LETTER

doi:10.1038/nature11631

The global diversity of birds in space and time

W. Jetz[1]*, G. H. Thomas[2]*, J. B. Joy[3]*, K. Hartmann[4] & A. O. Mooers[3]

Current global patterns of biodiversity result from processes that operate over both space and time and thus require an integrated macroecological and macroevolutionary perspective[1–4]. Molecular time trees have advanced our understanding of the tempo and mode of diversification[5–7] and have identified remarkable adaptive radiations across the tree of life[8–10]. However, incomplete joint phylogenetic and geographic sampling has limited broad-scale inference. Thus, the relative prevalence of rapid radiations and the importance of their geographic settings in shaping global biodiversity patterns remain unclear. Here we present, analyse and map the first complete dated phylogeny of all 9,993 extant species of birds, a widely studied group showing many unique adaptations. We find that birds have undergone a strong increase in diversification rate from about 50 million years ago to the near present. This acceleration is due to a number of significant rate increases, both within songbirds and within other young and mostly temperate radiations including the waterfowl, gulls and woodpeckers. Importantly, species characterized with very high past diversification rates are interspersed throughout the avian tree and across geographic space. Geographically, the major differences in diversification rates are hemispheric rather than latitudinal, with bird assemblages in Asia, North America and southern South America containing a disproportionate number of species from recent rapid radiations. The contribution of rapidly radiating lineages to both temporal diversification dynamics and spatial distributions of species diversity illustrates the benefits of an inclusive geographical and taxonomical perspective. Overall, whereas constituent clades may exhibit slowdowns[10,11], the adaptive zone into which modern birds have diversified since the Cretaceous may still offer opportunities for diversification.

Birds (class Aves) constitute a fascinating and widely-studied radiation. Analyses based on a very incomplete 'tapestry' phylogeny[12] suggested higher speciation and diversification rates in the tropics and in South relative to North America[13–15]. In addition, numerous geographically disparate clades are considered exceptional radiations, including both New and Old World warblers in the Northern Hemisphere[10,16], island radiations such as Darwin's finches[17], and the explosively diversifying white-eyes that span much of the southern Old World[18]. The prevalence and implications of such rapidly radiating clades have not been put in broader context: how characteristic are shifts in diversification, and to what extent do clade-specific and tree-wide variation in diversification rate contribute to diversity dynamics across the extant tree of the entire class? Where do these radiating lineages occur, and how much do they contribute to current-day patterns of diversity in the highly diverse tropics compared to relatively depauperate higher latitudes?

We address these questions using the first set of complete phylogenies of extant bird species (9,993 species, see Methods), compiled in a Bayesian framework, and a new species-level measure of past diversification rate. The phylogeny builds on previously established deeper relationships and combines molecular data for 6,663 species with taxonomic constraints for data-deficient species to more fully account for phylogenetic uncertainty. Lineages-through-time[8] and novel diversification-rates-through-time plots (Fig. 1) indicate that net diversification leading to extant lineages generally increased from approximately

