

# ECOLOGICAL LIMITS ON DIVERSIFICATION OF THE HIMALAYAN CORE CORVOIDEA

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Within regions, differences in the number of species among clades must be explained by clade age, net diversification rate, or immigration. We examine these alternatives by assessing historical causes of the low diversity of a bird parvorder in the Himalayas (the core Corvoidea, 57 species present), relative to its more species rich sister clade (the Passerida, ~400 species present), which together comprise the oscine passerines within this region. The core Corvoidea contain ecologically diverse species spanning a large range of body sizes and elevations. Despite this diversity, on the basis of ecological, morphological, and phylogenetic information, we infer that the best explanation for the low number of species within the Himalayan core Corvoidea is one in which ecology limits diversification and/or immigration. Within the core Corvoidea, body size is correlated with elevation: large species are found at high elevations, and small species at lower elevations. This contrasts with the presence of many small-bodied species spanning all elevations in the Passerida and many large bodied species at low elevations in the other orders of birds (the nonpasserines). Cladogenetic events leading to ecological differences between species in body size and shape mostly occurred millions of years ago, and the rate of evolutionary change has declined toward the present. Elevational distributions have been evolutionarily more labile, but are also associated with ancient cladogenetic events. We suggest the core Corvoidea occupy a restricted volume of ecological space in competition with other bird species, and this has limited in situ diversification and/or immigration.

**KEY WORDS:** Adaptive radiation, Corvoidea, diversity-dependence, ecological controls, Himalayas, Passerida, phylogeny.

Within a geographic region, clades often differ greatly in species richness. Clade size may vary for reasons reflecting both the timing of dispersal and differences in rates of speciation and extinction (Jablonski et al. 2006; Mittelbach et al. 2007; Roy and Goldberg 2007). First, ancestors of different clades may have colonized the region at different times, with older clades accumulating a greater number of species (Wiens et al. 2009). Second, speciation and/or extinction rates may differ between taxa as species numbers continue to increase from some starting point (Ricklefs 2006; Weir and Schluter 2007; Wiens 2007). Third, different clades may have different carrying capacities, resulting

from ecological limits on diversification (Weir 2006; Phillimore and Price 2008, 2009; Rabosky 2009; Vamosi and Vamosi 2011). Ongoing differences in speciation and extinction rates are sometimes classified together with ecological limits, because if ages are similar, differences in clade size must reflect differences in net diversification (Mittelbach et al. 2007). However, they represent quite different processes, analogous to intrinsic growth rate and carrying capacity, respectively, in the standard logistic equation of population growth (Rabosky 2009). In this article, we examine ecological limits as the cause of the relatively low diversity of the bird parvorder “core Corvoidea” (57 species) in the Himalayas.



The ecological limits hypothesis is a natural corollary of the classic conception of adaptive radiation. In the formal definitions of adaptive radiation by Simpson (1953) and Schluter (2000) a key feature is a rapid increase in species numbers, associated with ecological divergence and ecological opportunity. Because ecological and lineage diversification cannot be rapid for long, this logically implies that as environments fill up with species, the rate of both must slow (Burbrink and Pyron 2009; Gavrillets and Losos 2009; Phillimore and Price 2009; Mahler et al. 2010). This is for at least two reasons. First, at the end stages of an adaptive radiation, speciation proceeds allopatrically or parapatrically, producing ecologically similar sisters that are mutually unable to spread into each other's range: eventually ranges become so small that no further speciation is possible (Rosenzweig 1995; Weir and Price 2011). Second, ecological speciation (the association of divergent selection pressures with the generation of reproductive isolation) should slow as environments fill up (reviewed in Price 2008; Glor 2010). Studying the history of both ecological and lineage diversification within clades can be used to test the essential features of the ecological limits hypothesis (Mahler et al. 2010). That is the goal of this study.

The adaptive radiation/ecological limits hypothesis proposes a tight connection between species diversification and ecological diversification, implying that clades with low species diversity should also have low ecological diversity. The core Corvoidea provide an apparent exception, because within the Himalayas, limited species diversity is associated with great ecological diversity. Along two major niche dimensions (body size and elevational position) the core Corvoidea are more variable than their sister group the Passerida, despite containing less than one-sixth the number of species. In the core Corvoidea body mass ranges from 9 to >900 g, and species breed from 100 m to as high as 6000 m. The more species-diverse Passerida contain some species as small as 5 g, but none much larger than 120 g, and none that range to such high elevations. This suggests that other alternatives to ecological limits are more viable explanations for the low species diversity of the core Corvoidea. For example, both the core Corvoidea and the Passerida are thought to have entered Eurasia from Indonesia (Ericson et al. 2003; Barker et al. 2004; Jønsson et al. 2011). Barker et al. (2004) suggested that the ancestor(s) to the Eurasian core Corvoidea colonized at least 5 million years (MY) later than those of the Passerida, and this has contributed to their relatively low diversity.

The Himalayas contain the vast majority of habitats observed across Eurasia, with much variation in climate across a large elevational range (Grytnes and Vetaas 2002; Price et al. 2011). Thus, the region provides a suitable model to investigate the process of radiations on continents, which typically reflect much longer timescales than the more classic adaptive radiations on archipelagos and in lakes (Schluter 2000; Grant and Grant 2007; Losos

2010). The rise of the Himalayas was initiated by the collision of the Indian and Eurasian tectonic plates approximately 50 Ma (million years ago; Beck et al. 1995; Molnar et al. 2010), but more recent climate change within the region has clearly been important in affecting species composition, such as the arrival of the modern monsoon sometime after 10 Ma (Molnar et al. 2010), which is reflected by a large change in the mammalian fauna of northern Pakistan beginning at about 8 Ma (Badgley et al. 2008). It seems likely that changing environmental conditions over long timescales have driven the vast ecological and morphological diversity currently observed among species. This is supported by previous work on a large clade of Passerida, the Phylloscopidae, which are represented by 21 species within the Himalayas (Price 2010) and show ancient diversification in both body size and elevational distributions (Richman and Price 1992).

In this study, we use a time-dated phylogeny to examine the patterns of both lineage-splitting events among the Himalayan core Corvoidea and diversification along the dimensions of body size, morphological shape, and habitat occupied to assess the hypothesis of ecological limits. The core Corvoidea are found on all continents (except for Antarctica), having likely initially diversified in the New Guinea region (Jønsson et al. 2011). Some of the cladogenetic events leading to current Himalayan species almost certainly happened outside this region (notably in the New Guinea region), and the Himalayan representatives of the core Corvoidea comprise approximately 8% of the overall group (57 out of ~700 species). Thus, we are studying the build-up of a restricted fauna, rather than the whole clade. We interpret patterns of cladogenesis among the Himalayan species in terms of both speciation and extinction, and restrictions on dispersal of species from elsewhere into the Himalayas.

