1 Phenotypic similarity in sympatric crow species: evidence of social convergence?

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12 Abstract

13 Crows, rooks and ravens (*Corvus* spp.) display marked morphological and voice
14 similarities that have been hypothesised to stem from competitive interactions, as a case
15 of non-aposematic mimicry. Here, I test predictions of the mimicry hypothesis at the
16 macroevolutionary scale, examining whether species morphological and acoustic traits
17 covary with those of coexisting congeners, and whether phenotypic similarity has
18 facilitated the coexistence of related species after secondary contact. Body size and the
19 temporal patterns of the commonest call display high levels of similarity among
20 sympatric species, even after controlling for the effect of shared climate and habitat, and
21 phylogenetic constraints in the production of variation. When sister species differed in
22 these acoustic and morphological traits, their transition to secondary sympatry was
23 delayed relative to those with more similar traits. No similarity was found in the sexual
24 call of crows, suggesting that convergence occurs only when function does not favour
25 maintenance of species-specific traits. Crow similarities in morphological and acoustic

26 features may therefore be associated with coevolving interactions with congeners, in
27 line with a broad array of studies documenting convergence among species that interact
28 aggressively or forage communally.

Introduction

Closely related animal species that coexist in sympatry face significant and contrasting challenges. Competitive and reproductive interactions represent powerful agents of selection for organisms that share many traits through common ancestry (Schluter 2000; Pfenning and Pfenning 2009). The evolutionary outcome spans from the divergence in traits involved in resource use or reproduction to convergence (or parallelism) in agonistic displays (Brown and Wilson 1956; Abrams 1986; Tobias and Seddon 2009). Convergent evolution of key ecological traits is also promoted by selection stemming from shared habitat, climate, or predators (Brower 1996; Laiolo et al. 2015). These processes are clearly distinct, but the phenotypic targets often coincide. This is the case in body size or long-distance signals, which may be shaped by ecology and reproductive behaviour, as well as interspecific competitive interactions (Seddon 2005; Grether et al. 2013; Bothwell et al. 2015). When studying the evolution of these traits, interaction-driven divergence and environment-driven convergence have captured most attention. Competition-driven similarity may however also evolve, for instance in a context of heterospecific territorial defence or communal foraging. This evolutionary change, also labelled social, non-aposematic or competitive mimicry (Moynihan 1968; Cody 1969; Rainey and Grether 2007), often appears in birds. Examples are some toucans (Weckstein 2005), woodpeckers (Weibel and Moore 2005; Benz et al. 2015), suboscine passerines (Tobias and Seddon 2009, Tobias et al. 2014), minivets (Jönsson et al. 2010), orioles (Jönsson et al. 2016a), new world warblers (Losin et al. 2016), and larks (Laiolo 2012).

Crows, rooks and ravens (Corvidae, genus *Corvus* subgenus *Corvus*) display extremely low levels of variability in plumage colouration, voice, size and shape, an unusual conservatism given that crows inhabit all habitats and latitudes, including the

harshest extremes on earth (Madge and Burn 1984). The observation that even recently diverged and sympatric species strongly resemble one another (Goodwin 1986; Laiolo and Rolando 2003a; Haring et al. 2012) challenges the assumption that divergence is required to reduce the costs of interspecific interactions. Crows interact aggressively during breeding, but they often become gregarious and forage communally outside of breeding, protracting interspecific interactions year-round (Rowley 1973; Waite 1984; Goodwin 1986; Madge and Burn 1994; Rolando and Laiolo 1994; Bodey et al. 2009). These birds are keen in recognizing heterospecifics, and respond to their vocalizations with the proper behaviour (Wascher et al. 2012; Bilá et al. 2016). Goodwin (1986) first hypothesised that similarity may stem from the advantage, in terms of resource acquisition and defence, or protection from predation, of adopting intraspecific behaviours towards members of sympatric congeners during interspecific encounters.

Crow phenotypic convergence has been mentioned in a number of comparative studies (Laiolo and Rolando 2003a; Haring et al. 2012) but the mimicry hypothesis has never been explicitly addressed, either in sympatric vs. allopatric population comparisons at microevolutionary scales, or among species at macroevolutionary scales. At the present levels of knowledge, therefore, non-social hypotheses cannot be discarded, such as that of a generalized lack of divergence or selection on traits (Ackerly et al. 2006), or of convergence driven by shared pressures of the physical environment (Conte et al. 2012). In this study, I adopt a comparative, macroevolutionary framework to scrutinize the relationship between species co-occurrence patterns and acoustic and morphological similarity in the 46 species of the *Corvus* genus. Features such as morphology and the long-distance caw call are those that, together with black plumage, contribute to creating the crow-template that attracts or elicits following responses in related species as well as conspecifics (Goodwin 1986).