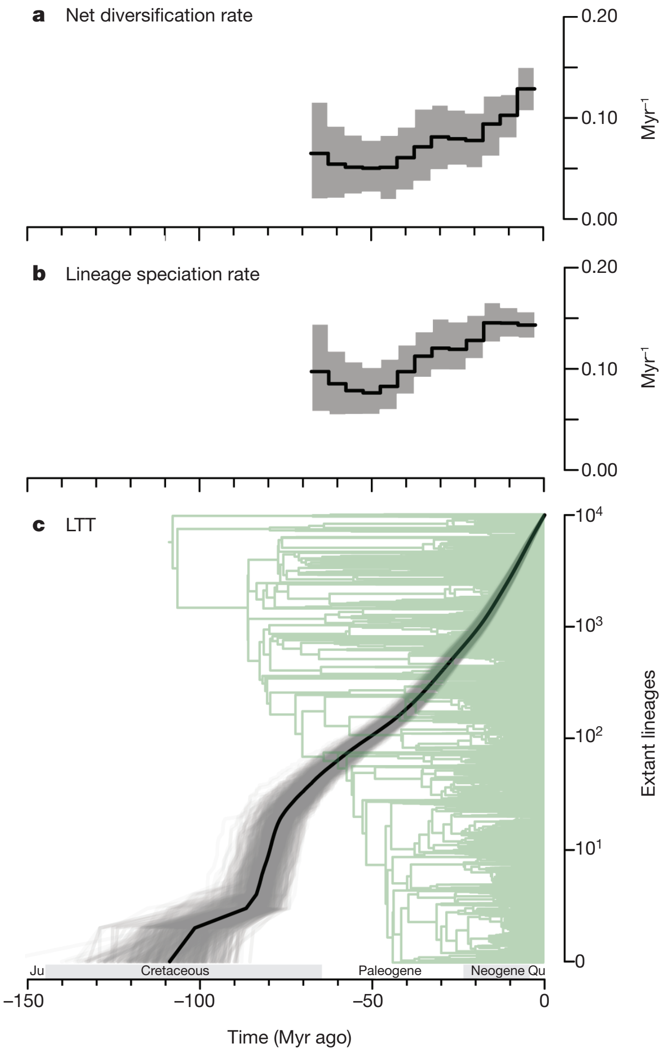

Figure 1 | Diversification of all birds through time. **a**, **b**, Estimates of the tree-wide lineage net diversification (speciation − extinction) rate (**a**) and speciation rate (**b**), calculated in 5 million year intervals (line segments). These are estimated to be very similar (see Supplementary Discussion). The shaded region represents the area between the 5th and 95th quantiles for 525 assessed trees with the mean rate traced in black. Intervals outside 67.5 and 2.5 Myr ago are not shown due to lack of data (≤30 lineages per interval) and the difficulty of accounting for ongoing speciation events, respectively. **c**, Lineage-through time plot for 1,000 trees (in grey), with mean waiting times to speciation in black. Green background is the tree depicted in Fig. 2. Geologic time periods are delineated at the bottom of the plot. Ju, Jurassic period; Qu, Quaternary period.

---

[1]Department of Ecology and Evolutionary Biology, Yale University, 165 Prospect Street, New Haven, Connecticut 06520-8106, USA. [2]Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK. [3]Department of Biological Sciences, Simon Fraser University, 8888 University Drive, Burnaby, British Columbia V5A 1S6, Canada. [4]Institute for Marine and Antarctic Studies, University of Tasmania, Private Bag 49, Hobart, Tasmania 7001, Australia.
*These authors contributed equally to this work.

50 million years (Myr) ago to at least 5 Myr ago. This contrasts markedly with patterns of decreasing net diversification reported for smaller clades for which a model of niche-filling coupled with long-term lineage competition[19] has been invoked[9,10,20–22].

By far the best model for diversification (median Akaike Information Criterion improvement over all other models $\gg$1,700; Supplementary Discussion and Table 1) is one where a subset of individual clades (identified in Fig. 2 and Table 1) are assigned their own constant and elevated diversification rates. This confirms a space- and time-dependent history of avian diversification, with most of the consistently identified rate increases occurring within the last $\sim$50 Myr. Several of these shifts confirm previously identified highly diverse clades with key morphological and behavioural innovations or environmental opportunities, including hummingbirds, parrots and a number of songbird lineages. Some additional young and rapidly radiating groups with rates of per-lineage species accumulation ≥ 0.25 species per million years (Table 1) stand out. These include the previously unrecognized rapid radiations of both ducks and geese, and of select gulls, as well as recognized rapid radiations of ovenbirds plus woodcreepers[23], and of white-eyes[18], all with extant diversity ranging from 44 to 300 species. Intriguingly, these recently rapidly radiating clades show no obvious restriction to parts of the phylogenetic tree (Fig. 2) or landmasses. Rapidly and slowly radiating clades are highly interspersed. Collectively, these tree-wide distributed bursts produce the overall average increase in tree-wide diversification rate (Fig. 1a). Importantly, these novel patterns assume rate constancy within clades, and so integrate (rather than conflict with) changing rates associated with, for example, diversity- or time-dependent slowdowns at smaller scales within individual clades[9,10,20].

To understand the consequences of rate variation across the tree for the present-day geographic variation in avian diversity in more detail, we calculate a new metric of species-level lineage diversification rate (DR) for every species. The measure captures the longer-term splitting rate leading to a given species, made possible by the full resolution of the phylogeny. It is directly related to clade level diversification rate measures (see Supplementary Methods), but offers species-level resolution. Mean species values range from 0.01 to 4.66 species Myr^{-1} and roughly follow a lognormal distribution (Fig. 2, centre) with a geometric mean of 0.157 species Myr^{-1} and only limited variation owing to captured phylogenetic uncertainty (Supplementary Discussion Fig. 4). The species level detail illustrates the marked heterogeneity in diversification rates beyond the main shifts and identifies numerous 'hot' sections of recent rapid radiations dispersed widely across the avian tree of life.