## Methods

### CORE CORVOIDEA

We followed Barker et al. (2004) in their definition of the core Corvoidea and used this classification to determine which Himalayan species to include. Following distributional ranges given in Rasmussen and Anderton (2005), we analyzed 56 species of core Corvoidea in this study. Martens et al. (2000) and Rasmussen and Anderton (2005) considered that the jungle crow, *Corvus macrorhynchos* species complex actually consist of three taxa, despite some authorities classifying it as a single species (Del Hoyo et al. 2009). Recent molecular work, including our own, show that *Corvus japonensis* and *Corvus leuillanti* are likely to be subspecies (Iwasa et al. 2002; K. Jønsson, pers. comm.), and their respective distributions in the Himalayas remain unclear. We therefore consider the jungle crow to form two species in the Himalayas, *Corvus culminatus* at lower elevations and

*C. japonensis* at higher elevations (Ali and Ripley 1987). The western and eastern forms of the nutcracker, *Nucifraga multi-punctata* and *Nucifraga caryocatactes*, were raised to full species level by Rasmussen and Anderton (2005) and it is probable that in some other groups, western and eastern forms will also be found to be sufficiently genetically divergent to be considered species (e.g., see Reddy 2008). Such species pairs, including the nutcrackers, may be considered essentially ecological equivalents, which are allopatric/parapatric replacements. Because we are concerned with diversification along ecological axes that promote sympatry, and to avoid issues with defining similar populations as species in general, we excluded one of the nutcrackers from most analyses. However, we confirmed that its inclusion did not alter any of the results we report.

### PHYLOGENY

We built a time-calibrated phylogeny from molecular data, using species of both the Passerida and core Corvoidea distributed broadly across the root of the Barker et al. (2004) tree. We used the following taxa (Tables S1–S4): (1) 57 Himalayan species of the core Corvoidea, (2) five other core Corvoidea species to provide calibration points, (3) 19 Passerida species, also used to help in the calibration, (4) the basal passerine (the endemic New Zealand wren *Acanthisitta chloris*) and a suboscine passerine (*Pachyramphus polychopterus*), (5) one species each from the passerine families Petrociidae and Picathartidae (*Tregellasia leucops* and *Picathartes gymnocephalus*), which have been proposed as sister groups to the Passerida (Ericson et al. 2003; Ericson and Johansson 2003; Barker et al. 2004; Jønsson et al. 2007). These latter species are not found in continental Asia, but we included them because if they are close outgroups to the Passerida, then the timing of their origination would represent the earliest opportunity for an ancestral lineage of the crown group Passerida to have dispersed from Australasia to Asia (Barker et al. 2004). In total, the calibrated tree contained 85 species.

We first generated a “backbone topology” to assess the relationships among 17 core Corvoidea taxa, the majority of which form genera, and whose monophyly had strong support in preliminary runs. DNA sequence data were obtained, either through our own sequencing or from GenBank, for one representative species within each of these groups, usually for two mitochondrial (ND2 and cytochrome b), and four nuclear (RAG-1, RAG-2, c-mos, and myoglobin-2) genes (Tables S1 and S2 for details on the mitochondrial genes and Tables S3 and S4 for the nuclear genes). We chose species with the most complete sequence data at these loci. Although we took all sequences from a single individual where possible, in a few cases we concatenated sequences from closely related congeners. Substitution models for each gene were selected using AIC (Akaike information criterion; Akaike 1974) in Jmodeltest 0.1.1 (Posada 2008). We partitioned the data between

these models and ran the analysis in MrBayes v.3.1.2. (Ronquist and Huelsenbeck 2003). Results are presented in the Appendix (Fig. A1). Strong support for the backbone topology was found at the majority of nodes.

To construct a time-calibrated species level phylogeny we then used up to 2184 bp of mitochondrial DNA sequences (ND2 and cytochrome b) for all 85 species in the program Beast v1.6.2 (Drummond and Rambaut 2007). We constrained monophyly at nodes between taxa of the core Corvoidea, for which posterior probability values were  $>0.95$  in the backbone topology. We used an uncorrelated log-normal relaxed-clock model, a GTR +  $\Gamma$  + I model of sequence evolution (selected as the best fitting substitution model for both genes in Jmodeltest 0.1.1 (Posada 2008)) and as a prior, the Yule model of speciation. Algorithms were run for 30,000,000 generations, and trees were sampled every 1000 generations. We used the program Tracer v1.5 (Rambaut and Drummond 2007) to visualize the distribution of parameters across Markov chain Monte Carlo (MCMC) iterations and to ensure models had reached stable distributions. We discarded 3000 trees as a burn-in. For the remaining trees the posterior probabilities of the median node heights were estimated using the maximum clade credibility method, and combined using TreeAnnotator v1.6.2 (Drummond and Rambaut 2007).

Previous attempts at dating the diversification of the core Corvoidea have relied on a single deep point calibration (*Acanthisittidae* vs. other passerines dated at 85–82 Ma) (Barker et al. 2004), with other studies using the derived dates as secondary calibrations (Jønsson et al. 2010). These dates are clearly very approximate, which may reflect both error in the age estimation of the calibration point, and rate heterogeneity among the lineages sampled (Lee 1999; Graur and Martin 2004). Currently the choice of an appropriate calibration for the root of passerine phylogenies is difficult, as no definitive fossils from the crown group suborders are known before about 25 Ma (Mayr 2005). In this study, we used both fossils and biogeographic events to date eight nodes distributed throughout the tree (Table 1). We used the divergence between *A. chloris* and other passerines (i.e., the basal splitting event in passerines; Hackett et al. 2008) to set an upper limit on the root of our tree. The biogeographic date used to calibrate this node (the separation of New Zealand from Australasia) has been suggested to be much more uncertain than the narrow range of dates (85–82 Ma) previously used (McLoughlin 2001; Irestedt et al. 2009). Here we employ a uniform prior using 85 Ma as the upper boundary, and the present day (0 Ma) as a lower boundary. The XML file used to produce the time-calibrated trees in BEAST is deposited in Dryad (<http://datadryad.org/resource/doi:10.5061/dryad.p9t061vc>).

