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A roadmap to identifying and filling shortfalls in Neotropical Ornithology

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Abstract

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

"I saw with regret, that whilst the number of accurate instruments was daily increasing, we were still ignorant"

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

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

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

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

Understanding the extent of our gaps in scientific knowledge requires identifying that which we do not know; recognizing these gaps also helps researchers ask questions that can best advance science. Birds may be the best known of all terrestrial biota, but data scarcity still plagues ornithology and Neotropical ornithology, in particular. The last 25 years, since Ted Parker's untimely death, have seen unprecedented changes in data collection, analysis, and availability. While the application of big-data approaches across large spatial, taxonomic, and temporal scales can fuel discovery, further advances are likely to be constrained by our inability to identify and prioritize research needs, as well as by a lack of basic knowledge about Neotropical birds. Shortfalls in our knowledge of biodiversity represent the gaps between realized knowledge and sufficient knowledge at the present day. Hortal et al. (2015) grouped biodiversity shortfalls into seven major domains related to systematics, biogeography, population biology, evolution, functional ecology, abiotic tolerances, and ecological interactions, combinations of which are needed to support effective conservation actions. Here, we discuss the importance and magnitude of each of these shortfalls relative to our knowledge of Neotropical birds, highlighting recent advances and proposing research priorities. In addition, we propose a new, eighth shortfall to specifically address the tremendous gap in basic natural history knowledge that still exists for a majority of Neotropical bird species—a gap that Ted Parker spent much of his life attempting to fill (Remsen 1997).

Systematics Domain: The Linnaean shortfall

Linnaean shortfalls (Lomolino 2004) represent the gap between the number of species formally described by scientists and the number of species that actually exist. In terms of taxonomic knowledge, ornithologists are fortunate relative to scientists working with other taxa, given that estimates suggest that more than 95% of avian species have been described (Mora et al. 2011, Scheffers et al. 2012). However, recent discoveries suggest that this estimate may have been too optimistic for the Neotropics. The race to describe the region's bird species reached its greatest intensity in the late 19th and early 20th centuries, often based on patchy specimen data from a taxon's geographic range and the methods were invariably pre-quantitative. A subsequent and largely unquestioned spate of 'lumping' of these forms, under the auspices of the polytypic 'biological' species concept (Mayr 1942, 1963,) has significantly impeded taxonomic progress (e.g., Sangster 2014 see the Darwinian shortfall and the revision of alpha taxonomy within polyphyletic species groups). A recent morphological and genetic assay by Barrowclough et al. (2016) contends that avian evolutionary diversity has been substantially underestimated, and that, under a phylogenetic species concept, we would recognize approximately 2 to 2.5 times the current number of biological species. In this vein, Navarro-SigüenzaI & Peterson (2004) proposed an alternative phylogenetic species taxonomy for the Mexican avifauna (which in the Neotropical realm includes the Yucatán Peninsula and southern lowlands, and most of the east and west coastlines and tip of the Baja California Peninsula) that resulted in splits affecting 135 'biological species', resulting in 323 new phylogenetic species of which 122 were new national endemics, increasing the national bird list by 18%.

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

Despite an arguably conservative approach to taxonomy, new species continue to be described on an annual basis from the Neotropical region, even from relatively well-inventoried areas (e.g., Fig. 1a). Between 1960 and 2016, 147 new species were described from South America and a further seven from Central America and Mexico (Brewer 2018). Ted Parker himself authored descriptions of three new bird species and seven subspecies, some of which may yet be elevated to species status in the future. Inspired by Parker, a number of his contemporaries have gone on to discover additional species. Most notable was a recent landmark volume in the Handbook of the Birds of the World series (de Hoyo et al. 2013) which published the descriptions of 15 new species from Amazonia (Whitney & Cohn-Haft 2013). This sudden rush of new Amazonian forms, not all of which have been formally recognised by all taxonomic bodies, reflects a broader changing picture of our understanding of the importance of acoustic (Remsen and Schulenberg 1997) and molecular tools in informing avian taxonomy (Remsen 2005). In most cases this re-evaluation of species assemblages will be reflected by redefining species limits, resulting in a significant increase in taxonomic ‘splitting’, but a smaller fraction of this unrecognised diversity will likely stem from completely undescribed new taxa.

