

## **Integrating multiple dimensions of biodiversity to inform global parrot conservation**

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1 **ABSTRACT**

2           Because biodiversity is increasingly threatened by habitat destruction and climate change,  
3 conservation agencies face challenges associated with an uncertain future. In addition to changes  
4 associated with climate and land use, parrots are threatened by hunting and capture for the pet  
5 trade, making them the most at-risk order of birds in the world. Parrots provide key ecosystem  
6 services, but remain understudied compared to other major bird orders despite their high  
7 extinction risk and ecological importance. Species richness is often used to identify high priority  
8 areas for conserving biodiversity. By definition, richness considers all species to be equally  
9 different. However, ongoing research emphasizes the importance of incorporating ecological  
10 functions (functional diversity) or evolutionary relationships (phylogenetic diversity) to more  
11 fully understand patterns of biodiversity, suggesting that using functional and phylogenetic  
12 information could improve conservation strategies. These distinctions among dimensions of  
13 biodiversity are important, because (1) areas of high species richness do not always represent  
14 areas of high functional or phylogenetic diversity, and (2) functional or phylogenetic diversity  
15 may better predict ecosystem function and evolutionary potential, which are essential for  
16 effective long-term conservation policy and management.

17           Our objective was to create a framework for identifying areas of high species richness,  
18 functional diversity, and phylogenetic diversity within the global distribution of parrots. We  
19 combined species richness, functional diversity, and phylogenetic diversity into an Integrated  
20 Biodiversity Index (IBI) to identify global biodiversity hotspots for parrots. We found important  
21 spatial mismatches among dimensions, which demonstrate that species richness is not always an  
22 effective proxy for other dimensions of parrot biodiversity. The IBI is an integrative and flexible  
23 index that can incorporate multiple dimensions of biodiversity, resulting in an intuitive and more

24 direct way of assessing comprehensive goals in conservation planning (i.e., healthy ecosystem  
25 functioning and climate change resilience).

## 26 **KEYWORDS**

27 c

28

## 29 **INTRODUCTION**

30 As we enter the early stages of the “Sixth Mass Extinction” (Ceballos et al. 2015),  
31 conservation agencies are struggling to face the challenges of a less certain future (Armsworth et  
32 al. 2015) as a consequence of habitat conversion and climate change (Urban et al. 2015). While  
33 most taxa are at risk, parrots (Psittaciformes) are especially so, as they are the most threatened  
34 order of birds, with ~43% of species listed as near-threatened or worse, and with ~28% listed as  
35 threatened or worse by the IUCN (IUCN 2015, Olah et al. 2016). Furthermore, 56% of parrot  
36 populations are currently thought to be in decline (IUCN 2015). However, estimates of bird  
37 density exist for only 25% of species, and those estimates suggest that parrot density is higher  
38 inside of protected areas than outside of them (Marsden & Royle 2014), demonstrating the  
39 critical importance of conservation action.

40 Parrots provide many important ecosystem functions, including invertebrate pest  
41 management, pollination, seed dispersal, and genetic-linking of plant communities, making them  
42 “keystone mutualists” (Tella et al. 2015, Blanco et al. 2015, Blanco et al. 2016). Parrots also  
43 forage on plants that are toxic and poisonous to many vertebrate species (Gilardi & Toft 2012,  
44 Blanco et al. 2015), allowing them to find food and persist in habitats where other frugivorous  
45 species cannot (Gilardi & Toft 2012). Given the critical ecosystem services parrots provide, their  
46 loss may have detrimental effects on the persistence of many plant species, thereby contributing

47 to ecosystem instability. Conversely, some parrot species have been spreading into new areas,  
48 primarily as a consequence of the pet trade, which has led to human/wildlife conflicts in Europe  
49 (White et al. 2019) and the introduction of 25 non-native species that now breed in the USA  
50 (Uehling et al. 2019).

51 In general, parrots have long generation times, low population densities, and high risk of  
52 being hunted or trapped (Pires 2012, Marsden & Royle 2014), all characteristics associated with  
53 high extinction risk (Bennett and Owens 1997, Cardillo et al. 2005). Predictably, parrot species  
54 that are larger-bodied and have longer generation times are generally found at relatively lower  
55 densities (Marsden & Royle 2014) and are more likely than are smaller parrot species to be  
56 obligate tree-cavity nesters (Renton et al. 2015), increasing extinction risk (Jones et al. 2006,  
57 Olah et al. 2016). Despite being the most-threatened order of birds, parrots are relatively  
58 understudied compared to other orders of birds (Brito & Orpea 2009, Ducatez & Lefebvre 2014).  
59 The lack of research may explain why density estimates, one of the most important factors in  
60 determining conservation status (Mace et al. 2008), are inadequate for most parrot species  
61 (Marsden & Royle 2014).

