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1 **AUK Special Feature: Neotropical Ornithology**

2 **A roadmap to identifying and filling shortfalls in Neotropical Ornithology**

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9

10 **Abstract**

11 Securing the long-term resilience of the world's most speciose avifauna, that of the
12 Neotropics, requires spatially and temporally explicit data to inform decisions. We examine
13 gaps in our knowledge of the region's avifauna through the lens of the biodiversity shortfall
14 concept: the gaps between realized knowledge and complete knowledge. This framework
15 serves as a useful tool to take stock of the last 25 years of Neotropical ornithological work
16 since the untimely death of Ted Parker. Here, we highlight seven key shortfalls: taxonomy,
17 distribution, abundance, evolutionary patterns, abiotic tolerances, species traits, and biotic
18 interactions. We then propose an eighth – and new – ‘Parkerian’ shortfall that reflects a lack
19 of basic natural history knowledge key both to understanding how species might respond to
20 environmental challenges. Bridging this shortfall will help reverse declines by informing
21 reintroduction, recovery network, and habitat restoration efforts. We discuss the challenges
22 imposed by each shortfall and how strategies such as citizen-science initiatives and
23 technological advances can either remedy or mitigate the uncertainty they generate.

24 *“I saw with regret, that whilst the number of accurate instruments was daily increasing, we*
25 *were still ignorant”*

26 — Alexander von Humboldt, Personal Narrative of Travels to the Equinoctial Regions of
27 America, During the Year 1799-1804 - Volume 1

28 *"Everything Ted saw in the field, he wrote down or dictated onto a tape; recording even*
29 *seemingly inconsequential details about birds was an obsession for him. Ted wrote notes so*
30 *that he would not forget what he had observed. ... He was constantly searching for patterns,*
31 *in distribution, foraging behavior, vocalizations, flock dynamics, in almost any aspect of*
32 *birds that attracted his attention"*

33 —Murray Gell-Mann, Gell-Mann, M. 1994. The Quark and the Jaguar. WH Freeman, New
34 York.

35 *Keywords: biodiversity shortfalls, tropical birds, taxonomy, distribution, abundance,*
36 *evolutionary patterns, abiotic tolerance, species traits, biotic interactions*

37 Understanding the extent of our gaps in scientific knowledge requires identifying that which
38 we do not know; recognizing these gaps also helps researchers ask questions that can best
39 advance science. Birds may be the best known of all terrestrial biota, but data scarcity still
40 plagues ornithology and Neotropical ornithology, in particular. The last 25 years, since Ted
41 Parker's untimely death, have seen unprecedented changes in data collection, analysis, and
42 availability. While the application of big-data approaches across large spatial, taxonomic, and
43 temporal scales can fuel discovery, further advances are likely to be constrained by our
44 inability to identify and prioritize research needs, as well as by a lack of basic knowledge
45 about Neotropical birds. Shortfalls in our knowledge of biodiversity represent the gaps
46 between realized knowledge and sufficient knowledge at the present day. Hortal et al. (2015)
47 grouped biodiversity shortfalls into seven major domains related to systematics,
48 biogeography, population biology, evolution, functional ecology, abiotic tolerances, and
49 ecological interactions, combinations of which are needed to support effective conservation

50 actions. Here, we discuss the importance and magnitude of each of these shortfalls relative to
51 our knowledge of Neotropical birds, highlighting recent advances and proposing research
52 priorities. In addition, we propose a new, eighth shortfall to specifically address the
53 tremendous gap in basic natural history knowledge that still exists for a majority of
54 Neotropical bird species—a gap that Ted Parker spent much of his life attempting to fill
55 (Remsen 1997).

56 **Systematics Domain: The Linnaean shortfall**

57 Linnaean shortfalls (Lomolino 2004) represent the gap between the number of species
58 formally described by scientists and the number of species that actually exist. In terms of
59 taxonomic knowledge, ornithologists are fortunate relative to scientists working with other
60 taxa, given that estimates suggest that more than 95% of avian species have been described
61 (Mora et al. 2011, Scheffers et al. 2012). However, recent discoveries suggest that this
62 estimate may have been too optimistic for the Neotropics. The race to describe the region's
63 bird species reached its greatest intensity in the late 19th and early 20th centuries, often based
64 on patchy specimen data from a taxon's geographic range and the methods were invariably
65 pre-quantitative. A subsequent and largely unquestioned spate of 'lumping' of these forms,
66 under the auspices of the polytypic 'biological' species concept (Mayr 1942, 1963,) has
67 significantly impeded taxonomic progress (e.g., Sangster 2014 see the Darwinian shortfall
68 and the revision of alpha taxonomy within polyphyletic species groups). A recent
69 morphological and genetic assay by Barrowclough et al. (2016) contends that avian
70 evolutionary diversity has been substantially underestimated, and that, under a phylogenetic
71 species concept, we would recognize approximately 2 to 2.5 times the current number of
72 biological species. In this vein, Navarro-Sigüenza & Peterson (2004) proposed an alternative
73 phylogenetic species taxonomy for the Mexican avifauna (which in the Neotropical realm
74 includes the Yucatán Peninsula and southern lowlands, and most of the east and west

75 coastlines and tip of the Baja California Peninsula) that resulted in splits affecting 135
76 ‘biological species’, resulting in 323 new phylogenetic species of which 122 were new
77 national endemics, increasing the national bird list by 18%.

78 Taxonomy does impact conservation efforts; although populations tend to be their focus,
79 taxonomic designations at the level of species can profoundly affect conservation agendas
80 and priorities (Hazevoet 1996, Peterson and Navarro-Sigüenza 1999), such that achieving a
81 consistent taxonomy is critical to bird conservation (Bates & Demos 2001). Rather than
82 resolve the persistent discord about species limits, critics argue that the widespread adoption
83 of more liberal and readily quantifiable definitions of species, such as the phylogenetic
84 species concept, would result in both an unmanageable number of names (Zachos 2013) and
85 issues of diagnosability that might vary greatly among taxonomists (Tobias et al. 2010).
86 Others assert that doubling or even tripling the number of Neotropical birds might not be
87 unmanageable given the numbers of species in most other groups of organisms
88 (Barrowclough et al. 2016), and quantitative methods abound to define diagnosability at the
89 morphological, signalling, and genetic levels (Sangster 2014).

90 Despite an arguably conservative approach to taxonomy, new species continue to be
91 described on an annual basis from the Neotropical region, even from relatively well-
92 inventoried areas (e.g., Fig. 1a). Between 1960 and 2016, 147 new species were described
93 from South America and a further seven from Central America and Mexico (Brewer 2018).
94 Ted Parker himself authored descriptions of three new bird species and seven subspecies,
95 some of which may yet be elevated to species status in the future. Inspired by Parker, a
96 number of his contemporaries have gone on to discover additional species. Most notable was
97 a recent landmark volume in the Handbook of the Birds of the World series (de Hoyo et al.
98 2013) which published the descriptions of 15 new species from Amazonia (Whitney & Cohn-
99 Haft 2013). This sudden rush of new Amazonian forms, not all of which have been formally

100 recognised by all taxonomic bodies, reflects a broader changing picture of our understanding
101 of the importance of acoustic (Remsen and Schulenberg 1997) and molecular tools in
102 informing avian taxonomy (Remsen 2005). In most cases this re-evaluation of species
103 assemblages will be reflected by redefining species limits, resulting in a significant increase
104 in taxonomic ‘splitting’, but a smaller fraction of this unrecognised diversity will likely stem
105 from completely undescribed new taxa.

