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The influence of wing morphology upon the dispersal, geographical distributions and diversification of the Corvides (Aves; Passeriformes)

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New species are sometimes known to arise as a consequence of the dispersal and establishment of populations in new areas. It has nevertheless been difficult to demonstrate an empirical link between rates of dispersal and diversification, partly because dispersal abilities are challenging to quantify. Here, using wing morphology as a proxy for dispersal ability, we assess this relationship among the global radiation of corvoid birds. We found that species distributions are associated with wing shape. Widespread species (occurring on both islands and continents), and those that are migratory, exhibit wing morphologies better adapted to long-distance flight compared with sedentary continental or insular forms. Habitat preferences also strongly predict wing form, with species that occur in canopies and/or areas of sparse vegetation possessing dispersive morphologies. By contrast, we found no significant differences in diversification rates among either the migratory or habitat classifications, but species distributed in island settings diversify at higher rates than those found on continents. This latter finding may reflect the elevated dispersal capabilities of widespread taxa, facilitating the radiation of these lineages across insular areas. However, as the correlations between wing morphology and diversification rates were consistently weak throughout our dataset, this suggests that historical patterns of diversification are not particularly well reflected by present-day wing morphology.

1. Introduction

The importance of dispersal in the formation of new species remains an unresolved question. Despite the need for populations to become geographically isolated from one another in the most common modes of speciation [1–4], the level of dispersal that maximizes rates of geographical isolation and ultimately diversification is unclear. While high dispersal capabilities may enhance the likelihood of colonizing new areas and the rate at which lineages become geographically isolated from one another [5], they may also facilitate continued gene flow among populations, inhibiting genetic differentiation and the accumulation of reproductive isolation [1,6–9]. Conversely, while low dispersal capabilities reduce the rate at which lineages colonize new areas, they may also limit gene flow between disconnected populations, facilitating their reproductive isolation [5]. Any empirical assessment of these relationships requires an explicit quantification of dispersal abilities; however, these are notoriously difficult to attain [8]. In this paper, we evaluate how a morphological proxy for flight performance (wing aspect ratio) correlates with long-distance seasonal movement, island presence, habitat preferences and lineage diversification among a global radiation of passerine birds.

Dispersal abilities are highly variable across animal groups [10–12]. While some taxa have the capacity to move over thousands of kilometres [13], others

are restricted to geographical areas that are many orders of magnitude smaller, likely reflecting their more limited potential for dispersal [5,11–12,14]. This heterogeneity in lineage dispersal ability has been suggested to explain variation in diversification rates, although the results of previous studies provide contradictory evidence about the shape and directionality of this relationship [7–9,15–19]. An improved understanding not only requires consideration of the life-history and ecological factors that lead lineages to disperse and colonize new areas, but also how landmass connectivity has determined the extent to which populations become geographically isolated from one another as a result of these events. Here, we assess the importance of these influences upon rates of lineage diversification among a taxonomically diverse avian group, the Corvides (*sensu* Cracraft [20]).

The Corvides are a radiation of approximately 790 species of passerine birds that are suggested to have originated within an area of variable landmass connectivity at the edge of the Australasian plate [21,22]. From here, several lineages independently colonized and diversified upon the world's major continental landmasses [21,22], whereas others radiated extensively throughout the island archipelagoes of the Indo-Pacific [23,24]. Increased dispersal abilities have been proposed to reflect the evolution of particular life-history and/or morphological traits [21,25], facilitating some lineages to undergo repeated range expansions, and diversify for longer periods of time [26]. In this respect, both the evolution of migratory behaviour and/or habitat preferences are potentially important factors, given that they can affect the propensity for lineages to disperse and colonize new areas, population connectivity and ultimately speciation [19,25,27,28]. However, their influence upon the evolution of wing morphology, the geographical distribution of species and their rates of lineage diversification, remains to be established.

A major problem in determining the relationship between dispersal and diversification is that dispersal is difficult to explicitly quantify [29,30]. For this reason, morphological proxies are regularly used to indirectly estimate dispersal abilities [16,31]. In birds, long-distance flight performance has been shown to be related to wing shape. Species possessing wings with high aspect ratios (relatively longer primary feathers compared with the secondaries) have increased abilities to sustain powered flight over long distances, compared with those whose aspect ratios are low [32–37]. High wing aspect ratios reduce the economic cost of flight by increasing lift relative to drag [38–40], and have been shown to correlate with longer overwater dispersal distances [8], longer natal dispersal distances [41] and the capacity to undertake migration [33,34,37]. In two of the most broad-scale comparative analyses to date, Claramunt *et al.* [8] and Weeks & Claramunt [9] proposed that wing morphology influences the rate at which diversification occurs in both continental and insular areas as result of its direct impact upon dispersal abilities. Here, we extend the analytical approach of these studies to test the consistency of these relationships among a speciose radiation of passerine birds that is extensively distributed throughout insular and continental settings. To do this, we first assess if global differences in the geographical distribution of corvoid species are related to their wing aspect ratios. Subsequently, we test if variation in wing morphology and rates of lineage diversification can be attributed to the evolution of migratory behaviour, habitat use or the colonization of islands.

