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Low ecological disparity in Early Cretaceous birds

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Ecological divergence is thought to be coupled with evolutionary radiations, yet the strength of this coupling is unclear. When birds diversified ecologically has received much less attention than their hotly debated crown divergence time. Here, we quantify how accurately skeletal morphology can predict ecology in living and extinct birds, and show that the earliest known assemblage of birds (= pygostylians) from the Jehol Biota (≈ 125 Ma) was substantially impoverished ecologically. The Jehol avifauna has few representatives of highly preservable ecomorphs (e.g. aquatic forms) and a notable lack of ecomorphological overlap with the pterosaur assemblage (e.g. no large or aerially foraging pygostylians). Comparisons of the Jehol functional diversity with modern and subfossil avian assemblages show that taphonomic bias alone cannot explain the ecomorphological impoverishment. However, evolutionary simulations suggest that the constrained ecological diversity of the Early Cretaceous pygostylians is consistent with what is expected from a relatively young radiation. Regardless of the proximate biological explanation, the anomalously low functional diversity of the Jehol birds is evidence both for ecological vacancies in Cretaceous ecosystems, which were subsequently filled by the radiation of crown Aves, and for discordance between taxonomic richness and ecological diversity in the best-known Mesozoic ecosystem.

1. Introduction

Birds thrive in environments across the globe and exhibit a striking array of ecologies [1], yet when and how birds achieved such staggering disparity remains contentious [2,3]. The debate surrounding bird origins has mostly centred on the controversial timing of crown divergences [2,4–7]. Understanding when birds radiated ecologically requires understanding their fossil record of disparity. We apply classical statistics and comparative methods [8] to predict ecology in fossil birds from the Early Cretaceous Jehol Biota from China based on ecological, morphological and phylogenetic data from extant avians. This allows us to quantify ecology in the oldest multitaxic assemblage of birds known [9]. After accounting for taphonomic biases, our results paint a picture of a functionally gap-filled assemblage lacking the diversity of ecologies that characterize modern assemblages.

2. Data and methods

(a) Ecomorphological correlations in extant birds

We compiled ecological data in the form of 16 binary, one continuous and two multistate variables describing habitat and diet for our extant species, then took limb measures and scored beak shape variables for 1375 specimens representing 630 extant genera in over 170 modern bird families (electronic supplementary material). Building on previous work [10–13], we computed the distances between taxa in ecological and morphological space separately, applied principal coordinate analyses to each data matrix to create continuous variable sets for both ecology, then used canonical correlations analysis (CCA) and phylogenetic CCA (pCCA [8]) to find how the morphological and ecological data were correlated both with and without

Table 1. Nearest neighbours of fossil taxa from CCA. Nearest five neighbours in CCA morphospace for taxa with known diet or habitat preferences; taxa consistent with preserved ecological evidence are shown in bold type. The probability of drawing a consistent extant genus at random (these values were used in the binomial test), and when the probabilities are weighted by CCA and pCCA distances, are shown. See the electronic supplementary material for a complete listing of nearest neighbours for Jehol taxa in CCA space.

fossil taxon	nearest neighbours	uniform prob.	CCA prob.	pCCA prob.
Jeholornis	*Buteo*, ***Ectopistes***, ***Macrocephalon***, ***Otidiphaps***, ***Strepera***	0.346	0.597	0.444
Sapeornis	***Crax***, ***Crossoptilon***, ***Francolinus***, ***Guttera***, ***Tetraogallus***	0.346	0.996	0.961
Jianchangornis	*Elanoides*, *Herpetotheres*, *Leptosomus*, *Micrastur*, *Surnia*	0.108	0.051	0.068
Confuciusornis	***Chionis***, *Gracula*, *Lophodytes*, *Pharomachrus*, *Rhynchopsita*	0.108	0.081	0.113
Hongshanornis	***Centropus***, ***Crypturellus***, ***Ixoreus***, ***Leptotila***, *Treron*	0.346	0.838	0.517
Archeorhynchus	***Aix***, ***Ectopistes***, *Nyctibius*, *Phibalura*, ***Pterocles***	0.395	0.395	0.352
Yanornis	***Burhinus***, *Dryocopus*, *Mergus*, *Otidiphaps*, *Uria*	0.013	0.204	0.059
Gansus	***Laterallus***, *Mimus*, *Pitta*, ***Porzana***, ***Sarothrura***	0.164	0.336	0.29
Piscivoravis	*Dumetella*, ***Laterallus***, *Mimus*, ***Sarothrura***, ***Steganopus***	0.108	0.174	0.16
Bohaiornis	***Amblyornis***, ***Crex***, ***Psophodes***, ***Pteroptochos***, ***Thinocorus***	0.395	0.424	0.524