This heterogeneity extends to the geographical prevalence of species with a signature of high past diversification. We find that the main geographic differences in diversification rate are east–west hemispheric, rather than latitudinal[14,15] (see below). Average rates are distinctly lower in the Eastern (east of 28° W, $\mathrm{DR} = 0.145$, $N = 5{,}810$) compared to the Western Hemisphere ($\mathrm{DR} = 0.177$, $N = 4{,}183$, $P_{\mathrm{avg}} < 0.05$, $f(P < 0.05) = 73/100$, Fig. 3). In contrast, there are no significant difference in rates ($P = 0.69$, $f(P < 0.05) = 0/100$) between Northern ($\mathrm{DR} = 0.161$, $N = 5{,}084$) and Southern Hemisphere species ($\mathrm{DR} = 0.154$, $N = 4{,}909$). Intriguingly, avian assemblages in Australia, Southeast Asia, Africa and Madagascar are characterized by particularly low average rates (below approximately 0.12 species Myr^{-1} in most locations, compared to a global mean of 0.16). These regions also harbour substantially fewer than expected of the 25% of species with highest diversification rate (<15% in most assemblages, Fig. 3d). One hypothesis for the patterns in Australia and Africa is regional density-dependent diversification, with early filling of ecological space by ancient radiations in their regions of origin[24]. Generally, high diversification rates and large relative prevalence of top diversification rate species are found throughout higher-latitude North America, parts of north Asia and southwest South America—the main breeding areas of several of the rapidly radiating clades identified in Table 1 (including warblers, ducks, gulls and woodpeckers). These regions have all been characterized by strong climatic fluctuations from the Pliocene to the present (with, for example, notable emergence and size fluctuations of wetland and forest breeding habitats), which supports the suggestion that the geography of past climate dynamics has had a major role for today's diversity patterns[1,4]. Isolated locations such as islands have been proposed to strongly facilitate rapid radiations through the reduction in gene flow and novel ecological opportunities they often present after initial colonization[17,25]. We confirm this globally, as non-pelagic birds with more than half of their range on islands ($N = 1{,}085$, $\mathrm{DR} = 0.203$) have much larger diversification rates than predominantly mainland birds ($N = 8{,}629$, $\mathrm{DR} = 0.153$; $P_{\mathrm{avg}} < 0.001$,

Table 1 | Rate shifts found in at least 25% of sampled trees.

Node	English	Scientific	Age	r	Species
G	Select gulls	Select Laridae	4.6 (0.0)	0.74	44
U	White-eyes, select babblers	Zosteropidae, select Timaliidae	8.1 (0.1)	0.49	113
N	Ovenbirds, woodcreepers	Dendrocolaptidae, Furnariidae	17.8 (0.1)	0.28	285
[O]	- Ovenbirds	- Furnariidae	13.6 (0.1)	0.31	223
C	Select ducks, geese	Anseriformes	10.8 (0.1)	0.28	109
T	Babblers, white-eyes	Timaliidae, Zosteropidae	17.7 (0.1)	0.27	355
Y	Weavers, estrildid finches	Ploceidae, Estrildidae	21.9 (0.2)	0.24	278
H	Woodpeckers and allies	Ramphastidae, Indicatoridae, Picidae	36.4 (0.3)	0.17	361
[I]	- Woodpeckers	- Picidae	23.8 (0.2)	0.21	220
X	Passeroidea songbirds	Passeroidea	35.7 (0.1)	0.20	1,418
D	Select hummingbirds	Select Trochilidae	20.7 (0.1)	0.19	266
R	Select sylvioid songbirds	Select Sylvioidea	33.3 (0.1)	0.17	1,031
[S]	- Subset	- Subset	29.1 (0.1)	0.19	704
Q	Passerida songbirds	Passerida	44.7 (0.1)	0.16	3,574
M	New World suboscines	Tyrannides	52.4 (0.2)	0.16	1,227
P	Select Corvida songbirds	Select Corvida	32.1 (0.2)	0.16	442
F	Gulls, terns, auks, skuas, jaegers	Stercorariidae, Alcidae, Laridae	21.1 (0.1)	0.15	131
V	Muscicapoidea songbirds	Muscicapoidea	38.8 (0.1)	0.14	732
[W]	- subset	- Subset	29.4 (0.2)	0.15	603
J	Parrots, songbirds	Psittaciformes, Passeriformes	77.2 (0.2)	0.14	6,320
[L]	- Most songbirds	- Passeriformes	66.8 (0.2)	0.14	5,964
A	Fowl	Galloanserae	78.7 (0.2)	0.08	448
[B]	- Landfowl	- Galliformes	53.9 (0.3)	0.13	267
K	True parrots	Psittacidae	35.6 (0.3)	0.13	330
E	Pigeons, doves	Columbidae	33.4 (0.1)	0.12	289

Rate shifts were identified using MEDUSA[5] (see Fig. 2 for position and prevalence). Pairs of nested shifts are combined when younger shifts (in square brackets) were depressed by the presence of older to <10% occurrence. 'Node' refers to position on example tree (Fig. 2), 'Age' of node is the mean age in units million years (with s.e. calculated across trees) calculated across the posterior sample of trees and 'r' is the mean per lineage diversification rate (in units of Myr^{-1}, s.e. across trees <0.01 for all) estimated for focal nodes of given species richness ('Species'). All clade-level rate estimates were inferred using Laser[28]. The background rate as estimated with MEDUSA was $r = 0.056$ Myr^{-1}. Support for nodes was 1.00 for all except U (0.02), T (0.73), S (0.48), P (0.85) and E (0.93).