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

Sensational rediscoveries such as that of Kaempfer's Woodpecker (*Celeus obrieni*) in 2006 (Fig. 1c), formerly known only from the type specimen collected in 1926, and now known to occur in bamboo groves over a huge swath of eastern Brazil, attests to the ease with which even charismatic species may elude ornithologists (Leite et al. 2013, Dornas et al. 2014). Major range extensions of difficult-to-detect species like owls, nightjars, and rails offer hope that these families may still harbour undescribed taxa. Some species may be forever lost to discovery, and we also need to redouble our effects to look for historic continental extinctions by searching carefully through museum drawers and hunting for subfossils. The Cryptic

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

Filling the Linnaean shortfall will require increased financial support for alpha taxonomy work and associated, collaborative expeditions to inaccessible or previously unsampled Neotropical locations. Underpinning these efforts must be stronger peer-recognition of the field of taxonomy, which is often viewed as 'low impact' in academic assessments (Agnarsson & Kuntner 2007), and also much greater support in general for the curation and use of museum collections associated with universities and other research institutions. Strengthening partnerships and increasing capacity for natural history collections within Latin America will be especially important as incoming generations of field ornithologists and students are well poised to discover the next wave of avian species.

Biogeographic domain – The Wallacean shortfall

Wallacean shortfalls represent gaps in our knowledge concerning geographic range limits and predicted distributions (Lomolino 2004), which remain a fundamental challenge to biogeographers and conservation biologists alike. Historically, in the absence of systematic surveys, general range maps were usually constructed from presence-only data from museum specimens and opportunistic citations of species in the technical and scientific literature (Anderson 2012). Wallacean shortfalls remain especially pervasive in the Neotropics given the inaccessibility of remote regions such as mountain ranges or corners of Amazonia that also sustain Linnaean shortfalls. Although ornithologists and birders are improving our understanding of coarse-scale ranges for many species – as evidenced by the relatively frequent discovery of major range extensions – our knowledge of specific habitat associations and derived distributions remains poor for most species and regions (Engler et al. 2017) and especially in the tropics (Orihuela-Torres et al. 2020).

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

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

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

Lack of basic knowledge of where and when species occur is a major obstacle for effective design of biodiversity conservation strategies. Resolving all Wallacean shortfalls may be a mammoth task but solutions can be simple, such as requiring increased support for organizations in Neotropical countries who are interested in working in out-of-the-way places. Important shortfalls might be remedied in high-priority regions, for example, by schemes such as the Rapid Assessment Program (RAP) that Ted Parker designed and directed for Conservation International (Remsen and Schulenberg 1997) and which was continued in the Field Museum of Natural History’s Rapid Biological Inventory program (http://fm2.fieldmuseum.org/rbi/). Importantly, RAP expeditions are collaborations between North American and Neotropical experts and feed directly into capacity building and conservation planning within the host countries.

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

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

Population biology domain: The Prestonian Shortfall

The Prestonian shortfall reflects our lack of knowledge on spatial and temporal changes in abundance and related population dynamics (Cardoso et al. 2011). Data to estimate these state variables are more challenging to obtain than simple presence-absence data, largely due to low detection probabilities of many Neotropical bird species due to combinations of natural low population densities or sensitivity to disturbance, low vocalisation rates and structurally complex habitats which make visual detection difficult (Archaux et al. 2012, Robinson et al. 2018a). In addition, reaching survey locations may be prohibitively logistically challenging, especially in montane regions or in remote Amazonian interfluvial regions where and logistics cost may be prohibitive. These challenges are exacerbated by the high costs of long-term data collection and the potential for high variability in species abundance patterns that may necessitate more intensive sampling. In these respects, Wallacean and Prestonian shortfalls are inextricably-linked – we often collect information not just on species presence and absence, but also on relative or absolute abundance, all in one survey. Sampling effort also needs to represent the full gradient of land cover classes where a species can be found, in order to increase the accuracy of both distribution models and abundance estimates (e.g., Moura et al 2013). In general, spatio-temporal bias and class imbalance issues (e.g., too many zeros associated with rare species) related to most survey data are difficult to mitigate without large sample sizes, leading to inaccurate, or at best imprecise, estimates of abundance needed for many conservation planning efforts (Gaston & Rodrigues 2003, Mace 2004, Robinson et al. 2018b).

