

# Ecological and biogeographical predictors of taxonomic discord across the world's birds

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## Abstract

**Aim:** Species delimitation is fundamental to biology, but disagreement in species concepts and the application of those concepts can lead to substantial variation in species lists, with important implications for conservation. For birds, there are four widely used global checklists that vary in length and application. Here, we investigate the biogeographical and ecological predictors of taxonomic disagreement between the four world bird species lists.

**Location:** Global.

**Time period:** Present.

**Major taxa studied:** Birds.

**Methods:** We determined taxonomic agreement based on whether each bird species name represented only one species ('agreement'), that is, no authorities have split the species, or represented multiple species ('disagreement') including disputed splits recognised by some authorities. We examined taxonomic agreement for all birds and for each family and biogeographical region. We then modelled taxonomic agreement as a function of six biogeographical and ecological variables: latitude, island endemism, log(mass), forest dependency, primary diet, and migratory status.

**Results:** Overall taxonomic agreement was 89.5%, and the remaining 10th of taxonomic names represented disputed splits upon which the four authorities disagreed. We found that taxonomic agreement was lowest for species in Southeast Asia/Australasia and the Southern Ocean, understudied regions where islands have driven high levels of cryptic diversification. In contrast, agreement was highest in the temperate Northern Hemisphere where diversity is lower and research is more extensive. Agreement was also higher for large, migratory species living in open habitats.

**Main conclusions:** Taxonomic agreement was higher for species that are easier to study such as large, temperate species from open habitats. In addition, agreement was lower for lineages that are more likely to undergo cryptic divergence such as island endemics with intermediate forest dependency and mobility. Species with these traits should be the focus of taxonomic research in order to achieve reconciliation of the world's bird lists and to better conserve extant biodiversity.

## KEYWORDS

biogeography, body size, conservation, forest dependency, latitude, migration, ornithology, tropical ecology

## 1 | INTRODUCTION

The classification of species is a fundamental part of biology. Yet, despite the importance of species delimitation, few biologists can agree on the definition of 'species'. A plethora of species concepts exist (Zachos, 2016), reflecting the inherent difficulty of 'imposing a discrete system on a continuous process' (Zachos, 2018). Even Charles Darwin (1859) wrote in *On the Origin of Species* that 'No one definition has satisfied all naturalists; yet every naturalist knows vaguely what he means when he speaks of a species'. Many biologists are able to operate with a vague species concept, but ontological divides persist to this day. These divides have implications not just for taxonomy and evolutionary biology (Faurby et al., 2016), but also for the effective conservation of these species themselves (Agapow et al., 2004; Mace, 2004). Identifying predictors of taxonomic disagreement can, therefore, help target research in an effort to reconcile that disagreement.

Biologists, conservationists, and policy makers need to have species lists (Thomson et al., 2018) in order to carry out comparative studies (Pigot et al., 2020; Şekercioğlu et al., 2004; Sheard et al., 2020), identify biodiversity hotspots (Myers et al., 2000; Orme et al., 2005), recommend conservation priorities (Buechley et al., 2019; McGowan et al., 2020) or identify the determinants of biodiversity loss (Newbold et al., 2014). In biodiversity studies, simple concepts such as species richness or endemism fundamentally depend on being able to define species. Using different definitions can get different results. For example, applying species concepts based on phenotypic or evolutionary differentiation can lead to previously underappreciated levels of diversity and endemism (Peterson, 2006), to the identification of alternative biodiversity hotspots (Meijaard & Nijman, 2003), and to the recognition of far more species (Barrowclough et al., 2016) that have smaller population and range sizes and thus increased conservation concern (Agapow et al., 2004). To not recognise alternative species concepts is to overlook cryptic biodiversity that could easily be lost (Hazevoet, 1996) in an era of biodiversity collapse (WWF, 2020).

Even for birds, the most well-studied class of organisms, several world checklists vary significantly in the number of species (Garnett & Christidis, 2017). Fundamentally, these differences result from disagreements about whether or not a given taxon represents one species or many. Discrepancies in these lists arise from differing species concepts, from differences in how those concepts are applied, and from variation in the speed at which taxonomies can be revised (McClure et al., 2020). Historically, the taxonomy of birds has favoured the biological species concept (BSC) based on reproductive isolation and the inability of populations to hybridise (Mayr, 1942), resulting in lists of approximately 10,000 species. More recently, molecular techniques have revolutionised species delimitation, with some authorities elevating the evolutionary species concept (ESC) or phylogenetic species concept (PSC) based on lineage differentiation (Wiley, 1978; Wiley & Mayden, 2000), an approach already adopted by mammal taxonomists (Zachos, 2016). The tendency towards the use of ESC and PSC brings with it the recognition of many more

species based on phylogenetic differentiation (Agapow et al., 2004; Isaac et al., 2004), as species are 'split' into multiple species. And there may be many more yet to come, with one study estimating the existence of over 18,000 bird species based on the application of morphological or genetic definitions of species (Barrowclough et al., 2016).

In addition to general species concepts, authorities can disagree on how those concepts are applied (McClure et al., 2020). Speciation is a gradual process including a 'grey zone' where it can be difficult to determine species limits (De Queiroz, 2007). Even given the same species concept, authorities can disagree on precisely where to draw the species line (De Queiroz, 2007; Zachos, 2018). Taxonomists must use extensive evidence to reach those decisions (De Queiroz, 2007; Hey et al., 2003), and this evidence can be based on phylogenetics, morphology, behaviour (such as acoustics), or the extent of hybridization (Barrowclough et al., 2016; Tobias et al., 2010; Winker, 2009). For example, BirdLife International uses the Tobias criteria (Tobias et al., 2010), which emphasise phenotypic divergence in species delimitation. The amount of data available to reach taxonomic decisions will vary based on the number of observations and samples from the field or museum collections (Hey et al., 2003), and discrepancies will likely arise for data-deficient species. Thus, for every species, taxonomists are using various lines of evidence, and decisions may therefore vary based on the imbued importance and quantity of different pieces of evidence (De Queiroz, 2007; Hey et al., 2003).

