Integrating multiple dimensions of biodiversity to inform global parrot conservation

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Burgio, K. R., Davis, K. E., Dreiss, L. M., Cisneros, L. M., Klingbeil, B. T, Presley, S. J., van Rees, C. B., Willig, M. R., 2022. Integrating multiple dimensions of biodiversity to inform global parrot conservation. *Animal Biodiversity and Conservation*, 45.2: 189–202, Doi: https://doi.org/10.32800/abc.2022.45.0189

Abstact

Integrating multiple dimensions of biodiversity to inform global parrot conservation. In addition to changes associated with climate and land use, parrots are threatened by hunting and capture for the pet trade, making them one of the most at risk orders of birds for which conservation action is especially important. Species richness is often used to identify high priority areas for conserving biodiversity. By definition, richness considers all species to be equally different from one another. However, ongoing research emphasizes the importance of incorporating ecological functions (functional diversity) or evolutionary relationships (phylogenetic diversity) to more fully understand patterns of biodiversity, because (1) areas of high species richness do not always represent areas of high functional or phylogenetic diversity, and (2) functional or phylogenetic diversity may better predict ecosystem function and evolutionary potential, which are essential for effective long–term conservation policy and management. We created a framework for identifying areas of high species richness, functional diversity, and phylogenetic diversity within the global distribution of parrots. We combined species richness, functional diversity, and phylogenetic diversity into an Integrated Biodiversity Index (IBI) to identify global biodiversity hotspots for parrots. We found important spatial mismatches between dimensions, demonstrating species richness is not always an effective proxy for other dimensions of parrot biodiversity. The IBI is an integrative and flexible index that can incorporate multiple dimensions of biodiversity, resulting in an intuitive and direct way of assessing comprehensive goals in conservation planning.

Key words: Parrots, Biogeography, Phylogenetic diversity, Functional diversity, Conservation

Resumen

Integración de las múltiples dimensiones de la biodiversidad para fundamentar la estrategia mundial de conservación de los psitaciformes. Además de los cambios relacionados con el clima y el uso de la tierra, los psitaciformes están amenazados por la caza y la captura destinada al comercio de mascotas, lo que los convierte en uno de los órdenes de aves en mayor riesgo de extinción para el que las medidas de conservación son especialmente importantes. Para determinar las zonas de prioridad alta para la conservación de la biodiversidad, se suele utilizar la riqueza de especies. Por definición, la riqueza considera que todas las especies son igualmente diferentes entre sí. No obstante, los estudios que se están llevando a cabo en la actualidad hacen hincapié en la importancia de incorporar las funciones ecológicas (diversidad funcional) o las relaciones evolutivas (diversidad filogenética) para comprender mejor los patrones de la biodiversidad, ya que 1) las zonas con una elevada riqueza de especies no siempre son zonas con una elevada diversidad funcional o filogenética y 2) la diversidad funcional y la diversidad filogenética pueden predecir mejor la función de los ecosistemas y el potencial evolutivo, que son fundamentales para la elaboración y gestión de políticas de conservación eficaces a largo plazo. Hemos creado un marco para determinar las zonas dentro del área de distribución de los psitaciformes en las que la riqueza de especies, la diversidad funcional y la diversidad filogenética son elevadas. Asimismo, hemos combinado la riqueza de especies, la diversidad funcional y la diversidad filogenética en un índice integrado de biodiversidad (IBI por su sigla en inglés), que permite determinar puntos de biodiversidad críticos para los psitaciformes. Hemos observado importantes discrepan-

ISSN: 1578–665 X
eISSN: 2014–928 X

cias entre las dimensiones, lo que pone de manifiesto que la riqueza de especies no siempre es una buena aproximación de las otras dimensiones de la biodiversidad de psitaciformes. El IBI es un índice integrador y flexible que puede incorporar múltiples dimensiones de la biodiversidad, lo que conlleva que sea una forma intuitiva y directa de evaluar los objetivos generales en la planificación de la conservación.

Palabras clave: Psitaciformes, Biogeografía, Diversidad filogenética, Diversidad funcional, Conservación

Received: 11 VIII 21; Conditional acceptance: 22 X 21; Final acceptance: 24 V 22

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Introduction

As we enter the early stages of the 'Sixth Mass Extinction' (Ceballos et al., 2015), conservation agencies are struggling to face the challenges of a less certain future (Armsworth et al., 2015) as a consequence of habitat conversion and climate change (Urban, 2015). While the population–level responses of avian taxa to anthropogenic pressures are mixed (Radchuk et al., 2019), parrots (Psittaciformes) appear to be especially vulnerable, and are among the most threatened orders of birds (Butchart et al., 2004), with many species and populations subject to diverse and largely consistent threats across several continents (Martin et al., 2014; Berkunsky et al., 2017; Olah et al., 2018). Furthermore, 38 % of parrot populations in the Neotropics show declining trends in abundance (Berkunsky et al., 2017), while of 15 large parrot species researched in Africa and Madagascar, 12 (75 %) showed evidence of population declines in parts of their geographical range (Martin et al., 2014). However, estimates of population density exist for only 25 % of parrot species, and those estimates suggest that parrot density is higher inside of protected areas than outside of them (Marsden et al., 2015), demonstrating the critical importance of conservation action.

Some parrot species have been linked to important ecosystem functions, including invertebrate pest management, pollination, seed dispersal, and genetic–linking of plant communities, making these species 'keystone mutualists' (Tella et al., 2015, Blanco et al., 2015, 2016; Baños–Villalba et al., 2017). Some parrots also forage on plants that are toxic or poisonous to many vertebrate species (Gilardi and Toft, 2012; Blanco et al., 2015), allowing them to find food and persist in habitats where other frugivorous species cannot do so (Gilardi and Toft, 2012); moreover, this behavior may also confer benefits of reduced parasitism (Masello et al., 2018). Given the critical ecosystem services parrots provide, their loss may have detrimental effects on the persistence of many plant species, thereby contributing to ecosystem instability. Conversely, some parrot species have been spreading into new areas, primarily as a consequence of the pet trade, which has led to human–wildlife conflicts in Europe (White et al., 2019) and the introduction of 25 non–native species that now breed in the USA (Uehling et al., 2019).

In general, parrots have long generation times, and low population densities, both life history traits that are associated with increased extinction risk (Bennett and Owens 1997; Cardillo et al., 2005). Parrots are also disproportionately targeted for hunting and trapping, with > 68 % of populations in the Neotropics and 11 of 15 (> 73 %) of assessed large parrots in Africa and Madagascar affected by capture for the pet trade, and millions of parrots being exported for trade in recent decades (Martin et al., 2014, Berkunsky et al., 2017; Martin, 2018; Olah et al., 2018). With the exception of colony–nesting species (Wermundsen, 1998; Masello et al., 2006), parrot species that are larger–bodied and have longer generation times are generally found at relatively lower densities (Marsden et al., 2015) and are more likely than are smaller parrot species to be obligate tree–cavity nesters (Renton et al., 2015). All of these factors are associated with elevated extinction risk in parrots (Jones et al., 2006, Olah et al., 2016). Despite this high level of threat, parrots have only recently been the subject of increasing research interest, and information on conservation–relevant parameters has been slow to accumulate (Masello and Quillfeldt, 2002; Brito and Orpea, 2009, Ducatez and Lefebvre, 2014; Martin et al., 2014; Olah et al., 2018). The previous lack of research may explain why density estimates, one of the most important factors in determining conservation status (Mace et al., 2008), are unreliable for most parrot species (Martin et al., 2014; Marsden et al., 2015).

