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# Macroevolutionary convergence connects morphological form to ecological function in birds

Alex L. Pigot<sup>1,2,13\*</sup>, Catherine Sheard<sup>2,3,13</sup>, Eliot T. Miller<sup>4,5</sup>, Tom P. Bregman<sup>2,6</sup>, Benjamin G. Freeman<sup>7</sup>, Uri Roll<sup>2,8</sup>, Nathalie Seddon<sup>2</sup>, Christopher H. Trisos<sup>2,9</sup>, Brian C. Weeks<sup>10,11</sup> and Joseph A. Tobias<sup>2,12\*</sup>

<sup>1</sup>Centre for Biodiversity and Environment Research, Department of Genetics, Evolution and Environment, University College London, London, UK.

<sup>2</sup>Department of Zoology, University of Oxford, Oxford, UK. <sup>3</sup>School of Biology, University of St Andrews, St Andrews, UK. <sup>4</sup>Cornell Lab of Ornithology, Ithaca, NY, USA. <sup>5</sup>Department of Biological Sciences, University of Idaho, Moscow, ID, USA. <sup>6</sup>Future-Fit Foundation, London, UK. <sup>7</sup>Biodiversity Research Centre, University of British Columbia, Vancouver, British Columbia, Canada. <sup>8</sup>Mitrani Department of Desert Ecology, Jacob Balaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Beer-Sheva, Israel. <sup>9</sup>African Climate and Development Initiative, University of Cape Town, Cape Town, South Africa. <sup>10</sup>School for Environment and Sustainability, University of Michigan, Ann Arbor, MI, USA. <sup>11</sup>Department of Ornithology, American Museum of Natural History, New York, NY, USA. <sup>12</sup>Department of Life Sciences, Imperial College London Silwood Park, Ascot, UK. <sup>13</sup>These authors contributed equally: Alex L. Pigot, Catherine Sheard. \*e-mail: [a.pigot@ucl.ac.uk](mailto:a.pigot@ucl.ac.uk); [j.tobias@imperial.ac.uk](mailto:j.tobias@imperial.ac.uk)

# SUPPLEMENTARY INFORMATION

1. Supplementary Methods
2. Supplementary Tables (1-4)
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As separate Excel files:

Supplementary Database 1: Species morphological PC scores and ecological niche assignments ( $n = 9963$  species).

Supplementary Database 2: Phenotypically matched family pairs ( $n = 91$  pairs), along with their diet, divergence time, geographic and foraging niche overlap.

# 1. Supplementary Methods

## Quantifying intra-specific trait variation and measurer effects

Substantial intra-specific variation in traits could invalidate analyses based on species mean trait values<sup>1</sup>. To examine whether this is an issue in our dataset, for each individual trait we fitted a linear mixed effects model across all individuals ( $n = 52,870$ ), including species as a random effect. We found that most of the variance in traits occurs across (98.25%) rather than within (1.75%) species, justifying the use of species mean values.

Our dataset contains measurements compiled by 93 researchers. Most contributors generated data from a wide range of taxonomic or ecological groups of species, but in some cases there was clustering of measurements with particular researchers focussing on specific groups of taxa. Although all measurers followed a set of strictly standardised measurement procedures, it is important to consider the potential influence of measurer effects. To address this issue, we collected replicate measurements of the same individual specimen for 2752 specimens across 2523 species. Each specimen was measured by two different measurers, involving a total of 35 different measurers. For each trait, we conducted a linear mixed effects model including species, individual and measurer identity as nested random effects. The % of total variance attributable to measurer was minor, varying from 0.19% (wing length) to 1.39% (beak width) (mean = 0.74%, Extended Data Fig. 2). Given the overwhelming dominance of interspecific differences in explaining trait variation in our dataset we do not include additional corrections for measurer identity. Linear mixed effects models were fitted in the R package lme4<sup>2</sup>.

## 2. Supplementary Tables

**Supplementary Table 1.** Description of species traits and % of variance attributed to intraspecific differences (from a variance components analysis).

Trait (mm)	Description	% variance within species
Beak length (tip-to-nares)	Distance from the anterior edge of the nostrils to the tip	1.39
Beak length (culmen)	Distance along the culmen from the base of the beak to the tip	1.71
Beak width	Width of beak at the anterior edge of the nostrils	2.49
Beak depth	Vertical height of beak at the anterior edge of nostrils	1.62
Tarsus length	Distance from the middle of the rear ankle joint, i.e. the notch between the tibia and tarsus, to the end of the last scale of the acrotarsium	1.71
Wing length (mm)	Distance between the carpal joint to wing tip	0.72
Secondary length (mm)	Distance between the carpal joint to the tip of the first secondary feather	1.33
Tail length (mm)	Distance from the tip of the longest rectrix to the point at which the two central rectrices protrude from the skin	2.99
Body mass (g)	Mass	NA

Estimates of intraspecific variation are not available for body mass.

