

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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- 446

Table 1: Functional attributes that reflect niche axes (functional components) were used to estimate functional biodiversity of parrot assemblages for each 500 km² grid cell.

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

447

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 (Δ IBI), illustrating that correlation on a global level does not predict congruence of hotspots of each dimension at smaller spatial scales. To calculate Δ IBI, we scaled the results of panels (a) and (d) to 0-1 (to make them comparable) and subtracted S from IBI, resulting in Δ 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.

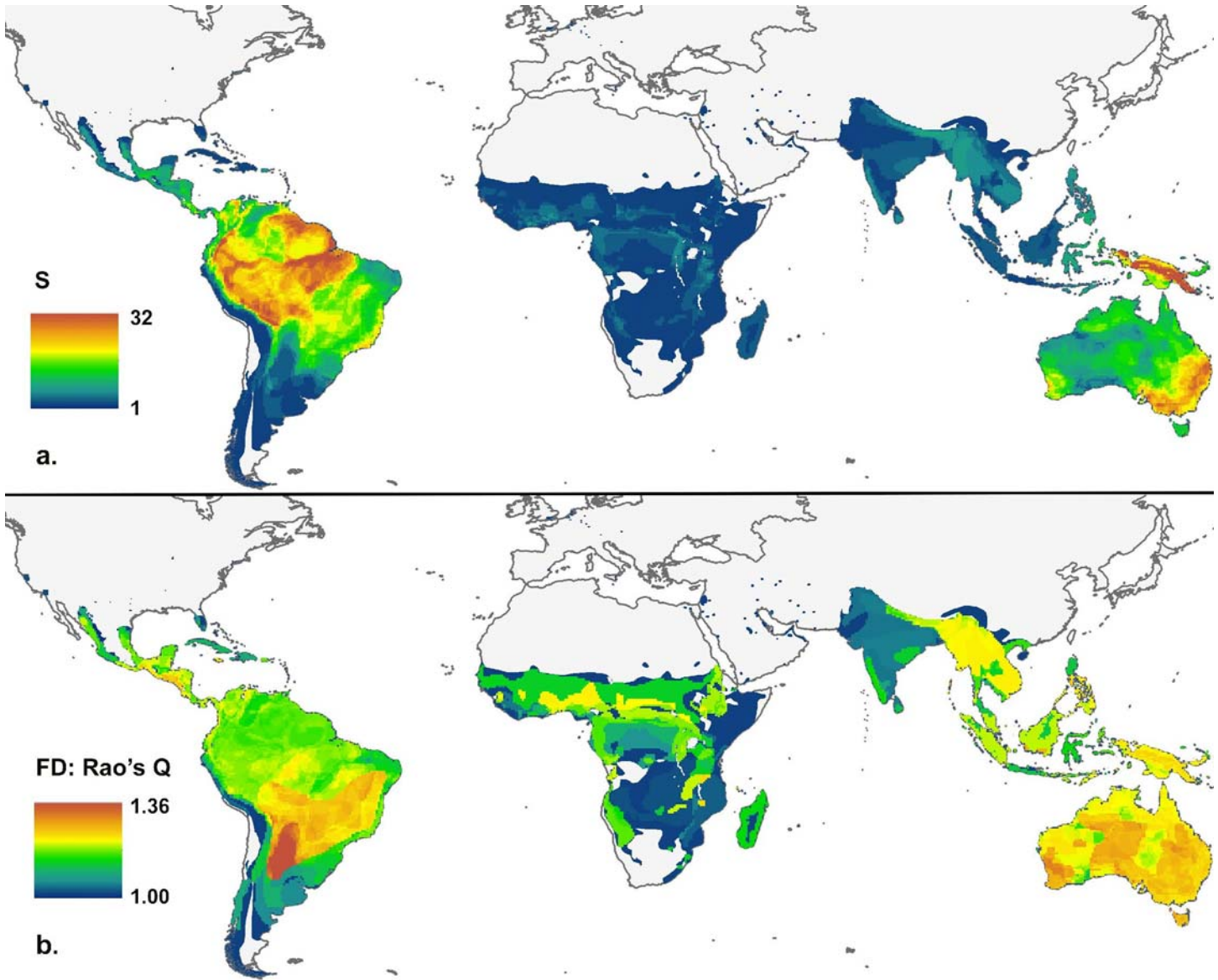


Figure 1

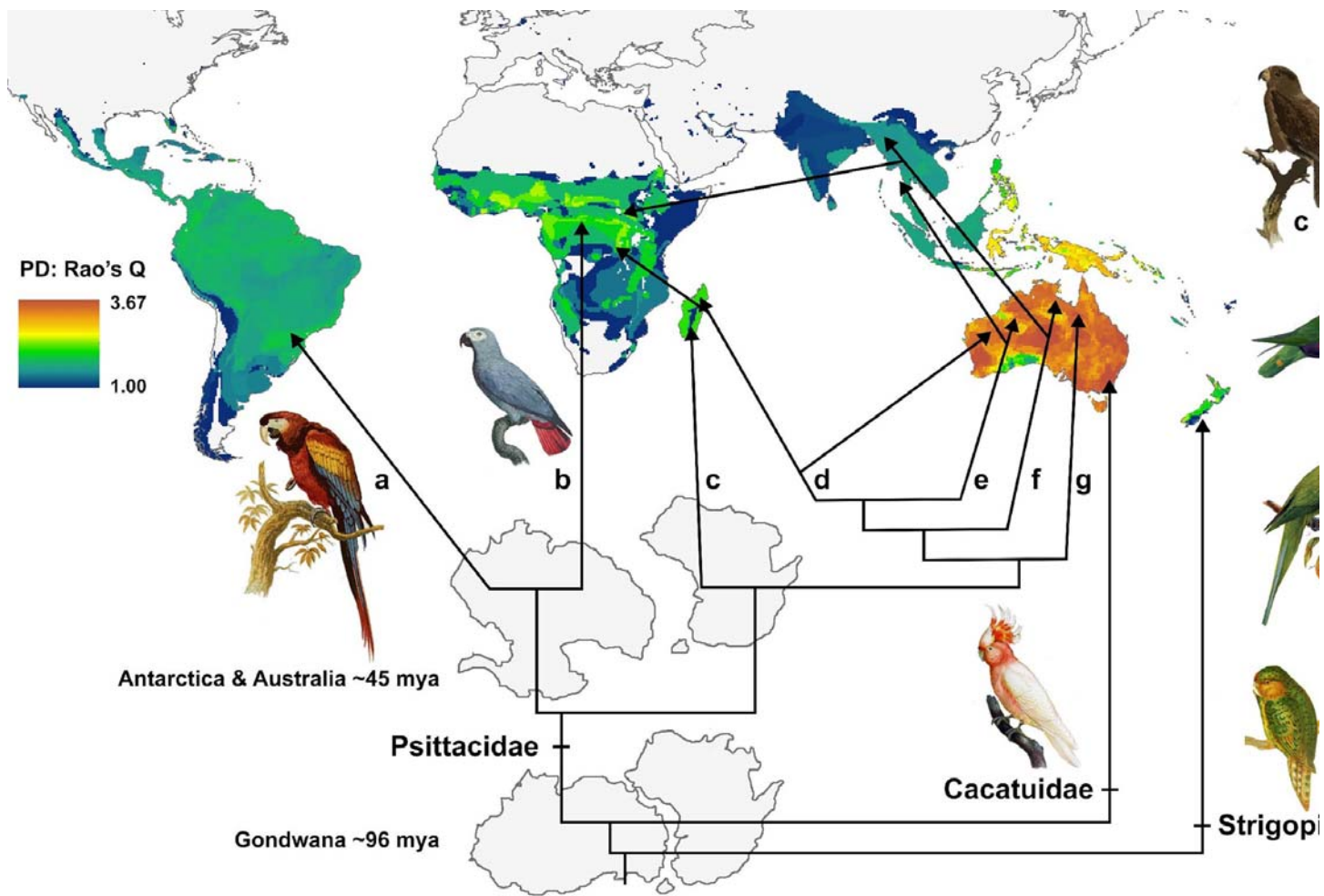


Figure 2

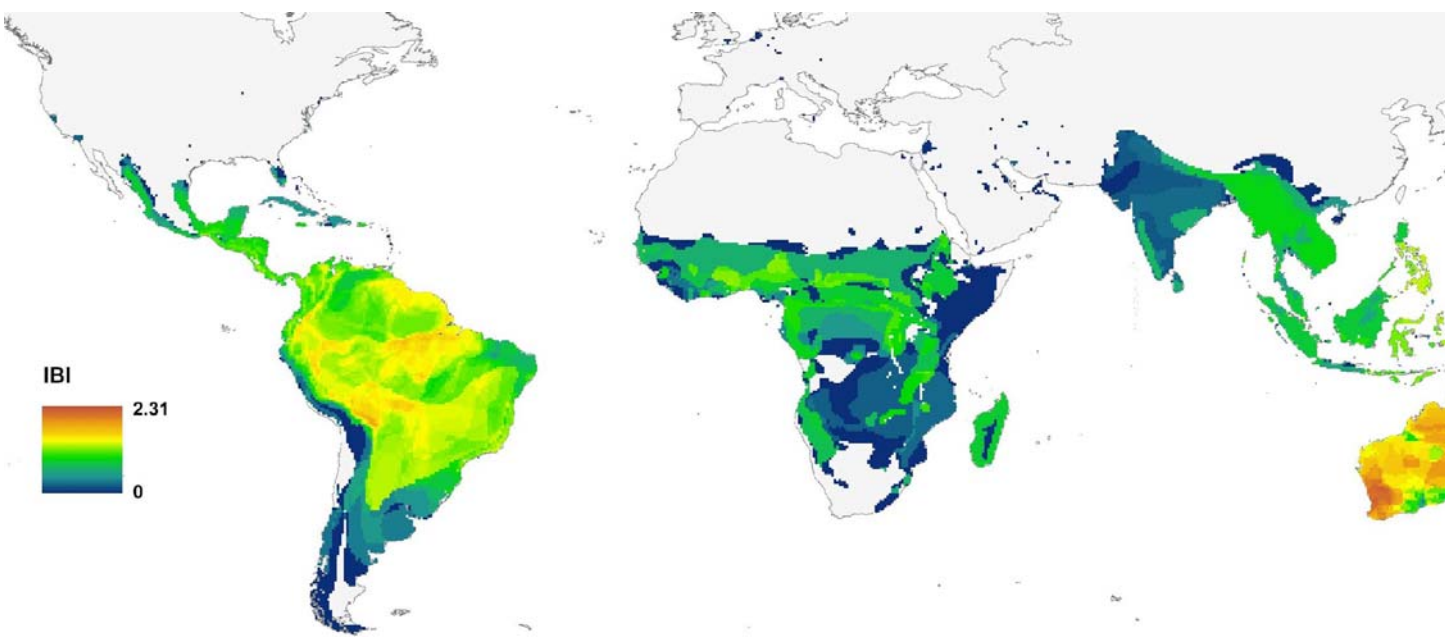


Figure 3

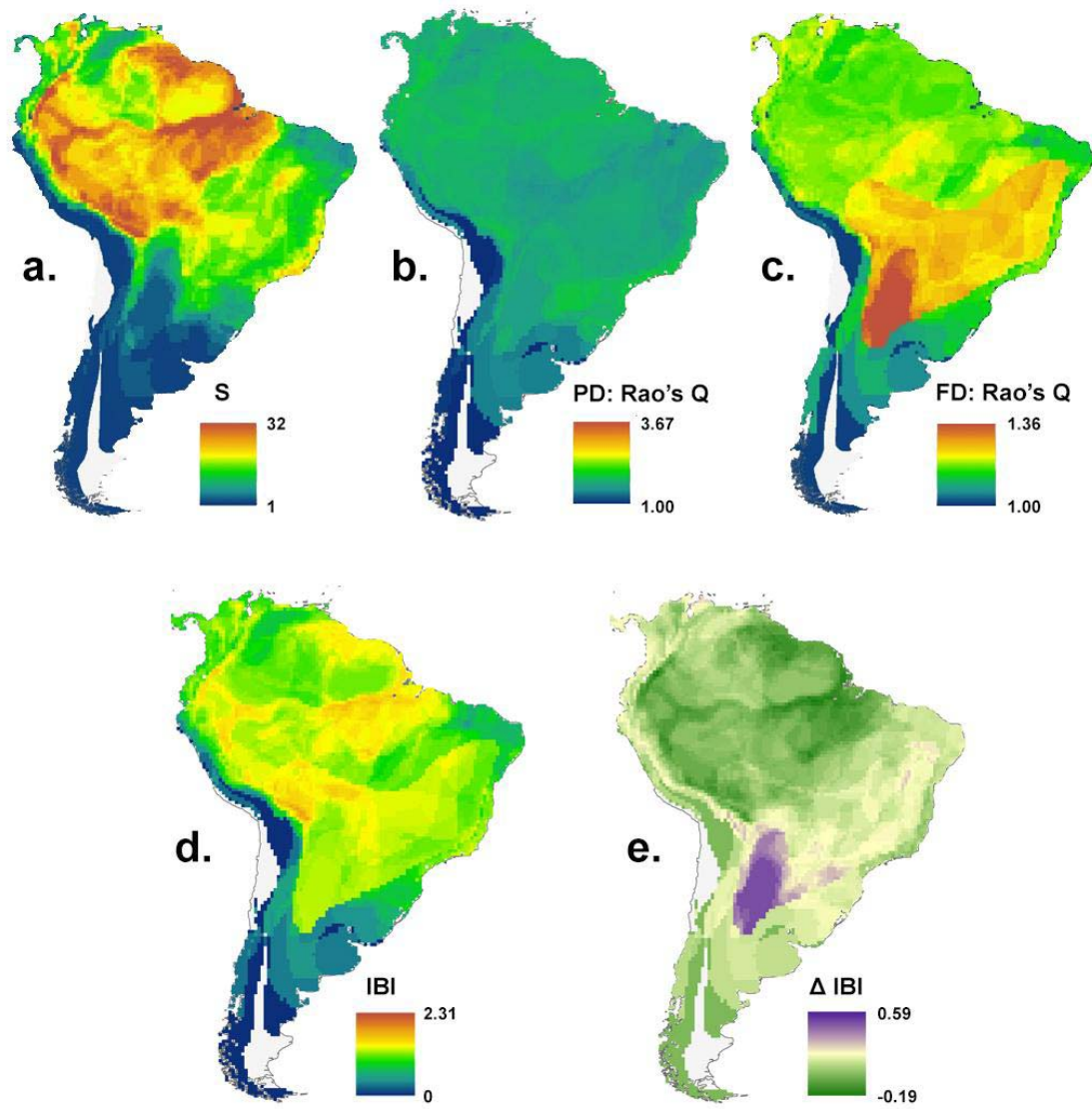


Figure 4