Variation in taxonomic agreement is not evenly distributed across bird families or countries (McClure et al., 2020) and it is critical to understand the drivers of this variation. What attributes cause taxonomic authorities to disagree on species limits? Discrepancies can arise from multiple sources and biases. A major source of disagreement likely arises from the geographical biases in research effort. In the understudied tropics, there may be less information (e.g., genetic or acoustic data) on which to base species delimitation decisions (Feeley et al., 2017; Harris et al., 2011; Rosenzweig et al., 2008; Titley et al., 2017). Disagreement may also be higher for island-restricted taxa. On separate islands it is difficult to implement the BSC as interbreeding cannot be tested, yet evolutionary distinctiveness can be assessed under the ESC. Research may also be biased at the species level towards large species from open habitats, which are easier to study. If a species is easier to observe and study, taxonomists likely have more data on which to base taxonomic decisions, and so different authorities are more likely to agree (limiting 'Type II uncertainty', Hey et al., 2003). Another important component of taxonomic disagreement could be cryptic lineages that are more likely to undergo divergence and occupy the 'grey zone'. If populations diverge genetically, this will favour species delimitation based on phylogeny. Yet other facets such as phenotypic differences may be at different stages of divergence. Thus, traits linked to a propensity for diversification such as island endemism, forest dependency or migratory capacity (Ashby et al., 2020; Claramunt et al., 2012; Rolland et al., 2014; Salisbury et al., 2012) may also be linked to taxonomic disagreement. Specifically, island endemics with low migratory capacity that depend on forest may be more likely to

diversify genetically and occupy the grey zone. Yet authorities may disagree on whether the genetic, phenotypic or behavioural divergence is sufficient to split a taxon.

In a recent study, McClure et al. (2020) analysed taxonomic agreement in the world's raptor species. They compared four major checklists, restricted to just the birds of prey, and calculated the percentage of taxonomic concepts agreed upon by all authorities. They also investigated variation in agreement between countries and taxonomic families. However, the study did not investigate the ecological correlates of taxonomic agreement, that is, the species-specific traits that could lead to higher or lower levels of agreement between taxonomic authorities. The study was also limited to raptors, which comprise 5.8% of all bird species. In this study, we analyse taxonomic agreement across > 11,000 species of birds, and explore the ecological traits associated with taxonomic agreement across all species.

We first examined the four major world bird lists to assess the levels of taxonomic agreement, and investigated how the level of agreement varies across families and biogeographical regions. Next, we investigated the predictors of taxonomic agreement: latitude, island endemism, body mass, forest dependency, primary diet and migratory status. We hypothesised that agreement would be highest for species that are most readily encountered (Neate-Clegg et al., 2020) and, therefore, studied, that is, large, migratory species from temperate regions with low forest dependency. In contrast, we hypothesised that the species with lowest agreement would be tropical, forest-dependent species, as these are some of the most cryptic and hard-to-study species. By demonstrating which families, regions, and ecological traits are associated with taxonomic discord, we aim to highlight groups of species that should receive more attention from evolutionary ecologists, phylogeneticists, and taxonomists in the future in order to agree upon a single global taxonomy for birds (McClure et al., 2020).

## 2 | METHODS

### 2.1 | Species checklists

In this study we focused on the four most prominent checklists of the world's birds (Garnett & Christidis, 2017), each with its own merits and applications (McClure et al., 2020). The Howard and Moore Checklist of the Birds of the World (hereafter 'Howard and Moore'; Dickinson & Remsen, 2013) was one of the original world bird lists, and is still implemented in museum curations around the world (McClure et al., 2020). The eBird/Clements Checklist of Birds of the World (hereafter 'Clements'; Clements et al., 2019) is the taxonomy followed and curated by the Cornell Lab of Ornithology and it is employed in all of their programs including the global citizen science platform eBird, the multimedia repository Macaulay Library, and the recently created online compendium *Birds of the World* (<http://birdsoftheworld.org>, Billerman et al., 2020), which has taken up the mantle of global bird species descriptions from the *Handbook of the Birds of the World Alive* (HBW; del Hoyo et al., 2019). Pertinent to

conservation scientists throughout the world, the Handbook of the Birds of the World and BirdLife International Digital Checklist of the Birds of the World (hereafter 'BirdLife'; del Hoyo et al., 2019) is the taxonomy curated by BirdLife International, which is used when assessing threat risks to birds for inclusion on the International Union for Conservation of Nature (IUCN) Red List. This taxonomy is also used for other globally important agreements such as the Convention on Migratory Species. All three of these checklists employ the BSC. Finally, the International Ornithological Community (IOC) World Bird List (hereafter 'IOC'; Gill et al., 2020) applies an ESC to species delimitation. These four world checklists differ in many regards and are followed by different scientific journals. They also differ in how regularly they are updated. The IOC checklist is updated biannually, and the Clements and BirdLife lists annually, while Howard and Moore has not been updated since 2014.

In August 2020, we downloaded the IOC World Bird List version 10.2 ('Comparison of IOC 10.2 with other world lists'), which compares several world bird lists. We reduced the dataset to the four world bird lists: IOC v10.2 (updated July 2020), BirdLife v4 (updated December 2019), Clements v2019 (updated August 2019), and Howard and Moore v4.1 (updated 2014). We filtered the results to contain only species, removing subspecies. We removed all extinct species as it can be difficult to assess taxonomic affiliation for these species.

### 2.2 | Assessing taxonomic agreement

In this study we were concerned with the sources of taxonomic 'splits', rather than the results of those splits, and we were interested in the traits that led to disagreement between authorities on what should be split. We thus chose to assign a single taxonomic name to each disputed species split, rather than representing in the dataset each taxonomic concept (*sensu* McClure et al., 2020) or daughter species that resulted from the split. Doing so reduced pseudo-replication in the subsequent analysis. For example, if we were to include all 13 disputed daughter species of *Erythropitta erythrogaster* in the dataset, we would be representing similar ecological data 13 times for one disputed split. In addition, we did not consider name changes, synonymy or differences in spelling (e.g., gender) as disagreements because, even if authorities disagreed on the name, they still agreed on the species' existence.