phylogenetic data. For pCCA, we used the sequence-based trees, rather than the full 'supertrees', of Jetz *et al.* [3] for 576 of the genera. This procedure produces a matrix of scores transformed such that morphology and ecology are maximally mutually correlated for extant birds.

(b) Testing ecological predictions for fossil birds

We assessed how well extant bird ecomorphology predicted ecology in stem birds by exploiting the fact that fossil birds occasionally preserve extrinsic ecological evidence [14,15]. Gut contents are preserved in eight Early Cretaceous pygostylians (plus the nearest relative of pygostylians, *Jeholornis*) [16–23] and aquatic habits are inferred for the non-Jehol ornithurine *Gansus* based on the preservation of webbed feet [24]. Li *et al.* [21] and Zheng *et al.* [23] have interpreted the 'gastroliths' in *Bohaiornis* and *Yanornis* as potentially unrelated to herbivory; however, for consistency, we treated the presence of stones in the digestive tract as evidence of some herbivory in all taxa and used our ecomorphological results to test their interpretations.

We tested the predictive power of extant bird ecomorphology in stem birds by two main ways. First, we found the five extant nearest neighbours in CCA space to the each of the 10 testable extinct taxa (those that preserve ecological evidence; table 1). We evaluated how many of those five extant nearest neighbours were consistent with the preserved ecological evidence for each testable extinct taxon. As each ecological category is present in extant birds at different frequencies, the extinct taxa vary in their expected number of consistent analogues (e.g. more extant eat seeds than eat fish, so extinct taxa with preserved seeds expected to have more consistent nearest neighbours; chance of matching each fossil given in table 1). We determined the probability of finding as many or more consistent analogues in the five nearest neighbours for each testable extinct taxon using the binomial distribution. The product of these individual binomial probabilities is the chance of finding as many or more matches across all 10 testable extinct taxa simultaneously (i.e. the overall *p*-value reported below).

For our second approach, we incorporated the distances between extinct taxa and their extant analogues to better capture uncertainty. We modelled the probability an extant genus is chosen as an analogue for an extinct taxon as decaying exponentially with the morphological distance between them. In this model, the more morphologically dissimilar an extant taxon is from an extinct taxon, the less likely it will be chosen as an

analogue. We used the distances in both CCA and pCCA space to find the probability of choosing a consistent analogue for each of the testable extinct taxa (table 1; see the electronic supplementary material). The exponential decay rate was fitted by maximizing the probability of drawing a consistent modern analogue for all extinct taxa with ecological evidence simultaneously using the function optimize() in R.

(c) Accounting for taphonomic biases

Although modern bird assemblages across the world occupy similar portions of morphospace [25], not all members of a given living assemblage are equally likely to be preserved. If species were preserved randomly with respect to morphology, the estimates of disparity in a fossil assemblage would be unbiased. However, ecological factors (such as aquatic habits) and morphological factors (such as body size) may influence preservation potential, especially in birds [2]. To account for such biases, we compare morphospace occupation between the Jehol assemblage, extant avifaunas and fossil/subfossil assemblages from the Quaternary (collectively referred to as subfossil assemblages, 35 total). These collections range in age from 40 000-year-old fossils to modern death assemblages (median age of 2556 years old; see the electronic supplementary material). Young deposits were chosen to minimize the effects of ecological and evolutionary differences between the ancient and modern avifaunas, so as to more readily detect preservation biases.