**Supplementary Table 2.** Trait loadings for beak space and % of variance accounted for by each principal component axis ( $n = 9963$  species).

Trait	PC1	PC2	PC3	PC4
Beak length (culmen)	0.46	0.47	-0.01	-0.75
Beak length (tip-to-nares)	0.52	0.55	0.02	0.66
Beak width	0.47	-0.46	0.76	-0.01
Beak depth	0.55	-0.52	-0.65	0.02
Variance %	84.2	13.0	1.7	1.1
Cumulative variance	84.2	97.2	98.9	100

**Supplementary Table 3.** Trait loadings for phenotype space and % of variance accounted for by each principal component axis ( $n = 9963$  species).

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9
Beak length (culmen)	0.22	-0.42	0.30	-0.26	0.08	-0.10	0.07	0.01	0.77
Beak length (tip-to-nares)	0.23	-0.67	0.23	-0.26	0.05	0.08	-0.04	0.06	-0.60
Beak width	0.23	-0.26	-0.37	0.41	0.01	0.06	0.75	-0.11	0.01
Beak depth	0.28	-0.29	-0.39	0.47	0.13	-0.05	-0.65	-0.06	0.11
Tarsus length	0.23	0.26	0.13	-0.06	0.86	0.00	0.06	-0.34	-0.09
Wing length	0.26	0.10	-0.15	-0.28	-0.30	0.66	-0.10	-0.53	0.07
Tail length	0.21	0.07	-0.58	-0.56	-0.06	-0.54	0.02	-0.07	-0.06
Secondary length	0.25	0.14	-0.26	-0.18	0.22	0.44	0.02	0.76	0.07
Body mass	0.74	0.34	0.36	0.19	-0.31	-0.23	0.00	0.10	-0.10
Variance %	83	6.1	3.8	3.2	2.1	0.8	0.5	0.3	0.2
Cumulative variance	83	89.2	93	96.2	98.3	99.1	99.6	99.9	100