The primary drivers of population decline and extinction risk in parrots include habitat loss or alteration (particularly for logging or agriculture), persecution as crop pests, capture for the global pet trade, and hunting for food (Martin et al., 2014). Of these, logging, agriculture, and capture for the pet trade simultaneously affect > 55 % of parrot populations in the Neotropics (Berkunsky et al., 2017), with apparently similar levels of incidence among large parrot species in Africa and Madagascar (Martin et al., 2014). In Oceania, logging affects the largest proportion of species (23%), followed by agriculture, hunting and trapping and invasive species (18 %, 17 %, 16 %, respectively); with invasive species including sugar gliders (*Petaurus breviceps*), fox (*Vulpes vulpes*), and feral cats (*Felis* catus) as a major threat primarily in New Zealand and Tasmania (Olah et al., 2018).

Over the past few decades, one of the most common methods for identifying areas of highest conservation priority has been based on the 'hotspot concept' (Reid, 1998; Myers et al., 2000), which uses existing species range maps to prioritize conservation efforts where species richness or richness of endemic species is highest. More recently, the multidimensional nature of biodiversity has emerged as a critical consideration for conservation prioritization and management (Mazel et al., 2014; Brum et al., 2017; Pollock et al., 2017) and considerations of irreplaceability and complementarity have supplemented the hotspot concept in spatial prioritization approaches (Andelman and Willig, 2003; Zonation and Marxan in Moilanen et al., 2009). Regions of high functional diversity (a measure of ecological trait diversity within an assemblage) or phylogenetic diversity (a measure of evolutionary diversity within an assemblage) may not coincide with areas with high species richness (for mammals; Safi et al., 2011; Mazel et al., 2014; Brum et al., 2017). Consequently, calls to incorporate phylogenetic or functional biodiversity into conservation planning have arisen in recent decades (Mace et al., 2003; Diaz et al., 2007). Phylogenetic or functional diversity may be better indicators of community resilience than is species richness (Naeem et al., 2012). Conserving functional diversity is critical for maintaining ecosystem functions (Naeem et al., 2012), and thus for maintaining critical ecosystem services, making it an important consideration in conservation (Chan et al., 2006; Diaz et al., 2007; Cimon–Morin et al., 2013; Kosman et al., 2019). Nonetheless, cases that incorporate functional diversity in conservation research are rare (but see Devictor et al., 2010; Mazel et al., 2014; Kosman et al., 2019). Maintaining the capacity for future adaptation is an important consideration for communities undergoing rapid climatic and environmental changes, suggesting that phylogenetic diversity should be given consideration when determining conservation goals (Naeem and Li, 1997; Cardinale et al., 2012). Moreover, the loss of phylogenetic or functional diversity may be a better indicator than is the loss of species richness in quantifying ecosystem vulnerability (Srivastava et al., 2012).

The limited availability of data at appropriate scales, and the complex nature of metrics used to quantify functional or phylogenetic diversity, have previously inhibited incorporation of this information into spatial conservation planning for protected areas (Brum et al., 2017; Pollock et al., 2017). A phylogenetic supertree for the world’s parrots (Burgio et al., 2019) and an improved suite of functional diversity metrics that emphasize the summed functional uniqueness of species within parrot communities throughout the world (Kosman et al., 2019), are now available. These developments have provided data and methods that can complement the standard use of species richness to set parrot conservation goals (Kosman et al., 2019). However, a method to integrate taxonomic, phylogenetic, and functional information into a single comprehensive biodiversity metric to guide conservation decisions in general, or parrot conservation decisions in particular, has not been developed. Here, we create a framework to identify areas of high species richness, functional diversity, and phylogenetic diversity within the global distribution of parrots by combining these recent innovations in parrot biodiversity research with existing data on global species distributions. We separately calculated species richness, functional diversity, and phylogenetic diversity, and then combined them into an Integrated Biodiversity Index (IBI) to identify global biodiversity hotspots to aid in parrot conservation. In addition, we specifically searched for important spatial mismatches between the components of this integrated metric to identify situations in which species richness is not an effective proxy for other dimensions of parrot biodiversity.

Material and methods

Data collection

We used range maps for all 398 extant species of parrot (Birdlife International, 2015) following the taxonomy of del Hoyo et al. (2014) to inform spatially–explicit estimates of biodiversity at a global scale. We estimated functional diversity using two types of data: categorical (binary) and mensural traits (table 1). For each data type, we used a suite of traits that reflect particular niche axes and define functional components. Categorical traits included components of diet, foraging strategy, and foraging location, whereas mensural traits comprise body size and range size. For each categorical trait, a species received a '1' if it exhibited the characteristic and a '0' if it did not. For each body size, we used the average value for each species based on measurements of multiple adults, when available. We obtained trait data for all parrot species from the literature (Burgio et al., 2019 for more details about this previously described and published dataset). We calculated phylogenetic diversity for each community using branch lengths from the phylogenetic supertree for all 398 extant parrots by Burgio et al. (2019).

Analyses

Biodiversity indices

We created a grid in ArcMap v.10.3 (ESRI, Redlands, CA, USA), using the Cylindrical Equal Area projection, with each grid cell measuring 50 x 50 km (hereafter 'grid cell'). For each grid cell (n = 21,078), we estimated species richness as the number of species with a range overlapping the cell. We estimated phylogenetic and functional diversity for each cell using Rao's quadratic entropy (Rao's Q: Botta–Dukát, 2005). Rao's Q measures the average difference between all pairs of species, thereby reflecting multivariate dispersion. We obtained the average phylogenetic or functional distances among species from pairwise dissimilarity matrices for the phylogenetic and functional components, as well as separately for each of the six functional categories. For the phylogenetic supertree, we populated a pairwise dissimilarity matrix via the 'cophenetic' function of the R package 'ape' (v.3.5; Paradis et al., 2004). We used the Gower metric from the R package 'cluster' (v.2.0.4; Maechler et al., 2012) to calculate pairwise functional dissimilarity matrices.

To allow meaningful comparisons among dimensions, we transformed each metric into its effective number of species or Hill number (hereafter numbers equivalent). The numbers equivalent is the number of maximally dissimilar species that is required to produce an empirical value of a diversity metric (Jost, 2006). This transformation facilitates intuitive interpretation of differences among assemblages and dimensions because indices are expressed in the same units (Jost, 2006, Chao et al., 2014). Species richness is its own numbers equivalent, because it is expressed in number of species. We transformed Rao's Q values into numbers equivalents using R functions developed by De Bello et al. (2010).

Integrated biodiversity index

The integrated biodiversity index (IBI) combines numbers–equivalent–transformations of Rao's Q for phylogenetic and functional diversity (all traits combined) with species richness. We scaled each dimension of biodiversity to a range from 0 to 1 so that each would have equal opportunity to contribute to the IBI value. Without such scaling, species richness would likely dominate spatial patterns of biodiversity. The IBI is the sum of the scaled representations of species richness (S), functional diversity (FD), and

Table 1. Functional attributes that reflect niche axes (functional components) were used to estimate functional biodiversity of parrot assemblages for each 500 km^2 grid cell: Fc, functional component; At, Attribute; Tv, trait values.

Tabla 1. Atributos funcionales que reflejan las dimensiones (componentes funcionales) que empleamos para estimar la biodiversidad funcional de las comunidades de psitaciformes respecto de cada cuadrícula de 500 km^2: Fc, componente funcional; At, Atributo; Tv, valores de los rasgos.