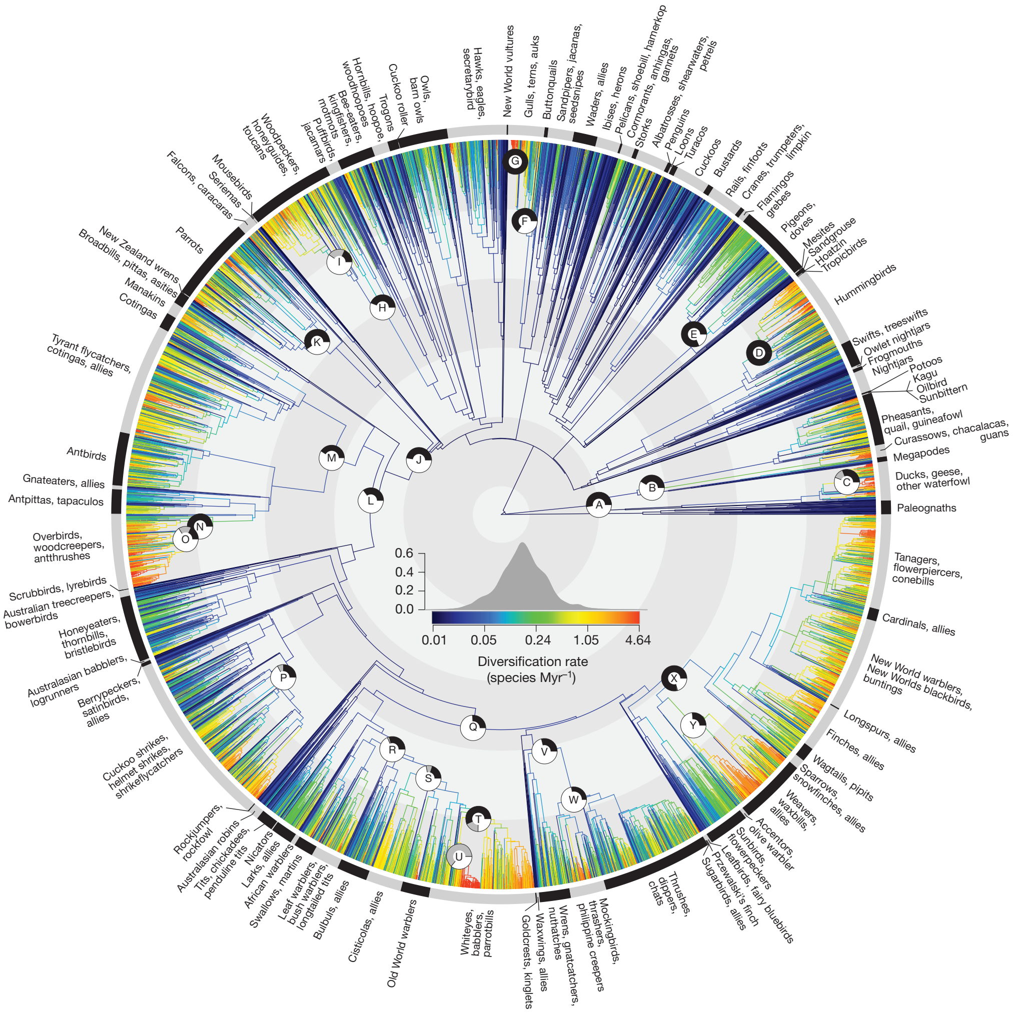

Figure 2 | Diversification across the avian tree. Diversification rate shifts identified by MEDUSA and the species level diversification rate metric (DR) are displayed on a representative avian tree. Nodes with shifts in diversification rate identified in at least 25% of the tested trees are indicated by pie-charts (labelled A–Y, see Table 1). Black and grey areas show the proportion of trees with a shift at the focal node and with shifts that are nested within (more recent than) the focal node, respectively. Shifts are counted only once (for example, shifts at node U do not contribute to the prevalence of nested shifts at node T). Prevalence of shifts may be lowered by a 'trickle-down' effect where combinations of nested shifts are rarely identified in the same tree (see also Supplementary Discussion Fig. 6 for discussion). Branches are coloured according to the mean diversification rate of descendant branches. We colour branches for visualization purposes to highlight tree-wide variation in diversification rate and do not analyse values for internal branches. Diversification rate quantifies the splitting rate along branches leading to a species and offers species-level detail for clade-level diversification rate (see Supplementary Methods). The inset shows the scale and frequency distribution of diversification rate values across species. Concentric grey circles show time from the present in 20 million year intervals.