106 Though visiting remote or inaccessible regions remains a priority for finding new species, the
107 recent spate of discoveries in relatively well-visited regions reminds us that we must remain
108 diligent everywhere, especially in megadiverse regions which have suffered extensive habitat
109 loss. Hotspots for new species in recent years have included the Andean foothills and
110 outlying ridges, Western Amazonian interfluvial regions ((Whitney & Cohn-Haft 2013: Fig
111 1b), and remarkably still the Brazilian Atlantic Forest (Lees & Pimm 2015). That species
112 could remain undetected in some of these regions given the relative ease of access and long
113 history of ornithological fieldwork is more a reflection of the small population sizes and
114 hyper-fragmented habitats of many of these new species that now stand on the brink of global
115 extinction (Lees & Pimm 2015). Finding these last species is thus a critical task for
116 conservation biologists.

117 Sensational rediscoveries such as that of Kaempfer's Woodpecker (*Celeus obrieni*) in 2006
118 (Fig. 1c), formerly known only from the type specimen collected in 1926, and now known to
119 occur in bamboo groves over a huge swath of eastern Brazil, attests to the ease with which
120 even charismatic species may elude ornithologists (Leite et al. 2013, Dornas et al. 2014).

121 Major range extensions of difficult-to-detect species like owls, nightjars, and rails offer hope
122 that these families may still harbour undescribed taxa. Some species may be forever lost to
123 discovery, and we also need to redouble our efforts to look for historic continental extinctions
124 by searching carefully through museum drawers and hunting for subfossils. The Cryptic

125 Treehunter (*Cichlocolaptes mazarbarnetti*), for example, was described from museum
126 specimens, seemingly after its global extinction (Mazar-Barnett and Buzzetti 2014, Lees &
127 Pimm 2015). The marine realm may also continue to be a source of new taxa, especially
128 among cryptic Procellariiformes (Harrison et al. 2013) which may again be spurred on by
129 advances in the use of DNA and acoustic analyses.

130 Filling the Linnaean shortfall will require increased financial support for alpha taxonomy
131 work and associated, collaborative expeditions to inaccessible or previously unsampled
132 Neotropical locations. Underpinning these efforts must be stronger peer-recognition of the
133 field of taxonomy, which is often viewed as ‘low impact’ in academic assessments
134 (Agnarsson & Kuntner 2007), and also much greater support in general for the curation and
135 use of museum collections associated with universities and other research institutions.

136 Strengthening partnerships and increasing capacity for natural history collections within Latin
137 America will be especially important as incoming generations of field ornithologists and
138 students are well poised to discover the next wave of avian species.

139 **Biogeographic domain – The Wallacean shortfall**

140 Wallacean shortfalls represent gaps in our knowledge concerning geographic range limits and
141 predicted distributions (Lomolino 2004), which remain a fundamental challenge to
142 biogeographers and conservation biologists alike. Historically, in the absence of systematic
143 surveys, general range maps were usually constructed from presence-only data from museum
144 specimens and opportunistic citations of species in the technical and scientific literature
145 (Anderson 2012). Wallacean shortfalls remain especially pervasive in the Neotropics given
146 the inaccessibility of remote regions such as mountain ranges or corners of Amazonia that
147 also sustain Linnaean shortfalls. Although ornithologists and birders are improving our
148 understanding of coarse-scale ranges for many species – as evidenced by the relatively

149 frequent discovery of major range extensions – our knowledge of specific habitat associations
150 and derived distributions remains poor for most species and regions (Engler et al. 2017) and
151 especially in the tropics (Orihuela-Torres et al. 2020).

152 Incomplete knowledge of physiognomic (e.g., elevation) and habitat associations results in
153 general polygons as the only form of representing a species' range and distribution, in
154 contrast to the detailed products being generated for some North American species across the
155 full annual cycle (Fink et al. 2018). Although efforts exist to update these maps using more
156 recent observations (e.g., Map of Life <https://mol.org/>), these maps are likely to fail to
157 represent the true geographic extent of occurrence and abundance across a species'
158 distributional range. Most species may also have disjunct or patchy distributions that are
159 poorly depicted in current range maps (Diamond 1980). Because Wallacean shortfalls are
160 exaggerated by spatio-temporal biases in data collection (e.g., between wet and dry seasons in
161 Amazonia when regions can become difficult to access), they are more challenging to fill
162 than Linnaean shortfalls. These seasonal biases make understanding phenomena such as
163 migration particularly complicated and often reinforce the pervasive assumption of residency
164 which may mask partial and altitudinal migration across the region (e.g., Lees & Martin
165 2014, Lees 2016, Fig. 1c; but see also Areta and Juhant 2019). Indeed, the distribution of
166 many common Nearctic–Neotropical migrants, such as the Black-billed Cuckoo (*Coccyzus*
167 *erythrophthalmus*) and Veery (*Catharus fuscescens*), remain poorly described during non-
168 breeding seasons, which not only can lead to overestimation of true range size (Remsen
169 2001), but causes us to overlook inter-seasonal dynamics and the importance of multiple
170 regions for migratory species (Heckscher et al. 2011, 2015, Renfrew et al. 2013). Ultimately,
171 these knowledge gaps can seriously undermine our ability to predict the impacts of potential
172 threats and identify habitat needs for species through their annual life cycle, including
173 migratory stop-over sites that might be critical to sustain populations (Bayly et al. 2018).

174 Cottee-Jones et al. (2016) designated these issues with migratory species the ‘movement
175 shortfall’.

176 Wallacean shortfalls do not apply to individual species alone, rather they can extend to entire
177 guilds. For example, pelagic avifauna in the Neotropics have been the subject of relatively
178 few dedicated offshore surveys, though recent work has unearthed a number of biogeographic
179 surprises (e.g., Klein et al. 2012; Lees et al. 2015). Data loggers and satellite tags hold
180 promise to substantially improve our knowledge of the non-breeding distribution of many
181 seabird species, as evidenced by the new discovery that both Desertas (*Pterodroma deserta*
182 Ramírez et al. 2013) and Zino’s (*P. madeira*; Zino et al. 2011) Petrels occur off the coast of
183 Brazil. Movement technologies have also been employed for terrestrial guilds of species and
184 have revealed, for example, the hitherto unknown wintering grounds of the Caribbean Martin
185 (*Progne dominicensis*; Perlut et al. 2017) and a North American population of Black Swift
186 (*Cypseloides niger borealis*; Beason et al. 2012), as well as new insights into migration routes
187 and timing for the more common Purple Martin (*Progne subis*) (Fraser et al. 2013). Major
188 shortfalls persist, however, for other closely related, yet difficult to identify, species in the
189 aerial insectivore guild, such as Peruvian (*Progne murphyi*) and Sinaloa (*P. sinaloae*)
190 Martins, as well as many species of Neotropical swifts.