Type of data	Fc	At	Tv
Categorical			
	Diet	Carrion	1.0
		Invertebrates	1.0
		Snails	1.0
		Pollen	1.0
		Nectar	1.0
		Flower	1.0
		Seed	1.0
		Nut	1.0
		Fruit	1.0
		Plant matter	1.0
		Roots	1.0
		Fungi	1.0
	Foraging strategy	Glean	1.0
		Dig	1.0
		Scavenge	1.0
		Graze	1.0
		Flower probe	1.0
		Excavate	1.0
	Foraging location	Water	1.0
		Ground	1.0
		Vegetation	1.0
		Subcanopy	1.0
		Canopy	1.0
Mensural			
	Body size	Mass	Mean (g)
		Lenght	Mean (cm)
		Tarsus	Mean (mm)
		Culmen	Mean (mm)
		Wing	Mean (mm)
		Tail	Mean (mm)
	Range size	Area	km^2

phylogenetic diversity (PD) for a particular grid cell (i):

$$\text{IBI} = \sum_i \frac{S_i - S_{min}}{S_{max} - S_{min}} + \frac{FD_i - FD_{min}}{FD_{max} - FD_{min}} + \frac{PD_i - PD_{min}}{PD_{max} - PD_{min}}$$

As a consequence of the numbers equivalent transformation and scaling functions, IBI values range from 0 to 3 and equally weight each dimension of diversity (a value of '0' would mean low combined biodiversity while a value of '3' would be highest in combined biodiversity).

Results

Species richness of parrots is highest in the Amazon Basin of South America, along the southeastern coast of Australia, and in the mountainous region of New Guinea (fig. 1A). Functional diversity is highest in the dry Chaco of South America (fig. 1B). Our measure of functional diversity represents multivariate dispersion, which is greatest for assemblages that represent many functional types, but that have low redundancy in those functions. Dry Chaco parrot assemblages have low species richness (fig. 1A) and species that differ greatly from each other in functional traits associated with diet and foraging location. Phylogenetic diversity is highest in Australia, arising primarily from the diversification of multiple subfamilies within the Psittacidae, and the fact that cockatoos (Cacatuidae), which represent a deep split in the parrot phylogeny (fig. 2), are endemic to Australia and Oceania.

IBI is highest in Australia and New Guinea (fig. 3), and moderate in northern and central South America. For example, in South America, species richness is highest in the Amazon Basin (fig. 4A), phylogenetic diversity is fairly evenly distributed throughout the

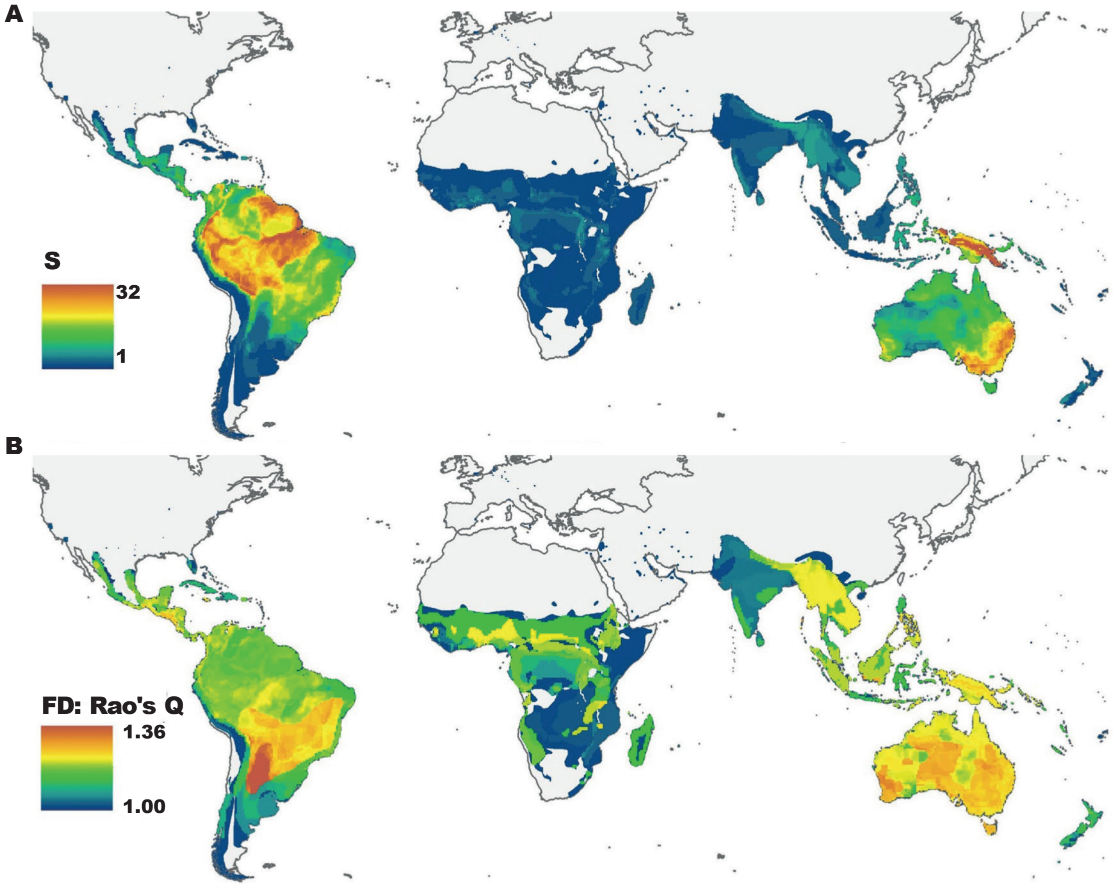

Fig. 1. Global map of: A, parrot species richness (S); and B, functional diversity (FD: Rao's Q, based on Hill numbers). Functional traits in the analysis include: diet, foraging location, foraging strategy, body size and shape characteristics, and range size.

Fig. 1. Mapa mundial de: A, la riqueza de especies de psitaciformes (S); y B, la diversidad funcional (FD por su sigla en inglés: Q de Rao, basada en números de Hill). Los rasgos funcionales del análisis son: la dieta, el lugar de alimentación, la estrategia de alimentación, la talla corporal, las características de forma y el tamaño del área de distribución.

continent (fig. 4B), and functional diversity is highest in the dry Chaco (fig. 4C). Although IBI equally weights each of the three dimensions (fig. 4D), considerable spatial mismatches exist between hot spots of species richness and IBI (fig. 4E, 5).

Discussion

In general, most of Australia, the island of New Guinea, and to a lesser extent, the Amazon Basin, evince the highest values of IBI. This corroborates past findings from studies on species richness, and emphasizes that the most diverse hotspots for parrot conservation are understudied and in urgent need of future research (Brito and Orpea, 2009; Ducatez and Lefebvre, 2014; Wilson et al., 2016), In addition, research on functional singularity of parrot species (a measure of species–level functional uniqueness) found that the parrot communities of these same regions comprise many species with highly unique and distinctive functional traits despite being communities with relatively low species richness (Kosman et al., 2019).

