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NICHE EXPANSION AND ADAPTIVE DIVERGENCE DRIVES THE GLOBAL RADIATION OF CROWS AND RAVENS

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The processes that allow some lineages to diversify rapidly at a global scale remain poorly understood. Although earlier studies emphasized the importance of dispersal, global expansions expose populations to novel environments and may also require adaptation and diversification across new niches. In this study, we investigated the contributions of these processes to the global radiation of crows and ravens (genus *Corvus*). Combining a new phylogeny with comprehensive phenotypic and climatic data, we show that *Corvus* experienced a massive expansion of the climatic niche that was coupled with a substantial increase in the rates of species and phenotypic

32 **diversification. The initiation of these processes coincided with the evolution of traits**
33 **that promoted dispersal and niche expansion. Our findings suggest that rapid global**
34 **radiations may be better understood as processes in which high dispersal abilities**
35 **synergise with traits that, like cognition, facilitate persistence in new environments.**
36 Rapid global radiations –defined as rapid evolutionary diversifications of lineages that are
37 accompanied by the colonization of a large fraction of the planet– have been documented in
38 nearly all domains of Life¹⁻³. Despite representing much of current diversity, it is presently
39 unclear why some clades only radiate regionally whereas others become global in similarly
40 short timescales. Current understanding suggests that global radiations are facilitated by
41 exceptional dispersal abilities⁴⁻⁷. These allow the expansion of species ranges and increase
42 the frequency of long-distance dispersal events (e.g., to remote islands or between
43 continents), multiplying the opportunities for allopatric speciation (Fig. 1). However, global
44 radiations often occur across highly dissimilar environments (e.g., across large climatic
45 gradients⁷) and may therefore involve exposure to resources, competitive regimes,
46 predation pressures and climatic conditions that can largely differ from those experienced
47 in the past. Thus, we expect that rapid global radiations may not only be facilitated by a
48 capacity to disperse over long distances, but also by an exceptional ability to respond to
49 new environmental challenges^{8,9}. If so, global radiations should involve a considerable
50 amount of adaptive diversification driven by environmental differences (for example,
51 through ecological speciation¹⁰⁻¹²) (Fig. 1).

52

53 Here, we investigate the importance of adaptive processes in global radiations, asking
54 whether they are associated with niche expansions and parallel pulses of rapid speciation
55 and phenotypic divergence^{10,13}. We address these questions in the genus *Corvus* (crows and
56 ravens), a prominent group within the avian family *Corvidae* that has expanded across the
57 world occupying almost all of Earth's biomes (from hottest deserts to the arctic regions),
58 branching out into at least 46 distinct species¹⁴. In sharp contrast, the diversification of all
59 other genera in *Corvidae* has resulted in far fewer species (≤ 20 species) and the
60 colonization of geographically restricted regions of the planet¹⁵. We begin by building a
61 time-calibrated phylogeny of the superfamily *Corvoidea* to assess whether the
62 diversification of *Corvus* is a fast global radiation. Having shown that the genus exhibits

63 significantly faster speciation rates than its background clade, we then ask whether the
64 rapid accumulation of new species in *Corvus* was coupled with a burst of morphological
65 and ecological diversification. To further interpret the results, we also investigate whether
66 the predicted burst of diversification not only was preceded by the acquisition of traits that
67 facilitate dispersal, but also by those that facilitate the invasion of new ecological niches.
68 Specifically, we focus on body size and encephalization, traits that in birds are thought to
69 increase competitive ability¹⁶, tolerance of novel conditions^{17,18} and improve the capacity to
70 exploit novel ecological opportunities^{19,20}. Our findings across a variety of ecological and
71 phenotypic traits consistently support the notion that the global radiation of crows and
72 ravens was enabled by the joint evolution of an exceptional capacity for long-distance
73 dispersal and an equally impressive ability to exploit new ecological opportunities and
74 adapt to them.

75

76 **Results**

77 *Molecular phylogeny*

78 Our time-calibrated phylogeny of the superfamily Corvoidea (Fig. S1), the parent clade that
79 contains Corvidae, recovered well-supported relationships between species (see Methods)
80 and was highly consistent with previously proposed phylogenetic hypotheses²¹. Our dating
81 estimates indicate that Corvidae started to diversify between 18 and 22 Ma, and that *Corvus*
82 began radiating between 8.8 to 11.3 Ma (around 10 Ma). These findings confirm earlier
83 estimates, which place the *Corvus* radiation on a similarly short timescale²¹⁻²³ and are
84 consistent with the earliest fossils that can unambiguously be assigned to the genus
85 *Corvus*^{24,25}.

86

87 *Dynamics of species diversification*

88 We applied BAMM²⁶ and MEDUSA²⁷ on the maximum clade credibility tree (hereafter
89 MCC tree) to ascertain whether *Corvus* exhibited different diversification dynamics than
90 the rest of Corvidae. In BAMM, we found that the best supported shift configurations
91 involved a single rate increase either at the base of *Corvus* (frequency = 0.36) or at the node
92 separating *Corvus* from its sister genus *Coloeus* (frequency = 0.28) (Fig. 2a and Fig. S2a).
93 Faster rates of diversification in *Corvus* were also detected when comparing mean rates

94 across the posterior set of trees (Fig. S3a). Similarly, a cohort analysis²⁸ confirmed that
95 *Corvus* exhibits macroevolutionary dynamics well detached from all other Corvidae (Fig.
96 S4a). Consistent with these findings, BAMM analyses indicate a significant decay in
97 speciation rates within Corvidae, conspicuously interrupted by a secondary peak of
98 speciation around 10 Ma, the estimated time of origin of *Corvus* (Fig. S2c). MEDUSA
99 analyses on the MCC tree and on the posterior set of trees also indicate that *Corvus* at least
100 double the mean background diversification rate of its family (Figs. S2b and S5a).

101

102 BAMM and MEDUSA can robustly identify nodes or areas within a tree where
103 diversification rates have shifted but are unable to distinguish the exact combination of
104 speciation and extinction that may have driven such shifts²⁹. Thus, we confirmed the
105 existence of heterogeneity in diversification dynamics within Corvidae by evaluating
106 changes in the dynamics of pulled speciation rates²⁹ (hereafter PSR). We note that PSR
107 variation over time is completely identifiable, given that PSR do not depend on parametric
108 assumptions about speciation and extinction rates and all models in a congruent set—as
109 defined by²⁹—share a common PSR curve. As such, analysis of PSR variation is a robust
110 complementary approach to BAMM and MEDUSA analyses. Visualization of PSR
111 variation through time within the family Corvidae confirms our initial findings (Fig. S2c).
112 Specifically, we observe a decay in speciation rates over time interrupted by a secondary
113 peak of speciation around 10 Ma, the estimated time of origin of *Corvus* (Fig. 2b). Thus,
114 our results suggest that, at a minimum, *Corvus* exhibited significantly different
115 diversification dynamics than its background clade and was able to accumulate a much
116 higher number of species per unit of time than closely related genera.

117

118 *Dynamics of phenotypic diversification*

119 If the observed burst of species diversification in *Corvus* resulted from adaptive processes
120 (e.g., ecological speciation), then we predict that this burst should be associated with a
121 parallel increase in eco-morphological diversification^{10,13}. We begin testing this prediction
122 through an analysis of various morphological traits with well-proven locomotory and
123 ecological relevance^{30–35}. Our list of traits includes linear measurements of two elements of
124 the upper limbs (i.e., humerus and ulna), three elements of the lower limbs (i.e., femur,

125 tibiotarsus and tarsometatarsus) and the length, width, and height at the middle point of the
126 upper beak (Table S1). We also characterized shape variation of the beak through
127 geometric morphometrics (supplementary file 1). Linear and geometric morphometrics
128 datasets were analysed independently by generating separate morphospaces through
129 phylogenetic principal components analyses, *p*PCA³⁶. Both of these *p*PCAs were
130 individually optimized under the models of evolution that presented the best relative fit³⁷.