191 Lack of basic knowledge of where and when species occur is a major obstacle for effective
192 design of biodiversity conservation strategies. Resolving all Wallacean shortfalls may be a
193 mammoth task but solutions can be simple, such as requiring increased support for
194 organizations in Neotropical countries who are interested in working in out-of-the-way
195 places. Important shortfalls might be remedied in high-priority regions, for example, by
196 schemes such as the Rapid Assessment Program (RAP) that Ted Parker designed and directed
197 for Conservation International (Remsen and Schulenberg 1997) and which was continued in
198 the Field Museum of Natural History’s Rapid Biological Inventory program

199 (<http://fm2.fieldmuseum.org/rbi/>). Importantly, RAP expeditions are collaborations between
200 North American and Neotropical experts and feed directly into capacity building and
201 conservation planning within the host countries.

202 Though tropical conservation efforts can benefit from rapid assessment programs at specific
203 sites, they are unlikely to be a panacea to remedy large data gaps across vast areas. Large-
204 scale citizen science initiatives and publicly available data repositories are now in a position
205 to fill many of these knowledge gaps on bird distributions by moving beyond collecting
206 presence-only data to collect location-specific information on species presence-absence and
207 even relative abundance. These programs vary from organically grown web resources such as
208 the Brazilian WikiAves initiative (<http://www.wikiaves.com.br/>), which has amassed over
209 2.9M bird images through 2020, to more science-driven, institutionally supported programs
210 like eBird (www.eBird.org) that has amassed nearly a billion bird records worldwide
211 (Sullivan et al. 2017), including more than 19 million media specimens available for
212 scientific study. Participation in eBird is increasing rapidly in neotropical countries, with
213 dedicated web portals (e.g., AvesAves in Mexico), data fields needed to inform species
214 distribution models (e.g., effort, location, presence-absence), embedded protocols for large-
215 scale monitoring programs (e.g., International Shorebird Survey, Latin America Program for
216 Wild Birds - PROALAS), and a network of national and regional reviewers exchanging
217 knowledge of bird distributions with a growing army of skilled observers. As an example of
218 the power of this program to collect information that is useful to predict species distributions,
219 34,000 people in 173 countries found 6,942 bird species and gathered more than 185 million
220 records during a 24-hr birding period known as Global Big Day in 2019
221 (<https://ebird.org/globalbigday>). The increased focus on data quality in citizen-science
222 programs has improved the application of these data to inform species distribution models,

223 improving our ability to accurately predict the extent of species occurrence at various spatial
224 and temporal scales (Engler et al. 2017).

225 Species distribution models (SDMs) using climate and topography are good at predicting the
226 potential niche/distribution of a species. However, deeper information on habitat associations,
227 effects of fragmentation, dispersal, harvesting and other factors are needed to properly predict
228 the realised niche/distribution of the species - this relates to other shortfalls but is important
229 for conservation (VanDerWal et al. 2009). In addition, the uncertainty around predicted
230 occurrence probabilities can be used to identify areas of high uncertainty where more
231 observations are needed (Guillera-Arroita 2017). Overall, the use of existing platforms for
232 data collection and storage (e.g., eBird and Birdtrack for birds), especially those that can
233 provide information on both presence and absence of species at specific locations and archive
234 verifiable media specimens, will facilitate the ability of governments and other stakeholders
235 to use observations collected from citizen scientists, as well as increase the value of expert-
236 led assessments such as RAP.

237 **Population biology domain: The Prestonian Shortfall**

238 The Prestonian shortfall reflects our lack of knowledge on spatial and temporal changes in
239 abundance and related population dynamics (Cardoso et al. 2011). Data to estimate these
240 state variables are more challenging to obtain than simple presence-absence data, largely due
241 to low detection probabilities of many Neotropical bird species due to combinations of
242 natural low population densities or sensitivity to disturbance, low vocalisation rates and
243 structurally complex habitats which make visual detection difficult (Archaux et al. 2012,
244 Robinson et al. 2018a). In addition, reaching survey locations may be prohibitively
245 logistically challenging, especially in montane regions or in remote Amazonian interfluvial
246 regions where and logistics cost may be prohibitive. These challenges are exacerbated by the

247 high costs of long-term data collection and the potential for high variability in species
248 abundance patterns that may necessitate more intensive sampling. In these respects,
249 Wallacean and Prestonian shortfalls are inextricably-linked – we often collect information not
250 just on species presence and absence, but also on relative or absolute abundance, all in one
251 survey. Sampling effort also needs to represent the full gradient of land cover classes where a
252 species can be found, in order to increase the accuracy of both distribution models and
253 abundance estimates (e.g., Moura et al 2013). In general, spatio-temporal bias and class
254 imbalance issues (e.g., too many zeros associated with rare species) related to most survey
255 data are difficult to mitigate without large sample sizes, leading to inaccurate, or at best
256 imprecise, estimates of abundance needed for many conservation planning efforts (Gaston &
257 Rodrigues 2003, Mace 2004, Robinson et al. 2018b).

258 Estimating changes in abundance is one of the costliest monitoring objectives for any
259 taxonomic group. Not surprisingly, then, estimating population size for most Neotropical
260 birds remains out of reach except for extreme cases where species are so rare that each
261 individual may be counted as, for example, the Orange-bellied Antwren (*Terenura sicki*;
262 Pereira et al. 2014, Fig 2b). The same may also be true for some colonial species restricted to
263 a relatively small number of breeding sites which may be remotely detected by satellite
264 (Fretwell et al. 2017), drone (Hodgson et al. 2017) or even kite (Delord et al. 2015). Most of
265 our information on changes in abundance comes from statistical models used to estimate
266 relative abundance and these are few in number (Buckland et al. 2008, Denes et al. 2017,
267 Gomez et al. 2017, Kuichi et al, 2018). Estimates of relative abundance can be modelled
268 across time, and, although estimates of population size are likely to be far from perfect, the
269 overall trajectory of the population can be highly informative (Robinson et al, 2018b).
270 Traditionally, estimation of population trends required standardized and optimized sampling
271 protocols, including by citizen scientists (Sauer et al, 2011), but more recent advances have

272 been made to use opportunistically collected citizen-science data to estimate trends in relative
273 abundance that can go some way towards correcting for both spatial bias and class imbalance
274 (Robinson et al. 2017). Advances in species distribution modelling have leveraged patchy and
275 sparse data (Fink et al. 2010) to estimate relative abundance across the entire range of
276 widespread species (Fig 2b) throughout their full annual cycle, and these new dynamic
277 abundance models have been shown to improve the prioritization of areas for conservation
278 (Johnston et al. 2019). Moreover, local occupancy probabilities derived from SDMs have
279 been found to be positively correlated with local abundance in a range of animal and plant
280 groups (Weber et al. 2017). Although low densities of data from many parts of the Neotropics
281 result in poor predictive performance, newer SDMs still perform well in data-poor regions,
282 such as Central America, even with relatively sparse spatial sampling coverage (Fink et al.
283 2020a).