We explicitly characterize the ways in which preservation distorts morphological disparity by comparing these subfossil assemblages with extant assemblages from the same geographical regions. The modern assemblages include 38 bird conservation regions from across North America for which we had more than two-thirds coverage at the generic level (data from ebird.org; see the electronic supplementary material) and Yellowstone National Park, a modern climatic analogue to the Jehol [26], as well as occurrence in nine counties comprehensively vouchered in the Field Museum collections (see the electronic supplementary material).

We also tested whether the Jehol birds known from multiple specimens occupied a different region of morphospace than those known from singletons using Hotelling's T^2 test. This approach can only say that the two groups are not significantly different at the current sampling level (i.e. a non-significant difference is not the same as no difference), but serves as a supplement to the other taphonomic analysis by at least quantifying
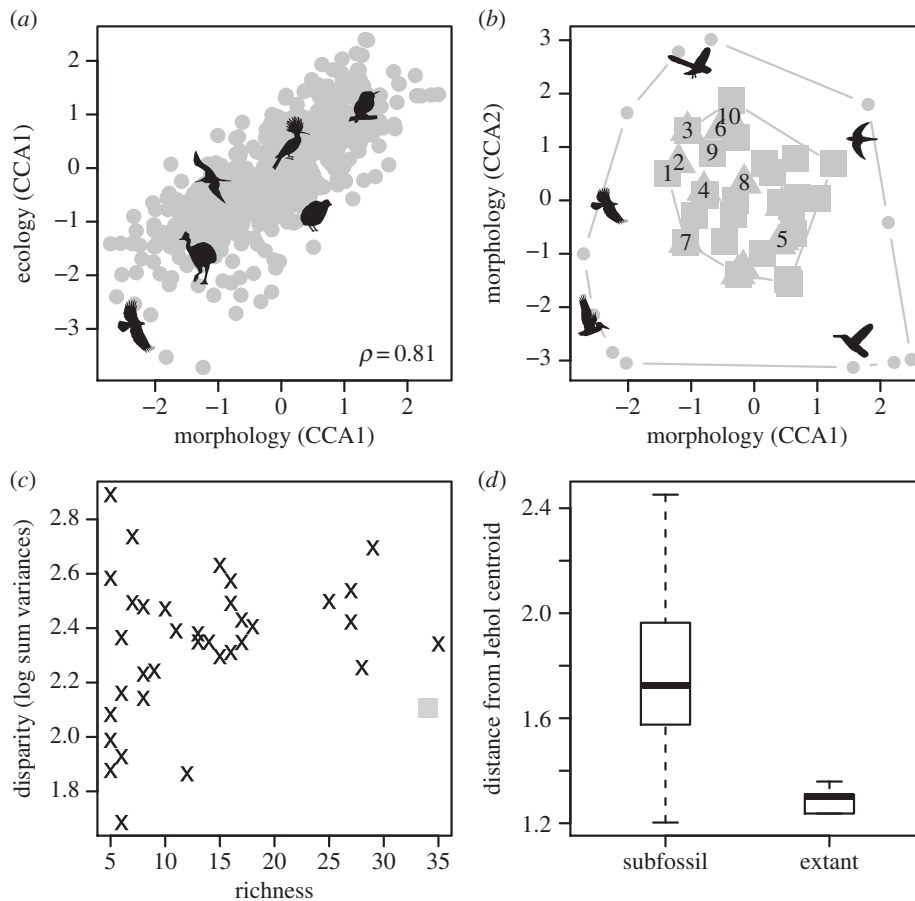
Figure 1. Ecomorphospace evolution and interpretation. (*a*) Correlation between ecology and morphology along the first phylogenetic canonical axis (Spearman's $\rho = 0.81$). (*b*) Ecomorphospace occupation of all birds (circles) and the Jehol birds known from multiple (triangles) and single (squares) specimens. Numbered taxa as in table 1. (*c*) Log sum of variances from the all 14 CCA axes plotted against generic richness of fossil birds for the Jehol (square) and Quaternary assemblages (crosses). (*d*) Distances from the centre (means and medians of all axes) of the Jehol assemblage to the centre of the extant and subfossil/fossil assemblages, showing the expectation for taphonomic processes is to shift an assemblage away from the Jehol.

whether the morphological bias in preservation is strong enough to be detected.