The caw call is common to all species and is given in a variety of situations, from social interactions, and recruitment to food, to mobbing and alarming (Thompson 1982; Conner 1985; Laiolo and Rolando 2003a; Martens et al. 2000). Bill and body size also have self-assertive functions and are themselves a cue during interactions (Richner 1989; Saino and Scatizzi 1991), apart from influencing the structure of vocalizations (Laiolo and Rolando 2003a). I addressed variation in the above characteristics, for which I expect convergence. I also examined the rattle, a call mediating sexual interactions characterized by marked specific distinctiveness (Goodwin 1986; Laiolo and Rolando 2003b). Neither divergence nor convergence is expected for this call, uttered by mates in close contact (Goodwin 1986), thus with little possibility for specific confusion or acoustic degradation.

In a scenario of divergent character displacement, the evolutionary differentiation of phenotypic traits should lead to a faster transition to sympatry of closely related species (Pigot and Tobias 2013). In species that use these traits in interspecific communication, convergence should promote coexistence. To test this prediction of the mimicry hypothesis I analysed the influence of acoustic and morphometric differentiation on the process of transition to sympatry of the youngest lineages after their initial allopatric split. I then analysed acoustic and morphometric evolution under the selective regimes imposed by co-occurring congeners and the environment (e.g., habitat and climate), and constrained by phylogeny (Hansen 1997; Seddon 2005). For the mimicry hypothesis to be supported, congener caw and morphology should influence the evolution of the same traits in coexisting species. Alternatively, if the environment-driven convergence hypothesis is true, the climate or the habitat, rather than the phenotype of sympatric congeners, should explain patterns of sympatric similarity. Eventually, the hypothesis of a lack of diversification should be supported by

strong phylogenetic constraints hampering evolutionary shifts, and nondivergence involving all traits.

Materials and methods

ACOUSTIC DATA

For this study, I completed personal data and recordings from the British Library published in previous studies (Laiolo and Rolando, 2003a and b) with new records from Xeno-canto, AVoCet and the Macaulay Library (Table S1). The resulting sample consists of 1223 caws (Fig. 1A) from 46 *Corvus* species and 215 rattles (Fig. 1B) from 35 species. Here I provide a brief summary of the process of selection of acoustic variables, more extensively detailed in Supplementary Tables S1 and S2. I took into account several acoustic variables per call type, and selected those with high levels of interspecific variation also partially explained by phylogeny. This screening aimed at limiting the noise of variation within species induced by motivation, social status, functional intraspecific significance, or non-biological forms of transmission (e.g., culture), which may modify the innate template of calls in a species' repertoire (Gwinner 1964; Heinrich and Marzluff 1991; Verbeek and Caffrey 2002). Five variables of the caw ($0.39 < K < 0.56$; $P < 0.05$) and two of the rattle ($0.35 < K < 0.53$; $P < 0.05$) had a significant phylogenetic signal and were considered in further analyses. Variables with no significant phylogenetic signal tend to correlate with the former, but have higher levels of within-species variability that likely hinder the influence of common ancestry (18% among- and 27% within-individual variability, as compared to 15% and 17% of variables with significant phylogenetic signal; details in Tab. S1). I am therefore confident that I am not excluding the most probable candidates for convergence, but rather the noise of intraspecific variation.

The five caw variables (call and pulse durations, fundamental and maximum carrying frequencies, and frequency range) were then reduced to two principal components by a Phylogenetic Principal Component Analysis (Revell 2009). The first component correlated with frequency variables (hereafter CawPC1: $0.64 < \text{loadings} < 0.74$, Variance explained: 35%) and the second to temporal ones (CawPC2: $0.67 < \text{loadings} < 0.77$, Variance explained: 25%) (Tab. S1). Since phylogenetically-informed principal components may alter data phylogenetic structure and bias results (Polly et al. 2013; Uyeda et al. 2015), the robustness of analyses was also assessed with raw variables, which also permitted accounting for variable measurement errors (standard errors). No variable reduction procedure was applied to rattle variables, since just two variables passed the above criteria (carrying frequency, hereafter RattleF, and pulse duration, RattleDP) and were uncorrelated between each other ($R = 0.05$, $P = 0.72$). Analyses were implemented with Avisoft-SASLab Pro (Avisoft Bioacoustics, Germany) and the R package *phytools* (Revell 2012).