Aside from multiple dimensions of biodiversity, considerations of spatial scale are necessary for effective conservation planning from an applied perspective. For example, most natural resource management agencies and conservation initiatives are regional or local in their scope and capabilities, and cannot engage in global conservation planning. For instance, the Neotropics score rather low (fig. 2) in phylogenetic diversity compared to other regions because only one subfamily (Arinae) is endemic there. However, functional diversity is highest in the Chaco region of South America, likely because it is a harsh environment with low productivity; it likely cannot support multiple populations or taxa that perform

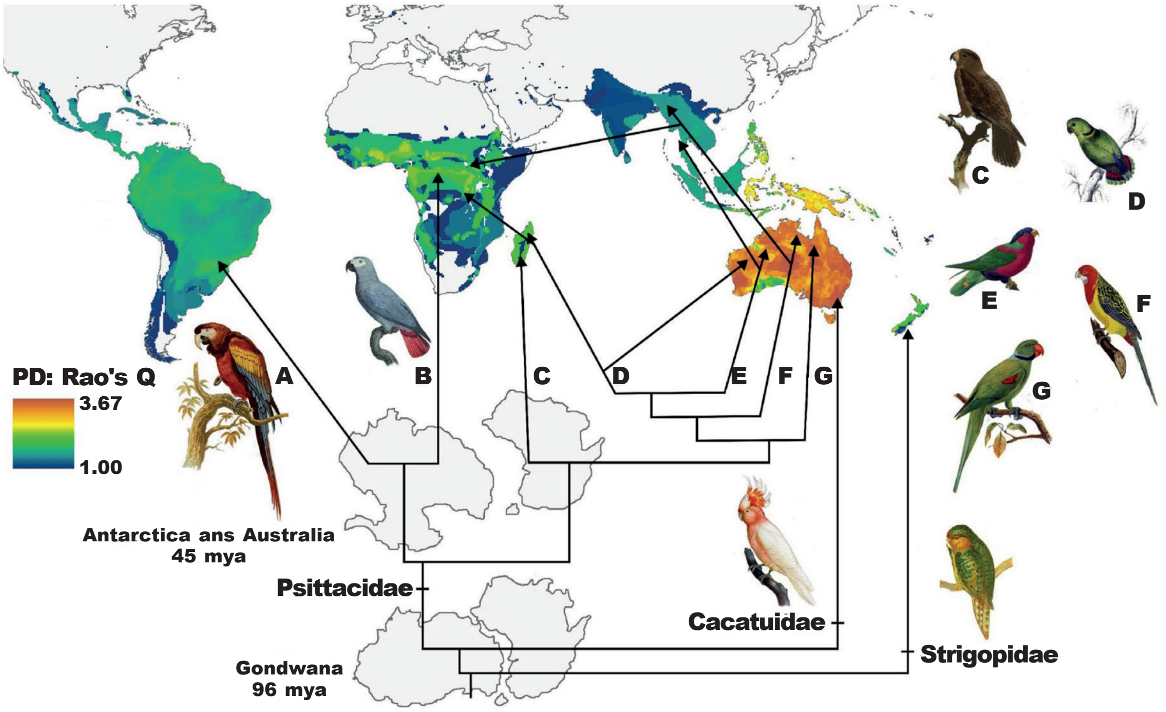

Fig. 2. Global map of phylogenetic diversity (PD) of parrots (Rao's Q, based on Hill numbers) associated with a diagrammatic representation of the diversification of major clades and their biogeographic affinities. Images of Gondwanaland were redrawn from Li and Powell (2001), with paths of dispersal obtained from Schweizer et al. (2010). Subfamilial designations on the cladogram are: A, Arinae; B, Psittacinae; C, Coracopseinae; D, Agapornithinae; E, Loriinae; F, Platycercinae; and G, Psittaculinae. (All parrot images are Public Domain)

Fig. 2. Mapa mundial de la diversidad filogenética (PD por su sigla en inglés) de los psitaciformes (Q de Rao, basada en números de Hill) combinado con la representación de la diversificación de los principales clados y sus afinidades biogeográficas. Las imágenes de Gondwana se extrajeron de Li y Powell (2001) y los patrones de dispersión se obtuvieron de Schweizer et al. (2010). Las designaciones de las subfamilias en el cladograma son: A, Arinae; B, Psittacinae; C, Coracopseinae; D, Agapornithinae; E, Loriinae; F, Platycercinae; y G, Psittaculinae (todas las imágenes de psitaciformes son de dominio público).

similar functions. The Arinae subfamily diversified relatively quickly (Davies et al., 2007; Wright et al., 2008) and is the most species–rich subfamily in the parrot phylogeny, accounting for the discrepancies between dimensions of biodiversity in South America (fig. 4). Maps of functional and phylogenetic diversity generated using only species of parrots found in the Neotropics (i.e., the Arinae) likely would identify different areas of continental conservation concern than those presented here (fig. 2, 4).

The areas we identified as high priorities generally correspond with results from other global prioritization research, but with a few notable exceptions. For instance, Myers et al. (2000), who initiated the 'hotspots' concept, and included a wide variety of taxa, also identified Brazil's Cerrado and the southern expanse of the tropical Andes as areas of high priority; but did not prioritize central Australia. Research restricted to considerations of species–level functional distinctiveness of parrots (Kosman et al., 2019), also identified New Guinea, Australia, and the Cerrado as areas of high priority for parrot conservation. Recent research has incorporated spatial prioritization and multiple dimensions of diversity. For instance, high priority areas for birds (Pollock et al., 2017) and mammals (Brum et al., 2017) are the Andes, equatorial Africa, Indonesia, and New Guinea, which coincide well the patterns of high IBI for parrots, though our results also emphasize southeastern Australia and the Amazon Basin, likely due to the unique diversification pattern of parrots.

The incorporation of socioeconomic data into conservation decisions can help anticipate new risks and adapt management targets accordingly (Armsworth et al., 2015). For example, high levels of urbanization correlate with an increased number of threatened parrot species, and a country's GDP (per capita) is associated with higher threat level (Butchart et al., 2015; Olah et al., 2016). Combining

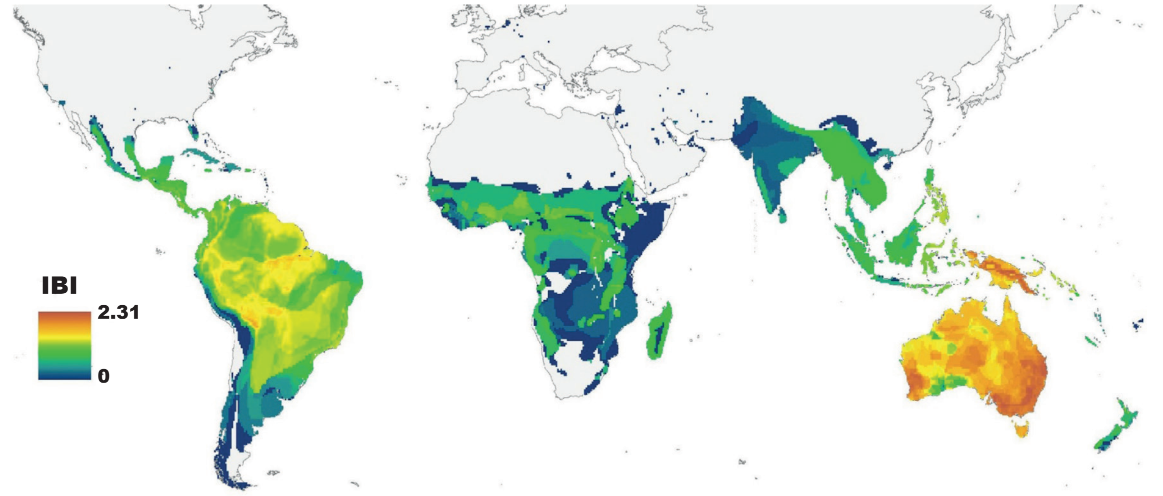

Fig. 3. Global map of the integrated biodiversity index (IBI) for parrots, which is the sum of numbers equivalents of species richness, phylogenetic diversity, and functional diversity for each grid cell, with each of the three components scaled from 0 to 1.

Fig. 3. Mapa mundial del índice integrado de biodiversidad (IBI por su sigla en inglés) para los psitaciformes, que es la suma de los números equivalentes de la riqueza de especies, la diversidad filogenética y la diversidad funcional de cada cuadrícula, los tres van de 0 a 1.

the IBI approach with socioeconomic variables could identify areas within countries where high levels of these risk factors coincide with high biodiversity to facilitate conservation prioritization and early intervention before extinction debt is generated by the excess accumulation of population stressors (e.g. habitat loss and increased hunting).