62 In addition to the effects of climate change and habitat loss resulting from agriculture or  
63 logging, other anthropogenic activities such as hunting and trapping are among the biggest  
64 threats to parrots (Snyder et al. 2000, Olah et al. 2016). Logging and agricultural conversion of  
65 habitats disproportionately affect parrots because a majority of parrot species (~70%) are forest-  
66 dependent (Olah et al. 2016). Most parrot species (~78%) also rely on tree-cavities for nesting  
67 (Renton et al. 2015), and nesting in some species is limited to a few tree species (Renton and  
68 Brightsmith 2009).

69 Over the past few decades, one of the most common methods for identifying areas of  
70 highest conservation priority has been based on the “hotspot concept” (Reid 1997, Myers et al.  
71 2000), which uses existing species range maps to prioritize conservation efforts where species  
72 richness or richness of endemic species is highest. More recently, the multidimensional nature of  
73 biodiversity has emerged as a critical consideration for conservation (e.g., Isaac et al. 2007,  
74 Mazel et al. 2014, Brum et al. 2017, Pollock et al. 2017) and considerations of irreplaceability  
75 and complementarity have supplemented the hotspot concept via spatial prioritization approaches  
76 (e.g. Andelman and Willig 2002, 2003; Zonation and Marxan; reviewed in Moilanen et al. 2009).  
77 Regions of high functional diversity (a measure of ecological trait diversity within an  
78 assemblage) or phylogenetic diversity (a measure of evolutionary diversity within an  
79 assemblage) may not coincide with areas with high species richness (e.g. for mammals; see Safi  
80 et al. 2011, Mazel et al. 2014, Brum et al. 2017). Consequently, calls to incorporate phylogenetic  
81 or functional biodiversity into conservation planning have arisen over the last couple of decades  
82 (Mace et al. 2003, Diaz et al. 2007).

83 Limited availability of data at appropriate scales, and the complex nature of metrics used  
84 to quantify functional or phylogenetic diversity, have inhibited until very recently the  
85 incorporation of this information into conservation planning approaches that prioritize land for  
86 protection (e.g. Brum et al. 2017, Pollock et al. 2017). Phylogenetic or functional diversity may  
87 be better indicators of community resilience than is species richness (Naeem et al. 2012).  
88 Conserving functional diversity is critical for maintaining ecosystem functions (Naeem et al.  
89 2012), and thus for maintaining critical ecosystem services, making it an important consideration  
90 in conservation (Chan et al. 2006, Diaz et al. 2007, Cimon-Morin et al. 2013, Kosman et al.  
91 2019). Nonetheless, cases that incorporate functional diversity in conservation research are rare

92 (but see Devictor et al. 2010 and Mazel et al. 2014). Maintaining the capacity for future  
93 adaptation is an important consideration for communities undergoing rapid climatic and  
94 environmental changes, suggesting that phylogenetic diversity should be given consideration  
95 when determining conservation goals (Naeem and Li 1997, Cardinale et al. 2012). Moreover, the  
96 loss of phylogenetic or functional diversity may be a better indicator than is the loss of species  
97 richness in quantifying ecosystem vulnerability (Srivastava et al. 2012).

98 Here, we created a framework to identify areas of high species richness, functional  
99 diversity, and phylogenetic diversity within the global distribution of parrots. We separately  
100 calculated species richness, functional diversity, and phylogenetic diversity, and then combined  
101 them into an Integrated Biodiversity Index (IBI) to identify global biodiversity hotspots to aid in  
102 parrot conservation. Important spatial mismatches between dimensions indicate situations in  
103 which species richness is not an effective proxy for other dimensions of parrot biodiversity.

## 104 **METHODS**

### 105 **Data collection**

#### 106 *Distribution data*

107 We used range maps for all 398 extant species of parrot (Birdlife International 2015)  
108 following the taxonomy of del Hoyo et al. (2014) to inform spatially-explicit estimates of  
109 biodiversity at a global scale.