MORPHOLOGICAL, PHYLOGENETIC AND ECOLOGICAL DATA

The average and standard error of bill and wing length per species were calculated from published literature (Madge and Burn 1994; Laiolo and Rolando 2003a; Tab. S2). All comparative analyses were based on phylogenetic information obtained from the calibrated phylogeny of Jönsson et al. (2016b), which has the greatest taxonomic coverage, and includes sequence data for the largest number of species, among those published thus far (Tab. S3). Information on aspects of species β -niche (habitat and climate) that may condition signal structure and morphology was obtained from global climate models and remote-sensing data, handled with QGIS 2.12.3 (Quantum GIS Development Team, 2012). *Corvus* range maps were kindly provided by BirdLife International and NatureServe (2012) in a polygon format. Originals were redrawn for

clades split off by Jönsson et al. (2016b) and Gill and Donsker (2016) by following Madge and Burn (1994). Maps were resampled to a reference gridded system of 30-arcmin resolution, totalling 69,142 cells with presence/absence data of each species and including the distribution of the entire group (Fig. 1C). I described climate variation by means of the 19 bioclimatic variables representing annual and seasonal trends of temperature and precipitation of the World Clim database (resolution of 30-arcsec; <http://www.worldclim.org/current>). A principal component analysis was run to summarize variation of these variables in the reference gridded system with 69,142 cell entries, which generated five components explaining 93% of climatic variation (hereafter, ClimatePC1, 2, 3, 4, 5; Tab. S2 and S4). I also accounted for vegetation density, downloading digital layers of the MODIS Vegetation Continuous Field VCF (15-arcsec resolution; <http://glcf.umd.edu/data/vcf/>) (Tab. S2). Within the range of each species, the average and standard error of climate principal components and of the index of vegetation density were calculated. Species averages of morphological and ecological traits retained a significant phylogenetic signal ($0.35 < K < 0.78$; $P < 0.05$).

Species' co-occurrence or segregation patterns were quantified by identifying significantly positive pairwise species associations. By applying the approach proposed by Veech (2013) to a species presence/absence matrix, I calculated the probability that any two species would co-occur at a frequency greater than the observed frequency if they were distributed independently of one another among cells. This method is based on probabilities of co-occurrence rather than on randomizations or simulations (Veech 2013). It permitted the identification of the set of species that positively co-occurred, a grouping confirmed by alternative indices of complementarity, such as the C-score (Tab. S5). These analyses were implemented with the R packages *letsR* (Vilela and Villalobos 2015), and *cooccur* (Griffith et al. 2015).

STATISTICAL ANALYSES

I first analysed whether caw, rattle, morphological and ecological differentiation influenced the transition to secondary sympatry of the youngest species (sister species) after their initial allopatric split. Then, in an expanded analysis not restricted to sister-taxa, I addressed the factors that may condition the evolution of caw, rattle and morphological traits of species, i.e. climatic niche and habitat, phylogeny as well as the phenotypic value of co-occurring species. According to the mimicry hypothesis, a return to sympatry of sister species should be hampered by high levels of differentiation or, in other words, be facilitated by similarities in caws and morphology. These traits should also coevolve with the caws and morphology of coexisting congeners when controlling for the influence of the physical environment and phylogeny.

The influence of phenotypic and ecological differentiation on the probability of co-occurrence of sister species