**Supplementary Table 4.** Description of foraging niches within specialist trophic niches.

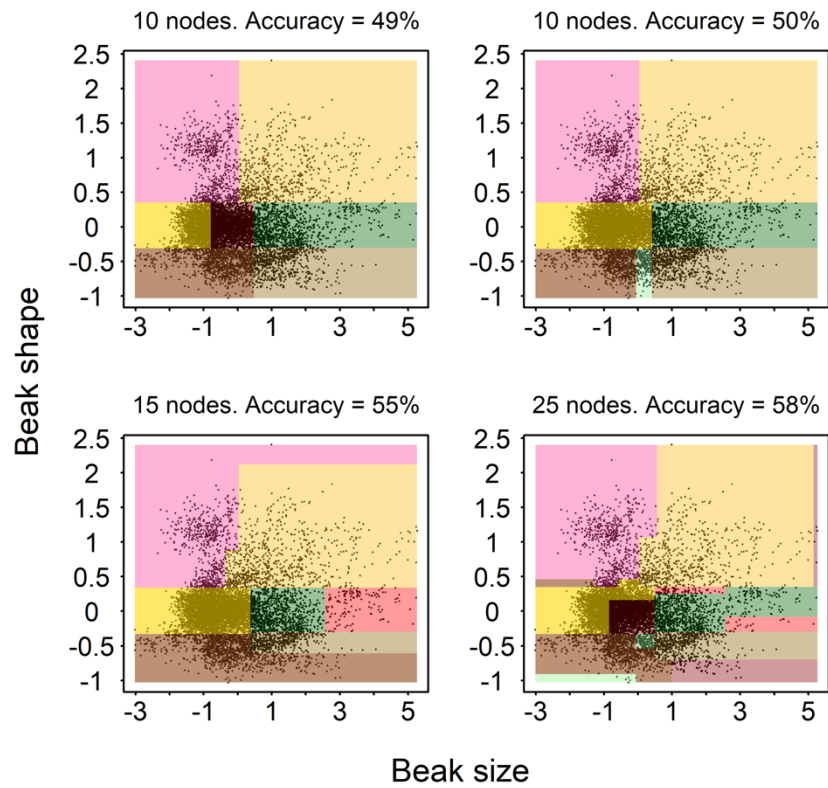
<b>Scavenger</b> ( <i>n</i> = 22)	<b>Scavenger Ground</b> ( <i>n</i> = 22) – species eating carrion (dead animal or fish remains) on the ground (e.g. vultures).
<b>Invertivore</b> ( <i>n</i> = 4765)	<b>Invertivore Aerial</b> ( <i>n</i> = 278) – species capturing flying invertebrates on the wing (e.g. swallows, swifts). Often described as ‘screening’ or ‘hawking’. In contrast to ‘ <b>Invertivore Sally air</b> ’, characterized by continuous and extended flight with multiple items captured before landing.
	<b>Invertivore Sally air</b> ( <i>n</i> = 317) – species capturing flying invertebrates in mid-air, with the attack starting from a perch (i.e. branch, rock, fence post, telegraph wire, etc.) and then returning to a perch (e.g. jacamars, kingbirds, etc). ‘Hawking’ will sometimes refer to this category, but the key distinguishing feature is that only a single prey item is captured before returning to a perch.
	<b>Invertivore Sally surface</b> ( <i>n</i> = 343) – species capturing invertebrates (including arachnids, worms, molluscs, etc.) attached to the substrate (e.g. leaves, twigs, branches, rock faces, etc) following an aerial attack manoeuvre (e.g. flight, pounce, jump, hover).
	<b>Invertivore Sally ground</b> ( <i>n</i> = 245) – species capturing invertebrates on the ground following an aerial attack manoeuvre (e.g. flying, gliding, dropping or pouncing) (e.g. chats, shrikes, kiskadee etc). The aerial manoeuvre may be followed by brief hopping toward prey (e.g. terns).
	<b>Invertivore Glean arboreal</b> ( <i>n</i> = 1792) – species capturing invertebrates attached to the substrate (e.g. leaves, twigs, branches, grass, bamboo, stems, hanging dead-leaves [not dead leaves on the ground] etc). No aerial attack manoeuvre is involved.
	<b>Invertivore Bark</b> ( <i>n</i> = 339) – species capturing invertebrates attached to or concealed within large branches and trunks of trees (e.g. woodpeckers, treecreepers, woodcreepers, wallcreepers, nuthatches, sittelas, nuthatches, vangas, etc., including honeyguides). This is distinguished from ‘ <b>Invertivore Glean arboreal</b> ’ by at least one criterion. First, the species employs specialized methods for moving over surfaces which are often, but not always vertical, vertical and too large to be gripped by the closed foot (including creeping, climbing or scaling). Second, the species extracts prey from in/under the bark using specialized methods (including hammering, probing or chiselling). Also includes species capturing insects from rock and cliff-faces (though not just on boulders), habitually perching on or clinging to large mammals and species that feed on honey and beeswax.
	<b>Invertivore Ground</b> ( <i>n</i> = 1026) – species capturing invertebrates on the ground. In contrast to ‘ <b>Invertivore Sally ground</b> ’, the search and attack manoeuvres take place on the ground (e.g. thrushes). This includes species standing on the ground and gleaning insects from vegetation (e.g. tinamous or larks) but excludes species that jump or sally upwards to capture prey from vegetation (‘ <b>Invertivore Sally surface</b> ’) or the air (‘ <b>Invertivore Sally air</b> ’). The ground is dry and thus excludes aquatic habitats (e.g. beaches, estuaries, wetlands, marshes [‘ <b>Aquatic predator Ground</b> ’]).
<b>Aquatic predator</b> ( <i>n</i> = 757)	<b>Aquatic predator Ground</b> ( <i>n</i> = 314) – species capturing invertebrates or vertebrates while standing in aquatic habitats (including beaches, estuaries, wetlands and marshes) (e.g. storks, herons, shorebirds). Prey may be captured on the ground or on/under water. This category includes species capturing aquatic prey (e.g. fish) or terrestrial prey in aquatic habitats (e.g. grasshopper).
	<b>Aquatic predator Perch</b> ( <i>n</i> = 44) – species capturing invertebrates or vertebrates on/under water following a direct attack flight from a perch (e.g. kingfisher).
	<b>Aquatic predator Aerial</b> ( <i>n</i> = 87) – species capturing invertebrates or vertebrates on/under water during continuous flight (including dipping, hovering, pattering, snatching). In contrast to ‘ <b>Aquatic predator Perch</b> ’, prey item is identified while flying (not from perch). The predators body may partially submerge but does not plunge beneath the surface (see ‘ <b>Aquatic predator Plunge</b> ’). Includes kleptoparasitic species capturing fish by chasing other piscivores and forcing them to regurgitate (e.g. skuas, frigatebirds).
	<b>Aquatic predator Plunge</b> ( <i>n</i> = 59) – species capturing invertebrates or vertebrates by plunging under water following continuous flight. The predators body submerges entirely beneath the surface, with the prey captured either by the momentum of the plunge or following propelled swimming.