#### 110 *Trait and phylogenetic data*

111 We estimated functional diversity using two types of data: categorical (binary) and  
112 mensural traits (Table 1). For each data type, we used a suite of traits that reflect particular niche  
113 axes and define functional components. Categorical traits included components of diet, foraging

114 strategy, and foraging location, whereas mensural traits comprise body size and range size. For  
115 each categorical trait, a species received a “1” if it exhibited the characteristic and a “0” if it did  
116 not. For each body size, we used the average value for each species based on measurements of  
117 multiple adults, when available. We obtained trait data for all parrot species from the literature  
118 (see Burgio et al. [2019] for more details) and range size data from Birdlife International (2015).  
119 We calculated phylogenetic diversity for each community using branch lengths found in a  
120 recently-published time-calibrated phylogenetic supertree for all 398 extant parrots (Burgio et al.  
121 2019).

## 122 **Analyses**

### 123 ***Biodiversity indices***

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

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

143

#### 144 ***Integrated Biodiversity Index***

145 The Integrated Biodiversity Index (IBI) combines numbers equivalent transformations of  
146 Rao's Q for phylogenetic and functional diversity (all traits combined) with species richness. We  
147 scaled each dimension of biodiversity to a range from 0 to 1 so that each would have equal  
148 opportunity to contribute to the IBI value. Without such scaling, species richness would likely  
149 dominate spatial patterns of biodiversity. The IBI is the sum of the scaled representations of  
150 species richness (S), functional diversity (FD), and phylogenetic diversity (PD) for a particular  
151 grid cell (*i*):

$$IBI = \sum_i \left[ \frac{(S_i - S_{min})}{(S_{max} - S_{min})} + \frac{(FD_i - FD_{min})}{(FD_{max} - FD_{min})} + \frac{(PD_i - PD_{min})}{(PD_{max} - PD_{min})} \right]$$

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

155

## 156 **RESULTS**



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

167 IBI is highest in Australia and New Guinea (Fig. 3), and moderate in northern and central  
168 South America. For example, in South America, species richness is highest in the Amazon Basin  
169 (Fig. 4a), phylogenetic diversity is fairly evenly distributed throughout the continent (Fig. 4b),  
170 and functional diversity is highest in the dry Chaco (Fig. 4c). Although IBI equally weights each  
171 of the three dimensions (Fig. 4d), considerable spatial mismatches exist between hot spots of  
172 species richness and IBI (Figs. 4e, S1).

173

## 174 **DISCUSSION**

175 In general, most of Australia, the island of New Guinea, and to a lesser extent, the  
176 Amazon Basin, evince the highest values of IBI. Because parrots and regions with the highest  
177 levels of species richness are generally understudied (Brito & Orpea 2009, Ducatez & Lefebvre  
178 2014, Wilson et al. 2016), the results of IBI analysis helps to focus future research on parrots in  
179 areas of greatest need.

180           Aside from multiple dimensions of biodiversity, considerations of spatial scale are  
181 necessary for effective conservation planning. For example, most conservation agencies are  
182 regional or local in scale, and cannot engage in global conservation planning. For instance, the  
183 Neotropics score rather low (Fig. 2) in phylogenetic diversity compared to other regions because  
184 only one subfamily (Arinae) is endemic there. However, functional diversity is highest in the  
185 Chaco region of South America, likely because it is a harsh environment with low productivity;  
186 it likely cannot support multiple populations that perform similar functions. The Arinae  
187 subfamily diversified relatively quickly (Davies et al. 2007, Wright et al. 2008) and is the most  
188 species-rich subfamily in the parrot phylogeny, accounting for the discrepancies between  
189 dimensions of biodiversity in South America (Fig. 4). Maps of functional and phylogenetic  
190 diversity generated using only species of parrots found in the Neotropics (i.e. the Arinae) likely  
191 would identify different areas of continental conservation concern than those presented here  
192 (Figs. 2 & 4).