131

132 The *p*PCA of linear measurements was optimized with a BM model of evolution (Table
133 S2). The first three components in this analysis (i.e., LIN1-LIN3) collectively explained
134 94% of variation in linear measurements and reflected functionally relevant variation in
135 body size, beak dimensions (mainly height), and relative wing length (Table S3). Within
136 these components, the genus *Corvus* exhibits the greatest level of morphological variation
137 among Corvidae, particularly in LIN1 and LIN2. Body size (LIN1) is on average larger in
138 *Corvus* than in other Corvidae and shows twice as much variation as the second most
139 variable genus of the family (i.e., *Cyanocorax*) (Fig. 3a). As for variation in beak height
140 (LIN2), *Corvus* also exhibits the greatest disparity in its family, being 2.75 times greater
141 what is observed in the second most variable genus (i.e., *Cyanocorax*) (Fig. 3a). In birds,
142 variation in both traits (body size and beak shape) is linked to differences in ecologies,
143 including resource partitioning^{9,38,39} and shifts in climatic niche⁴⁰⁻⁴² and therefore, the
144 increase in phenotypic disparity observed in *Corvus*, likely reflects an increase in
145 ecological diversification. Critically, we find evidence that wing shape — measured as
146 “hand-wing index” (HWI), a well-known proxy for wing aspect ratio and dispersal ability
147 in birds (see⁴³ and references therein)— significantly covaries with both body size (LIN1)
148 and relative wing length (LIN3) ($F = 4.21$, p -value < 0.001 and $F = 40.56$, p -value < 0.001 ,
149 respectively, Fig. S6). This covariation confirms that *Corvus* has not only longer wings but
150 also a greater potential for long-distance dispersal than most of its close relatives.

151

152 We used three complementary approaches to investigate whether the observed
153 morphospace expansion in *Corvus* was indeed accompanied by accelerated rates of
154 phenotypic evolution: BAMM⁴⁴, MOTMOT⁴⁵ and BROWNIE⁴⁶. Each of these methods
155 relies on different analytical approaches to test for rate heterogeneity across a tree. BAMM

156 and MOTMOT are designed to identify the most likely position and magnitude of rate
157 shifts in a phylogeny with no a-priori assumptions regarding shift locations. BROWNIE, on
158 the other hand, enables testing alternative hypotheses on potential rate shifts at specific
159 nodes of the tree (e.g., the split between *Corvus* and all other Corvidae). Our results are
160 consistent across all three alternatives. In our analysis of body size (LIN1), both BMM
161 and MOTMOT detected a single rate increase, either at the base of *Corvus* (MOTMOT and
162 BMM shift configuration frequency = 0.2), at the split between *Coloelus* and *Corvus*
163 (BMM shift configuration frequency = 0.23), or at the split between *Nucifraga* and the
164 *Coloelus* / *Corvus* clade (BMM shift configuration frequency = 0.28) (Fig. 2c and S7).
165 These findings, as well as a related cohort analysis (Fig. S4b), suggest that acceleration of
166 body size evolution was initiated either at or slightly before the origin of *Corvus*. We note,
167 however, that regardless of the actual location of that shift, mean rates of body size
168 evolution were higher in *Corvus* than in the neighbouring clades in both the MCC tree and
169 in the posterior set of trees (Fig. 2, S3b, S5b and S7). Accordingly, we used the BROWNIE
170 approach to compare a single rate model against a two rates model with a shift at the node
171 that separates *Corvus* from all other Corvidae. Likelihood-ratio tests indicate that the two-
172 rates model is always better supported across the entire posterior set of trees, when we
173 compute rates according to the two-rates model, these are significantly higher in *Corvus*
174 than in other Corvidae (Fig. S8a).

175

176 In our analyses of beak height (LIN2), both BMM and MOTMOT detected a single sharp
177 rate increase either at the base of *Corvus* or within it, specifically, in the clade that contains
178 most of the species in the genus (Figs. 2c, S4c and S7). Once again, this finding was
179 confirmed by the observation that rates of LIN2 evolution are higher in *Corvus*, both within
180 the MCC tree and within the posterior set of trees (Fig. S5b and S7). A similar pattern was
181 also observed with BROWNIE (Fig. S8b). In sharp contrast, neither BMM, MOTMOT
182 nor BROWNIE detected rate heterogeneity in the evolution of relative wing length, LIN3,
183 either within the MCC tree (Figs. S4d, S7), or across the posterior set of trees (Fig. S3b and
184 S5b, S8c).

185

186 We then explored the evolution of beak shape using a geometric morphometric approach. A
187 *p*PCA of superimposed landmark coordinates (see methods) optimized with an Early Burst
188 model of evolution (Table S2), indicates that *Corvus*-specific variation in beak shape either
189 resembles (area of the α -convex hull in GM1 - GM2 morphospace: *Corvus* = 0.017; other
190 Corvidae = 0.024; Fig. 3c) or even surpasses that of all other Corvidae (area of the α -
191 convex hull in GM2 - GM3 morphospace: *Corvus* = 0.019; other Corvidae = 0.014; Fig.
192 3d). In agreement with previous analyses using linear beak measurements, BAMM and
193 MOTMOT indicate that the diversification of beak shape also accelerated within *Corvus*
194 (Fig. S9-S10). Such rate increases were consistently observed with all other methods and
195 across our entire posterior set of trees (Fig. S3c, S5c and S11). Follow up analyses with a
196 phylogenetic MANOVA of centroid sizes on superimposed landmark coordinates indicated
197 that beak size and beak shape components covary (Pillai's trace= 0.64, p-value = 0.01). To
198 address this issue, we recomputed the *p*PCA and the rates of evolution on allometric-free
199 beak shape residuals. Although lower in magnitude, these new metrics produced
200 qualitatively identical patterns to those obtained with the initial shape components (Fig.
201 S12 - S15, S3d and S5d). Based on these findings, we conclude that even though some of
202 the evolution of beak shape in *Corvus* was likely a reflection of changes in beak size (and
203 likely, body size), there is nevertheless strong evidence indicating that *Corvus* beaks also
204 responded independently to selection during the radiation process.

205

206 We further assessed temporal dynamics of morphological diversification in Corvidae by
207 plotting phenotypic disparity through time (DTT)⁴⁷. Specifically, we plotted the mean
208 subclade disparity at each node of the phylogeny against node age and compared it against
209 a null model with a pure Brownian Motion (BM) model of evolution and a single rate for
210 the entire tree. This null model specifically estimates the amount of disparity that can be
211 expected from a simple process of stochastic evolution⁴⁸ and therefore serves as an
212 appropriate baseline for comparison. Empirical DTT plots indicate that most morphological
213 traits exhibited a clear decrease in phenotypic disparity over the first half of the
214 diversification of the family Corvidae (Figs. 4a, b). However, most of these decays were
215 conspicuously interrupted by new pulses of phenotypic disparity that began ca. 10 Ma (i.e.,
216 at the origin of *Corvus*). These empirical patterns are clearly different from the Brownian

217 expectations based on a single model of evolution, which show a linear decrease through
218 time (Fig. 4a-b for findings on the MCC tree and Fig. S16a-b for confirmation across the
219 posterior set of trees).

220

221 To confirm that these effects were indeed produced by the acceleration of rates of evolution
222 in *Corvus*, we simulated phenotypic disparity using the rate variation estimated by BAMM
223 for LIN1, LIN2, GM1, GM2 and GM3 (i.e., the traits for which BAMM detected *Corvus*-
224 specific rate accelerations). Reassuringly, the medians and 95% confidence intervals (CI) of
225 these simulations are broadly consistent with the observed patterns of divergence in all
226 traits (Fig. S17a-b). Additionally, we note that when empirical DTT plots were recomputed
227 excluding *Corvus* from the phylogeny, we did not observe any secondary pulses in
228 disparity (Fig. S18a-b). These two findings strongly indicate that the increase in phenotypic
229 disparity observed in Corvidae ca. 10 Ma can be specifically attributed to the acceleration
230 of phenotypic evolution within *Corvus*.