For every possible species name across the four lists, we assigned a single taxonomic name. When all lists recognised the same species (a full match; Table 1A, Supporting Information Table S1) that species was assigned its own taxonomic name. However, for many species, one or more authorities did not recognise the species (a mismatch; Table 1A, Supporting Information Table S1). Some of these taxonomic mismatches resulted from genuine, recently discovered species (i.e., not resulting from splits) that were not yet recognised by certain authorities (e.g., *Oreotrochilus cyanolaemus*, blue-throated hillstar, discovered in 2017). For those newly discovered species, the mismatch did not arise as a result of a disputed taxonomic split, and

**TABLE 1** Examples of how taxonomic agreement is assessed in this study

A					
IOC 10.2	Clements 2019	H&M 4.1	BirdLife v4	Full match	Taxonomic name
<i>Acanthis flammea</i>	<i>Acanthis flammea</i>	<i>Acanthis flammea</i>	<i>Acanthis flammea</i>	Yes	<i>Acanthis flammea</i>
<i>Acanthis cabaret</i>	<i>Acanthis cabaret</i>			No	<i>Acanthis flammea</i>
<i>Acanthis hornemanni</i>	<i>Acanthis hornemanni</i>	<i>Acanthis hornemanni</i>		No	<i>Acanthis flammea</i>
<i>Loxia pytyopsittacus</i>	<i>Loxia pytyopsittacus</i>	<i>Loxia pytyopsittacus</i>	<i>Loxia pytyopsittacus</i>	Yes	<i>Loxia pytyopsittacus</i>
<i>Loxia scotica</i>	<i>Loxia scotica</i>	<i>Loxia scotica</i>	<i>Loxia scotica</i>	Yes	<i>Loxia scotica</i>
<i>Loxia curvirostra</i>	<i>Loxia curvirostra</i>	<i>Loxia curvirostra</i>	<i>Loxia curvirostra</i>	Yes	<i>Loxia curvirostra</i>
<i>Loxia sinesciuris</i>	<i>Loxia sinesciuris</i>			No	<i>Loxia curvirostra</i>
<i>Loxia leucoptera</i>	<i>Loxia leucoptera</i>	<i>Loxia leucoptera</i>	<i>Loxia leucoptera</i>	Yes	<i>Loxia leucoptera</i>
<i>Loxia megaplaga</i>	<i>Loxia megaplaga</i>	<i>Loxia megaplaga</i>	<i>Loxia megaplaga</i>	Yes	<i>Loxia megaplaga</i>

B		
Taxonomic name	Species represented	Agreement
<i>Acanthis flammea</i>	3	0
<i>Loxia pytyopsittacus</i>	1	1
<i>Loxia scotica</i>	1	1
<i>Loxia curvirostra</i>	2	0
<i>Loxia leucoptera</i>	1	1
<i>Loxia megaplaga</i>	1	1

Note: See text for full names of the checklists (H&M = Howard and Moore). In table A, the four major world bird lists are compared. Where all authorities recognise a species (i.e., full match) the species is assigned its own taxonomic name. Where one or more authorities do not recognise a species, that species is assigned the taxonomic name of the parent species from which it is split. In table B, the number of species that each taxonomic name represents is counted. The taxonomies agree when a taxonomic name represents one species, but disagree when a taxonomic name represents multiple species.

there is no parent species to assign as a taxonomic name, so we assigned the recognised species name as their taxonomic name.

Yet the vast majority of taxonomic mismatches resulted from whether certain authorities recognised a taxon as a subspecies of another species or as a full species in its own right. For example, the four authorities disagree on whether or not the crossbill *Loxia curvirostra* is split into multiple species. IOC and Clements recognise both *L. curvirostra* (red crossbill) and the split *L. sinesciuris* (Cassia crossbill, endemic to southern Idaho), while BirdLife and Howard and Moore do not yet agree on this split, recognizing only one species, *L. curvirostra* (Table 1A). For every case of taxonomic mismatch, we searched for the disputed species in Avibase—The World Bird Database (<http://avibase.bsc-eoc.org>) to determine the parent species from which the disputed split derives. For example, in the case of *L. sinesciuris*, we assigned it the name of the parent species *L. curvirostra*. Once this process was completed, every species had been assigned a taxonomic name, either its universally recognised species name (for full matches), or the name of its parent species (for mismatches). We then tabulated how many times each taxonomic name was represented across the lists (Table 1B, Supporting Information Table S2). For example, *L. curvirostra* was represented twice (once for *L. curvirostra* and once for *L. sinesciuris*) while *L. scotica* (Scottish crossbill) was represented only once.

Where a taxonomic name was represented only once, we assigned a '1', meaning that all authorities agreed on what that name

circumscribed. Where a taxonomic name was represented more than once, we assigned a '0', meaning that at least one authority disagreed on what that name circumscribed. To use the previous example, all four authorities agree on what *L. scotica* describes so it received a 1, but they do not agree on what *L. curvirostra* describes so it received a 0.

After assigning agreement and disagreement to all taxonomic names, we calculated the total taxonomic agreement that is, the proportion of taxonomic names universally accepted across lists. We also calculated agreement by taxonomic family and biogeographical region. Biogeographical region consisted of 19 groups based on classical biogeographical realms or combinations of those realms (Supporting Information Table S3), and these were assigned to each species based on their range maps (del Hoyo et al., 2019). Because the four lists also do not agree on the number and names of the families, we used the IOC family names, as IOC features the most families and is the most regularly updated. However, we also provide an assessment of the agreement of family names across authorities.

### 2.3 | Ecological trait analysis

We analysed how taxonomic agreement varied over several biogeographical and ecological traits. All of these traits were taken from BirdBase, a global trait dataset of the world's birds regularly used

in comparative analyses (see Buechley et al., 2019; Neate-Clegg et al., 2020; Şekercioğlu et al., 2019). We first matched the assigned taxonomic name to a species name in BirdBase. We then identified six variables of interest: latitude, island endemism, log(mass), forest dependency, primary diet, and migratory status. As putative splits tend to have very similar ecologies to their parent species, we assumed that the trait data for parent species also applied to the putative daughter species. Some variables, however, cannot be applied to both parent and daughter species. For example, many daughter species are island endemics (e.g., *Troglodytes beani*, *Pipilo socorroensis*), when their parents are not (*Troglodytes aedon*, *Pipilo maculatus*). For these species, we determined whether or not at least one species name under each taxonomic name was an island endemic, creating a binary variable (yes/no) for island endemism. We also considered using BirdLife's threat status categorization but chose not to as threat status is based on the taxonomic concepts recognised by BirdLife and so cannot be applied to parent species.

