ECOGRAPHY

Research

Contrasting patterns of diversification in a bird family (Aves: Gruiformes: Rallidae) are revealed by analysis of geospatial distribution of species and phylogenetic diversity

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Ecography
42: 500–510, 2019
doi: 10.1111/ecog.03783

Subject Editor: Susanne Fritz
Editor-in-Chief: Miguel Araújo
Accepted 26 July 2018

Geospatial patterns in the distribution of regional biodiversity reflect the composite processes that underpin evolution: speciation, dispersal and extinction. The spatial distribution and phylogeny of a globally widespread and species rich bird family (Rallidae) were used to help assess the role of large-scale biogeographical processes in diversity and diversification. Here, we examine how different geostatistical diversity metrics enhance our understanding of species distribution by linking occurrence records of rail species to corresponding species level phylogeny. Tropical regions and temperate zones contained a large proportion of rail species richness and phylogenetic diversity whilst small islands in Australian, Oceanian and Oriental regions held the highest weighted and phylogenetic endemism. Our results suggest that habitat connectivity and dispersal were important ecological features in rail evolution and distribution. Spatial isolation was a significant driver of diversification where islands in Oceania were centres of neo-endemism with recent multiple and independent speciation events and could be considered as nurseries of biodiversity. Palaeo-endemism was mostly associated with older stable regions, so despite extensive long distance range shifting these areas retain their own ancient and distinct character. Madagascar was the major area of palaeo-endemism associated with the oldest rail lineages and could be considered a museum of rail diversity. This implies a mixture of processes determine the current distribution and diversity of rail clades with some areas dominated by recent 'in situ' speciation while others harbour old diversity with ecological traits that have stood the test of time.

Keywords: phylogenetic endemism, phylogeny, biodiversity

Introduction

The spatial discontinuity in the diversity of life has been of interest to biogeographers and evolutionary ecologists since Wallace (Wallace 1876). Although it is well established that biological diversity is unevenly distributed (Gaston 2000), there is still much we do not understand about the regional patterns of diversity and the

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evolutionary processes that underpin the distribution of current clades (Wiens 2007, Harrison and Cornell 2008, White and Hurlbert 2010, Belmaker and Jetz 2015). Speciation, extinction and range shifting all contribute to regional species richness and endemism but the temporal and geographic scale of each may differ. Even where spatial patterns and environmental conditions have been long recognised as controls, the processes and drivers remain unsolved (Rohde 1992, Huston 1999, Nekola 1999, Gaston et al. 2007, Ricklefs 2010, Hawkins et al. 2012). Meta-analysis of global diversity trends can highlight key patterns but conceal lineage specific variation that could be informative about mechanisms. In contrast, the use of spatial data and phylogenetic signal allow quantification of biodiversity and examination of processes causing the distribution and diversification of clades (Mishler et al. 2014, Pellens and Grandcolas 2016).

Detailed analysis of particular lineages has provided insights, although biogeographers are sometimes distracted by instances with low lineage diversity. In particular, relict lineages such as the Tuatara *Sphenodon punctatus* in New Zealand (Jones and Cree 2012) and the Wollemi Pine *Wollemia nobilis* in Australia (Macphail et al. 2013) provide tantalizing hints of the past composition and distribution of biota, but their minimal lineage diversity and distant phylogenetic relationships to other living organisms show extensive extinction of close relatives (Habel et al. 2010, Grandcolas et al. 2014, Grandcolas and Trewick 2016). Inferences drawn from speciose lineages with global representation should be more informative and revealing of the relative contribution of historical, spatial and ecological features that shape regional-scale species richness. Linking patterns of diversity to process is challenging, but recently developed phylodiversity metrics can provide a useful impartial view of the way biodiversity varies in global clades. These quantitative approaches can strengthen our inferences of the processes that lead to the assembly of communities (Mishler et al. 2014, Rosauer and Jetz 2014). Importantly such approaches are highly appropriate to examine spatial patterns of diversity and quantify the amount of evolutionary history or distinctiveness of a set of species because they take into account not only their geographic range but also the length of branches on the phylogeny.

The parsimonious interpretation of global patterns of diversity across different organismal groups is that regional level processes are of general importance in driving biodiversity (Ricklefs and Schluter 1983, Gaston 2000, Ricklefs 2004, Qian et al. 2009, García-R et al. 2012). In birds, biodiversity tends to be highest in tropical and subtropical areas with species associated with longer branches residing at lower latitudes (Blackburn and Gaston 1996, Jetz et al. 2004, Orme et al. 2006, Weir and Schluter 2007). More youthful diversification (lineage splitting) is associated with geologically young oceanic islands such as Galapagos finches (Grant and Grant 2008), Hawaiian honeycreepers (Lerner et al. 2011) and Madagascan vangas (Jønsson et al. 2012), but each of these examples involves limited clade depth and spatial sampling. Avian species richness differs substantially among clades and regions and it is uncertain whether local patterns help explain unevenness in the distribution of diversity in widespread speciose bird groups. Broadly distributed and species-rich lineages provide an opportunity to contrast evolutionary processes driving diversity spanning a wide spatiotemporal extent (Yuan et al. 2016).