(d) Comparing with evolutionary expectations

The origin time and rate of lineage diversification of Pygostylia are, due to their extremely patchy fossil record, unknown. This hinders our ability to evaluate whether specific factors such as competition must be invoked to explain restricted morphospace in the Jehol. The Jehol birds are strongly time-averaged and from one geographical area, making them an underestimate of pygostylian disparity. We estimated rates of morphological evolution in Aves using the 576 genera for which we have both morphological and phylogenetic data from the sequence-based phylogenies of Jetz *et al.* [3]. Morphological rates were estimated allowing for a rate shift along the tree [27]. We used the posterior distribution of morphological rate in Aves as bounds for the rates plausible in pygostylians. Through simulations, we examined whether disparity of the Jehol fell within the bounds of realistic expectations as defined by extant avian disparity, as direct testing is impossible without a time-calibrated phylogeny of Pygostylia. As evolutionary covariance reduces expected disparity, we biased ourselves towards simulating high disparity by using a star phylogeny of Jehol birds across a suite of root ages (from 175 Ma, slightly older than *Anchiornis* [28], to 130 Ma). We used this suite of realistic root ages and the posterior distributions of morphological evolutionary rates from Aves to calculate boundaries on how much disparity a diffusive process is expected to have produced in the Jehol pygostylians using the equation presented by O'Meara *et al.* [29].

3. Results

Our analyses of modern birds show that morphology is a strong predictor of ecology (figure 1*a*). For all taxa except *Jianchangornis*, at least one of the closest five modern birds in CCA space is consistent with extrinsic data (median = 2.5), and the probability of doing as well or better for all 10 testable taxa combined is highly significant (*p*-value < 1.1×10^{-8}). Further, when the probability of selecting an analogue was weighted by distance in CCA space, only *Jianchangornis* and *Confuciusornis* had notably lower probabilities of being matched compared with random, with most taxa having a significant increase in probability (table 1). The confirmation that morphology correlates strongly with ecology in extant birds and the extant bird ecomorphological correlations predict preserved ecological evidence in stem birds significantly better than random, allowing us to confidently compare the morphological disparity of the entire Jehol assemblage as a proxy for its ecological disparity in comparisons with modern and subfossil avifaunas.

The Jehol bird assemblage is ecologically impoverished compared with both extant and recent fossil assemblages (figure 1*b,c*). Overall, the ecological disparity [30] present in the Jehol avifauna is dominated by ground-foraging granivores/insectivores, similar to sparrows or pigeons (e.g. *Longicrusavis*), although the Jehol does have kingfisher-like arboreal faunivores (most longipterygids, e.g. *Shanweiniao*) and cuckoo or myna-like generalists (e.g. *Eoconfuciusornis*,

Pengornis). Swifts, storks, swans and other aerial and aquatic specialist birds characteristic of modern ecosystems lack robustly supported analogues in this ancient assemblage (see the electronic supplementary material).

