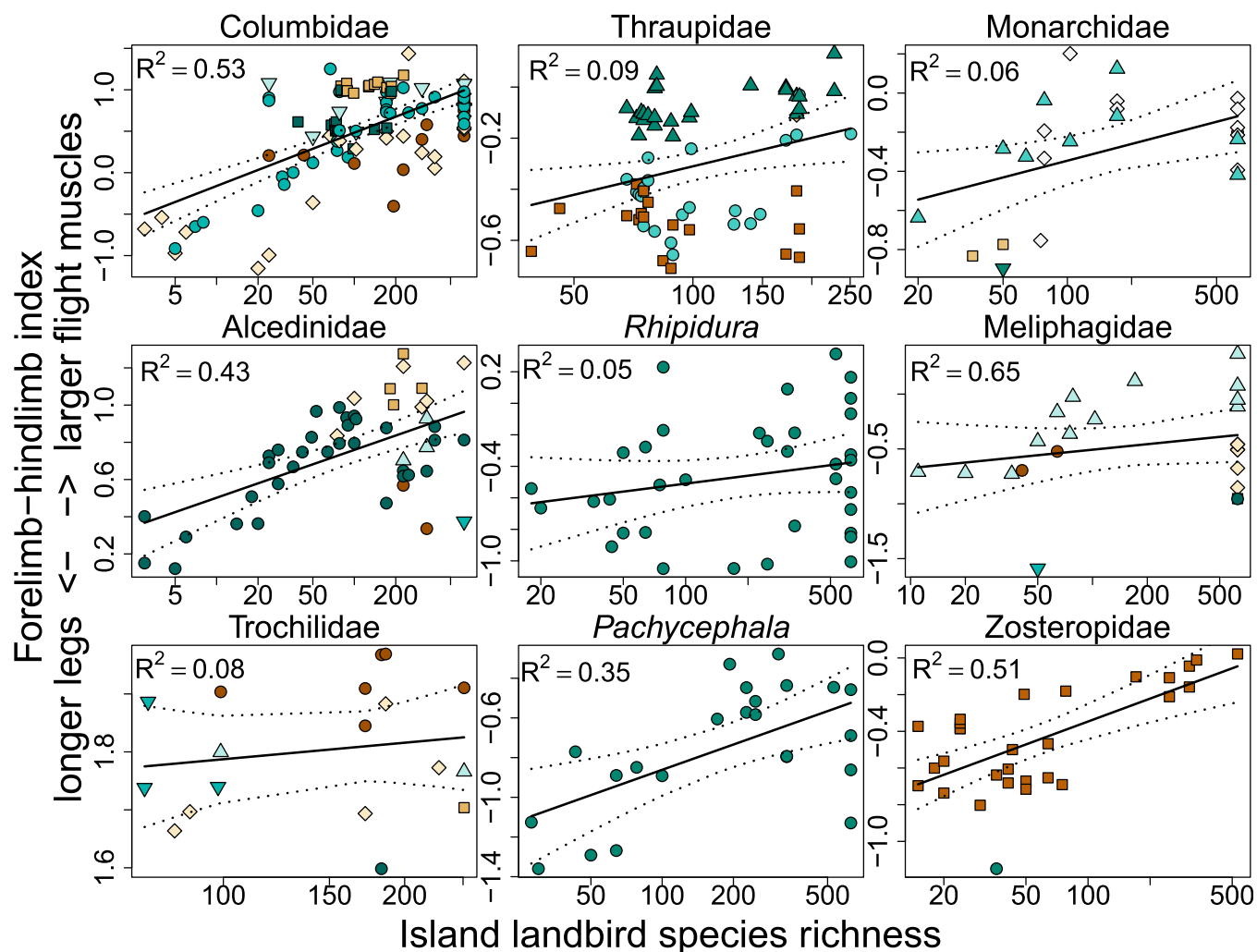


Fig. 2. Larger flight muscles and shorter legs are positively correlated with island species richness (Table 1 and *SI Appendix*, Table S2). Each point is a population mean. Solid black lines are linear regression lines and dashed lines are 95% confidence bands. R^2 values are partial R^2 for landbird species richness in linear regressions that include genus as a predictor variable where applicable (*SI Appendix*, Tables S2 and S4). That is, they estimate the proportion of variation explained by species richness that cannot be explained by genus alone. Differently colored and shaped points within a family indicate different genera (see *SI Appendix*, Fig. S15 for a key to genera).

is most likely attributable to depauperate ecological communities rather than the physical properties of small islands.

Lower predation pressure on islands with low raptor species richness and no mammalian predators might release landbirds from the need for large, powerful flight muscles that facilitate rapid escape. Islands of lower species richness tend to have less diverse sets of competitors, predators, habitats, and food sources (16, 21, 27). Raptor species richness and overall landbird species richness were tightly correlated ($P < 0.001$, $R^2 = 0.90$, df: 1 and 78), but raptor species richness was consistently the best predictor of changes in keel and leg lengths (Table 1). Additional reduction in the forelimb-hindlimb index of island birds was attributable to the absence of native mammalian predators (Table 1). Raptor species richness is likely an informative index of the predation pressure that raptors exert on island birds because when only one or a few raptor species are present on an island, those species tend to be generalist predators; whereas, raptors that specialize on eating birds tend to occur only on islands of high species richness (16, 27). Specialized predators likely exert stronger pressure to maintain rapid escape abilities. Hence, the lack of bird-specialist predators on islands with few raptor

species may allow for reduced energetic investment in flight muscles and concomitant increase in hindlimb size.

Smaller flight muscles likely result in slower maximal flight speeds and slower takeoffs, with longer legs potentially compensating for small flight muscles (25, 28–30). Birds use a leg thrust to generate initial forward velocity during takeoff (28, 29). Flight is extremely costly at airspeeds close to zero, and power requirements decrease as velocity increases to moderate flight speeds (30). Birds' leg thrusts allow their wings and flight muscles to begin generating lift at airspeeds significantly greater than zero, thereby reducing the overall power required for lift production (30). Longer legs provide a longer lever, increasing force generation during the leg thrust that initiates takeoff. Theoretically, this change should reduce the power required from the flight muscles while also reducing the overall speed of escape from a predator, although this prediction has yet to be experimentally tested. Longer legs may have evolved as a result of this functional (28, 29) and/or energetic tradeoff with flight muscle size, because similar tradeoffs occur across the bird phylogeny and within individuals across ontogeny (25). In this way, selection for reduced flight muscles may have indirectly caused leg length to increase. An alternative explanation for longer legs on

depauperate islands is that they may have been directly favored via selection for perch generality and ground foraging (5, 12). Birds on islands of low species richness tend to use a wider variety of habitats, food sources, and perch types (5, 31, 32). Songbirds have been found to evolve longer legs on islands in association with variable perch types (5, 12). Similarly, longer legs are associated with increased terrestriality and walking. If reduced interspecific competition resulting in the use of greater perch variety is the primary driver of the evolution of longer legs on islands of low species richness, we would expect to see this pattern exclusively in birds that use perches in a variety of ways while foraging (e.g., clinging, hanging, hopping, or walking). Instead, even hummingbirds and kingfishers, which tend not to cling, hang, hop, or walk, have longer legs on islands of lower species richness. This phenomenon suggests that biomechanical compensation for small flight muscles is an important cause of elongated legs in volant island birds.

Our results provide new perspective on the evolution of flightlessness. Previous workers have focused on the causes and consequences of the evolution of flightlessness on islands (e.g. (15, 16, 19, 33, 34), but the possibility that volant species are subject to similar mechanisms has not been addressed. We suggest that the profound shape change exhibited during the transition to flightlessness is the extreme manifestation of a predictable pattern of avian evolution in response to ecological release from predators. Certain taxa, like rails, are more likely to reach the extreme state (15, 16, 18). The majority of landbirds that colonize islands, however, appear to be affected similarly, even those that are destined to never evolve flightlessness. Taxa including fruit doves, monarch flycatchers, tanagers, white-eyes, whistlers, fantails, honeyeaters, kingfishers, and hummingbirds exhibited morphological changes along the trajectory toward flightlessness, despite flight ability being integral to their modes of foraging and breeding. The range of variation in the forelimb-hindlimb index reflects a continuum of locomotory modes, from highly aerial to flightless. In insular communities, a shift in the balance of directional selection pressures causes incremental changes along this continuum. Consistent with this idea, McCall et al. (33) found that flightlessness is most likely to evolve in taxa that already have short wings relative to their body mass.

Our results have two major implications for mechanisms of diversification. First, the vulnerability of volant island birds to introduced predators, partly attributable to an evolved reduction in vigilance (“island tameness”; refs. 35 and 36), is exacerbated by reduced physical capacity for escape via flight, increasing extinction risk (37). Second, systematic reduction in flight muscle size could propel taxon cycles (38) by reducing the probability of over-water dispersal from small-island populations. The latter would inhibit interisland gene flow, causing island populations to evolve on independent trajectories, each with reduced probability of undergoing subsequent expansion and diversification.

Materials and Methods

Data Collection. For the comparison of continents versus islands, we used bird specimens that were collected by us and many colleagues using standard museum methods (23, 24). Each bird was weighed, and the pectoralis major and supracoracoideus muscles were extracted and weighed. Flight muscle mass scaled isometrically with body mass; accordingly, we calculated relative flight muscle size by dividing total flight muscle mass by body mass. Species values were obtained by taking the mean of the average male measurement and average female measurement. All mass data were associated with specimens archived at the Museum of Southwestern Biology (University of New Mexico), Centro de Ornitología y Biodiversidad (Lima, Peru), or Florida Museum of Natural History (University of Florida).

To address forelimb and hindlimb dimensions in island bird populations across a range of insularity, we used museum skeletal specimens from historic to modern collections, focusing on 15 well-represented taxa: Trochilidae; *Macropygia*, *Ducula*, *Ptilinopus*, *Columbina*, and *Zenaidura aurita* (Columbidae); Alcedinidae; Zosteropidae; *Rhipidura* (Rhipiduridae); Meliphagidae;

Monarchidae; *Pachycephala* (Pachycephalidae); *Coereba flaveola*, *Tiaris*, and *Loxigilla* (Thraupidae). Because the flight muscles attach to the sternal keel, keel size is closely related to flight muscle size. A single measurement, the diagonal length of the keel, which encompasses both length and depth, was the best predictor of flight muscle size and correlated strongly with flight muscle mass both within and among species (*SI Appendix, SI Materials and Methods*). We measured all available skeletal specimens of our focal island taxa at five natural history museums with large avian skeletal collections. One person (N.A.W.) made all of the following measurements from each skeletal specimen: diagonal keel length and the lengths of the coracoid, humerus, femur, and tarsometatarsus. Specimens missing any of these elements were excluded from analyses.

Data on island area, landbird species richness, and raptor species richness were compiled from the literature (16, 27, 39–42) for each island from which we had bird skeletal measurements. We included regularly occurring resident or migrant species, but excluded vagrants and rarities. We coded islands for the presence/absence of native mammals that might predate birds.

Analyses. We tested whether island-restricted species have evolved smaller flight muscles than their continental relatives by conducting PGLSs in R with packages *ape* and *nlme* (43–45) using a phylogenetic tree for birds (46) and species averages of relative flight muscle sizes. Species found on both continents and islands (including migrants) were coded as continental. We coded species as “island-restricted” if they were not regularly found on any continent or island larger than 200,000 km². We chose this cutoff because large islands are continent-like in their ecology (e.g., New Guinea has roughly the same landbird species richness as Australia) and because this cutoff was a natural break point in the data. Our dataset included species restricted to islands larger than 450,000 km² and smaller than 200,000 km², but none in between (*Dataset S1*). We restricted analyses to landbirds only (i.e., excluded ducks, seabirds, shorebirds, and grebes). Our dataset included average relative flight muscle sizes for 868 species, of which 59 of were restricted to islands, and 38 were restricted to islands smaller than 200,000 km².

To test whether flight muscle size and leg lengths were related to landbird species richness, raptor species richness, mammalian predators, or island area, we analyzed skeletal measurements multiple ways. We used principal component analysis on length measurements of the coracoid, humerus, femur, and tarsometatarsus to account for body size, because the first principal component (PC1) of this analysis included all four variables, loading roughly equally and in the same direction. We used the residuals of a linear model of the skeletal element of interest (i.e., keel length and tarsometatarsus length) by PC1 as a body size-corrected estimate of the character. All results presented are these body size-corrected estimates rather than raw values. Because in most cases keel length and leg length were evolving in concert and were strongly negatively correlated (*SI Appendix, Fig. S1 and Table S1*), we created a shape index to characterize small flight muscles and long legs. This forelimb-hindlimb index was the second principal component (PC2) from a principal component analysis on keel length and leg length measurements. Both keel and leg length loaded equally and in the same direction in PC1, and in opposite directions in PC2. PC2 explained 25% of the variation when analyzed across the entire dataset.