$f(P < 0.05) = 100/100$). Many islands, particularly those inhabited by passerines in the Pacific, North Atlantic and Caribbean, stand out for their high diversification rates, for example, as shown by the dramatic white-eye radiation (Table 1). As might be expected on the basis of species richness alone, passerines ($N = 5{,}966$, $\mathrm{DR} = 0.179$) have on average much higher diversification rate values than non-passerines ($N = 4{,}027$, $\mathrm{DR} = 0.131$), a difference captured by the diversification rate increase observed at the base of the Passeriformes (node 'L' in Table 1, Fig. 2). Accordingly, passerines have a strong influence on the geographic patterns of highest diversification rate (Fig. 3b, c). However, both major groups harbour high and low diversification rate species and both have major hemispheric differences as well as higher rates on islands. Intriguingly though, non-passerines, especially through groups such as water birds, and some gulls and woodpeckers, drive the higher rates in Asia and also show high rates in North America. Passerines show significant recent radiations in temperate Asia and North America. In particular due to the ovenbird and woodcreeper clades, passerines contribute strongly to high average diversification rates and present richness in South America, especially south of the core rainforest belt. We propose that over the past 10–20 Myr the expansion of core temperate habitats[4] as well as mountain uplifts and, more recently, the retreat of high-latitude glaciations (followed by range expansions and speciation), all contributed to these distinctive patterns.

These geographic patterns add an important dimension to perspectives that have emphasized latitude[15] as a predictor of both diversification rate and standing diversity. In a highly simplifying global latitudinal view (Fig. 4), high diversification rate species in all tropical lowland regions seem generally outnumbered by species of lower diversification rate. Overall, the simple hypothesis that latitudinal diversity differences result from raw variation in net rates by latitude is rejected: mean diversification rate shows no significant trend with absolute latitude or between the tropics and higher latitudes (Fig. 4). This finding is consistent with the hypothesis that the greater combined age and expanse of tropical moist forests has facilitated greater species accumulation without necessarily facilitating greater rates of diversification[4]. The equatorial dip in average diversification rates is followed by a peak in the slightly drier and (over the past 10 Myr)

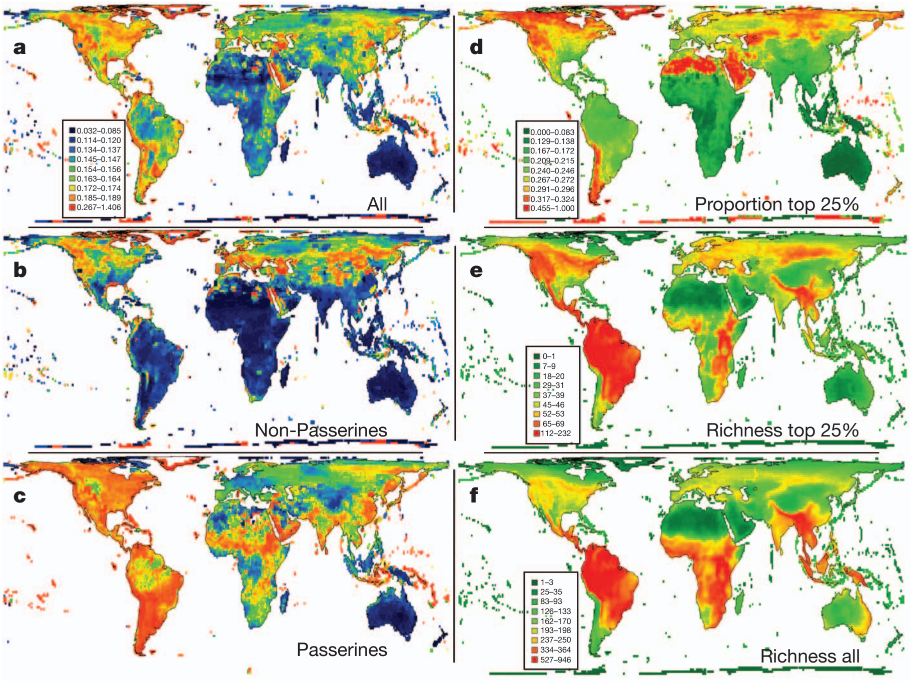

Figure 3 | Geographic variation in species-level lineage diversification rate and the richness of high-diversification rate species. **a**–**c**, Mean assemblage diversification rate (see Fig. 2), calculated as the geometric mean of all species in a grid cell assemblage, weighted by the inverse of their range size. **a**, All species; **b**, non-passerines; **c**, passerines. This visualization limits the overbearing (pseudo-replicating) effect wide-ranging species have on perceived spatial patterns of assemblage summaries[4]. **d**–**f**, Relative (**d**) and absolute (**e**) richness of top 25% diversification rate species (DR $\geq$ 0.243 species Myr^{-1}); **f** shows the richness of all 9,993 bird species for comparison. Grid cell size is 110 × 110 km for all panels (Behrman projection).

climatically more dynamic regions at around 10–15° in both hemispheres and an overall decrease towards the high latitudes. However, as our spatial results indicate, the outcome of any such latitudinal comparisons, excepting perhaps a narrow equatorial band, will depend on hemisphere and region, and the inclusion, prevalence and current evolutionary dynamics of particular clades (see also ref. 3).