The Rallidae is one such globally distributed bird group with clades spanning local and continental regions and a signature of high extinction dynamics (Ripley 1977, Garcia-R et al. 2014a, b). Phylogenetic analysis of approximately 70% of recognized rail species diversity including several extinct taxa provides the opportunity to assess the differences in lineage diversity among regions and so infer the influence of landscape history on species richness and community structure. Species diversity and regional composition varies, probably reflecting differing rates of speciation and extinction in response to features of local habitat stability. We used state of the art phylogenetic distance metrics to look for areas where rails have recently diversified and areas where older lineages may have persisted during periods of environmental change to test whether old diversity is tied to the tropics and young diversification is linked to oceanic islands and/or higher latitudes. We discuss biodiversity patterns in rails in terms of differing regional histories. Is rail diversity, when branch lengths from a phylogeny are used, evenly distributed around the globe, or do different processes operate in different places? How are rail phylogenetic diversity, diversification and endemism related to different geographical settings?

Material and methods

Phylogeny

We used the most complete dated phylogeny of the family Rallidae (Garcia-R et al. 2014a) to calculate the spatial metrics (Supplementary material Appendix 1 Fig. A1a). This phylogeny was obtained from fragments of three mitochondrial (cyt*b*, COI and 16S) and two nuclear (FGB7 and RAG-1) genes from 70% (91 species out of ~130) of the species within the family, including four recently extinct species, and 22 of 33 extant genera (Supplementary material Appendix 1 Fig. A1b). The phylogeny included the vast majority of valid and available Rallidae (Supplementary material Appendix 1 Table A1). *Sarothrura rufa, Canirallus kioloides* and *C. beankaensis*, that brought the total to 94 species in the previous study (Garcia-R et al. 2014a), were excluded from the present analysis because they are outside of the family and more closely related to *Heliornis fulica* (Heliornithidae).

Spatial data

We extracted occurrence records from the global biodiversity information facility (GBIF, <www.gbif.org>, last accessed in May 2017) database for taxa included in the most complete rail phylogeny available (Garcia-R et al. 2014a). We removed from the GBIF dataset any records that were not georeferenced, or related to captive specimens and/or unknown localities. For recently extinct species we added data from selected literature (Ripley 1977, Olson 1985, Ripley and Beehler 1985, Taylor 1998). Our final data set contained 1 033 872 records of 91 species of rails. Individual records consisted of documented instances of occurrences for each species in areas defined by 100 × 100 km grid cells. The coordinate information was projected into an Albers Coordinate system (ESRI:54009) to obtain equal-area square grid cells. Classification of major geographic regions of the world follow Holt et al. (2013).

Patterns in the spatial distribution of diversity and endemism

To evaluate the distribution of diversity and endemism we calculated four biodiversity metrics in each grid cell. Species richness (SR) and weighted endemism (WE) were used to evaluate the distribution of taxonomic diversity (richness). SR is the absolute number of species and WE is the sum of the proportions of species ranges represented in each equal-area square grid cells (Crisp et al. 2001, Laffan and Crisp 2003, Lee and Mishler 2014, Laffan et al. 2016). We also employed phylogenetic diversity (PD) which uses phylogenetic branch lengths to evaluate the evolutionary diversity contained within a grid cell (Faith 1992, Chao et al. 2010) and phylogenetic endemism (PE) which is a range-weighted index to assess the branches of the phylogenetic tree restricted to a given location (Rosauer et al. 2009). PE for an area is the sum of weighted branch lengths, where each branch is weighted by the fraction of its geographic range represented by the given area. In this work, PD and PE are scaled to represent the proportion of variation within the tree represented by the given taxa and the total length of the tree divided between branches according to their relative lengths (Rosauer et al. 2009). Biodiversity metrics were calculated using Biodiverse 0.19 (Laffan et al. 2010), via a pipeline (<https://github.com/NunzioKnerr/biodiverse_pipeline>) developed in R ver.3.0.2 (R Development Core Team). A redundancy test calculated as 1 – [richness/(number of samples)] was performed to identify overall sampling in each grid cell whilst a bi-plot of branch length versus bootstrap score based on the Maximum Likelihood tree was performed to evaluate the effect of phylogenetic uncertainty in the calculation of the analyses presented here.

Identifying areas of significant phylogenetic diversity and endemism

Relative phylogenetic diversity (RPD), relative phylogenetic endemism (RPE) and categorical analysis of neo- and palaeo-endemism (CANAPE) enables interpretation from lineage diversity and can be used to infer ecological processes likely implicated in the distribution of endemism (Mishler et al. 2014). RPD and RPE allow a generalizable comparison of biodiversity assessments that takes into account the topology of the tree by using the ratios of PD and PE observed on the actual tree with those on a hypothetical tree with the same topology but equal branch lengths. CANAPE identifies regions of geographically restricted long or short branches. It finds grid cells that have significantly high PE and subsequently assesses the RPE score (which is calculated as the ratio of PE from the actual tree to PE from the alternate tree) for each significant cell. CANAPE categorizes centres of endemism that are classified at phylogenetic and spatial levels according to the branch lengths of the spatially restricted branches within them. Four types of area endemism can be identified in CANAPE: neo-, palaeo-, mixed- and super-endemism (Fig. 1). Areas with neo- and palaeo-endemism both have overrepresentation of phylogenetic branches that otherwise occur rarely. The overrepresentation of range-restricted long or short branch lengths in a selected location is compared to what would be expected if the same number of terminal taxa had been selected at random from the tree. An area that has significantly more range-weighted short branches (significantly low RPE) in a phylogeny is considered an area of neo-endemism while an area with significantly long branches (significantly high RPE) is an area of palaeo-endemism.