Estimating changes in abundance is one of the costliest monitoring objectives for any taxonomic group. Not surprisingly, then, estimating population size for most Neotropical birds remains out of reach except for extreme cases where species are so rare that each individual may be counted as, for example, the Orange-bellied Antwren (*Terenura sicki*; Pereira et al. 2014, Fig 2b). The same may also be true for some colonial species restricted to a relatively small number of breeding sites which may be remotely detected by satellite (Fretwell et al. 2017), drone (Hodgson et al. 2017) or even kite (Delord et al. 2015). Most of our information on changes in abundance comes from statistical models used to estimate relative abundance and these are few in number (Buckland et al. 2008, Denes et al. 2017, Gomez et al. 2017, Kuichi et al, 2018). Estimates of relative abundance can be modelled across time, and, although estimates of population size are likely to be far from perfect, the overall trajectory of the population can be highly informative (Robinson et al, 2018b). Traditionally, estimation of population trends required standardized and optimized sampling protocols, including by citizen scientists (Sauer et al, 2011), but more recent advances have been made to use opportunistically collected citizen-science data to estimate trends in relative abundance that can go some way towards correcting for both spatial bias and class imbalance (Robinson et al. 2017). Advances in species distribution modelling have leveraged patchy and sparse data (Fink et al. 2010) to estimate relative abundance across the entire range of widespread species (Fig 2b) throughout their full annual cycle, and these new dynamic abundance models have been shown to improve the prioritization of areas for conservation (Johnston et al. 2019). Moreover, local occupancy probabilities derived from SDMs have been found to be positively correlated with local abundance in a range of animal and plant groups (Weber et al. 2017). Although low densities of data from many parts of the Neotropics result in poor predictive performance, newer SDMs still perform well in data-poor regions, such as Central America, even with relatively sparse spatial sampling coverage (Fink et al. 2020a).

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

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

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

Evolution domain: The Darwinian shortfall

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

In recent years, far more emphasis has been placed on clarifying species status for contentious taxa than investigating geographic variation within species that is critical for understanding evolutionary relationships. It has been argued that many avian subspecies are poorly supported and often arbitrarily demarcated subdivisions of geographic gradients in character variation (Zink 2004). The diagnoses for most subspecies have not been revisited in recent years and are typically weak, with only some poor qualitative descriptions of morphological characters without recourse to statistical analyses (Remsen 2005). For example, neither morphological (Handford 1985) nor mitochondrial phylogeographic structure analyses (Lougheed et al. 2013) support the subspecific taxonomy of the Rufous-collared Sparrow (*Zonotrichia capensis*). Conversely, some poorly described subspecies eventually prove to represent undescribed or cryptic new species, once geographic variation (especially behavioural/vocal) within widespread taxa is better understood e.g. the Black-billed Thrush (*Turdus ignobilis*) complex (Cerqueira et al. 2016). Preliminary analyses indicate that others demand attention e.g. the Sooty- headed/Yungas Tyrannulet (*Phyllomyias griseiceps*/*weedeni*) complex (Harvey et al. 2014). Full genome analyses are challenging our concepts of how species should be defined, with some long-cherished biological species such as Blue-winged (*Vermivora cyanoptera*) and Golden-winged (*V. chrysoptera*) warblers shown to be minimally distinct (Toews et al. 2016), whilst deep and phylogenetically informative divisions have been uncovered in other species (e.g. Harvey & Brumfield 2015, Cadena et al. 2019, Fig 2c). The public availability of large databases such as GENBANK (http://www.ncbi.nlm.nih.gov/genbank) has done much to facilitate this rapid rise in knowledge acquisition of the evolutionary relationships among birds.