We conducted PGLS analysis on the entire skeletal dataset, with island population as the unit for analysis and island population means calculated from individual-level data (*Dataset S2*). This analysis required a phylogenetic tree that included relationships among island populations. Therefore, we patched hypothesized relationships among island populations into a species-level tree from Jetz et al. (46), largely derived in its major clades from Hackett et al. (47). We used published phylogeographic studies (48–54) as the basis for hypothesized relationships among island populations. For taxa without published phylogeographic studies, we hypothesized relationships based on subspecies differentiation, relationships among populations of similar species on the same islands, and geographic proximity of islands (see *SI Appendix, Figs. S2–S10* for resulting phylogenetic trees). We performed AIC model selection to test which combination of four variables (raptor species richness, landbird species richness, island area, or presence/absence of mammalian predators) best predicted morphology, eliminating models with uninformative parameters (55).

We also conducted nonphylogenetic linear regression analyses with each morphological character of interest as a function of landbird species richness and island area, respectively, using both population-level means and individuals as units of analysis. We conducted these analyses within each genus or, where sampling within one particular genus was limited, within a family (e.g., Trochilidae, Monarchidae, Meliphagidae). Taxa for which we only had a few island populations were excluded to allow for more clade-specific analyses (e.g., members of Alcedinidae outside of the genus *Todiramphus*).

The resulting 15 focal taxa for the nonphylogenetic analyses included 339 (93%) of the 366 island populations analyzed above.

To test predictions of the island rule as traditionally defined (4), we examined how the slope of the regression of body size vs. island species richness within each genus correlates with mean body size across genera. For each genus with sample $n \geq 10$ and island populations $n > 3$, we performed a linear regression between body size (PC1) and species richness ($n = 19$ genera). We regressed the coefficient of the relationship between body size and species richness against mean body size of the genus. We repeated the analysis with the slope set to 0 for taxa in which the linear regression of body size by species richness was not statistically significant at $P < 0.05$. We performed this analysis for all taxa together, and also for Columbidae and Passeriformes separately. If the taxa in our study follow the island rule, we would expect the relationship to be positive: Small-bodied species should have negative relationships between island species

richness and body size, whereas large-bodied taxa should become smaller as island species richness decreases (SI Appendix, Fig. S11).

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Supporting Information Appendix for

An avian island rule: evolution toward flightlessness

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This file includes:

Supplemental Text

Supporting References

Figs. S1-S15

Tables S1-S5

Code and data required to reproduce all analyses and figures in this paper is available at <https://github.com/coereba/islands>

Supplemental Text

Supplemental materials and methods

We analyzed three distinct datasets. Analysis 1: species means of relative flight muscle mass; Analysis 2: means of skeletal characters for each island population (i.e., one value for each species on each island); and Analysis 3: skeletal measurements of individuals.

Analysis 1: We tested whether island-restricted species have evolved smaller flight muscles than their continental relatives by conducting phylogenetic generalized linear models (PGLS) in R with packages *ape* and *nlme* (1-3) using a phylogenetic tree for birds (4) and species averages of relative flight muscle sizes. Species found on both continents and islands (including migrants) were coded as continental. We coded species as “island-restricted” if they were not regularly found on any continent or island larger than 200,000km². We chose this cutoff because large islands are continent-like in their ecology (e.g., New Guinea has roughly the same landbird species richness as Australia) and because this was a natural break point in the data: our dataset included species restricted to islands larger than 450,000km² and smaller than 200,000km², but none in between. We restricted analyses to landbirds only (i.e., excluded ducks, seabirds, shorebirds, and grebes). Our dataset included average relative flight muscle sizes for 868 species. Only 59 of these are restricted to islands, and only 38 of these are restricted to islands smaller than 200,000km². We determined which model among null, Brownian motion, Ornstein-Uhlenbeck, and Pagel’s lambda models best described the flight muscle data using AIC. In all cases Pagel’s lambda models were the best fit and thus were used for the correlation structure in PGLS analyses.

Analyses 2 and 3: To test whether flight muscle size and leg lengths are related to island species richness or area, we analyzed skeletal measurements multiple ways. First, we used principal component analysis on length measurements of the coracoid, humerus, femur, and tarsometatarsus to account for body size, as the first principal component (PC1) of this analysis included all four variables loading roughly equally and in the same direction. We used the residuals of a linear model of the skeletal element of interest (i.e., keel length and tarsometatarsus length) by PC1 as a body size-corrected estimate of the

character. All results presented are these body size-corrected estimates rather than raw values. Because in most cases keel length and leg length were evolving in concert and were strongly negatively correlated (Fig. S1, Table S1), we created a shape index to characterize small flight muscles and long legs. This forelimb-hindlimb index was the second principal component (PC2) from a principal component analysis on keel length and leg length measurements. Both keel and leg length loaded equally and in the same direction in PC1, and in opposite directions in PC2. PC2 explained 25% of the variation when analyzed across the entire dataset.

Analysis 2A: We conducted phylogenetic generalized least squares linear model (PGLS) analysis on the entire skeletal dataset, with island population as the unit for analysis, and island population means calculated from individual-level data. The PCA was conducted across all individuals, with PC1 and residual values averaged for each island population. This analysis required a phylogenetic tree that included relationships among island populations. Therefore, we grafted hypothesized phylogenies of island populations onto a species-level tree from Jetz et al. (4), largely derived in its major clades from Hackett et al. (5). We used published phylogeographic studies (6-12) as the basis for hypothesized relationships among island populations. For taxa without published phylogeographic studies, we hypothesized relationships based on subspecies limits, relationships among populations of similar species on the same islands, and geographic proximity of islands.

While conducting phylogenetic comparative analyses across populations rather than species is not ideal, there is not a feasible alternative. We note that species taxonomy is currently under revision for many of our island taxa, and recent studies have suggested that many island populations that are currently considered to be conspecific actually comprise reproductively isolated, monophyletic lineages (7, 9, 12). Even island populations that have not yet reached biological species designation may be effectively isolated from related populations and experiencing independent evolutionary trajectories. Thus we analyzed each of the 366 island populations as an independent lineage.

Analysis 2B: We conducted non-phylogenetic linear regression analyses with the character of interest by species richness and island area, respectively, on population-level data. We used the same methods as in analysis 2A for calculating island population means. We conducted these analyses within each genus, or, where sampling within any particular genus was limited, within a family (e.g., Trochilidae, Monarchidae, Meliphagidae). These analyses included most of the 366 island populations analyzed in Analysis 2A. A few taxa were excluded to allow for more clade-specific analyses (e.g., members of Alcedinidae outside of the genus *Todiramphus*). More inclusive but less clade-specific analyses (i.e., analyses including all members of a family) yielded very similar results to those presented.

Analysis 3A: We conducted linear regression analyses with the character of interest by species richness and island area, respectively, with the individual specimen as the unit of analysis. We conducted PCAs separately for each taxon of interest. Sex and species were included as covariates in multiple regressions. We report the full model for each morphological character by species richness in Tables S4 and S5. As in analysis 2B, we conducted these analyses within each genus, or, in a few cases where sampling within one genus was limited, within a family. More inclusive but less clade-specific analyses yielded very similar results to those presented.

Analysis 3B: To test predictions of the island rule, we examined how the body size of the focal taxon affected the relationship between body size and species richness and island area, respectively. For each genus with sample $n \geq 10$ and island populations $n > 3$, we performed a linear regression between body size (PC1) and species richness. We regressed the coefficient of the relationship between body size and species richness against mean body size of the genus. We repeated the analysis with the slope set to 0 for taxa in which the linear regression of body size by species richness was not statistically significant at $p < 0.05$. We performed this analysis for all taxa together, and also for Columbidae and Passeriformes separately. If the taxa in our study follow the island rule, we would expect the relationship to be positive: small-bodied species should have negative relationships between island species richness and body size, whereas large-bodied taxa should become smaller as island species richness decreases (Fig. S11).

Relationship between keel length and flight muscle mass

Individual-level analyses: We reduced our dataset to individual specimens for which we had both flight muscle masses and skeletal measurements. Keel length was strongly correlated with flight muscle mass across all individuals ($p < 0.001$, adj. $R^2 = 0.81$, df: 1 and 165). We conducted a PCA across this entire dataset to correct for body size, as described above. Body size-corrected keel length was positively correlated with relative flight muscle size ($p < 0.001$, adj. $R^2 = 0.58$, df: 1 and 165).

We then focused on within-lineage relationships between keel length and flight muscle size. In *Coereba flaveola* body size-corrected keel length was positively correlated with relative flight muscle size ($p = 0.004$, adj. $R^2 = 0.22$, df: 1 and 30; results were nearly identical when correcting for body size using PC1 from the PCA run above, or when a new PCA was conducted using only *Coereba flaveola* samples). Likewise, in the pigeon *Macropygia mackinlayi* keel length was positively correlated with flight muscle size (body size-corrected: $p = 0.0029$, adj. $R^2 = 0.61$, df: 1 and 9; raw length and mass values, uncorrected for body size: $p = 0.0049$, adj. $R^2 = 0.56$). These were the only two species for which we had at least 10 samples with both skeletal and flight muscle mass data. Looking across individuals in the fruit-dove genus *Ptilinopus*, we also found that keel length was positively correlated with flight muscle size (body size-corrected: $p < 0.001$, adj. $R^2 = 0.63$, df: 1 and 15; not body size-corrected: $p < 0.001$, adj. $R^2 = 0.85$). Similar results were found for the *Zosterops* white-eyes (body size-corrected: $p = 0.0019$, adj. $R^2 = 0.50$, df: 1 and 13; not body size-corrected: $p < 0.001$, adj. $R^2 = 0.63$) and the *Rhipidura* fantails (body size-corrected: $p = 0.14$, adj. $R^2 = 0.12$, df: 1 and 11; not body size-corrected: $p < 0.001$, adj. $R^2 = 0.90$).

Species average analyses: We calculated species averages of the skeletal measurements, including PC1 and body size-corrected characters, and combined this dataset with the dataset on species averages of flight muscle masses. We used phylogenetic generalized linear models (PGLS) as described in the methods above to test how keel length and flight muscle size were related across species in a phylogenetic context. Species averages of body size-corrected keel length were positively correlated with relative flight muscle sizes (PGLS: $p < 0.001$, $R^2 = 0.47$, df: 41). Likewise, keel length uncorrected for body size was strongly correlated with flight muscle mass (PGLS: $p < 0.001$, $R^2 = 0.65$, df: 41).

While skeletal proxies for flight muscle size such as keel length are highly correlated with flight muscle mass, measurements taken on skeletal specimens are more precise and accurate. Our flight muscle data were collected over the span of a decade by dozens of specimen preparators, often in less than ideal field conditions, whereas one investigator (N.A.W.) made all skeletal measurements in the comfort of museum collections. Additionally, flight muscle mass varies within an individual in response to body condition, migration, season, and breeding, but skeletal structures are less labile. These naturally occurring variations in flight muscle mass along with measurement error likely account for much of the variation left unexplained by keel length.

Evolution toward flightlessness in island birds

Our findings that birds evolve smaller flight muscles and longer legs on smaller, species-poor islands are robust to analytic method, taxonomic scale, and island system. Our data come from populations on oceanic and continental islands in the Pacific and Caribbean. They include Old World kingfishers, Old World and New World doves and pigeons, hummingbirds (New World-restricted), and both Old and New World families of passerines. We reach the same conclusions whether testing the question across lineages in a phylogenetic comparative framework or when focusing on within-species or within-genera comparisons and whether we use island population means or individual values as the units of analysis (Tables S2-S4).

Analysis 1: Pagel's lambda correlation structure best described the flight muscle mass data. Across all landbirds, island-restricted species had smaller flight muscles than their continental relatives (PGLS: $p < 0.001$; df: 866). Relative flight muscle size is mechanistically tied to flight style and body plan, and displays high phylogenetic signal (Pagel's $\lambda = 0.89$). Family alone explains 71% of the variation in relative flight muscle size across birds ($p < 0.001$; df: 104 and 847). For family Columbidae (pigeons and doves), we had data on 59 species, 8 of which are restricted to islands smaller than 200,000km² (13.6%). This was the only family for which we had data on >4 island-restricted species and >4 continental species. Within Columbidae, relative flight muscle mass exhibited less phylogenetic signal (Pagel's $\lambda = 0.23$) and there was little difference between the fit of the null model and Pagel's lambda correlation structure (AIC -222.6 and -222.0, respectively). Island-restricted columbids had smaller relative flight muscles than their continental relatives in both PGLS ($p < 0.001$, df: 57) and non-phylogenetic linear regression ($p < 0.001$, adj. $R^2 = 0.26$, df: 57).

Analysis 2: Pagel's lambda correlation structure best described the keel length, tarsometatarsus length, and forelimb-hindlimb index data, with each exhibiting high phylogenetic signal (Pagel's $\lambda = 0.95, 0.98, \text{ and } 0.97$, respectively). Body size-corrected keel length and the forelimb-hindlimb index correlated positively with island species richness and island area, while body size-corrected tarsometatarsus length correlated negatively with island species richness and island area. This was the case for phylogenetic generalized linear models and non-phylogenetic linear regressions of island population means (Tables 1, S2, S3).

We focus on only islands in this study, but when data from Australian populations are included, the results are similar. Australia's landbird species richness similar to that of New Guinea, and morphological traits are similar for relatives on Australian and New Guinea.