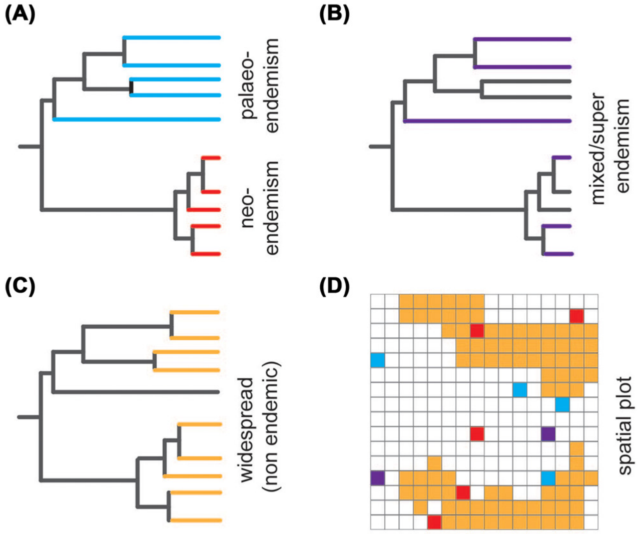

Figure 1. Illustration of the way CANAPE analysis categories express the spatial occurrence of phylogenetic diversity. The occurrence of numerous lineages on range-weighted long branches (blue branches in subtree A) in a limited area results in an inference of palaeo-endemism (blue grid cells in spatial plot D), whereas the occurrence in a limited area of lineages on range-weighted short branches (red branches in subtree A) indicates neo-endemism (red grid cells in spatial plot D). Areas of mixed or super endemism (purple grid cells in spatial plot D) are those with an assemblage consisting of locally endemic lineages on range-weighted long and short branches (purple branches in subtree B). Areas (orange grid cells in spatial plot D) with assemblages dominated by branches that are not significantly long and short after range weighting (orange branches in subtree C) are not considered endemic sites. If a branch is not found in a cell it will have zero weight and no weighted branch length.

Geographic areas of mixed- and super-endemism contain both neo- and palaeo-endemics, but are distinguished by areas of super-endemism exhibiting extremely high significance for PE on both the observed and alternate tree (using a one-tailed test, 0.01 level). Identifying areas that are hotspots of neo- or paleo-endemism has biogeographic and conservation implications because they help to generate inferences of distinctive evolutionary history and the processes that shape biodiversity. Statistical significance of these indices was evaluated using a randomization test with the standard null model (Mishler et al. 2014) in Biodiverse (Laffan et al. 2010). We ran 999 iterations of randomization and used R scripts to visualise the results. During each iteration, species (tree tips) were randomly allocated to the landscape, with the constraint that the richness of each cell was held constant and the same as in the original data set.

Data deposition

Phylogenetic trees have been deposited in TreeBASE (<www.treebase.org) with submission ID 22491.

Results

Patterns in the distribution of diversity and endemism

Spatial patterns of species richness (SR) and phylogenetic diversity (PD) were uneven but visually similar to one another and statistically correlated ($r^2=0.934$, $p < 0.001$). Each major landmass contains regions of moderate to high SR and PD (Fig. 2a, b), but the grid cells with the highest rail diversity lie in the Panamanian, Neotropical and Australian regions. These regions contain up to 13 species with a PD value of 0.28, that suggests more than a quarter of the tree is present. In contrast, the highest values of weighted (WE) and phylogenetic endemism (PE) were recovered for grid cells encompassing Australian, Oceanian and Oriental islands (Fig. 3a, b). Both metrics identify the Chatham Islands (east of New Zealand) as having high endemism, but WE was also high for the Solomon Islands whereas PE was high for Calayan Island (Philippines), Sulawesi (Indonesia) and Papua New Guinea. We found a weak correlation of both SR and PD with PE (SR-PE, $r^2=0.114$, $p > 0.05$ and PD-PE, $r^2=0.102$, $p > 0.05$), suggesting that the metrics expressed different features of spatial diversity. The variation in these metrics is not the product of arbitrary sampling because the GBIF data set is rich in rail occurrence information (Supplementary material Appendix 1 Fig. A2). We note too that there is little uncertainty about the tree topology as the only low bootstrap scores were restricted to very short branches (Supplementary material Appendix 1 Fig. A3). A small percentage of the boostrap supports values are less than 70%, which likely have little overall influence in well-sampled grid cells because the well-supported long branches contribute most of the PD (Gonzalez-Orozco et al. 2016).