2. Material and methods

(a) Phylogenetic, character and spatial data

We obtained an estimate of the phylogenetic relationships among 789 species of the Corvides from Jønsson *et al.* [42], in which the species' limits correspond to those proposed by the IOC v. 2.7 [43]. The phylogeny was generated using sequence data from 665 species, and was calibrated using fossil and biogeographic information sampled across a broad temporal and taxonomic range. The remaining 124 species that had no sequence data available at the time of the tree generation were added as polytomies to the maximum clade credibility (MCC) tree of Jønsson *et al.* [42] using taxonomic information largely reflecting species placements in the *Handbook of the Birds of the World* [44]. The branch lengths subtending these species were inferred using the polytomy resolution method [45]. Owing to the limited variation in branch lengths and topology in the resulting pseudo-posterior distribution of phylogenies, the comparative analyses relating to the evolution of wing morphology were performed on an MCC tree derived from this distribution, after seven species for which wing measurements were unavailable were pruned out (see Jønsson *et al.* [42] for further information on the methods used to generate the phylogeny). The results from the comparative analyses (see below) on the complete phylogeny were in concordance with those in which the added species (those without DNA sequence data available) were excluded (see electronic supplementary material, figure S1 and appendix A). The complete species-level phylogeny used in these analyses can be downloaded from Dryad (http://dx.doi.org/10.5061/dryad.fd4m0).

Breeding range estimates for the 782 measured corvoid species were obtained from an expert-validated database [46], in which species presence was recorded at the $1° \times 1°$ scale. We followed the classifications proposed by Marki *et al.* [25] to determine the propensity for seasonal movement and the continental/island distribution of all species. We considered 80 species to undertake seasonal movement (generally more than 1000 km) between the breeding and wintering grounds, with the remaining 702 species determined to be sedentary. Species were classified as island dwelling if the islands upon which they occur were separated from continental areas by deep water bodies. In this respect, the tectonic origin of the island could be from either continental or oceanic plates. However, the separation of these areas from continents by deep water allows us to infer that their colonization probably involved overwater dispersal, rather than intermittent land bridges formed when sea levels were lower than at the present time. Species that occurred on both islands and continents were classified as widespread. In total, we considered 171 island species, 520 continental species and 91 widespread species. Finally, we also classified species based on habitat preferences following information from the *Handbook of the Birds of the World* [44]. All species were considered to be present in one of three habitat classes; open, dense or mixed. Our aim in these classifications was to broadly differentiate species by the foliage density in which they are commonly found, and whether or not they occur in interior forest ('dense' excluding predominantly canopy species), more open areas ('open'), or in a combination of both ('mixed'). The character states of all species are listed in electronic supplementary material, table S1.

(b) Morphological data and calculation of the hand wing index

The ability to sustain long-distance flight has been shown to correlate with a high aspect ratio of the wing [32,37], which we quantified among the Corvides using the hand wing index (herein HWI) proposed by Claramunt *et al.* [8]:

$$HWI = 100 \ x \left(\frac{WL - SL}{WL} \right).$$

Wing length (WL) was measured from the carpal joint of the wing to the tip of the longest primary feather. Secondary length (SL) was measured to the tip of the first secondary feather, also from the carpal joint (see fig. 2 of Claramunt et al. [8] for an illustration of both measures). P.Z.M. measured WL and SL on 4344 museum specimens of the Corvides, representing 99% (782/789) of the species present in our phylogenetic tree. We measured male specimens when possible, although in a few cases when these were poorly represented in the respective collections, we supplemented them with measurements from females. An average of 5.6 ± 1.2 specimens were measured per species. All measurements and corresponding museum voucher numbers are provided in electronic supplementary material, table S2.

(c) Spatial analyses

To assess geographical variation in the distribution of species that differ in their wing shape, we first ranked all species by their HWI values, before dividing our overall distributional database into quartiles. Species in the first quartile are those that have relatively more rounded wings (the longest primary and secondary feathers being similar in length), whereas species in the fourth quartile have wings that are longer, with more projected tips. We computed the species richness patterns of the four quartiles at the $1° \times 1°$ scale, and regressed the grid-cell richness of each HWI quartile against that of the overall Corvides using linear models. Subsequently, we examined the spatial pattern of the residuals, which allows us to infer geographical areas that have an over- or underrepresentation of species in the different HWI quartiles.