Our choice of a constant-rate birth model as a prior on diversification is conservative with respect to clade-level rate heterogeneity, increasing diversification towards the present and major hemispheric differences in lineage-diversification rate. Our results are also robust to differing phylogenetic hypotheses, including currently existing alternative backbone topologies and the inclusion of data-deficient species (see Supplementary Discussion). Indeed, our tree distribution was designed to both integrate the latest taxonomic data and to capture remaining phylogenetic uncertainty given current knowledge; this means it will not be suitable for some questions in avian systematics. In addition, the age of origination of crown group birds and the absolute diversification rates will be contingent on the specific fossil constraints used. Ongoing discovery of cryptic species may further affect rate estimates, especially in the tropics where taxonomists have been less active. Further, and importantly, our inference is necessarily limited to lineages leading to present-day species and cannot account for the non-random extinction of entire clades (for example, of the entire moa clade in New Zealand). Finally, the illustrated spatial patterns tie diversification rate to the occurrence of species today rather than the time of their origination when the distribution of bioclimatic zones and species may have been different. Nonetheless, the uncovered geographic heterogeneity in diversification rates seems pervasive and provides a first global integration of species-level diversification rate variation across both time and space. It may be that birds are distinctive in their pattern of an increasing diversification rate from ~50 Myr ago to the recent: the overall adaptive zone into which modern birds have diversified since at least the early Eocene may not be saturated, and opportunities for diversification may be expanding. Alternatively, if the evidence for saturation in other taxa is not due to sampling

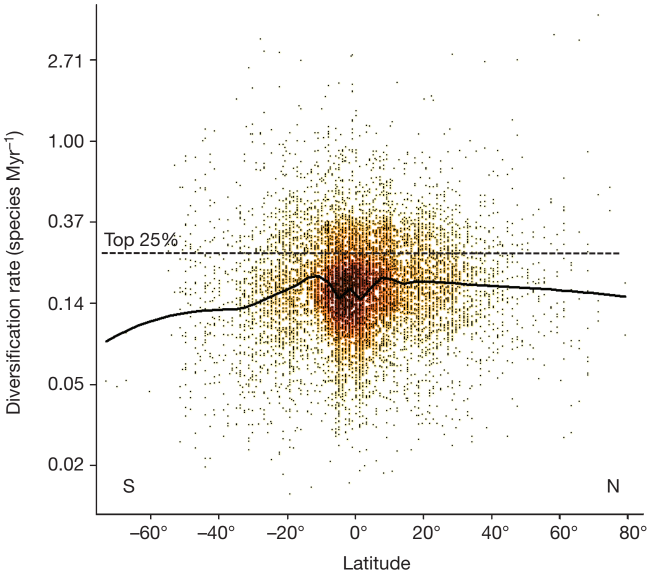

Figure 4 | Latitudinal gradient in species-level lineage diversification rate. Each black point represents a single species diversification rate (DR) at the centroid latitude of its global breeding range. Only the 75% species with small to moderate latitudinal extent (<26.4°, N = 7,493) are included to ensure comparable centroid positions (see Supplementary Discussion Fig. 7 for very similar patterns and results including all species). There is no significant association between diversification rate and absolute centroid latitude ($P_{\mathrm{avg}} = 0.51$, $f(P < 0.05) = 0/100$) or for intra- (<23° latitude) against extra-tropical centroid location ($P_{\mathrm{avg}} = 0.16$, $f(P < 0.05) = 31/100$). The solid line is a loess smooth over all data (span = 0.2, degree = 2). The dashed line indicates the threshold identifying the quartile of species with highest diversification rate (DR $\geq$ 0.243 Myr^{-1}). Darker brown shading highlights greater density of species points.

issues[26], then the difference may be due to the novel combined scale and resolution of our analyses, and smaller clades that are geographically or ecologically bounded may indeed saturate[9–11]. We will need to compare global complete trees such as the one we present here with well-characterized component clades. We predict that constraint-induced slowdowns in net diversification will appear at smaller ecological and geographic scales, but that these do not combine to produce the same pattern at broader scales. This would be consistent with a classical view of multiple and ongoing, individually constrained adaptive radiations as a main driver of biodiversification[19].