Areas of significant phylogenetic diversity and endemism

For rails, grid cells with significantly high RPD were mostly in scattered locations within the Neotropical, Afrotropical and Oriental regions (Fig. 5a), whereas cells with significantly low RPD were mostly in Australia and Oceania, as well as the Nearctic and Neotropics. Significantly low RPE was recorded in scattered locations through South America and Pacific islands, while significantly high RPE was mostly in Africa and Madagascar (Fig. 4b). CANAPE analyses indicated areas with many range-restricted taxa that exist around the globe, but most centres of mixed- and super-endemism were in tropical regions below the equator (Fig. 5). Islands in northern (e.g. Hawaii and Guam) and southwest (e.g., Lord Howe Island and Auckland Islands) Pacific and north-east of the Oriental region (Calayan Island in the Philippines) were identified as centres of neo-endemism, whereas centres of palaeo-endemism were predominantly in Madagascar and surrounding islands and scattered through tropical Africa, Neotropical and Oriental regions.

Discussion

Geospatial heterogeneity in the reported biodiversity metrics suggests mixed regional variation in rates of dispersal, speciation and extinction in rails. Species richness and phylogenetic diversity metrics show areas with greatest rail diversity in both tropical and temperate zones, whereas weighted and phylogenetic endemism (WE and PE) indicated an overall trend of increasing diversity toward tropical and/or insular areas (Fig. 3a, b). Moreover, relative phylogenetic diversity (RPD) and relative phylogenetic endemism (RPE) showed a contrasting pattern with significantly high values in tropical parts of South America, Africa and Asia (blue cells in Fig. 4a, b), suggesting that these places may have acted as refugia during recent climate changes or are the result of ecological competition (Nekola 1999, Mishler et al. 2014). The resulting phylogenetic overdispersion implies unrelated taxa are able to occupy the same space, perhaps by partitioning habitats (Cody and Diamond 1975, Webb et al. 2002, Barnagaud et al. 2014, Garcia-R et al. 2016). Predominantly low RPD and RPE in Australasia and oceanic islands in Oceania may reflect habitat filtering based on phylogenetically conserved traits of closely related taxa (e.g. several extant and extinct species of *Gallirallus*). The Neotropical and Nearctic regions also present low values of RPD (red cells in Fig. 4a). However, in this case they might indicate areas where recent evolutionary diversification has occurred across environmental gradients (i.e. niche conservatism) or partitions of similar ecological conditions (e.g. *Fulica* coots associated with lake systems), as indicate by taxonomic diversification with high rates of