	<b>Aquatic predator Surface</b> ( $n = 73$ ) – species capturing invertebrates or vertebrates on/under water whilst swimming on the water surface. In contrast to ‘ <b>Aquatic predator Perch</b> ’ or ‘ <b>Aquatic predator Aerial</b> ’ there is no direct attack flight. The species may dip under the water but, in contrast to ‘ <b>Aquatic predator Dive</b> ’, contact with the surface is maintained.
	<b>Aquatic predator Dive</b> ( $n = 134$ ) – species capturing invertebrates or vertebrates under water by diving from the surface (not the air, see ‘ <b>Aquatic predator Perch</b> ’ and ‘ <b>Aquatic predator Plunge</b> ’).
<b>Vertivore</b> ( $n = 311$ )	<b>Vertivore Aerial</b> ( $n = 20$ ) – species captures vertebrate prey during flight. Both predator and prey are in flight (e.g. peregrine, hobby, falcon)
	<b>Vertivore Air to surface</b> ( $n = 54$ ) – species captures prey on branches or the ground by diving from the air, usually after circling or hovering in flight. Includes quartering flight (e.g. kestrels, kites, some owls).
	<b>Vertivore Perch</b> ( $n = 190$ ) – species captures prey on branches or the ground by diving from a perch (e.g. many owls, eagles).
	<b>Vertivore Ground</b> ( $n = 6$ ) – species capturing prey on the ground, including eggs in ground nests, while they themselves are also walking or running on the ground (e.g. secretary bird, seriemas, ground hornbills).
	<b>Vertivore Arboreal</b> ( $n = 6$ ) – species capturing prey from foliage, branches, epiphytes, cavities, bark or other arboreal substrate while perched on the substrate. There is no flight attack involved. This includes eating bird chicks from arboreal nests and drinking blood while perched on mammals (e.g. oxpeckers).
<b>Nectarivore</b> ( $n = 507$ )	<b>Nectarivore Hover</b> ( $n = 318$ ) – species feeding on nectar or other plant exudates (e.g. sap) while in flight (e.g. hummingbirds).
	<b>Nectarivore Glean</b> ( $n = 184$ ) – species feeding on nectar or other plant exudates (e.g. sap) while perched, including nectar predators that pierce corollas (e.g. sunbirds, flowerpiercers). Species feeding on honey (e.g. honeyguides) included under ‘ <b>Invertivore Bark</b> ’.
<b>Granivore</b> ( $n = 662$ )	<b>Granivore Arboreal</b> ( $n = 185$ ) – species foraging on seeds, grains and nuts taken from vegetation (e.g. trees, grass stems) while perched (e.g. seedeaters, finches).
	<b>Granivore Ground</b> ( $n = 408$ ) – species foraging on fallen seeds, grains and nuts collected from the ground (e.g. partridges, pheasants, finches).
<b>Herbivore terrestrial</b> ( $n = 93$ )	<b>Herbivore (T) Arboreal</b> ( $n = 13$ ) – species foraging on leaves, buds, blossom, or other vegetation (except fruit, seeds and nectar). The food is taken from above ground, generally while the species is perching on branches or other stems. Generally, a small part of diet, except for the hoatzin, plantcutters.
	<b>Herbivore (T) Ground</b> ( $n = 73$ ) – species foraging on grass, leaves, buds, blossom, or other vegetation (not fruit or seeds) taken while the species is on the ground (e.g. geese). The vegetation may itself be off the ground.
<b>Herbivore aquatic</b> ( $n = 82$ )	<b>Herbivore (A) ground</b> ( $n = 9$ ) – species foraging on aquatic vegetation (including seeds) either below or above the water surface (algae, pondweed, waterside vegetation). The species collects vegetation while under water, sitting on the water surface or wading.
	<b>Herbivore (A) surface</b> ( $n = 47$ ) – species foraging on aquatic vegetation (including seeds) on/under water whilst swimming on the water surface. The species may dip under the water but, in contrast to ‘ <b>Herbivore (A) dive</b> ’, contact with the surface is maintained.
	<b>Herbivore (A) dive</b> ( $n = 13$ ) – species foraging on aquatic vegetation (including seeds) under water by diving from the surface.
<b>Frugivore</b> ( $n = 1030$ )	<b>Frugivore Aerial</b> ( $n = 88$ ) – species foraging on fruits in flight, including those that hover to pluck fruit from bushes and trees (e.g. oilbird, some manakins).
	<b>Frugivore Glean</b> ( $n = 894$ ) – species foraging on fruits while perched (not in flight) above ground and plucking fruits from vegetation (e.g. toucans, hornbills).
	<b>Frugivore Ground</b> ( $n = 20$ ) – species foraging on fruits lying on the ground (e.g. trumpeters).