By employing multiple calibration points, as we do here, the accuracy of date estimations should improve. This is because the average distance between calibrated and uncalibrated nodes is

**Table 1.** Dates entered into the BEAST analysis as calibration points, all set with uniform priors.

Calibration taxon	Sister taxa in tree	Calibration source	Date used (millions of years)	Calibration type	Reference
<i>Chlorospingus pileatus</i>	<i>Chlorospingus tacarcunae</i>	Biogeographic (age of Talamanca uplift)	4.6	Hard maximum boundry	Weir et al. (2008)
<i>Myadestes obscures</i>	<i>Myadestes unicolor</i>	Biogeographic (age of main Hawaiian islands)	5.2	Hard maximum boundry	Miller et al. (2007)
<i>Passerina cyanea</i>	<i>Cyanocopsa cyanooides</i>	Fossil <i>Passerina</i> species	4.5	Hard minimum boundry	Becker (1987)
<i>Pomarea iphis</i>	<i>Pomarea dimidiata</i>	Biogeographic (end of volcanism on Eiao island)	5.1	Hard maximum boundry	Cibois et al. (2004)
<i>Sylvia rueppelli</i>	<i>Sylvia melanothorax</i>	Biogeographic (reformation of Cyprus)	5.4	Hard maximum boundry	Böhning-Gaese et al. (2003)
<i>Cyanocitta stelleri</i>	<i>Cyanocorax mystacalis</i> / <i>Gymnorhinus cyanocephalus</i>	Fossil <i>Miocitta</i>	15	Hard minimum boundry	Becker (1987)
<i>Fringilla montifringilla</i>	<i>New world nine primaried oscines</i> (7 species)	Fossil tentative identification as a Parulidae	18	Hard minimum boundry	Becker (1987)
<i>Acanthisitta chloris</i>	All other passerines	Biogeographic (separation of New Zealand from Australia)	85	Hard maximum boundry	Gaina et al. (1998); Li and Powell (2002); Hackett et al. (2008)

reduced (Linder et al. 2005), and an increased number of calibrations distributed broadly throughout a phylogeny can improve modeling of rate heterogeneity. However, there remain many general uncertainties associated, which include the choice of node at which to apply the calibration (Sanderson 2002; Near et al. 2005; Rutschmann et al. 2007), molecular clock assumptions (Sanderson 2002; Weir and Schluter 2008), and the use of valid priors (Fleischer et al. 1998; Ho and Phillips 2009). Many of our results depend on an approximately ultrametric tree, but not on absolute dates, and we confirmed results on a set of trees produced using other methods (e.g., one in which we built a tree without fossils).

**ECOLOGICAL DATA**

We obtained body mass data for 490 species of passerines and nonpasserines believed to occur in the Himalayas (Rasmussen and Anderton 2005) from Dunning (2008), supplemented by our own field data (Price 1979; Price and Jamdar 1990). Among the nonpasserines we included only forest species, and excluded gamebirds and birds of prey, which we consider more ecologically distinct and less likely to interact with the core Corvoidea than the other groups (Price et al. 2011). We were missing data for approximately 100 species, although many are considered rare or

only theoretically in the region (Rasmussen and Anderton 2005). We used the average of mean male and mean female mass, where possible, and the median where only the range of body masses (minimum and maximum) was given in Dunning (2008). Midpoint elevational ranges of the same 490 species were taken from Price et al. (2011) who give ranges in both the southeast and northwest Himalayas. If the species occurred in both localities, we used the average across the localities.

In addition, JK measured two males of each species of the core Corvoidea from study skins at the Chicago Field Museum of Natural History, for tarsus, wing length, and beak length, beak depth, and beak width (beak measurements were all taken from the front edge of the nares). Data are provided in Table S5. By measuring two individuals, the within-species variance is reduced by 50% when compared to measuring a single individual, but little extra is gained from measuring a third. Using analyses of variance (ANOVAs) we found that more than 97% of the variance for all traits was between species. We used principal component analysis on the correlation matrix of the log-transformed measurements (including mass), and investigated patterns in the evolution of PC1 and PC2. We did not correct for phylogeny in our extraction of the principal components (cf. Revell 2009), because the summary measures (i.e., PC1 and PC2 scores) gave readily interpretable

**Table 2.** Correlations of principal component scores with log-transformed morphological measurements, as measured on museum specimens (mass from Dunning 2008).

Character	PC1	PC2
Tarsus, mm	0.91	0.39
Beak length, mm	0.96	-0.18
Beak depth, mm	0.97	-0.06
Beak width, mm	0.97	-0.2
Wing length, mm	0.97	-0.04
Body mass, log (g)	0.98	0.11
Proportion variance explained	0.92	0.04

loadings (Table 2) and we are mostly concerned with collapsing the data.

### LINEAGE DIVERSIFICATION

Analyses of near-complete bird phylogenies show strong evidence for a slowdown in lineage splitting events toward the present (Phillimore and Price 2008, 2009). This is usually attributed to a declining speciation rate (Rabosky and Lovette 2008), and consistent with an approach toward an ecological carrying capacity (Phillimore and Price 2009), suggesting ecological limits on diversification (Rabosky 2009). However, sampling a subset of species from a larger phylogeny creates a slowdown in the observed lineage-splitting events, because older nodes tend to be included in the sample whereas younger ones do not (Pybus and Harvey 2000). Following Pybus and Harvey (2000) we assessed slowdowns against a simulated pure-birth model.

Only 8% of the overall core Corvoidea are analyzed in our phylogeny, and one model would be to consider the entire clade of the core Corvoidea as the sample space from which species have been randomly drawn to fill the Himalayas. This is an extreme null model and at a minimum, the only relevant extra-limital nodes on a tree of the complete core Corvoidea should be those that have actually led to at least one Himalayan species (see Weir 2006). For example, according to Sibley and Monroe (1990), 60 species are restricted to Australia and/or New Zealand, 167 to Africa, 101 to the Americas, and a further 37 are endemic species with restricted ranges on Pacific islands. The majority of these species are irrelevant to the build-up of Himalayan diversity. We therefore considered two alternative sample spaces from which to draw Himalayan species. These are the 117 species with populations in continental Eurasia (including Southeast Asia) or the 244 species which are found in Eurasia and/or the Indonesian islands, according to the compilation of Sibley and Monroe (1990). Using Geiger in R (Harmon et al. 2008; R Development Core Team 2010), we simulated 1000 trees containing either 117 or 244 species, respectively, and then randomly sampled 56 species from the tree. We then computed the  $\gamma$ -statistic (a large negative value for  $\gamma$  implies a declining rate of lineage splitting, Pybus and Harvey 2000) for