284 Unlike the situation at temperate latitudes, there are relatively few structured, long-term
285 ornithological studies to monitor changes in relative abundance across Neotropical species
286 over time (Robinson and Curtis 2020). Such studies are necessary given that their duration
287 gives a broader overview of the minimum timeframe needed to estimate trends in abundance
288 (~ 10yrs), which can be used to make inferences on minimum viable population size (Reed et
289 al. 2003). Despite being critical for national, regional, and global species assessments (e.g.,
290 IUCN Red List), our capacity to estimate total population size for most species remains
291 constrained by a paucity of data. Museum specimens and historical data can be helpful for
292 providing a broader context to understand historic local extinctions (Kattan et al. 1994,
293 Moura et al. 2014), which may pre-date any type of monitoring efforts and provide a sense of
294 the context for current population trend estimates.

295 Although citizen science holds a great deal of promise in filling these shortfalls,
296 participants will require careful guidance from experts in wildlife population monitoring to

297 make sure that we not only increase the quantity of information, but also its quality. The
298 application of best practices for collecting information, as well as the use of established
299 sampling protocols developed to inform a broad range of statistical models (e.g., PROALAS
300 for bird counts; Ruiz-Gutiérrez et al. 2018), will make the best use of monitoring resources.
301 Another field with considerable potential to fill the Prestonian shortfall is automated acoustic
302 monitoring of bird vocalisations (Leach et al. 2016). Although still in its infancy,
303 developments in automated song recognition, falling costs of hardware, and increased
304 interest, both from ornithologists and from other biological disciplines, will see a rapid
305 growth in our ability to collect information on species' presence-absence, to express relative
306 abundance as inferred from calling intensity and to detect shifts in distribution within entire
307 bird communities across potentially vast areas (Priyadarshani et al. 2018).

308 Beyond understanding abundance, data on population dynamics of Neotropical
309 species are even more costly and difficult to obtain. Although there are some notable long-
310 term projects that have resulted in contributions of population vital rates for Neotropical
311 species (Brawn et al, 1999, reviewed in Ruiz-Gutierrez et al. 2012), there are relatively few
312 contributions relative to the number of long-term banding projects underway in various parts
313 of the Neotropics. Since 2012, there have only been a handful of published studies that look
314 at survival rates for adults (e.g., Thomson and Estades 2012), and even fewer exist overall
315 that look at survival during other critical life stages (e.g. juvenile survival). Ruiz-Gutierrez et
316 al. (2012) suggest that this is largely due to overall low capture probabilities of Neotropical
317 residents, small sample sizes due to the low number of mist nets (e.g., 10-15 nets) commonly
318 used to sample what are often low-density bird communities, and inconsistencies between
319 field protocols and requirements of capture-recapture models used to estimate population
320 vital rates. Ruiz-Gutiérrez et al. (2012) provide guidelines for sampling designs that facilitate

321 the estimation of avian vital rates from banding, as part of long-term research projects as well
322 as larger, coordinated banding efforts.

323 **Evolution domain: The Darwinian shortfall**

324 Darwinian shortfalls reflect a lack of knowledge about the evolutionary tree of life. Diniz-
325 Filho et al. (2013) identified three aspects that contribute to this shortfall: (a) a lack of fully
326 resolved phylogenies; (b) limited knowledge of edge lengths and problems with absolute time
327 calibrations; and, (c) a lack of evolutionary models to link phylogenies to ecological traits
328 and life-history variation. Attempts to reduce the impact of these knowledge gaps has to start
329 with knowledge of the terminal tips of the phylogenies and understanding their topological
330 relationships to the other tips. The tips may refer to species or subspecies, many of which, at
331 a molecular level, may be insufficiently distinct to be called either phylogenetic species or
332 ‘evolutionary significant units’ (Barrowclough et al. 2016). This is nominally the domain of
333 the Linnaean shortfall – understanding how many species there are – and this basic
334 taxonomic work is needed to define the biodiversity units of greatest interest to conservation
335 biologists (Rojas-Soto et al. 2010).

336 In recent years, far more emphasis has been placed on clarifying species status for
337 contentious taxa than investigating geographic variation within species that is critical for
338 understanding evolutionary relationships. It has been argued that many avian subspecies are
339 poorly supported and often arbitrarily demarcated subdivisions of geographic gradients in
340 character variation (Zink 2004). The diagnoses for most subspecies have not been revisited in
341 recent years and are typically weak, with only some poor qualitative descriptions of
342 morphological characters without recourse to statistical analyses (Remsen 2005). For
343 example, neither morphological (Handford 1985) nor mitochondrial phylogeographic
344 structure analyses (Lougheed et al. 2013) support the subspecific taxonomy of the Rufous-

345 collared Sparrow (*Zonotrichia capensis*). Conversely, some poorly described subspecies
346 eventually prove to represent undescribed or cryptic new species, once geographic variation
347 (especially behavioural/vocal) within widespread taxa is better understood e.g. the Black-
348 billed Thrush (*Turdus ignobilis*) complex (Cerqueira et al. 2016). Preliminary analyses
349 indicate that others demand attention e.g. the Sooty-headed/Yungas Tyrannulet (*Phyllomyias*
350 *griseiceps/weedeni*) complex (Harvey et al. 2014). Full genome analyses are challenging our
351 concepts of how species should be defined, with some long-cherished biological species such
352 as Blue-winged (*Vermivora cyanoptera*) and Golden-winged (*V. chrysoptera*) warblers
353 shown to be minimally distinct (Toews et al. 2016), whilst deep and phylogenetically
354 informative divisions have been uncovered in other species (e.g. Harvey & Brumfield 2015,
355 Cadena et al. 2019, Fig 2c). The public availability of large databases such as GENBANK
356 (<http://www.ncbi.nlm.nih.gov/genbank>) has done much to facilitate this rapid rise in
357 knowledge acquisition of the evolutionary relationships among birds.

358 Nevertheless, avian phylogenies are far more complete than for any other major taxonomic
359 group. For example, there is now a complete global phylogeny available for all birds (Jetz et
360 al. 2012), albeit with remaining uncertainties about positions of deep branches in the tree and
361 with inductive inference, rather than measurement, guiding some genetic placements. New
362 family-level phylogenies for Neotropical bird families are appearing on a regular basis (e.g.,
363 Derryberry et al. 2011, McGuire et al. 2014) catalysed by rapid progress in DNA sequence
364 technology, bioinformatics, molecular genetics, and phylogeny reconstruction. In fact, since
365 1993, there has been an explosion of phylogenetic studies of Neotropical birds and a
366 proliferation of molecular laboratories at universities and museums, including in several
367 Neotropical countries facilitating major multi-taxon assessments (e.g., Silva et al. 2019). This
368 explosion was made possible by the regular collection of tissue samples for genetic analysis
369 as part of regular biodiversity collecting, as pioneered by Ted Parker and his colleagues

370 during the 1980s. Despite this overall progress in understanding evolutionary relationships in
371 recent decades, the phylogenetics and historic biogeography of many diverse Neotropical
372 species groups remain unresolved, hampering our ability to identify and conserve biodiversity
373 hotspots of greatest evolutionary significance.