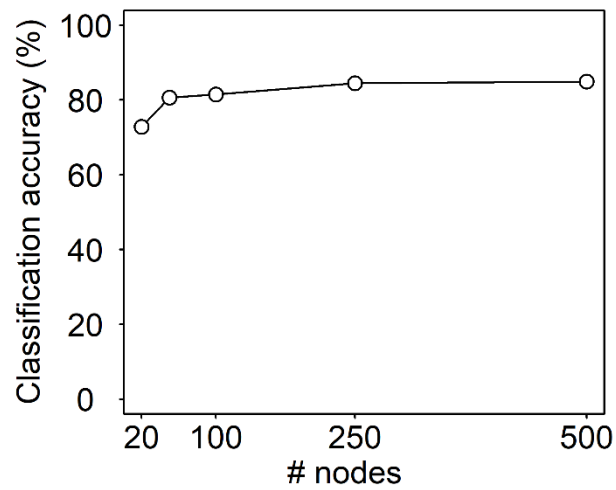
$n$  = number of species within each specialist trophic and foraging niche. The number of species within a trophic niche is generally greater than the sum of the constituent foraging niches because some species ( $n = 628$ ) use multiple foraging manoeuvres and substrates in relatively equal proportions and are classed as foraging generalists.



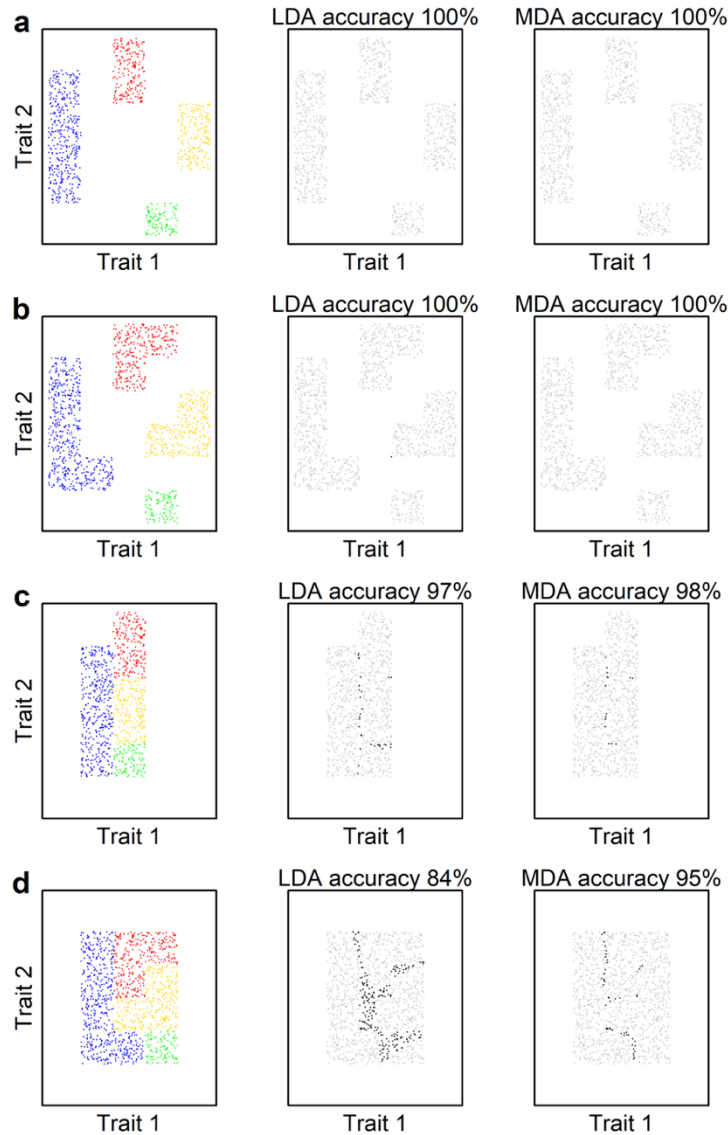
### 3. Supplementary Figures



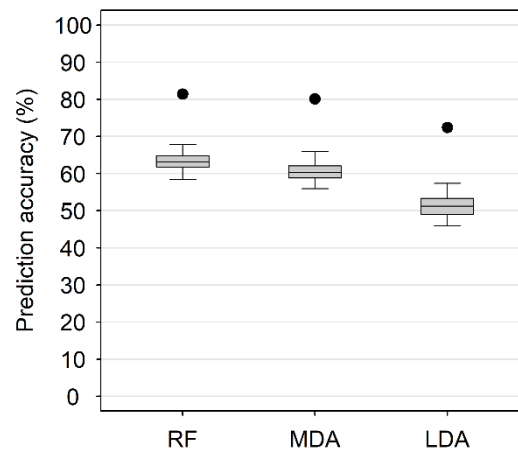
**Supplementary Figure 1. Examples of the partitioning of morphospace into distinct hypervolumes corresponding to different trophic niches.** Each plot shows the result a single decision tree randomly selected from a Random Forest model using the first two dimensions of beak morphospace. The random selection of trait axes at each node in the tree leads to stochastic variation across trees in how morphospace is partitioned (i.e. no single tree represents an optimal partitioning of morphospace) (a-b). Increasing the number of terminal nodes in the tree allows for more irregularly shaped hypervolumes, increasing the predictive accuracy of the decision tree (c-d).