193           The areas we identified as high priorities generally correspond with results from other  
194 global prioritization research, but with a few notable exceptions. For instance, Myers et al.  
195 (2000), who initiated the “hotspots” concept, and included a wide variety of taxa, also identified  
196 Brazil’s Cerrado and the southern expanse of the tropical Andes as areas of high priority; but did  
197 not prioritize central Australia. Recent research has incorporated spatial prioritization and  
198 multiple dimensions of diversity. For instance, high priority areas for birds (Pollock et al. 2017)  
199 and mammals (Brum et al. 2017) are the Andes, equatorial Africa, Indonesia, and New Guinea,  
200 which coincide well the patterns of high IBI for parrots, though our results also emphasize  
201 southeastern Australia and the Amazon Basin, likely due to the unique diversification pattern of  
202 parrots.

203           The incorporation of socioeconomic data into conservation decisions can help anticipate  
204 new risks and adapt management targets accordingly (Armsworth et al. 2015). For example, high  
205 levels of urbanization correlate with an increased number of threatened parrot species, and a  
206 country's GDP (per capita) increases the threat level (Olah et al. 2016, Butchart et al. 2015).  
207 Such an approach could identify areas within countries with increasing urbanization and  
208 increasing per capita GDP, with relatively high levels of diversity, to allow early intervention,  
209 before the effects of processes that lead to extinction (e.g. habitat loss and increased hunting) are  
210 irreversible.

211           If a conservation agency were to decide that hotspots of species richness were sufficient  
212 to set priorities for parrot conservation in South America, they would focus on the Amazon Basin  
213 (Fig. 4a), largely ignoring the high degree of functional diversity in the dry Chaco, which has the  
214 highest functional diversity of parrots in the world (Fig. 4c). However, by incorporating multiple  
215 aspects of biodiversity in the IBI, these aspects of biodiversity are weighted equally (Fig. 4d),  
216 allowing conservation agencies to make more informed decisions. Importantly, any particular  
217 dimension of biodiversity can be emphasized (or de-emphasized) within the IBI framework  
218 depending on the goals of a particular project. The mismatch between species richness and IBI  
219 (Figs 4e, S1) illustrates the importance of all aspects of biodiversity, and the problems with  
220 assumptions that protecting one dimension means that other dimensions are protected effectively.  
221 Spatial mismatches among hotspots of different dimensions have also been documented for  
222 mammals (Mazel et al. 2014). Conservation planners and practitioners should consider the scale  
223 and goals of conservation plans and should incorporate relevant information into an integrated  
224 framework to understand the relative value of particular policy options before taking action.

225           Although we do not explore extinction risk specifically, parrot species with larger ranges  
226 generally are at less risk of extinction, whereas parrot species with larger bodies or that are more  
227 dependent on forest may be at increased risk for extinction (Jones et al. 2006, Olah et al. 2016).  
228 Because these, and other traits, may be good indicators of extinction risk for parrots, it may be  
229 useful to consider each functional component separately. Mapping the areas of relatively low  
230 diversity in traits such as body size (Fig. S2), location (Fig. S4), or range size (Fig. S6), may be a  
231 good first step in identifying assemblages that may be at greater risk for extinction. Critically,  
232 simultaneous consideration of all components of functional diversity can obscure important  
233 patterns that are relevant to particular conservation issues (Spasojevic & Suding 2012, Lopez et  
234 al. 2016). Conservation agencies concerned primarily with protecting ecosystem functioning or  
235 ecosystem services may wish to focus on diet and foraging strategy diversity (Figs S3 and S5,  
236 respectively), as opposed to functional diversity.

237           The network of conservation areas in France provides different levels of protection for  
238 bird species richness, phylogenetic diversity, and functional diversity (Devictor et al. 2010). A  
239 potential extension of our framework could evaluate how well particular dimensions of  
240 biodiversity are protected, as a means of weighting the IBI equation to emphasize or de-  
241 emphasize particular dimensions when prioritizing areas to protect. Similarly, measures such as  
242 “ED” (Evolutionary Distinctiveness; Isaac et al. 2007), “EDGE” (Evolutionary Distinctiveness /  
243 Globally Endangered; Isaac et al. 2007), and “EDR” (Evolutionary Distinctiveness Rarity; Jetz et  
244 al. 2014) can be added or can replace phylogenetic diversity to ensure that distinct clades of the  
245 parrot tree are given more weight when assessing conservation priorities.