Testing the island body size rule

Analysis 3B: There was no significant relationship between body size and the direction of body size change on islands (non-significant slopes set to 0: all taxa: $p=0.65$, $R^2=0.01$, df: 1 and 17; Columbidae: $p=0.73$, $R^2=0.03$, df: 1 and 4; Passeriformes: $p=0.24$, $R^2=0.19$, df: 1 and 7; non-significant slopes included: all taxa: $p=0.52$, $R^2=0.02$, df: 1 and 17; Columbidae: $p=0.74$, $R^2=0.03$, df: 1 and 4; Passeriformes: $p=0.25$, $R^2=0.19$, df: 1 and 7). Additionally, visual examination of the pattern reveals no trend, significant or otherwise (figs. S12-S14). The possible exception is passerines (fig. S14), which appear to exhibit a positive relationship between the change in body size with species richness and body size. This relationship is not statistically significant, however, and there are only 9 genera of sufficient sampling to include in analyses. We caution that the entire body size range for passerines in our dataset is not large: 5.5g (*Tiaris bicolor*) to 54.0g (*Pachycephala pectoralis*). Additionally, the differences in size between the small-bodied passerines which become larger on small islands of low species richness and the large-bodied passerines which become smaller on these islands is not great. The genus *Myzomela* (6.6-17.9g, mean 11.4g) exhibits a significant negative relationship between body size and species richness, while the similarly sized genus *Myiagra* (9.8-24.1g, mean 14.2g) exhibits a significant positive relationship (Table S5). Likewise, the closely related *Coereba flaveola* (mean 9.9g) and *Loxigilla* (mean 20.6g) tanagers change body size on islands in opposite ways (Table S5). Perhaps with more data we might find support for the island rule in passerines. When considered in sum, however, the taxa in our study do not follow the island rule.

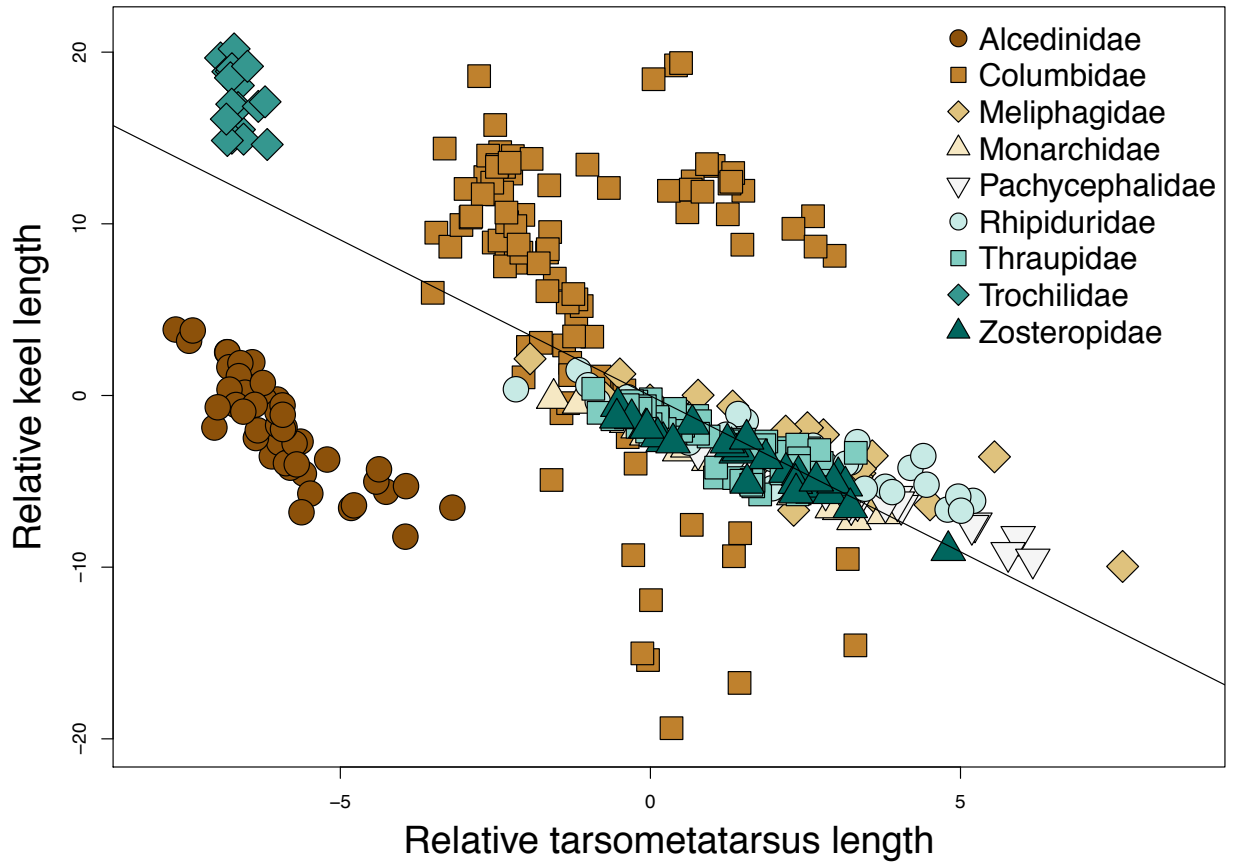
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Additional Supporting Figures

Fig. S1. Keel length is negatively correlated with tarsometatarsus length within and across taxa. Relative lengths of the keel and tarsometatarsus are the residuals of a regression of keel and tarsometatarsus lengths, respectively, by the first principal component, an indicator of overall body size (see supplemental methods, section “analyses 2 and 3”). Each point is an individual sample.



Figs. S2-S10. Avian populations on islands of low species richness have repeatedly evolved smaller flight muscles and longer legs (Tables 1, S2). Colors of tree tips and boxes represent island landbird species richness. The positions of colored squares represent population means of the forelimb-hindlimb index. Gray box-and-whisker plots behind the colored squares show the first and third quartiles, with whiskers extending to 1.5 times the inner quartile range or the outermost data point within that range. Dashed vertical lines represent clade means of the forelimb-hindlimb index. Grayscale circles and diamonds indicate the residuals of regressions of keel and tarsometatarsus lengths by body size (PC1), respectively. Darker points indicate smaller keels and shorter legs for a given body size, while lighter points indicate larger keels and longer legs.

Fig. S2. Columbidae (pigeons and doves)

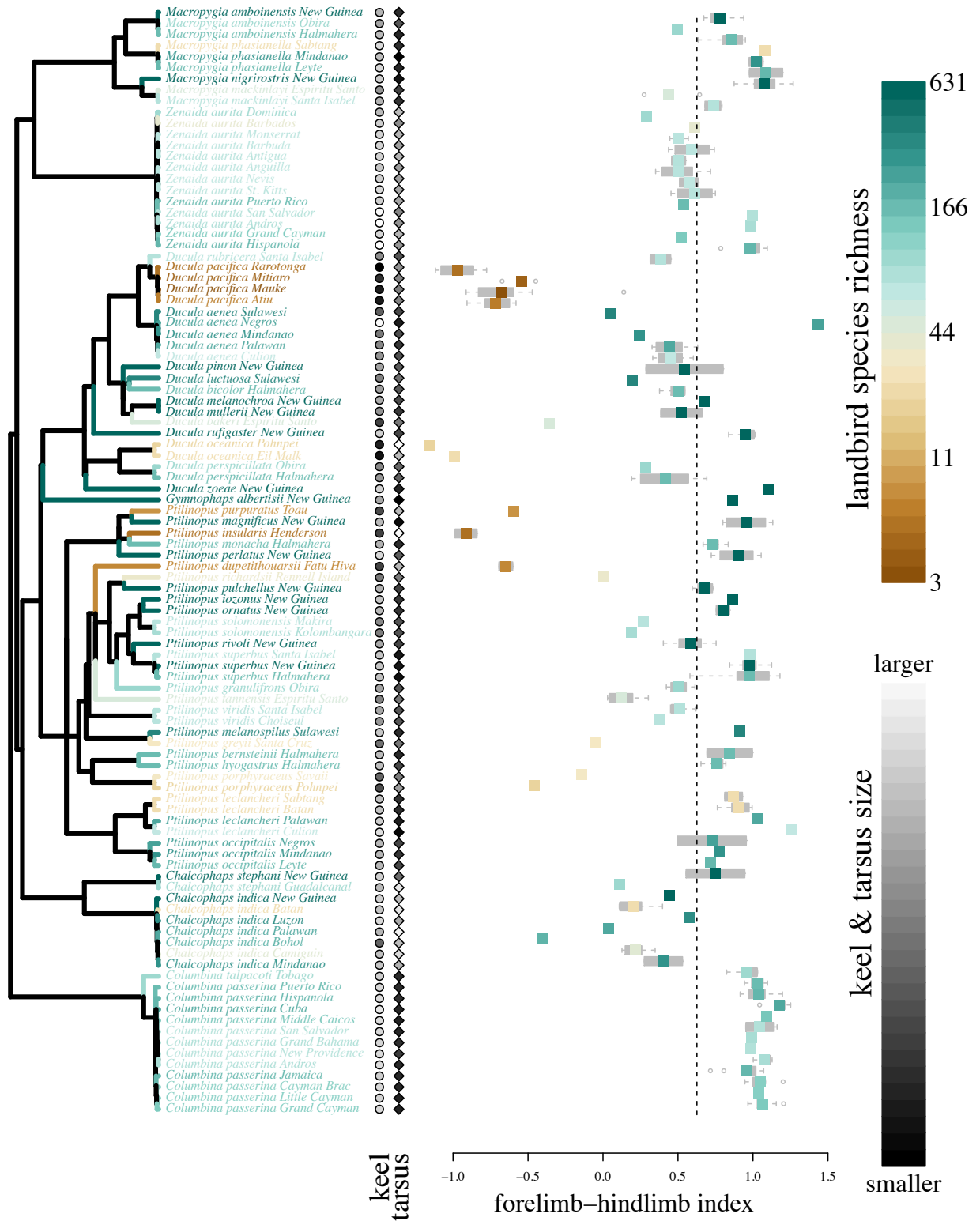


Fig. S3. Alcedinidae (kingfishers)

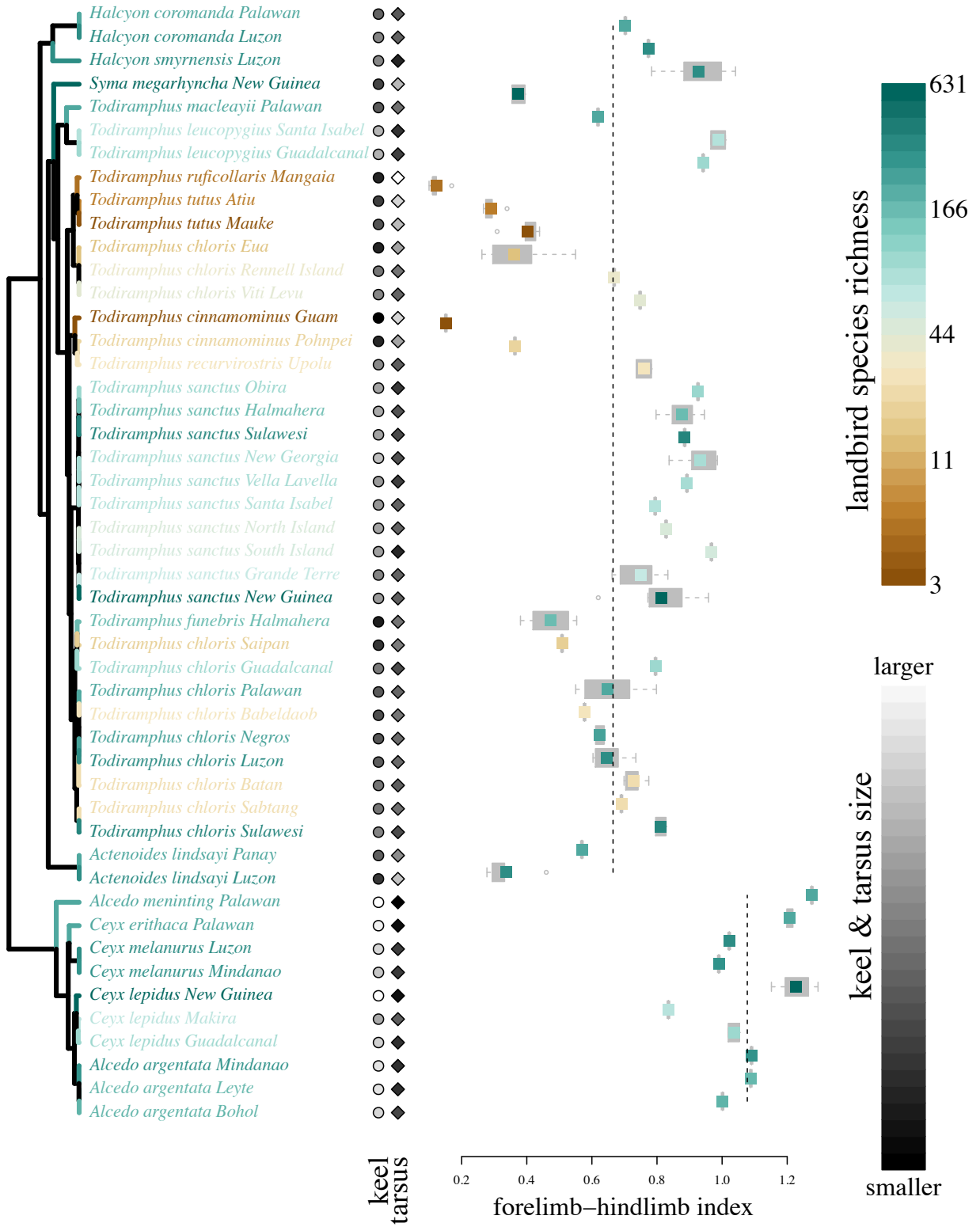


Fig. S4. Thraupidae (tanagers)