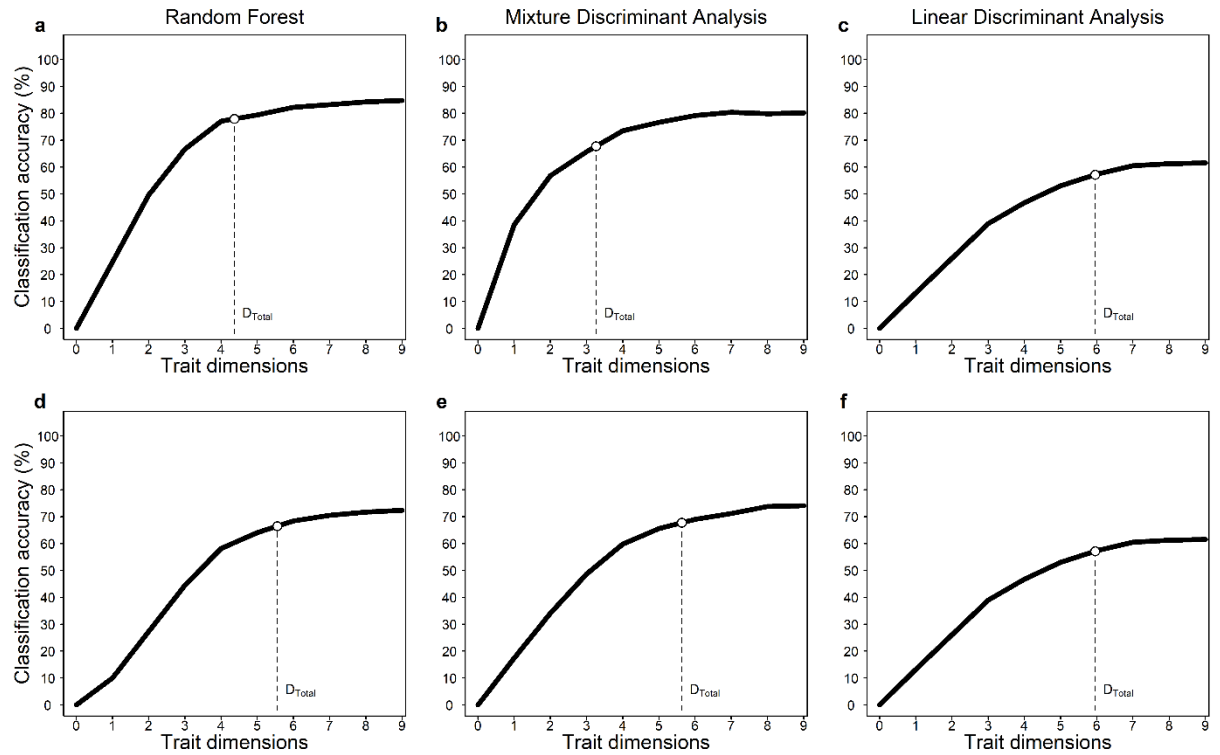
**Supplementary Figure 2. Predictive accuracy of Random Forest models.** Data show classification accuracy (%) of RF models predicting specialist trophic niches ( $n = 9$ ) of all birds ( $n = 9,963$  species) as a function of the maximum number of terminal nodes per decision tree. Allowing the growth of larger decision trees increases predictive accuracy by allowing more irregularly shaped niches (see **Supplementary Figure 1**). However, predictive accuracy remains high even when tree growth is strongly constrained (e.g. 73% with 20 terminal nodes).