231

232 *Geographic variation and dynamics of climatic diversification*

233 Our analyses indicate that the genus *Corvus* recolonized most of the areas occupied by
234 other Corvidae and collectively extended the geographic distribution of the family by
235 almost 30% as it moved into regions like Australasia, northern and southern Africa,
236 Madagascar, and the Arabian Peninsula (Fig. 5a-b). This massive geographic expansion is
237 even more remarkable when considering that the second most widely distributed genus in
238 Corvidae (i.e., *Pica*) occupies only a third of the area occupied by *Corvus* (Fig. S19).
239 We took advantage of the vast amount of georeferenced records for Corvidae in eBird⁴⁹ to
240 investigate whether the geographic expansion of *Corvus* was accompanied by a parallel
241 expansion in climatic niche. We used a principal components analysis⁵⁰ to describe the
242 main axes of variation in the climate space occupied by all Corvidae. Of the two main axes
243 identified, the first one, CLIM1, captured primarily a temperature gradient, whereas the
244 second one, CLIM2, captured a gradient in precipitation (Table S4). Visualization of scores
245 of these two axes revealed that while most of the genera in Corvidae occupy relatively
246 small climatic niches, *Corvus* is broadly distributed in climate space (Fig. 5c). Even more
247 striking, the climatic niche of *Corvus* almost completely encompasses that of other

248 Corvidae and further expands it toward warmer (i.e., more negative values in CLIM1, Fig.
249 5c), wetter (i.e., more positive values in CLIM2, Fig. 5c) and drier habitats (i.e., more
250 negative values in CLIM2, Fig. 5c). Not surprisingly, the rates of evolution estimated for
251 both climate axes are generally elevated in *Corvus* as compared to the rest of the family
252 (Fig. 2d, Fig. S20-S22, S3e and S5e). Just as with morphology, the DTT plots for climatic
253 niche components indicate that increasing levels of climatic disparity were primarily
254 produced during the last 10 Ma (Fig. 4c). Here too, these patterns are robust to phylogenetic
255 uncertainty (Fig. S3e and S5e, S16c), and better approximated by a model in which rates of
256 evolution are assumed to be accelerated in *Corvus* (Fig. S17c). In this case, though,
257 significant levels of disparity are still detected in recent times if *Corvus* is excluded from
258 the analysis (Fig. S18c), highlighting the fact that a remarkable amount of climatic niche
259 evolution is also observed in the genera *Pica* and *Urocissa* (see Fig. S20). On a related
260 note, we also found that the genus *Corvus* exhibits the highest number of sympatric species
261 among Corvidae, which indicates that it could have also experienced higher levels of
262 interspecific competition than its closest relatives (Fig. S23).

263

264 *Phenotypic drivers of global radiation*

265 To assess whether the remarkable ecological and lineage diversification of *Corvus* was
266 potentially triggered, as predicted, by the joint evolution of exceptional capacities both
267 disperse and respond to ecological challenges, we now take a closer look at the traits that
268 help distinguish *Corvus* from other Corvidae. We previously showed that *Corvus* differs
269 from most of its close relatives in two key traits related to long distance dispersal and
270 competitive ability: large bodies and long wings relative to the body (Fig. 3a, b).

271 Additionally, extensive natural history accounts and ethological experiments suggest that
272 *Corvus* may also excel in cognitive ability (e.g. ^{51,52}), a feature that is known to increase the
273 ability to tolerate novel environmental conditions^{17,18} and exploit novel ecological
274 opportunities¹⁹. Relative brain size provides a principled way to compare cognitive
275 capacity across bird species, as it is known to correlate positively with behavioural
276 flexibility⁵³, learning⁵⁴, memory⁵⁵, neuron number⁵⁶, and the volume of pallial areas
277 associated with general-domain cognition⁵⁷. We thus evaluated whether body size, relative
278 wing length, and relative brain size increased in value with the origin of *Corvus* (around 10

279 Ma) and maintained comparatively higher values during the early burst of diversification of
280 this genus. Both predictions are strongly supported by our data. Specifically, morphological
281 comparisons show that crows and ravens exhibit larger relative brain sizes than other
282 Corvidae (phylogenetic ANOVA with Pagel's lambda = 0.75, $F = -0.15$, $p\text{-value} = 0.054$;
283 Fig. S24), as well as larger bodies and higher HWI (see results in previous sections).
284 Moreover, ancestral state reconstructions detect substantial increase in mean relative brain
285 size, HWI, and body size at the origin of *Corvus* and indicate that these traits maintained
286 comparatively higher values within this genus throughout its entire radiation process (Fig.
287 6a-c). Importantly, the initial increase in reconstructed values and the maintenance of such
288 high values thereafter are also visible in family-wide averages (Fig. 6d) when *Corvus* is
289 included in these metrics (compare with Fig. S25 for when it is not). Additionally, we note
290 that neither BAMM, MOTMOT nor BROWNIE detect significant rate shifts in relative
291 brain size within Corvidae (Fig. S26). Although diversification in body size significantly
292 increased in *Corvus*, most of the ancestral and current body sizes in *Corvus* are bigger than
293 all other Corvidae (Fig. 2a and 6a).

294

295 **Discussion**

296 Our analyses show that in approximately 10 Ma, crows and ravens experienced a massive
297 geographic expansion that allowed them to re-occupy and even surpass the already broad
298 climatic niche of other Corvidae. In parallel with this geographic and niche expansion,
299 *Corvus* experienced accelerated rates of species diversification accompanied by a
300 remarkable fast expansion of the morphospace. *Corvus* for instance, exhibits the greatest
301 amount of body size variation and the highest rates of body size evolution in Corvidae. In
302 terms of beak shape, crows and ravens not only reproduced many of the shapes already
303 present in their family, but also evolved entirely new beak types in short time-periods (e.g.,
304 *Corvus crassirostris* and *Corvus moneduloides*). Because these morphological traits have a
305 well-established adaptive basis^{9,38,39}, our findings support the notion that the global
306 radiation of crows and ravens cannot merely be understood as the result of dispersal and
307 (non-adaptive) allopatric speciation, but also of considerable adaptive divergence driven by
308 ecological factors¹⁰⁻¹².

309

310 The exact ecological and geographic processes behind the *Corvus* diversification are yet to
311 be determined. One possibility is that the colonization of vastly different climates induced
312 adaptive diversification in body size (e.g., “Bergmann’s rule”⁴⁰) and beak morphology^{41,42}.
313 Additionally, it is possible that some of the morphological divergence observed in *Corvus*
314 was driven by the encounter of new ecological opportunities on islands^{58,59}. Consistently
315 with this interpretation, *Corvus* exhibits the highest rate of island colonization in its family
316 (including at least 15 insular endemics) and is one of the few corvids that reached remote
317 archipelagos like Hawaii (3,800 km from mainland), Guam (1,800 km from mainland) and
318 New Zealand (1,700 km from mainland). Additionally, insular species tend to occupy the
319 periphery of *Corvus*’ morphospace and have produced some of its most divergent beak
320 shapes (Fig. 3a and c-d). Given that many *Corvus* are currently sympatric (Fig. S23), some
321 fraction of the observed divergence could also reflect character displacement driven by
322 interspecific competition⁶⁰.

323
324 The remarkable key adaptations behind the outstanding dispersal ability of *Corvus* and its
325 capacity to tolerate new environmental conditions and invade new ecological niches are
326 also insufficiently understood. Our results suggest a number of potential candidates:
327 elongated wings, bigger bodies, and larger relative brains. Elongated wings are generally
328 correlated with an enhanced potential for dispersal among birds⁶¹ and Corvidae in particular
329 (Fig S6). Large bodies confer significant advantages in interspecific competition¹⁶, and may
330 therefore represent a significant asset during range expansion¹⁶. A large brain, relative to
331 body size, provides the neural basis for behavioural innovation and learning, features that
332 are known to facilitate persistence in new environments and the adoption of new resource
333 opportunities^{17,62}. We note that the rapid radiation of *Corvus* was preceded by the evolution
334 of all three of these traits (Fig. 6), and therefore conclude that it is plausible that they may
335 have triggered the rapid diversification of the clade.