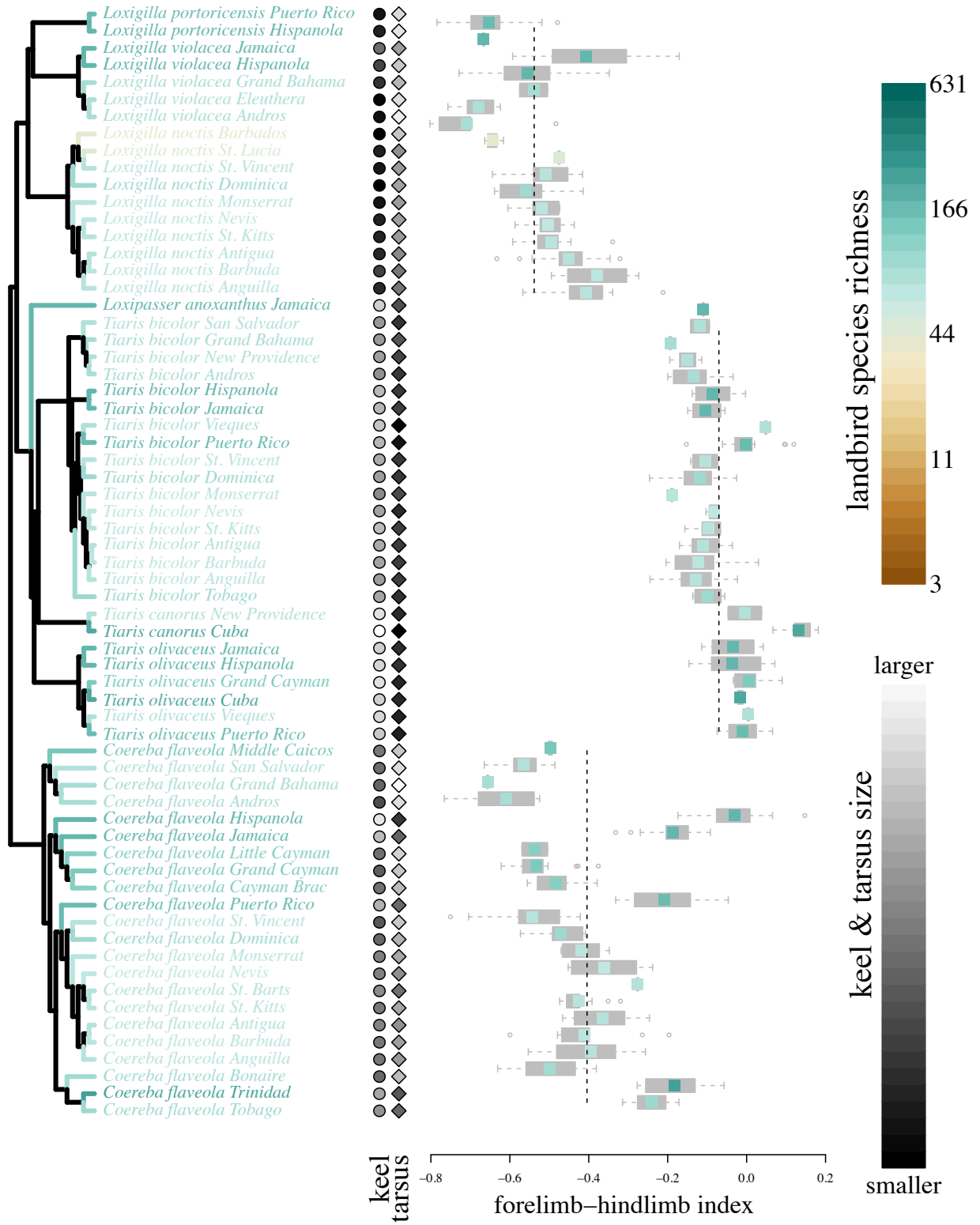


Fig. S5. Meliphagidae (honeyeaters)

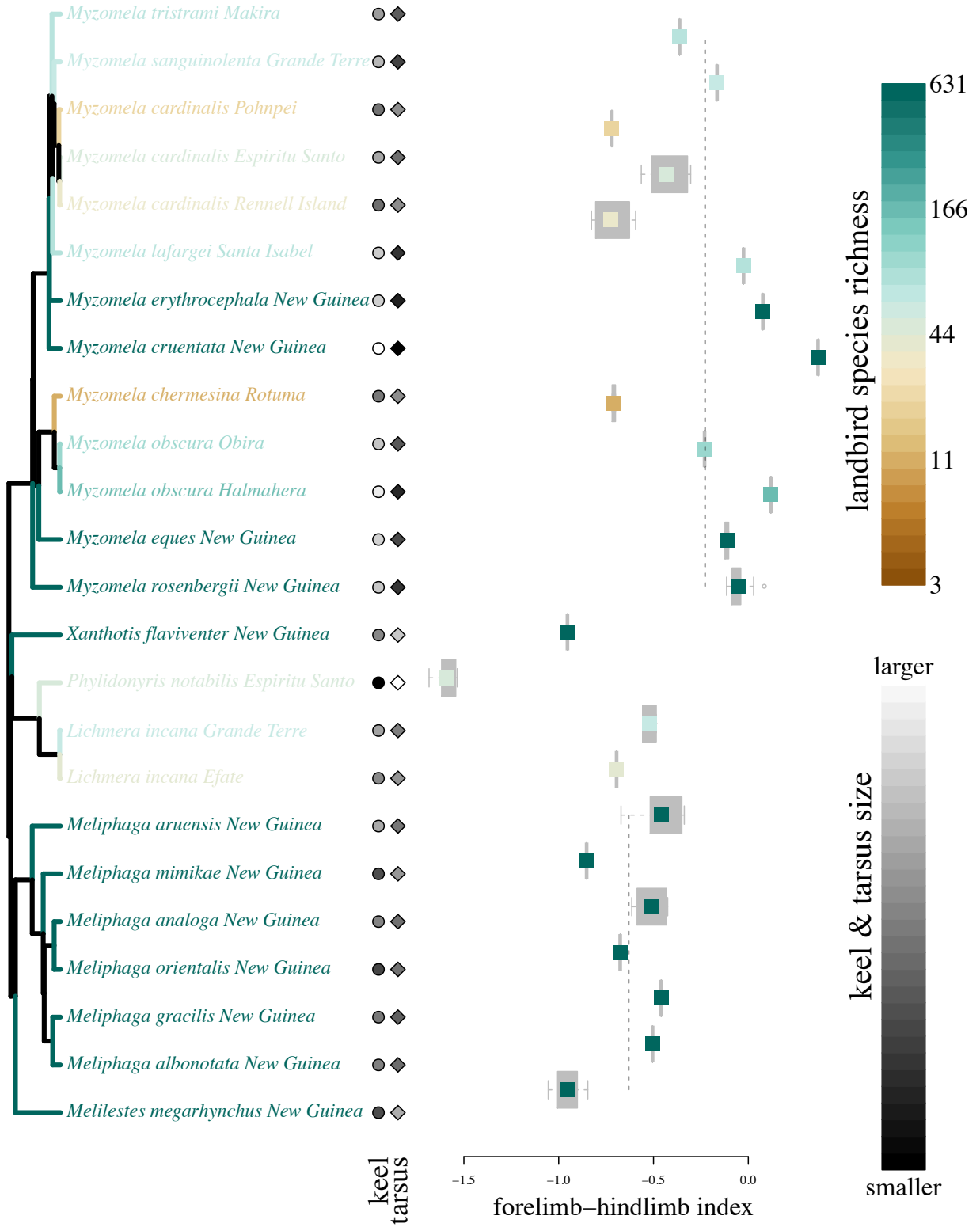


Fig. S6. Zosteropidae (white-eyes)

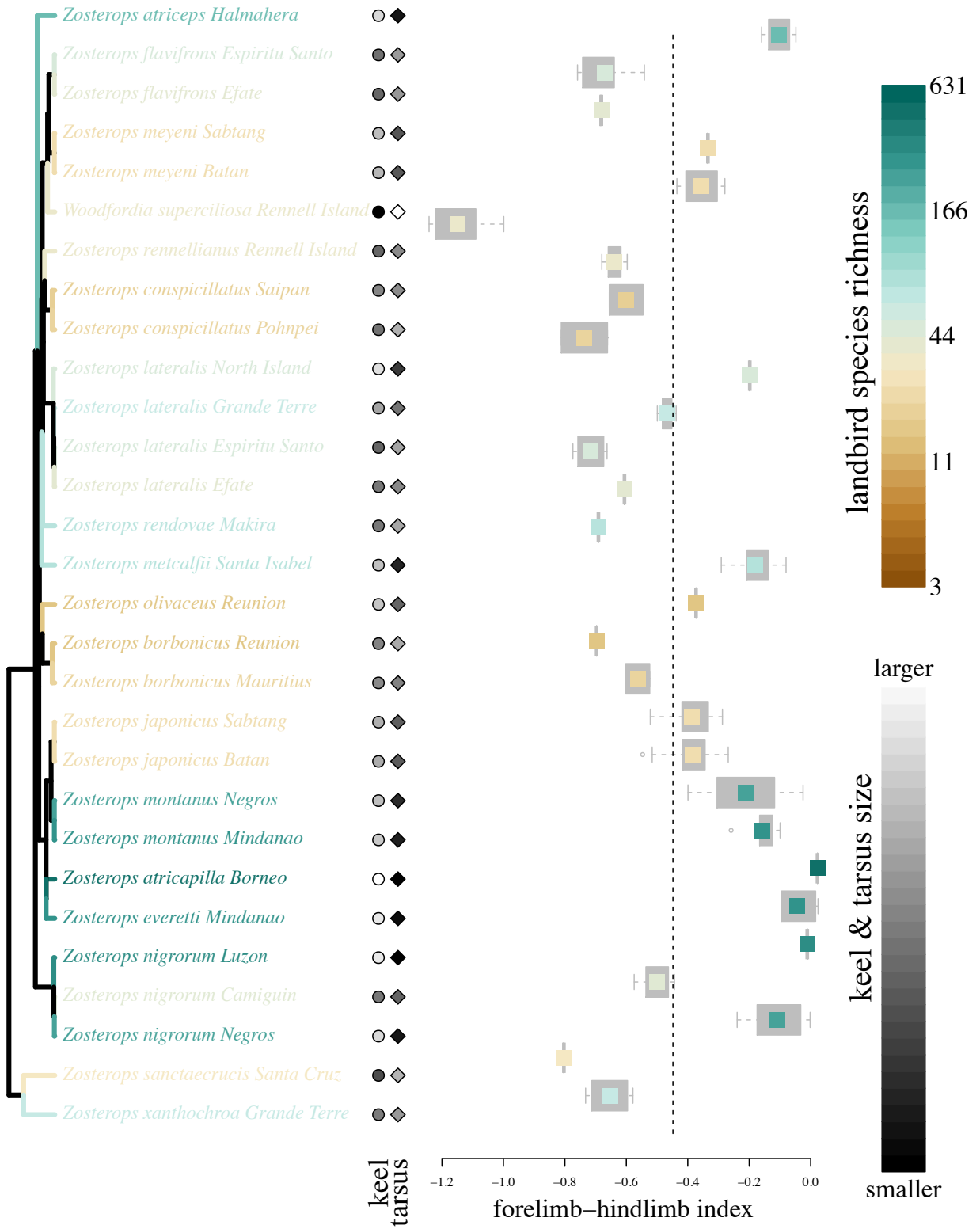


Fig. S7. Pachycephalidae (whistlers)