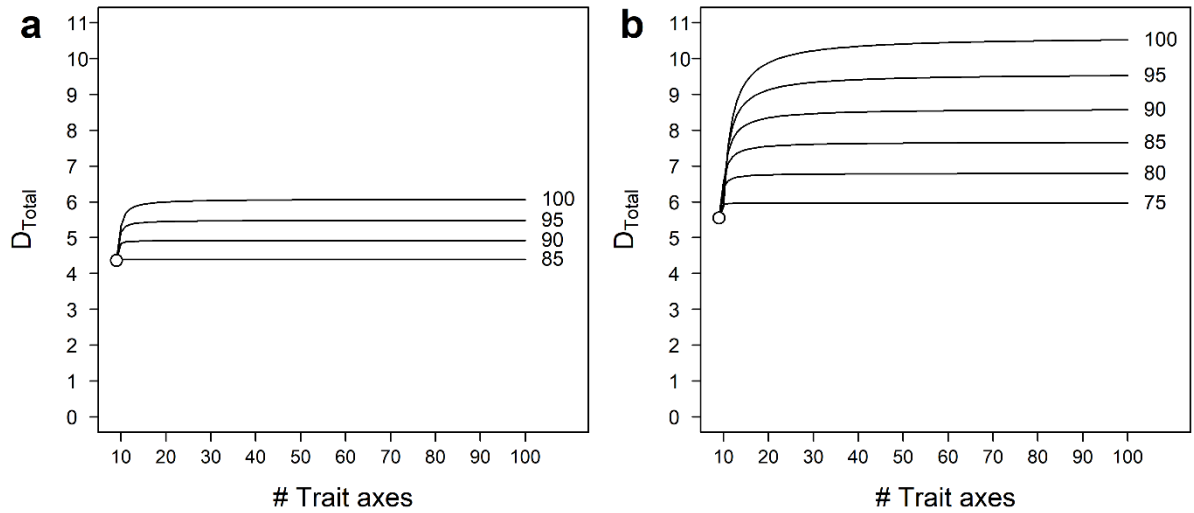
**Supplementary Figure 3. Effects of niche shape on the predictive accuracy of Linear (LDA) and Mixture Discriminant Analysis (MDA).** Four hypothetical morphospaces are shown in which different niches (colours) occur either as (a,b) isolated clusters or (c,d) interlocking tiles, and where niches have (a,c) regular or (b,d) irregular shapes. In all cases, there is no overlap in species niches, leading to a perfect association between morphology and ecology. Left column shows the distribution of niches in morphospace; centre and right-hand columns show the location of species with niches correctly (grey) or incorrectly (black) predicted according to LDA and MDA, respectively. **a-b**, when niches occupy isolated clusters, LDA and MDA predictive accuracy is 100%. **c**, when niches abut in morphospace some species are misclassified. **d**, when niches abut and have irregular shapes, species around the boundaries of each niche are misclassified leading to a reduction in predictive accuracy (LDA = 84% accuracy; MDA = 95% accuracy). In all scenarios, predictive accuracy of a Random Forest model is 100%.



**Supplementary Figure 4. The expected match between avian traits and trophic niches arising from shared phylogenetic history.** Boxplots show the predictive accuracy of three alternative classification algorithms— Random Forest (RF), Mixture Discriminant Analysis (MDA), and Linear Discriminant Analysis (LDA)—used to estimate trophic niches with the full nine-dimensional morphospace (points) for  $n = 6,666$  species with both morphological and genetic data. In each case, overall classification accuracy exceeds that expected under the evolutionary null model (box and whiskers show 50% interquartile range and 95% confidence interval). The null model incorporates a multi-rate process of Brownian trait evolution whereby rates of evolution can vary both across lineages and over time.



**Supplementary Figure 5. Estimating dimensionality of avian niche space using alternative classification algorithms** Random Forest (a,d), Mixture Discriminant Analysis (b,e) and Linear Discriminant Analysis (c,f). Accuracy curves indicate the cumulative maximum predictability of (a-c) trophic and (d-f) foraging niches in morphospaces consisting of different numbers of trait dimensions. Points indicate the dimensionality of niche space ( $D_{Total}$ ) according to Levene's index.



**Supplementary Figure 6. Estimated total dimensionality ( $D_{Total}$ ) of morphospace is robust to the inclusion of additional hypothetical trait axes.** Results are shown for (a) specialist trophic niches and (b) foraging niches. In addition to the nine measured traits, we simulated the effects of including additional hypothetical trait axes, up to a total of 100 axes. We assume that each additional trait axis has an equal contribution in accounting for the variation in niches currently unexplained by our empirical nine-dimensional morphospace. This assumption is conservative, because any variation in the relative contribution of these additional trait axes would lead to smaller increases in  $D_{Total}$  than estimated here. Thus, our simulations are best interpreted as providing an upper bound on  $D_{Total}$  from measuring additional trait axes.  $D_{Total}$  also depends on the assumption of whether these additional trait axes would enable ecological niches to be predicted with complete accuracy (i.e. 100%) or whether some variation in niches is inherently unpredictable. Assuming lower levels of maximum predictive accuracy (e.g. 85%) leads to less sensitivity in estimates of  $D_{Total}$  to variation in the number of trait axes.