336
337 The exceptional behavioural flexibility of *Corvus* is particularly evident in its extant
338 species, which collectively display the greatest number of behavioural innovations reported
339 for any avian genus⁶³ and are frequent colonizers of human cities⁶⁴ thanks in part to their
340 ability to exploit new resources⁶⁵ and their flexibility in nest site choices⁶⁶. This exceptional

341 behavioural flexibility could nevertheless challenge the idea that exposure to divergent
342 selection played a major role in the diversification of the clade. Specifically, behavioural
343 flexibility (just as phenotypic plasticity⁶⁷) is often portrayed as a potential inhibitor of
344 evolutionary change because it increases an individual's ability to survive and reproduce
345 even with an inappropriate phenotype⁶⁸⁻⁷¹. How, then, could the early evolution of large-
346 relative brain sizes have subsequently facilitated the evolution of new phenotypes in
347 *Corvus*? The answer to this question could lie on theoretical and empirical work that
348 suggests that although behavioural flexibility can reduce the strength of selection, it cannot
349 avoid it altogether, especially when the new selective pressures are very different from
350 those that a species faced in its ancestral niche^{12,69,72-80}. Thus, it is possible that exceptional
351 capacities for behavioural flexibility enabled ancestral *Corvus* to colonize habitats that were
352 very different than the ones they had most recently evolved in, and that their ability to
353 persist under suboptimal conditions allowed selection to subsequently improve the match
354 between their phenotypes and the new environment^{81,82}.

355

356 In conclusion, we have shown that the global radiation of crows and ravens was
357 characterised by bursts of phenotypic and species diversification associated with parallel
358 expansions of geographic ranges and ecological niches. Because colonization success is
359 often limited by ecological factors¹², these findings suggest that crows were able to
360 colonize the entire globe very quickly not only because they had an exceptional capacity to
361 reach distant locations but also a remarkable ability to persist in suboptimal environments
362 and adapt quickly to new conditions. Beyond the specifics of this case study, our findings
363 more generally indicate that rapid global radiations can be better understood as processes in
364 which dispersal synergises with traits that, like cognition, facilitate survival in suboptimal
365 habitats and ultimately promote the expansion of ecological niches.

366

367 **Methods**

368 **PHYLOGENETIC ANALYSES**

369 We computed a new phylogeny of the superfamily Corvoidea, the parent clade containing
370 the family Corvidae. Working at this large phylogenetic scale allowed us to use multiple
371 calibration points distributed across the superfamily (external to Corvidae) and allowed us

372 to compare the diversification rates computed for *Corvus* and Corvidae, with the
373 background rates in their ancestral clade. To build the phylogeny we used the gene
374 supermatrix provided by Jönsson *et al.*²¹ and updated all missing species in the superfamily
375 with new data from GenBank (GenBank was accessed in late 2017, Table S5). The final
376 dataset included eight nuclear and four mitochondrial genes (see supplementary methods).
377 All genes were aligned through a translation alignment algorithm implemented in
378 TranslatorX (<http://translatorx.co.uk>; ⁸³). Phylogenetic analyses were conducted with the
379 package BEAST v.2.4.8⁸⁴ based on an uncorrelated log-normal relaxed clock and a “Yule
380 process” tree prior. We used the same calibrations used in²¹ to estimate our phylogeny in
381 units of time. The best nucleotide substitution model and partition strategy was estimated
382 through a reversible-jump algorithm⁸⁵, as implemented in the plugin RB in the package
383 BEAST. Tracer version 1.6⁸⁶ was used to confirm convergence and good mixing of each
384 MCMC chain. We calculated the MCC tree with median node heights using TreeAnnotator
385 (also included in BEAST package), setting the posterior probability limit at 0.5. 11 species
386 (four species for which we had morphological data and seven species for which we had
387 climatic data) and that were not available in GenBank were added manually to the MCC
388 tree and to all trees in our posterior following taxonomic and biogeographic criteria. We
389 performed a sensitivity analysis to assess the effect of the added species in our results (see
390 supplementary methods for details on taxon allocation and results of the sensitivity
391 analyses).

392

393 **DYNAMICS OF SPECIES DIVERSIFICATION**

394 We used BAMM v2.5.0²⁶ to infer species diversification rates on the MCC tree of the
395 superfamily Corvoidea (only containing species available in GenBank). This analysis was
396 based on two independent rjMCMC, each reliant on four chains with a thinning interval of
397 10,000 generations and a total chain length of 30 million generations. Prior settings were
398 generated in the R package BAMMtools v2.1.7⁴⁴. After discarding the first 10% of
399 generations as “burn-in”, we assessed convergence of the MCMCs by visualizing the traces
400 of both runs and computing the potential scale reduction factors and the effective sample
401 sizes of each parameter. Species diversification rates across the phylogeny were interpreted
402 by visualizing the means of the marginal posterior density of the rates estimated for each

403 branch. We also visualized and interpreted the best supported shift configurations (i.e.,
404 frequencies ≥ 0.2 in the 95% credible shift set) on the MCC tree and performed a
405 macroevolutionary cohort analysis that estimated the pairwise probability that any two tips
406 in the phylogeny shared the same diversification rate²⁸. Finally, we computed and
407 visualized the median diversification rate through time. To integrate phylogenetic
408 uncertainty into our BAMM analyses, we ran a single rjMCMC chain of 30 million
409 generations across a sample of 100 tree topologies randomly selected from the BEAST
410 posterior distribution (posterior set of trees). For each chain, we extracted the mean
411 marginal densities of rates for all tips of and compared them across the 100 trees. All
412 BAMM outputs were analysed using the R package BAMMtools⁴⁴.

413

414 Aside from BAMM, we also ran MEDUSA in the R package geiger v2.0.6.4⁸⁷ to evaluate
415 birth-death and Yule models while setting shifts between diversification regimes at both
416 nodes and stems. Finally, we used the function `fit_hbd_psr_on_grid` (R package Castor
417 v1.6.7⁸⁸) to fit PSR in homogenous birth-death models on a time grid (evaluated at 8
418 points) when investigating variation in diversification dynamics over time in the family
419 Corvidae. Lower and upper bounds for PSR were set to 0 and 5 respectively.

420

421 **PHENOTYPIC DATA COLLECTION, MORPHOSPACE GENERATION AND** 422 **DYNAMICS OF PHENOTYPIC DIVERSIFICATION**

423 The use of osteological specimens allowed us to include three species of extinct *Corvus* in
424 the study (*Corvus moriorum* from Chatham Island/New Zealand and *Corvus impluviatus*
425 and *Corvus viriosus* from Hawaii). We acquired linear measurements in 93 species (237
426 specimens) and geometric morphometrics of beak shape in 96 species (213 specimens). All
427 measurements were obtained from high definition photographs taken from standardised
428 positions, using the software ImageJ v1.52⁸⁹. To describe beak shape in the geometric
429 morphometric approach, we placed landmarks at the mid-point of the cranio-facial hinge
430 (landmark 1), at the lower margin at the level of the maximum of curvature at the rostral
431 end of the *fossa et fenestra antorbitalis* (landmark 2) and at the tip of the beak (landmark
432 3). These were complemented by 11 equally spaced semilandmarks between landmark 1
433 and 3, and by nine equally spaced semilandmarks between landmarks 2 and 3 (Fig. S27).

434 Within each species, the landmark coordinates of all specimens were superimposed by
435 means of a Generalized Procrustes analysis⁹⁰, where the position of semilandmarks was
436 optimized by allowing them to slide along their respective curves to minimize bending
437 energy. Superimposed coordinates were then projected to a tangent space, from which we
438 calculated the mean shape per species to be used for all downstream analyses. All the
439 aforementioned GM procedures were performed using the function *gpa* in the package
440 *geomorph* v3.2.1^{91,92}. In addition to the morphological data specifically collected for this
441 study, we also collated wing shape data (HWI) from a published source⁴³.

