

Reporting Summary

Nature Research wishes to improve the reproducibility of the work that we publish. This form provides structure for consistency and transparency in reporting. For further information on Nature Research policies, see [Authors & Referees](#) and the [Editorial Policy Checklist](#).

Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

- | n/a | Confirmed |
|--------------------------|--|
| ☐ | ☒ The exact sample size (n) for each experimental group/condition, given as a discrete number and unit of measurement |
| ☐ | ☒ A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly |
| ☐ | ☒ The statistical test(s) used AND whether they are one- or two-sided
<i>Only common tests should be described solely by name; describe more complex techniques in the Methods section.</i> |
| ☐ | ☒ A description of all covariates tested |
| ☐ | ☒ A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons |
| ☐ | ☒ A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals) |
| ☐ | ☒ For null hypothesis testing, the test statistic (e.g. F , t , r) with confidence intervals, effect sizes, degrees of freedom and P value noted
<i>Give P values as exact values whenever suitable.</i> |
| ☐ | ☒ For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings |
| ☐ | ☒ For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes |
| ☐ | ☒ Estimates of effect sizes (e.g. Cohen's d , Pearson's r), indicating how they were calculated |

Our web collection on [statistics for biologists](#) contains articles on many of the points above.

Software and code

Policy information about [availability of computer code](#)

Data collection tpsDig.2, tpsRelw, TreeAnnotator (Beast2), MorphoJ (v.1.0.6), Resistant Procrustes Software (available online at: <https://sites.google.com/site/resistantprocrustes/>).

Data analysis MorphoJ(v.1.0.6), R statistical environment (geomorph v.3.0.7.), BayesTraits V2.0.2.

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors/reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Research [guidelines for submitting code & software](#) for further information.

Data

Policy information about [availability of data](#)

All manuscripts must include a [data availability statement](#). This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A list of figures that have associated raw data
- A description of any restrictions on data availability

All relevant raw data (landmark data and phylogenies) will be made available via the University of Bristol's DataBris repository. All the R code used in this article will be made available via the University of Bristol's DataBris repository.

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	Using a sample of 436 bird species across virtually all families of landbirds (i.e: Inopinaves, defined as Telluraves + Opisthocomus hoazin, Prum et al. 2015) and state-of-the-art geometric morphometrics and phylogenetic comparative methods, we quantify evolutionary interdependence between the bird beak and braincase (cranial integration) in every avian lineage to test whether this condition promotes or constrains evolution. We find high levels of integration across most clades of landbirds. Even more surprisingly, we find that the two textbook examples of adaptive radiations in birds, Darwin's finches and Hawaiian honeycreepers, rapidly evolved a large range of beak shapes despite tight cranial integration. This is highly unexpected. We show that, contrary to conventional thinking, tight cranial integration actually facilitated, rather than constrained, diversification in two of the archetypal examples of adaptive radiation.
Research sample	Our study includes 128 families of landbirds giving a total of 436 species. All but five families within the landbird radiation are represented in our sample (Philepittidae, Sapayoidae, Dasyornithidae, Urocynchramidae and Aegithinidae). These families are either monotypic or have an extremely reduced diversity, and often regarded as belonging within other passerine families 44. Sampling was non-random and aimed to capture the maximum beak morphological disparity within each family, with a special focus on Darwin's finches and Hawaiian honeycreepers (represented in our sample by ~70% and ~ 60 % of their extant diversity, respectively).
Sampling strategy	Sampling was non-random and aimed to cover all the known families of landbirds (Inopinaves). Furthermore, a previously crowd-sourced sample of beak shapes was used aimed to capture maximum beak shape disparity within each of the studied families. One specimen per species was used as the focus of our study is macroevolutionary (between species).
Data collection	Skulls were photographed following standard procedures in macrophotography to ensure minimal distortion. Landmark data was collected using these photographs and standard software in geometric morphometrics. Shape data was extracted from this landmark data following state-of-the-art procedures in geometric morphometrics. All technical details are given in the Methods section of the article.
Timing and spatial scale	Museum specimens were photographed over the years 2015, 2016 and 2017 during at least ten visits to the skeletal collections of ornithology of the National History Museum (Tring, UK) and the Smithsonian National Museum of Natural History (Washington, D.C., USA).
Data exclusions	No data was excluded.
Reproducibility	All the analyses were repeated more than once to verify the methodological procedures were correct. Proof of this could be submitted upon request. Furthermore, our data is analyzed using three different analytical situations to stress the importance of some issues in the correct quantification of trait covariation using current methods in geometric morphometrics and phylogenetic comparative methods. We propose a pipeline to identify and novel solutions to solve these issues.
Randomization	This is not relevant to our study. Bird species were assigned to the clades in which they are recovered in our phylogenetic hypothesis (maximum clade credibility tree from a population of trees produced by a previous and large phylogenomic study).
Blinding	This is not relevant to our study. Only the first author, G.N., collected the data.
Did the study involve field work?	☐ Yes ☒ No

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology
☒	☐ Animals and other organisms
☒	☐ Human research participants
☒	☐ Clinical data

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging