THE SPATIAL AND TEMPORAL CHANGES OF FUNCTIONALLY RARE LANDBIRD SPECIES IN NORTH AMERICA RELATIVE TO URBANIZED AREAS

by

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ABSTRACT

THE SPATIAL AND TEMPORAL CHANGES OF FUNCTIONALLY RARE LANDBIRD SPECIES IN NORTH AMERICA RELATIVE TO URBANIZED AREAS

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Human population growth is believed to be the cause of the current mass extinction event across many taxa, mediated through degradation of natural habitats. This loss of habitat is related to land-use change as human population growth typically leads to intensifying urbanization, which, in turn, negatively affects biodiversity. The value of biodiversity cannot be underestimated since it ensures stable ecosystem functioning and a steady supply of ecosystem services. This relationship is best described in terms of the functional diversity concept which states that species within biological communities vary in the redundancy of their functional roles and provides a framework to quantify the value of these taxa based on species traits. Predicting the effects of human-borne disturbances on functional diversity in communities is essential and allows one to highlight those species in greatest need of conservation for the sake of ecosystem functioning.

In the work presented here, I analyzed data from the North American Breeding Bird Survey and eBird covering Canada, the United States, and Mexico from 2000 to 2021, combined with data on 23 functional traits, to calculate regional rarity and functional distinctiveness of 680 breeding bird species. I found that functional distinctiveness and numerical rarity of species were related such that rare species tended to be functionally distinctive and their loss was expected to disproportionately affect functional diversity.

Functional distinctiveness and numerical rarity can be combined in a metric of the functional rarity of communities. Functional rarity is distributed unevenly across the continent, and there are clear hotspots that indicate communities in the greatest need of conservation. The functional rarity of North American breeding birds has increased across North America over the past two decades. Moreover, this increase was more likely to occur in urbanized areas, implying that urban disturbance invokes a form of environmental filtering and causes functional

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eradication in biological communities. These findings suggest more attention to the conservation of urban ecosystems is sorely needed.

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To my beloved Aksyniia who did not let me give up.

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The data used in this thesis were collected by thousands of citizen scientists — participants of the North America Breeding Bird Survey and eBird. This work is based solely upon their effort, their thousands of hours spent in the field, and the hard work of the teams that maintain these marvelous and huge endeavors.

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INTRODUCTION

Anthropogenically induced global change, a multifaceted and sophisticated set of phenomena (Daily et al. 1994, Ehrlich and Ehrlich 2009, Carpenter et al. 2009), has led to rapid biodiversity loss manifested by habitat change and fragmentation (Brooks et al. 2002), invasions of exotic species (Galiana et al. 2014), overharvesting (Jackson 2001), climate change (Bálint et al. 2011, Harley 2011), and pollution (McLaughlin and Mineau 1995, Geiger et al. 2010). An outcome of population growth has been increasing urbanization, an outward expansion of cities that is an ongoing process which drives habitat loss and converts land cover into impervious surface (Seto et al. 2012) and negatively affects properties of biological populations (Moll et al. 2019, Murray et al. 2019), communities (McKinney 2006), and whole ecosystems (Li et al. 2019). Ecological communities associated with urban areas are thought to be novel in their composition relative to natural communities, leading to urbanized biological populations possessing altered behavioral, physiological, and morphological traits (Grimm et al. 2008a). The effects of urbanization might go even deeper because of associated creation of areas required to maintain urban population of humans (i.e., agricultural conversion) that are not impervious themselves but pose a threat to biodiversity attributed to homogenization, fragmentation, and loss of suitable habitats (Daily et al. 2001, Ricketts et al. 2001). Further intensification of urbanization is expected to reduce diversity in biological communities (Aronson et al. 2014, La Sorte et al. 2018) and increase rates of species extinction (Czech et al. 2000, Shochat et al. 2010, Fattorini 2011) making the effects of global change on biota even more devastating. In fact, the current mean rate of vertebrate species loss is approximately two orders higher than natural background rates (Ceballos and Ehrlich 2002); populations of terrestrial vertebrates are estimated to show 25% decline in abundance and invertebrates — 45% since the pre-industrial era (Dirzo et al. 2014); as of 2004, 23% of vertebrate species, 57% of invertebrate species, and 70% of plant species evaluated are threatened with extinction (Baillie et al. 2004), and many of these species are not likely to survive the present century (Pimm et al. 1995).

The role of extinction in shaping ecological communities is obviously one of the main factors determining the composition of these communities. For example, classical theories of community assembly processes, such as MacArthur-Wilson's equilibrium theory of island biogeography, treat species richness as a function of local extinction rates along with

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colonization rates, and community composition is thought to be determined by the equilibrium between these two processes; from this perspective, if an observed species richness is an equilibrium point between the flow of colonizing species into an island of suitable habitat and extinction of species due to disturbance and interspecific interactions, then, with all else being equal, an increase in extinction rates will result in a rapid decrease of species richness (MacArthur and Wilson 1963, Simberloff and Wilson 1969). The global extinction rates caused by human influence are much higher than natural background rates — often labeled as the "extinction crisis", or the "sixth mass extinction" (Brooks et al. 2002, Ceballos and Ehrlich 2002, Wake and Vredenburg 2008, Ceballos et al. 2015) — could cause more than a simple turnover in species composition, but a rapid loss of taxonomic, functional, and phylogenetic diversity, alterations in biogeochemical properties in ecosystems, and, consequently, malfunctions in ecosystem functioning (Naeem et al. 2012) with a further decline in ecosystem services provided to humans (Ehrlich and Mooney 1983).

Ecosystem Functioning and Services

The concept of ecosystem services, defined as "conditions and processes through which natural ecosystems, and the species that make them up, sustain and fulfill human life" (Daily 1997, p. 3) (Table 1), is often useful for the purpose of illustrating the importance of ecosystem functioning to the general public, although it is considered to be less relevant to ecologists and more meaningful to economists (Toman 1998). Ecosystem services are typically classified into provisioning (e.g., food, fibers, genetic resources, biochemicals, fresh water), regulating (e.g., air quality, climate, water, erosion, disease, pests, pollination), supporting (e.g., soil formation, primary production, nutrient and water cycling), and cultural services (recreation, education, aesthetics) (Wallace 2007). Ecosystem functioning can be viewed from a variety of perspectives relative to the utilitarian value to humans: from ecosystem benefits that directly affect human well-being through the use of ecosystem goods (e.g., food) and services (e.g., waste elimination) that are estimated to have a monetary value twice as big as the world's overall gross national product (Costanza et al. 1997), down to ecosystem processes and functions that occur irrespective of human benefit and may or may not produce associated goods and services (La Notte et al. 2017). While ecosystem services are often taken for granted, the future human population growth and associated global change will likely cause a decrease in accessibility to

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Table 1. Operational definitions of the major terms used

Term	Definition and reference
Biological diversity	variability in communities and ecosystems (Hubbell 2001, Magurran 2004)
Community	a group of species that occur in space and time and have similar resource requirements (Chesson 2000, Begon et al. 2006)
Disturbance	a factor that causes temporary and localized shifts in demographic rates and may potentially cause a reduction in biomass (Grime et al. 1987, Mouillot et al. 2013)
Ecosystem functioning	a sum of ecosystem processes, i.e., physical, chemical, and biological transformations of matter and energy involving organisms and their interactions with other organisms and the environment (Scherer-Lorenzen et al. 2022)
Ecosystem services	conditions and processes through which natural ecosystems, and the species that make them up, sustain and fulfill human life (Daily 1997)
Functional distinctiveness	characteristics of a species having traits dissimilar from those of other species in the community (Violle et al. 2017)
Functional divergence	characteristics of a community which relates to the overall species deviance from the average trait value within a community (Villéger et al. 2008, Mouchet et al. 2010)
Functional diversity	the value and range of functional traits of the organisms present in a given ecosystem (Díaz and Cabido 2001)
Functional rarity	feature of a species that integrates both functional distinctiveness and taxonomic scarcity at the local scale, or both functional uniqueness and taxonomic restrictedness at the regional scale (Violle et al. 2017)
Functional trait	any trait which impacts fitness indirectly via its effects on growth, reproduction and survival (Violle et al. 2007)
Local scale	a scale within one community (Violle et al. 2017)
Numerical rarity	a feature of species with low abundance in terms of its biomass, number of individuals, or occurrence (Violle et al. 2017), having a low abundance or range size relative to other species (Gaston 1994)
Rarity	the feature of a species that implies its uniqueness relative to other species
Regional scale	a scale of metacommunities and/or regional pool of species (Violle et al. 2017); the boundaries of regions defined here correspond to the bird conservation regions (Sauer et al. 2003)
(Species) trait	any phenological, morphological, physiological, reproductive, or behavioral characteristic of an individual that can be assigned to a species (Kissling et al. 2018)
Taxonomic diversity	a measure of species composition in terms of both the number of species and their relative abundances (Legendre and Legendre 1998)
Urban gradient	an abstract ordering of changes in land cover, land use, and human activity caused by urbanization (Cadenasso et al. 2006)

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common benefits (Cazalis et al. 2018, Roy et al. 2018) mediated through biodiversity loss (Mace et al. 2012). Native ecosystems are more effective than restored ones (Benayas et al. 2009), so extinction of species and degradation of ecosystems should be avoided to allow for stable supply of ecosystem services (Ehrlich and Mooney 1983). It is less detrimental to preserve the integrity of an ecosystem than to restore it both in terms of economic value and ecosystem functioning.

The concept of ecosystem services and ecosystem functions may leave a misleading impression that ecosystems exist and function for human well-being (Schröter et al. 2014). Rather, ecosystem services and goods are the direct byproducts of ecosystem processes, such as primary production, decomposition, pollination, soil formation, nutrient cycling, etc. (Truchy et al. 2015). Ecosystem functioning has many facets, which all seem to be an outcome of biological diversity. For example, primary biomass is strongly and positively related to plant taxonomic diversity (Hector et al. 1999, 2011, Hooper et al. 2005, Tilman et al. 2012, 2014). Increasing plant diversity (Oelmann et al. 2007) and maintaining the natural state of ecosystems (Likens et al. 1970) are also accompanied by higher nutrient retention and clean water supplies. Finally, high community diversity ensures resistance to invasion by exotic species (Fargione and Tilman 2005) that can cause massive economic losses (Pimentel et al. 2005). Yet, ecosystem functioning is much more complex and includes a variety of ecosystem processes much than what is typically considered such as productivity, nutrient retention, stability, and invasibility (Mittelbach and McGill 2019).

Rarity in the Context of Biological Diversity

There is no doubt in the value of biodiversity for ecosystem functioning and, therefore, for human well-being (Engelhardt and Ritchie 2001, Balvanera et al. 2006, Brockerhoff et al. 2017), therefore, conservation of biological diversity is an important issue (Randall 1991). From a purely ecological perspective, the diversity of ecological communities is a function of the distribution of species abundances within communities — one of the most universal and oldest of ideas in ecology (Magurran 2004). Phenomenological descriptions of species abundance distributions were firstly provided by Motomura in 1932 (Whittaker 1972) as a geometric series of decreasing species abundances. Other classic species abundance models included log-series and lognormal models. Log-series models implied that the most common abundance class was observations of single individuals, or singletons, with every next abundance class following a

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simple reducing log-series (Fisher et al. 1943). Lognormal models, instead, implied that species of intermediate abundance classes were the most common, if viewed on a logarithmic scale of species abundance (Preston 1948, 1962a, 1962b). Species abundance modeling received a lot of attention in the second half of twentieth century, yielding a variety of models (McGill et al. 2007) that explained observed patterns via random processes (MacArthur 1957, 1960) or more sophisticated mechanisms (Tokeshi 1990, 1993, 1996, Hubbell 1997, 2006, McGill and Collins 2003, Volkov et al. 2003), but the most striking observation was that both empirical distributions and models had one particular feature in common (Kunin and Gaston 1993, McGill et al. 2007, Chase 2013): some species are abundant, but the vast majority is rare (Magurran 2004). In fact, biological diversity is often quantified using prevalence of rare species in communities, which is reflected in numerous diversity metrics based on the distribution of species abundances (Mendes et al. 2008, Hubbell 2013, Kondratyeva et al. 2019).

The prevalence of rare taxa within biological communities is the very reason for the vulnerability of biological diversity to abnormally increased extinction rates since rare taxa are more likely to go extinct (Terborgh 1974, Courchamp et al. 2006). Moreover, some species may be considered to be "functionally extinct" even if there is a viable population, meaning that a population size is under some threshold that will likely lead to extinction in other taxa (Säterberg et al. 2013). Similarly, species populations may continue existing due to delayed effects of habitat destruction — so-called extinction debt — although their extinction is only a matter of time (Tilman et al. 1994, Jackson and Sax 2010). Since the current extinction crisis threatens biological diversity globally, it also threatens ecosystem functioning, hence, ecosystem goods and service supply. The primary question is, therefore, how to mitigate the devastating effects of global change on rare taxa and subsequent biodiversity loss.

One might suggest that the ecological effect of rare species is negligible compared to abundant taxa, thus, rare species might not necessarily be expected to be integral to ecosystem function. For example, the mass ratio hypothesis posits that the productivity of an ecosystem is mainly determined by dominant taxa so that rare taxa are not required for stable ecosystem functioning (Díaz et al. 2003, Pakeman et al. 2011); moreover, an excess in number of taxa may even destabilize entire ecosystems (May 1972, Putman 1994) — an assumption based on properties of multivariate mathematical systems. The mass ratio hypothesis has several caveats that do not allow one to simply dismiss the importance of rare taxa in favor of dominant species.

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For example, the hypothesis was originally formulated for plants that typically occupy a single trophic level as opposed to animal taxa that differ in their position within a trophic web. Indeed, there are top-predators that can shape an entire ecosystem even though their abundance is low due to the loss of energy when biomass flows between trophic levels (Elton 1927, Simberloff 2012, Trebilco et al. 2013). Such so-called keystone species have effects on the community that are disproportionately large relative to their abundance (Paine 1966, 1969, 1980, Power et al. 1996). Keystones are hardly predictable by species-level traits, their roles are rather context-dependent (i.e., community composition, location, environmental productivity) and often determined by their position in a food web or via removal experiments (Menge et al. 1994, Power et al. 1996, Berlow et al. 2004, Jordán 2009). In any case, the definition of keystone species tentatively implies rarity relative to biomass — as opposed to dominant taxa whose effects on ecosystems may be explained simply by their high abundance defined within the mass ratio hypothesis (e.g., trees, grasses, corals) (Power et al. 1996).

Rarity, however, does not always necessarily mean being prone to extinction. Rabinowitz (1981) separates seven forms of rarity based on habitat specificity, geographic range, and population size. The fossil record suggests that geographic range size played the primary role in the extinction of many taxa, and local abundance had little effect on extinction risk (Harnik et al. 2012). Some taxa may be rare due to high levels of specialization (Harcourt et al. 2002, Swarts et al. 2010) (i.e., a narrow ecological niche may result in a lower likelihood that a habitat is suitable), but this mechanism is not upheld for every case (Williams 2005).

Ecological Niche

An ecological niche can be defined as the set of requirements needed for a species to survive in a given environment (Chase and Leibold 2003). Such a definition might be considered oversimplified, given the breadth of classical and contemporary definitions.

The Grinnellian niche consists of a set of environmental conditions necessary for species existence, while a species morphology, physiology, and behavior may be explained by adaptation to the environment (Grinnell 1917, James et al. 1984). The Grinnellian approach is particularly useful for species distribution modeling because it connects environmental space (i.e., a set of tolerable values of environmental parameters) and geographic space (i.e., a set of suitable areas) (Peterson 2003, Peterson et al. 2011): as an example, the term was first suggested

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by Grinnell to explain the restricted range of the California Thrasher *Toxostoma redivivum* as a function of the distribution of Chaparral plant associations to which the bird is adapted by having strong feet and legs, short wings, ability to run, non-conspicuous plumage, and nests located within dense foliage (Grinnell 1917). Because of the temporal variability in habitat requirements, the shape of a niche is not fixed and can change depending on context (Soberón and Peterson 2020). If, however, environmental conditions change more quickly than a species can adapt, niche tracking can occur, when species follow limiting environmental boundaries through geographic space to remain in favorable conditions (Tingley et al. 2009).

The Eltonian perspective, however, views the niche as a position of a species within a trophic web (Elton 1927, Whittaker et al. 1973), which may be useful in identifying keystone species, particularly in so-called "wasp-waist" ecosystems where there are few species linking trophic levels (Jordán 2009). The original definition of an Eltonian niche as the role that a species plays in a community might be considered vague, and even with modern development of food web, the data required to construct an Eltonian niche are scarce and thus one might need to examine similar taxa as a proxy to understanding niche space (Peterson et al. 2011, Dehling and Stouffer 2018).

The Hutchinsonian niche views a species as an *n*-dimensional hypervolume (Hutchinson 1957) on axes of biotic (or bionomic) and abiotic (or scenopoetic) variables (Hutchinson 1978, Soberón 2007). Hutchinson suggested that a niche can be divided into fundamental (i.e., pre-interactive space describing the fundamental requirements of a species when isolated from interspecific competition) and realized niche (i.e., the component that accounts for the limitations of a fundamental niche due to species interactions, primarily, competition).

Contemporary perspectives of niches are typically a composite of Grinnellian, Eltonian, and Hutchinsonian concepts. For example, Chase and Leibold (2003) incorporate resource-ratio theory (Tilman 1980) to link Grinnellian and Eltonian perspectives: within this paradigm, a niche is not only the set of requirements, but also an effect of species on resource availability and environment. Another example of the development of the niche concept is the BAM-model, which states that area occupied by a species lies within an intersection of biotic (B) and abiotic (A) conditions that result in positive population growth rate, and movement realm (M) (i.e., area available for dispersal). The approach distinguishes (i) fundamental niche, where population growth rate can be theoretically positive due to suitable abiotic conditions, (ii) potential niche,

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where a species can coexist with other taxa but may not occur everywhere due to geographical constraints, and (iii) realized niche – sites where a species does occur directly (Soberón 2007). The BAM-model also suggests that a realized niche may be larger than fundamental because of source-sink dynamics (i.e., dispersal of individuals into areas with conditions that do not allow the local populations to have a positive population growth rate) (Pulliam 1988, 2000, Holt 2009).

A species' niche can be described as a set of trait values coding abiotic environmental conditions for modeling a Grinnellian niche, which is commonly used in making predictions on geographic distribution of suitable habitats (Elith et al. 2011) or organism-/species-level traits (Table 1) related to the biology of species, which is more common within a Hutchinsonian perspective (Hutchinson 1959). Among a plethora of traits that can be applied to describe a species, functional traits are the most informative, meaning a characteristic of species which "impacts fitness indirectly via its effects on growth, reproduction and survival" (Violle et al. 2007). In terms of functional traits, a niche can be then defined as a "region of the functional space containing all the trait combinations displayed by the individuals of a species" (Carmona et al. 2016). Functional traits are expected to be useful as parameters, thresholds, or estimations in a dynamic system model of energy and mass exchange between organisms and environment (Kearney et al. 2021). In other words, functional traits must be related to resource utilization and interspecific effects, therefore affecting ecosystem functioning.

Differences in functional traits among species, their niches, and, thus, resource consumption, are a key to understanding the mechanisms behind the role of diversity in ecosystem functioning and stability. The effect of taxonomic diversity on productivity can be explained by the fact that if species differ in their phenology, physiology, nutrient or habitat requirements (i.e., have different niches) and there is a large number of species for a complementarity among niches to result in a broad community niche, then niche complementarity is expected to lead to more efficient resource use by the community as a whole (Fig. 1) (Fargione et al. 2007, Marquard et al. 2009, Blüthgen and Klein 2011, Kühsel and Blüthgen 2015). Ecosystem stability, on the other hand, may be ensured because of the portfolio effect: a diversity of species that fluctuate with time independently of each other due to differential response to temporal environment variability are more likely to yield a stable temporal trend in productivity merely because of an overlap in random deviations of productivity of single species (Tilman et al. 1998). If species niches overlap considerably, community

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stability may result because of an inherent redundancy (i.e., if one species goes extinct, another will replace it with similar function (Fig. 1)) (Miñarro and García 2018). Another possible explanation to observed patterns is the sampling effect, whereby higher diversity increases the probability that one of the species will be highly productive (Aarssen 1997, Huston 1997). The sampling effect has been shown to be at play in early stages of community development (Cardinale et al. 2007). Both niche complementarity and sampling effect imply that high diversity determines high productivity, although the latter does not highlight the importance of differences in species niches (Fig. 1).

It is still unclear if functional traits alone can be used to predict a species effect on ecosystem functioning. On the one hand, those traits that are associated with interspecific relationships may be used to identify keystone species (Libralato et al. 2006). On the other hand, values of such traits are difficult to obtain and require labor-intensive removal experiments or data on food web structure. An early definition stated that a keystone is, in fact, a single-species functional group (Bond 1994, Jordán 2009), so that one would make a vague prediction that functionally distinctive species (i.e., dissimilar from other species in a community based on a combination of traits (Violle et al. 2017)) are vital for ecosystem functioning. Some authors (e.g., McGill et al. 2006) have even suggested that functional traits could be used to predict community structure, and there is limited evidence that functional distinctiveness may determine rarity or abundance of taxa (Baastrup-Spohr et al. 2015, Umaña et al. 2017). Such relationship could also have been predicted from niche theory (i.e., specialists are expected to have lower abundance, see Umaña et al. 2017).

Rare Species and Ecosystem Functioning

The role of rare species in ecosystem functioning may be not limited to some of them being keystone species — indeed, only a minor fraction of species within communities can be considered keystone (Power et al. 1996). Even given the common misuse of the label “keystone species” wherein the term is applied to rare, dominant, charismatic, or flagship species despite not adhering to the classic definition (Piraino and Fanelli 1999), every taxa, whether rare or not, cannot be considered as keystone. It does beg the question of whether rare taxa that are not keystone are still important to communities.

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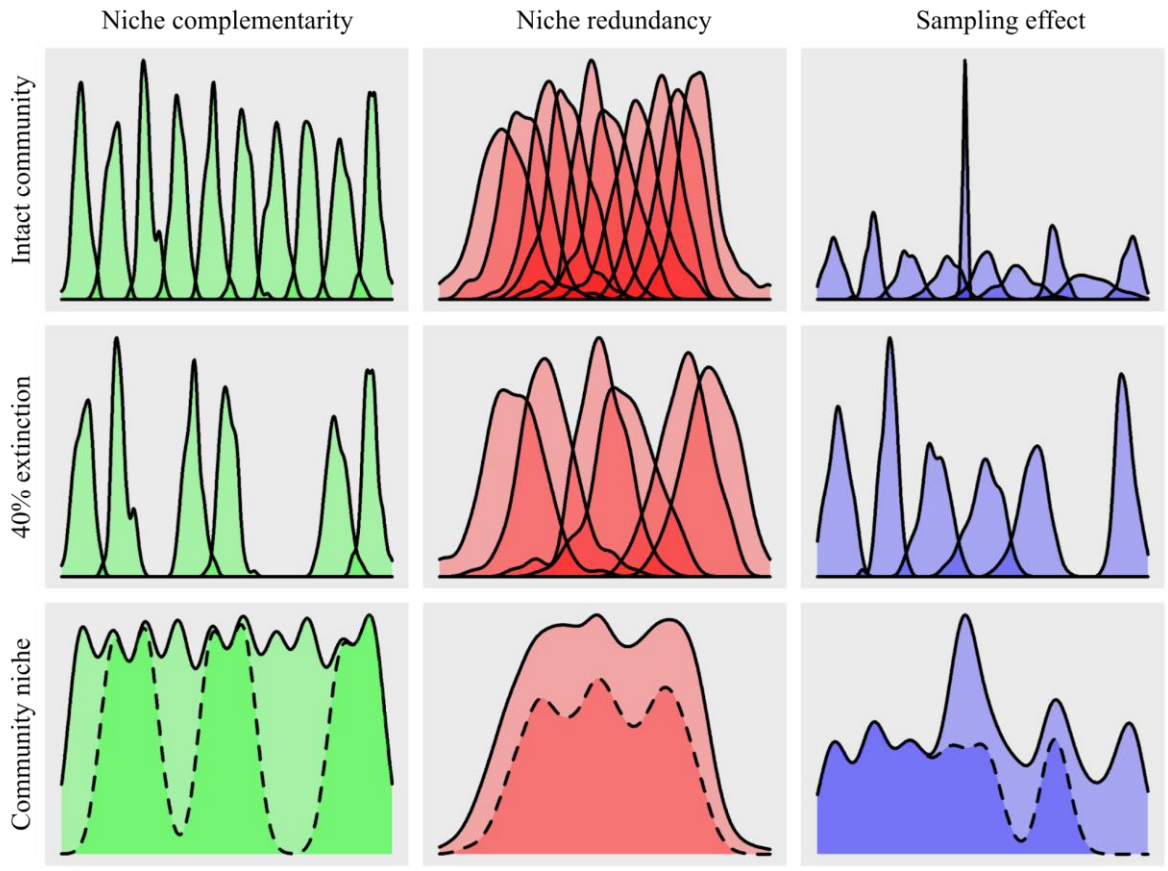

Fig. 1. A conceptual model of extinction effect on resource use by a community under different scenarios: niche complementarity, niche redundancy, and sampling effect

Rarity itself is also not clearly defined. Although the meaning of rarity may seem intuitively obvious, it is not easy quantify rarity (Gaston 1994). While some authors define rare species as singletons (Novotný and Basset 2000), this might be a poor practice because it is susceptible to sampling bias: the number of observed singletons depends on the completeness of a sampling effort (Longino et al. 2002). An alternative approach would be to define species as rare depending on abundance rank (i.e., being in the lower quartile) within a distribution of values reflecting their numbers, such as abundance, biomass, or occurrence etc. (Gaston 1994). A more modern approach would be to base rarity of a species on the probability of being assigned to a cluster of rare or abundant species by a clustering algorithm (Balbuena et al. 2021). Almost all approaches define rarity within a dichotomous rare/abundant framework, usually based on a

definition of rarity as having a low abundance or range size relative to other species (Gaston 1994).

Rarity of species may also be related to the interaction of a species' life history and environmental conditions (Flather and Sieg 2007, Vellak and Ingerpuu 2007), though there is an paucity of studies addressing the ecological causes of species rarity. The connection between rarity and niche properties can be made through the fact that due to niche differentiation, two coexisting species are extremely unlikely to have identical niches (MacArthur and Levins 1967, Schoener 1974, Stubbs and Bastow Wilson 2004), therefore, a given set of environmental conditions will likely have different suitability for each member of a community, leading to variation in abundance and, consequently, rarity of some of the species within this community (McGill and Collins 2003).

Neutral models of community composition, although, predict that the majority of species will be rare without any assumption on niche difference: for example, MacArthur's broken-stick model yields a species-abundance curve similar to an empirical one based only on an assumption that resource partitioning among species occurs randomly (MacArthur 1957, 1960). Hubbell's unified neutral theory (Hubbell 1997, 2001), moreover, is capable of yielding even more realistic species-abundance curves based on an assumption of a random replacement of dead individuals and slow speciation in a community irrespective of species niche differences. From the perspective of neutral models, the rarity of species may be nothing more than an outcome of stochastic processes rather than a function of particular species traits.

Whether species rarity is related to niche or not, two species with very similar habitat requirements cannot coexist. Thus, diversity within ecological communities implies a diversity of species requirements (Hutchinson 1959, 1961). If environmental conditions shift, as in the case of global change, individual taxa may change geographic distribution (Tingley et al. 2009). At the level of communities and ecosystems, however, it also suggests that a dominant species may not be favored by a new suit of environmental conditions. The observations of fluctuations in community structure may support this hypothesis: for example, while rare species tend to be good colonizers, go extinct and recolonize local ecosystems, common species vary in abundance with time much less (Henderson and Magurran 2014). One likely explanation for this pattern, in my opinion, is that environmental conditions often vary around a point suitable for a set of

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abundant species whereas rare species never become abundant since they are in suboptimal conditions or even go extinct when these conditions fall out of their tolerance limits.

When there is a considerable disturbance, environmental conditions may approach an optimum for some rare species in a community, in which case such species may increase their abundance following a decrease in dominant species (that at this point face unfavorable conditions) ensuring the stable functioning of an ecosystem. Rare species provide an insurance effect (Yachi and Loreau 1999): in a moment in time or point of space, only a few species are in their ecological optimum while other — rare — species are in their zones of stress or intolerance but may turn out to be significantly valuable to ecosystem functioning when conditions change and other species move away from their optimum. The community and, thus, ecosystem are expected to be resistant to disturbances due to the insurance effect (Yachi and Loreau 1999). Moreover, given that there is a constant dispersal of community members among ecosystems and consistent spatial variability in disturbance, some communities may act as sources of species that can replace less adapted to disturbances species in disturbed ecosystems, which would buffer and maintain ecosystem functioning as well (Loreau et al. 2003).

Community resistance, i.e., the strength of perturbation needed to shift a community to a different configuration (Pimm 1984), seems to be extremely dependent on biological diversity. There are three main hypotheses of ecosystem functioning response to disturbances: (i) the rivet-redundancy hypothesis associated with the niche redundancy hypothesis suggests that initial community composition is redundant to some extent so that there is some buffer for disturbance that does not affect ecosystem functioning up to some threshold despite loss of species through extinction (Ehrlich and Ehrlich 1981); (ii) the proportional decline hypothesis consistent with niche complementarity suggests that a drop in ecosystem functioning is a linear function of species extinction (Loreau and Hector 2001, Loreau et al. 2001); and (iii) the facilitative hypothesis suggests that a small change in diversity will lead to a catastrophic drop in functioning attributed to facilitation among species (Cardinale et al. 2002, Flather and Sieg 2007). The rivet-redundancy hypothesis is the most apparent of the hypotheses (Cardinale et al. 2011), suggesting that there is some redundancy in species functioning within ecosystems that, up to some limit, allows some taxa to go extinct without a considerable decrease in the ability of ecosystems to function properly (Fig. 1). From this perspective, rare taxa emerge to be vital for

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ecosystem conservation because their preservation, especially those that perform non-redundant, unique roles, ensures ecosystem functioning and supply services (Dee et al. 2019).

Effect of Disturbances on Ecosystems

It should thus be clear that ecosystem functioning can vary with respect to responses to species extinctions mediated through disturbance events. But the effect of disturbance on species diversity may differ as well. In fact, disturbance, to some extent, can promote diversity, which is known as the intermediate disturbance hypothesis (Grime 1973, Connell 1978). If one defines disturbance as a factor that causes reduction in biomass (Grime et al. 1987), there is a threefold effect of disturbance on biodiversity: low disturbance levels allow the dominant species to outcompete other taxa, high disturbance cannot be tolerated by the majority of species, whereas intermediate disturbance levels limit the competitive abilities of good competitors which allows efficient colonizers to coexist with competitors and results in an overall highly diverse community (Chesson and Huntly 1997, Townsend et al. 1997). Yet, the intermediate disturbance hypothesis has been a subject to criticism since the limited support of it seems to be context-dependent (Mackey and Currie 2001, Shea et al. 2004, Bongers et al. 2009, Fox 2013).

Urbanization can be considered a disturbance. At the landscape level, urbanization causes land use shifts towards developed, impervious areas (Morse et al. 2003, Antrop 2004, Alig et al. 2004, Grimm et al. 2008b), which is less suitable for wildlife than intact natural areas, mainly due to habitat loss and pollution. Additionally, urbanization causes habitat fragmentation (York et al. 2011), having deleterious effects on biodiversity as well due to a decrease in habitat availability (Fahrig 2003). Effects of habitat fragmentation, though, are not straightforward because of the complexity of the concept: fragmentation as a "process during which a large expanse of habitat is transformed into a number of smaller patches of smaller area isolated from each other by the matrix of habitats unlike the original" (Fahrig 2003, p. 490) is associated with patch isolation and habitat loss, a primary cause of population declines and species extinction (Taylor et al. 1993, Bender et al. 1998), whereas fragmentation *per se* may cause habitat heterogeneity that makes a landscape suitable for a variety of species up to some limit (Fahrig 1997, Fahrig et al. 2011). At a smaller scale, urbanization acts as a disturbance, causing a decrease in primary productivity and resource availability (Li et al. 2019), toxification by pollutants, and high exposure to parasites (Morse et al. 2003, Murray et al. 2019).

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The effect of urbanization, as is any kind of disturbance, on ecosystem functioning may be unclear: on the one hand, it can promote diversity due to the intermediate disturbance effect, but on the other hand, it can decrease diversity because of increased extinction rates. In the case of urbanization, it seems to not be feasible to globally exclude the cause of disturbance (i.e., human population growth) for the sake of conservation (Holdren and Ehrlich 1974, Six et al. 2004, Ehrlich and Ehrlich 2009). This does not mean the inevitability of decline in global biodiversity and ecosystem functioning, though, since urban areas may have a potential for conservation by themselves (Tratalos et al. 2007, Shwartz et al. 2014, Chamberlain et al. 2019, Dubovyk et al. 2020), particularly if species of conservation concern are adapting to urban disturbances (Partecke and Gwinner 2007). The areas affected by urbanization outside of developed areas are critical to maintaining the urban areas, i.e., countryside, has also been shown a great potential for conservation (e.g., as source habitat for urban populations) suggesting that there is a hope for biological diversity in the face of global change (Daily et al. 2001, Ricketts et al. 2001, Horner-Devine et al. 2003).

Taxonomic and Functional Diversity

To measure the effects of disturbances on biological diversity, one would first need to define diversity in this context. In the diversity of definitions (DeLong 1996, Kaennel 1998, Magurran 2004), biological diversity *sensu lato* is "the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic systems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems" (Heywood 1995, p. 8). In a more strict and quantitative definition, biological diversity is related to species richness and relative species abundance in a community (Hubbell 2001, Magurran 2004, Mittelbach and McGill 2019). A community itself refers to a group of species that occur in space and time (Begon et al. 2006), although the definition (Table 1) implies that these species are limited to a group of phylogenetically related taxa with similar resource requirements (Chesson 2000, Mittelbach and McGill 2019), often referred to as an "ensemble" (Fauth et al. 1996). Legendre and Legendre (1998) define biological diversity as a combination of two parameters, referring to the number of species and the shape of the species abundance distribution. They define it as "a measure of species composition in terms of both the number of species and their relative abundances [...], a synthetic biotic index which captures

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multidimensional information relative to the species composition of an assemblage or a community" (Legendre and Legendre 1998).

With regards to the above-mentioned relationship between ecosystem functioning and urbanization, there is a question how to quantify both. Urbanization effects are often studied within the context of an urban gradient, a nebulous concept due to the lack of a standard definition of urbanization as an ecological rather than social phenomenon (Warren and Lepczyk 2012, Moll et al. 2019). Urbanization effects are mediated through habitat loss, land cover change, and habitat fragmentation, so that it makes sense to quantify the urban gradient in terms of land use, e.g., amount of impervious surface within some area (Morse et al. 2003). Ecosystem functioning, on the other hand, refers to a plethora of processes and a facet chosen to quantify it depends strongly on a part of an ecosystem that is being investigated. One would argue that biological diversity might be a useful proxy to ecosystem functioning, based on both phenomenological observation of correlation between the two (Hooper et al. 2005, Tilman et al. 2014, Truchy et al. 2015, Weisser et al. 2017) and the strong theoretical framework that connects them mechanistically (Yachi and Loreau 1999, Loreau and Hector 2001, Cardinale et al. 2002, 2007, Loreau et al. 2003, Scherer-Lorenzen et al. 2022). From this perspective, it seems justified to infer the effect of urbanization on ecosystem functioning in a fashion similar to how the effects of urbanization have been examined relative to biological diversity.

The most common approach to quantifying diversity is through the use of indices based on species abundance. Other than simply reporting the number of species in a community (i.e., species richness), Shannon's and Simpson's indices are the most popular methods among ecologists (Gorelick 2006), although there are dozens of other measures (Legendre and Legendre 1998, Magurran 2004). Shannon's index is highly biased by sample size (Peet 1974) and should be standardized by species richness (Pielou 1975, Magurran 2004). The information yielded by this index is vague when applied to ecological communities (Camargo 2008). Similar criticism can be found toward virtually any diversity index (Peet 1974, Smith and Grassle 1977, Gamito 2010), which suggests that the whole concept of diversity measures is useless: "the term 'species diversity' has been defined in such various and disparate ways that it now conveys no information other than 'something to do with community structure'" (Hurlbert 1971). Yet, these measures of taxonomic diversity are extensively used, likely, mainly due to their convenience and simplicity of calculations.

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Taxonomic diversity measures are based on the notion of species (or other taxa) being discrete categories of organisms. Such an approach ignores taxonomic identities and the fact that taxa comprising a community vary in their functional roles and evolutionary history (Jarzyna and Jetz 2016). In other words, a hypothetical set of individuals composed of a plant, a fungus, and an animal would have the same taxonomic diversity as a set of individuals from one taxonomic family of birds as long as the respective ratios of species abundances are the same. This implies that measures of taxonomic diversity lead to a loss of information regarding the functional and phylogenetic characteristics of a community (Safi et al. 2011, Cardoso et al. 2014), making any inference based on taxonomic diversity metrics limited.

An alternative way to measure diversity is to incorporate functional or phylogenetic components. Functional diversity is the variety of functional traits of the organisms that occur in an ecosystem (Díaz and Cabido 2001). A focus on functional facets of diversity rather than taxonomic can reveal more general rules of community assembly (Mittelbach and McGill 2019). The most primitive estimation of functional diversity, analogous to species richness for taxonomic diversity, would include the number of functional groups defined as sets of organisms having similar responses to the environment and similar effects on ecosystem functioning (Díaz and Cabido 2001). This quantification would critically depend on identities of groups chosen and their number, which makes diversity of functional groups biased and uninformative (Petchey and Gaston 2006). Multidimensional mathematical methods have been useful in more informative measurement of functional diversity, assuming that species or individuals can be viewed as points in a multidimensional space of functional traits (Carmona et al. 2016), resulting in a variety of metrics (Cadotte et al. 2011, van der Plas et al. 2017). Among these, three major independent facets of functional diversity are most commonly used: functional richness, functional evenness, and functional divergence (Mason et al. 2005, Villéger et al. 2008). All three require quantifying species-level functional distinctiveness (Table 1), i.e., the degree to which a species or individuals are similar or differ from other community members (Carmona et al. 2016). From this perspective, functional diversity is a diversity of species ecological niches.

Functional richness relates to the range of functional characteristics observed in a community to reveal the amount of functional space occupied by organisms within a community (Carmona et al. 2016), which relates to the maximum width of a community niche (Fig. 1). Functional richness can be quantified as a convex hull volume (Cornwell et al. 2006) to show the

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range of functionally marginal species but it does not account for relative position of proximal species within a multidimensional trait space. Functional evenness relates to the pattern of species distribution within a multidimensional space, irrespective of whether it is uniform or clumped (Ricotta et al. 2014). This facet is usually measured by sum of cluster tree branch lengths weighted by species abundance (Villéger et al. 2008, Mouchet et al. 2010). This measure is ambiguous in its ecological interpretation (i.e., what does a clumped or even distribution imply?) and there is some evidence of inconsistency in metric values (Gaëlle and Jean-Claude 2018).

Functional divergence (Table 1) refers to the degree to which the abundance in functional trait space of the organisms composing a community is distributed toward the extremes of its functional volume (Carmona et al. 2016). It is calculated as a function of mean functional distinctiveness of each species within the community (Villéger et al. 2008, Mouchet et al. 2010) and shows how far, on average, species are in trait space from a community centroid — an abstract hypothetical species that represents the community niche — implying the range of ecological functions and environmental conditions under which a community can function properly. Functional divergence is the metric that relates most strongly to the characteristics of individual species.

From the perspective of a functional diversity framework, species may vary in functional redundancy, a property with important implications for conservation management. If two species face the same threat of extinction, one might be interested in which species needs more intensive conservation effort, given that resources for conservation are limited and it may be not feasible to preserve every species (Wilson et al. 2006). In most scenarios, the most unique species would be preferred, since redundant taxa are presumed to be less valuable and unique species provide more benefits to ecosystem functioning (Jain et al. 2014, Leitão et al. 2016, Jousset et al. 2017, Dee et al. 2019). This idea is incorporated into the framework of functional rarity (Table 1) to aid in identifying the species that possess the most unique combinations of functional traits, species that are most vulnerable to extinction based on scarcity of abundance (Grenié et al. 2017, Violle et al. 2017). Using such metrics, one may choose to prioritize taxa whose protection is expected to result in the greatest protection of rapidly declining biological diversity and functioning of ecosystems.

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Avian Communities as a Model System

Understanding functional diversity requires not only accurate data on species abundances but also acknowledges the variability of species detectability (Palacio et al. 2020). It also involves the need for a complete dataset of species trait values that can be used for determining functional distinctiveness (Lavorel et al. 2008). To study the effects of urbanization on functional diversity, one requires the species abundance dataset distributed across an urban gradient, and trait data available for the complete suite of taxa. Both criteria are often met when studying birds.

Avian communities are convenient subjects for a study of the effects of urbanization on biota (Marzluff 2016): at least 20% of all bird species and 70% of all bird families are found in and around cities, including many taxa in decline (Fernández-Juricic and Jokimäki 2001). Generally high species diversity among climate zones and the ability to detect birds readily makes them a practical suite of taxa for testing theoretical ecological principles with relatively large datasets (Lennon et al. 2001, Petchey et al. 2007). Data on avian assemblages have been used extensively to test global changes such as land cover shifts on ecological communities (Newbold et al. 2015). Birds are also important components of ecosystems and are often associated with seed dispersal, primary productivity, nutrient cycling, and trophic interactions (Cooke et al. 2019, Loiseau et al. 2020). The diversity of birds often covaries with diversity of other taxa (Kati et al. 2004, Toranza and Arim 2010, Tisseuil et al. 2013), suggesting to some extent that birds may be used as indicators of hotspots of diversity that can be prioritized for conservation (Reid 1998).

The availability of data on avian species abundances and distribution in developed countries is mostly possible because of birding — a common hobby of lay citizens where they observe birds recreationally (Sekercioglu 2002, Callaghan et al. 2021, Randler 2021, Squires et al. 2021). As of 2016, there were 45 million birders in the U.S. alone, according to the U.S. Fish and Wildlife Service (https://www.census.gov/library/publications/ 2018/demo/ fhw-16-nat.html). It makes volunteers the most important source of data on biodiversity (Roy et al. 2012). Nowadays, there are large-scale bird population monitoring schemes running thanks to the tremendous efforts by volunteers worldwide (Hagemeijer et al. 1997, Newson et al. 2005, Jiguet et al. 2005, Kéry and Royle 2009, Doxa et al. 2010). These datasets are a great example of the power of a citizen science approach, which means collecting, categorizing, transcribing, and/or analyzing data collected by citizens that are not classically trained as scientists (Bonney et

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al. 2014). There are a few national-wide bird survey programs in the U.S., such as Audubon Christmas Bird Count (Niven et al. 2004, Butcher et al. 2005, Meehan et al. 2019) and the United States Geological Survey's Breeding Bird Survey (Sauer et al. 2003, Ziolkowski et al. 2010, Sauer and Link 2011, Link et al. 2017, Sauer et al. 2017b) that have been collecting data for decades, as well as state-level atlas projects (Ankori-Karlinsky et al. 2022).

Such programs are examples of structured citizen science projects with defined objectives, strict survey designs, and rigorous data collection protocols, that may discourage potential participants and limit the amount of data collected (Kelling et al. 2019). There is an even bigger potential in data-intensive citizen science projects that emphasize collecting as much of data as possibly (Kelling et al. 2009, Hochachka et al. 2012). eBird (https://ebird.org/home) is a good example of a data-driven project: a platform for birders to report and view observation records (Sullivan et al. 2009, 2014, Johnston et al. 2021). The semi-structured design of data-driven citizen science allows scientists to control the quality of data, sampling effort, and environmental conditions by filtering observations that meet certain criteria without putting such constraints on citizen observers (Kelling et al. 2009, 2019, Hochachka et al. 2012). This approach has allowed eBird to amass (as of 17 February 2022) a database that contains over 63 million observations of 10,624 bird species submitted by over 739,000 observers. Such publicly available datasets allow one to test a variety of ecological questions at large spatial scales.

Effects of Urbanization on Avian Communities

Some of the features associated with increasing urbanization and its effects on avian communities are well known. For example, an increase in overall abundance but a decline in species richness has been described (Marzluff et al. 2001, MacGregor-Fors et al. 2012). On the other hand, there is a lack of knowledge about the drivers and mechanisms of such changes. Studies are typically conducted as case studies of particular cities and, thus, it is unclear whether patterns observed can be drawn more generally for other cities (Beissinger and Osborne 1982). For example, the presence of human-provided resources in urban ecosystems can explain the abundance of avian and mammal predators, which also shapes the abundance of prey that may include taxa that are particularly vulnerable to nest predation (Stracey and Robinson 2012). Such nest predation may favor larger taxa, those that can defend nests against predators, or smaller taxa that may have more cryptic nests. Such findings tend to be idiosyncratic and have not

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resulted in an overarching consensus among studies (Kaisanlahti-Jokimäki et al. 2012, Stracey and Robinson 2012). Besides influencing predator numbers, urbanization also alters the ratio of functional groups of birds (Petchey et al. 2007, Marzluff and Rodewald 2008, Rodewald 2012, Aronson et al. 2014, Marzluff 2016, Galewski and Devictor 2016) to such an extent that some species associated with urban locations have significantly increased in abundance over the last few decades (Sauer and Link 2011). This finding implies that by investigating changes of functional rarity, one could determine underlying mechanisms responsible for changes in avian community structure that are driven by increasing urbanization.

Additional resources available in urban ecosystems may be one of the most important factors shaping avian communities, since a resource in general (i.e., a factor that leads to higher population growth rates with increasing availability and which is consumed by a population (Tilman 1980)), are the baseline terms upon which competition, coexistence, niche differentiation and many more ecological concepts are based. Life in cities clearly offers a supply of some critical resources for birds, such as additional food (Anderies et al. 2007, Foltz et al. 2015) and nesting sites (Blewett and Marzluff 2005, Tella et al. 2014, Tomasevic and Marzluff 2017).

Besides the passive availability of resources associated with cities, humans actively engage in feeding birds intentionally. At first glance, it might appear to benefit avian populations, especially in winter when food is scarce and critical for survival given low temperatures (Robb et al. 2008). The amount of resources that humans provide to birds is enormous: the Americans alone are estimated to feed 450 million kg of seeds annually (Jones and James Reynolds 2008). Such supplementary feeding can result in maladaptive shifts in diet, mainly a lack of vitamins and microelements, resulting in developmental defects that are potentially lethal for birds (e.g., angel wing deformations associated with eating bread (Zsivanovits et al. 2006)). Another potential harm from feeding birds is that bird feeders constitute hubs of infectious disease transmission (Brown and Hall 2018). For example, bird feeders are thought to be responsible for outbreaks of finch trichomonosis, Paridae pox, passerine salmonellosis, and mycotoxin poisoning (Lawson et al. 2018). Even when supplementary feeding decreases winter mortality, it causes high competition and subsequent lack of resources for chicks during the breeding season (Jansson et al. 1981, Plummer et al. 2015), and improper nutrient balances may jeopardize egg laying (e.g., the “junk-food hypothesis” states that consuming easily available food may turn out

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to be a reason for lower reproductive success (Grémillet et al. 2008)). Supplementary feeding is also biased towards particular taxa, and may favor invasive species, causing shifts in community structure that may result in local extinction (Galbraith et al. 2015) and a subsequent decrease in species richness (Oro et al. 2013). Supplementary feeding can also lead to increased predation pressure as well, given that bird feeders can become zones of attraction to potential predators because of the locally high density of prey (Hanmer et al. 2017) and increasing probability of finding a nest (Selva et al. 2014). Finally, availability of supplementary food may select for beak morphology associated with extracting food from feeders and remaining in temperate areas with supplementary resources rather than migrating seasonally (Plummer et al. 2015).

There is a price to be paid for the benefits of urban life: high resource abundance is often associated with high rates of air and soil pollution. Industrial and transport emissions result in high concentrations of potentially harmful heavy metals (Scheifler et al. 2006, Coeurdassier et al. 2012, Meillère et al. 2016, Birnie-Gauvin et al. 2016). Constant noise pollution is another factor that disrupts behavior and reproduction that relies heavily on vocal cues, causing changes in bird songs with potential effect on reproductive success and community structure (Nemeth and Brumm 2009, Francis et al. 2009, 2011, Ciach and Fröhlich 2017, Duquette et al. 2021). Artificial light is another source of pollution that has significant costs for birds because behavioral patterns of many species are associated with light levels throughout the day and season (Kempenaers et al. 2010, Dominoni 2015, Raap et al. 2017). Yet, it remains unclear to what extent these factors introduce stressors to birds associated with urban environments (Bonier 2012, Rebolo-Ifrán et al. 2015).

Overall, urbanization seems to act as a strong environmental filter that favors specific species within a regional pool. Those taxa that have higher competitive ability for abundant resources and an ability to adapt to the threats associated with living in an urban environment, such as increased predation, disease, toxicity, stress, light and noise pollution. There are groups of species that vary in their ability to survive within urban environments (e.g., urban avoiders, suburban adapters, and urban exploiters), and the question is whether urbanization results in changes in functional diversity associated with particular functional traits (Croci et al. 2008, Pennington and Blair 2012, Rodewald 2012). The line of evidence suggests that urban disturbance does lead to a decrease in functional diversity (Devictor et al. 2007, La Sorte et al. 2018, Palacio et al. 2018, Matuoka et al. 2020), which is expected when species richness

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responds to levels of disturbance in a hump-shaped curve as predicted by the intermediate disturbance hypothesis (Mouillot et al. 2013). Though there are, however, studies that have demonstrated that urbanization promotes functional diversity because of increases in habitat diversity (Oliveira et al. 2018), patterns of functional diversity are inconsistent among different urban locations (Morelli et al. 2021).

Summary

Global biodiversity is under threat because of human population growth and subsequent global changes. Despite the natural resilience of ecosystems, their functions are particularly vulnerable to disturbances, population declines, and species extinction. Any change in ecosystem functioning will likely result in a reduction of ecosystem services, which in turn puts humans at greater risk.

Functional diversity can be used as a predictor of important ecosystem processes to reveal unique, functionally rare taxa that one cannot afford to lose. Functional rarity has the potential to bridge theoretical ecology and applications in conservation biology to maximize the benefit of conservation management relative to ecosystem functioning. In the context of limited resources for conservation and the increasing threat of global change, finding spatial hotspots of functional rarity could be used as a powerful tool for decision making and optimizing current and future efforts.

Purpose of the Study

This study aimed to reveal the spatiotemporal patterns of functional rarity in avian communities across continental North America. Functional rarity was calculated for avian communities correcting for variation in species detection probabilities. Such data allowed me to calculate functional distinctiveness of each species using a database of species functional traits, and functional rarity as a function of species functional distinctiveness and numerical rarity.

Given the complex nature of both urban disturbance and functional rarity, it is not obvious what the relationship is between the two, if any. If urbanization acts as an environmental filter, trait variation is expected to be lower in urban areas, so that there will be lower mean local and regional functional distinctiveness of species comprising a community. On the other hand, habitat fragmentation associated with urbanization may promote habitat diversity and increase

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the range of functional traits in a community, having a totally opposite effect. Therefore, the shape of relationship between functional rarity and urbanization is unknown and requires investigation (Fig. 2).

There were three main objectives in this study:

1) *To develop a means to identify functionally rare taxa and the communities within which they are found*. Functional rarity, as an indicator of value of a species to ecosystems, does not always reflect conservation rarity derived simply from geographical range and abundances. The International Union for Conservation of Nature (IUCN) status, which is derived from range and abundance data does not always correspond to functional rarity, as some taxa can have high functional value yet be labeled as a species of Least Concern or with non-evaluated status (Loiseau et al. 2020). An important caveat is that functional rarity is related more to the importance of ecosystem functioning rather than to the risk of extinction. Global conservation assessment schemes typically highlight assessment scores relative to population size, geographic range, or population trends. A positive correlation between functional distinctiveness and abundance rarity would imply that protection of rare taxa automatically leads to preservation of unique species traits, which would support the use of assessments like IUCN status.
2) *To identify spatial hotspots of functional rarity and their distribution throughout the urban gradient*. Because current conservation efforts are driven by metrics of rarity associated with abundance and spatial extent, there has been limited study of hotspots relative to ecologically important taxa. Functionally rare species are not distributed evenly but, instead, have distinct hotspots, areas with high conservation value (Loiseau et al. 2020). This implies that hotspots of functional rarity could serve as areas of more concentrated focus, given their limited scope and conservation importance.
3) *To determine if the spatial distribution of hotspots of functionally rare bird species have changed relative to land cover changes associated with increasing urbanization during the last 20 years*. If bird species composing avian communities are gradually adapting to urban disturbances, one could expect changes in the overall relationship between functional rarity and urban land cover. The relationship between rates of change in land use and corresponding change in the structure of bird communities could be used to determine the overall effect on functionally rare species and the value of urban areas for conservation.

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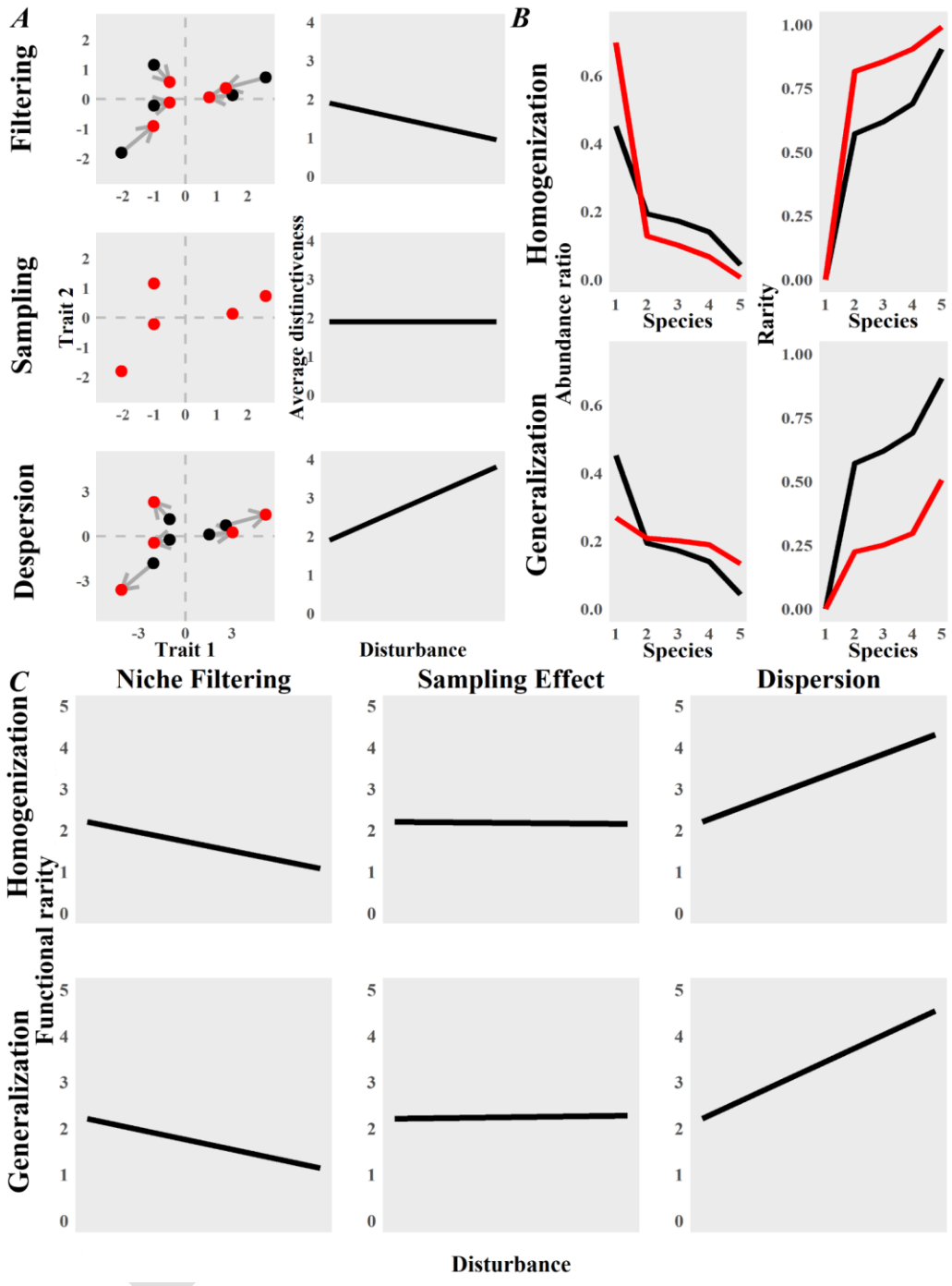

Fig. 2. Potential responses of functional rarity to a disturbance (C) under different assumptions on (A) effect of the disturbance on functional diversity (niche filtering, sampling effect, or dispersion due to habitat heterogeneity) and (B) species abundance distribution (homogenization, or higher dominance, and generalization, or higher evenness); red color denotes changes after the disturbance

A PRIMER OF QUANTIFICATION OF FUNCTIONAL DIVERSITY AND RARITY OF SPECIES

The design of data analysis was based on two separate datasets: community structure and species functional traits. Community structure refers to abundances of species comprising a community, with data on species counts extracted from two data sources: the North American Breeding Bird Survey (hereafter BBS) and eBird. The data filtered from one dataset were limited by the other and vice versa: the BBS data used in this project were limited to the period of 2000–2021 because eBird data was consistently collected after 2000 (Fig. 3). BBS program consists of standardized surveys with strict sampling rules, so that the data from the semi-structured eBird dataset were filtered to correspond to the BBS sampling scheme. Given that these two sources utilize different taxonomies, they were converged into a unified taxonomy for this project defining 703 taxa. For each of these species, the data on 23 functional traits related to the effects of a focal species on other species and surrounding habitat comprised the second dataset. The two datasets combined provided the means to reveal the patterns of functional diversity and rarity across North America.

Dataset on Species Abundances

The dataset on species abundances was used to describe the taxonomic composition of avian communities: each observation was a combination of relevant metadata (location and date of an observation) and a vector of species abundances extracted from both the BBS and eBird datasets.

The species identities were not consistent among the datasets: BBS used the taxonomy approved by the 60th supplement to the American Ornithological Society's checklist of North American birds (Chesser et al. 2019), whereas eBird used the Clements checklist (August 2021 update) of Birds of the World approved by the American Birding Association (Clements 2007). These two taxonomies may or may not recognize some species as subspecies or vice versa: BBS (AOS) taxonomy includes 757 separated taxa, among which there were 669 species and 15 subspecies considered in this project, and there were 713 species with overall 1,988 subspecies recognized by eBird in North America.

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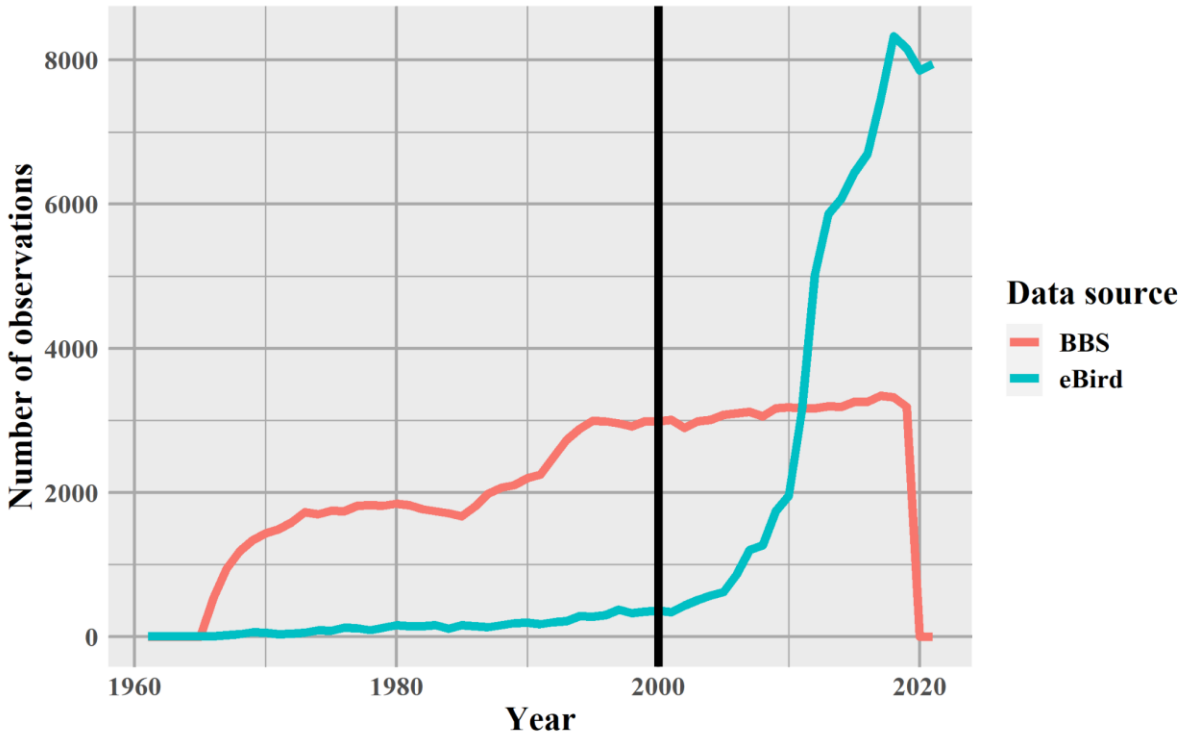

Fig. 3. The numbers of observation events in Breeding Bird Survey and eBird datasets in North America since 1960, the black line denotes the time range of present study

To deal with this issue, I merged both datasets into 703 unique taxa (Fig. 4, Appendix A) based on the species list used in the BBS with additions related to the fact that the BBS species list is relevant mainly for the continental U.S. and Canada — species that occur in Mexico but do not occur within the U.S. were taken from Ehrilch et al. (1988). Data from Central America (Belize, Costa Rica, El Salvador, Guatemala, Honduras, Nicaragua, and Panama) were not considered in this study because of the lack of consistent data on species occurrences in these regions (Ramírez-Albores et al. 2021).

Each observation was accompanied by the following metadata: latitude and longitude of starting point of each census (coordinate system WGS 1984, decimal degrees), date of an observation, location identifier in an original source, location identifier within the whole project, source dataset, and bird conservation region (see below). Unique project location identifiers were assigned to groups of points within 0.1 degrees, which corresponds to approximately 2 km at 81° N and 11 km at 15° N. Non-species taxa (i.e., so-called “slash” taxa — when an observer was not

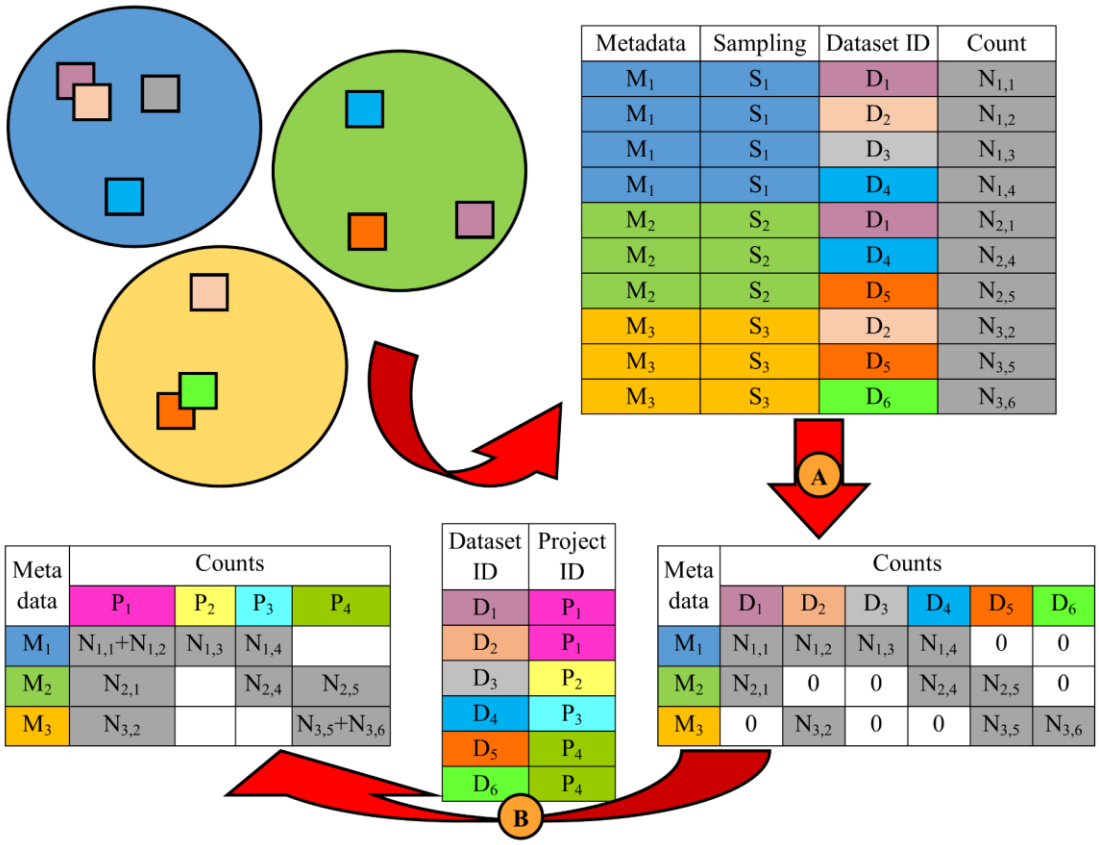

Fig. 4. Workflow of operations leading to the transformation of a species abundances dataset into community structure data (A) and reduction of subspecies taxonomic categories (B)

sure of a species identification and provided the information on possible species identities) and hybrids were ignored.

Breeding Bird Survey Data

BBS has been conducted every year since 1966 (except 2020 due to the global pandemic) on fixed 39.4 km (24.5 mi) routes that are supposedly selected at random among secondary roads of each state or province (Boulinier et al. 1998b). Typically, the surveys are conducted during June, although late May is acceptable in southern regions and early July in northern regions (Sauer and Link 2011). Each BBS route consists of 50 points 800 m (0.5 mi)

apart from each other: the observers are asked to conduct the survey of all birds seen and heard within a 400-m radius of each point for 3 min starting 30 min before local sunrise (Sauer and Link 2011).

The BBS dataset was downloaded from https://www.pwrc.usgs.gov/bbs/RawData/. It contained the data on weather conditions during each sampling effort, routes, and species counts. The species counts were available in two options: species counts aggregated in groups of ten points and overall count for a route, and separate point counts were available for the surveys conducted after 1997.

The dataset provides the locations of a starting point of each route only. Anecdotal evidence suggests that the United States Geological Survey possesses the data on location of every point count since 1997 (Boulinier et al. 1998b, Barnagaud et al. 2017), but these data do not seem to be freely available. Therefore, the data extracted for this study refer to individual BBS surveys, providing substantial information on community structure (Catano et al. 2020).

Only the observations that meet official BBS criteria on weather, date, time, and route completion were used, yielding 55,662 valid observations since 2000.

eBird Data

The eBird dataset (all years, all countries) was downloaded from the eBird web site (https://ebird.org/data/download) in November 2021, and thus included all observations up to October 2021. The dataset was filtered using the auk R package (Johnston et al. 2021, R Core Team 2022) based on the following filters: complete checklists (i.e., an observer had acknowledged that the submitted check list contained all species he/she could recognize), country was set to the U.S., Canada, and Mexico, protocol was set to traveling, traveled distance was set to 32.2–48.3 km (20–30 mi), which is similar to 39.4 km surveyed in BBS counts, and the time of sampling was set to 150–600 minutes which corresponds to a range between minimum possible timing of one completion of a BBS route (3 min × 50 points = 150 min) and 10 hrs that would be needed to walk at a pace of 3.94 km/h through the whole route as a worst-case scenario. The upper limit might seem exaggerated, but since BBS does not provide the data on time of sampling, it is unclear what sampling duration should be used when filtering the eBird dataset. Besides, the distribution of sampling duration in the dataset used is clearly right-skewed

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(Fig. 13), which suggests that the observations yielded by slow and long travels are rare and unlikely to produce a substantial sampling bias.

Observations that duplicated effort within the BBS dataset were deleted from eBird dataset. Such observations were defined as those occurring on the same day and within 0.1° from each other based on latitude and latitude. Overall, 101,072 observations have left from the eBird dataset after this step.

Unlike the BBS dataset, where all species were considered to be breeding at the time of observation and which ignores the fact that the timing of breeding may vary among taxa, the eBird dataset has been collected during different seasons, so that the data contained observations of some species as breeding though in reality they had a migrant or vagrant status at the time of the observation. To deal with that, approximate breeding period was described for each species using the information provided by the Birds of the World project (https://birdsoftheworld.org/) which combines data from peer-reviewed sources edited by recognized specialists in the biology of particular species, and wherein all observations of individuals occurring outside of the breeding season were ignored. After the removal of all out-of-breeding season observations and those that were located in the sea or the ocean, the eBird dataset contained 36,250 observations.

Bird Conservation Regions

Bird conservation regions (BCRs) were designed to reflect large-scale geographical areas that have relatively homogeneous climatic conditions and, hence, co-occurring bird species. Avian conservation in North America uses the BCRs that reflect homogeneity of bird communities, habitats, and resource management issues (Sauer et al. 2003) and can be used for ecologically meaningful division into regions (Fig. 5).

Correction for Detection Probability

In any monitoring survey, no real count of species is being obtained, but some sort of count statistic (i.e., number of individuals detected). The success with which an observer detects individuals can be described as a detection probability denoting the probability with which an individual that occupies a patch is observed. Detection probability is thought to be always less than one, meaning that there is always a chance for an observer to miss an observation of an individual animal (MacKenzie et al. 2002). A number of factors affect detection probability that

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Fig. 5. Bird Conservation Regions of North America, according to North American Bird Conservation Initiative

can be related to particular features of individual taxa (e.g., prey species that behave cautiously not to draw a predator's attention, leading to a low detection probability by an observer) or behavioral responses to environmental variables, such as habitat type (e.g., a bird is expected to be more cautious in an open habitat), weather (e.g., birds are less active in harsh weather conditions), sunlight and time of the day/year (e.g., affecting phenological response in mating behavior, such as singing, that increases detectability), etc. (Anderson et al. 2015). Moreover, species detectability also depends on abundance, which may lead to an overestimation of abundance in common taxa and an underestimation in rare ones (Tanadini and Schmidt 2011). Overall, detection probability is a highly heterogeneous parameter that varies among species, habitats, and environmental conditions, and should be accounted for when estimating community-level diversity metrics, especially functional diversity (Boulinier et al. 1998b, Palacio et al. 2020). Duration of sampling effort is another important parameter (i.e., when sampling is longer, it is more likely that a rare taxa will be detected (Colwell and Coddington 1994)), so that it was important to account for sampling effort when filtering the eBird dataset to join it with BBS.

One of the largest sources of bias when conducting community-level studies based on datasets like BBS or eBird is that comparisons of counts among species is not appropriate. The observed count is a function of abundance and detection probability, and thus observed counts among species should not be treated as a true reflection of actual abundances when determining community structure and composition. In the case of BBS, the issue of detection bias might be more critical than with eBird because the BBS sampling scheme restricts the time of sampling to 30 min before sunrise, which biases against the detection of nocturnal species (Sauer et al. 2017a).

A detectability/occupancy framework provides a means to deal with detection bias. From the perspective of this model, an observed species count is a product of a stochastic process described by the probability of detection, p, and the probability of occurrence, ψ. Within a spatially defined sampling space, or region, only a subset of plots are sampled (MacKenzie et al. 2006). In the case presented here those subsets of plots correspond, for example, to active BBS routes. A fraction of sampling sites occupied by a particular species correspond to occurrence ψ, but the fact that detection is not perfect within each site and not all individuals that are present are observed implies that any estimates of regional abundance (that are later used to estimate

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species rarity) will be lower than reality — and the fact that detectability varies among species creates an even larger bias. To incorporate detection probability, a repeated sampling design is required, which is not the case for BBS sampling (i.e., there is only one sampling event per year per route) and repeated sampling is rare within the eBird dataset. An alternative approach is assuming that a species is present within a group of points within a BBS route, and, so, if a species is present for at least one point within the route, one could calculate the detection probability as the fraction of points within which a species was detected (Boulinier et al. 1998b). This alternative approach does not require temporal replication and would not be applicable to the semi-structured eBird dataset.

N-mixture models have been used to estimate real abundances from observed counts (Royle 2004). These models view site-specific species counts as independent random variables distributed according to an assumed statistical distribution (e.g., Poisson or negative binomial), assuming constant detection probability. N-mixture models rely heavily on assumptions, namely correspondence of data to assumed statistical distributions, parameter values not being extreme, and data are accurate — rarely the case in bird counts with double counting, variation in population size and detection probability (Link et al. 2018).

The real species abundance within a region is not fixed, but there is some uncertainty related to population fluctuations and statistical reasons. Confidence intervals of estimates of regional abundance that account for the BBS monitoring scheme and variation in species detectability can be calculated following Stanton et al. (2019):

$$N \approx \frac{\sum_{j=1}^{m} \sum_{i=t}^{T} {Y_{ij}}/{n}}{m} \frac{a}{A} \left(\frac{r}{C_D}\right)^2 C_P C_T$$

where Y refers to species count in year i at route j, n is the number of times route j was surveyed between years $i = t \ldots T$, m is the number of routes within a region, a is the area of a region in km^2, A = 25.1 km^2 is the assumed area covered by one BBS count (given that there are 50 points with a search radius of r = 400 m, $50 \times 0.4^2 \times \pi \simeq 25.133$), and three variables ($C_D$, C_P, and C_T) related to detection probability: C_D refers to distance-detection adjustment (i.e., distance needed to detect a bird given its behavior, e.g., loud individuals may be heard over greater distances), C_P refers to pair adjustment (i.e., amount of undetected individuals; e.g., silent females associated

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with an individual singing male that has been detected), and C_T is time-of-day adjustment (i.e., level of activity during the time of sampling; e.g., morning hours).

Since the data in this study were analyzed separately for each year to reflect temporal changes, Stanton's formula may be simplified to

$$N = \frac{1}{m}\sum_{j=1}^{m} Y_j \frac{a}{A}\left(\frac{400}{C_D}\right)^2 C_P C_T$$

to estimate the population size of each species within a region.

For the three detection probability adjustment parameters, Stanton et al. (2019) suggested the following procedures: C_D is estimated as a random draw from a uniform distribution with known lower and upper limits; C_P is estimated as a random draw from a truncated normal distribution with known mean, where standard deviation is assumed to be equal to 0.13, and lower and upper bounds; C_T is estimated as a random draw from a lognormal distribution with known mean and SD. Among these parameters, estimation for common species seems to be the most sensitive to distance adjustment, whereas the abundance of rare species is likely to be inaccurate (Stanton et al. 2019). The parameter values used in the analysis reported here were taken for 406 species provided (Stanton et al. 2019); for species not found in Stanton et al. (2019), a mean value of parameter for similar taxa (within a genus or, in rare cases, family) was used instead. To account for variability of sampling distance within the eBird dataset, the area covered by one sampling effort A was also derived from a drawn from an empirical distribution of sampling distances within a BCR in a given year (i.e., A = [*sampling distance*/39.43 km] × [$50\times0.4^2\times\pi$]), rather than using a constant value of 25.1 km^2. The estimation procedure was run 500 times for each species, BCR, and year, and the median of a simulated distribution was assumed to be representative and proportional to the regional species abundance. This approach deviated from Stanton's et al. (2019) correction, which returned a confidence interval rather than a point estimate, but such approach was needed to reduce the computation time required for an analysis of large datasets.

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Numerical Rarity

Although the concept of rarity may seem straightforward, its quantification is anything but simple. In abstract terms, a species that is rare is opposite to a species that is numerically dominant. An easy way to separate species into rare and non-rare is to partition a set of species in a community into two groups based on a particular threshold (Gaston 1994). This threshold can be determined based on a distribution of any species-specific metric that reflects an ecological value of interest within an ecosystem (e.g., abundance, occurrence, biomass, range, etc.). A common approach is to divide species in a community along a gradient of abundant to rare is based and to use a threshold of 25th percentile of such a metric so that 75% of the species in a community are considered abundant and 25% are considered rare (Gaston 1994, Magurran 2004).

More detailed discrete schemes exist to evaluate species rarity. For example, the International Union for Conservation of Nature's (IUCN) Red List conservation status distinguishes among extinction risk levels (extinct, extinct in the wild, critically endangered, endangered, vulnerable, near threatened, and of least concern) based on species abundance dynamics and range area that are thought to predict the risk of extinction (Baillie et al. 2004, Rodrigues 2006). Yet, although conservation statuses are more valuable for conservation management, such a declaration rarely reflects a species' role within communities, and requires intense sampling and evaluation by experts, which makes relying on such designations inappropriate for the majority of taxa in this study.

Alternative means of quantifying rarity in a useful way that acknowledges abundance of a focal species within the context of community structure do exist. For example, one alternative is to use the probability of species being classified as rare by means of a fuzzy clustering algorithm (Balbuena et al. 2021). This approach returns a value ranging between 0 and 1, but, unfortunately, this method is computationally expensive, which is not practical for large datasets. This approach is also binary given that clustering is expected to classify a species into either rare or abundant categories.

Classical rarity weighting techniques include taking the ratio of the most dominant species relative to a focal species, the ratio of a focal species relative to the most dominant one subtracted from 1, and scoring based on an abundance rank (Sólymos and Fehér 2005, Dapporto and Dennis 2008, Leroy et al. 2012). These metrics provide biased estimates of rarity weights for

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species of intermediate abundance (Leroy et al. 2012). The method suggested by Leroy et al. (2012) deals with this problem by introducing a continuous rarity weighting procedure with an adjustable parameter of rarity cut-off level that corresponds to a Gaston's threshold of abundance (by default, 25%): species with abundance lower than the cut-off level exponentially increase with distance between their abundance and the cut-off level rarity weight (Leroy et al. 2012, 2013). According to this method, a rarity weight can be calculated as

$$w_{Leroy} = \exp\left[-\left(\frac{N_i}{N_{\max}}\eta + 1\right)^2\right]$$

where N_i is a focal species abundance, N_{max} is the most numerically dominant species abundance, and η is an adjustment coefficient fitted for a given cut-off point (Leroy et al. 2012). In the work presented here, the rarity cut-off level was assumed to equal 25%. To adjust the method for my purposes, the table values of the coefficient η corresponding to arbitrary abundance values were fed to a linear model to estimate the values of η that corresponded to intermediate abundances that were not provided by Leroy et al. (2012). The relationship between abundance and η seems to be reciprocal, i.e., $\eta = f(N) = 1/N^x$, so that firstly I estimated the value of x at which the sum of squared residuals of a model was at its minimum (x = 1.17) and secondly this linear model was used to estimate a value of η for a given species abundance (Fig. 6).

One of the disadvantages of Leroy's method is that the rarity cut-off adjustment coefficient (i.e., the rarity weight itself), is dependent of absolute species abundances. The abundance values used in this work were not abundances per se, but estimates of abundances extrapolated on whole regions, resulting in very large values (i.e., $10^2 – 10^8$) so that η did not vary considerably. This approach had the potential to create bias in rarity weights assigned for species in BCRs with small areas because their extrapolated abundances were related to a region's size. Rarity should be estimated within the context of community irrespective of its size (i.e., based on relative species abundances), which cannot be used with Leroy's method.

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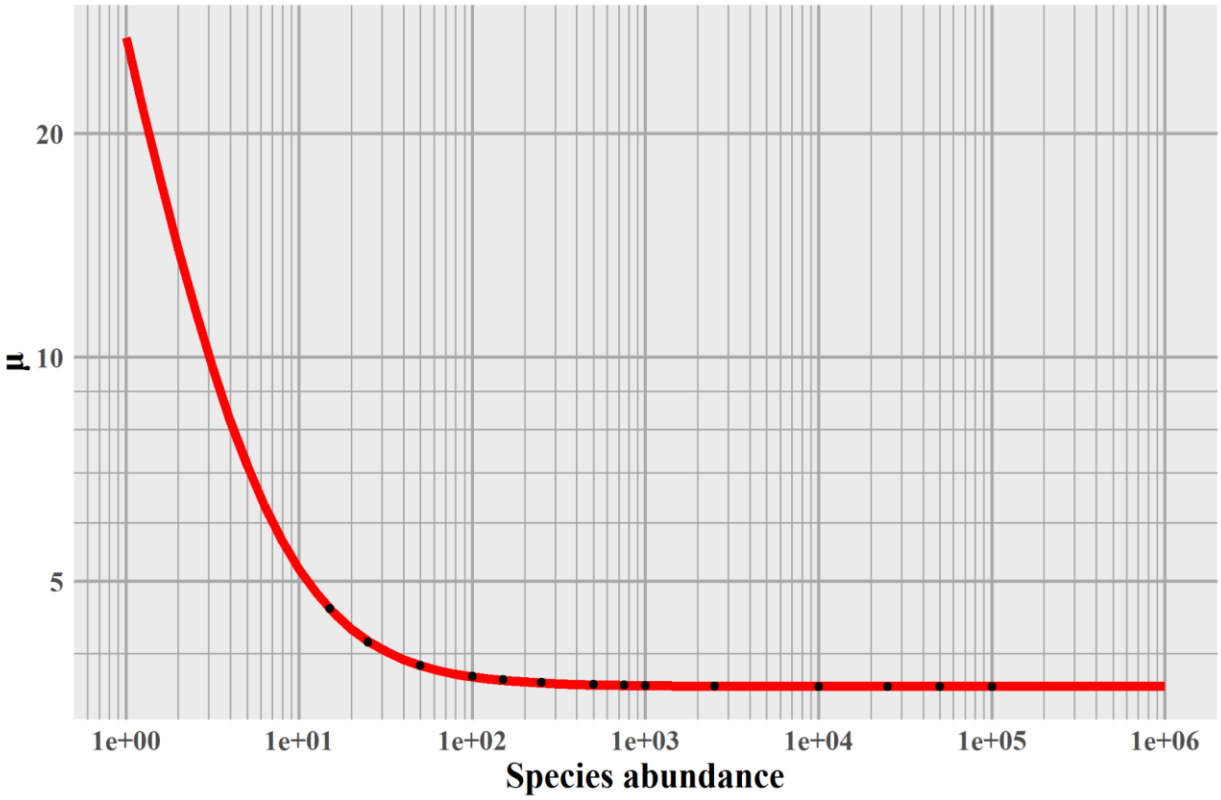

Fig. 6. The extrapolated values of rarity cut-off adjustment coefficient η as a function of species abundances based on arbitrary abundance values (black points)

To deal with this problem, I used the independently developed log-rarity metric

$$w_{log} = \frac{\log(N_i/N_{\max})}{\min[\log(N_i/N_{\max})]}$$

which was normalized between 0 and 1 so that the rarest species always had a weight of 1 and the most dominant species had a weight of 0. The relationship between log-rarity and abundance is linear on a log-scale of species abundances.

Dataset on Species Traits

Functional diversity is based on multidimensional trait space, but there are many traits that an organism possesses, and virtually all of them can be found to be relevant (Tilman 1999). For

example, using traits relevant to the Grinnellian niche might be useful for modeling the spatial distribution of a species and may concomitantly reveal habitat requirements. The Grinnellian niche, however, does not really reveal much about the functional role of particular species (Dehling and Stouffer 2018). For a meaningful estimation of functional role, one would need traits related to species trophic requirements and resource consumption, reproductive output, biomass and other components related to that species' effects on ecosystems. In the work presented here, I used 23 functional traits that can be partitioned into categories of ecological influence and importance within habitat filtering:

1. ***resource consumption*** is thought to be related to habitat choice by organisms (Francis et al. 2011, Pontarp and Petchey 2016) based on the assumption that the presence of resources required by an organism is the basic prerequisite for its existence (Lele et al. 2013);
    a. ***food resources*** needed to meet energetic demands of an organism, one of the most important resource type explaining community structure (Hairston et al. 1960, Oksanen et al. 1981, Hairston and Hairston 1993);
    b. ***other resources*** needed to maintain stable population growth, such as resources needed for nesting, which may act as a limiting resource and affect biomass flows in ecosystem due to use of construction materials for nest building (Martin et al. 2004, Wiebe 2011);
2. ***effect intensity*** in terms of species traits that predict local abundance and short-term population dynamics that result in the amount of resources allocated by an individual (Boggs 1992);
    a. ***reproductive*** traits affect the rate at which a population is being replenished and the amount of new individuals that are consuming resources, affecting overall fitness of species (Pianka 1970);
    b. ***life history*** traits affect the amount of resources consumed by one individual during its lifetime (Stearns 1976, Karl and Fischer 2008);
3. ***biotic interactions*** related to the position of an organism within a trophic web and related to a species being keystone within a community (Libralato et al. 2006, Dehling and Stouffer 2018).

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The trait variables used in works related to functional diversity in birds are typically limited to a small number and are often binary or continuous (Petchey et al. 2007), with the potential for a loss of information about functional similarity of species. To avoid it, I used three types of variables:

- continuous, either constrained (i.e., with a minimum possible value of 0 and maximum possible value of 1, e.g., probabilities) or not (e.g., body mass),
- categorical, so that species could be assigned one category among a fixed set of possible values, and
- discrete distributions (i.e., there was a set of variables corresponding to one trait that described a distribution of this trait among fixed categories so that the sum of the variable values for a species was always 100%).

An overview of the traits used, their group of ecological importance, and type are shown in Table 2.

The dataset on species traits was compiled using a set of available literature sources describing biology and life history of North American birds (Ehrlich et al. 1988, Wilman et al. 2014, Sheard et al. 2020, Billerman et al. 2022). In a case when a trait value was unknown, it was assumed based on sister taxa (e.g., a mean value for a genus).