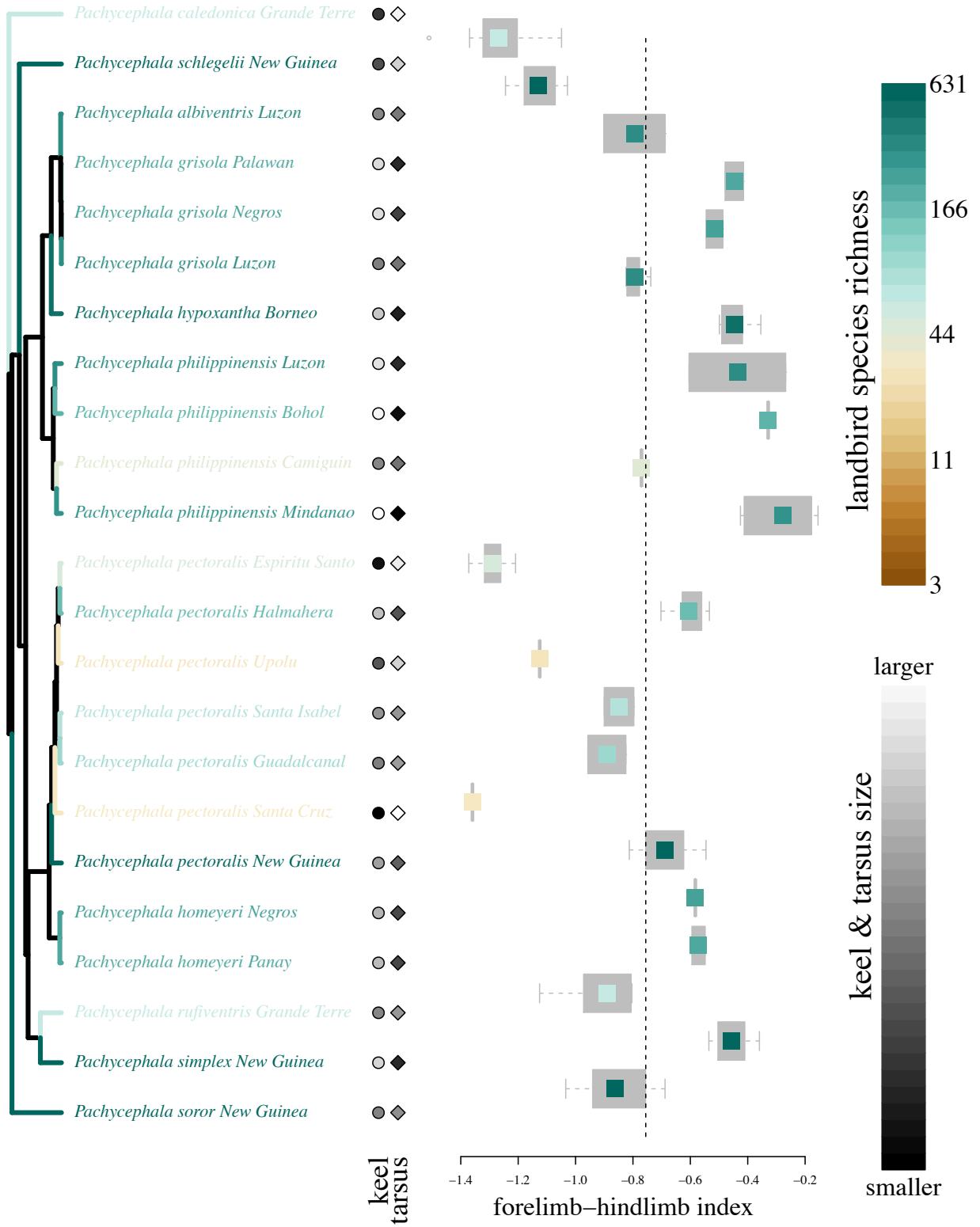


Fig. S8. Monarchidae (Old World flycatchers)

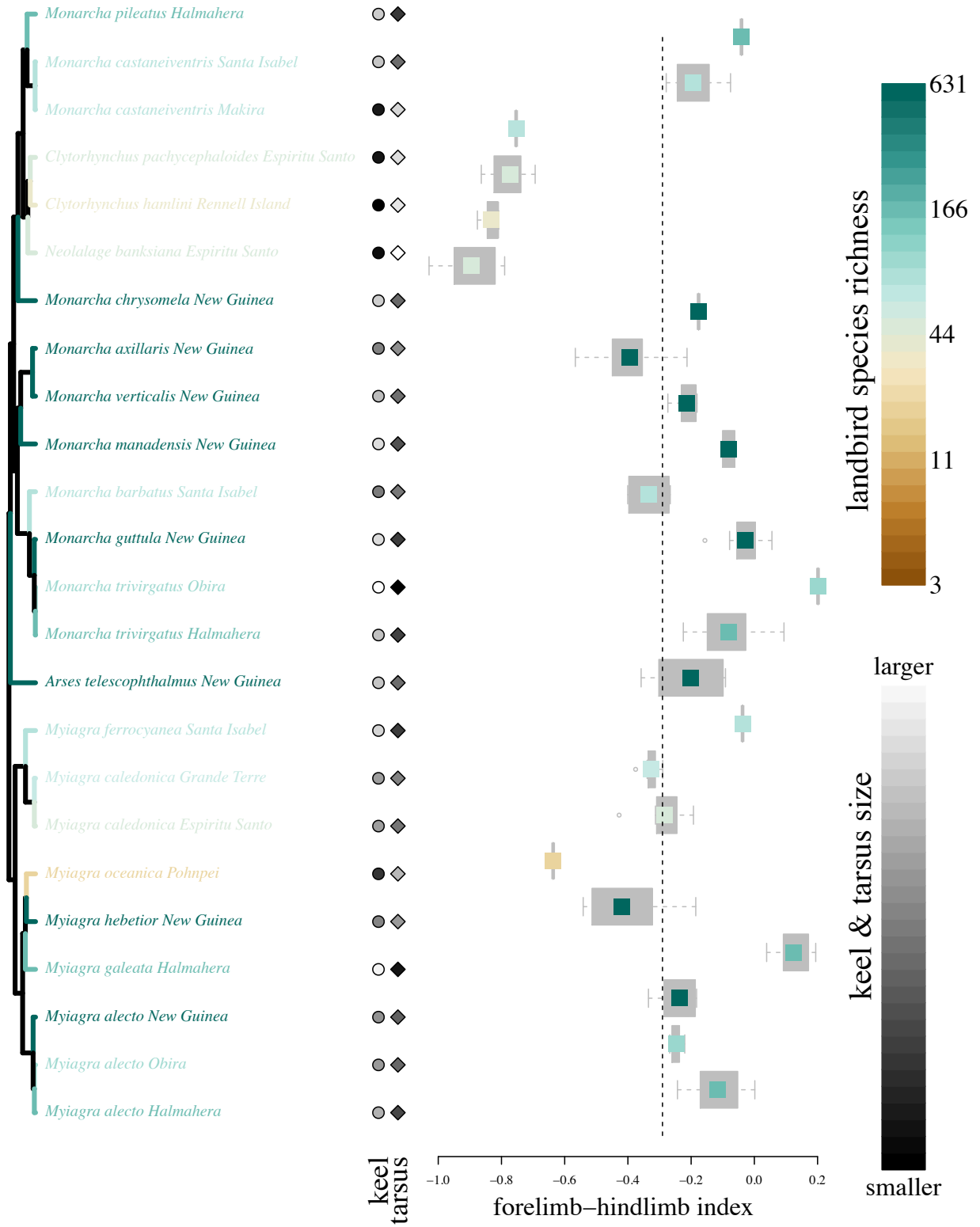


Fig. S9. Rhipiduridae (fantails)

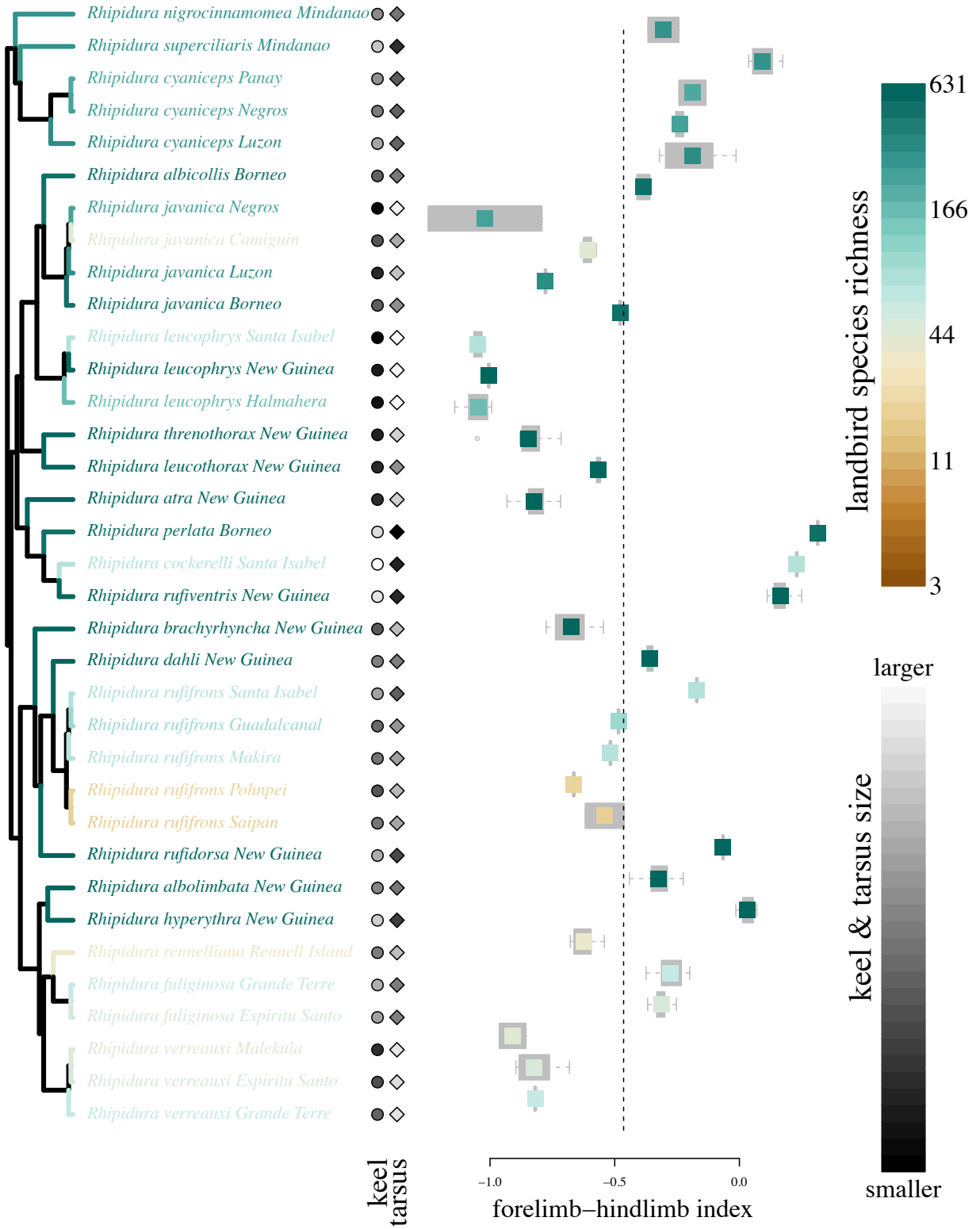


Fig. S10. Trochilidae (hummingbirds)

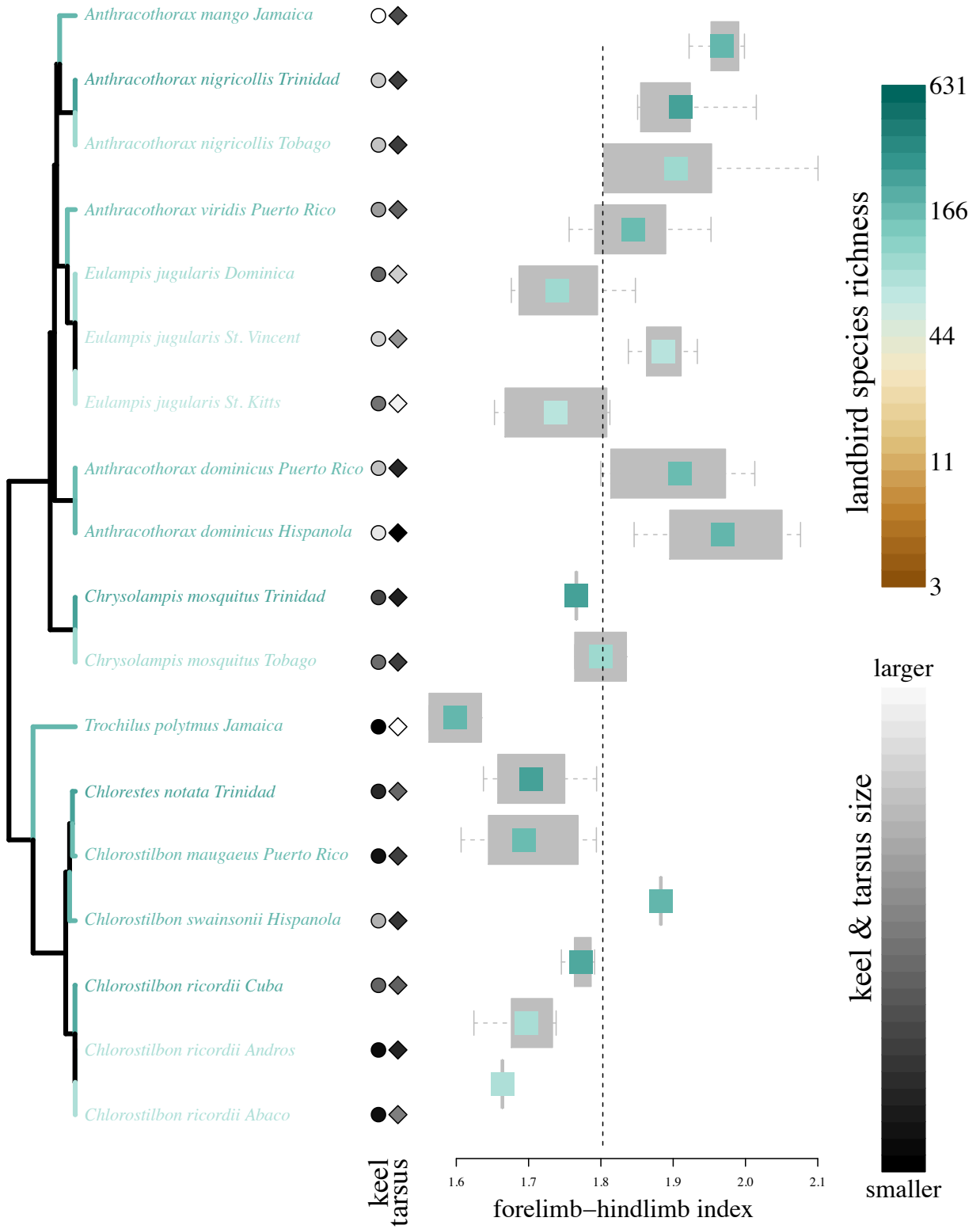


Fig. S11. Predictions of the island rule. Small-bodied taxa should become larger on islands of lower species richness, and thus exhibit a negative relationship between body size and species richness. Large-bodied taxa should become smaller on islands of low species richness, and thus exhibit a positive relationship between body size and species richness. If most taxa truly are evolving toward an idealized or equilibrium body size, body size changes should be greatest for taxa at the extremes of body size. Some taxa may not change body size consistently on islands, and thus have slopes of 0. These should be primarily medium-sized taxa.