246           Climate change will have direct and indirect effects on species range shifts (Jones et al.  
247 2016). Direct effects are based on the physiological tolerances of species, which will track their

248 climatic niches as spatial patterns of temperature and precipitation change. Indirectly, climate  
249 change will affect land-use patterns by humans (Turner et al. 2010), which may limit or form  
250 barriers against the dispersal of individuals (Faleiro et al. 2013). Preserving connectivity among  
251 habitat patches may be a key element of effective conservation strategies in the face of climate  
252 change (Schmitz et al. 2015), further supported here by the areas we identify as high diversity,  
253 including the belt across central South America (Fig. 4). The effects of recent climate change  
254 have been greater at high elevations and in tundra compared to tropical and subtropical lowlands  
255 (Seddon et al. 2016) that harbor most species of parrots. Nonetheless, many parrot species occur  
256 in areas that are sensitive to climate change. Based on a combination of species richness and the  
257 number of threatened species and endemic species, Indonesia, Brazil, Australia, Colombia, and  
258 Bolivia are the five highest priority countries for parrot conservation action (Olah et al. 2016).

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

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**Table 1: Functional attributes that reflect niche axes (functional components) were used to estimate functional biodiversity of parrot assemblages for each 500 km<sup>2</sup> grid cell.**

<b>Type of Data</b>	<b>Functional Component</b>	<b>Attribute</b>	<b>Trait Values</b>
<b>Categorical</b>	<b>Diel</b>	Carnion	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
		<b>Foraging Strategy</b>	Clean
	Dig		1, 0
	Scavenger		1, 0
	Graze		1, 0
	Flower probe		1, 0
	Excavate		1, 0
	<b>Foraging Location</b>		Water
		Ground	1, 0
Vegetation		1, 0	
Subcanopy		1, 0	
Canopy		1, 0	
<b>Mensural</b>	<b>Body Size</b>	Mass	Mean (g)
		Length	Mean (cm)
		Tarsus	Mean (mm)
		Culmen	Mean (mm)
		Wing	Mean (mm)
		Tail	Mean (mm)
	<b>Range Size</b>	Area	km <sup>2</sup>

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## FIGURE LEGENDS

**Figure 1.** Global map of parrot (a) 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.

**Figure 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 from the Public Domain.

**Figure 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.

**Figure 4.** Graphical comparison of (a) species richness (S), (b) phylogenetic (PD), and (c) functional (FD) diversity patterns as well as (d) IBI of South America and (e) the difference between species richness (S) and IBI ( $\Delta$  IBI), illustrating that correlation on a global level does not predict congruence of hotspots of each dimension at smaller spatial scales. To calculate  $\Delta$  IBI, we scaled the results of panels (a) and (d) to 0-1 (to make them comparable) and subtracted S from IBI, resulting in  $\Delta$  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.