METHODS SUMMARY

Phylogenetic tree construction. Pseudo-posterior samples of complete avian trees were assembled as follows. (1) Every bird species was assigned to one of 158 clades identified using a backbone phylogeny[27]. (2) Relaxed-clock trees were generated for each clade from sequence data. (3) Relaxed-clock trees for entire clades were generated combining species with and without genetic data: species without genetic information (3,330) were placed within their clade using constraint structures consistent with consensus trees from step (2) plus taxonomic information and branching times sampled from a pure birth model of diversification. (4) Final trees were assembled from the clade distributions plus samples of dated backbone trees from (one of two) distributions constructed using relaxed molecular clock techniques, 15 genes, ten fossil constraints and extensive topology constraints derived from published sources. For further information see Supplementary Methods, for trees, see Supplementary Results or http://birdtree.org.

Diversification analyses. We compared diversification models on 525 sampled trees: seven models fit smooth changes in rate[28], one searches for tree-wide rate shifts[29] and one identifies clades that have significantly elevated or depressed diversification rates relative to the entire tree[5]. To visualize diversification through time we estimated tree-wide speciation and extinction rates in five-million-year intervals using TreePar[29].

We measured the species-level lineage diversification rate (DR) for every species i as the inverse of its mean equal splits measure[30]:

$$\mathrm{DR}_i = \left(\sum_{j=1}^{N_i} l_j \frac{1}{2^{j-1}}\right)^{-1}$$

where N_i = number of edges on path from species i to the root and l_j = length of the edge j.

Comparative diversification rate analyses. For comparisons of diversification rate we used phylogenetic generalized least squares across 100 trees and list average P values and frequency (f) of trees with $P < 0.05$. For the island–mainland comparison we excluded 279 predominantly pelagic species.

Spatial analysis. We compiled non-invasive breeding distributions from the literature and select updates (see Supplementary Methods). We extracted these ranges over a 110 km equal area grid in Behrman projection excluding cells with <30% dry land or without off-shore islands, resulting in 2.43×10^6 occurrence records over 12,850 cells.

Received 5 April; accepted 28 September 2012.

1. Mittelbach, G. G. *et al.* Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecol. Lett.* **10,** 315–331 (2007).
2. Ricklefs, R. E. A comprehensive framework for global patterns in biodiversity. *Ecol. Lett.* **7,** 1–15 (2004).
3. Linder, H. P. Plant species radiations: where, when, why? *Phil. Trans. R. Soc. B* **363,** 3097–3105 (2008).
4. Jetz, W. & Fine, P. V. A. Global gradients in vertebrate diversity predicted by historical area-productivity dynamics and contemporary environment. *PLoS Biol.* **10,** e1001292 (2012).
5. Alfaro, M. E. *et al.* Nine exceptional radiations plus high turnover explain species diversity in jawed vertebrates. *Proc. Natl Acad. Sci. USA* **106,** 13410–13414 (2009).
6. Smith, S. A., Beaulieu, J. M., Stamatakis, A. & Donoghue, M. J. Understanding angiosperm diversification using small and large phylogenetic trees. *Am. J. Bot.* **98,** 404–414 (2011).
7. Roelants, K. *et al.* Global patterns of diversification in the history of modern amphibians. *Proc. Natl Acad. Sci. USA* **104,** 887–892 (2007).
8. Nee, S., Mooers, A. O. & Harvey, P. H. Tempo and mode of evolution revealed from molecular phylogenies. *Proc. Natl Acad. Sci. USA* **89,** 8322–8326 (1992).
9. Phillimore, A. B. & Price, T. D. Density-dependent cladogenesis in birds. *PLoS Biol.* **6,** e71 (2008).
10. Rabosky, D. L. & Lovette, I. J. Density-dependent diversification in North American wood warblers. *Proc. R. Soc. B* **275,** 2363–2371 (2008).
11. Weir, J. T. Divergent timing and patterns of species accumulation in lowland and highland neotropical birds. *Evolution* **60,** 842–855 (2006).
12. Sibley, C. G. & Ahlquist, J. E. *Phylogeny and Classification of Birds: a Study in Molecular Evolution* (Yale Univ. Press, 1990).
13. Ricklefs, R. E. Global variation in the diversification rate of passerine birds. *Ecology* **87,** 2468–2478 (2006).
14. Cardillo, M., Orme, C. D. L. & Owens, I. P. F. Testing for latitudinal bias in diversification rates: an example using New World birds. *Ecology* **86,** 2278–2287 (2005).
15. Weir, J. T. & Schluter, D. The latitudinal gradient in recent speciation and extinction rates of birds and mammals. *Science* **315,** 1574–1576 (2007).
16. Price, T., Lovette, I. J., Bermingham, E., Gibbs, H. L. & Richman, A. D. The imprint of history on communities of North American and Asian warblers. *Am. Nat.* **156,** 354–367 (2000).
17. Grant, P. R. & Grant, B. R. *How and Why Species Multiply: the Radiation of Darwin's Finches* (Princeton Univ. Press, 2011).
18. Moyle, R. G., Filardi, C. E., Smith, C. E. & Diamond, J. Explosive Pleistocene diversification and hemispheric expansion of a "great speciator". *Proc. Natl Acad. Sci. USA* **106,** 1863–1868 (2009).
19. Simpson, G. G. *The Major Features of Evolution* (Columbia Univ. Press, 1953).
20. Etienne, R. S. *et al.* Diversity-dependence brings molecular phylogenies closer to agreement with the fossil record. *Proc. R. Soc. B* **279,** 1300–1309 (2012).
21. Morlon, H., Parsons, T. L. & Plotkin, J. B. Reconciling molecular phylogenies with the fossil record. *Proc. Natl Acad. Sci. USA* **108,** 16327–16332 (2011).
22. Ezard, T. H. G., Aze, T., Pearson, P. N. & Purvis, A. Interplay between changing climate and species' ecology drives macroevolutionary dynamics. *Science* **332,** 349–351 (2011).
23. Derryberry, E. P. *et al.* Large-scale continental radiation: the neotropical ovenbirds and woodcreepers (Aves: Furnariidae). *Evolution* **65,** 2973–2986 (2011).
24. Ericson, P. G. P. Evolution of terrestrial birds in three continents: biogeography and parallel radiations. *J. Biogeogr.* **39,** 813–824 (2012).
25. Price, T. *Speciation in Birds* (Roberts, 2008).
26. Cusimano, N. & Renner, S. S. Slowdowns in diversification rates from real phylogenies may not be real. *Syst. Biol.* **59,** 458–464 (2010).
27. Hackett, S. J. *et al.* A phylogenomic study of birds reveals their evolutionary history. *Science* **320,** 1763–1768 (2008).
28. Rabosky, D. L. LASER: a maximum likelihood toolkit for detecting temporal shifts in diversification rates from molecular phylogenies. *Evol. Bioinform. Online* **2,** 247–250 (2006).
29. Stadler, T. Mammalian phylogeny reveals recent diversification rate shifts. *Proc. Natl Acad. Sci. USA* **108,** 6187–6192 (2011).
30. Redding, D. W. & Mooers, A. O. Incorporating evolutionary measures into conservation prioritization. *Conserv. Biol.* **20,** 1670–1678 (2006).