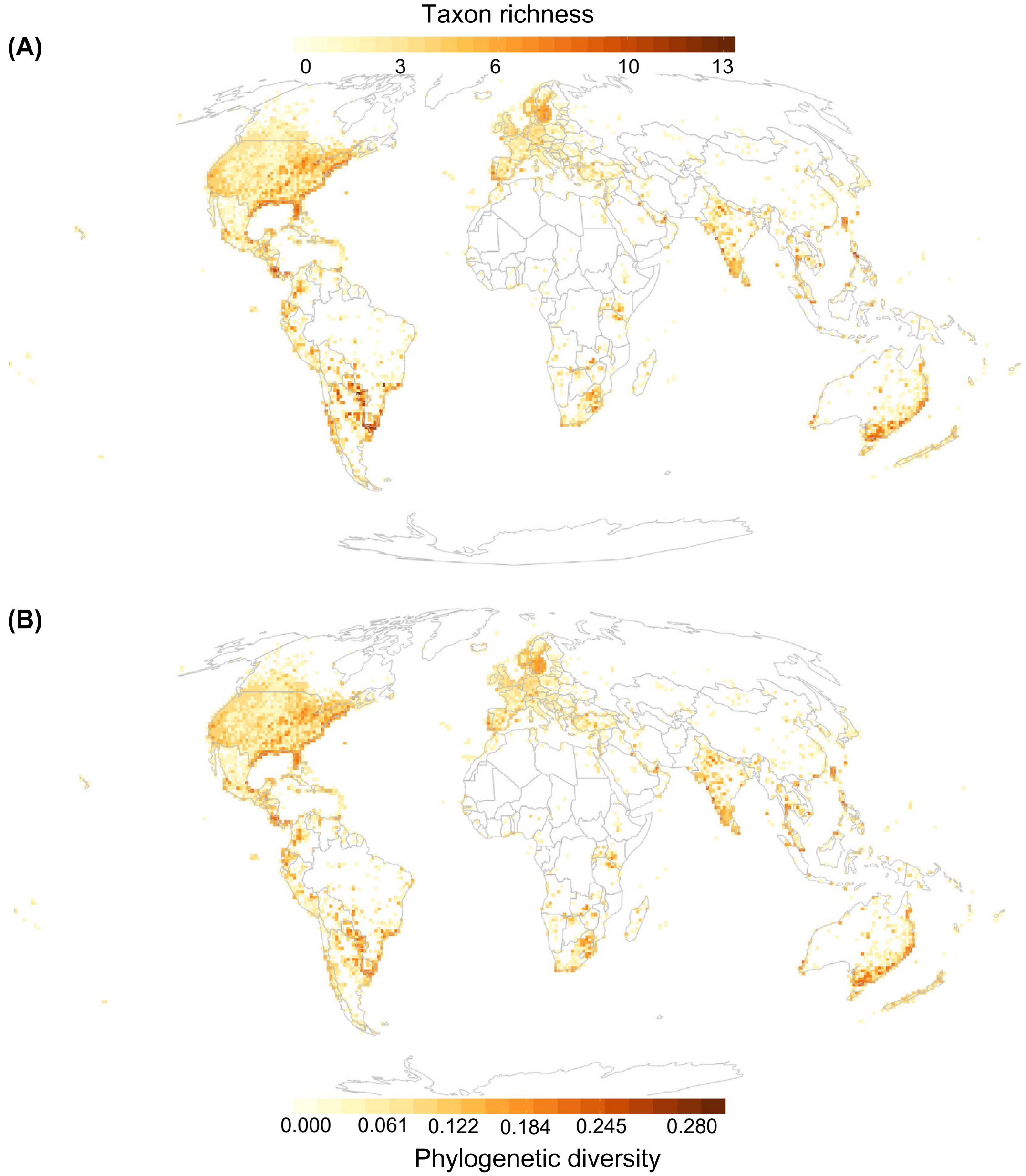

Figure 2. Global extent patterns of observed diversity for 91 species (4 extinct and 87 extant) of rails (Aves: Rallidae) using species richness (SR) and phylogenetic diversity (PD). Values are given as the fraction of total tree length. (A) SR is the number of species present in a grid cell. (B) PD is the portion of a phylogeny in a grid cell represented by the sum of the branch lengths from the root of the phylogeny to the tips (Faith 1992).

secondary sympatry (Barnagaud et al. 2014, Andersen et al. 2015).

Deep clade diversity (palaeo-endemism) associated with tropical regions is consistent with the idea that these places are evolutionary refugia or museums of diversity (Jablonski et al. 2006). For instance, Madagascar contains the majority of deep phylogenetic palaeo-endemism in rails (e.g. the habitat generalist *Dryolimnas cuvieri* and the forest-dwelling *Mentocrex kioloides*, Goodman et al. 2011) and the importance of this island as a centre of endemism is supported by studies on other birds (Jetz et al. 2014) and mammals (Wilmé et al. 2006, Rosauer and Jetz 2014). Madagascar presents three major massifs and a humid eastern biome with forest patches acting as refugia during periods of drier climate that facilitate species accumulation, allopatric speciation and numerous evolutionary radiations linked to pronounced regional and local environmental gradients (Wilmé et al. 2006, Vences et al. 2009, Jetz et al. 2012, Brown et al. 2014).

Areas of neo-endemism were in Australian, Oceanian and the Oriental regions, and especially on oceanic islands. Diversification on islands is associated with several flightless rail species of recent origin after dispersal of volant