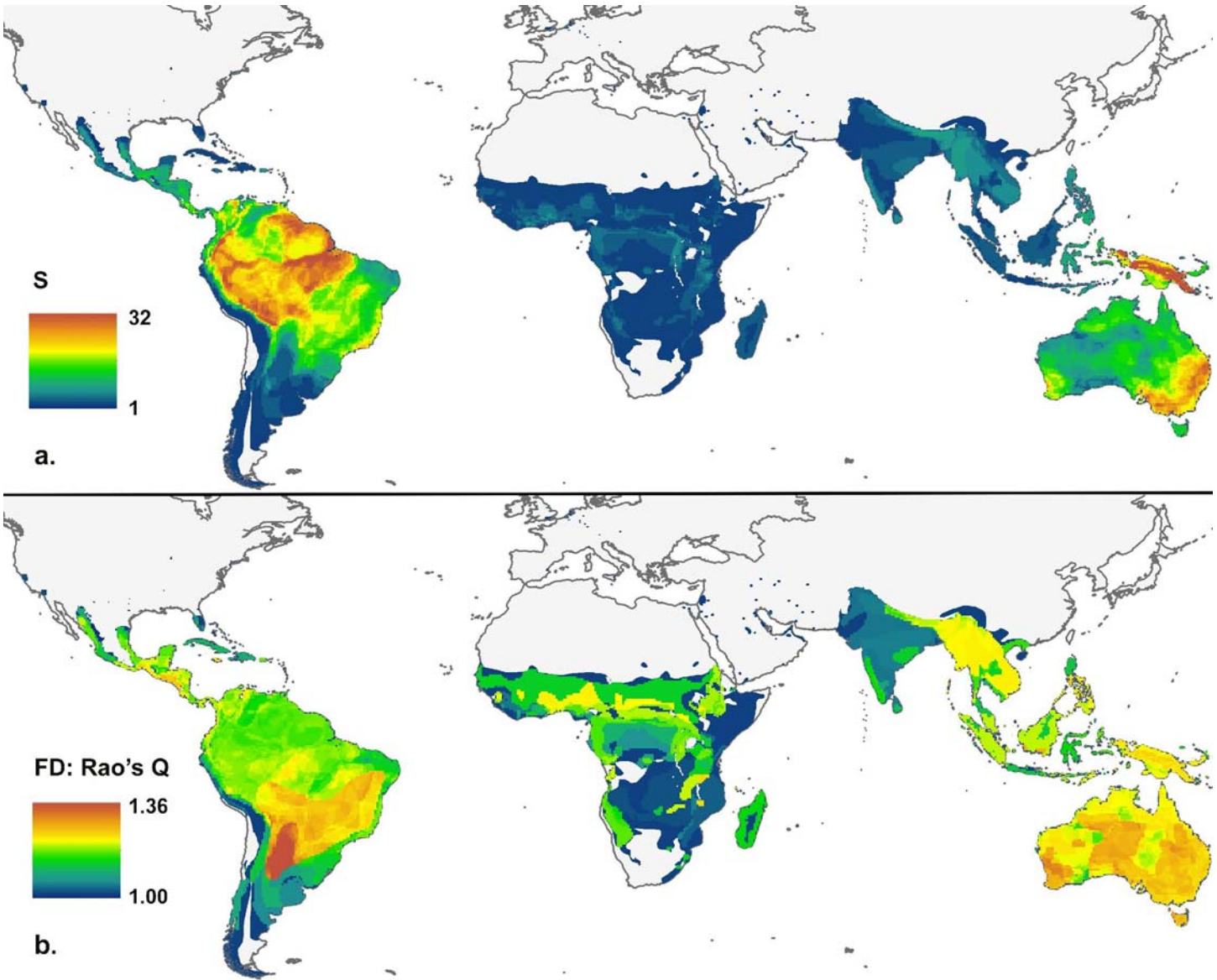


Figure 1