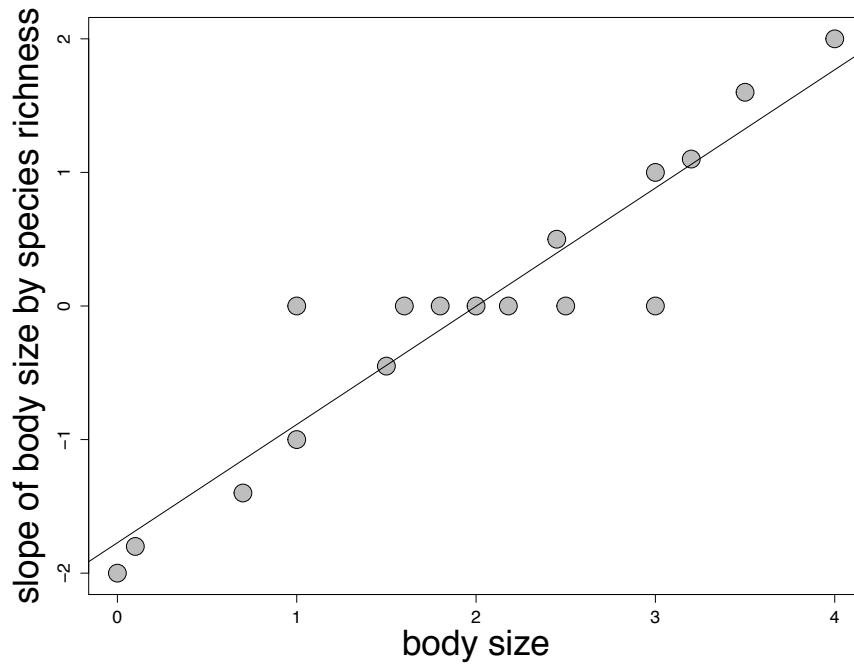


Fig. S12. The relationship between body size and island species richness for each genus (y-axis) and mean body size for the genus (x-axis). The size of each point represents the R^2 value for the linear regression model of body size by species richness for that genus. Clade is indicated by color.

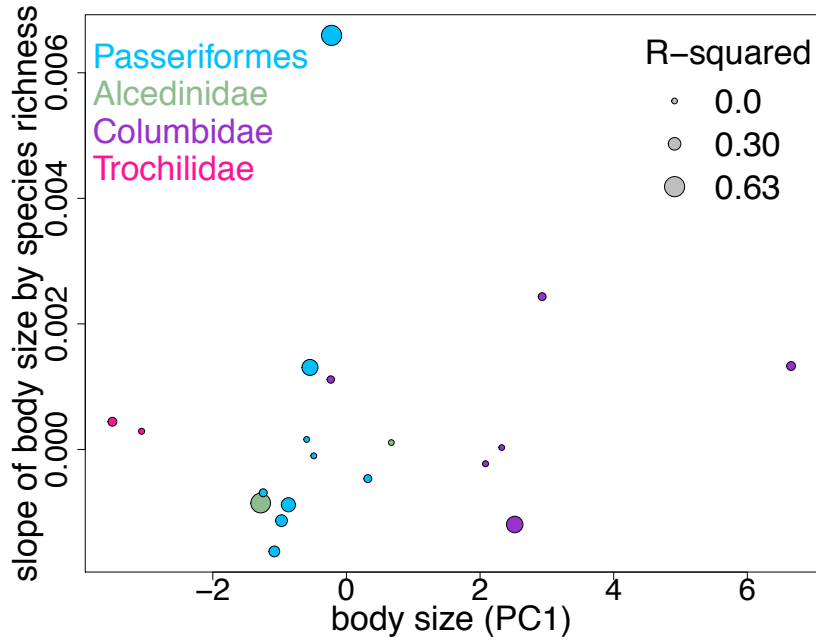


Fig. S13. The relationship between body size and island species richness for each genus (y-axis) and mean body size for the genus (x-axis) for Columbidae. The size of each point represents the R^2 value for the linear regression model of body size by species richness for that genus.

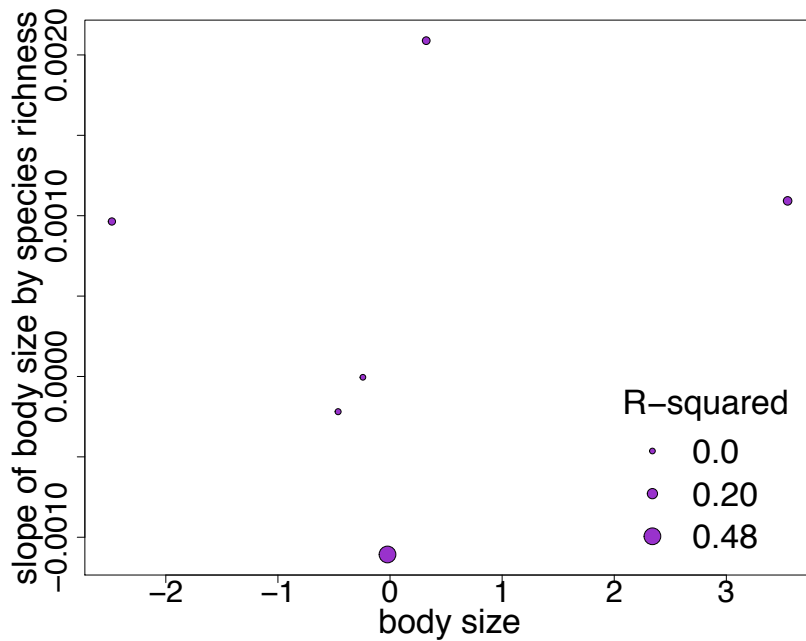


Fig. S14. The relationship between body size and island species richness for each genus (y-axis) and mean body size for the genus (x-axis) for Passeriformes. The size of each point represents the R^2 value for the linear regression model of body size by species richness for that genus.

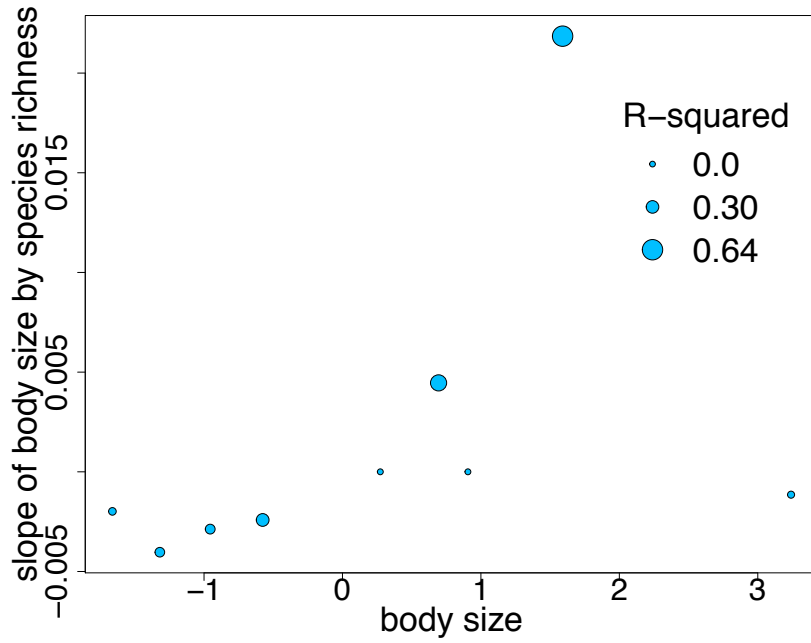


Fig. S15. Legend for genera in Fig. 2 of main text.

Columbidae

- *Chalcophaps*
- *Columbina*
- ◇ *Ducula*
- △ *Gymnophaps*
- ▽ *Macropygia*
- *Ptilinopus*
- *Zenaida*

Monarchidae

- *Arses*
- *Clytorhynchus*
- ◇ *Monarcha*
- ▲ *Myiagra*
- ▽ *Neolalage*

Alcedinidae

- *Actenoides*
- *Alcedo*
- ◇ *Ceyx*
- △ *Halcyon*
- ▽ *Syma*
- *Todiramphus*

Meliphagidae

- *Lichmera*
- *Melilestes*
- ◇ *Meliphaga*
- △ *Myzomela*
- ▽ *Phylidonyris*
- *Xanthotis*

Trochilidae

- *Anthracothorax*
- *Chlorestes*
- ◇ *Chlorostilbon*
- △ *Chrysolampis*
- ▽ *Eulampis*
- *Trochilus*

Thraupidae

- *Loxigilla*
- ◇ *Loxipasser*
- *Coereba*
- ▲ *Tiaris*

Zosteropidae

- *Woodfordia*
- *Zosterops*

Supporting Tables

Table S1: Keel and tarsometatarsus lengths are negatively correlated in most taxa. Linear models of body size-corrected keel length predicted by body size-corrected tarsometatarsus length for each focal taxon.

taxon	coefficient	p-value	adj. R ²	df
<i>Ptilinopus</i>	-3.67	<0.001	0.64	1 and 112
<i>Ducula</i>	-7.32	<0.001	0.49	1 and 60
<i>Columbina</i>	-0.49	0.45	0.0	1 and 73
<i>Macropygia</i>	-4.20	<0.001	0.46	1 and 43
<i>Zenaida aurita</i>	-3.67	<0.001	0.31	1 and 37
<i>Coereba flaveola</i>	-0.62	<0.001	0.34	1 and 237
<i>Loxigilla</i>	-0.91	<0.001	0.22	1 and 195
<i>Tiaris</i>	-0.15	0.32	0.0	1 and 175
<i>Todiramphus</i>	-1.99	<0.001	0.78	1 and 87
Zosteropidae	-0.66	<0.001	0.59	1 and 126
Trochilidae	-6.26	<0.001	0.63	1 and 72
Rhipiduridae	-0.58	<0.001	0.55	1 and 116
Meliphagidae	-0.78	<0.001	0.49	1 and 54
Monarchidae	-0.88	<0.001	0.62	1 and 121
Pachycephalidae	-0.46	<0.001	0.60	1 and 82

Table S2: Results for models predicting the relationship between the forelimb-hindlimb index and island characteristics in non-phylogenetic analyses. The dependent variable in each model is the forelimb-hindlimb index: the second principal component from a PCA of keel length and tarsometatarsus length. Greater values of the forelimb-hindlimb index indicate larger flight muscles and shorter legs. Island population means are the units of analysis (analysis 2B). Island area and species richness values are log-transformed. Models are linear regressions.