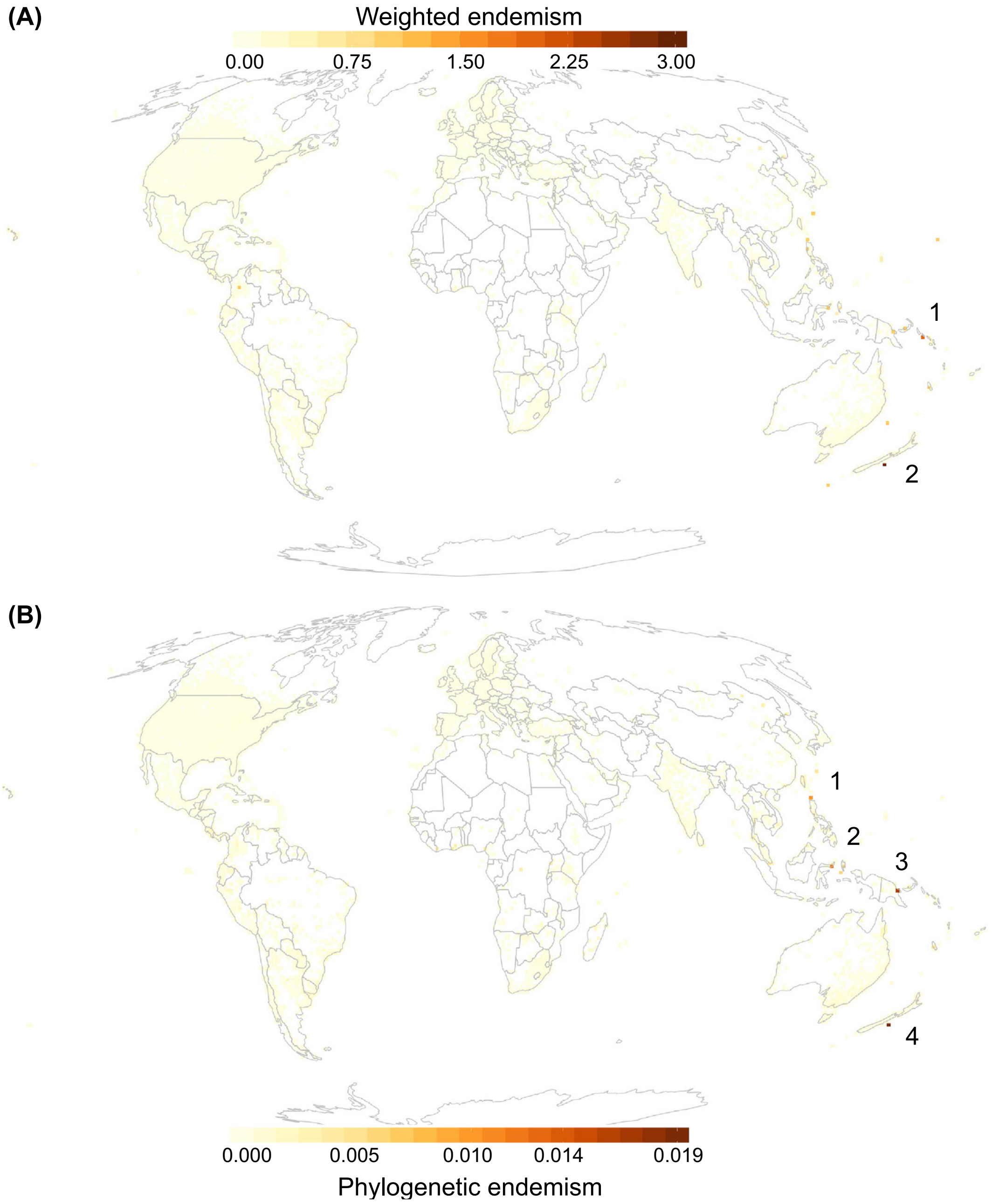

Figure 3. World spatial patterns of observed diversity for 91 species (4 extinct and 87 extant) of rails (Aves: Rallidae) using weighted endemism (WE) and phylogenetic endemism (PE). Values are given as the fraction of total tree length. (A) WE is the fraction of the range of each taxon occurring across the sampling area (Crisp et al. 2001, Laffan et al. 2016). In this case, the highest WE values are present in Solomon archipelago (1) and Chatham Islands (2). (B) PE refers to the degree of spatial restriction or geographic range of phylogenetic branches of the tree in a particular grid cell (Rosauer et al. 2009). In this case, the highest PE values are found in The Philippines (1), Sulawesi (2), Papua New Guinea (3) and Chatham Islands (4).

colonisers from continental locations (Trewick 1997a, b, Slikas et al. 2002, Garcia-R et al. 2014a, Garcia-R et al. 2016). In most cases neo-endemism involves rapid phenotypic (e.g. hindlimb and forelimb size) shifts associated with local ecological conditions, including the absence of terrestrial mammal predators (Olson 1985, Steadman 1995, Mayr and Diamond 2001, Kirchman 2009, Kirchman 2012, Garcia-R and Trewick 2015, Garcia-R et al. 2016). Several species of *Gallirallus* have independently evolved flightless insular endemics. On the Chatham islands for instance, three now extinct endemic species of (or allied to) *Gallirallus* (*Diaphorapteryx hawkinsi*, *G. modestus* and *G. dieffenbachii*) spanned a broad size and ecological range, including extreme bill size dimorphism in the smallest (Trewick 1997b, Cooper