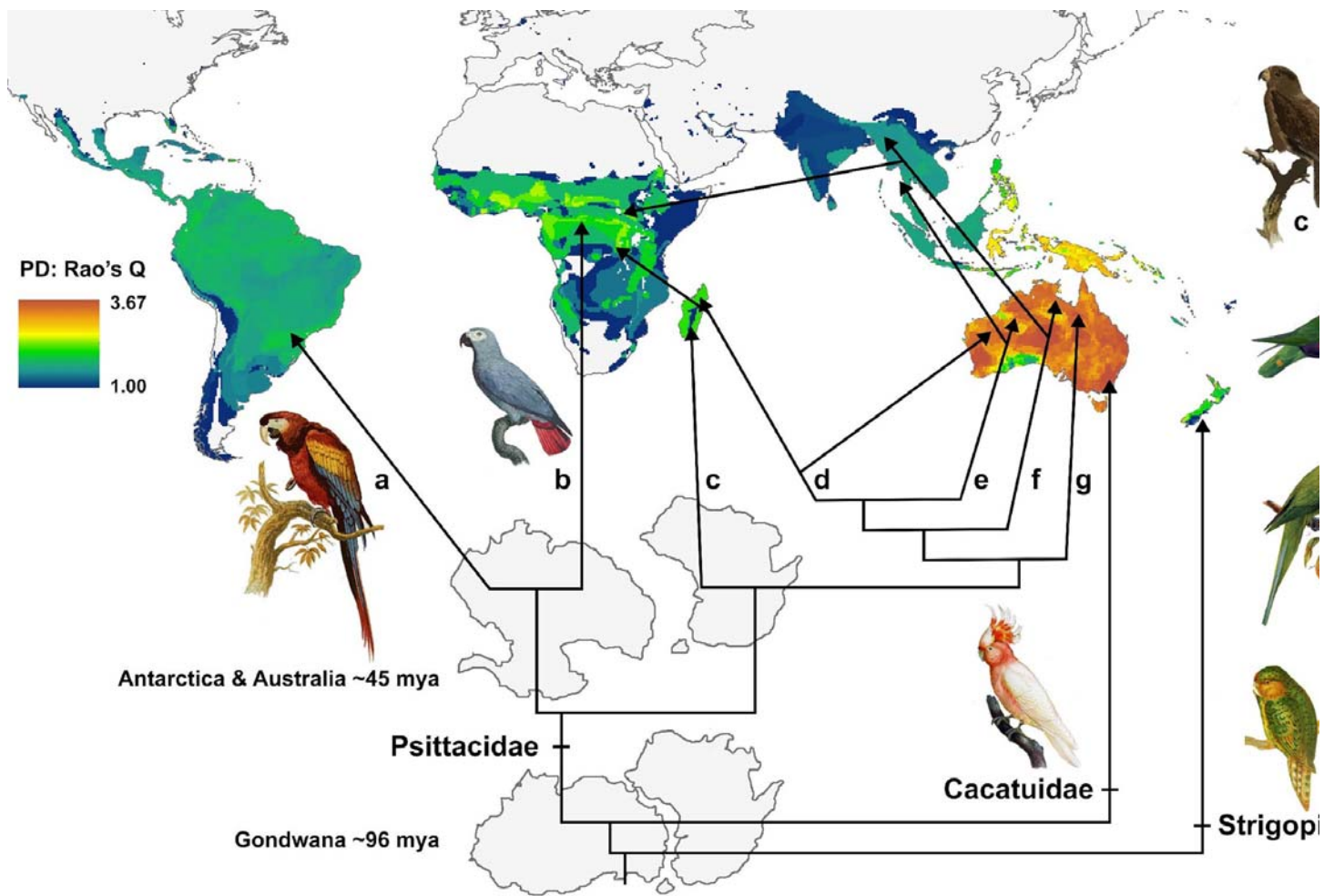
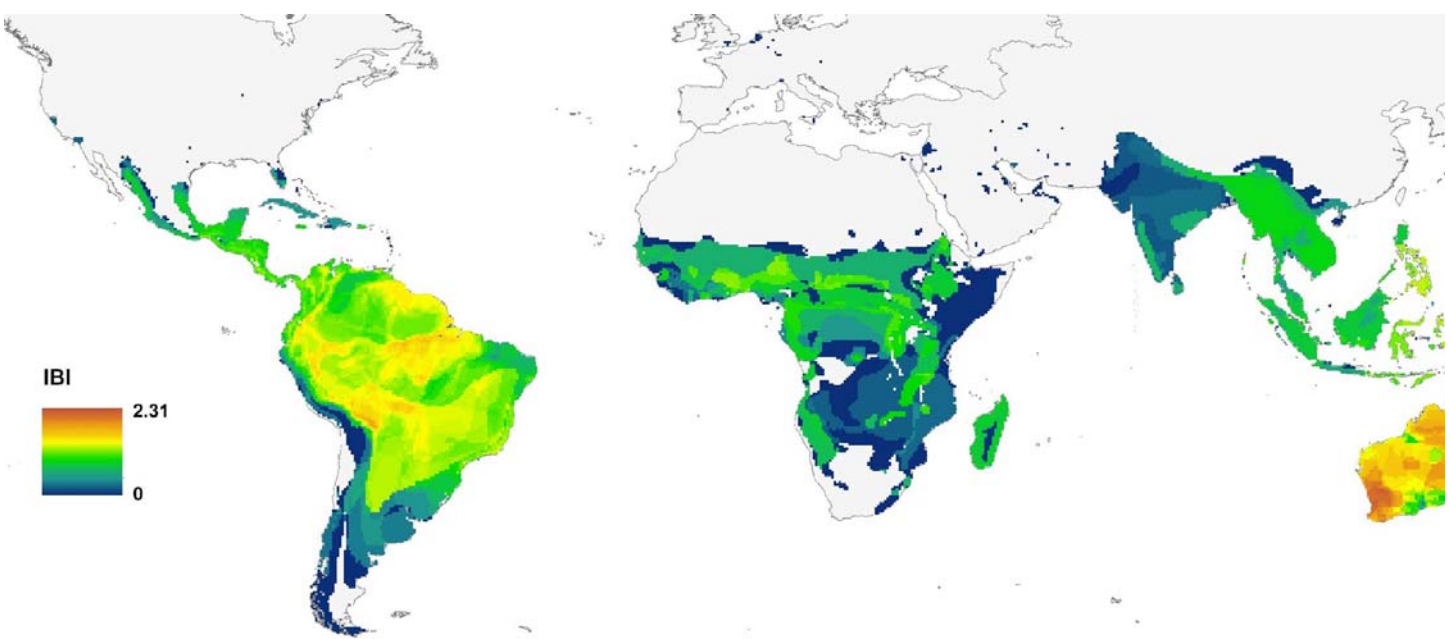