taxon	predictor variable(s)	AIC	coefficient	model p-value	adj. R ²	df
all taxa	richness	811.8	0.31	<0.001	0.04	1, 364
all taxa	area	824.7	0.05	0.08	0.01	1, 364
all taxa	richness + family	252.0	0.40	<0.001	0.80	9, 356
all taxa	family	356.9		<0.001	0.73	8, 357
<i>Ptilinopus</i>	richness	31.1	0.68	<0.001	0.56	1, 31
<i>Ptilinopus</i>	area	44.6	0.23	<0.001	0.34	1, 31
<i>Ducula</i>	richness	28.0	0.74	<0.001	0.66	1, 20
<i>Ducula</i>	area	32.7	0.33	<0.001	0.57	1, 20

taxon	predictor variable(s)	AIC	coefficient	model p-value	adj. R ²	df
<i>Columbina</i>	richness	-33.9	0.16	0.17	0.09	1, 11
<i>Columbina</i>	area	-32.5	0.01	0.39	0.0	1, 11
<i>Macropygia</i>	richness	4.8	0.15	0.46	0.0	1, 7
<i>Macropygia</i>	area	5.5	0.02	0.76	0.0	1, 7
<i>Zenaida aurita</i>	richness	1.9	0.19	0.60	0.0	1, 11
<i>Zenaida aurita</i>	area	-0.82	0.11	0.11	0.14	1, 11
<i>Coereba flaveola</i>	richness	-19.4	0.47	0.02	0.20	1, 20
<i>Coereba flaveola</i>	area	-18.9	0.08	0.03	0.19	1, 20
<i>Loxigilla</i>	richness	-24.9	-0.09	0.51	0.0	1, 15
<i>Loxigilla</i>	area	-28.4	-0.05	0.06	0.16	1, 15
<i>Tiaris</i>	richness	-61.0	0.22	0.006	0.26	1, 23
<i>Tiaris</i>	area	-56.5	0.03	0.06	0.11	1, 23
<i>Todiramphus</i>	richness	-15.9	0.26	<0.001	0.43	1, 30
<i>Todiramphus</i>	area	-10.3	0.11	<0.001	0.32	1, 30
Zosteropidae	richness	-2.8	0.42	<0.001	0.42	1, 27
Zosteropidae	area	4.6	0.13	0.003	0.26	1, 27
Trochilidae	richness	-23.7	0.09	0.51	0.0	1, 16
Trochilidae	area	-23.7	0.02	0.52	0.0	1, 16
<i>Rhipidura</i>	richness	34.5	0.17	0.20	0.02	1, 33
<i>Rhipidura</i>	area	34.5	0.07	0.20	0.02	1, 33
Meliphagidae	richness	30.7	0.17	0.27	0.01	1, 22
Meliphagidae	area	31.1	0.06	0.36	0.00	1, 22
Monarchidae	richness	8.9	0.28	0.02	0.18	1, 22
Monarchidae	area	11.8	0.09	0.10	0.08	1, 22
<i>Pachycephala</i>	richness	7.3	0.42	0.003	0.32	1, 21
<i>Pachycephala</i>	area	14.7	0.10	0.13	0.06	1, 21

Table S3: Results for analyses predicting the relationship between body size and island characteristics. Island population means are the unit of analysis (analysis 2B). Island area and species richness values are log-transformed. Models are linear regressions.

taxon	predictor variable(s)	AIC	coefficient	model p-value	adj. R ²	df
<i>Ptilinopus</i>	richness	80.9	0.023	0.92	0.0	1, 31
<i>Ptilinopus</i>	area	80.9	-0.005	0.96	0.0	1, 31
<i>Ducula</i>	richness	54.1	0.52	0.022	0.20	1, 20
<i>Ducula</i>	area	54.7	0.23	0.030	0.17	1, 20
<i>Columbina</i>	richness	-0.92	0.15	0.71	0.0	1, 11
<i>Columbina</i>	area	-1.77	0.045	0.36	0.0	1, 11
<i>Macropygia</i>	richness	23.2	-0.43	0.43	0.0	1, 7
<i>Macropygia</i>	area	21.6	-0.25	0.18	0.13	1, 7

taxon	predictor variable(s)	AIC	coefficient	model p-value	adj. R ²	df
<i>Zenaida aurita</i>	richness	2.7	0.44	0.26	0.03	1, 11
<i>Zenaida aurita</i>	area	3.1	0.08	0.32	0.0	1, 11
<i>Coereba flaveola</i>	richness	-12.1	-0.24	0.30	0.0	1, 20
<i>Coereba flaveola</i>	area	-12.0	-0.04	0.32	0.0	1, 20
<i>Loxigilla</i>	richness	6.0	1.3	<0.001	0.50	1, 15
<i>Loxigilla</i>	area	4.0	0.29	<0.001	0.56	1, 15
<i>Tiaris</i>	richness	-39.5	-0.16	0.16	0.04	1, 23
<i>Tiaris</i>	area	-37.7	-0.01	0.57	0.0	1, 23
<i>Todiramphus</i>	richness	57.2	0.04	0.82	0.0	1, 30
<i>Todiramphus</i>	area	57.3	-0.01	0.85	0.0	1, 30
Zosteropidae	richness	35.5	-0.20	0.26	0.01	1, 27
Zosteropidae	area	33.9	-0.12	0.09	0.07	1, 27
Trochilidae	richness	8.2	-0.43	0.23	0.03	1, 16
Trochilidae	area	6.9	-0.13	0.11	0.10	1, 16
<i>Rhipidura</i>	richness	67.9	0.02	0.92	0.0	1, 33
<i>Rhipidura</i>	area	67.7	-0.03	0.67	0.0	1, 33
Meliphagidae	richness	64.9	0.29	0.34	0.0	1, 22
Meliphagidae	area	64.8	0.13	0.33	0.0	1, 22
Monarchidae	richness	38.8	-0.17	0.43	0.0	1, 22
Monarchidae	area	39.0	-0.06	0.52	0.0	1, 22
Pachycephalidae	richness	23.9	-0.54	0.007	0.27	1, 21
Pachycephalidae	area	24.7	-0.22	0.010	0.24	1, 21

Table S4: Results for Analysis 3A, predicting shape with island species richness and area. The dependent variable in each model is the forelimb-hindlimb index: the second principal component from a PCA of keel length and tarsometatarsus length. Greater values of the forelimb-hindlimb index indicate larger flight muscles and shorter legs. Each data point is one specimen. Island area and species richness values are log-transformed. Models are linear regressions. P-values for each parameter are from ANCOVAs. Area and richness were positively correlated with the shape variable unless “(-)” follows the term in the “predictor variable(s)” column, indicating a negative correlation between the shape variable and the predictor variable of interest.

taxon	predictor variable(s)	model p-value	adj. R ²	p-values for each parameter	df
<i>Ptilinopus</i>	richness	<0.001	0.41		1, 112
<i>Ptilinopus</i>	area	<0.001	0.26		1, 112
<i>Ptilinopus</i>	richness + species + sex	<0.001	0.92	richness <0.001; species <0.001; sex: 0.07	23, 90
<i>Ducula</i>	richness	<0.001	0.43		1, 60
<i>Ducula</i>	area	<0.001	0.38		1, 60
<i>Ducula</i>	richness + species + sex	<0.001	0.60	richness <0.001; species: 0.008; sex: 0.004	13, 48
<i>Columbina</i>	richness	0.25	0.0		1, 73
<i>Columbina</i>	area	0.68	0.0		1, 73
<i>Columbina</i>	richness + species + sex	0.03	0.08	richness: 0.23; species: 0.07; sex: 0.03	3, 71
<i>Macropygia</i>	richness	<0.001	0.42		1, 43
<i>Macropygia</i>	area	<0.001	0.30		1, 43
<i>Macropygia</i>	richness + species + sex	<0.001	0.66	richness <0.001; species <0.001; sex: 0.48	5, 39
<i>Zenaida aurita</i>	richness	0.008	0.15		1, 37
<i>Zenaida aurita</i>	area	<0.001	0.27		1, 37
<i>Zenaida aurita</i>	richness + sex	0.01	0.18	richness: 0.007; sex: 0.16	2, 36
<i>Coereba flaveola</i>	richness	<0.001	0.40		1, 237
<i>Coereba flaveola</i>	area	<0.001	0.61		1, 237
<i>Coereba flaveola</i>	richness + sex	<0.001	0.46	richness <0.001; sex <0.001	2, 236
<i>Loxigilla</i>	richness	<0.001	0.08		1, 195
<i>Loxigilla</i>	area	0.08	0.01		1, 195
<i>Loxigilla</i>	richness +	<0.001	0.17	richness <0.001; species	4,

taxon	predictor variable(s)	model p-value	adj. R ²	p-values for each parameter	df
<i>Tiaris</i>	species + sex richness	<0.001	0.42	<0.001; sex: 0.11	192 1, 175
<i>Tiaris</i>	area	<0.001	0.36		1, 175
<i>Tiaris</i>	richness + species + sex	<0.001	0.53	richness <0.001; species <0.001; sex <0.001	4, 172
<i>Todiramphus</i>	richness	<0.001	0.60		1, 87
<i>Todiramphus</i>	area	<0.001	0.51		1, 87
<i>Todiramphus</i>	richness + species + area	<0.001	0.82	richness <0.001; species <0.001; sex: 0.10	9, 79
Zosteropidae	richness	<0.001	0.23		1, 126
Zosteropidae	area	0.06	0.02		1, 126
Zosteropidae	richness + species + sex	<0.001	0.87	richness <0.001; species <0.001; sex: 0.02	19, 108
Trochilidae	richness	<0.001	0.17		1, 72
Trochilidae	area	<0.001	0.30		1, 72
Trochilidae	richness(-) + species + sex	<0.001	0.77	richness <0.001; species <0.001; sex <0.001	12, 61
Trochilidae	area + species + sex	<0.001	0.77	area <0.001; species <0.001; sex <0.001	12, 61
<i>Rhipidura</i>	richness	0.28	0.00		1, 116
<i>Rhipidura</i>	area	0.77	0.00		1, 116
<i>Rhipidura</i>	richness + species + sex	<0.001	0.90	richness <0.001; species <0.001; sex <0.001	22, 95
Meliphagidae	richness	<0.001	0.42		1, 54
Meliphagidae	area	<0.001	0.38		1, 54
Meliphagidae	richness + species + sex	<0.001	0.83	richness <0.001; species <0.001; sex: 0.001	21, 34
Monarchidae	richness	<0.001	0.28		1, 121
Monarchidae	area	<0.001	0.12		1, 121
Monarchidae	richness + species + sex	<0.001	0.82	richness <0.001; species <0.001; sex <0.001	20, 102
<i>Pachycephala</i>	richness	<0.001	0.25		1, 82
<i>Pachycephala</i>	area	0.05	0.03		1, 82
<i>Pachycephala</i>	richness + species + sex	<0.001	0.60	richness <0.001; species <0.001; sex: 0.89	12, 71

Table S5: Results for Analysis 3A. Each data point is one specimen. Island area and species richness values are log-transformed. Models are linear regressions. P-values for each parameter are from ANCOVAs. “Keel” and “tarso” are the residuals of regressions of keel length and tarsometatarsus length, respectively, by PC1, to correct for overall body size. Unless otherwise noted, area and richness were positively correlated with keel length and negatively correlated with tarsometatarsus length. The relationship between richness or area and PC1 is indicated by (-) following area/richness for a negative correlation and (+) for a positive correlation.

taxon	model	predictor variable(s)	model p-value	adj. R ²	p-values for each parameter	df
<i>Columbidae</i>						
<i>Ptilinopus</i>	keel	richness	<0.001	0.38		1, 112
<i>Ptilinopus</i>	keel	area	<0.001	0.24		1, 112
<i>Ptilinopus</i>	keel	area + species + sex	<0.001	0.88	area <0.001; species <0.001; sex: 0.3	23, 90
<i>Ptilinopus</i>	keel	richness + species + sex	<0.001	0.88	richness <0.001; species <0.001; sex: 0.3	23, 90
<i>Ptilinopus</i>	tarso	area	<0.001	0.21		1, 112
<i>Ptilinopus</i>	tarso	richness	<0.001	0.34		1, 112
<i>Ptilinopus</i>	tarso	area + species + sex	<0.001	0.92	area: 0.99; species <0.001; sex: 0.4	23, 90
<i>Ptilinopus</i>	tarso	richness + species + sex	<0.001	0.92	richness: 0.97; species <0.001; sex: 0.4	23, 90
<i>Ptilinopus</i>	PC1	area(-)	0.40	0.00		1, 112
<i>Ptilinopus</i>	PC1	richness(-)	0.41	0.00		1, 112
<i>Ptilinopus</i>	PC1	area(-) + species + sex	<0.001	0.92	area: 0.004; species <0.001; sex <0.001	23, 90
<i>Ptilinopus</i>	PC1	richness(-) + species + sex	<0.001	0.92	richness: 0.005; species <0.001; sex <0.001	23, 90
<i>Ducula</i>	keel	richness	<0.001	0.60		1, 60
<i>Ducula</i>	keel	area	<0.001	0.53		1, 60
<i>Ducula</i>	keel	richness +	<0.001	0.74	richness: 0.42;	13,

taxon	model	predictor variable(s)	model p-value	adj. R ²	p-values for each parameter	df
		species + sex			species <0.001; sex: 0.02	48
<i>Ducula</i>	keel	area + species + sex	<0.001	0.74	area: 0.93; species <0.001; sex: 0.02	13, 48
<i>Ducula</i>	tarso	richness	<0.001	0.32		1, 60
<i>Ducula</i>	tarso	area	<0.001	0.27		1, 60
<i>Ducula</i>	tarso	richness + species + sex	<0.001	0.60	richness: 0.65; species <0.001; sex: 0.02	13, 48
<i>Ducula</i>	PC1	area(+)	<0.001	0.20		1, 60
<i>Ducula</i>	PC1	richness(+)	<0.001	0.24		1, 60
<i>Ducula</i>	PC1	richness(-) + species + sex	<0.001	0.79	richness <0.001; species <0.001; sex: 0.002	13, 48
<i>Columbina</i>	keel	richness	0.16	0.01		1, 73
<i>Columbina</i>	keel	area	0.06	0.03		1, 73
<i>Columbina</i>	keel	richness + species + sex	0.02	0.09	richness: 0.43; species: 0.01; sex: 0.1	3, 71
<i>Columbina</i>	keel	area + species + sex	0.009	0.11	area: 0.13; species: 0.009; sex: 0.09	3, 71
<i>Columbina</i>	tarso	richness	0.27	0.00		1, 73
<i>Columbina</i>	tarso	area	0.35	0.00		1, 73
<i>Columbina</i>	tarso	richness + species + sex	0.02	0.09	richness: 0.06; species: 0.02; sex: 0.29	3, 71
<i>Columbina</i>	PC1	area(+)	0.01	0.07		1, 73
<i>Columbina</i>	PC1	richness(+)	0.04	0.05		1, 73
<i>Columbina</i>	PC1	richness(+) + species + sex	<0.001	0.46	richness <0.001; species <0.001; sex: 0.03	3, 71
<i>Macropygia</i>	keel	richness	<0.001	0.37		1, 43