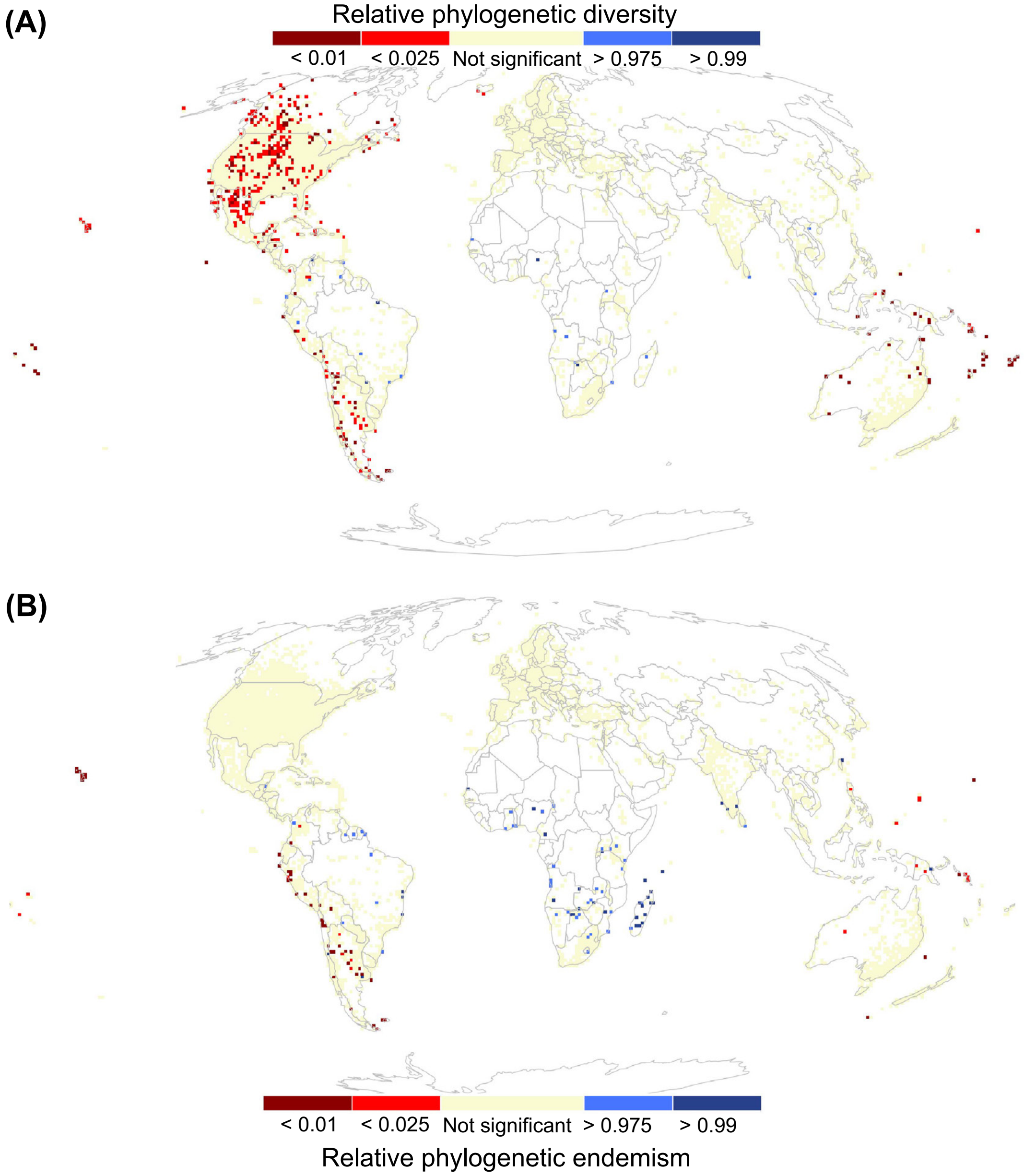

Figure 4. (A) Relative phylogenetic diversity (RPD) of rails. RPD is the PD measured on the actual tree divided by the PD measured on a comparison tree (Mishler et al. 2014). Red grid cells indicate values with significantly lower RPD than expected; that capture less PD given the number of branches and might present phylogenetic clustering. Blue grid cells indicate values that contain significantly more RPD than expected; capturing greater PD and might present phylogenetic overdispersion. Beige cells have values that are not statistically significant. (B) Relative phylogenetic endemism (RPE) of rails. RPE is PE measured on the actual tree divided by PE measured on the comparison tree (Mishler et al. 2014). The red cells show values that contain significantly lower RPE than expected; the blue cells present values that contain significantly higher RPE than expected.

and Tennyson 2004), but examples in other genera include the forest-dwelling Henderson island crake *Porzana/Zapornia atra* and open country grazing Takahe *Porphyrio hochstetteri* in New Zealand. The most likely explanation for the detection of these areas with species on short branches and their recognition as centres of neo-endemism lies in their degree of physical isolation and small populations coupled with rare long distance colonisations (Barton and Mallet 1996, Ricklefs 2003, Moyle et al. 2009, Andersen et al. 2014). Long-distance dispersal, resulting in occupation of extended geographic areas and mixed ecological conditions, is a recognised trait in some rails, but its biological importance and historical effect may be localised and short term. Many oceanic islands in the Pacific remained isolated during climate cycles of the Pleistocene (Hall 2009, Lohman et al. 2011) and were colonized by flying rails that lose their capability