(d) Phylogenetic comparative analyses

We assessed differences in the diversification rates and values of the HWI between the migratory, island/continent and habitat classifications, using phylogenetic generalized least-squares regression and ANOVA (PGLSANOVA), implemented in the R package caper [47]. For the HWI values, we assessed the differences among all corvoid species and their predictor variables simultaneously. To determine variation in diversification rates among our predictor variables (insularity, habitat preferences and migratory behaviour), we follow a similar approach to that of Weeks & Claramunt [9]. First, we determined well supported monophyletic clades of more than one species (supported by posterior probability values greater than or equal to 0.95 in the phylogeny of Jønsson et al. [42]) in which all members share the same character state (for example, all species being present on islands). We then quantified the character states of these clades among the other predictor variables, before calculating the method of moments diversification rate estimator [48], which reflects log(number of species within a clade)/crown clade age (herein $\log(N)/T$). We then assessed (i) significant differences in diversification rates among all predictor variables and (ii) the relationships between diversification rates and mean HWI across clades. To determine the consistency of these results among the overall Corvides, we also estimated historical diversification rates among all species using two alternative methodologies; DR [49] and BAMM [50]. More detailed methodology and a description of the results using these approaches can be found in electronic supplementary material, appendix A.

3. Results

(a) Spatial variation in the hand wing index

The species richness patterns among the HWI quartiles generated from the overall dataset show high spatial heterogeneity, which varies greatly with latitude (figure 1). The residual patterns of the first and second HWI quartiles show that species that have relatively short and rounded wings are overrepresented in the tropics and underrepresented in temperate areas (figure S2). Conversely, the third quartile shows a slight tendency for species overrepresentation in temperate areas, which becomes much stronger in the fourth quartile (species with the longest and most projected wing tips; figure S2). These latter patterns highlight the northern areas of the Palaearctic and parts of the Oriental region to be overrepresented with species, and the tropics as underrepresented. Australia is further notable for having a greater number of fourth quartile species than predicted given the overall richness patterns (figure S2). Only species that have intermediate or high values of the HWI are present on the most remote islands of the Pacific (figure 1). Although these analyses control for variation in species richness among grid-cells, it should be noted that the absolute numbers of over- or underrepresented species are influenced by the underlying gradient in species diversity (electronic supplementary material, figure S3), which reflects the origins and heightened diversification of the group within the Indo-Pacific, followed by subsequent worldwide phylogenetic expansion [21].

(b) Comparisons of the hand wing index and diversification rates between the migratory, insular and habitat classifications

The HWI values among the 782 measured species are illustrated on the MCC tree in figure 2. The results from our PGLSANOVA show that HWI is significantly predicted by all variables (migratory behaviour, habitat and insularity; full model; $F = 56.1$, $R^2 = 0.29$, $p < 0.001$; electronic supplementary material, table S3). Considering the ability to undertake seasonal movement, we found that migratory species had significantly higher values of the HWI compared with those that were sedentary ($R^2 = 0.24$, $t = 7.5$, $p < 0.001$; figure 3). Differences in the HWI values were also recovered between the habitat classes, with the open and mixed habitat species having significantly higher values compared with those occurring in habitats with dense foliage ($R^2 = 0.06$, $t = 5.1$, $p < 0.001$; figure 3). However, when comparing the differences in $\log(N)/T$ among monophyletic clades of the migratory and habitat classifications, we found no significant differences among the character states (migratory behaviour; $R^2 = 0.01$, $t = 1.5$, $p = 0.29$; habitat; $R^2 = 0.05$, $t = 0.57$, $p = 0.13$; figure 3 and electronic supplementary material, tables S4 and S5).