## 4. Supplementary Acknowledgements

We thank Chris Cooney, Ally Phillimore, and Gavin Thomas for discussion and technical support. For access to museum specimens and help with logistics, we thank Hein van Grouw, Mark Adams, and Robert Prys-Jones (Natural History Museum, Tring, UK), Lydia Garetano, Kaiya Provost and Paul Sweet (American Museum of Natural History), David Allan and Mmatjie Mashao (Durban Natural Science Museum, Durban, South Africa), Guilherme Brito (Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil), Marcus Chua (Lee Kong Chian Natural History Museum, National University of Singapore, Singapore), Santiago Claramunt (Royal Ontario Museum, Canada), Mario Cohn-Haft (Instituto Nacional de Pesquisas da Amazônia, Manaus), Clem Fisher (Liverpool Museum), Jon Fjeldsa and Carsten Rahbek (Zoological Museum, University of Copenhagen, Denmark), Sylke Frahnert (Museum of Natural History, Berlin, Germany), Jerome Fuchs (Muséum National d'Histoire Naturelle, Paris, France), Natalia Garcia (Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina), Isabel Gomez (Coleccion Boliviana de Fauna, Museo Nacional de Historia Natural, La Paz, Bolivia), Juan Carlos Gonzalez (University of the Philippines Los Banos, Museum of Natural History, Los Banos, Philippines), Peter Hosner (National Museum of Natural History, Smithsonian Institution, Washington, USA), Ron Johnstone (Western Australian Museum, Welshpool, Australia), René Marie Lafontaine (Royal Belgian Institute of Natural Sciences, Brussels, Belgium), John McCormack and James Maley (Moore Laboratory of Zoology, Occidental College, Los Angeles, California, USA), Luciano Naka and Victor Leandro (Federal University of Pernambuco, Recife, Brazil), Peter Njoroge (National Museums of Kenya, Nairobi), He Peng (National Zoological Museum of China, Institute of Zoology, Chinese Academy of Sciences), Matt Rayner (Auckland War Memorial Museum, Auckland, New Zealand), Van Remsen, Vivien Chua and Oscar Johnson (Louisiana State University), Gary Stiles (Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia), Brian Schmidt (Smithsonian Museum of Natural History, USA), Paul Schofield (Canterbury Museum, Christchurch, New Zealand), Luis Fabio Silveiro (Museu de Zoologia da Universidade de Sao Paulo, Sao Paulo, Brazil), Ildiko Szabo (Beatty Biodiversity Museum, Vancouver, Canada), Till Topfer (Research Museum Alexander Koenig, Bonn, Germany), Jeremiah Trimble (Harvard Museum of Comparative Zoology), Rolly Urriza (Philippine National Museum, Manila, Philippines), Thomas Valqui (Centro de Ornitología y Biodiversidad, Lima, Peru), David Willard, Ben Marks and Bobby Lauer (Field Museum of Natural History, Chicago, USA), and Kristof Zyskowski (Yale Peabody Museum). For help with data collection and management, we thank Nico Alioravainen, Sebastián Aveldaño, Phil Birget, Matheus Bitencourt, Rauri Bowie, Maritza Cabrera, M.P. Camelo, Monica Lynn Carlson, Phil Chapman, Dominic Chesire, Nigel Collar, Eden Cottee-Jones, Ross Crates, Ben Daly, Bianca Darski, Elizabeth Derryberry, K. Eldridge, Lincoln Fishpool, Michaela Forthuber, Juan Carlos Gonzalez, Ada Grabowska-Zhang, Michael Harvey, Jeffrey Tyler Howard, Gabriel Jamie, Sam Jones, Maura Jurado, Robert Lauer, Tom Lawrence, Bicheng Li, Hevana Lima, Maria Livrand, Rosalbina Butron Loayza, Yingqiang Lou, Hannah MacGregor, James Maley, Tom Matthews, Rebekah Mayhew, Jay McEntee, Camilla Meneses, Edson Mlamba, Delaney Morrow, Monte Neate-Clegg, Martin Paeckert, Tony Parker, Faansie Peacock, He Peng, Henry Pollack, Robert Pople, Frank Rheindt, Steve Rogers, Sarah Rosenberg-Wohl, Abigail Rothrauff, Sonia Salazar, Celeste Santos, Henrike Schulte to Bühne, Lankani Somarathna, Nicolas Soulages, Cassie Stoddard, Daniel Swindlehurst, Till Topfer, Natasha Turner, Claire Vincent, Junfu Wang and Yoshika Willis. Additional sources of funding were provided by the Oxford Martin School and Royal Society (NS); National Science Foundation Postdoctoral Fellowship in Biology (No. 1523695) (BF); National Science Foundation (1402506) and Edward Rose (Cornell Lab of Ornithology) postdoctoral

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[http://www.clker.com/cliparts/f/7/9/a/11949848182045168189eagle\\_01.svg.med.png](http://www.clker.com/cliparts/f/7/9/a/11949848182045168189eagle_01.svg.med.png)  
<http://phylopic.org/image/05cd7d8c-6b2c-4b97-b7b8-053559019eeb/>



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