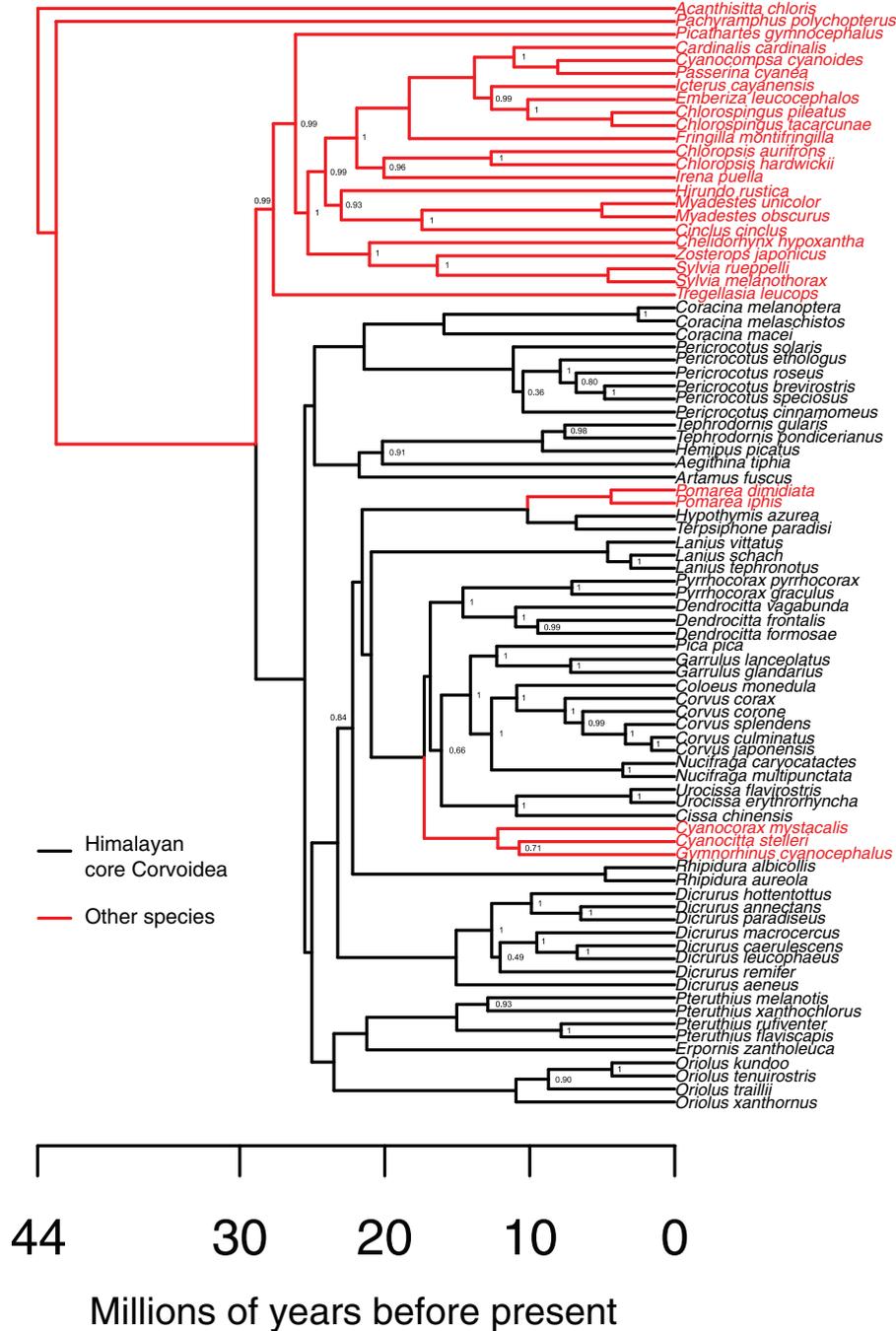
both the simulations and 1000 time-calibrated phylogenies from the post burn-in sample (pruned to contain the 56 relevant species) and calculated the proportion of simulated trees which had a value of  $\gamma$  less than that on any of the time-calibrated trees.

### ECOLOGY AND MORPHOLOGY

Significance of correlations between the ecological and morphological traits was assessed using the independent contrasts method (Felsenstein 1985), implemented in the R package APE (Paradis et al. 2004; R Development Core Team 2010). The contrast method assumes Brownian motion, which, as we show below, is rejected. This is unlikely to create a large bias in our results (Díaz-Uriarte and Garland 1996), but to confirm significance we repeated the analysis using phylogenetic least squares regression (PGLS), in the R package caper (Orme et al. 2011; R Development Core Team 2010). PGLS uses a branch length transformation ( $\lambda$ ) that maximizes the fit of the phylogeny to Brownian motion. Results were consistent between methods, and we present only the contrast statistics.

We also used independent contrasts to analyze rates of ecological and morphological diversification. Under the Brownian motion null hypothesis, all contrasts are independently drawn from a normal distribution and should show no pattern on the tree. Therefore, any nonrandom pattern in the distribution of contrasts on the tree indicates deviation from Brownian motion (Garland 1992; Freckleton and Harvey 2006; Mahler et al. 2010). We obtained standardized contrasts based on the branch-lengths of the tree in Figure 1, pruned to contain only the 56 species of Himalayan core Corvoidea. Following Freckleton and Harvey (2006), we regressed their absolute values against the node distance from the root of the tree. We also used the maximum likelihood procedure of Mahler et al. (2010) to obtain the linear fit of the squared contrast values against node distance, which provides a direct estimate of how the Brownian motion rate parameter changes with time (Mahler et al. 2010). A negative slope implies much evolution early in the radiation and relatively little late (Richman 1996), whereas a positive relationship demonstrates much evolution late in the radiation, but is consistent with either a constant high rate of change through time (Richman and Price 1992; Ackerly et al. 2006) or evolution restricted to the more recent past (Ackerly et al. 2006; Losos 2010). To assess uncertainty in the phylogenetic reconstructions, we obtained a post burn-in sample of 1000 time-calibrated trees (each pruned to the relevant 56 species), and then calculated independent contrasts and the regression statistics on each of these trees.

Finally, we compared results from the contrast analyses with Blomberg et al.'s  $K$  statistic (Blomberg et al. 2003) using Picante in R (Kembel et al. 2010).  $K$  values of 1 imply phylogenetic signal consistent with Brownian motion,  $K > 1$  implies phylogenetic signal greater than Brownian motion (tip species more similar than expected), and  $K < 1$  implies signal less than Brownian motion.



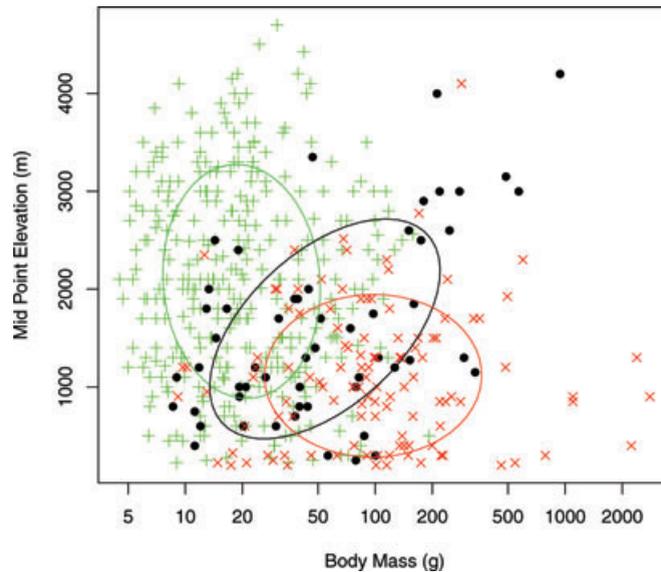
**Figure 1.** Time-calibrated phylogeny for the Himalayan core Corvoidea, based on protein-coding mitochondrial DNA sequences with the topology fixed according to nuclear and mitochondrial data (Appendix). Himalayan core Corvoidea are shown in black. Other taxa were used to assist in the time calibrations and were pruned from the final tree for subsequent analyses, as was one species of the Himalayan core Corvoidea, *Nucifraga multipunctata* (see Methods). Numbers either to the left or right of nodes are posterior probability values.