With respect to the island/continental distributions, widespread taxa (species distributed on both continents and islands) have significantly higher HWI values relative to those found strictly on either continents or islands, which did not significantly differ from one another ($R^2 = 0.1$, $t = 5.9$, $p < 0.001$; figure 3). Insular and widespread species also had significantly higher values of net diversification in contrast with continental species ($R^2 = 0.2$, $p < 0.001$; figure 3 and electronic supplementary material, table S6). Differences in diversification rates estimated among all species using DR and BAMM support these findings (electronic supplementary material, appendix A). However, the relationships between HWI and diversification rates were weak throughout our analyses. We found no significant correlations when evaluating these relationships among the three different predictor variables (insularity: slope $= 0.05$, $R^2 = 0.02$, $p = 0.23$; habitat: slope $= -0.12$, $R^2 = 0.03$, $p = 0.15$; and migratory behaviour: slope $= 0.54$, $R^2 = 0.01$, $p = 0.29$; figure 3), or when assessing them throughout the radiation as a whole (electronic supplementary material, figure S4).
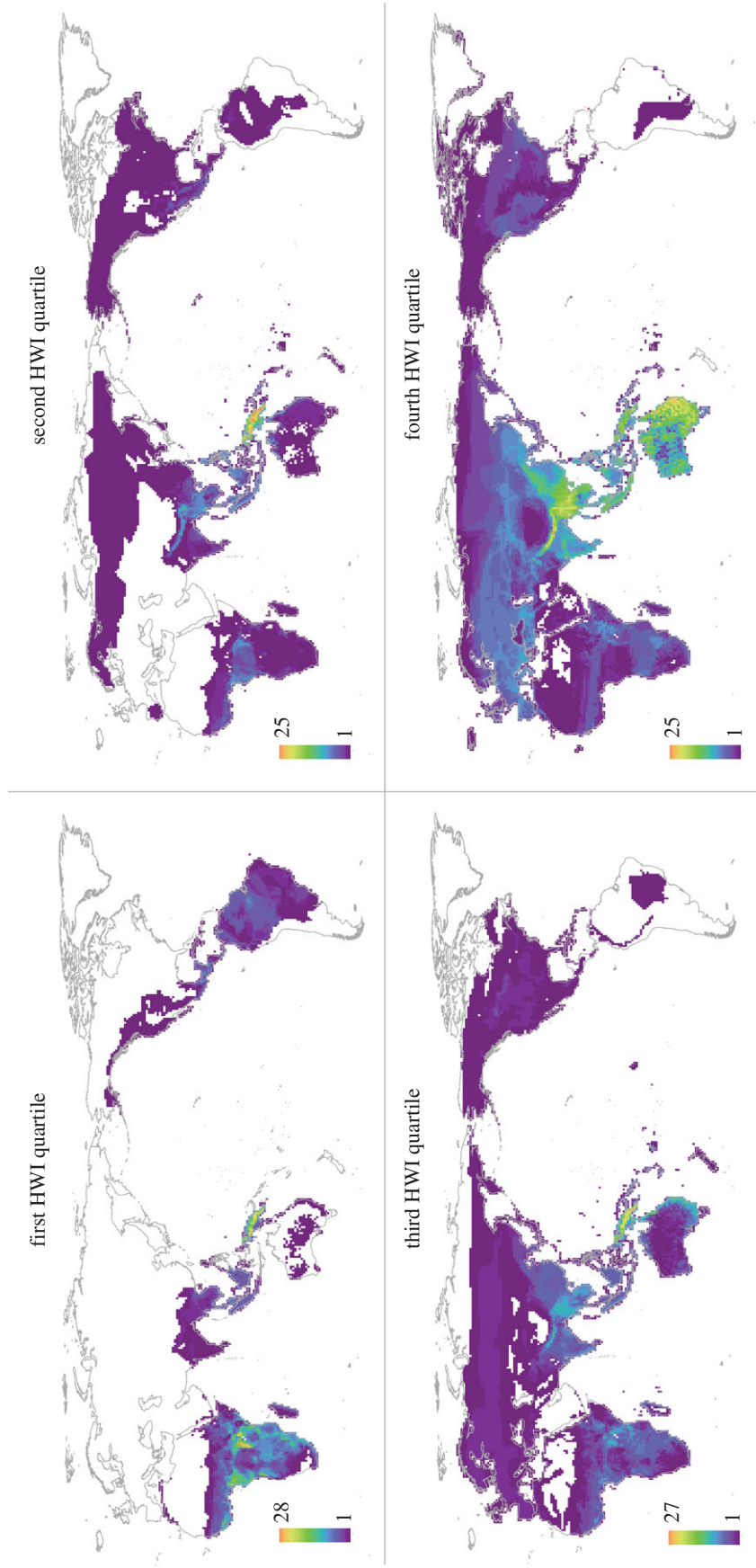