The morphological disparity (sum of variances) of the Jehol assemblage is substantially lower than Quaternary sites of comparable richness (figure 1*c*), and the centre (means and medians of morphological axes) is significantly closer to modern assemblages than subfossil ones (figure 1*d*). When comparing only modern assemblages with fossil data from the same geographical region, it becomes clear that the expected shift in centre due to taphonomic bias is away from the Jehol (paired Wilcoxon: $V = 20$, $p < 6 \times 10^{-6}$). Although the Quaternary deposits are not perfect taphonomic analogues, the stark shift in location between modern and geographically coincident fossil assemblages strongly suggests that taphonomic artefacts alone cannot explain the ecomorphological vacancies in the Jehol assemblage. Species of Jehol birds known from multiple individuals have a higher preservation potential than those known from only a single specimen, but the Hotelling's T^2 test found no significant difference in the location in morphospace of genera known from single or multiple specimens ($n = 24/10$, $p = 0.75$). The distance between the Jehol and other fossil avifaunas, and the failure to find a strong difference between well-preservable and poorly preservable taxa, together provide robust evidence that taphonomic bias is not strong enough to produce the observed ecological vacancies alone, and that biological factors (such as disparification rates) must be invoked. Using rates of morphological evolution estimated from the extant tree of Aves, our simulations show that the disparity observed in the Jehol (an underestimate of global pygostylian disparity) falls well within the expected bounds for a young radiation (figure 2).

4. Discussion

Both our reconstructed ecologies for individual taxa and analyses based on claw curvature [31] detect a large fraction of ground foragers in the Early Cretaceous assemblage. Functional analysis of wing proportions supports strong flight capabilities in many Jehol birds [12], although analysis of furcula shape has suggested a 'soaring' flight mode in several species [13], including *Sapeornis* and *Yanornis*. Although *Yanornis* is known to have eaten fish [16,23], which is potentially consistent with a soaring flight mode, both *Yanornis* and *Sapeornis* are reconstructed in our analyses as more ground-foraging, which is much more consistent with the seeds in the diet of *Sapeornis* and the gastrolith evidence in *Yanornis*. Bell & Chiappe [11], using a principal components analysis of limb elements, also reconstructed *Sapeornis* as an aerial forager and reconstructed many Jehol taxa as overlapping marine species, while our reconstructed analogues are overwhelmingly terrestrial, which makes them consistent with non-marine deposition of the formations. With regard to qualitative descriptions, *Bohaiornis* is known to have possessed recurved claws, pointed teeth and gastroliths [21], and is reconstructed here as being similar to arboreal taxa that eat both insects and plant matter (e.g. *Amblyornis*, a bowerbird).

The Jehol assemblage is a composite, incorporating birds from several formations spanning almost 11 Myr [9]. These
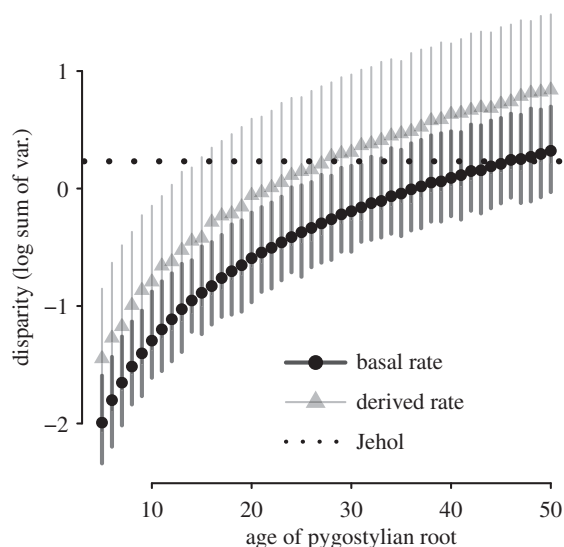

Figure 2. Results of evolutionary simulations showing time to evolve disparity. The results from simulating at different root ages versus the predicted disparity are shown, with the rates drawn from the posterior for the basal avian rate of phenotypic divergence shown in black, the elevated passerine rate in grey and the disparity of the Jehol assemblage denoted by the dotted horizontal line.