442

443 We used PCAs to generate morphospaces for both linear and geometric morphometric
444 datasets. Morphospaces were computed in the R package *mvMORPH* v1.1.1³⁶ by
445 calculating the covariance matrices of our datasets through the *mvgl*s function, using the
446 rotation-invariant “ridge quadratic null” penalty, and accounting for intra-specific variation
447 and measurement errors in the model fit (i.e., setting the option *SE* to *TRUE*). Given that
448 mis-specifying the evolutionary model can lead to erroneous inferences in phylogenetic
449 PCA³⁷, we fitted three different models and used the best fitting one for downstream
450 analyses. The models considered were Brownian motion (BM, in which evolutionary rates
451 are constant and the mean expected trait change is zero), Early Burst (EB, a variant of the
452 BM model in which rates decrease over time) and Ornstein-Uhlenbeck (OU, evolutionary
453 rates are constant, but traits are pulled towards a single optimum value)⁹³. The relative fit of
454 these alternatives was assessed through the generalized information criterion (GIC) using
455 the GIC function also in the package *mvMORPH*. The covariance matrix obtained by the
456 best model was then converted to a correlation matrix and used to estimate the PCA with
457 the function *mvgl*s.pca (also included in *mvMORPH*). To interpret shape variation along
458 the three first PC axes (see results), we predicted the landmark configurations at the
459 extremes of each PC axes by means of the code provided in³⁶ (see function in
460 supplementary file 2). Predicted shapes at PC extremes were compared to the global mean
461 shape by means of a thin-plate spline deformation grid using the function *plotRefToTarget*
462 from the package *geomorph*⁹². Additionally, beak shape disparities were compared among
463 Corvidae using α -convex hulls computed through the function *ahull* from the R package
464 *alphahull* v2.1⁹⁴.

465

466 Beak sizes were estimated by means of centroid sizes, defined as the square root of the sum
467 of the squared distances between the centre of the landmark configuration and each
468 landmark⁹⁵. We applied a PL-MANOVA⁹⁶ of centroid size against landmarks of species'
469 mean shape configurations (with functions `mvgl`s and `manova.gls` from the package
470 `mvMORPH`), using a Pillai test, an EB model and 1,000 permutations, to test for the
471 existence of shape-size allometry across species⁹⁷. To address this issue, we used the
472 function `mvgl`s to obtain a size-free correlation matrix that was subsequently used to
473 estimate the phylogenetic PCA as described before. All PCA plots were visualized by
474 means of the function `phylomorphospace`⁹⁸ (from the R package `phytools` 0.7-70⁹⁹) to
475 facilitate the phylogenetic interpretation of shape variation.

476

477 We used BAMM with identical model settings as those described in our lineage
478 diversification analyses, to explore the evolutionary dynamics of Corvid morphology based
479 on the first three PC axes of phenotypic variation (in both linear and geometric
480 morphometric data). We assessed rate heterogeneity across the MCC tree and the posterior
481 set of trees by means of the same approaches described earlier for species diversification.
482 We also analysed morphological data with the function `transformPhylo.ML` from the
483 package `motmot` v2.1.3⁴⁵, setting the minimum clade size to infer a rate shift at five species
484 and the maximum of rate regimes in the phylogeny at four. We implemented BROWNIE⁴⁶
485 through the function `brownie.lite` in `phytools` 0.7-70⁹⁹. For each tree in our posterior set, we
486 fitted two alternative models of evolution: one assuming a single rate parameter across the
487 entire phylogeny and another one assuming independent rates for the *Corvus* clade
488 (including stem) and the remaining Corvidae ("noncensored" model in⁴⁶). The two-rates
489 models were fitted by assigning branches to each of the target clades with the function
490 `paintSubTree` (also in `phytools` 0.7-70⁹⁹). Model support was evaluated through a likelihood
491 ratio tests against the χ^2 distribution⁴⁶. The mean subclade disparity through time (DTT)
492 of phenotypic PCs was computed with the function `dtc` (package Geiger⁸⁷), using average
493 squared Euclidean distances. We compared observed DTT patterns against two sets of
494 simulations, one assuming a single BM rate across the entire tree and the other assuming
495 the rate heterogeneity estimated by BAMM (with accelerated rates within *Corvus*, see

496 function in supplementary file 2). Simulations were based on 1,000 replicates after which
497 we computed 95% CI.

498

499 **GEOGRAPHIC AND CLIMATIC DIVERSIFICATION**

500 To compare the geographic expansion of *Corvus* with the rest of genera in Corvidae, we
501 generated presence-absence matrices at a resolution of 0.1° by 0.1° for each corvid genera
502 based on shapefiles provided by BirdLife International (downloaded in Feb 2019¹⁰⁰). With
503 these, we first plotted and compared geographic distributions and areas among corvid
504 genera as well as between *Corvus* and other Corvidae using a Wagner IV equal-area
505 projection. To explore climatic diversification in Corvidae, we downloaded all observations
506 of species in the family from eBird⁴⁹, following the criteria described in Callaghan et al.¹⁰¹
507 and restricting our search from January 2010 to May 2020 (more than 30 million
508 observational records). To reduce redundancy in these data and to avoid potential sampling-
509 related and geographical biases, we subsampled the set of observations to a single locality
510 per species per cell at an approximate resolution of 11x11 km. All species distributions
511 were subsequently visualized to filter out gross errors, such as localities in atypical
512 continents or within water bodies. We then extracted the climatic variables associated with
513 each georeferenced observation using the function “extract” in the package raster¹⁰² and
514 climate data from WorldClim¹⁰³ (<https://www.worldclim.org>) at a resolution of 1.5
515 minutes. The PCA of the background climatic space was produced from the combined
516 dataset for all corvids using the function `dudi.pca` in R package `ade4` v. 1.7-16a¹⁰⁴. For
517 broad-level comparisons we approximated the position of each species in climatic niche
518 space as their mean values in the first two PCA axes. Climatic variation across species was
519 visualized through the function `phylomorphospace`⁹⁸ in `phytools` 0.7-70⁹⁹ to facilitate
520 phylogenetic interpretation. Finally, we also used our curated eBird dataset to estimate the
521 number of unique sympatric assemblages of congeneric species in each genus. A proxy for
522 the levels of potential competition among closely related species (see function in
523 supplementary file 2).

524

525 **DYNAMICS OF RELATIVE BRAIN SIZE EVOLUTION**

526 We measured brain volumes of 76 species (197 specimens) of Corvids, by filling the brain
527 cavity of skulls with 1 mm glass microballoons (GB 01, conservation resources UK
528 limited) of known density and weighing these microballoons with a digital scale at 0.01
529 gram precision. We converted weights to volumes using their known density (Table S6)
530 and obtained relative brain volumes by regressing log-transformed absolute mean brain
531 volumes against log-transformed mean femur lengths. We chose femur length as a proxy
532 for body size because this metric is readily available for all species (including extinct ones)
533 and it is the osteological measure that more closely covaries with body fresh weight in
534 Corvoidea ($cor = 0.9$) (Fig. S28).

535

536 We used phylogenetic linear regression models in phylolm (R package phylolm¹⁰⁵) to
537 compute residual brain sizes, under four different models of evolution: BM,
538 OUrandomRoot (OU process with a stationary distribution for the ancestral state at the
539 root) and OUfixedRoot (OU process with an estimated ancestral state at the root) and EB
540 (early burst). Additionally, we fitted one more phylolm model using Pagel's lambda (a
541 weighing parameter that estimates the extent to which tip similarities can be explained by a
542 BM process). Residual brain sizes for downstream analyses were extracted from the best
543 fitting model given AIC scores¹⁰⁶ (i.e., the model with Pagel's lambda). We note that as
544 expected, brain residuals are uncorrelated with body size (phylogenetic regression: $F = -$
545 0.01 , p -value = 0.89). We also used phylolm to test for relative brain size differences
546 between *Corvus* and the rest of the family Corvidae (phylogenetic ANOVA), comparing
547 the supports of all previously described models.

548

549 The dynamics of relative brain evolution were characterized with BAMM, MOTMOT and
550 BROWNIE using the settings described in earlier sections. To study variation in body size
551 (femur length), HWI and relative brain size through time, we projected the phylogeny into
552 spaces defined by phenotypic values using the function phenogram in the R package
553 phytools⁹⁹. Additionally, we visualized the average ancestral state values of each trait at
554 different time points using the function ace in the package ape¹⁰⁷. To better assess the
555 effects of *Corvus* we compared these macroevolutionary patterns with those obtained after
556 removing all species in this genus from the phylogeny and recomputing the averages.