Based on latitudinal distribution, we split species into three groups: tropical (species' entire range lies between the Tropics of Cancer and Capricorn), temperate (species' entire range lies outside the tropics) and trans-latitude (species range covers both temperate and tropical regions). As with biogeographical realm, these latitudinal classifications were based on the species range maps (del Hoyo et al., 2019). Migratory status consisted of four categories: full migrant, altitudinal migrant, irregular movements (e.g., nomadic or irruptive), and sedentary. Forest dependency data came from BirdLife International and also consisted of four categories: 'high', 'medium', 'low' and 'non-forest' (Birdlife International, 2020). We had initially also considered a primary habitat variable but the co-occurrence of this variable with forest dependency led to a high variance inflation factor (Zuur et al., 2010).

All analyses were carried out in R version 3.2.4 (R Core Team, 2020). For all taxonomic names, we ran a generalised linear mixed model with a binary response variable (1/0, agree/disagree) and binomial error structure, which contained all six variables of interest as fixed effects. The model also included genus nested within taxonomic family (IOC) as random effects to account for similarities between related species. Once we had created the general model, we used the function 'dredge' from the R package *MuMIn* (Bartoń, 2020) to run models for every possible subset of variables (60 models), to rank those models based on Akaike Information Criterion corrected for small sample sizes ( $AIC_c$ ), and to provide model weights for each model (Burnham & Anderson, 2002). We considered the model with the lowest  $AIC_c$  to be the model best supported by the data, and the ratio between the weight of this model and the weight of the next best model gave the degree of superiority of the best model. We also present summaries of the other competing models within  $\Delta AIC_c < 6$  (Harrison et al., 2018). To compare the importance of the variables among the competing models, we summed the model weights. Finally, we used likelihood ratio tests (LHR) to determine the significance of the categorical variables in the top-ranked model.

As the Howard and Moore checklist has not been updated in several years, it is potentially a large source of taxonomic disagreement

compared to the other checklists, which are updated at least annually. We, therefore, decided to re-run the analyses excluding Howard and Moore, assigning taxonomic names based on mismatches across the three remaining lists (Supporting Information Tables S4, S5). We repeated the modelling process of general model construction and multi-model inference.

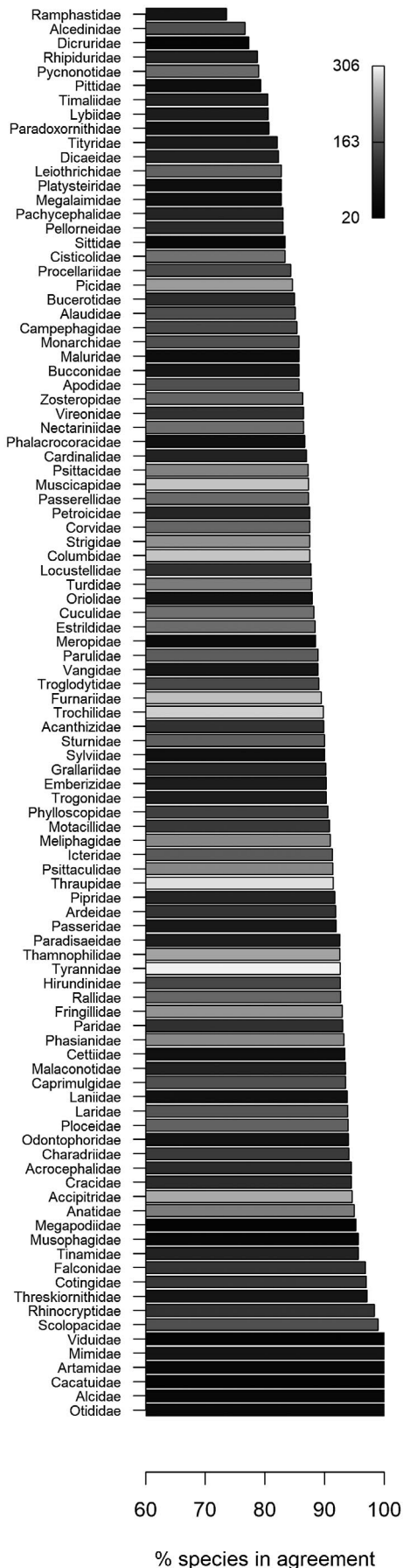
### 3 | RESULTS

Across the four world bird lists, a total of 11,389 extant species names were recognised (Supporting Information Table S1). BirdLife recognised the most extant species (10,988), followed by IOC (10,802) and Clements (10,565), with Howard & Moore recognising the fewest (10,039). Of the 11,389 unique species across the lists, 9,894 were recognised by all authorities (full matches) while 1,495 (13.1%) were mismatches (Supporting Information Table S1). Of these mismatches, 18 were genuine, recently discovered species (i.e., not resulting from splits) that were not yet recognised by all authorities while three were species split from extinct taxa. These 21 species were assigned their own taxonomic name and added to the full matches. Thus, after assigning a taxonomic name to each species, we identified 9,915 taxonomic names (Supporting Information Table S2). Of these names, 8,873 names were assigned to only one species that is, all authorities agreed on what that species circumscribed. The overall taxonomic agreement was therefore 89.5%. The remaining taxonomic names were assigned to anywhere from two to 15 species (median = 2, mean = 2.4). The taxonomic name with the most representation, *Ceyx lepidus*, is a small kingfisher from Southeast Asia recognised as only one species by Howard and Moore but split into up to 15 species by other authorities.