## Results

### PHYLOGENY

The time-calibrated tree is shown in Figure 1. The topology of the backbone to the tree is largely consistent with earlier analyses, with some exceptions described in the Appendix. We infer that the most recent common ancestors to the crown Passerida and

Himalayan crown core Corvoidea existed at 25 Ma (95% confidence limits [CL] from the Bayesian sample, 23–28 Ma) and 26 Ma (23 Ma, 28 Ma CL), respectively, with divergence of these two groups at about 29 Ma (26 Ma, 32 Ma CL). These dates are somewhat younger than those suggested by Barker et al. (2004) based on the fixed *Acanthisitta* date. They reflect our inclusion



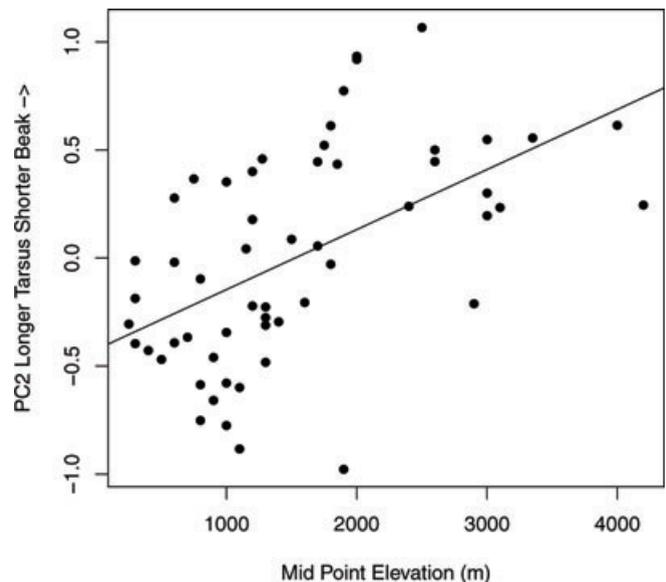
**Figure 2.** Scatter of mid-point elevational range (m) versus log body mass (g) within the Himalayas, for the Passerida (+), core Corvoidea (•), and forest nonpasserines (x). Ellipses are the 50% predictive intervals of the points.

of uncertainty in the Bayesian prior, which in itself reflects uncertainty in both the timing of the separation of New Zealand from Australia (McCloughlin 2001; Irestedt et al. 2009) and the origination of the lineage leading to *Acanthisitta* (Worthy et al. 2010).

### ECOLOGICAL ATTRIBUTES

Figure 2 shows a plot of the mid-point of the elevational position against body mass for all species, separated into three groups: the nonpasserines, the Passerida, and the core Corvoidea. The nonpasserines tend to occupy relatively low elevations but have a wide range of body masses at these elevations. The Passerida are generally small bodied but cover the entire elevational gradient. The core Corvoidea lie between these two groups, and unlike these groups show a correlation of body size with elevation: large species tend to be found at high elevations, where they replace the nonpasserines (correlation between log body mass and midpoint elevation,  $r = 0.49$ ,  $N = 56$ ,  $P < 0.001$ , correlation between contrasts [with no intercept in the model],  $r = 0.38$ ,  $P = 0.004$ ). The correlation of elevation with PC1 based on the museum measurements was similar to that for body mass ( $r = 0.42$ ,  $P = 0.001$ ), although this is not significant after phylogenetic correction ( $r = 0.32$ ,  $P = 0.07$ ).

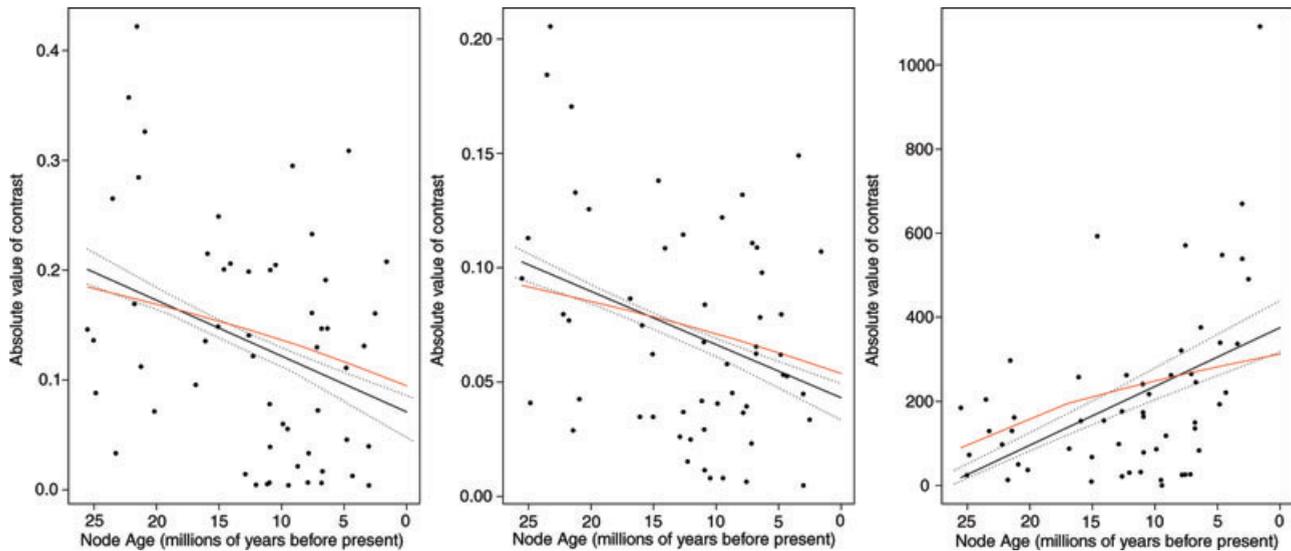
PC2 represents a shape measure, corresponding to the relative size of tarsus and beak measures (Table 2, higher values of PC2 indicate longer tarsi relative to beak size). As in the case of body mass, PC2 is correlated with midpoint elevation (Fig. 3,  $r = 0.52$ ,  $N = 56$ ,  $P < 0.001$ , correlation between contrasts,  $r = 0.36$ ,  $P = 0.001$ ). Species with high tarsus/beak ratios live at higher elevations.