557

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576

577 **Author contributions**

578 JGP, CB and DS conceived the study. JGP and FS collected data. JGP analysed the data
579 with help from CB, AK, and MP. JGP, CB and DS wrote the manuscript. JGP produced the
580 figures. All co-authors edited the manuscript.

581

582 **Data availability**

583 Data are available as tables S2, S7, S8 and supplementary file 1.

584

585 **Code availability**

586 The custom code used in this study is provided in supplementary file 2.

587

588 **References**

- 589 1. Magallón, S., Sánchez-Reyes, L. L. & Gómez-Acevedo, S. L. Thirty clues to the exceptional
590 diversification of flowering plants. *Ann. Bot.* **123**, 491–503 (2019).
- 591 2. Shi, J. J. & Rabosky, D. L. Speciation dynamics during the global radiation of extant bats.
592 *Evolution (N. Y.)*. **69**, 1528–1545 (2015).
- 593 3. Nicolai, M. P. J. & Matzke, N. J. Trait-based range expansion aided in the global radiation
594 of Crocodylidae. *Glob. Ecol. Biogeogr.* **28**, 1244–1258 (2019).
- 595 4. Coyne, J. A. & Orr, H. A. Speciation Sinauer Associates. *Sunderland, MA* **276**, 281 (2004).
- 596 5. Price, T. & others. *Speciation in birds*. (Roberts and Co., 2008).
- 597 6. Moyle, R. G., Filardi, C. E., Smith, C. E. & Diamond, J. Explosive Pleistocene
598 diversification and hemispheric expansion of a “great speciator”. *Proc. Natl. Acad. Sci.* **106**,
599 1863–1868 (2009).
- 600 7. Van Bocxlaer, I. *et al.* Gradual adaptation toward a range-expansion phenotype initiated the
601 global radiation of toads. *Science*. **327**, 679–682 (2010).
- 602 8. Phillimore, A. B. & Price, T. D. Ecological influences on the temporal pattern of speciation.
603 *Speciat. patterns Divers. Cambridge Univ. Press. Cambridge, UK* 240–256 (2009).
- 604 9. Price, T. D. *et al.* Niche filling slows the diversification of Himalayan songbirds. *Nature*
605 **509**, 222–225 (2014).
- 606 10. Nosil, P. *Ecological speciation*. (Oxford University Press, 2012).
- 607 11. Naciri, Y. & Linder, H. P. The genetics of evolutionary radiations. **1060**, 1055–1072 (2020).
- 608 12. Price, T. D. & Sol, D. Introduction: genetics of colonizing species. *Am. Nat.* **172**, S1–S3
609 (2008).
- 610 13. Schluter, D. *The ecology of adaptive radiation*. (Oxford University Press, 2000).
- 611 14. Gill, F. & Donsker, D. IOC World Bird List (v 8.1). 2018. (2018).
- 612 15. Del Hoyo, J., Del Hoyo, J., Elliott, A. & Sargatal, J. *Handbook of the birds of the world*. vol.
613 1 (Lynx edicions Barcelona, 1992).
- 614 16. Cassey, P. Are there body size implications for the success of globally introduced land
615 birds? *Ecography*. **24**, 413–420 (2001).
- 616 17. Fristoe, T. S., Iwaniuk, A. N. & Botero, C. A. Big brains stabilize populations and facilitate
617 colonization of variable habitats in birds. *Nat. Ecol. Evol.* **1**, 1706–1715 (2017).
- 618 18. Sayol, F. *et al.* Environmental variation and the evolution of large brains in birds. *Nat.*
619 *Commun.* **7**, 1–8 (2016).
- 620 19. Sol, D. Revisiting the cognitive buffer hypothesis for the evolution of large brains. *Biol. Lett.*
621 **5**, 130–133 (2009).

- 622 20. Lefebvre, L. & Sol, D. Brains, lifestyles and cognition: are there general trends? *Brain.*
623 *Behav. Evol.* **72**, 135–144 (2008).
- 624 21. Jönsson, K. A. *et al.* A supermatrix phylogeny of corvid passerine birds (Aves: Corvides).
625 *Mol. Phylogenet. Evol.* **94**, 87–94 (2016).
- 626 22. Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K. & Mooers, A. O. The global diversity of
627 birds in space and time. *Nature* **491**, 444–448 (2012).
- 628 23. Marki, P. Z. *et al.* Breeding system evolution influenced the geographic expansion and
629 diversification of the core Corvoidea (Aves: Passeriformes). *Evolution.* **69**, 1874–1924
630 (2015).
- 631 24. Kessler, J. E. Evolution of Corvids and their Presence in the Neogene and the Quaternary in
632 the Carpathian Basin. *Ornis Hungarica* **28**, 121–168 (2020).
- 633 25. Olson, S. L., Rasmussen, P. C. & others. Miocene and Pliocene birds from the Lee Creek
634 Mine, North Carolina. *Smithson. Contrib. to Paleobiol.* **90**, 233–365 (2001).
- 635 26. Rabosky, D. L. Automatic detection of key innovations, rate shifts, and diversity-
636 dependence on phylogenetic trees. *PLoS One* **9**, (2014).
- 637 27. Alfaro, M. E. *et al.* Lineage-specific diversification rates and high turnover in the history of
638 jawed vertebrates. *Proc Natl Acad Sci USA* **106**, 13410–13414 (2009).
- 639 28. Rabosky, D. L., Donnellan, S. C., Grudler, M. & Lovette, I. J. Analysis and visualization of
640 complex macroevolutionary dynamics: an example from Australian scincid lizards. *Syst.*
641 *Biol.* **63**, 610–627 (2014).
- 642 29. Louca, S. & Pennell, M. W. Extant timetrees are consistent with a myriad of diversification
643 histories. *Nature* **580**, 502–505 (2020).
- 644 30. Kulemeyer, C., Asbahr, K., Gunz, P., Frahnert, S. & Bairlein, F. Functional morphology and
645 integration of corvid skulls—a 3D geometric morphometric approach. *Front. Zool.* **6**, 2
646 (2009).
- 647 31. Zeffler, A., Johansson, L. C. & Marmebro, Å. Functional correlation between habitat use and
648 leg morphology in birds (Aves). *Biol. J. Linn. Soc.* **79**, 461–484 (2003).
- 649 32. Wang, X., McGowan, A. J. & Dyke, G. J. Avian wing proportions and flight styles: first step
650 towards predicting the flight modes of Mesozoic birds. *PLoS One* **6**, (2011).
- 651 33. Corbin, C. E., Lowenberger, L. K. & Gray, B. L. Linkage and trade-off in trophic
652 morphology and behavioural performance of birds. *Funct. Ecol.* **29**, 808–815 (2015).
- 653 34. Kennedy, J. D. *et al.* The influence of wing morphology upon the dispersal, geographical
654 distributions and diversification of the Corvides (Aves; Passeriformes). *Proc. R. Soc. B Biol.*
655 *Sci.* **283**, 20161922 (2016).