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Figure 1. Maps of species richness among 1° × 1° grid-cells for quartiles defined from ranks of all corvoid species based on their values of the HWI. The first quartile contains species with the lowest values of the HWI and represents those that have the shortest wings relative to their width, whereas the fourth quartile contains species with the highest values, which thus are those with the longest most projected wing tips.
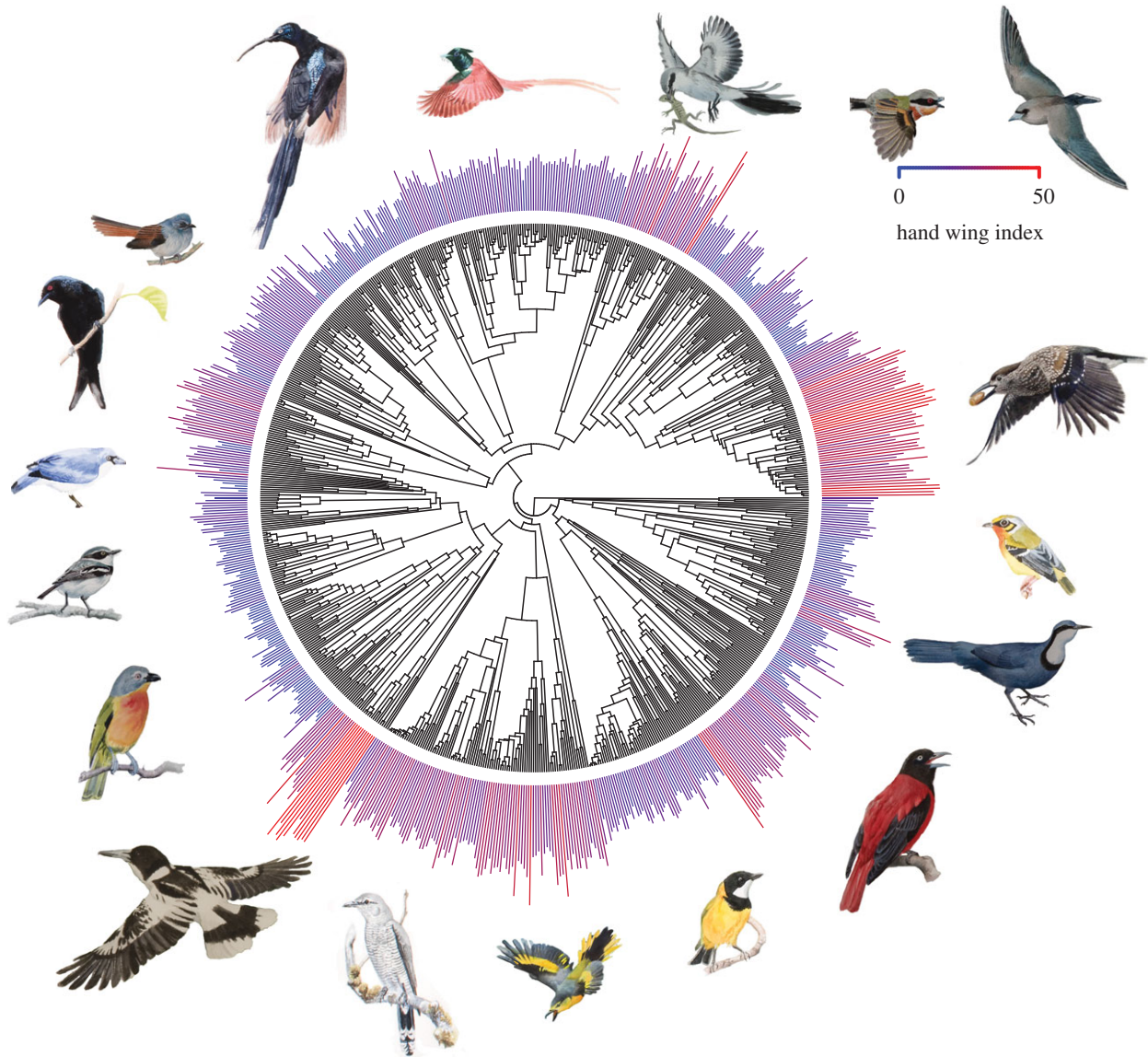
Figure 2. Maximum clade credibility tree illustrating values of the wing aspect ratio (HWI) for 782 species of the Corvides. Blue colours represent lower values of the HWI and red colours indicate higher values. The corresponding wing shapes are illustrated at either end of the scale bar (left: *Batis crypta*, right: *Artamus cyanopterus*). The species shown around the edge of the phylogeny represent members of the major clades found close to the respective tips. The species illustrated in a clockwise order from the top of the phylogeny are as follows: *Terpsiphone paradisi, Lanius sphenocercus, Nucifraga caryocatactes, Pteruthius xanthochlorus, Ptilorrhoa caerulescens, Oriolus traillii, Pachycephala pectoralis, Pericrocotus flammeus, Coracina fimbriata, Cracticus mentalis, Malaconotus cruentus, Batis soror, Cyanolanius madagascarinus, Dicrurus adsimilis, Rhipidura cyaniceps* and *Epimachus meyeri*. J.F. provided all illustrations.