The level of taxonomic agreement varied greatly across families. Of the 99 families containing at least 20 taxonomic names, agreement varied from 100 to 73.5% (Figure 1). Six of the 99 families had 100% taxonomic agreement (Otididae, Alcidae, Cactuidae, Artamidae, Mimidae and Viduidae). The families with the lowest taxonomic agreement included Ramphastidae (73.5%), Alcedinidae (76.7%), Dicuridae (77.3%), Rhipiduridae (78.7%), Pycnonotidae (78.9%) and Pittidae (79.3%). The four authorities also differed in their recognition of family names. IOC recognised the most families (251), followed by Clements (248), BirdLife (242), and Howard and Moore (235). Taxonomic agreement also varied significantly across biogeographical regions. The highest levels of agreement (Figure 2a) were found in the Nearctic (95.1%), Palaearctic (93.5%) and Holarctic (92.9%) regions. The lowest levels of agreement were found in Southeast (69.8%), Southern Ocean (76.2%) and cosmopolitan (76.5%) species.

The top-ranked model based on  $AIC_c$  contained latitude, island endemism, log(mass), forest dependency, and migration (Table 2). This model had a weight of .67, which was over 5 times greater than the next best model, which contained all variables. Across the four competing models within  $\Delta AIC_c < 6$ , latitude, island endemism, and forest dependency appeared in all of the models (Table 2). Across





**FIGURE 1** Taxonomic agreement in birds across the International Ornithological Community (IOC) bird families of the world. Only families containing  $\geq 20$  taxonomic names are shown and they are ordered by level of agreement. Families are coloured according to species richness from the least rich (black) to the most speciose (white)

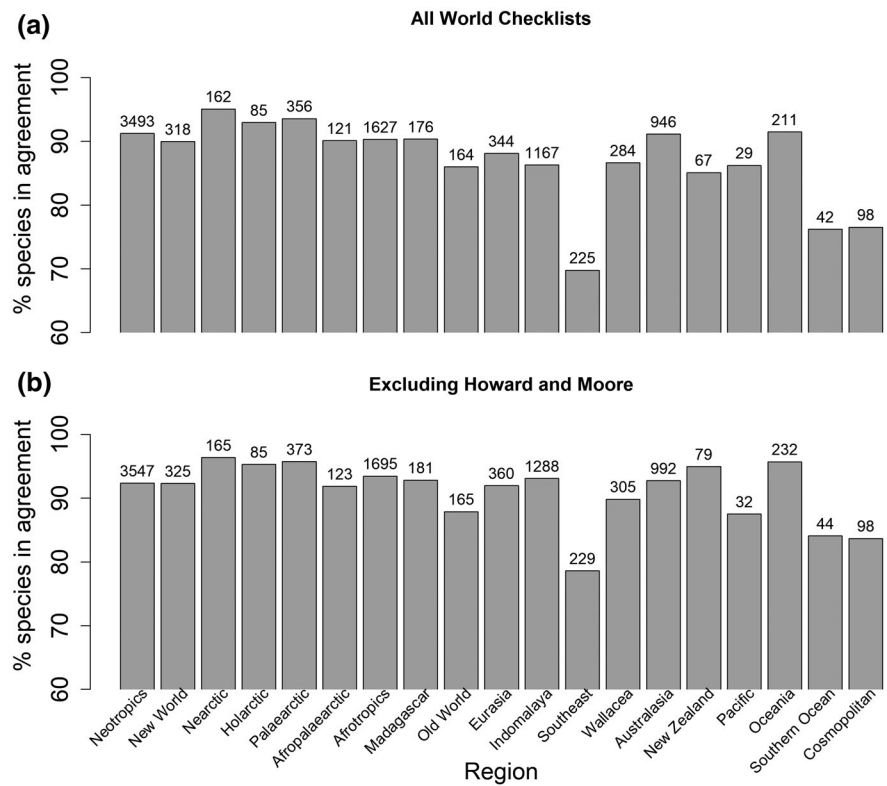
competing models, latitude, island endemism, and forest dependency all had a summed weight of c. 1, while log(mass) had a summed weight of .91, and migration had a summed weight of .89.

Agreement varied significantly by latitude (Figure 3a; LHR:  $\chi^2 = 41.3$ ,  $p < .001$ ) with the highest agreement for temperate species (92.4%) and the lowest for trans-latitude species (87.3%) with intermediate agreement for tropical species (89.9%). Taxonomic names that included at least one island endemic showed lower taxonomic agreement (83.9%) than taxonomic names with no island endemism (91.2%; Figure 3b;  $\chi^2 = 106.1$ ,  $p < .001$ ). The level of agreement increased significantly with body mass (Figure 3c;  $0.073 \pm 0.030$ ,  $t = 2.45$ ,  $p = .014$ ). Taxonomic agreement varied significantly with forest dependency (Figure 3d; LHR:  $\chi^2 = 45.7$ ,  $p < .001$ ) with the highest level of agreement for non-forest species (92.9%) and the lowest agreement for species of medium forest dependency (86.5%). Finally, taxonomic agreement varied significantly with migratory status (Figure 3e; LHR:  $\chi^2 = 9.5$ ,  $p = .023$ ). Full migrants had the highest agreement (90.6%) and altitudinal migrants had the lowest agreement (86.5%).

After dropping the Howard and Moore checklist from the analyses, a total of 11,361 extant species were recognised (Supporting Information Table S4). Of these species, 10,310 were recognised by all authorities while 1,051 had mismatches. We identified 10,318 taxonomic names (Supporting Information Table S5), including seven genuine, newly discovered species that were not yet recognised by all authorities and one species split from an extinct taxon. Of these names, 9,530 names were assigned to only one species, resulting in taxonomic agreement of 92.4%. Thus, removing Howard and Moore increased the level of taxonomic agreement. Of the families containing at least 20 taxonomic names, nine families had 100% taxonomic agreement (Otididae, Alcidae, Threskiornithidae, Cacatuidae, Rhinocryptidae, Artamidae, Mimidae, Passeridae and Viduidae) while the six families with the lowest agreement were Ramphastidae (75.0%), Lybiidae (80.45%), Alcedinidae (83.2%), Pycnonotidae (84.3%), Ptilonorhynchidae (85.0%) and Tityridae (85%).