Nevertheless, avian phylogenies are far more complete than for any other major taxonomic group. For example, there is now a complete global phylogeny available for all birds (Jetz et al. 2012), albeit with remaining uncertainties about positions of deep branches in the tree and with inductive inference, rather than measurement, guiding some genetic placements. New family-level phylogenies for Neotropical bird families are appearing on a regular basis (e.g., Derryberry et al. 2011, McGuire et al. 2014) catalysed by rapid progress in DNA sequence technology, bioinformatics, molecular genetics, and phylogeny reconstruction. In fact, since 1993, there has been an explosion of phylogenetic studies of Neotropical birds and a proliferation of molecular laboratories at universities and museums, including in several Neotropical countries facilitating major multi-taxon assessments (e.g., Silva et al. 2019). This explosion was made possible by the regular collection of tissue samples for genetic analysis as part of regular biodiversity collecting, as pioneered by Ted Parker and his colleagues during the 1980s. Despite this overall progress in understanding evolutionary relationships in recent decades, the phylogenetics and historic biogeography of many diverse Neotropical species groups remain unresolved, hampering our ability to identify and conserve biodiversity hotspots of greatest evolutionary significance.

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

Functional ecology domain: The Raunkiæran shortfall

A lack of knowledge about species-specific traits and their ecological functions has been termed the Raunkiæran shortfall (Hortal et al., 2015) after Christen C. Raunkiær the Danish botanist. The last few years have seen several heavily populated global databases that describe birds in terms of their functional traits, rather than their taxonomic or phylogenetic affiliations. These databases have built on the phenomenal legacy of the first comprehensive trait database of Neotropical birds assembled by Parker et al. (1996). Subsequent databases have, for instance, covered fairly crude measures of body mass, diet, habitat, and foraging stratum data (Wilman et al. 2014) at a global level, but finer-tuned datasets are now becoming available extending to, for example, bill morphology of thousands of species (Cooney et al. 2017). Trait datasets previously available for certain clades and regions have now been published at global scales for almost all bird species, including morphological traits linked to trophic niches (Pigot et al. 2020) and dispersal ability (Sheard et al. 2020) and work on collecting data on plumage traits is ongoing (https://www.zooniverse.org/projects/ghthomas/project-plumage). Functional trait-based approaches are used in a wide range of applications in ecological and evolutionary research; traits are viewed as phenotypic attributes affecting their fitness, that of other organisms, and the ecosystems they inhabit (Violle et al. 2007). Quantitative trait values lend themselves to easy comparisons between and among populations, species, and communities subject to different environmental conditions.

Quantitative trait data have been used, for example, in studies of the loss of ecosystem services such as seed dispersal and top-down control of herbivory (Bregman et al. 2016). Such studies can then provide insight into the relative contribution of different species in providing such services. In the latter case species that contributed most to network organization were at higher risk of extinction. Use of species traits and deeper information on how individual species interact with each other within an ecological network analysis framework has shown particular promise in identifying the key role of particular bird species in maintaining forest ‘health’ (e.g., Sebastian-Gonzalez et al. 2017), and what likely happens when such species are lost. For example, Vidal et al. (2014) found that the species that contributed most to plant–frugivore interaction network organization in an Atlantic Forest system were at higher risk of extinction. The loss of such species has impacts that cascade to communities, driving for example, rapid evolutionary changes in seed size (Galetti et al. 2013) with knock-on effects on other ecosystem services such as carbon storage (Bello et al. 2015).

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

Abiotic tolerance domain: The Hutchinsonian shortfall

The Hutchinsonian shortfall represents a lack of understanding of the responses and tolerances of species to varying abiotic conditions. Rosado et al. (2016) argued that this needs to be subdivided into the Grinnellian shortfall, which reflects a lack of knowledge about responses of species to a given environmental driver, and the true Hutchinsonian shortfall, reflecting uncertainty about the functional roles of species. Nuances aside, the shortfall is itself directly influenced by the Wallacean shortfall; in order to understand environmental tolerance we must first have a clear idea of where species are in time and space. If observations of any given taxon cover a representative sample of environmental gradients within their range, then data collection bias may not be too troubling for modelling efforts (Oliveira et al. 2016). Interpolated surfaces of predicted species distributions can be 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 development of semi-mechanistic models at the community level to model climate change impacts on biodiversity. Such a conceptual integrated modelling framework approach (Mokany et al. 2015) would retain the features of existing correlative community-level models to deal with shortfalls, while including mechanistic processes in predicting how diversity will change over time as environmental conditions vary.