taxon	model	predictor variable(s)	model p-value	adj. R ²	p-values for each parameter	df
<i>Macropygia</i>	keel	area	<0.001	0.22		1, 43
<i>Macropygia</i>	keel	richness(-) + species + sex	<0.001	0.64	richness: 0.84; species <0.001; sex: 0.51	5, 39
<i>Macropygia</i>	tarso	richness	<0.001	0.34		1, 43
<i>Macropygia</i>	tarso	area	<0.001	0.25		1, 43
<i>Macropygia</i>	tarso	richness + species + sex	<0.001	0.52	richness: 0.13; species <0.001; sex: 0.11	5, 39
<i>Macropygia</i>	PC1	richness(-)	0.86	0.00		1, 43
<i>Macropygia</i>	PC1	area(-)	0.26	0.01		1, 43
<i>Macropygia</i>	PC1	richness(-) + species + sex	<0.001	0.81	richness: 0.77; species <0.001; sex: 0.009	5, 39
<i>Zenaida aurita</i>	keel	richness	<0.001	0.28		1, 37
<i>Zenaida aurita</i>	keel	area	<0.001	0.41		1, 37
<i>Zenaida aurita</i>	keel	richness + sex	0.001	0.27	richness <0.001; sex: 0.43	2, 36
<i>Zenaida aurita</i>	tarso	richness	0.15	0.03		1, 37
<i>Zenaida aurita</i>	tarso	area	0.03	0.10		1, 37
<i>Zenaida aurita</i>	tarso	richness + sex	0.25	0.02	richness: 0.15; sex: 0.42	2, 36
<i>Zenaida aurita</i>	PC1	richness(+)	0.04	0.08		1, 37
<i>Zenaida aurita</i>	PC1	area(+)	0.04	0.09		1, 37
<i>Zenaida aurita</i>	PC1	richness(+) + sex	<0.001	0.33	richness: 0.02; sex <0.001	2, 36
Thraupidae						
<i>Coereba flaveola</i>	keel	richness	<0.001	0.21		1, 237
<i>Coereba flaveola</i>	keel	area	<0.001	0.38		1, 237
<i>Coereba flaveola</i>	keel	richness + sex	<0.001	0.37	richness <0.001; sex <0.001	2, 236

taxon	model	predictor variable(s)	model p-value	adj. R ²	p-values for each parameter	df
<i>Coereba flaveola</i>	keel	area + sex	<0.001	0.52	area <0.001; sex <0.001	2, 236
<i>Coereba flaveola</i>	tarso	richness	<0.001	0.31		1, 237
<i>Coereba flaveola</i>	tarso	area	<0.001	0.38		1, 237
<i>Coereba flaveola</i>	tarso	richness + sex	<0.001	0.39	richness <0.001; sex: 0.06	2, 236
<i>Coereba flaveola</i>	tarso	area + sex	<0.001	0.46	area <0.001; sex: 0.004	2, 236
<i>Coereba flaveola</i>	PC1	richness(-)	<0.001	0.13		1, 237
<i>Coereba flaveola</i>	PC1	area(-)	<0.001	0.18		1, 237
<i>Coereba flaveola</i>	PC1	richness(-) + sex	<0.001	0.37	richness <0.001; sex <0.001	2, 236
<i>Loxigilla</i>	keel	richness	<0.001	0.12		1, 195
<i>Loxigilla</i>	keel	area	<0.001	0.08		1, 195
<i>Loxigilla</i>	keel	richness + species + sex	<0.001	0.32	richness <0.001; species <0.001; sex: 0.18	4, 192
<i>Loxigilla</i>	tarso	richness	0.02	0.02		1, 195
<i>Loxigilla</i>	tarso	area	0.24	0.00		1, 195
<i>Loxigilla</i>	tarso	richness + species + sex	<0.001	0.12	richness <0.001; species <0.001; sex: 0.14	4, 192
<i>Loxigilla</i>	PC1	richness(+)	<0.001	0.62		1, 195
<i>Loxigilla</i>	PC1	area(+)	<0.001	0.56		1, 195
<i>Loxigilla</i>	PC1	richness(+) + species + sex	<0.001	0.87	richness <0.001; sex <0.001; species <0.001	4, 192
<i>Tiaris</i>	keel	richness	<0.001	0.25		1, 175
<i>Tiaris</i>	keel	area	<0.001	0.23		1, 175
<i>Tiaris</i>	keel	richness + species + sex	<0.001	0.40	richness <0.001; species: 0.003; sex <0.001	4, 172

taxon	model	predictor variable(s)	model p-value	adj. R ²	p-values for each parameter	df
<i>Tiaris</i>	tarso	richness	<0.001	0.12		1, 175
<i>Tiaris</i>	tarso	area	<0.001	0.10		1, 175
<i>Tiaris</i>	tarso	richness + species + sex	<0.001	0.28	richness <0.001; species <0.001; sex: 0.73	4, 172
<i>Tiaris</i>	PC1	richness(-)	<0.001	0.07		1, 175
<i>Tiaris</i>	PC1	area(-)	0.009	0.03		1, 175
<i>Tiaris</i>	PC1	richness(+) + species + sex	<0.001	0.37	richness <0.001; species <0.001; sex: 0.01	4, 172
Alcedinidae						
<i>Todiramphus</i>	keel	richness	<0.001	0.56		1, 87
<i>Todiramphus</i>	keel	area	<0.001	0.46		1, 87
<i>Todiramphus</i>	keel	richness + species + sex	<0.001	0.72	richness <0.001; species <0.001; sex: 0.32	9, 79
<i>Todiramphus</i>	tarso	richness	<0.001	0.62		1, 87
<i>Todiramphus</i>	tarso	area	<0.001	0.52		1, 87
<i>Todiramphus</i>	tarso	richness + sex + species	<0.001	0.87	richness <0.001; species <0.001; sex: 0.03	9, 79
<i>Todiramphus</i>	PC1	richness(+)	0.18	0.00		1, 87
<i>Todiramphus</i>	PC1	area(+)	0.54	0.00		1, 87
<i>Todiramphus</i>	PC1	richness(-) + species + sex	<0.001	0.83	richness: 0.001; species <0.001; sex: 0.71	9, 79
Zosteropidae	keel	richness	<0.001	0.11		1, 126
Zosteropidae	keel	area	0.29	0.00		1, 126
Zosteropidae	keel	richness + species + sex	<0.001	0.74	richness <0.001; species <0.001; sex: 0.06	19, 108
Zosteropidae	tarso	richness	<0.001	0.30		1,

taxon	model	predictor variable(s)	model p-value	adj. R ²	p-values for each parameter	df
Zosteropidae	tarso	area	0.03	0.03		126 1,
Zosteropidae	tarso	richness + species + sex	<0.001	0.91	richness <0.001; species <0.001; sex: 0.01	126 19, 108
Zosteropidae	PC1	richness(-)	0.02	0.03		1, 126
Zosteropidae	PC1	area(-)	0.03	0.03		1, 126
Zosteropidae	PC1	richness(-) + species + sex	<0.001	0.94	richness <0.001; species <0.001; sex: 0.22	19, 108
Trochilidae	keel	richness	<0.001	0.14		1, 72
Trochilidae	keel	area	<0.001	0.23		1, 72
Trochilidae	keel	richness(-) + species + sex	<0.001	0.78	richness <0.001; species <0.001 sex <0.001;	12, 61
Trochilidae	keel	area + species + sex	<0.001	0.79	area <0.001; species <0.001; sex <0.001	12, 61
Trochilidae	tarso	richness	0.01	0.07		1, 72
Trochilidae	tarso	area	<0.001	0.21		1, 72
Trochilidae	tarso	richness(+) + species + sex	<0.001	0.57	richness <0.001; species <0.001; sex: 0.01	12, 61
Trochilidae	tarso	area + species + sex	<0.001	0.58	area <0.001; species <0.001; sex: 0.01	12, 61
Trochilidae	PC1	richness(-)	<0.001	0.17		1, 72
Trochilidae	PC1	area(-)	<0.001	0.14		1, 72
Trochilidae	PC1	richness(+) + species + sex	<0.001	0.95	richness <0.001; species <0.001; sex <0.001	12, 61
Rhipiduridae <i>Rhipidura</i>	keel	richness(-)	0.19	0.01		1, 116
<i>Rhipidura</i>	keel	area(-)	0.11	0.01		1,

taxon	model	predictor variable(s)	model p-value	adj. R ²	p-values for each parameter	df
<i>Rhipidura</i>	keel	richness(-) + species + sex	<0.001	0.80	richness: 0.004; species <0.001; sex <0.001	116 22, 95
<i>Rhipidura</i>	keel	area(+) + species + sex	<0.001	0.80	area <0.001; species <0.001; sex <0.001	22, 95
<i>Rhipidura</i>	tarso	richness	0.004	0.06		1, 116
<i>Rhipidura</i>	tarso	area	0.06	0.02		1, 116
<i>Rhipidura</i>	tarso	richness + species + sex	<0.001	0.93	richness <0.001; species <0.001; sex <0.001	22, 95
<i>Rhipidura</i>	PC1	richness(+)	0.10	0.01		1, 116
<i>Rhipidura</i>	PC1	area(-)	0.89	0.00		1, 116
<i>Rhipidura</i>	PC1	richness(+) + species + sex	<0.001	0.91	richness <0.001; species <0.001; sex 0.003	22, 95
Meliphagidae	keel	richness	<0.001	0.24		1, 54
Meliphagidae	keel	area	<0.001	0.22		1, 54
Meliphagidae	keel	richness + species + sex	<0.001	0.84	richness <0.001; species <0.001; sex <0.001	21, 34
Meliphagidae	tarso	richness	<0.001	0.52		1, 54
Meliphagidae	tarso	area	<0.001	0.47		1, 54
Meliphagidae	tarso	richness + sex + species	<0.001	0.73	richness <0.001; species: 0.008; sex <0.001	21, 34
Meliphagidae	PC1	richness(+)	0.73	0.0		1, 54
Meliphagidae	PC1	area(-)	0.71	0.0		1, 54
Meliphagidae	PC1	richness(-) + species + sex	<0.001	0.92	richness: 0.22; species <0.001; sex: 0.006	21, 34
Monarchidae	keel	richness	<0.001	0.24		1, 121

taxon	model	predictor variable(s)	model p-value	adj. R ²	p-values for each parameter	df
Monarchidae	keel	area	<0.001	0.14		1, 121
Monarchidae	keel	richness(-) + species + sex	<0.001	0.81	richness <0.001; sex <0.001; species <0.001	20, 102
Monarchidae	tarso	richness	<0.001	0.22		1, 121
Monarchidae	tarso	area	0.001	0.09		1, 121
Monarchidae	tarso	richness(+) + species + sex	<0.001	0.88	richness <0.001; species <0.001; sex: 0.03	20, 102
Monarchidae	PC1	richness(-)	0.22	0.00		1, 121
Monarchidae	PC1	area(-)	0.15	0.01		1, 121
Monarchidae	PC1	richness(+)+ species + sex	<0.001	0.89	richness <0.001; species <0.001; sex <0.001;]	20, 102
Pachycephalidae						
<i>Pachycephala</i>	keel	richness	<0.001	0.20		1, 82
<i>Pachycephala</i>	keel	area	0.01	0.06		1, 82
<i>Pachycephala</i>	keel	richness + species + sex	<0.001	0.32	richness <0.001; species: 0.01; sex: 0.18	12, 71
<i>Pachycephala</i>	tarso	richness	<0.001	0.37		1, 82
<i>Pachycephala</i>	tarso	area	0.001	0.12		1, 82
<i>Pachycephala</i>	tarso	richness + species + sex	<0.001	0.82	richness <0.001; species <0.001; sex: 0.03	12, 71
<i>Pachycephala</i>	PC1	richness(-)	0.19	0.01		1, 82
<i>Pachycephala</i>	PC1	area(-)	0.002	0.10		1, 82
<i>Pachycephala</i>	PC1	richness(-) + species + sex	<0.001	0.36	richness: 0.11; species <0.001; sex: 0.58	12, 71
<i>Pachycephala</i>	PC1	area(-) + species + sex	<0.001	0.41	area <0.001; species <0.001; sex: 0.46	12, 71