- 656 35. Pigot, A. L. *et al.* Macroevolutionary convergence connects morphological form to
657 ecological function in birds. *Nat. Ecol. Evol.* 1–10 (2020).
- 658 36. Clavel, J., Aristide, L. & Morlon, H. A penalized likelihood framework for high-dimensional
659 phylogenetic comparative methods and an application to new-world monkeys brain
660 evolution. *Syst. Biol.* **68**, 93–116 (2019).
- 661 37. Uyeda, J. C., Caetano, D. S. & Pennell, M. W. Comparative analysis of principal
662 components can be misleading. *Syst. Biol.* **64**, 677–689 (2015).
- 663 38. Leyequién, E., de Boer, W. F. & Cleef, A. Influence of body size on coexistence of bird
664 species. *Ecol. Res.* **22**, 735–741 (2007).
- 665 39. Grant, P. R. Bill size, body size, and the ecological adaptations of bird species to
666 competitive situations on islands. *Syst. Biol.* **17**, 319–333 (1968).
- 667 40. Meiri, S. & Dayan, T. On the validity of Bergmann’s rule. *J. Biogeogr.* **30**, 331–351 (2003).
- 668 41. Friedman, N. R. *et al.* Evolution of a multifunctional trait: shared effects of foraging ecology
669 and thermoregulation on beak morphology, with consequences for song evolution. *Proc. R.*
670 *Soc. B* **286**, 20192474 (2019).
- 671 42. Friedman, N. R., Harmáčková, L., Economo, E. P. & Remeš, V. Smaller beaks for colder
672 winters: Thermoregulation drives beak size evolution in Australasian songbirds. *Evolution.*
673 **71**, 2120–2129 (2017).
- 674 43. Sheard, C. *et al.* Ecological drivers of global gradients in avian dispersal inferred from wing
675 morphology. *Nat. Commun.* **11**, 1–9 (2020).
- 676 44. Rabosky, D. L. *et al.* BAMM tools: an R package for the analysis of evolutionary dynamics
677 on phylogenetic trees. *Methods Ecol. Evol.* **5**, 701–707 (2014).
- 678 45. Thomas, G. H. & Freckleton, R. P. MOTMOT: Models of trait macroevolution on trees.
679 *Methods Ecol. Evol.* **3**, 145–151 (2012).
- 680 46. O’Meara, B. C., Ané, C., Sanderson, M. J. & Wainwright, P. C. Testing for different rates of
681 continuous trait evolution using likelihood. *Evolution.* **60**, 922–933 (2006).
- 682 47. Harmon, L. J., Schulte, J. A., Larson, A. & Losos, J. B. Tempo and mode of evolutionary
683 radiation in iguanian lizards. *Science.* **301**, 961–964 (2003).
- 684 48. Slater, G. J., Price, S. A., Santini, F. & Alfaro, M. E. Diversity versus disparity and the
685 radiation of modern cetaceans. *Proc. R. Soc. B Biol. Sci.* **277**, 3097–3104 (2010).
- 686 49. Sullivan, B. L. *et al.* eBird: A citizen-based bird observation network in the biological
687 sciences. *Biol. Conserv.* **142**, 2282–2292 (2009).
- 688 50. Broennimann, O. *et al.* Measuring ecological niche overlap from occurrence and spatial
689 environmental data. *Glob. Ecol. Biogeogr.* **21**, 481–497 (2012).

- 690 51. Heinrich, B. *Ravens in winter*. (Simon and Schuster, 2014).
- 691 52. Taylor, A. H., Hunt, G. R., Medina, F. S. & Gray, R. D. Do New Caledonian crows solve
692 physical problems through causal reasoning? *Proc. R. Soc. B Biol. Sci.* **276**, 247–254 (2009).
- 693 53. Lefebvre, L., Reader, S. M. & Sol, D. Brains, innovations and evolution in birds and
694 primates. *Brain. Behav. Evol.* **63**, 233–246 (2004).
- 695 54. Rensch, B. Increase of learning capability with increase of brain-size. *Am. Nat.* **90**, 81–95
696 (1956).
- 697 55. Roth, T. C., LaDage, L. D., Freas, C. A. & Pravosudov, V. V. Variation in memory and the
698 hippocampus across populations from different climates: a common garden approach. *Proc.*
699 *R. Soc. B Biol. Sci.* **279**, 402–410 (2012).
- 700 56. Olkowicz, S. *et al.* Birds have primate-like numbers of neurons in the forebrain. *Proc. Natl.*
701 *Acad. Sci.* **113**, 7255–7260 (2016).
- 702 57. Sayol, F., Lefebvre, L. & Sol, D. Relative brain size and its relation with the associative
703 pallium in birds. *Brain. Behav. Evol.* **87**, 69–77 (2016).
- 704 58. Garcia-Porta, J. & Ord, T. J. Key innovations and island colonization as engines of
705 evolutionary diversification: A comparative test with the Australasian diplodactyloid geckos.
706 *J. Evol. Biol.* **26**, (2013).
- 707 59. Losos, J. B. & Ricklefs, R. E. Adaptation and diversification on islands. *Nature* **457**, 830–
708 836 (2009).
- 709 60. Stuart, Y. E. & Losos, J. B. Ecological character displacement: glass half full or half empty?
710 *Trends Ecol. Evol.* **28**, 402–408 (2013).
- 711 61. Jenkins, D. G. *et al.* Does size matter for dispersal distance? *Glob. Ecol. Biogeogr.* **16**, 415–
712 425 (2007).
- 713 62. Sol, D. *et al.* Evolutionary divergence in brain size between migratory and resident birds.
714 *PLoS One* **5**, (2010).
- 715 63. Ducatez, S., Sol, D., Sayol, F. & Lefebvre, L. Behavioural plasticity is associated with
716 reduced extinction risk in birds. *Nat. Ecol. Evol.* **4**, 788–793 (2020).
- 717 64. Sayol, F., Sol, D. & Pigot, A. L. Brain size and life history interact to predict urban tolerance
718 in birds. *Front. Ecol. Evol.* **8**, 58 (2020).
- 719 65. Baltensperger, A. P. *et al.* Seasonal observations and machine-learning-based spatial model
720 predictions for the common raven (*Corvus corax*) in the urban, sub-arctic environment of
721 Fairbanks, Alaska. *Polar Biol.* **36**, 1587–1599 (2013).
- 722 66. Kövér, L. *et al.* Recent colonization and nest site selection of the Hooded Crow (*Corvus*
723 *corone cornix* L.) in an urban environment. *Landsc. Urban Plan.* **133**, 78–86 (2015).

- 724 67. Oostra, V., Saastamoinen, M., Zwaan, B. J. & Wheat, C. W. Strong phenotypic plasticity
725 limits potential for evolutionary responses to climate change. *Nat. Commun.* **9**, 1–11 (2018).
- 726 68. Dukas, R. & Ratcliffe, J. M. *Cognitive ecology II*. (University of Chicago Press, 2009).
- 727 69. Huey, R. B., Hertz, P. E. & Sinervo, B. Behavioral drive versus behavioral inertia in
728 evolution: a null model approach. *Am. Nat.* **161**, 357–366 (2003).
- 729 70. Fox, R. J., Donelson, J. M., Schunter, C., Ravasi, T. & Gaitán-Espitia, J. D. Beyond buying
730 time: the role of plasticity in phenotypic adaptation to rapid environmental change. (2019).
- 731 71. Aboitiz, F. Behavior, body types and the irreversibility of evolution. *Acta Biotheor.* **38**, 91–
732 101.
- 733 72. Wcislo, W. T. Behavioral environments and evolutionary change. *Annu. Rev. Ecol. Syst.* **20**,
734 137–169 (1989).
- 735 73. Sol, D., Stirling, D. G. & Lefebvre, L. Behavioral drive or behavioral inhibition in evolution:
736 subspecific diversification in Holarctic passerines. *Evolution.* **59**, 2669–2677 (2005).
- 737 74. Mayr, E., Mayr, E., Mayr, E. & Mayr, E. *Animal species and evolution*. vol. 797 (Belknap
738 Press of Harvard University Press Cambridge, Massachusetts, 1963).
- 739 75. Mayr, E. The emergence of evolutionary novelties. *Evol. after Darwin* **1**, 349–380 (1960).
- 740 76. Hardy, A. C. *The living stream: evolution and man*. (Harper & Row, 1967).
- 741 77. Wyles, J. S., Kunkel, J. G. & Wilson, A. C. Birds, behavior, and anatomical evolution. *Proc.*
742 *Natl. Acad. Sci.* **80**, 4394–4397 (1983).
- 743 78. Plotkin, H. C. *The role of behavior in evolution*. (MIT press, 1988).
- 744 79. Lande, R. Models of speciation by sexual selection on polygenic traits. *Proc. Natl. Acad.*
745 *Sci.* **78**, 3721–3725 (1981).
- 746 80. West-Eberhard, M. J. Phenotypic plasticity and the origins of diversity. *Annu. Rev. Ecol.*
747 *Syst.* **20**, 249–278 (1989).
- 748 81. Sol, D. & Price, T. D. Brain size and the diversification of body size in birds. *Am. Nat.* **172**,
749 170–177 (2008).
- 750 82. Sayol, F., Lapiedra, O., Ducatez, S. & Sol, D. Larger brains spur species diversification in
751 birds. *Evolution.* **73**, 2085–2093 (2019).
- 752 83. Abascal, F., Zardoya, R. & Telford, M. J. TranslatorX: multiple alignment of nucleotide
753 sequences guided by amino acid translations. *Nucleic Acids Res.* **38**, W7–W13 (2010).
- 754 84. Bouckaert, R. *et al.* BEAST 2: a software platform for Bayesian evolutionary analysis. *PLoS*
755 *Comput. Biol.* **10**, (2014).
- 756 85. Bouckaert, R., Alvarado-Mora, M. V, Pinho, J. R. & others. Evolutionary rates and HBV:
757 issues of rate estimation with Bayesian molecular methods. *Antivir Ther* **18**, 497–503