Biotic interactions domain: The Eltonian shortfall

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

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

One of the most striking examples of species interactions of conservation concern involves the recent discovery that survival of the insular endemic Golden Lancehead (*Bothrops insularis*) snake relies on the seasonal arrival of its prey – migrant *Elaenia* flycatchers, drifted off course to the snake's tiny island redoubt - the Ilha da Queimada Grande off the coast of SE Brazil (Marques, et al. 2012). At a broader scale, knowledge of the keystone role of army ants in Neotropical forests is nothing new, but only recently has the magnitude of these interactions started to become better documented—for instance over 300 species of animals are thought to be dependent on single army ant species: *Eciton burchellii* (Rettenmeyer et al. 2011). In the case of many bird species, this relationship amounts to parasitism of the ants, rather than the long-thought mutualism (Wrege et al. 2005). Knowing the critical importance of these interspecies interactions, both local and widespread, we must wonder at how many additional examples await discovery within Neotropical bird communities. Work on parasites and their impacts on Neotropical bird populations, especially in the context of global change are even more limited but are now known to be potentially extremely important at least in insular systems (Bulgarella et al. 2018).

New analytical techniques and statistical frameworks are shedding light on interspecific behaviors and associations, and ways to estimate species interactions (Rota, 2016). Joint-species distribution models can now accommodate species traits and interactions and can include habitat-associations at multiple levels, including detection probability (Ovaskainen et al, 2019). This last point can be an important factor when the detection probability of species is influenced both by density-dependent call rates and by the presence of the other species. Network analyses also offer a useful conceptual framework to understand the complexity of biological systems in providing metrics to assess the strengths of interactions at the species level (Bascompte et al. 2006). Understanding the consequences for communities of the gradual erosion of species from ecological networks is crucial to determine their resilience to environmental change. The existence of any thresholds, after which community collapses are precipitated, will be depend on both the degree of ecological redundancy for species within the system and the responses of keystone species to habitat loss (Guimarães et al. 2011). Combining community-level data with life-history traits permits investigation of the role of inter-specific competition to be explored across environmental gradients (e.g. Bregman et al. 2015) to understand the consequences for ecosystem function.

Natural History domain: The new Parkerian shortfall

In addition to formal approaches to understanding physical and functional traits of species, a lack of basic natural history knowledge for most Neotropical bird species greatly impedes our ability to fill the Raunkiaerian and other shortfalls. We hereby term this specific knowledge gap the Parkerian shortall. This shortfall reflects the fundamental importance of basic natural history in underpinning our understanding of species' limits and phylogenetic relationships, geographic distributions, and ecological requirements. During his relatively short career, Ted Parker used his singular skills of observation and meticulous record-keeping to reveal how behavioural and microhabitat specializations contribute to avian biodiversity (e.g., Remsen and Parker 1983), as well as the relationship between foraging behaviour and habitat selection in understanding a species' biogeography and phylogenetic position (Remsen and Schulenberg 1997).

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

A lack of knowledge of the foraging behaviour and diet of individual species continues to impede our ability to understand ecological processes such as seed dispersal and pollination, and to understand habitat requirements and the degree of threats from anthropogenic change with basic biological information lacking for many species (see gaps in the new Birds of the World platform https://birdsoftheworld.org/). For example, as of 1 May 2020, 110 Neotropical species were missing from the Macaulay Library archive, and 96 New World species missing from xeno-canto (hence their vocal behaviour is unknown or unavailable for study) and even basic nest descriptions are not listed for 328 of a sample of 1018 Neotropical species across nine families (Table 1). Continuing to populate these data resources will be a major step towards filling the Parkerian shortfall and providing the raw material for filling shortfalls in other domains.