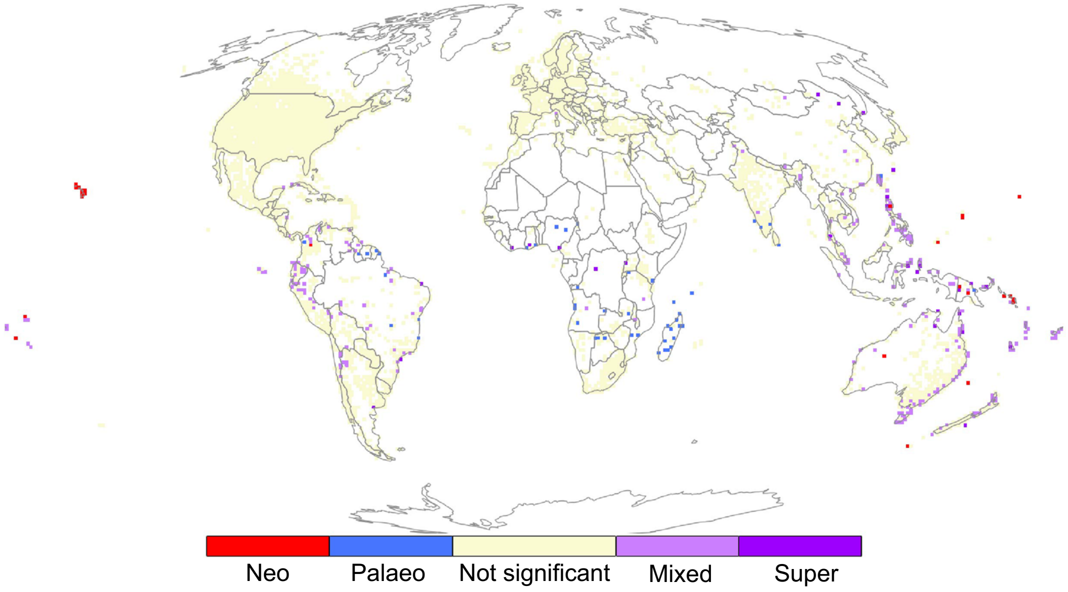

Figure 5. Centres of endemism for rails mapped from CANAPE categories of phylogenetic endemism (Mishler et al. 2014). Red grid cells indicate locations inferred as 'centres of neo-endemism' and blue grid cells indicate locations inferred as 'centres of palaeo-endemism'. Purple grid cells indicate a mix of neo-endemism and palaeo-endemism with the most statistically significant ones (dark purple) termed 'centres of super-endemism'.

for further long-distance dispersal (e.g. *Porphyrio, Lewinia* and *Gallirallus*). These species evolved into flightless endemics when flight was not integral to foraging, social interaction, or predator avoidance (Garcia-R and Trewick 2015, Garcia-R et al. 2016, Garcia-R et al. 2017). However, most endemism on each of these islands reflects a small number of flightless species (e.g. *Gallirallus wakensis* in Wake Island, *Porzana/Zapornia palmeri* in Hawaii, *Nesoclopeus poecilopterus* in Fiji, *Gallinula pacifica* in Samoa) that have unfortunately become extinct after human settlements in the late Holocene (Steadman 1989, Steadman 2006).

Overall, our analyses suggest that rail diversity reflects regional differences of diversification and extinction in response to local conditions. Habitat heterogeneity, patchiness, past climate dynamics and geographic barriers are probably the most important factors in diversification in the New and Old worlds. Madagascar and some areas of Africa and South America may represent tropical refugia containing most representation of old rail clades that matched with ancestral niches of many extant clades (Rahbek and Graves 2001, Orme et al. 2005, Hawkins et al. 2007, Weir and Schluter 2007, McCain 2009). Island archipelagos, on the other hand, show high endemism resulting from colonisation and adaptation to local conditions.

The indices used here make a robust and unique case study to explore biodiversity centres of rails in terms of evolutionary histories and potential refugia, but they also contribute important information to conservation efforts. Our analyses clearly identified islands as global centres of rail endemism, a pattern found in plants and other vertebrates (Kier et al. 2009, Jetz et al. 2012, Rosauer and Jetz 2014). High values of neo-endemic richness on islands emphasize their outstanding importance for global conservation of genetic resources whilst palaeo-endemic areas deserve particular conservation attention, as they have species that are taxonomically isolated and represent a larger amount of unique evolutionary history (Kier et al. 2009). In particular, areas identified as containing both super- and mixed-endemism are especially important because they harbour globally rare taxa on both long old and short young evolutionary branches. Most areas of mixed and super-endemism were found in tropical forests of Central Africa, Australia, Amazonia and the Pacific. Tropical forests appear to have retained lineages that suffered higher extinction rates elsewhere leading to range contraction. These 'mega' diverse hotspots represent both museums of old diversity and cradles of young diversification (Jablonski et al. 2006) that result from taxonomic accumulation of lineages colonising during period of climate instability (Voris 2000, Lohman et al. 2011, Smith et al. 2014, Bacon et al. 2015). The retention of areas with rich assemblages and development of multi-scale approaches to conserving unique evolutionary diversity require analyses of this sort.

Although we detected some empty grid cells that may not be truly empty of the species concerned (e.g. in Africa and parts of central and northern Asia), the power of the approach will continue to increase as GIS records of taxon locations accumulate. The completeness of current sampling available on the GBIF database can be considered a limitation but GBIF bird data are disproportionately better sampled and curated than other taxon groups (Maldonado et al. 2015, Amano et al. 2016, Troudet et al. 2017) and our results are consistent with the distribution and diversity of rails and patterns inferred for other vertebrates. It must be the case that at least some species have not been mapped to grid cells in which they actually occur. Related to this is the likelihood that some grid cells are now empty of species they naturally contained through human activity. Accommodating ecological change in the Anthropocene may require use of additional modelling tools (Moat et al. 2018, Ware et al. 2018). Analyses of spatial diversity may also be influenced by tips missing from the phylogeny, a common problem in biogeography as well (Crisp et al. 2011). Of the currently recognised species names missing from our analysis (Supplementary material Appendix 1 Table A2), most are on islands and/or have near relatives on short phylogenetic branches. This may mean that the extent of neoendemism is underestimated, but at least some of these putative species are likely synonyms or variants of species with more extensive spatial range that is included in our study. Others are certainly extinct and most of the localities where they were found have already been shown to be places of neo-, mixed- or super-endemism.

Acknowledgements – We received comments and critical feedback from Richard C. Winkworth, Nunzio Knerr, the Ecography subject editor and two anonymous referees that improved the manuscript.

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Supplementary material (Appendix ECOG-03783 at <www.ecography.org/appendix/ecog-03783>). Appendix 1.