formations are largely lacustrine in deposition, with volcanic eruptions thought to have caused the mass deaths (see [9] and references therein). In our analyses, we also included *Gansus*, a web-footed water bird from the nearly co-eval Xiagou Formation of western China. Selecting taxa from a more spatio-temporally restrictive unit (e.g. the Yixian Formation alone) and excluding the water bird *Gansus* would only make the assemblage look even more depauperate and would exclude one of the most readily preserved taxa (*Gansus*). By incorporating birds from different units, we have increased the overall disparity, and made our tests for differences between the Jehol assemblage and modern/subfossil avifaunas conservative. Likewise, the Jehol biota derives from many sites over a much larger area than our recent subfossil sites, which are predominately single-locality examples. This makes the lower disparity of the Jehol assemblage all the more aberrant, as sedimentological differences between the Yixian and Jiufotang Formations suggest multiple preserved environments [9]. Although competition with pterosaurs has been debated as important in early bird evolution [32], the vacancies observed in the Jehol may simply reflect its temporal proximity to the origin of Pygostylia.

The earliest assemblage of birds is ecologically impoverished, and is biased towards both small-bodied and terrestrial birds. Although taphonomic filters certainly exist, and we cannot remove their influence, we demonstrate that such filters alone fail to explain the paucity of large-bodied or aquatic forms, and may not be able to fully explain the absence of small-bodied forms, either. Nor were such filters strong enough to create a significant difference in morphology between birds known from multiple specimens and those known only as singletons at the current sampling size.

Based on our simple modelling experiments, the disparity observed in the Jehol assemblage fits within the bounds expected for a young radiation diffusing through morphospace (figure 2). Rates of morphological evolution are controlled by a suite of biotic factors, ranging from ecological forces like competition (possibly with pterosaurs and

non-avian maniraptorans) to intrinsic factors such as rates of mutation [33] and degree of developmental integration [34]. Understanding the degree to which different evolutionary factors contributed to the limited disparity of early birds is beyond the scope of current data, but our analyses robustly demonstrate that taphonomy alone cannot explain the ecological vacancies observed.

In general, the fossil record suggests that clades saturate morphospace quickly, with much of the major ecomorphological diversity occurring early in the evolutionary history of clades [1]. Recent advances in ecology and comparative methods provide a rigorous framework explaining that such 'early bursts' are to be expected when ecological opportunity exists [35]. These empirical and theoretical studies support a model of expanding the contours of morphospace before filling up the interior. Our analysis provides a framework for inferring ecology from morphology in extinct taxa, and helps to integrate palaeontological data in ecoevolutionary analyses while facilitating comparisons between the ecological evolution of birds and other clades, such as mammals.

Across the Mesozoic, mammals were competitively excluded from the larger-bodied niches their Cenozoic descendants ultimately filled [36,37]. However, Mesozoic mammals convergently evolved many of the specialized aquatic, scansorial, fossorial and gliding ecomorphs seen in their Cenozoic relatives [37], whereas only a few bird remains from the Mesozoic yet speak to a greater ecological diversity [38,39] (although see [40,41]). Competition with non-avian dinosaurs could explain the body-size bias in both mammals and birds, though potential competition with pterosaurs has been invoked as a possible constraint on early avian diversity. Such assertions are difficult to test given our present understanding of the ecology of those extinct taxa. Furthermore, based on our modelling experiment, we suggest that insufficient time to radiate can explain much, if not all, of the ecological vacancies in the Jehol avifauna. Further ecosystem-level analyses of functional diversity in Mesozoic assemblages are needed to refine and test competition hypotheses.

While the timing of avian taxonomic diversification remains controversial [6], understanding the history of ecological diversification of birds is an important, understudied parallel line of inquiry. Knowing which niches birds occupied across the Cretaceous is critical for determining how disparate potential crown avians may have been by the K–Pg boundary, and whether crown clades lineages experienced a rapid radiation into new niches following K–Pg extinction or not. Here, we have provided a rigorous method for testing ecomorphological reconstructions in fossil taxa and a baseline for disparity through an analysis of the hitherto best-sampled Cretaceous bird fauna. We find that this early bird fauna was less ecologically diverse than modern equivalents, with a preponderance of ground-foraging forms, and that the unoccupied niche space is probably tied to the rate of radiation through intrinsic limits or coupled with the effects of competition.

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