374 A community's phylogenetic diversity (after Faith 1992), calculated as the sum of branch
375 lengths between root and tips on a phylogenetic tree, is becoming an increasingly established
376 metric to assess biological integrity alongside taxonomic diversity (species richness) and
377 functional diversity (incorporating species trait information). Integrating information on the
378 phylogenetic positions of species provides information about the legacy of evolutionary
379 processes (e.g., speciation) into conservation assessments (e.g., Edwards et al. 2015, Lees et
380 al. 2016) and may add more conservation value to more evolutionary distinct species
381 regarded as having greater irreplaceability (Fig 3a, b). There is growing evidence that
382 increased phylogenetic diversity predicts some measures of enhanced ecosystem functioning
383 (Cadotte, et al. 2012, Cadotte 2013), and, if this proves to be a general rule, then phylogenetic
384 diversity might well provide a powerful tool for evidence-based conservation strategies given
385 that collecting phylogenetic data is often considerably easier than collecting detailed trait
386 data.

387

388 **Functional ecology domain: The Raunkiæran shortfall**

389 A lack of knowledge about species-specific traits and their ecological functions has been
390 termed the Raunkiæran shortfall (Hortal et al., 2015) after Christen C. Raunkiær the Danish
391 botanist. The last few years have seen several heavily populated global databases that
392 describe birds in terms of their functional traits, rather than their taxonomic or phylogenetic
393 affiliations. These databases have built on the phenomenal legacy of the first comprehensive

394 trait database of Neotropical birds assembled by Parker et al. (1996). Subsequent databases
395 have, for instance, covered fairly crude measures of body mass, diet, habitat, and foraging
396 stratum data (Wilman et al. 2014) at a global level, but finer-tuned datasets are now
397 becoming available extending to, for example, bill morphology of thousands of species
398 (Cooney et al. 2017). Trait datasets previously available for certain clades and regions have
399 now been published at global scales for almost all bird species, including morphological traits
400 linked to trophic niches (Pigot et al. 2020) and dispersal ability (Sheard et al. 2020) and work
401 on collecting data on plumage traits is ongoing
402 (<https://www.zooniverse.org/projects/ghthomas/project-plumage>). Functional trait-based
403 approaches are used in a wide range of applications in ecological and evolutionary research;
404 traits are viewed as phenotypic attributes affecting their fitness, that of other organisms, and
405 the ecosystems they inhabit (Violle et al. 2007). Quantitative trait values lend themselves to
406 easy comparisons between and among populations, species, and communities subject to
407 different environmental conditions.

408 Quantitative trait data have been used, for example, in studies of the loss of ecosystem
409 services such as seed dispersal and top-down control of herbivory (Bregman et al. 2016).
410 Such studies can then provide insight into the relative contribution of different species in
411 providing such services. In the latter case species that contributed most to network
412 organization were at higher risk of extinction. Use of species traits and deeper information on
413 how individual species interact with each other within an ecological network analysis
414 framework has shown particular promise in identifying the key role of particular bird species
415 in maintaining forest ‘health’ (e.g., Sebastian-Gonzalez et al. 2017), and what likely happens
416 when such species are lost. For example, Vidal et al. (2014) found that the species that
417 contributed most to plant–frugivore interaction network organization in an Atlantic Forest
418 system were at higher risk of extinction. The loss of such species has impacts that cascade to

419 communities, driving for example, rapid evolutionary changes in seed size (Galetti et al.
420 2013) with knock-on effects on other ecosystem services such as carbon storage (Bello et al.
421 2015).

422 This recent accumulation of knowledge of traits derived from specimen data suggests, at least
423 for those species for which sufficient museum specimens exist, that we are making progress
424 in making up this shortfall. However, a major characteristic of the Raunkiæran shortfall is
425 that the traits that are typically measured are often the simplest, rather than the most
426 functional (Hortal et al., 2015). There is an urgent need to use informative functional traits -
427 those linked to species' tolerance of abiotic and biotic conditions or to the effects of species
428 on ecosystems (Hortal et al., 2015). As such, more effort needs to be concentrated on
429 behavioral, physiological, and life history traits (Kingsolver et al. 2001) instead of simply
430 morphological ones.

431 **Abiotic tolerance domain: The Hutchinsonian shortfall**

432 The Hutchinsonian shortfall represents a lack of understanding of the responses and
433 tolerances of species to varying abiotic conditions. Rosado et al. (2016) argued that this needs
434 to be subdivided into the Grinnellian shortfall, which reflects a lack of knowledge about
435 responses of species to a given environmental driver, and the true Hutchinsonian shortfall,
436 reflecting uncertainty about the functional roles of species. Nuances aside, the shortfall is
437 itself directly influenced by the Wallacean shortfall; in order to understand environmental
438 tolerance we must first have a clear idea of where species are in time and space. If
439 observations of any given taxon cover a representative sample of environmental gradients
440 within their range, then data collection bias may not be too troubling for modelling efforts
441 (Oliveira et al. 2016). Interpolated surfaces of predicted species distributions can be
442 extremely important tools for seeking out relictual populations of rare species (Marini et al.

2010). However, consideration of recent habitat loss is important as current distributions for many species may reflect habitat availability in the Anthropocene that may be constrained given that humans tend to settle in biological hotspots (Cincotta et al. 2000). Some species may even be observed in suboptimal habitat types, which, if considered in isolation in a modelling framework, may result in misleading habitat suitability models and lead to perverse conservation decisions (Pulliam & Danielson 1991).

Understanding abiotic tolerance and the interaction between topography and climate will be crucial to predicting Neotropical bird responses to climate change coupled with other global change drivers, such as habitat loss, fragmentation and degradation, the invasion of exotic species, and parasites or pathogens that cause disease (Ehrlich & Pringle, 2008, Frishkoff et al. 2016). Threats from climate change to Neotropical birds are myriad and range from the collapse of montane climate envelopes as distributions are forced to move upslope (Sekercioglu et al. 2008, Freeman et al, 2018) to potential wholesale Amazonian die-back and switch to alternative stable ecosystem states (Malhi et al. 2008). Clearly, our ability to understand tolerances and threats is dependent on knowledge of species-specific physical and functional traits, highlighting a direct link between Raunkiaeran and Hutchinsonian shortfalls.