Figure 2





**Figure 3**

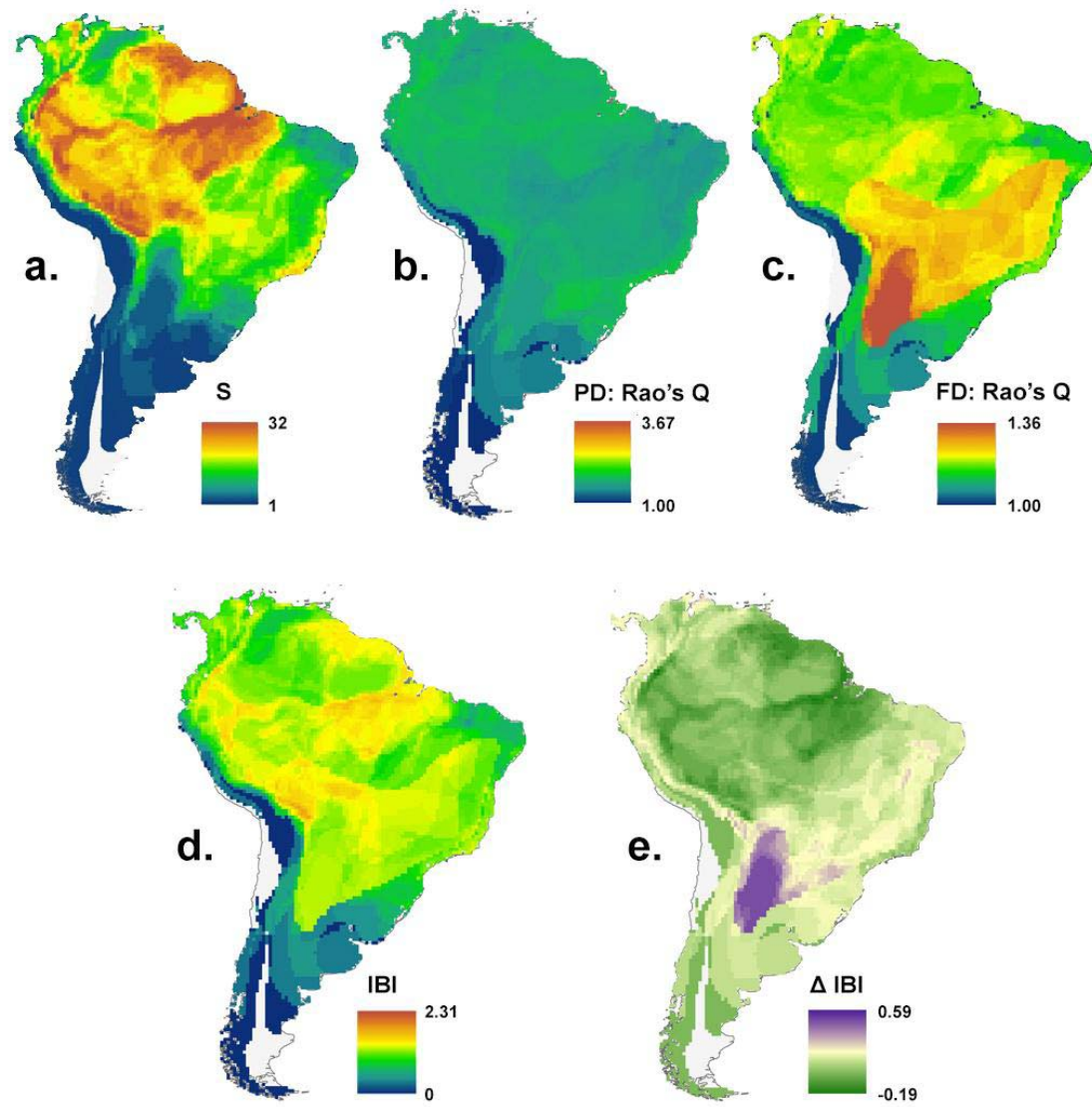


Figure 4