If a conservation practitioner were to use species richness as their only metric for spatial conservation prioritization of parrots in South America, they would focus on the Amazon Basin (fig. 4A), largely ignoring the high degree of functional diversity in the dry Chaco, which has the highest functional diversity of parrots in the world (fig. 4C). However, by incorporating multiple aspects of biodiversity in the IBI, these aspects of biodiversity are weighted equally (fig. 4D), allowing conservation agencies to make more informed decisions. Importantly, any particular dimension of biodiversity can be emphasized (or de–emphasized) within the IBI framework depending on the goals of a particular project. The mismatch between species richness and IBI (fig. 4E, 5) illustrates the importance of all aspects of biodiversity, and the problems with assumptions that protecting one dimension means that other dimensions are protected effectively. Spatial mismatches among hotspots of different dimensions have also been documented for mammals (Mazel et al., 2014). Conservation planners and practitioners should consider the scale and goals of conservation plans and should incorporate relevant information into an integrated framework to understand the relative value of particular policy options before taking action.

Although we do not explore extinction risk specifically, our framework may be applied to examine specific correlates of extinction risk among communities across space. Specifically, some of the traits and datasets used for IBI calculation in this study are associated with elevated extinction risk. For instance, parrot species with larger bodies or that are more dependent on forest habitat may be at increased risk for extinction (Jones et al., 2006; Olah et al., 2016). Depending on the source of threat to a given species or region, conservation planners may find it useful to consider some functional components of our IBI approach separately. This is a complementary approach to an aggregated metric like the IBI, and could be a valuable exercise in certain circumstances.

For example, mapping the areas of relatively low diversity in traits such as body size (fig. 1s in supplementary material), location (fig. 3s in supplementary material), or range size (fig. 5s in supplementary material), may be a good first step in identifying assemblages that may be at greater risk for extinction. This step may be particularly important because the simultaneous consideration of all components of functional diversity can obscure important patterns that are relevant to particular conservation issues (Spasojevic and Suding, 2012; Lopez et al., 2016). Conservation agencies concerned primarily with protecting ecosystem functioning or ecosystem services may wish to focus on diet and foraging strategy diversity (fig. 2s, 4s in supplementary material, respectively), as opposed to broader summary indices of diversity.

As demonstrated in this study, the three components of IBI are given equal weight. This was done to demonstrate the extent of spatial mismatch between

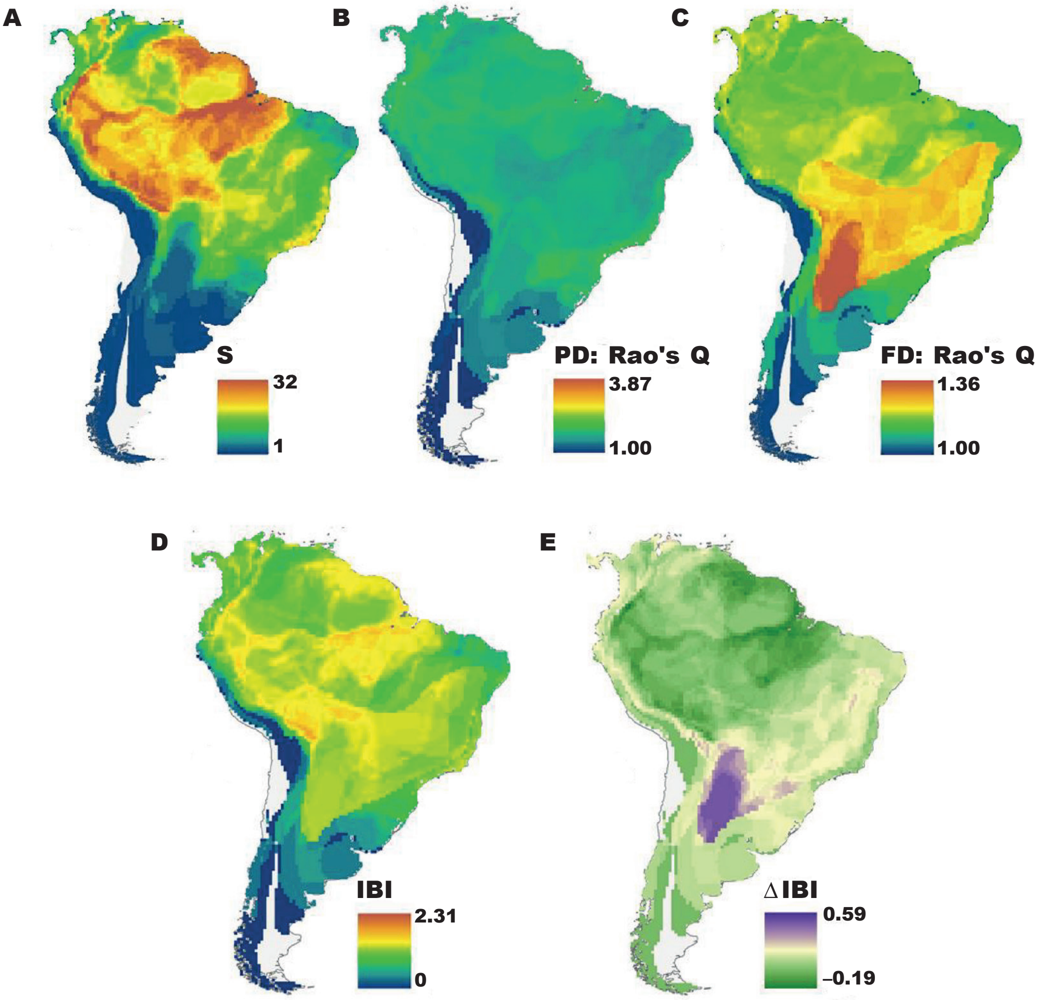

Fig. 4. Graphical comparison of: A, species richness (S); B, phylogenetic diversity (PD); and C, functional diversity (FD) patterns as well as D, IBI of South America and E, the difference between species richness (S) and IBI (∆IBI), illustrating that correlation on a global level does not predict congruence of hotspots of each dimension at smaller spatial scales. To calculate ∆IBI, we scaled the results of panels A and D to 0–1 (to make them comparable) and subtracted S from IBI, resulting in ∆IBI, which can range from –1 to 1. Positive scores (purple) are areas more emphasized by IBI, whereas negative scores (green) are areas more emphasized by species richness. Yellow scores indicate approximately equal emphasis.

Fig. 4. Comparación gráfica de los patrones de: A, la riqueza de especies (S); B, la diversidad filogenética (PD por su sigla en inglés); y C, la diversidad funcional (FD por su sigla en inglés), así como D, el índice integrado de biodiversidad (IBI por su sigla en inglés) de Sudamérica y E, la diferencia entre la riqueza de especies (S) y el IBI (∆IBI), lo que muestra que la correlación a escala mundial no permite predecir la congruencia de los puntos críticos de cada dimensión de biodiversidad en escalas espaciales más reducidas. Para calcular ∆IBI, transformamos los resultados de A y D en una escala de 0 a 1 (para poderlos comparar) y restamos S del IBI, lo que dio lugar a ∆IBI, que puede valer entre –1 y 1. Las puntuaciones positivas (en color violeta) indican las zonas con un IBI elevado, mientras que las negativas (en color verde) indican las zonas con una elevada riqueza de especies. Las puntuaciones intermedias (en color amarillo) indican zonas en las que el IBI y la riqueza de especies tiene aproximadamente el mismo peso.

phylogenetic and species richness indicators for illustrative purposes. For conservation implementation, decision–makers can easily assign weights to these different components as needed for prioritization or gap analysis. For example, a potential extension of our framework could evaluate how well particular dimensions of parrot biodiversity are protected, as a means of weighting the IBI equation to emphasize or de–emphasize particular dimensions when prioritizing areas to protect. The network of protected areas in