4. Discussion

Animal groups are highly variable in their ability to disperse and establish in new locations [10,11]. In combination, these differences are predicted to influence the rate at which lineages diversify and the geographical distributions of species [5,8,9,15]. The results of this study confirm these latter predictions among a global radiation of passerine birds, the Corvides. Species that are migratory, found in more open habitats or are distributed in both insular and continental settings, possess wing morphologies adapted for sustaining flight over long distances (figure 3). Taxa distributed on islands also have high rates of lineage diversification (figure 3), suggesting that wing morphology could have been an important influence in determining the potential for colonization and diversification in new areas. However, despite large variation in the distribution of corvoid species with different wing morphologies (figures 1

and S2), we consistently recovered weak and non-significant correlations between aspect ratios and diversification rates (electronic supplementary material, figure S4). This suggests that the influence of wing morphology upon dispersal (and ultimately speciation) is complex, and that the evolution of wing shape is potentially determined by multiple ecological selection pressures.

(a) The evolution of wing morphology and its influence on the distribution of corvoid species

Mobility and the propensity for dispersal are important components of avian ecology. Among the vast majority of lineages, these abilities are determined by flight, with wing morphology proposed to determine the distance over which flight can be sustained [32,34,37,51], in addition to manoeuvrability [52]. Bird species that have wing morphologies
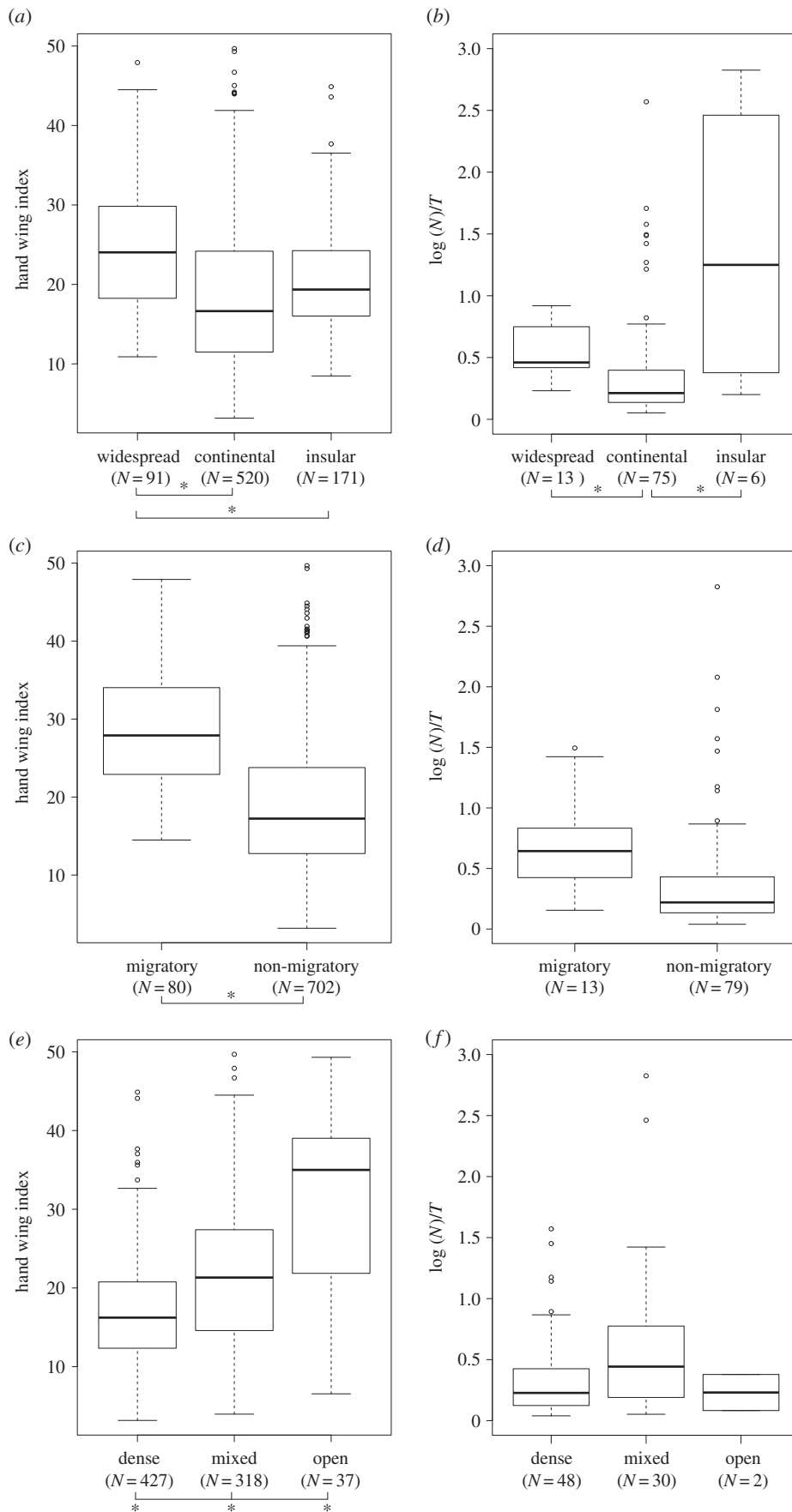
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Figure 3. Boxplots illustrating HWI (*a,c,e*) and log(*N*)/*T* (*b,d,f*) values among all species of the Corvides (*a,c,e*) and among monophyletic clades of the respective character states ((*b,d,f*), see §2 for further information about these definitions). Variation in these values are highlighted among taxa that are distributed on islands, continents or are widespread (present on both islands and continents), in (*a,b*). Here, islands are considered to be landmasses separated from continental areas by deep water bodies, and as such their colonization is likely to have involved overwater dispersal. Differences among species that undertake seasonal movement generally more than 1000 km from those that are more sedentary are highlighted in (*c,d*). Finally, differences among species found in open, dense or mixed habitat types are shown in (*e,f*). The numbers of species in the insular, continental, widespread, migratory, non-migratory, open habitat, dense habitat and mixed habitat classes are shown in parentheses. Asterisks highlight groups that have significantly different values of HWI or diversification rates.

adapted to undertake long-distance flight should theoretically have a greater potential to disperse to new and more remote areas, compared with those that do not. Our comparisons between the wing morphologies of migratory and sedentary species, and among those that occur in insular or continental settings, provide some evidence to support this idea (figure 3). However, in interpreting these results, it is necessary to consider that wing morphology is also important in other aspects of species ecology, including the capability to manoeuver and forage within the preferred habitat (figure 3), and therefore is likely to be subject to multiple selection pressures, some of which may be unrelated to dispersal ability.