Work on understanding climate change responses has focussed on modelling expected changes in species-specific distributions (Elith & Leathwick, 2009) based on observed changes in species distributions under past or future climate change scenarios. These have often focussed on altitudinal range shifts (Forero-Medina et al. 2011, Freeman et al. 2018). Other studies have drawn attention to the role of slope, aspect and soil composition in mediating community composition (e.g., Cintra & Naka 2011) which in turn mediate microhabitats used by birds (Stratford and Stouffer 2015). SDMs have become a key tool for ecologists to build quantitative models of climate change impacts on the spatial distribution of individual species (Thuiller, 2003). Mokany and Ferrier (2011) made a case for the

468 development of semi-mechanistic models at the community level to model climate change
469 impacts on biodiversity. Such a conceptual integrated modelling framework approach
470 (Mokany et al. 2015) would retain the features of existing correlative community-level
471 models to deal with shortfalls, while including mechanistic processes in predicting how
472 diversity will change over time as environmental conditions vary.

473

474 **Biotic interactions domain: The Eltonian shortfall**

475 The Eltonian shortfall is arguably the widest of all of the biodiversity shortfalls. It
476 encompasses the gaps in our knowledge of species' interactions and their effects on
477 individual survival and fitness. The complexity of biotic interactions likely peaks in the
478 humid tropics (Schemske et al. 2009), and the web of potential interactions that characterize
479 hyperdiverse tropical biotas are legion. They obviously do not stop at just those between one
480 bird species and the next but reflect the whole gamut of interactions between predators and
481 prey, mutualisms, transmission of parasites and pathogens, and even ecosystem engineering.
482 Bridging this shortfall by necessity requires knowledge of the basic ecology and natural
483 history of Neotropical birds, highlighted in the next shortfall; one cannot understand species
484 interactions and interdependence without this baseline knowledge. The slow drip of
485 publication of papers on natural history and community dynamics is iteratively chipping
486 away at the Eltonian shortfall. Exciting recent examples include the discovery that mixed
487 species flocks change their habitat use when flock-leading *Thamnomanes* antshrikes are
488 temporarily removed (Martínez et al. 2018) and the discovery that holes made by *Diglossa*
489 flowerpiercers facilitate nectar access for hummingbirds which are also 'illegitimate'
490 accessors of nectar resources (Gonzalez and Loiselle 2016).

491 Interactions between species have been shown to be highly sensitive to anthropogenic
492 change. Neotropical birds exhibit some of the most complex social mutualisms known to
493 science, including those observed between members of avian mixed-species flocks (Munn
494 1986)—interactions that may be highly sensitive to environmental change (Mokross et al.
495 2014). These changes must reach back further than recent land-use change with many
496 interspecies interactions likely having been lost following the extinction loss of almost the
497 entire Neotropical megafauna (Galetti et al. 2018). Large mammals and birds, for example,
498 may be extremely important for ecosystem function, and loss of co-occurring biodiversity
499 maintenance via trophic cascades and propagation of consumer impacts through food webs
500 may lead to trophic downgrading (Svenning et al. 2016). This loss can be reversed by re-
501 introducing key species in defaunated or restored forests, a process of trophic rewilding that
502 is likely to become a key conservation tool in the tropics as well as the temperate zone
503 (Galetti et al. 2017).

504 One of the most striking examples of species interactions of conservation concern involves
505 the recent discovery that survival of the insular endemic Golden Lancehead (*Bothrops*
506 *insularis*) snake relies on the seasonal arrival of its prey – migrant *Elaenia* flycatchers, drifted
507 off course to the snake’s tiny island redoubt - the Ilha da Queimada Grande off the coast of
508 SE Brazil (Marques, et al. 2012). At a broader scale, knowledge of the keystone role of army
509 ants in Neotropical forests is nothing new, but only recently has the magnitude of these
510 interactions started to become better documented—for instance over 300 species of animals
511 are thought to be dependent on single army ant species: *Eciton burchellii* (Rettenmeyer et al.
512 2011). In the case of many bird species, this relationship amounts to parasitism of the ants,
513 rather than the long-thought mutualism (Wrege et al. 2005). Knowing the critical importance
514 of these interspecies interactions, both local and widespread, we must wonder at how many
515 additional examples await discovery within Neotropical bird communities. Work on parasites

516 and their impacts on Neotropical bird populations, especially in the context of global change
517 are even more limited but are now known to be potentially extremely important at least in
518 insular systems (Bulgarella et al. 2018).

519 New analytical techniques and statistical frameworks are shedding light on interspecific
520 behaviors and associations, and ways to estimate species interactions (Rota, 2016). Joint-
521 species distribution models can now accommodate species traits and interactions and can
522 include habitat-associations at multiple levels, including detection probability (Ovaskainen et
523 al, 2019). This last point can be an important factor when the detection probability of species
524 is influenced both by density-dependent call rates and by the presence of the other species.

525 Network analyses also offer a useful conceptual framework to understand the complexity of
526 biological systems in providing metrics to assess the strengths of interactions at the species
527 level (Bascompte et al. 2006). Understanding the consequences for communities of the
528 gradual erosion of species from ecological networks is crucial to determine their resilience to
529 environmental change. The existence of any thresholds, after which community collapses are
530 precipitated, will be depend on both the degree of ecological redundancy for species within
531 the system and the responses of keystone species to habitat loss (Guimarães et al. 2011).

532 Combining community-level data with life-history traits permits investigation of the role of
533 inter-specific competition to be explored across environmental gradients (e.g. Bregman et al.
534 2015) to understand the consequences for ecosystem function.

535 **Natural History domain: The new Parkerian shortfall**

536 In addition to formal approaches to understanding physical and functional traits of species, a
537 lack of basic natural history knowledge for most Neotropical bird species greatly impedes our
538 ability to fill the Raunkiaerian and other shortfalls. We hereby term this specific knowledge
539 gap the Parkerian shortfall. This shortfall reflects the fundamental importance of basic natural

540 history in underpinning our understanding of species' limits and phylogenetic relationships,
541 geographic distributions, and ecological requirements. During his relatively short career, Ted
542 Parker used his singular skills of observation and meticulous record-keeping to reveal how
543 behavioural and microhabitat specializations contribute to avian biodiversity (e.g., Remsen
544 and Parker 1983), as well as the relationship between foraging behaviour and habitat
545 selection in understanding a species' biogeography and phylogenetic position (Remsen and
546 Schulenberg 1997).

547 One example of how natural history studies, inspired by Ted Parker, led to cascading
548 knowledge gains in other domains began with the recognition that a diverse foraging guild of
549 species in several families were extreme specialists on aerial leaf litter in tropical forests
550 (Remsen and Parker 1984, Gradwohl and Greenberg 1984). Subsequent behavioral and
551 ecological studies of this guild (Rosenberg 1997) increased our knowledge of mixed-species
552 flock dynamics and generated a new hypothesis of relationships within the speciose antbird
553 genus *Myrmotherula* (Hackett and Rosenberg 1990), which eventually led to the recognition
554 of a distinct new genus (Isler et al. 2006). Similarly, careful attention to microhabitat
555 differences among similar species, first noted by Parker, led to discovery of major range
556 extensions among Amazonian bamboo specialists (Parker et al. 1997) and the recognition of
557 many species, cryptic or otherwise, that are restricted to white sand forests (Alonso and
558 Whitney 2003, Adeney et al. 2016). Finally, there are numerous cases in which understanding
559 the subtle variation in vocalizations among species across barriers or habitats has led to major
560 taxonomic and biogeographic revisions within several Neotropical families, including, for
561 example, antbirds (Isler et al. 1998), tapaculos (Krabbe and Schulenberg 1997, Cadena et al.
562 2020), and woodcreepers (Rodrigues et al. 2013).