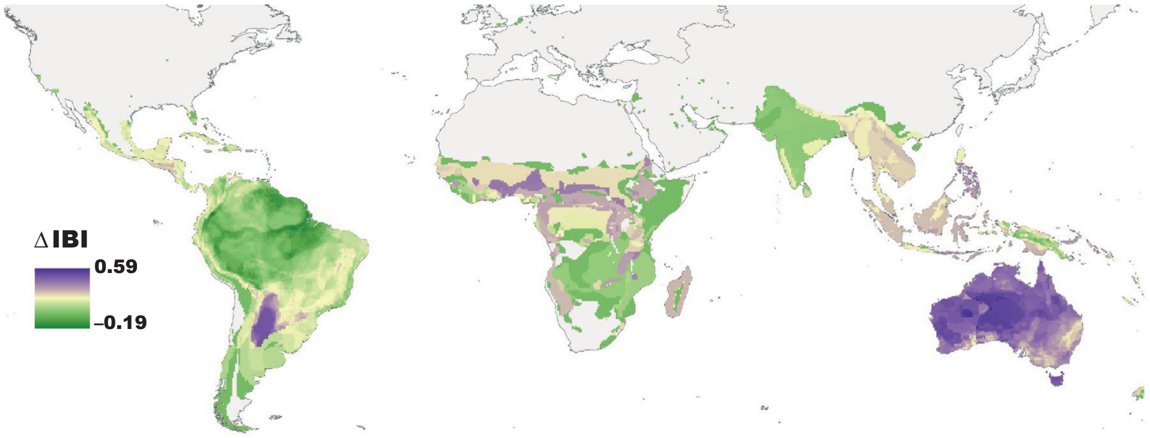

Fig. 5. Global map of mismatch between integrated biodiversity index (IBI) and species richness. Results shown in figures 1A and 3 are scaled from 0 to 1 (to make them comparable), and subtracted species richness (S) from (IBI), resulting in ∆IBI*,* which can range from –1 to 1. Positive scores (purple) are areas more emphasized by IBI, whereas negative scores (green) are areas more emphasized by species richness. Yellow scores indicate similar conclusions based on IBI or species richness.

Fig. 5. Mapa mundial de la discrepancia entre el índice integrado de la biodiversidad (IBI) y la riqueza de especies. Los resultados que se muestran en las figuras 1A y 3 se han transformado en una escala del 0 al 1 (para poderlos comparar) y se ha restado la riqueza de especies (S) del IBI, lo que da como resultado ∆IBI, que puede valer entre –1 y 1. Las puntuaciones positivas (en color violeta) indican las zonas con un IBI elevado, mientras que las negativas (en color verde) indican las zonas con una elevada riqueza de especies. Las puntuaciones intermedias (en color amarillo) indican que se pueden extraer conclusiones parecidas tanto en función del IBI como de la riqueza de especies.

France provides different levels of protection for bird species richness, phylogenetic diversity, and functional diversity (Devictor et al., 2010). Similarly, measures such as 'ED' (Evolutionary Distinctiveness; Isaac et al., 2007), 'EDGE' (Evolutionary Distinctiveness/Globally Endangered; Isaac et al., 2007), and 'EDR' (Evolutionary Distinctiveness Rarity; Jetz et al., 2014) can be added or can replace phylogenetic diversity to ensure that distinct clades of the parrot tree are given more weight when assessing conservation priorities.

Climate change will have direct and indirect effects on species distributions (Jones et al., 2016). Direct effects are based on the physiological tolerances of species, which will track their climatic niches as spatial patterns of temperature and precipitation change. Indirectly, climate change will affect land–use patterns by humans (Turner et al., 2010), which may limit or form barriers against the dispersal of individuals (Faleiro et al., 2013). Indirect effects can also be mediated by interspecific interactions, for example changes in nesting or foraging habitat availability from changes in the plant community, or exposure to novel predators from climate range shifts (Porfirio et al., 2016; Hambuckers et al., 2021).

Preserving connectivity among habitat patches may be a key element of effective conservation strategies in the face of climate change (Schmitz et al., 2015), further supported here by the areas we identify as high diversity, including the belt across central South America (fig. 4). The effects of recent climate change have been greater at high elevations and in tundra compared to tropical and subtropical lowlands (Seddon et al., 2016) that harbor most species of parrots. Nonetheless, many parrot species occur in areas that are sensitive to climate change. Based on a combination of species richness and the number of threatened species and endemic species, Indonesia, Brazil, Australia, Colombia, and Bolivia are the five highest priority countries for parrot conservation action (Olah et al., 2016), although several countries in the Neotropics (including Panama, Guyana, Surinam, French Guiana, Uruguay and the Greater and Lesser Antilles) represent data gaps and thus research priorities (Berkunsky et al., 2017). Olah et al. (2018)'s more recent analyses for Oceania also highlight New Caledonia, New Zealand (particularly the South Island), Tasmania, and the Moluccas as additional major priorities for parrot conservation.

Given the predicted extent and severity of effects of climate change, conservation agencies face a daunting task. Conservation planning must balance current protection needs with future expectations as species may become locally extinct, shift their ranges, or adapt to changing conditions, possibly leading to the production of novel assemblages. Additional complications for future conservation efforts include the push and pull between different scales of conservation prioritization (i.e. the 'actors' versus the 'stage'; Tingley et al., 2014). Although some conservation agencies may opt to focus on particular species due to public and political values (Mace, 2004), IBI is an integrative and flexible index that can incorporate multiple dimensions of biodiversity, resulting in the intuitive way to assess more than just species richness in conservation planning.

Acknowledgements

We thank R. K. Colwell, C. Rittenhouse, M. Rubega, B. Walker, and an anonymous reviewer for providing valuable feedback. K. R. Burgio was supported by National Science Foundation (NSF) grant #DGE–0753455. Many of the methods in this paper were developed in part by participation of K. R. Burgio, L. M. Dreiss, L. M. Cisneros, B. T. Klingbeil, S. J. Presley, and M. R. Willig in an NSF–funded project entitled 'The Dimensions of Biodiversity Distributed Graduate Seminar' awarded to S. Andelman and J. Parrish (DEB–1050680). S. J. Presley and M. R. Willig were supported by the Center for Environmental Sciences and Engineering at the University of Connecticut, as well as by an NSF award (DEB–1546686 and DEB–1831952).

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Supplementary material

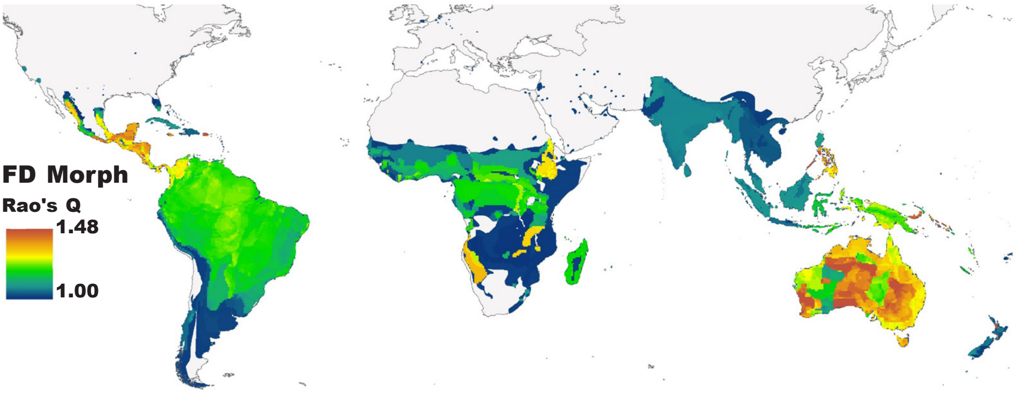

Fig. 1s. Global map of morphological trait diversity of parrots based on Rao's Q.