**Figure 3.** Correlation of shape (PC2) with mid-point elevation (m) within the core Corvoidea. Line is the least squares regression.

### LINEAGES THROUGH TIME

The mean  $\gamma$ -statistic (Pybus and Harvey 2000) calculated from 1000 samples of the time-calibrated tree (Fig. 1, pruned to contain 56 species of the Himalayan core Corvoidea) indicates that internal nodes are distributed disproportionately toward the root of this tree ( $\gamma = -4.43 \pm 0.21$ ) suggesting a slowdown in speciation events which led to the contemporary Himalayan core Corvoidea. This is significant when evaluating the simulated values of  $\gamma$  against those from the 1000 calibrated phylogenies, considering both Eurasian species alone ( $N = 117$ ,  $P < 0.001$ ), and Eurasian and Indonesian species together as the source pool ( $N = 244$ ,



**Figure 4.** Regression of absolute values of contrasts against time in the Himalayan core Corvoidea. *Left:* log mass (g); *Centre:* PC2; *Right:* elevation (m). Solid black line refers to the least squares regression on the maximum clade credibility tree. Dashed lines give the 0.025% and 0.975% quantiles of the regression coefficients for the contrasts calculated on a sample of 1000 trees. Note that the regressions produced by any of the 1000 sampled trees are significant ( $P < 0.05$ ) for all three traits (see text for  $P$  values based on the maximum clade credibility tree). Solid gray line (red in the online version) gives the model fit of the Brownian motion rate parameter, assuming it changes linearly with time (Mahler et al. 2010). Significance of the Mahler fits, by likelihood ratio tests are as follows: log mass ( $P = 0.04$ ), PC2 ( $P = 0.06$ ), elevation ( $P < 0.0001$ ).

$P = 0.049$ ). The observed slowdown could be a result of a genuine slowdown in the entire clade of the core Corvoidea, or a result of nonrandom establishment in the Himalayas. For example, species closely related to a Himalayan incumbent may be less likely to become established because of their ecological similarity, as we consider further in the discussion.

#### EVOLUTION OF ECOLOGICAL DIFFERENCES

Absolute standardized contrasts for log body mass are negatively correlated with distance from the root (Fig. 4;  $r = -0.33$ ,  $P = 0.01$ ), and the same is true for PC2 ( $r = -0.33$ ,  $P = 0.01$ ). This implies that much diversification in both traits took place early in the history of the group, at an estimated 25–18 Ma (Fig. 4, *left and centre*). These correlations reflect the presence of a few large contrasts representing early diversification events at the base of the tree, but they are not dependent on the phylogeny we present, and are present on all 1000 trees analyzed from the BEAST run (Fig. 4, legend). Unlike the morphological traits, contrasts of mid-point elevation are positively correlated with distance from the root ( $r = 0.46$ ,  $P < 0.001$ ; Fig. 4, *right*).

Blomberg et al.'s  $K$  statistic can be used to summarize the results for the three traits. We found greater than Brownian motion evolution in both log mass ( $K = 2.43$ ) and PC2 ( $K = 1.4$ ), but less in elevation ( $K = 0.49$ ). The  $K$  values of both body mass and PC2 showed highly significant phylogenetic signal when evaluated against a randomization test ( $P < 0.001$ ), however, the  $K$  value of elevation did not ( $P = 0.1$ ).

#### Discussion

In the theory of ecological limits, rates of speciation (Price 2008; Foote 2009; Rabosky 2009) as well as ecological and morphological evolution (Burbrink and Pyron 2009; Foote 2009; Mahler et al. 2010) slow through time. This decline is associated with niche space becoming filled. Here, we have studied the diversification of a monophyletic group of birds occurring within the Himalayas, the core Corvoidea. In accord with the ecological limits model, we find among these species a slowdown in both rates of lineage splitting and morphological diversification. We suggest these slowdowns are a consequence of restricted available niche space, and that this results at least partly from competition with other Himalayan bird groups (Fig. 2).

The slowdown in the cladogenetic events that have led to the present-day Himalayan core Corvoidea could arise in at least three different ways. First, it may represent extinction events that are nonrandomly dispersed on the phylogeny. Second, the slowdown in speciation could be going on within the core Corvoidea as a whole (about 700 species), followed by random dispersal into the Himalayas. Third, the slowdown may be a consequence of differential establishment, such that speciation across the whole group has not slowed, but instead only relatively distantly related species have colonized the Himalayas. Any of these three processes would lead to the observed slowdown, and it is possible that all have contributed. However, we suggest that all three are an expected manifestation of the same underlying process, viz.

ecological limits. First, if extinctions are nonrandom, a simple explanation is that turnover is happening within ecological adaptive zones, as close relatives replace each other (McPeck 2008). Second, range expansions are required for ongoing allopatric and parapatric speciation events (Rosenzweig 1995; Weir and Price 2011). Thus, if species are unable to expand their ranges in an ecologically full environment, this should lead to a decline in speciation (Phillimore and Price 2009).

With respect to range expansions, many of the Himalayan core Corvoidea have allopatric sisters that lie outside of the Himalayas (Sibley and Monroe 1990), and at least part of the reason for the observed slowdown must be a failure of these species to expand their ranges into the Himalayas. Under the ecological controls model, a failure to expand ranges is attributed to ecological similarity with incumbents, and therefore competitive exclusion (Phillimore and Price 2009). However, other explanations include barriers over which there has been insufficient time to cross, and incomplete reproductive isolation (Weir and Price 2011). Neither of these alternatives alone seem likely to account for the general failure of many close relatives to expand ranges into the Himalayas, given that many Himalayan species are also found in the neighboring regions of China and Southeast Asia (Sibley and Monroe 1990) and are likely to have acquired strong reproductive isolation from their relatives, having been long separated (Jönsson et al. 2011).

A relatively low ecological carrying capacity is consistent with the observed slowdown in lineage diversification within the Himalayan core Corvoidea. However, three alternative explanations could also contribute to the low species richness of the core Corvoidea, at least with respect to its sister group, the Passerida. An extreme “null model” is that the low richness represents the purely stochastic outcome of birth and death (e.g., Raup et al. 1973; Mitter et al. 1988). For example, if we compare the disparity in numbers of the 57 Himalayan core Corvoidea with the Himalayan Passerida (>400 Himalayan species), under a pure-birth model, and with an expectation of 250 species, the probability of producing a tree with <58 tips is 0.2 and that for a tree with >400 tips is 0.22 (eq. 4 of Nee et al. 1994), so this level of disparity is consistent with such a “random” model. But a model of “randomness” seems highly unrealistic, given such features as the past climatic history of the Himalayas, the patterns of morphological evolution within the group, and the presence of a slowdown in cladogenetic events. With respect to the slowdown, we simulated 1000 trees under the pure-birth model described above and found that every tree containing 57 species had a more positive estimate of Pybus and Harvey’s  $\gamma$  (i.e., showed less of a slowdown) than is observed in the data. This is because, in randomly generated trees, those with relatively few species have less speciation events early in their history, and more later (Phillimore and Price 2008), which is opposite to the pattern in our data.