After exclusion of Howard and Moore, agreement across regions was similar to that when Howard and Moore was included (Figure 2b). The top-ranked model based on  $AIC_c$  contained latitude, island endemism, forest dependency, and migration (Table 3). Another model with very similar support also contained log(mass). The weights of both models were around 50% higher than the weights of the next two models. Across the eight competing models within  $\Delta AIC_c < 6$ , latitude, island endemism, and forest dependency appeared in all of the models (Table 3). Across competing models, latitude, island endemism and forest dependency all had a summed

**FIGURE 2** Taxonomic agreement in birds across regions of the world. Comparisons are made between (a) four global checklists (IOC v10.2, BirdLife v4, Clements v2019, and Howard and Moore v4.1), and (b) the same checklists but excluding Howard and Moore. Numbers above bars show the total number of taxonomic names in each category. See text for full names of the checklists



**TABLE 2** Top-ranked models of the relationship between taxonomic disagreement and species-specific biogeographical and ecological variables for four checklists of the world's birds

Model	df	logLik	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	Weight
latitude + island + log(mass) + forest dependency + migration	13	-3,025.80	6,077.64	0.00	.64
latitude + island + log(mass) + diet + forest dependency + migration	15	-3,025.50	6,081.06	3.42	.12
latitude + island + log(mass) + forest dependency	10	-3,030.57	6,081.17	3.53	.11
latitude + island + forest dependency + migration	12	-3,028.78	6,081.59	3.95	.09
Null	3	-3,124.96	6,255.91	178.27	.00

Note: AIC<sub>c</sub> = Akaike Information Criterion corrected for small sample sizes; logLik = log-likelihood. Models are ranked based on AIC<sub>c</sub> and all models are shown within ΔAIC<sub>c</sub> < 6. We also provide the null model (no fixed effects). For each model we provide the model structure, degrees of freedom, log-likelihood, AIC<sub>c</sub>, ΔAIC<sub>c</sub>, and model weight.

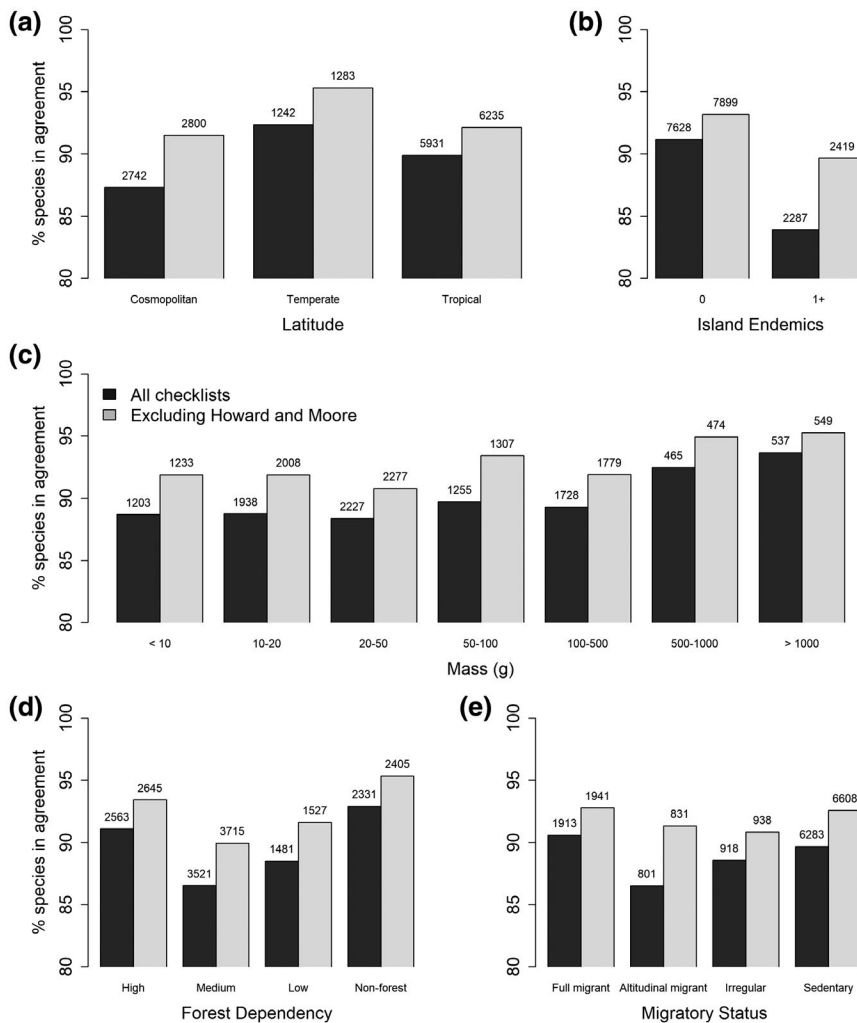
weight of *c.* 1, while migration had a summed weight of .60. The variables contained within the top-ranked model showed similar relationships with taxonomic agreement to the relationships from the results of the analyses including Howard and Moore (Figure 3).

## 4 | DISCUSSION

Birds are one of the best-known classes of organism, yet different authorities still do not agree on what constitutes a species. Across the four major world bird checklists, authorities agreed that 89.5% of taxonomic names represented full species. However, for over a 10th of taxonomic names, the four world checklists did not agree

on whether each name represented one species or multiple species. This may even underestimate finer-scale taxonomic disagreement, for if we had analysed disagreement among daughter species we would likely have found higher rates (McClure et al., 2020), and indeed, of the 11,389 possible species names, 13% were mismatches.