Fig. 1s. Mapa mundial de la diversidad de características morfológicas de los psitaciformes basada en la Q de Rao.

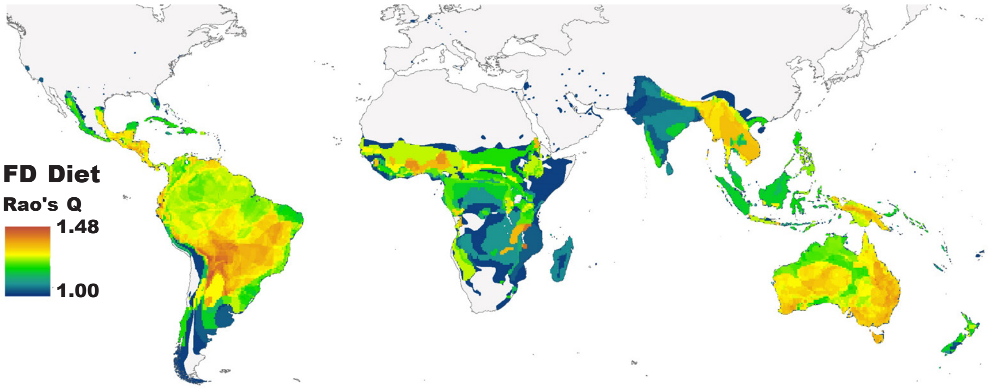

Fig. 2s. Global map of diet diversity of parrots based on Rao's Q.

Fig. 2s. Mapa mundial de la diversidad alimentaria de los psitaciformes basada en la Q de Rao.

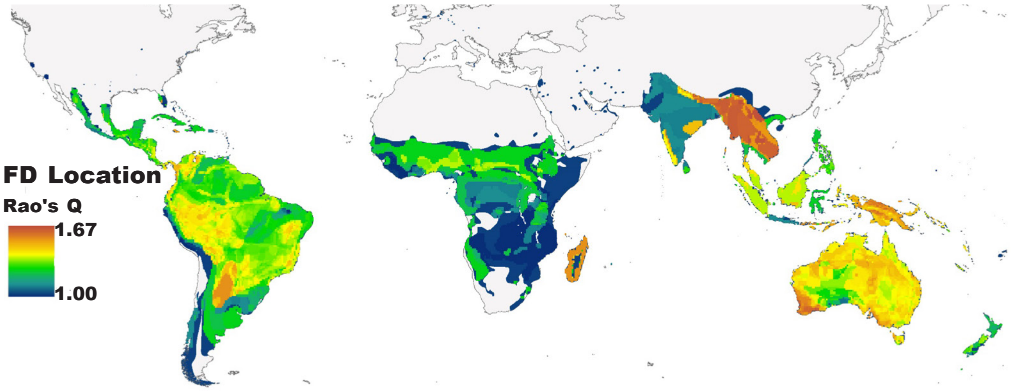

Fig. 3s. Global map of foraging location diversity of parrots based on Rao's Q.

Fig. 3s. Mapa mundial de la diversidad de lugares de alimentación de los psitaciformes basada en la Q de Rao.

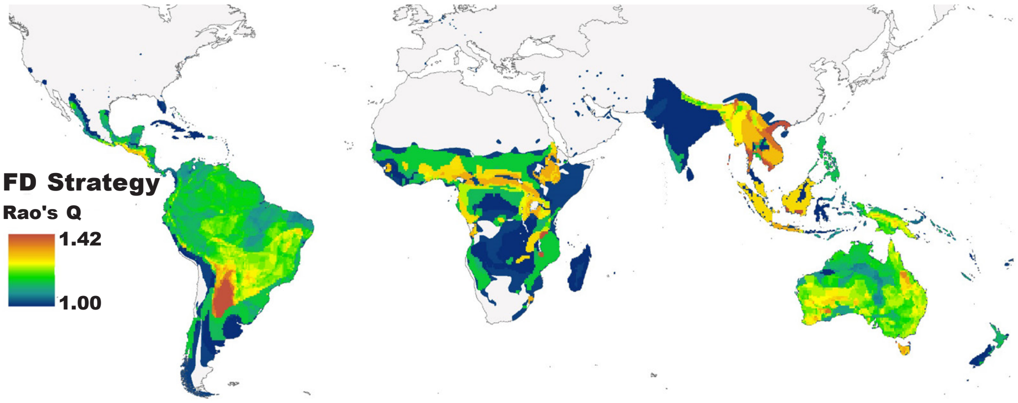

Fig. 4s. Global map of foraging strategy diversity of parrots based on Rao's Q.

Fig. 4s. Mapa mundial de la diversidad de estrategias de alimentación de los psitaciformes basada en la Q de Rao.

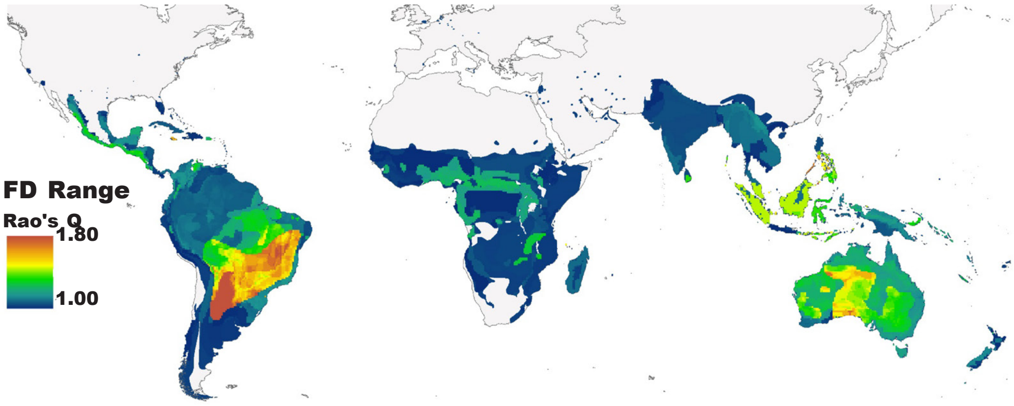

Fig. 5s. Global map of range size of parrots based on Rao's Q.

Fig. 5s. Mapa mundial del tamaño del área de distribución de los psitaciformes basado en la Q de Rao.

R code for quantifying Rao's Q for functional diversity.