563 A lack of knowledge of the foraging behaviour and diet of individual species continues to
564 impede our ability to understand ecological processes such as seed dispersal and pollination,

565 and to understand habitat requirements and the degree of threats from anthropogenic change
566 with basic biological information lacking for many species (see gaps in the new Birds of the
567 World platform <https://birdsoftheworld.org/>). For example, as of 1 May 2020, 110 Neotropical
568 species were missing from the Macaulay Library archive, and 96 New World species missing
569 from xeno-canto (hence their vocal behaviour is unknown or unavailable for study) and even
570 basic nest descriptions are not listed for 328 of a sample of 1018 Neotropical species across
571 nine families (Table 1). Continuing to populate these data resources will be a major step
572 towards filling the Parkerian shortfall and providing the raw material for filling shortfalls in
573 other domains.

574 Tackling the Parkerian shortfall requires greater valuation of basic natural history information
575 (Bartholomew 1986, Cotterill and Foissner 2010). This valuation needs to extend not just to
576 biodiversity inventories and taxonomy that fall in the broader natural history remit that we
577 earlier champion, but also of careful quantitative and qualitative observations of the ecology
578 of species that do not need to be hypothesis driven to be of merit. Such data has found
579 champions in the Neotropics across the decades, natural historians like Helmet Sick,
580 Alexander Skutch, and Edwin Willis, have paved the way for subsequent ornithologists by
581 filling in the gaps about life histories so fundamental to blockbuster global analyses of avian
582 traits. Of the contemporary cohort of field ornithologists, Harold Greeney stands out as an
583 author of several hundred ornithological papers that detailed the breeding biology of over 500
584 Neotropical bird species (e.g., Greeney et al. 2004, 2007, 2013). New technologies such as
585 camera traps and nest cams can help bridge this gap and further plug other shortfalls. The
586 discovery of interspecific nesting associations involving Plumbeous Kites (*Ictinia plumbea*)
587 and becards (*Pachyramphus* spp.) by Bodrati and Cockle (2017) is just one great example of
588 such work.

589 **Conclusions**

590 Our review reveals that, despite progress in plugging knowledge gaps in Neotropical
591 ornithology, some shortfalls, such as the Eltonian domain of biotic interactions, may persist
592 for decades to come. Moving forward, one of the most important steps is to encourage,
593 support, and value both basic science and natural history descriptions of Neotropical birds.
594 The ‘pervasive denigration of natural history’ (*sensu* Cotterill and Foissner 2010) includes
595 both the failure to appreciate and support biodiversity inventories and the failure of
596 scientometrics to quantify the importance of taxonomic and natural history publications.
597 Instead, we challenge the scientific community to better fund and recognize the contributions
598 of ornithologists working to fill the shortfalls that we have highlighted. In addition, increased
599 attention should be directed towards building capacity and cultivating partnerships with local
600 scientists and universities in Neotropical countries to mobilize the capacity that is needed to
601 adequately fill the many knowledge gaps that still exist across the various shortfalls described
602 in this paper.

603 Another factor to consider is that interest in birds stretches far beyond professional
604 ornithologists and includes a diverse group of amateur ornithologists, birdwatchers,
605 naturalists, and outdoor recreationists. Therefore, prospects for addressing shortfalls are
606 better than for other taxonomic groups. For example, much of the progress of the last two
607 decades in filling in shortfalls have come from non-scientists, a large cohort of whom are bird
608 tour guides with exceptional field expertise. For example, the Red de Monitoreo Comunitario
609 de Aves in Mexico, led by NABCI and CONABIO, has trained over 660 members across 15
610 Mexican states, contributed over 26,300 complete eBird checklists, playing a significant role
611 in generating critical information on the distribution and abundance of Neotropical birds
612 (CONABIO 2020). Encouraging the growing legions of birders to contribute to citizen-
613 science “big data” databases and archives is essential. Regional programs such as WikiAves
614 and global ones like xeno-canto have been invaluable in capturing would-be citizen scientists

615 and archiving rich media specimens. While these individual efforts should be supported, there
616 is also a growing need to connect across efforts such that data can effectively be combined
617 and synthesized. The eBird enterprise (Sullivan et al. 2017) has become a benchmark in
618 combining real-time information on distribution and abundance, with key data on natural
619 history (e.g., breeding codes) and the ability to link field observations with specimen archives
620 for photographs, video, and sound recordings. The continuing exponential growth of data
621 submitted to this platform will undoubtedly reveal additional insights into species
622 distributions, geographic variation, and behaviors that will lead to new taxonomic changes
623 and knowledge of ecological relationships. Promoting eBird as a unified platform for natural
624 history information on Neotropical birds could lead to major advances in filling knowledge
625 shortfalls.

626 As knowledge is amassed and published in an ever-expanding number of data repositories
627 and journals, we also must continue to synthesize information in standardized accounts, such
628 as the Birds of the World platform. These accounts are vital for tracking the boundaries of
629 our knowledge, and for inspiring new exploration and research to continue to fill knowledge
630 shortfalls. Until recently many of the scientific studies within the Neotropics were driven by
631 North Americans and Europeans visiting the Neotropical frontier. Fortunately, the past two
632 decades has observed an increase in ornithological research at universities across the
633 Neotropics, with dedicated lab groups and university programs equipped with modern field
634 and lab methods driving progress forward. These networks are both expanding and recruiting
635 a new generation of young ornithologists through the work of Professional organisations,
636 NGOs and birding clubs. Funding and supporting all of these efforts and programs is
637 essential.

638 Finally, we stand to gain much from new technologies and modelling applications to more
639 quickly assimilate knowledge in all domains. As just one example, radio-tracking arrays (e.g.,

640 Motus) may prove to be an excellent investment for tracking both local bird movements and
641 those at hemispheric scales, opening new frontiers in understanding dynamic avian
642 distributions and ecological relationships (Gomez et al, 2018). Similarly, advances in genetic
643 techniques and analyses are catalysts for rapid changes in our understanding of taxonomic
644 relationships – within species as well as across newly recognized bird families. Our greatest
645 progress in filling knowledge shortfalls will come from coordinating and synthesizing such
646 advances in order to increase our understanding of Neotropical avian diversity, patterns of
647 endemism, and especially threats that need to be addressed in conservation strategies. Even as
648 our scientific knowledge of Neotropical birds advances, however, an additional shortfall
649 looms—our ability to link the importance of birds for ecosystem functioning to issues of
650 broader conservation concern, such as improving food security. This is crucial given that
651 public support is fundamental in leveraging both the policy and human behavioural change
652 that are necessary to reduce current extinction rates.