I first identified the youngest (sister) species in the maximum clade credibility tree published by Jönsson et al. (2016), totalling 16 pairs. The resulting pairs agree with the phylogeny previously published by Haring et al. (2012) with respect to species in common. I assumed that the initial state of sister species was allopatric, as is typical in this group (Haring et al. 2012), and used continuous multi-state Markov models to model the transition to an irreversible state of secondary sympatry as an exponential function of time. In models, each pair of sister species contributed two observations: the state at time zero, established as allopatric, and that at the present (e.g., at the observed node age), categorized as sympatric when species positively co-occur (Tab. S5). After running a constant-rate model entering exclusively phylogenetic distance, I included as covariates differences between sister species in acoustic variables (CawPC1, CawPC2, RattleF, RattleDP), morphological variables (wing and bill length) and ecological

variables (vegetation density and ClimatePC1, 2, 3, 4, 5). These differences were calculated as the absolute contrasts (absolute values of differences) of the means of each variable or principal component. The fit of models including covariates over the constant-rate model was assessed by means of the Akaike Information Criterion corrected for small sample size (AIC_c) and likelihood ratio tests. The effect of covariates was assessed by hazard ratios, which are significant when the 95% CI does not include 1. If the transition to sympatry is hampered by trait dissimilarities, hazard ratios should be < 1 , and should be > 1 when divergence facilitates the transition. Given that the number of species with rattle data was lower than that of the other variables, models were initially run with the lowest sample of pairs (those with available rattle data, 10 pairs) for comparisons based on the Akaike Information criteria. They were then repeated excluding rattle data with the entire set of 16 pairs, to test the robustness of the above results for the rest of the variables, for which a larger sample of sister taxa was available. Multi-state models were run in R with the package *msm* (Jackson 2011).

Drivers of phenotypic similarity

~~In order to~~To analyse whether the acoustic or morphological characteristics of a species could be influenced by (i.e., match) those of coexisting congeners, the averages and variances of these features in positively co-occurring species were calculated and used as predictors of congener influence. Since the phenotypic characteristics of any given species could be both the target (response) and the agent of selection on coexisting species (predictor), this approach inevitably leads to non-independent response and predictor variables if all species combinations are considered. To overcome this bias, the species contributing to the dependent variable were selected among those that never (naturally) occurred among the co-existing species of others, a condition met by 13 species in the rattle dataset and 16 in the datasets of the other variables (Tab. S5). I used

this set of species to model variation of acoustic and morphological variables as a sum
 of random noise and a deterministic pull toward particular states determined by
 predictor variables, weighting by the measurement error (standard error) of response
 and predictor variables when available (Hansen 1997; Hansen et al. 2008). Analyses
 were run with *slouch* in R (Hansen et al. 2008), in which trait optima were modeled on
 environmental and social variables that also change over time, thus approximating the
 conditions of traits that may coevolve with species ecological niche and the phenotype
 of co-occurring congeners (Laiolo et al. 2015). In such models, the evolutionary lag was
 quantified by phylogenetic half-life $t_{1/2}$, which indicates the time to move halfway from
 the ancestral state to the primary optimum ($t_{1/2}$ attains high values when the process of
 adaptation is slow). As predictors for caw and rattle variables, I considered the two
 morphological traits, the five climate components, the index of vegetation density and
 the acoustic characteristics of co-occurring species (e.g., for CawPC1 as a response
 variable, I entered the average CawPC1 of the caws of co-occurring species). As
 predictors for wing and bill lengths, I considered the five climate components, the index
 of vegetation density and the morphological characteristics of co-occurring species
 (again, for wing length as a response variable, I entered the average wing length of co-
 occurring species). I used the AIC_c to assess the fit of models including different
 combinations of predictors, considering as equally probable models separated by less
 than three AIC_c points from the model with the lowest AIC_c .

~~In order to~~To discriminate between the direct and spurious (environment-driven)
 effect of social environment on species phenotypic characteristics, I also performed
 phylogenetic path analyses (von Hardenberg and Gonzalez-Voyer 2013). In cases of
 significant influence of both predictors, these analyses permit the testing of the relative
 importance of alternative causal models including the direct and indirect influences of

predictors on the response variable. Models were fit with PGLS regressions with the correlation structure of Martins and path model performances were assessed by an information criterion similar to AIC_c adapted to path analyses, the CIC_c , (details in Tab. S6). The R packages *caper* (Orme et al. 2012), *ape* (Paradis et al. 2004) and *nlme* (Pinheiro et al. 2012) were used.