Apart from the null model a second explanation for the reduced diversity of the core Corvoidea, at least with respect to the Passerida, is that the group dispersed into Eurasia more recently (Barker et al. 2004), resulting in less time for speciation (e.g., Stephens and Wiens 2003). It is difficult to assess this idea (even the colonization route of the Passerida, from Africa or Southeast Asia, has been disputed [Fuchs et al. 2006; Jönsson and Fjeldså 2006]). However, we have no direct support for a time argument because the ages of the crown group species are very similar (Fig. 1). Further, it is possible that a later arriving group has an advantage over an earlier arriving group. For example, from the fossil record of Europe, small nonpasserines were replaced by small passerines, beginning about 25 Ma (Mayr 2005). A third explanation for a disparity in species numbers between the two groups is that rates of diversification have remained constant through time, but at a higher rate in the more speciose group (e.g., Wiens 2007), perhaps because species in one clade share a trait which accelerates speciation, and this trait is not present in the other clade (e.g., Mitter et al. 1988; Vamosi and Vamosi 2011). Net diversification rates have certainly been higher in the Passerida relative to the core Corvoidea but neither time nor constant rates of diversification provide a complete explanation of the Himalayan core Corvoidea’s low species diversity, given the slowdown in lineage-splitting events among this group.

Among the core Corvoidea, we have studied the diversification of both body size and elevational range. These axes represent proxies for two important components of species ecology. Body size is likely strongly correlated with prey size (Vézina 1985), whereas elevational distribution relates to the range of habitats occupied. Elevation is correlated with morphology, specifically relative tarsus length. This may reflect adaptations to foraging in more open habitats at higher elevations, especially hopping and walking on the ground (as the high elevation Corvidae commonly do), whereas the low elevation species include many small flycatcher-like types such as *Hemipus* and *Terpsiphone*, found in trees and bushes. Within the core Corvoidea, elevation and body size are positively correlated and larger species are present at higher elevations. This correlation is consistent with effects of competition from other groups of birds (Fig. 2). First, the parvorder Passerida contains small-bodied species at all elevations (~400 species in the Himalayas), and second, the nonpasserines contain multiple large species at low elevations (among forest species, excluding gamebirds and birds of prey, ~130 species in the Himalayas).

If the Passerida and nonpasserines restrict ecological space into which the core Corvoidea can diversify, we should be able to detect this in terms of the rate of trait evolution through time. In accord with this, the rates of evolution in body size and shape (PC2) have slowed through time. For both traits, this reflects large differences among five ancient clades that diverged more

than 20 Ma (Corvidae, Laniidae, Monarchiidae, Dicuridae, and Rhipiduridae). Such ancient divergences may represent entry into new ecological zones (e.g., Burbrink and Pyron 2009), including the transition from foraging within forest to more open habitat (Jönsson et al. 2011).

A pattern of disproportionate diversification of body size and/or shape early in the radiation of a group has not been commonly observed in general surveys (Harmon et al. 2010), but has been noted previously for higher taxonomic groups of birds (Bennett and Owens 2002; Harmon et al. 2010), in a study of a single large clade of tropical birds (the Furnariidae; Derryberry et al. 2011), and in some case studies of reptiles (Burbrink and Pyron 2009; Mahler et al. 2010). Besides the core Corvoidea, another Himalayan group, the Old World leaf warblers (Phylloscopidae) also experienced early divergence in body size, albeit over only a twofold range (Richman and Price 1992; Richman 1996). However, the timing of the body size divergences between the Phylloscopidae and core Corvoidea are quite different, with major body size divergences occurring at an estimated 8–12 Ma in the Phylloscopidae (Price 2010). The Phylloscopidae are essentially a temperate group and originated close to the Himalayas (Johansson et al. 2007), whereas the core Corvoidea originated and diversified in the tropical Papuan region (Jönsson et al. 2011), and it was here where the large divergences in body size are likely to have occurred. We suggest that more generally, new radiations to produce coexisting species within a single elevational belt may often result in body size divergence.

In contrast to body size and shape, many elevational differences between species have evolved more recently. Either elevation has evolved only in the more recent past, or it has evolved frequently throughout the history of the group, including the recent past. The alternatives are not easily separated based on phylogenetic analysis alone (Ackerly et al. 2006; Losos 2010), but neither is a priori consistent with an ecological controls model. However, the Himalayas experienced large climate changes between 10 and 6 Ma and again after 4 Ma (Molnar et al. 2010). Thus, ecological opportunity along the elevation axis may have promoted a wave of invaders into the Himalayas (reflected by some very large contrasts in elevation close to the tips of the tree) at this time, and the process does seem to have declined more recently. Only a single large contrast in elevational range is observed in the past 2 MY (between *C. culminatus* and *C. japonensis*).

In conclusion, the process of diversification of the Himalayan core Corvoidea suggests that increasing saturation along two major niche dimensions, body size and habitat, has led to an associated slowdown in the accumulation of species within the Himalayas. More generally, limits on range expansion not only slow the build up of an avifauna but must also eventually slow speciation (Rosenzweig 1995; Phillimore and Price 2009). We conclude that ecological controls are likely one important mech-

anism whereby speciation rates are limited, along with other factors, such as intrinsic differences between clades in diversification rates, and factors which affect the colonization of regions (Ricklefs 2003; Wiens 2007; Vamosi and Vamosi 2011).