Dispersal and radiation out of the ancestral Indo-Pacific region are known to have occurred among many independent corvoid lineages [21,22], including the colonization of distant continental land masses such as Africa and South America. However, species distributed in the tropical areas of these continents have some of the lowest values of the HWI (figures 1 and S2), implying that their current abilities for long-distance flight are limited. This finding is seemingly contradictory to the apparent need for long-distance dispersal events in order to have reached these areas. Many of these groups forage mainly inside forest of dense shrubbery (e.g. *Batis, Laniarius, Platysteira, Malaconotus, Hylophilus* and *Vireolanius*), having wing morphologies that facilitate manoeuvrability within dense vegetation [52,53]. Hence, habitat preferences (particularly those associated with dense foliage) exert selection pressures on wing morphology (figure 3) that may indirectly affect the capacity for lineages to disperse over long distances. While it is possible that the distribution of these species reflects that predominantly poor long-distance fliers can on rare occasions disperse and establish in remote locations, an alternative explanation is that evolutionary changes in wing morphology (mediating dispersal ability) have occurred throughout the history of these lineages [9]. This latter hypothesis seems particularly likely, given the finding that wing morphology can evolve over relatively short timescales in some avian groups (e.g. following establishment in island settings [54]).

Although some corvoid lineages dispersed to and diversified on continents, others radiated extensively throughout island archipelagoes [23,24]. By considering islands as landmasses separated from continental areas by deep water channels, we infer that their colonization required overwater dispersal, which in many instances must have been over long distances. We found that widespread species had significantly higher HWI values than species that were strictly confined to islands, or to continents (figure 3; electronic supplementary material, table S3). This suggests that flight abilities, influenced by wing morphology, have been important in facilitating the colonization of islands, particularly those that are distantly located from continental areas. It is notable that only species with intermediate to high HWI values have colonized the most remote islands of the Pacific (figure 1).

The differences in HWI values between widespread and insular species imply that evolutionary changes in wing shape occur following the differentiation of island taxa from widespread forms. Intraspecific comparisons of insular and continental populations support this hypothesis and illustrate that the wing shapes of island taxa become relatively shorter and rounder post colonization [5,55,56]. Selection for a reduction in flight ability among island taxa may reflect that long-distance flight is a physiologically costly behaviour [55,57], which is unnecessary on islands that contain an abundance of available

resources [54,58]. It is also possible that island species become 'psychologically' flightless [59], such that they are reluctant to fly over water, even if they maintain the morphological apparatus to do so (e.g. [60]). Conversely, the high HWI values of the widespread species suggest that these taxa may be in a phase of geographical expansion, with a high capacity for dispersal (as proposed by Mayr & Diamond [7]). These results do not, however, preclude that island colonization may also occur among taxa that have wing morphologies less suited for long-distance dispersal. For example, weak fliers may on rare occasions disperse to distant islands (e.g. [61]), and island colonization could also occur in the absence of active flight, being aided by favourable tail winds.

The evolution of migration is another factor that may influence the geographical distribution and potential for corvoid species to disperse over long distances. We found that migratory corvoid species have significantly more projected wing tips compared with sedentary forms (figure 3). These morphologies have been shown to be prevalent among many avian lineages that are migratory [32–35,37,51], enabling long-distance flight between the breeding and non-breeding areas, which is necessary as a consequence of the seasonal availability of resources on the breeding grounds [62]. This finding explains why species with higher HWI values are overrepresented in northern temperate regions (figure S2), given that the extension of breeding ranges to the north is conditioned by the ability of many of these birds to leave these regions during winter. However, migratory habitats alone are unable to completely explain the geographical patterns of species overrepresentation in the upper HWI quartiles. For example, the large number of high HWI species present in Australia are made up by representatives of three families (Artamidae, Campephagidae and Monarchidae). Although migratory strategies, or nomadism, have evolved in many of these lineages, they are also considered to be strong fliers as a consequence of their general adaptations for using long aerial sallies to capture their food [44], suggesting the additional importance of foraging mode as a selection pressure on wing morphology.

(b) The influence of wing morphology upon lineage diversification

While dispersal leading to range expansion is a key stage in both allopatric and parapatric modes of speciation [1,2], in this study, we find wing morphology (which is potentially related to dispersal ability) to be weakly correlated with rates of lineage diversification among the Corvides (electronic supplementary material, figure S4 and tables S4–S6). Although a weak correlation might reflect that the true relationship between dispersal and diversification is hump-shaped, rather than linear (the 'intermediate dispersal hypothesis'; see [2,7–9]), adding quadratic terms to these models did not improve the statistical fit to our data. More likely, these findings reflect that the relationship between diversification and current flight ability is confounded by evolutionary changes in wing morphology as a result of ecological selection pressures relating to migratory behaviour, foraging modes, patterns of social organization or habitat use (figure 3).