Results

THE INFLUENCE OF PHENOTYPIC AND ECOLOGICAL DIFFERENTIATION ON THE PROBABILITY OF CO-OCCURRENCE OF SISTER SPECIES

In the sample of 10 species pairs with complete data, three models better explained the transition to secondary sympatry of *Corvus* species than the simple model including time only (all $\log\text{-LR test} > 6.62$, $P < 0.01$). These considered a transition delayed by species differences in either caw durations (CawPC2: hazard ratio = 0.38, CI: 0.15 - 0.95) or wing length (0.92, CI: 0.86 - 0.99) or accelerated by differences in ClimatePC3, the component positively correlated with temperature of the wet and warm quarter (hazard ratio = 51.9, CI = 1.24 - 2156) (Fig. 2A). Obviously, if similarities rather than dissimilarities are set as covariates, CawPC2 and wing length similarities assist the transition (hazard ratios = 2.6 and 1.1, respectively) and ClimatePC3 hampers it (0.16). Allopatric and sympatric sister species varied in the magnitude of differentiation of these traits (wing length and CawPC2: $t_9 > 2.3$, $P < 0.05$, climate PC3: $t_9 = 1.8$; $P = 0.10$, tested with PGLS regressions controlling for node phylogeny) (Fig. 2B). The performance of multi-state models including the other variables performed worse. In particular, models including rattle dissimilarities or CawPC1 were separated by over 6

AIC_c points from the best models and hazard ratios overlapped zero (RattleF: 0.001 - 60; RattleDP: 0.98 - 1.1; CawPC1: 0.50 - 1.18).

Given the low weight of rattle variables, models were also run excluding them, in the entire set of sister pairs (16). This permitted the assessment of the time of secondary contact, estimated at 4.06 ± 1.82 Myrs after lineage split. It also allowed the confirmation of the influence of caws and body size on the timing of co-occurrence in this larger dataset. The best model, separated by over 10 AIC_c points from the model with differences in climate PC3, was one including the interaction between differences in CawPC2 and wing length, with a hazard ratio of 0.64 (CI: 0.44-0.91; log-LR test 18.46, $P < 0.001$). This result indicates that species differing largely in caw temporal features as well as body size take more time to attain sympatry, reinforcing the results obtained with the lowest sample. Models run with raw variables confirmed results obtained with CawPC2, with caw duration as the covariate included in the best model (hazard ratio: 0 - 0.01; *log-LR test* 6.62, $P = 0.01$).

DRIVERS OF PHENOTYPIC SIMILARITY

Variables associated with the phenotypic characteristics of coexisting congeners were included in the best models explaining variation of CawPC2 and wing length. There was a positive correlation between these traits in target species and the respective trait value of coexisting congeners (Fig. 3; Tab. 1). Over 83% of variation in CawPC2 of target species was explained by the CawPC2 of coexisting congeners in combination with temperature of the cold and dry quarter, e.g. ClimatePC1 (32% and 50% of variation, respectively, when social and climate predictors were entered alone). Path analyses indicated that the influence of congeners' traits was direct and fully independent from that of climate. The pathway depicted in Fig. 3B outperformed models with no direct influence of the social surrounding ($\Delta\text{CICc} > 11.9$; Tab. S7). The

best model explaining variation in wing length included the average wing length of coexisting congeners (Fig. 3C), although it only explained 13% of variation and phylogeny had a marked influence (high half-life $t_{1/2}$) (Tab. 1).

Ecological predictors had a weak influence on CawPC1 and the two rattle variables, and no relevant matching with CawPC1 or rattle variables of coexisting congeners occurred. For these variables, no model outperformed a null model including the sole intercept, although a weak correlation was found between CawPC1, the index of vegetation density and climate PC1, and between RattleF and bill length (Tab. 1). Wing length had no marked effect on CawPC1 ($R^2 = 0.088$) and CawPC2 ($R^2 = 0.036$), meaning that traits influenced by the social environment, CawPC2 and wing length, were fully independent. The length of the bill varied allometrically with that of wings with no influence of other predictors (Tab. 1). When repeating models with raw caw variables instead of principal components, the effect of social predictors was confirmed while vegetation density slightly increased its influence, especially on fundamental frequencies (Table S7).

Discussion

The body sizes and durations of the caws of crows display high levels of similarity among sympatric species. Two lines of evidence support the hypothesis of social convergence at the macroevolutionary and macroecological scale of this study. First, the time after speciation until sister lineages come into secondary contact was influenced by differences in these phenotypic features, with delayed sympatry for young species giving caws of different durations and differing in body size. Secondly, social factors, expressed here as the average phenotype of co-occurring species, correlated significantly with variation in these traits in an expanded analysis not restricted to sister

taxa and partialling out environmental influences. Crow caw durations and body size did not covary, but their variation was significantly associated with the social as well as the physical environment (caw) or phylogenetic history (body size). Convergence in these features does not appear to be a case of interspecific social dominance mimicry (Prum and Samuelson 2012; Jönsson et al. 2016a), occurring when a subordinate species uses mimicry to minimize competitive interference with a dominant model taxon of larger body size. Corvids also base their dominance hierarchies on body size (Rolando 1988; Richner 1989; Rolando and Laiolo 1997), but sympatric crows lack size disparities, and both calls and body size differences must be minimized for secondary contact to take place.