Much of the variation in species recognition could be explained by differing species concepts. BirdLife, Clements, and Howard and Moore all employ the BSC (Mayr, 1942) while IOC uses the ESC (Buechley et al., 2019; Wiley, 1978; Wiley & Mayden, 2000). The BSC places the burden of proof on demonstrating reproductive incapability (Gill, 2014), and, as such, leads to more conservative checklists with fewer species. By contrast, the ESC places the burden of proof instead on demonstrating that species can interbreed successfully



**FIGURE 3** Biogeographical and ecological predictors of taxonomic agreement for the world's birds. The level of agreement was associated with (a) latitude, (b) island endemism, (c) log(mass), (d) forest dependency and (e) migratory status. Numbers above bars show the total number of taxonomic names in each category

**TABLE 3** Top-ranked models of the relationship between taxonomic disagreement and species-specific biogeographical and ecological variables for three checklists of the world's birds (excluding Howard and Moore)

Model	df	logLik	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	Weight
latitude + island + forest dependency + migration	12	-2,515.30	5,054.63	0.00	.27
latitude + island + log(mass) + forest dependency + migration	13	-2,514.36	5,054.76	0.12	.25
latitude + island + log(mass) + forest dependency	10	-2,517.75	5,055.53	0.90	.17
latitude + island + forest dependency	9	-2,518.76	5,055.54	0.90	.17
latitude + island + diet + forest dependency + migration	14	-2,515.19	5,058.43	3.80	.04
latitude + island + log(mass) + diet + forest dependency + migration	15	-2,514.22	5,058.49	3.86	.04
latitude + island + log(mass) + diet + forest dependency	12	-2,517.65	5,059.32	4.69	.03
latitude + island + diet + forest dependency	11	-2,518.71	5,059.45	4.82	.02
Null	3	-2,568.91	5,143.83	89.20	.00

Note: AIC<sub>c</sub> = Akaike Information Criterion corrected for small sample sizes; logLik = log-likelihood. Models are ranked based on AIC<sub>c</sub> and all models are shown within ΔAIC<sub>c</sub> < 6. We also provide the null model (no fixed effects). For each model we provide the model structure, degrees of freedom, log-likelihood, AIC<sub>c</sub>, ΔAIC<sub>c</sub>, and model weight.



(Gill, 2014), and generally leads to the recognition of more species (Agapow et al., 2004; Isaac et al., 2004). Thus, the application of the ESC by IOC could cause disagreement across the checklists even if the three BSC checklists agreed. Until relatively recently, the ESC approach of IOC resulted in the longest of the four checklists (Garnett & Christidis, 2017). However, in the last few years, the BirdLife checklist has jumped ahead to more than 11,000 species (including historically extinct species) as a result of a comprehensive taxonomic review of the world's birds by the organization (BirdLife International, 2016). In addition, McClure et al. (2020) found that in most cases the ESC led to similar species limits as the BSC (particularly between IOC and Clements) and that taxonomic disagreement likely stemmed not from the species concepts themselves, but from how they are applied. These facts alone demonstrate that it is not simply the species concept employed that accounts for variation in species recognition.

Besides the choice of species concepts, the four authorities also differ in how those concepts are applied. For example, the authorities differ in their usage of grey literature and local taxonomic experts (McClure et al., 2020). In addition, BirdLife employs the Tobias criteria (Tobias et al., 2010), which emphasises the importance of phenotypic divergence in putative species splits. As speciation is a continuum (Zachos, 2018), even authorities employing the same species concepts can reach different decisions because of the data available to them and how they weight different lines of evidence (De Queiroz, 2007; Hey et al., 2003). For example, taxonomists that emphasise morphological or acoustic divergence (Tobias et al., 2010) may draw a line earlier in the speciation process, while taxonomists that emphasise reciprocal monophyly (Moritz, 1994) may draw the line later after complete genetic separation (De Queiroz, 2007).

Despite its current use in museum collections around the world, the Howard and Moore checklist stands out as both the shortest (10,039 species), and oldest of the lists, having not received an update since 2014 (Dickinson & Remsen, 2013). In the last 6 years there have been countless taxonomic revisions recognised by the other three checklists and so much of the disagreement between all checklists could, therefore, be ascribed to the outdated Howard and Moore checklist. Indeed, when the Howard and Moore list is dropped from the comparisons, the number of taxonomic names jumped from 9,916 to 10,319, and the level of agreement rose from 89.5 to 92.4%. This result suggests that a least some of the taxonomic disagreement resulted from the lack of updates to Howard and Moore (McClure et al., 2020). The increase in agreement was particularly pronounced for taxonomic names that included at least one island endemic (Figure 3b), suggesting that many of the species that have been split since Howard and Moore's last revision were island endemics. Yet the removal of Howard and Moore clearly still leaves a great amount of disagreement, meaning that, even for checklists that are updated every year, the authorities do not agree on species delimitation. Thus, among the remaining three checklists, disagreement is more likely to be driven by differing species concepts, applications, and criteria (see above).

At the family level, taxonomic agreement varied widely (Figure 1). Of the six bird families (containing  $\geq 20$  taxonomic names) with the lowest taxonomic agreement, five of the families are centred primarily in the Palaeotropics, particularly Southeast Asia. Similarly, the Southeast region (a region comprising combinations of Indomalaya, Wallacea, Australasia and New Zealand; Supporting Information Table S3) received the lowest agreement compared to other regions (Figure 2). Southeast Asia has produced a great amount of taxonomic upheaval in recent years (Andersen et al., 2013; Brown et al., 2013; Irestedt et al., 2013; Sánchez-González & Moyle, 2011; Shakya et al., 2020). In particular, many species spread across archipelagos have been split by some authorities. Islands are a good example of how differing species concepts and applications can lead to taxonomic discord, and we found that taxonomic names that included at least one island endemic tended to have lower agreement (Figure 3b). It is impossible to test whether allopatric populations on different islands can reproduce to produce fertile young and many of them are phenotypically very similar (Gill, 2014), and yet many of these populations have been genetically isolated from one another for millions of years (Andersen et al., 2013; Irestedt et al., 2013), forming distinct, reciprocally monophyletic evolutionary lineages. These genetic lines of evidence have only recently become available to taxonomists.

In addition to the Southeast region, species in the Southern Ocean also had lower levels of taxonomic agreement (Figure 2a). Again, this disagreement results in part from the number of islands spread distantly across the ocean, which leads to potential population differentiation, and this result is corroborated by the importance of island endemism in the models. But rather than small forest birds, these islands are characterised by their seabirds, particularly Procellariiformes, Spheniscidae and Phalacrocoracidae. Many of these seabirds are far-ranging over thousands of kilometres (Phillips et al., 2007), contrasting with the low dispersal ability of tropical forest species (Sheard et al., 2020). However, high natal philopatry (Austin et al., 2004; Friesen, 2015; Munro & Burg, 2017), geographical isolation (Friesen, 2015), and oceanic currents (Clucas et al., 2018) promote low gene flow between populations. The isolation of these species, despite similar phenotypes, predisposes them to taxonomic uncertainty, and also makes them difficult to study (Munro & Burg, 2017).