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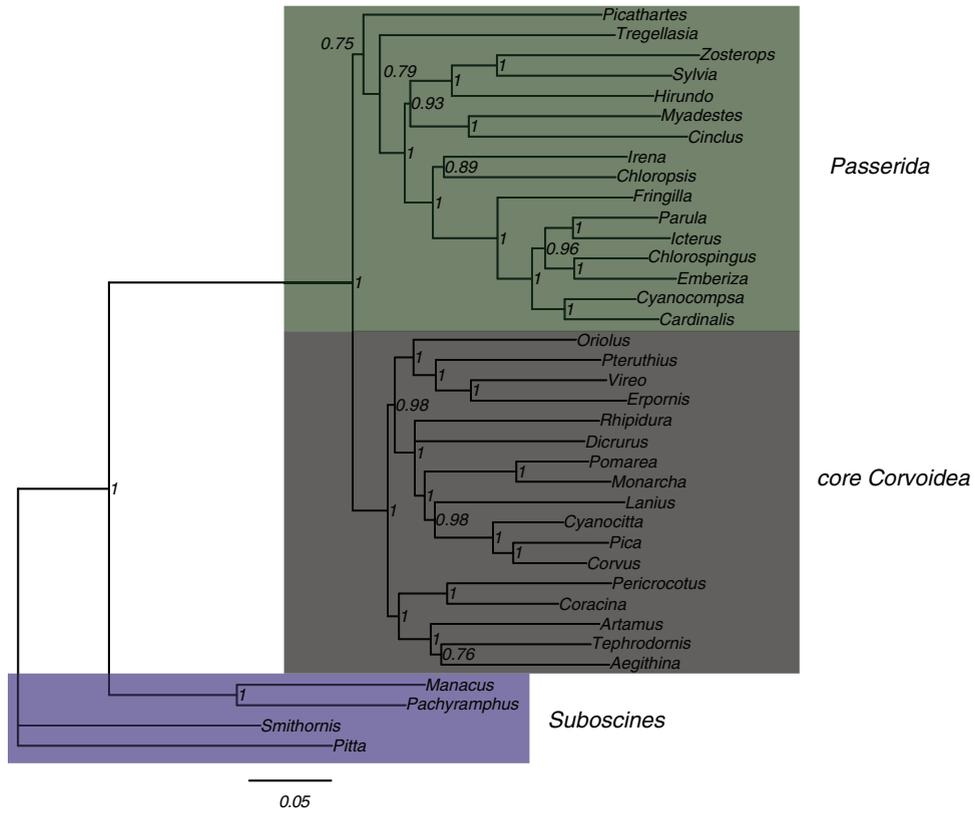
## Appendix

### CONSTRUCTION OF THE BACKBONE PHYLOGENY

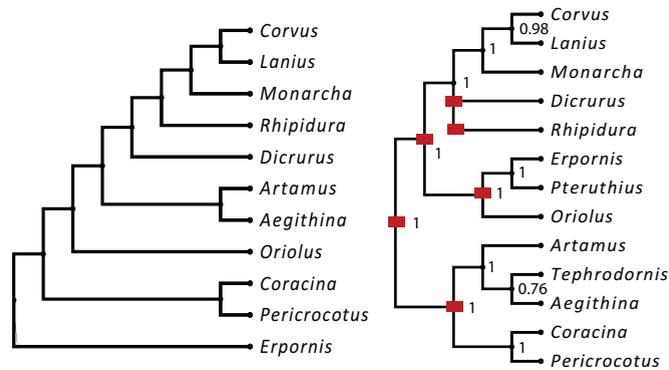
Barker et al. (2004) attempted to resolve the relationships among passerine families based on 4126 bases of the nuclear genes RAG-1 and RAG-2. This study was criticized for its over-reliance on the phylogenetic signal of a single gene, RAG-1 (Irestedt and Ohlson 2007). Our preliminary runs confirmed the individual monophyly of 17 groups of core Corvoidea (the majority of which form genera), on the basis of mitochondrial genes. To study relationships among these 17 Corvoidea groups and a further 20 groups of suboscines and Passerida, we used nuclear sequences from four genes (RAG-1 [2872bp], RAG-2 [1152bp], c-mos [607bp], myoglobin-intron 2 [714bp]) (obtained from GenBank) and mitochondrial sequences from two genes (cytochrome b 1143bp and ND2 1041bp) obtained from our own sequencing as well as GenBank (Tables S1–S4). We use the genus *Monarcha* as a surrogate for *Hypothymis* as previously both were amalgamated into a single genus and are believed to be closely related (Rasmussen and Anderton 2005).

All sequences were aligned using MAFFT v.6 (Katoh and Toh 2008) with further manual adjustments. Despite a number of indels in the nuclear dataset, sequences could be unambiguously aligned. Any gaps were treated as missing data. The nuclear dataset consisted of up to 5484 bp and the mitochondrial dataset 2184 bp. We obtained as much sequence as possible for each group, sometimes by combining across species (see Tables S1 and S2) but included only one sequence per group. We initially partitioned the dataset into individual genes, and selected the best fitting substitution models using AIC (Akaike 1974) in Jmodeltest 0.1.1 (Posada 2008). The GTR +  $\Gamma$  + I model was the best fitting model for all genes apart myoglobin, for which the GTR +  $\Gamma$  model provided the best fit. We concatenated alignments by their best fitting substitution model and performed the analysis in MrBayes v. 3.1.2 (Ronquist and Huelsenbeck 2003). Two independent runs each consisting of four Metropolis-coupled MCMC chains with two hot and two cold chains were run for a total of 6,000,000 generations with trees sampled every 250 generations. The first 2400 samples before the model had reached its target distribution were discarded as a burn in. Posterior probabilities were estimated from the consensus of the remaining trees.

Figure A1 shows the results. This confirms the reciprocal monophyly of a broad subset of the core Corvoidea and Passerida, but also shows that there is poor support for a sister relationship between the Passerida and the families Petrocidae and Picathartidae (represented by *T. leucops* and *P. gymnocephalus*, respectively), which are extra limital (cf. Barker et al. 2004). Some of the topology is in agreement with that of Barker et al. (2004), but there are well-supported differences (Figure A2). We confirm Reddy and Cracraft's (2007) finding that *Erpornis zantholeuca* and *Pteruthius* are sister groups. However, *Oriolus* is included as a member of this monophyletic group, forming the basal branch.



**Figure A1.** Backbone phylogeny constructed using multiple nuclear and mitochondrial genes (Tables S1–S4), produced using MrBayes v.3.1.2. Numbers either to the left or right of nodes are posterior probability values.



**Figure A2.** Inferred topology for genera of the Himalayan core Corvoidea, as suggested by Barker et al. (2004) based on two nuclear introns (*left*) and this study based on four nuclear introns and two mitochondrial DNA (mtDNA) genes (*right*). The node representing the divergence between *Dicrurus* and *Rhipidura* is collapsed, reflecting the results of the Bayesian analysis presented in Figure A1. Posterior probabilities are indicated. Incongruences between trees are shown by red boxes at the appropriate nodes.

## *Supporting Information*

The following supporting information is available for this article:

**Table S1.** Full species list of all Himalayan core Corvoidea sampled in this study and sources of mitochondrial genetic data.

**Table S1A.** Collection localities and dates for specimens not held in museums.

**Table S2.** GenBank accession numbers and associated references for the mitochondrial genes cytochrome b and ND2, for use in both the partitioned analysis and the time-calibrated phylogeny.

**Table S3.** Full list of core Corvoidea species used to compile the nuclear dataset for the partitioned analysis.

**Table S4.** Passerida and suboscine species used to compile the nuclear dataset for the partitioned analysis.

**Table S5.** Morphological measurements, mm; mean; and standard deviation based on  $N = 2$  males/species (from the Field Museum of Natural History, Chicago).

Supporting Information may be found in the online version of this article.

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