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655

656 **Data availability**

657 This is not a data paper.

658

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1066 Table 1. Lack of data on nest descriptions among Neotropical bird species as an example of
1067 the Parkerian shortfall in ornithological knowledge. Data collated from a random sample of
1068 1067 Neotropical species across nine families species accounts in Birds of the World
1069 (<https://birdsoftheworld.org>).

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Family	Neotropical breeding species	Nest undescribed
Cracidae	54	8 (15%)
Odontophoridae	29	8 (28%)
Columbidae	70	13 (19%)
Trochilidae	337	102 (30%)
Rallidae	51	9 (18%)
Accipitridae	61	6 (10%)
Falconidae	26	6 (23%)
Psittacidae	156	42 (27%)
Thamnophilidae	234	134 (43%)

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1078 Figure 1. Linnaean shortfalls may persist in areas that are remarkably well surveyed: a) an
1079 undescribed *Myornis* pygmy-tyrant which had evaded detection in historically well
1080 inventoried areas of north-east Brazil (Ciro Albano). Google Earth imagery has proven to be
1081 vital in planning surveys to plug Linnaean and Wallacean shortfalls in addition to many other
1082 conservation applications. Image b) depicts a view of the Cordillera Azul in Peru, a pre-
1083 Andean range that has been the scene of several new species discoveries in recent years, the
1084 process of finding suitable habitat is now greatly facilitated by open access high quality
1085 satellite data (imagery ©Google Earth) and c) Kaempfer's Woodpecker *Celeus obrieni* which
1086 was rediscovered in north-eastern Brazil in 2006 after 80 years as an enigma, it is now known
1087 to occupy a huge 861,000 km² range and suggests that even striking species may elude
1088 detection at sub-continental scales if they have high habitat specificity (A. C. Lees).

1089 Figure 2. a) Orange-bellied Antwren *Terenura sicki* a Critically Endangered endemic of
1090 northeast Brazil which is rare enough that all individuals within the population could easily
1091 be surveyed (A. C. Lees), b) seasonally-averaged estimated relative abundance map for Fork-
1092 tailed Flycatcher *Tyrannus savanna* (Fink et al. 2020b) derived from eBird data and a suite of
1093 environmental variables (*Tyrannus* illustration by Ian Lewington, used with permission from
1094 Birds of the World) and c) Bayesian tree showing phylogenetic relationships within the
1095 Tropical Andes clade of *Scytalopus* tapaculos revealing populations which likely merit
1096 additional study to clarify their taxonomic status (Cadena et al. 2020).

1097 Figure 3 a) Specimens of scythebills in the *Campylorhamphus procurvoides* complex (A. C.
1098 Lees) used in the description of a new Amazonian taxon – *cardosoi* (Portes et al. 2013);
1099 museum specimens like these can provide a wealth of morphological data and b) genetic data
1100 – here Mark Adams takes a toe-pad sample from a specimen of Variegated Antpitta *Grallaria*
1101 *varia* at the Natural History Museum at Tring (A. C. Lees). The widespread online
1102 availability of abiotic data facilitates modelling work that may result in significant

1103 distributional discoveries here, c) the relationship between rainfall and the seasonal
1104 distribution of the Ash-throated Casiornis *Casiornis fuscus* found by Lees (2015) to be a
1105 partial longitudinal migrant to Amazonia during the dry season (*Casiornis* illustration by
1106 Hilary Burn used with permission from Birds of the World).

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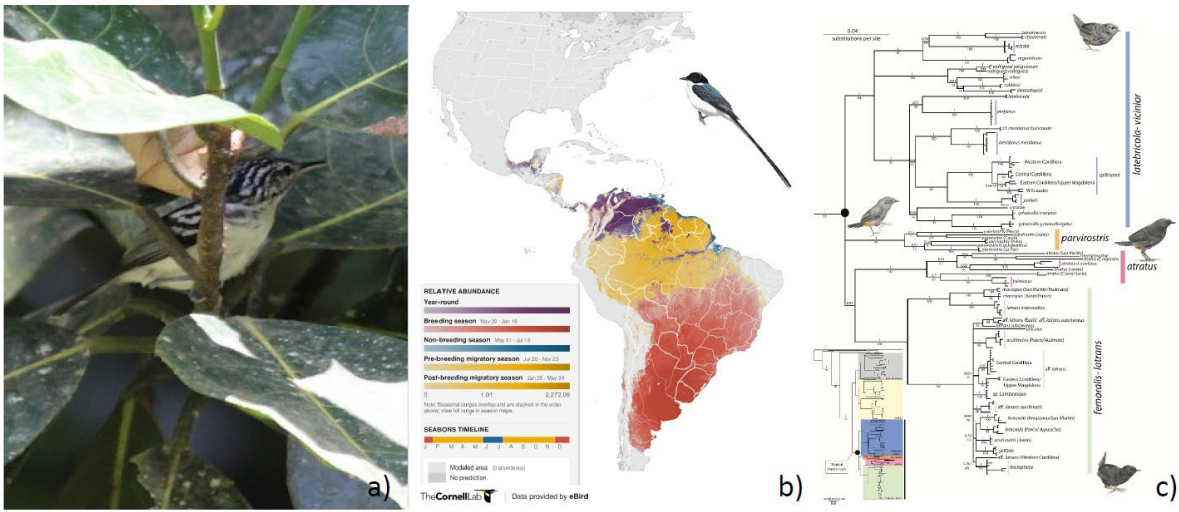
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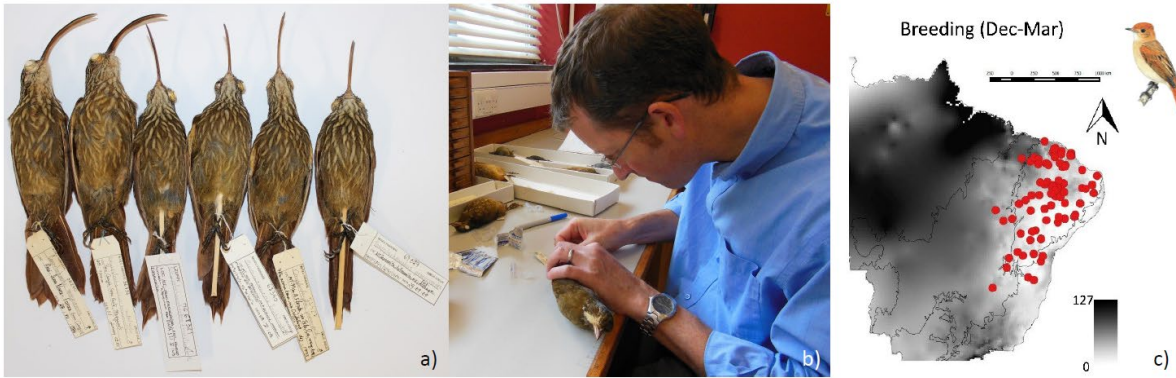
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1131 Figure 1.



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1135 Figure 3.