Elsewhere around the world, taxonomic agreement was highest in the temperate Northern Hemisphere (Nearctic, Palearctic and Holarctic regions; Figure 2a), which makes sense for two reasons. First, research is biased towards temperate regions (Feeley et al., 2017; Harris et al., 2011; Rosenzweig et al., 2008; Titley et al., 2017) and so there has been more opportunity to determine species limits. With more data and evidence available for temperate species, uncertainty in species delimitation is reduced (Hey et al., 2003), making taxonomic agreement more likely. Second, temperate species differ in many ways from tropical species that would lead to lower potential for cryptic speciation. In particular, tropical species have lower dispersal ability (Sheard et al., 2020)

and are more ecologically specialised than their temperate counterparts (Salisbury et al., 2012), which, coupled with dispersal barriers and competition, leads to high levels of allopatric speciation (Pigot & Tobias, 2013; Shakya et al., 2020) and cryptic diversity (Brown et al., 2013). Cryptic diversification can make it difficult to delimit species. The path to speciation includes changes in genetics and phenotype, and the extent to which different lines of evidence are valued could lead to discrepancies in species limits among taxonomic authorities. In contrast, the low diversity of temperate regions makes that diversity easier to quantify and understand.

The level of taxonomic agreement increased significantly with body mass, particularly for species > 500 g (Figure 3c). Large species are less numerous making taxonomic agreement more likely. Larger species are also easier to observe and study, reducing taxonomic uncertainty (Hey et al., 2003). Additionally, body size is correlated with lower diversity (Maurer et al., 1992) and linked to other life-history and ecological traits that produce low diversification rates in general. For example, large body size is associated with increased longevity (Valcu et al., 2014), smaller clutch sizes (Jetz et al., 2008), larger home ranges (Haskell et al., 2002), larger geographical ranges (Maurer et al., 1992) and reduced plumage dichromatism (Dale et al., 2015). These factors may interact in complex ways to inhibit diversification rates (Harvey et al., 2017; Owens et al., 1999), and lower diversification rates likely reduce the number of taxa occurring within the 'grey zone' of species divergence (De Queiroz, 2007).

The results for forest dependency and migratory status contained expected and unexpected outcomes. For example, the results supported our hypotheses that taxonomic agreement would be higher for non-forest or migratory species (Figure 3d,e). Like larger-bodied species, species of open habitats are easier to study (Hey et al., 2003) and tend to have higher dispersal ability (Pinto-Ledezma et al., 2017; Sheard et al., 2020; White, 2016), which inhibits lineage divergence. Open habitats also have fewer opportunities for niche partitioning (MacArthur & MacArthur, 1961; Pinto-Ledezma et al., 2017; Tews et al., 2004). Similarly, migratory species have wide ranges (Blackburn, 1996), with greater potential for gene flow (Arguedas & Parker, 2000; Pruett et al., 2008) and lower opportunity for cryptic speciation (Claramunt et al., 2012; Rolland et al., 2014), although migratory species can act as evolutionary sources of sedentary species (Gómez-Bahamón et al., 2020; Rolland et al., 2014). Migrants also spend their breeding season in temperate regions, particularly in the Northern Hemisphere, where most research takes place. Thus, a combination of positive research bias and lower levels of lineage divergence reduces the taxonomic uncertainty in migratory birds of open habitats (Hey et al., 2003).

For the opposite of these reasons, we expected taxonomic agreement to be lowest for sedentary species that are highly dependent on forest. Yet, while we found that agreement was indeed lower for these groups than for non-forest migrants, the lowest agreement was actually for altitudinal migrants with medium forest dependency. Species with medium forest dependency have, by

definition, an intermediate dependence on forest. Similarly, altitudinal migrants are somewhat intermediate in migratory syndrome between full migrants and sedentary species; they migrate, but over very short distances. Our results may, therefore, support the theory that intermediate dispersal ability leads to higher rates of diversification (Ashby et al., 2020; Claramunt et al., 2012) whereby sufficient dispersal capability is required to colonise new areas but not so much dispersal ability that gene flow prevents speciation. The greatest potential for cryptic lineage differentiation may, therefore, occur in lineages with intermediate forest dependence and intermediate mobility. These are species that are most likely to undergo intermediate levels of lineage divergence, with more taxa occurring in the 'grey zone' (De Queiroz, 2007), and more potential for taxonomic disagreement as different authorities apply different criteria to reach delimitation decisions.

Taken together, our results highlight two important and interrelated facets of taxonomic discord: factors driving divergence rates and factors affecting research bias. Taxonomic disagreement is higher in the understudied tropics and thus this study follows others (Harris et al., 2011; Sheldon, 2019; Titley et al., 2017) in encouraging more tropical research. Specific regions that should be the focus of taxonomic attention include Southeast Asia and the Southern Ocean. In order to reduce taxonomic uncertainty (Hey et al., 2003), more attention should be given to small-bodied, island species with medium-to-high forest dependency that undergo altitudinal migration or irregular movements. These biogeographical and ecological traits point to areas of research that could lead to taxonomic revision and reconciliation (Mace, 2004; McClure et al., 2020). As anthropogenic change continues, it is more important than ever to reach taxonomic agreement so that critical species, habitats and regions receive appropriate levels of conservation (Agapow et al., 2004; Hazevoet, 1996; Peterson, 2006; Sangster, 2000; Thomson et al., 2018).

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## AUTHOR CONTRIBUTIONS

MHCNC conceptualised and designed the study. MHCNC, JDB and ÇHŞ collected and curated the data. MHCNC performed the analyses and wrote the first draft. ÇHŞ supervised the project and provided intellectual insights. All authors contributed substantially to revisions.

## DATA AVAILABILITY STATEMENT

We provide all data on taxonomic mismatches as Supporting Information (Tables S1, S2, S4, S5).

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## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section.

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