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

Conclusions

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

Another factor to consider is that interest in birds stretches far beyond professional ornithologists and includes a diverse group of amateur ornithologists, birdwatchers, naturalists, and outdoor recreationists. Therefore, prospects for addressing shortfalls are better than for other taxonomic groups. For example, much of the progress of the last two decades in filling in shortfalls have come from non-scientists, a large cohort of whom are bird tour guides with exceptional field expertise. For example, the Red de Monitoreo Comunitario de Aves in Mexico, led by NABCI and CONABIO, has trained over 660 members across 15 Mexican states, contributed over 26,300 complete eBird checklists, playing a significant role in generating critical information on the distribution and abundance of Neotropical birds (CONABIO 2020). Encouraging the growing legions of birders to contribute to citizen-science "big data" databases and archives is essential. Regional programs such as WikiAves and global ones like xeno-canto have been invaluable in capturing would-be citizen scientists and archiving rich media specimens. While these individual efforts should be supported, there is also a growing need to connect across efforts such that data can effectively be combined and synthesized. The eBird enterprise (Sullivan et al. 2017) has become a benchmark in combining real-time information on distribution and abundance, with key data on natural history (e.g., breeding codes) and the ability to link field observations with specimen archives for photographs, video, and sound recordings. The continuing exponential growth of data submitted to this platform will undoubtedly reveal additional insights into species distributions, geographic variation, and behaviors that will lead to new taxonomic changes and knowledge of ecological relationships. Promoting eBird as a unified platform for natural history information on Neotropical birds could lead to major advances in filling knowledge shortfalls.

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

Finally, we stand to gain much from new technologies and modelling applications to more quickly assimilate knowledge in all domains. As just one example, radio-tracking arrays (e.g., Motus) may prove to be an excellent investment for tracking both local bird movements and those at hemispheric scales, opening new frontiers in understanding dynamic avian distributions and ecological relationships (Gomez et al, 2018). Similarly, advances in genetic techniques and analyses are catalysts for rapid changes in our understanding of taxonomic relationships – within species as well as across newly recognized bird families. Our greatest progress in filling knowledge shortfalls will come from coordinating and synthesizing such advances in order to increase our understanding of Neotropical avian diversity, patterns of endemism, and especially threats that need to be addressed in conservation strategies. Even as our scientific knowledge of Neotropical birds advances, however, an additional shortfall looms—our ability to link the importance of birds for ecosystem functioning to issues of broader conservation concern, such as improving food security. This is crucial given that public support is fundamental in leveraging both the policy and human behavioural change that are necessary to reduce current extinction rates.

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Data availability

This is not a data paper.

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

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%)

Figure 1. Linnaean shortfalls may persist in areas that are remarkably well surveyed: a) an undescribed *Myornis* pygmy-tyrant which had evaded detection in historically well inventoried areas of north-east Brazil (Ciro Albano). Google Earth imagery has proven to be vital in planning surveys to plug Linnaean and Wallacean shortfalls in addition to many other conservation applications. Image b) depicts a view of the Cordillera Azul in Peru, a pre-Andean range that has been the scene of several new species discoveries in recent years, the process of finding suitable habitat is now greatly facilitated by open access high quality satellite data (imagery ©Google Earth) and c) Kaempfer's Woodpecker *Celeus obrieni* which was rediscovered in north-eastern Brazil in 2006 after 80 years as an enigma, it is now known to occupy a huge 861,000 km^2 range and suggests that even striking species may elude detection at sub-continental scales if they have high habitat specificity (A. C. Lees).