With respect to migration, the establishment of lineages in their wintering areas has been suggested, on occasion, to promote substantial radiation (e.g. [27,63]). However, the results of our analysis revealed no significant differences in rates of lineage diversification between migratory and non-migratory

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clades (electronic supplementary material, table S4 and appendix A). It is possible that evolutionary lability in migratory behaviour (by which we refer to the propensity to transition between migratory and non-migratory forms) is of greater significance in determining the establishment and diversification of lineages in new areas, rather than whether a species is migratory or non-migratory at the present time. Yet, given the relatively small number of migratory corvoid species, migration *per se* is likely to be a relatively unimportant mechanism facilitating speciation events across the overall clade. Habitat use may represent another important influence on the relationship between dispersal and diversification, with the strata at which a species occurs previously having been inferred to be a key determinant of speciation rates in birds [19]. This previous finding is also somewhat inconsistent with our results, which illustrate similar rates of diversification among corvoid species that vary in habitat types (figure 3; electronic supplementary material, appendix A). Differences in how habitat use was defined, the taxonomic scale and the spatial extents of these studies all potentially contribute to these discrepancies. We do not rule out that an interaction between habitat use and dispersal could be an important influence determining connectivity between populations, and hence the likelihood of speciation, but such differences may be difficult to detect in our data, given the coarse nature of our habitat classifications and the interspecific focus of our study.

In contrast with the overall similarity in diversification rate values between the migratory and habitat classifications, clades distributed on islands (either strictly or as widespread taxa) are apparently diversifying at higher rates compared with those found on continents (figure 3; electronic supplementary material, appendix A), corroborating the findings of Marki *et al*. [25]. Several reasons could explain the differences in diversification dynamics among these areas. First, the colonization of new islands is likely to lead to instant geographical isolation from the source populations, which may result in genetic differentiation, and eventually the formation of reproductive isolation [2,9]. Dispersal and establishment throughout fragmented island landscapes may therefore increase rates of speciation among these lineages. Islands also tend to be species-depauperate environments, which in some cases have a prevalence of available resources in novel habitats [56] that could enhance ecological differentiation and ultimately diversification rates. However, island lineages also tend to experience higher rates of extinction relative to continental forms [2], and variation in the ability of these areas to maintain lineages over historical timescales is therefore an additional factor likely to influence the differences in diversification dynamics.

The results from the island/continental comparisons are consistent with the idea that evolutionary lability in dispersal abilities is an important determinant of diversification rates. Widespread species have wing morphologies better suited for long-distance dispersal relative to insular forms, implying that their abilities to reach new locations are comparatively higher. Lineages that diversify at high rates throughout insular settings are therefore likely to be those that have been labile in their dispersal capacity through time [5,7] (i.e. they have transitioned between high and low dispersal capacities throughout their history). As such, the differentiation of island taxa from widespread forms may reflect a transition from high to low dispersal capacity, as evidenced by their HWI values. Although Weeks & Claramunt [9] found a negative relationship between dispersal and diversification among

birds distributed throughout Australasian archipelagoes, it is conceivable that the results of both studies are consistent with the hypotheses of evolutionary lability in dispersal. This is because clades with low HWI values and high current diversification rates may not necessarily have had low HWI values throughout their history, with evolutionary changes in wing morphology occurring post island colonization. For example, species from the family Rallidae, which were reported as having some of the highest rates of diversification but lowest HWI values by Weeks & Claramunt [9], were also acknowledged to undergo rapid evolutionary changes in wing morphology [54]. In concordance with Weeks & Claramunt [9], we suggest that periods of range expansion and geographical isolation occur in a manner that are coupled with changes in dispersal ability through time, but that it is the rate at which these changes occur that is most important in determining the dynamics of diversification. However, a major difference in our results with those of Claramunt *et al*. [8] and Weeks & Claramunt [9] is that we fail to recover any significant associations (be they linear or unimodal) between diversification rates and HWI (figure 3; electronic supplementary material, figure S4 and tables S4–S6). This is despite a much greater sample of species and geographical area over which these relationships were tested. Should evolutionary lability in dispersal abilities (and wing form) be the true determinant of diversification rates (rather than consistently low, intermediate or high rates of dispersal), current wing shape may provide a potentially misleading picture about the relationship between rates of historical dispersal and diversification.

5. Conclusion

The movement capabilities and geographical distributions of birds are better known than for any other organismal group, facilitating investigation into how these factors influence the diversity and distribution of lineages. In this study, among a global radiation of passerine birds, we demonstrate that lineages differing in their wing morphologies also vary in their spatial distributions. These differences are correlated with species' propensity to undertake seasonal movement, habitat preferences and with their presence in insular and continental settings. While movement strategies and habitat use have had a more limited influence on lineage diversification, colonization and radiation in island settings have led to many recent speciation events. These events involved over-water dispersal, and may have been influenced by the evolution of wing morphologies that are best suited for long-distance movement. However, in spite of the patterns presented here, the degree to which dispersal abilities change throughout the timescale of speciation, and across large taxonomic groups, remains unclear. One important step forward will be to explicitly determine how lineage dispersal relates to the movement of individuals across a range of taxa. Although rapid developments in direct tracking technology may soon facilitate such studies, determining historical dispersal capabilities will continue to be challenging.

electronic supplementary material, table S1). Phylogenetic data: http://dx.doi.org/10.5061/dryad.fd4m0.

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