- 758 (2013).
- 759 86. Rambaut, A. & Drummond, A. J. Tracer v1. 4. (2007).
- 760 87. Harmon, L. J., Weir, J. T., Brock, C. D., Glor, R. E. & Challenger, W. GEIGER:
761 investigating evolutionary radiations. *Bioinformatics* **24**, 129–131 (2008).
- 762 88. Louca, S. & Louca, M. S. Package ‘castor’. (2017).
- 763 89. Rasband, W. S. & others. ImageJ. (1997).
- 764 90. Rohlf, F. J. & Slice, D. Extensions of the Procrustes method for the optimal superimposition
765 of landmarks. *Syst. Biol.* **39**, 40–59 (1990).
- 766 91. Adams, D. C. & Otárola-Castillo, E. geomorph: an R package for the collection and analysis
767 of geometric morphometric shape data. *Methods Ecol. Evol.* **4**, 393–399 (2013).
- 768 92. Adams, D. C., Collyer, M., Kaliontzopoulou, A. & Sherratt, E. Geomorph: Software for
769 geometric morphometric analyses. (2016).
- 770 93. Chira, A. M. & Thomas, G. H. The impact of rate heterogeneity on inference of
771 phylogenetic models of trait evolution. *J. Evol. Biol.* **29**, 2502–2518 (2016).
- 772 94. Rodríguez Casal, A. & Pateiro López, B. Generalizing the convex hull of a sample: the R
773 package alphahull. (2010).
- 774 95. Zelditch, M. L., Swiderski, D. L. & Sheets, H. D. *Geometric morphometrics for biologists: a
775 primer*. (Academic Press, 2012).
- 776 96. Clavel, J. & Morlon, H. Reliable phylogenetic regressions for multivariate comparative data:
777 illustration with the MANOVA and application to the effect of diet on mandible morphology
778 in Phyllostomid bats. *Syst. Biol.* **69**, 927–943 (2020).
- 779 97. Dujardin, J.-P., Le Pont, F. & Baylac, M. Geographical versus interspecific differentiation of
780 sand flies (Diptera: Psychodidae): a landmark data analysis. *Bull. Entomol. Res.* **93**, 87–90
781 (2003).
- 782 98. Sidlauskas, B. Continuous and arrested morphological diversification in sister clades of
783 characiform fishes: a phylomorphospace approach. *Evolution (N. Y.)*. **62**, 3135–3156 (2008).
- 784 99. Revell, L. J. phytools: an R package for phylogenetic comparative biology (and other
785 things). *Methods Ecol. Evol.* **3**, 217–223 (2012).
- 786 100. International, B. BirdLife International and handbook of the birds of the world (2017) Bird
787 species distribution maps of the world. (2017).
- 788 101. Callaghan, C. T., Nakagawa, S. & Cornwell, W. K. Global abundance estimates for 9,700
789 bird species. *Proc. Natl. Acad. Sci.* **118**, (2021).
- 790 102. Hijmans, R. & van Etten, J. raster: raster: Geographic data analysis and modeling. *R Packag.
791 version* **517**, 2 (2014).

- 792 103. Fick, S. E. & Hijmans, R. J. WorldClim 2: new 1-km spatial resolution climate surfaces for
793 global land areas. *Int. J. Climatol.* **37**, 4302–4315 (2017).
- 794 104. Dray, S., Dufour, A.-B. & others. The ade4 package: implementing the duality diagram for
795 ecologists. *J. Stat. Softw.* **22**, 1–20 (2007).
- 796 105. Ho, L. S. T. *et al.* Package ‘phylolm’. (2018).
- 797 106. Akaike, H. Information theory and an extension of the maximum likelihood principle. in
798 *Selected Papers of Hirotugu Akaike* 199–213 (Springer, 1998).
- 799 107. Paradis, E., Claude, J. & Strimmer, K. APE: analyses of phylogenetics and evolution in R
800 language. *Bioinformatics* **20**, 289–290 (2004).

801

802 **Figures**

803

804 **Figure 1. Conceptual depictions of the contributions of dispersal abilities and**
805 **adaptability in (global) diversifications.** Increased capacity to disperse over long
806 distances creates more frequent opportunities for allopatric speciation (blue arrows) and
807 exposes lineages to new environments (orange arrows). Traits that facilitate survival and
808 local adaptation under suboptimal conditions prevent local extinction upon arrival and give
809 lineages the opportunity to evolve in response to optimizing selection from the new
810 environmental conditions. These adaptive processes further increase the chances of
811 diversification through ecological speciation.

812

813 **Figure 2. Rates of species, phenotypic and climatic diversification in Corvidae.** Family-
814 wide variation in rates of (a) species diversification, (c) phenotypic diversification and (d)
815 climatic diversification as estimated with BAMM. Circles indicate the alternative position
816 of shifts in shift configurations with a frequency higher than 0.2 for linear measurements
817 and 0.05 for climate (diameter and grey shading is proportional to the frequency). Squares
818 indicate shifts detected by MEDUSA (red) and MOTMOT (black). LIN1 = body size;
819 LIN2 = beak height; CLIM1 = Temperature gradient; and CLIM2 = Precipitation gradient.
820 (b) Speciation rates through time as estimated by pulled speciation rates. Grey shaded area
821 depicts 95% credible intervals.

822

823 **Figure 3. Morphological diversity in the family Corvidae.** Upper panels (a-b) depict the
824 morphospace derived from a phylogenetic PCA on linear measurements. Lower panels (c-
825 d) depict the morphospace of beak shape derived from a phylogenetic PCA on data
826 obtained through geometric morphometrics. Black lines depict phylogenetic relationships
827 among species. Blue regions highlight the extent of the beak morphospace occupied by
828 *Corvus*. Peripheral graphs in the bottom panels depict thin-plate spline deformation grids to
829 help visualize extreme shapes along each axis.

830

831 **Figure 4. Evolution of phenotypic disparity in Corvidae.** Mean subclade disparity
832 through time (DTT) for (a) linear measurements and (b) beak shape obtained through
833 geometric morphometrics. Dashed lines indicate median subclade DTT based on 1,000
834 simulations of character evolution under a Brownian motion model with a single tree-wide
835 rate of change. Grey shaded areas depict 95% credible intervals for DTT estimated in
836 simulation. Vertical dashed lines indicate the onset of diversification of the genus *Corvus*.

837

838 **Figure 5. Distributions and climatic niche of *Corvus* and Corvidae.** World distributions
839 of (a) all species of Corvidae excluding *Corvus* and (b) all species of *Corvus*. (c) Climatic
840 space occupied the family Corvidae. Black lines depict phylogenetic relationships among
841 species. (d) DTT for climatic diversification in the family Corvidae. The vertical dashed
842 line indicates the onset of diversification of the genus *Corvus*. Grey shaded areas depict
843 95% credible intervals for DTT estimated in simulation.

844

845 **Figure 6. Evolution of body size (as estimated from femur length), wing shape (as**
846 **estimated by “hand-wing index”, HWI), and relative brain size in the family**
847 **Corvidae.** The vertical positions of nodes in phenograms (a-c) depict the reconstructed
848 values of a given trait, whereas their horizontal position (i.e., time of divergence) and
849 connectivity reflect the underlying phylogeny (*Corvus* branches are highlighted in red). (d)
850 Clade-wide patterns of variation in the mean ancestral body size, HWI, and relative brain
851 size through time.