Conversely, there was no evidence for mimicry in the rattle call, as expected for a signal addressed to mates in close contact (Chamberlain and Cornwell 1971; Conner 1985). There was some evidence that this vocalization may be influenced by bill size, as is typical of trilled vocalizations (Podos 2001). Species ecological preferences also followed their own evolutionary trajectory: sympatric crows do not share ecological preferences more than allopatric ones, and dissimilarities in CimatePC3 rather accelerated the transition to sympatry in one of the selected transition models. This is the sole result supporting a pattern of limiting similarity in crows, and is in line with observations of other mimic complexes in birds that also exhibit variation in ecology and habitat preferences (Prum 2014).

The fact that caw and body size similarity also involves relatively old sympatric lineages suggests that it may have arisen after initial divergence. However, it is also possible that species with similar phenotype because of slow divergence, lack of genetic variation or directional selection were more likely to achieve secondary sympatry and co-occur extensively. These forms of nondivergence can be viewed as alternative, more

parsimonious mechanisms of convergence (Losos 2011; Tobias et al. 2014), which may have hampered body size variation in crows (Saino and Scatizzi 1991, this study), as in many avian lineages (Harmon et al. 2010). In the case of vocalizations, however, the classic view of convergence (following initial divergence) appears to better fit the observed variation patterns. First, the short phylogenetic half-lives ($t_{1/2}$; Tab. 1) of the caw duration component denotes weak phylogenetic inertia and prompt evolutionary shifts in response to predictors, which explain a large portion of variance in this feature. Secondly, the fact that shared climatic conditions contribute to convergence in caw durations and, albeit slightly, caw frequencies, suggests that the caw call is fully exposed to the action of natural and social selection. Vocalizations given in multiple contexts and for different receivers are expected to evolve faster than signals with more limited functions (Wheatcroft and Price 2014), and indeed the most recent crow lineages diverge in some acoustic features of their caws (Palestrini and Rolando 1996; Martens et al. 2000).

Even if social factors emerge as potential drivers of crow caw and body size similarity, several open questions remain. Direct evidence of convergent agonistic character displacement, the initial process that drives divergence between sympatric and allopatric conspecific populations and convergence between sympatric heterospecific populations, is required to link macroevolutionary patterns with the micro-evolutionary process of adaptation (Tobias and Seddon 2009, Laiolo 2013). It is also unclear why crows, which are well known for their superb learning skills (Emery 2006), should base their interspecific interactions on mimicry rather than on learning their specific signals, as they do with non-crow heterospecifics (Marzluff et al. 2012; Wascher 2012). One possible explanation is that mimicry assures more flexible and complex interspecific relationships than communication based on learning, which is often limited to warning

signals in an anti-predatory context (Marzluff et al. 2012; Wheatcroft and Price 2013).
Social selection, in this sense, may become especially effective in refining mimicry
among closely related congeners, which already display high levels of structural affinity
because of common ancestry (Tobias and Seddon 2009; Losin et al. 2016).

In conclusion, this first attempt to test predictions of the mimicry hypothesis
provides evidence that crow similarities in morphological and acoustic features may be
associated with coevolving interactions with congeners, but also with bioclimatic
preferences and intrinsic constraints to differentiation. Selection leading to
environmental fit can act simultaneously with natural selection on interspecific social
functions, and focusing on environmental convergence is clearly an oversimplification
in the context of the evolution of multifunctional traits (Tobias et al. 2014) and of
mimicry in general (Rainey and Grether 2007). Although the results of this study are
consistent with a broad array of studies documenting convergence among closely
related co-existing species, future empirical work requires downscaling to micro-
evolutionary processes to link convergence and adaptation.

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SUPPORTING INFORMATION

Table S1: Details of acoustic repertoire, analyses and variable selection criteria.

Table S2: Dataset used in this study.