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

Figure 3 a) Specimens of scythebills in the *Campylorhamphus procurvoides* complex (A. C. Lees) used in the description of a new Amazonian taxon – *cardosoi* (Portes et al. 2013); museum specimens like these can provide a wealth of morphological data and b) genetic data – here Mark Adams takes a toe-pad sample from a specimen of Variegated Antpitta *Grallaria varia* at the Natural History Museum at Tring (A. C. Lees). The widespread online availability of abiotic data facilitates modelling work that may result in significant distributional discoveries here, c) the relationship between rainfall and the seasonal distribution of the Ash-throated Casiornis *Casiornis fuscus* found by Lees (2015) to be a partial longitudinal migrant to Amazonia during the dry season (*Casiornis* illustration by Hilary Burn used with permission from Birds of the World).

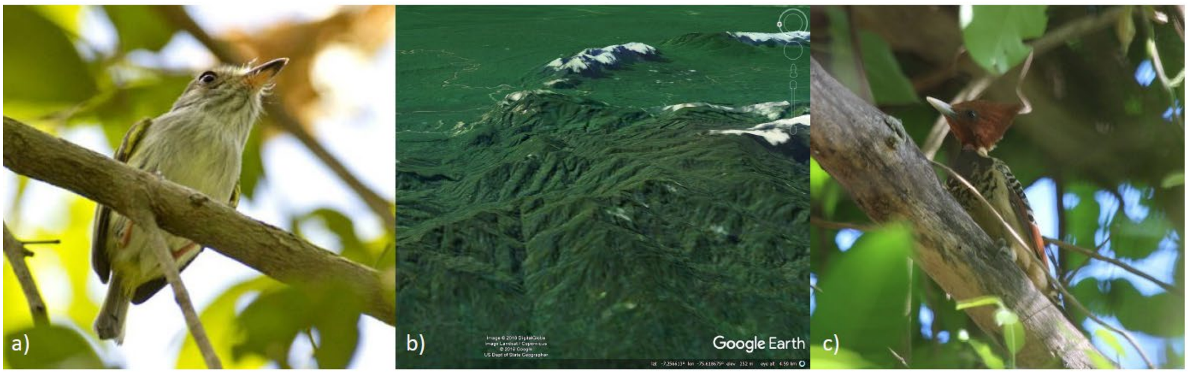

Figure 1.

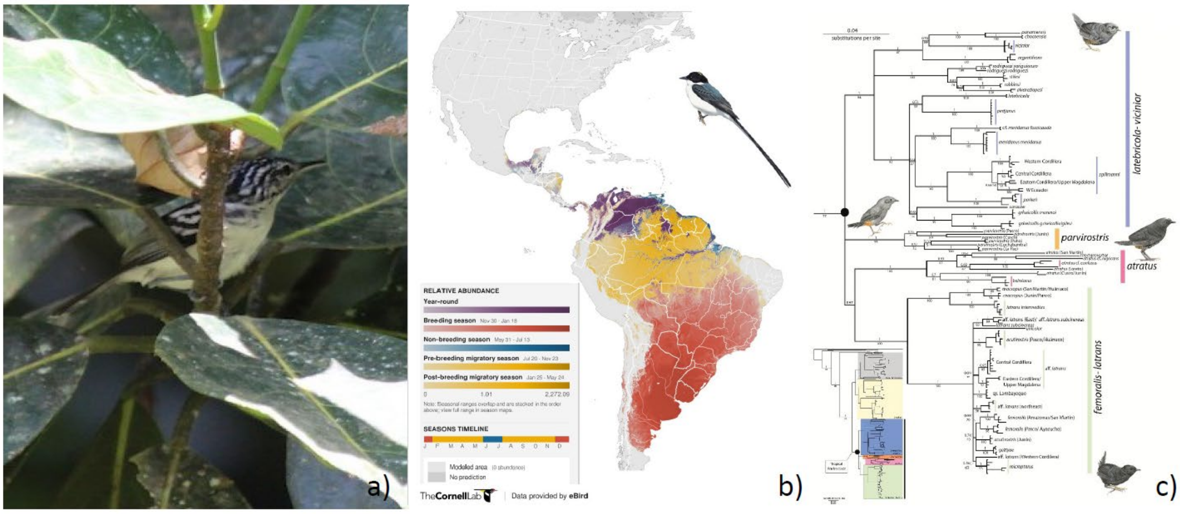

Figure 2.

Figure 3.