Código R para cuantificar la Q de Rao para la diversidad funcional.

```
#Code from: Integrating multiple dimensions of biodiversity to inform global parrot conservation
        #Corresponding Author: Kevin R. Burgio: kevin.burgio@gmail.com

#set working directory
setwd(".../FD")

#load packages and source code
source("Rao.r")
library(cluster)
library (ade4)

########### COMM 1 ############
Parrot_Comm=read.table("Parrot_Comm_1_Fixed.txt", h=T)
tParrot_Comm = t(Parrot_Comm)

##AllTraits
All_Traits=read.table("All_Traits.txt", h=T)
useD=daisy(All_Traits[,1:30], metric="gower",weights = c(1/6, 1/6, 1/6, 1/6, 1/6, 1/6, 1/12, 1/12, 1/12,
1/12, 1/12, 1/12, 1/12, 1/12, 1/12, 1/12, 1/12, 1/12, 1/5, 1/5, 1/5, 1/5, 1/5, 1/6, 1/6, 1/6, 1/6, 1/6, 1/6))
useRaoJ = Rao(sample=tParrot_Comm, dfunc=useD, dphyl=NULL, weight=F, Jost=T, structure=NULL)
write.csv(useRaoJ$FD$Alpha,"FD_All_NR_Comm_1_Results_1.csv")

##MorphTraits
Morph_Traits=read.table("Morph_Traits.txt", h=T)
useD=daisy(Morph_Traits, metric="gower")
useRaoJ = Rao(sample=tParrot_Comm, dfunc=useD, dphyl=NULL, weight=F, Jost=T, structure=NULL)
write.csv(useRaoJ$FD$Alpha,"FD_Morph_Comm_1_Results_1.csv")

##DietTraits##
Diet_Traits=read.table ("Diet_Traits.txt", h=T)
useD=daisy(Diet_Traits, metric="gower")
useRaoJ = Rao(sample=tParrot_Comm, dfunc=useD, dphyl=NULL, weight=F, Jost=T, structure=NULL)
write.csv(useRaoJ$FD$Alpha,"FD_Comm_1_Results_1.csv")

##WhereTraits##
Location_Traits=read.table ("Location_Traits.txt", h=T)
useD=daisy(Location_Traits, metric="gower")
useRaoJ = Rao(sample=tParrot_Comm, dfunc=useD, dphyl=NULL, weight=F, Jost=T, structure=NULL)
write.csv(useRaoJ$FD$Alpha,"FD_Location_Comm_1_Results_1.csv")

##HowTraits##
Strategy_Traits=read.table ("Strategy_Traits.txt", h=T)
useD=daisy(Strategy_Traits, metric="gower")
useRaoJ = Rao(sample=tParrot_Comm, dfunc=useD, dphyl=NULL, weight=F, Jost=T, structure=NULL)
write.csv(useRaoJ$FD$Alpha,"FD_Strategy_Comm_1_Results_1.csv")

##RangeSizeTraits##
Range_Traits=read.table ("Range_Traits.txt", h=T)
useD=daisy(Range_Traits, metric="gower")
useRaoJ = Rao(sample=tParrot_Comm, dfunc=useD, dphyl=NULL, weight=F, Jost=T, structure=NULL)
write.csv(useRaoJ$FD$Alpha,"FD_Range_Comm_1_Results_1.csv")

########### COMM 2 ####################
Parrot_Comm=read.table("Parrot_Comm_2_Fixed.txt", h=T)
tParrot_Comm = t(Parrot_Comm)
```

```
##AllTraits
All_Traits=read.table("All_Traits.txt", h=T)
useD=daisy(All_Traits[,1:30], metric="gower",weights = c(1/6, 1/6, 1/6, 1/6, 1/6, 1/6, 1/12, 1/12, 1/12,
1/12, 1/12, 1/12, 1/12, 1/12, 1/12, 1/12, 1/12, 1/12, 1/5, 1/5, 1/5, 1/5, 1/5, 1/6, 1/6, 1/6, 1/6, 1/6, 1/6, 1/1))
useRaoJ = Rao(sample=tParrot_Comm, dfunc=useD, dphyl=NULL, weight=F, Jost=T, structure=NULL)
write.csv(useRaoJ$FD$Alpha,"FD_All_NR_Comm_2_Results_1.csv")

##MorphTraits##
Morph_Traits=read.table("Comm_2_Morph_Fixed.txt", h=T)
useD=daisy(Morph_Traits, metric="gower")
useRaoJ = Rao(sample=tParrot_Comm, dfunc=useD, dphyl=NULL, weight=F, Jost=T, structure=NULL)
write.csv(useRaoJ$FD$Alpha,"FD_Morph_Comm_2_Results_1.csv")

##DietTraits##
Diet_Traits=read.table ("Diet_Traits.txt", h=T)
useD=daisy(Diet_Traits, metric="gower")
useRaoJ = Rao(sample=tParrot_Comm, dfunc=useD, dphyl=NULL, weight=F, Jost=T, structure=NULL)
write.csv(useRaoJ$FD$Alpha,"FD_Comm_2_Results_1.csv")

##WhereTraits##
Location_Traits=read.table ("Location_Traits.txt", h=T)
useD=daisy(Location_Traits, metric="gower")
useRaoJ = Rao(sample=tParrot_Comm, dfunc=useD, dphyl=NULL, weight=F, Jost=T, structure=NULL)
write.csv(useRaoJ$FD$Alpha,"FD_Location_Comm_2_Results_1.csv")

##HowTraits##
Strategy_Traits=read.table ("Strategy_Traits.txt", h=T)
useD=daisy(Strategy_Traits, metric="gower")
useRaoJ = Rao(sample=tParrot_Comm, dfunc=useD, dphyl=NULL, weight=F, Jost=T, structure=NULL)
write.csv(useRaoJ$FD$Alpha,"FD_Strategy_Comm_2_Results_1.csv")

##RangeSizeTraits##
Range_Traits=read.table ("Range_Traits.txt", h=T)
useD=daisy(Range_Traits, metric="gower")
useRaoJ = Rao(sample=tParrot_Comm, dfunc=useD, dphyl=NULL, weight=F, Jost=T, structure=NULL)
write.csv(useRaoJ$FD$Alpha,"FD_Range_Comm_2_Results_1.csv")
```

R code for quantifying Rao's Q for phylogenetic diversity.

Código R para cuantificar la Q de Rao para la diversidad filogenética.

```
#Code from: Integrating multiple dimensions of biodiversity to inform global parrot conservation
        #Corresponding author: Kevin R. Burgio: kevin.burgio@gmail.com

#Set working directory containing .tre files
setwd(".../PD")

#Load libraries and source code
source("Rao.r")
library(cluster)
library (ade4)
library(ape)
library(picante)

parrot_tree <- read.tree("ParrotTree_060517.tre") ## in this tree Cacatua ducorpsii is misspelled as Ca-
catua ducopsii. The comm files have been adjusted to reflect the misspelling

#### COMM 1 #### had to split the community files in half (but keep all species in each file) because
R cannot handle a vector of ~2 GB

parrot_comm = read.table("Parrot_Comm_1_Fixed_2.txt", h=T)
pruned_phylo_parrot = prune.sample(parrot_comm, parrot_tree)
print (pruned_phylo_parrot)

plot(pruned_phylo_parrot, cex = .01)
print(pruned_phylo_parrot$tip.label)

#populate pairwise dissimilarity matrix
pairwise.dist.mat = cophenetic(pruned_phylo_parrot)
parrot_comm1 = parrot_comm[,pruned_phylo_parrot$tip.label]
tparrot_comm = t(parrot_comm1)
gc()
useRaoJ = Rao(sample=tparrot_comm, dfunc=NULL, dphyl=pairwise.dist.mat, weight=F, Jost=T,
structure=NULL)

#Write to file
write.csv(useRaoJ$TD$Alpha,"TD_Comm_1_Results.csv",sep="")
write.csv(useRaoJ$PD$Alpha, "PD_Comm_1_Results.csv",sep="")

####COMM2

parrot_comm = read.table("Parrot_Comm_2_Fixed_2.txt", h=T)
pruned_phylo_parrot_2 = prune.sample(parrot_comm, parrot_tree)
print (pruned_phylo_parrot_2)

plot(pruned_phylo_parrot_2, cex = .01)
print(pruned_phylo_parrot_2$tip.label)

#populate pairwise dissimilarity matrix
pairwise.dist.mat = cophenetic(pruned_phylo_parrot)
parrot_comm2 = parrot_comm[,pruned_phylo_parrot_2$tip.label]
tparrot_comm2 = t(parrot_comm2)
gc()
useRaoJ2 = Rao(sample=tparrot_comm2, dfunc=NULL, dphyl=pairwise.dist.mat, weight=F, Jost=T,
structure=NULL)

#write to file
write.csv(useRaoJ2$TD$Alpha,"TD_Comm_2_Results.csv",sep="")
write.csv(useRaoJ2$PD$Alpha, "PD_Comm_2_Results.csv",sep="")
```