Table S3: Phylogeny of the 46 species of the genus *Corvus* sungenus *Corvus*.

Table S4: Results of Principal Component Analysis performed on bioclimatic variables.

Table S5. List of positive spatial associations among species.

Table S6. Details on phylogenetic path analyses.

Table S7. Models with raw caw variables.

Figure captions

FIGURE 1. A. Sonogram of the caw of a Mariana crow, *Corvus kubaryi* (Andria Kroner, XC254699, Xeno-Canto). **B.** Sonogram of the rattle of a Torresian crow, *Corvus orru* (Emma I. Greig, ML201285, Macaulay Library) **C.** Geographic variation in *Corvus* species richness worldwide.

FIGURE 2. A. Accumulation of secondary sympatry (%) with time since speciation in 10 pairs of sister species. The best three models of transition to sympatry are depicted, including as covariates differences in the principal component positively correlated with caw durations (Δ CawPC2), the principal component positively correlated with temperature of the wet and warm quarter (Δ ClimatePC3), and -body size (Δ Wing length), together with the model with no covariate (Null model). **B.** Average differences ($\pm$ SE) between the abovementioned variables in sympatric and allopatric sister species. Significant differences as emerging from PGLS regressions are shown. * $P < 0.05$

FIGURE 3. A. Relationship between the residuals of CawPC2 (partialling out the effect of ClimatePC1) of a given species and the average CawPC2 of the species that positively co-occur with it, as from the dataset of the SLOUCH regressions. **B.** Diagram of the best models explaining variation in CawPC2, as inferred by phylogenetic path analyses. **C.** Relationship between the wing length ($\pm$ SE) of a given species and the average wing length ($\pm$ SE) of the species that positively co-occur with it, as from the dataset of the SLOUCH regressions. CawPC2 is the principal component positively correlated with caw durations; ClimatePC1 is the principal component positively correlated with temperature of the cold and dry quarter, and negatively correlated with seasonality.

Fig. 1.

Fig. 2

Fig. 3.

Table 1. List of the top ranking models explaining phenotypic variation in *Corvus* species, and predictors included in these models. I considered as equally-probable best models those separated by less than three AIC_c points from the model with the lowest AIC_c, which are highlighted in bold. Optima were modelled on a sample of 16 species for caws and morphological features, and for 13 species for rattles, to allow the independence of response and predictor acoustic variables. Optimal slopes indicate the expected adaptive variation of traits as these were free of phylogenetic constraints, while evolutionary slopes indicate the observed variation due to both adaptation and phylogeny. The value of $t_{1/2}$ measures trait dependence on ancestral values and represents the time (in Myrs) to lose half of the ancestral influence; the stationary variance v_y measures deviations from primary optima because of random drift and unmeasured evolutionary forces.

Response variable	Model	Slope of the evolutionary regression (SE)	Slope of the optimal regression (SE)	AIC _c	R^2	$t_{1/2}$	v_y
CawPC1	Null model	-	-	103.62	-	3	26
	Index of vegetation density	0.21 (0.10)	0.12 (0.06)	103.73	21.09	3	23
	ClimatePC1	1.42 (0.68)	0.98 (0.46)	103.79	21.00	3	23
CawPC2	CawPC2 of co-existing species + ClimatePC1	0.51 (0.10) - 0.84 (0.13)	0.62 (0.13) - 1.00 (0.17)	66.43	83.00	1	1
	Null model	-	-	85.26	-	1	7
RattleF	Null model	-	-	20.70	-	0.1	0.1
	Bill length	-0.017 (0.09)	-0.017 (0.09)	21.85	29.40	0.1	0.1
	Wing length	-0.02 (0.02)	-0.02 (0.02)	23.82	11.18	0.1	0.1

RattleDP	Null model	-	-	3.17	-	1	0.1
	Bill length	0.003 (0.008)	0.004 (0.009)	7.51	12.0	1	0.1
Wing length	Wing length of co-existing species	0.48 (0.07)	0.98 (0.15)	321.4	12.96	4	100
	ClimatePC3	8.47 (4.77)	5.74 (3.21)	526.8	57.5	2	100
Bill length	Wing length	0.16 (0.03)	0.33 (0.06)	120.3	56.93	4	42
	Wing length + Bill length of coexisting species	0.16 (0.03) +0.05 (0.32)	0.63 (0.14) - 0.11 (1.58)	124.9	57.5	10	60