Supplementary Information is available in the online version of the paper.

Acknowledgements We thank D. Redding for critical input in the early stages of this project; A. Mimoto, F. Ronqvist and M. Teslenko for help modifying MrBayes; I. Martyn for coding; R. Bowie, J. McGuire, A. Cooper, K. Burns and M. Sorenson among others, for unpublished phylogenetic material or information; M. Benton, T. Ezard, T. Price, M. Donoghue, J. Beaulieu, J. Belmaker, P. M. Hull, D. Field, N. Longrich, V. Saranathan, M. Steel, H. Morlon, J. Brown, A. Phillimore, R. Fitzjohn, R. Etienne, W. Stein and especially T. Stadler for data, important input and/or discussion; G. Smith, C. Schank, D. Thiele, T. M. Lee, F. La Sorte, C. Edwards, K. Ashton and J. Hazelhurst for help with spatial and phylogenetic data collection and management; C. Schank for help preparing the tree visualizations. This work was carried out using the BlueFern Supercomputing Facilities (http://www.bluefern.canterbury.ac.nz), University of Canterbury, the Advanced Computing Research Centre, University of Bristol (http://www.bris.ac.uk/acrc/) and the Interdisciplinary Research in Mathematics and Computer Sciences Centre, Simon Fraser University (http://www.irmacs.sfu.ca). This work was partly supported by NSF grants DBI 0960550 and DEB 1026764 and NASA Biodiversity Grant NNX11AP72G (W.J.); the Natural Environment Research Council (Postdoctoral Fellowship grant number NE/G012938/1 and the NERC Centre for Population Biology) (G.H.T.); and NSERC Canada, the Wissenschaftskolleg zu Berlin, the Yale Institute for Biospheric Sciences and Simon Fraser University (A.O.M.). Most importantly, we thank the many avian systematists and phylogeneticists who have contributed their data to public databases and so made our study possible.

Author Contributions W.J., A.O.M., and G.H.T. conceived of the study; K.H., W.J., J.B.J., A.O.M. and G.H.T. developed the methods; W.J., J.B.J. and G.H.T. collected the data; W.J., J.B.J. and G.H.T. conducted the analyses; W.J., J.B.J., A.O.M. and G.H.T. wrote the paper. W.J., J.B.J, G.H.T. and A.O.M. contributed equally to the study.

Author Information Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of the paper. Correspondence and requests for materials should be addressed to W.J. (walter.jetz@yale.edu) or A.O.M. (amooers@sfu.ca).