Six of the traits (diet, diurnal feeding, nocturnal feeding, diet items, feeding method, feeding substrate) are related to diet and are determined by a community's effectiveness at nutrient retention (Forister and Jenkins 2017). The diet category (fruit and nectar eaters, invertebrate eaters, omnivores, plant and seed eaters, and carnivores [vertebrates, fish, and/or carrion]) reflects the trophic grouping of each species. Diurnal and nocturnal feeding were treated as non-exclusive binary variables, indicating day/night activity; nocturnal activity is not widespread among most avian taxa, with the exception of owls and nightjars, and likely is a good predictor of functional distinctiveness (Park et al. 1940). Diet items were represented as a distribution of food types (invertebrates, endothermic vertebrates, ectothermic vertebrates, fish, unknown vertebrates, carrion, fruits, nectar, seeds, green parts of plants, and human food leftovers) consumed by a particular taxon, approximating its position within a food web (Gray et al. 2015). Feeding methods reflected feeding behavior, which is related to the portion of resource space used by a species (Mitchell 1981). Feeding methods included the following categories: digging (removing surface soil, rocks, and/or understory to find food), ground gleaning

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Table 2. List of species traits, their group of ecological influence, variable type, and source of the data

Trait	Type	Primary Reference†
Food resources		
Diet	categorical	E, W, B
Diurnal feeding	continuous (0/1)	E
Nocturnal feeding	continuous (0/1)	E
Diet items	distribution	E, W, B
Feeding method	distribution	E, B
Feeding substrate	distribution	E, W, B
Other resources		
Nest type	categorical	E, B
Nest substrate	distribution	E, B
Reproduction		
Breeding system	categorical	E, B
Chick development at hatching	categorical	E, B
Nest aggregation	categorical	B
Clutch size	continuous	E, B
First breeding age	continuous	B
Number of clutches a year	continuous	E, B
Breeding success	continuous (0…1)	B
Life history		
Adult annual survival	continuous (0…1)	B
Average biomass	continuous	E, B
Maximum lifespan	continuous	B
Biotic interactions		
Hand-wing index	continuous	S
Kleptoparasitism	continuous (0…1)	E
Nest dependency	continuous (0…1)	B
Nest parasitism	continuous (0…1)	E, B

Notes: † References correspond to Billerman et al. 2022 (B), Ehrlich et al. 1988 (E), Sheard et al. 2020 (S), and Wilman et al. 2014 (W).

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(picking up items from the surface), foliage gleaning (taking items from foliage and small branches), bark gleaning (excavating, drilling, and removing items from bark), gleaning while hovering (removing items from plants while in the air), hover and pouncing (hovering before swooping or dropping down on prey), hawking (short flights from a perch), aerial foliage (capturing items mid-air during continuous flights), aerial foraging (chasing and catching prey in air or snatching it from a perch), swoops (snatching prey up from ground after a gliding descent), high patrol (soaring at high altitude looking for prey), low patrol (searching flight at low altitudes, i.e., height of a tree), high dives (dropping from height into water), skimming (low flight over water, with or close to penetrating the surface with bill), surface dives (floating and diving underwater), surface dips (taking items underwater while floating), dabbing (taking items with more than half of the body being underwater), stalking and striking (hunting in water by standing above it motionless), and probing (taking items located beneath the surface of a solid substrate while standing on it). Feeding substrate reflected the location of resources within an ecosystem and its spatial distribution determining resource partitioning and niche differentiation (MacArthur 1958). Feeding substrate consisted of following categories: mud, below water level, within the water column, tree, ground, understory, middle to high parts of trees (trunk, bark, branches), canopy (leaves and small branches), air, dumps and dumpsters. Overall, these traits (diet, diurnal/nocturnal feeding, diet items, feeding methods, and feeding substrate) are expected to represent the position of species in a food web fully enough to assume its effect on ecosystem functioning.

Other resources that are important to birds relate to nest building because such resources presumably are limiting and predict competition for nesting sites, species occurrence, and, overall, community structure (Blewett and Marzluff 2005, Wiebe 2011, Tomasevic and Marzluff 2017). Nest type relates to evolutionary history (Winkler and Sheldon 1993), and in the work presented here it was treated as a categorical trait, so that each species could be assigned to one type: no nest (i.e., laying eggs on bare ground), parasitism (does not require building a nest, but is dependent on other species' nests presence), scrape (a simple depression with a rim to prevent eggs from rolling), crevice (a crack in a cliff or between rocks), burrow (chamber in the end of a burrowed tunnel), cavity (excavated or natural cavity in a limb or trunk of a tree), platform (structure large enough for a bird to land), saucer (shallow cup with a small rim built of small branches and other materials), cup (hemispherical nest with a large rim), spherical (i.e., enclosed

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with a small entrance), chamber (spherical nest hidden within a substrate), oven (a specific chamber with an explicit roof and small entrance), gourd (a chamber made of clay and saliva, typically attached to a vertical surface), and pendant (an elongate sack suspended from a branch). Nest substrate is expected to be more variable within a species than nest shape, so that this trait was assumed to be discretely distributed among the following categories: bank (river/lake/sea banks, steep slopes near the water), ground (among rocks, roots of live or fallen trees, bare soil), grass, cliff (natural crevices and/or ledges of cliffs), artificial structures (poles, antennas, and buildings), shrubs, deciduous trees, coniferous trees, snags and dead limbs, cacti, tangles (vines, brambles, brush piles), and floating on water (e.g., anchored to emerged or submerged vegetation).

Traits related to reproduction were expected to relate intensity of effect a species has on ecosystem functioning, since species with large offspring that breed frequently might affect matter and energy fluxes due to mass effects (Tomlinson et al. 2014). Breeding system was expected to relate to local density, so that each species was assumed to be one of the following: cooperative (two or more females simultaneously breed in the same nest with or without non-breeding helpers), polygynandrous (two or more males mate with two or more females exclusively), promiscuous (males and females mate indiscriminately), lekking (females survey the males' competitive displays), polyandrous (one female mates with more than one male), polygynous (one male mates with more than one female), and monogamous (one male mates with one female).

The mean age of first reproduction indicates the time of individual affecting ecosystem functioning directly due to resource consumption without an indirect effect through offspring. Nest aggregation (solitary, loosely colonial, or strongly colonial) was coded as a categorical trait. A strongly colonial species would be expected to have a strong effect on ecosystem functioning due to its high local density but be more limited in nesting location choice. The mean number of successful clutches per year is also important as it shows the fecundity of a species and its reproductive output per unit of time. Clutch size was also considered, along with both lower and upper limits. Breeding success was defined as the probability of a breeding pair to produce an egg that survives until fledging and successfully transitions into independent movement and feeding. Number of clutches per year, clutch size, and breeding success combined are expected to be a good predictor of the effect of a species' reproduction on ecosystems. Chick development

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time within the nest is highly related to species' phylogeny (Temrin and Tullberg 1995); this trait was considered categorical (precocial 2 [chicks are mobile, downy at hatching, able to follow the parents and find food], precocial 3 [mobile, downy, follow parents, but food needs to be shown by parents], precocial 4 [mobile, downy, follow parents and are fed], semiprecocial [mobile, but remain at rest and fed], semialtricial 1 [immobile, downy, eyes are open, but fed], semialtricial 2 [immobile, downy, eyes are closed, and fed], and altricial [immobile, featherless, eyes closed, and fed]).

Other life history traits are also related to the effect of species on ecosystem functioning, as well as being important for conservation efforts (Crouse et al. 1987). For example, mean body mass might be an obvious morphometric parameter that predicts resource consumption. Maximum lifespan is also essential in determining the amount of resources consumed by an individual over its lifetime; although mean lifespan would be more meaningful, data on maximum lifespan is more easily obtained, especially for rare taxa. Finally, mean adult survival is relevant for conservation purposes, since species with low survival probability might be more threatened by extinction (Crouse et al. 1987).

The traits related to biotic interactions might be the most important ones in the context of a species' functional role, but, at the same time, the most difficult to estimate. Among traits used in the work presented here, kleptoparasitism was related to diet and defined as the proportion of diet obtained by parasitizing other species. Nest dependency (i.e., to what extent a species relies on other species for finding a suitable nest location [e.g., owls that breed in nest holes but are dependent on large woodpeckers creating nest cavities]), and nest parasitism (i.e., relying on other individuals, either conspecifics or other species, for egg incubation) are biotic interaction traits related to reproduction. All three of these traits were quantified as ratios, representing the levels at which such a behavior is typical for a species. Some morphological parameters were also used as a proxy for biotic interactions. For example, hand-wing index, calculated as $100\times(D_K/L_W)$ where L_W is the wing length (between the carpal joint and the tip of the longest primary feather) and D_K is Kipp's distance (difference between L_W and secondary length [i.e., from the carpal joint to the tip of the first secondary feather]), is related to diet and dispersal ability (Claramunt et al. 2012, Kennedy et al. 2016, Sheard et al. 2020). These characters play an important functional role in the ecosystems, for example, for seed dispersal (Schubert and Walters 2022).

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Functional Distinctiveness

Functional distinctiveness is a characteristic of a species having traits dissimilar from those of other species in a community (Violle et al. 2017). Functional distinctiveness, at the species level, and divergence, at the community level, are components of functional diversity based on species-level calculations, unlike, for example, functional richness or evenness that are derived from community-level metrics (Villéger et al. 2008, Mouchet et al. 2010). Functional distinctiveness is quantified as a distance between a particular species and a community centroid within multidimensional trait space, where the community centroid corresponds to a set of weighted-by-species-abundances mean trait values within a community (Villéger et al. 2008, Mouchet et al. 2010, Carmona et al. 2016, Violle et al. 2017). And while this definition is useful when working with continuous or binary variables corresponding to functional traits, other types of data, such as distributions and categorical variables, add complexity to the calculations of functional distinctiveness.

A conventional community centroid would be a vector of weighted mean trait values

$$\bar{\mathbb{C}} = \left(\bar{\mathbb{C}}_t : \bar{\mathbb{C}}_t = \frac{1}{S} \sum_{s=1}^{S} \mathbb{C}_{s,t} \right)$$

where a pool of community species traits takes the form of matrix $\mathbb{C}_{s,v}$, where $s = 1 \ldots S$ is a species among total S species, and $t = 1 \ldots T$ is a trait among T traits to which corresponds variable(s) v.

Because traits used in the work presented here include continuous, categorical, and discrete distributional forms, a centroid consists of different types of data. Therefore, if a trait variable v corresponding to a trait t was continuous, then the community centroid would take the form of

$$\bar{\mathbb{C}}_v = \frac{1}{S} \sum_{s=1}^{S} \mathbb{C}_{s,v}.$$

For categorical variables an element of a community centroid was represented as a frequency of distribution of each alternative category value within a community,

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$$\bar{\mathbb{C}}_v = \{n_j : n_j = (\sum_{\mathbb{C}_{s,v}=j} 1)/S \; \forall \; j\},$$

yielding a set of occurrences of each category *j* of a trait variable *v* within *S* species.

Finally, distributed traits were written in sets of variables representing the percentage of population exhibiting a particular trait value, so that a centroid value for such trait variables *v* would equal a weighted mean, ensuring that in a centroid the sum of values corresponding to all possible trait values would equal 1 (Fig. 7). Thus, there could be more than one trait variable *v* that corresponds to one trait *t* that is a distribution.

Calculating functional distinctiveness corresponds to a transformation of the matrix $\mathbb{C}$, which refers to traits of a community's species pool, into a matrix $\mathbb{D}$ of distances to a centroid estimated for each trait (denoted here as trait-distinctiveness), that can later be summarized to overall individual species' distinctiveness.

Calculation workflow of a trait-distinctiveness $\mathbb{D}_{s,t}$ differed based on the type of trait. For continuous variables, trait-distinctiveness was assumed to be equal to the difference between a species' trait value and centroid value, so that

$$\mathbb{D}_{s,t} = |\mathbb{C}_{s,t} - \bar{\mathbb{C}}_t|.$$

Distance between a species and a centroid for categorical variables could be based on the frequency of observed categories among the species pool (i.e., on a simple matching function (Legendre and Legendre 1998)), but such an approach would have led to a loss of information about similarity between the categories (e.g., one would agree that saucer and cup nests are more similar to each other than saucer and cavity). Therefore, dissimilarity matrices $\mathbb{S}_t$ were built for each categorical variable that contained presumed and arbitrary distances between the categories (Appendix B), and trait-distinctiveness for such traits was calculated as

$$\mathbb{D}_{s,t} = \frac{\sum_{i=1}^{J} (\bar{\mathbb{C}}_t)_{i'} \cdot (\mathbb{S}_t)_{i,j=\mathbb{C}_{i,j}}}{\max\left((\mathbb{S}_t)_{i,j=\mathbb{C}_{i,j}}\right)},$$

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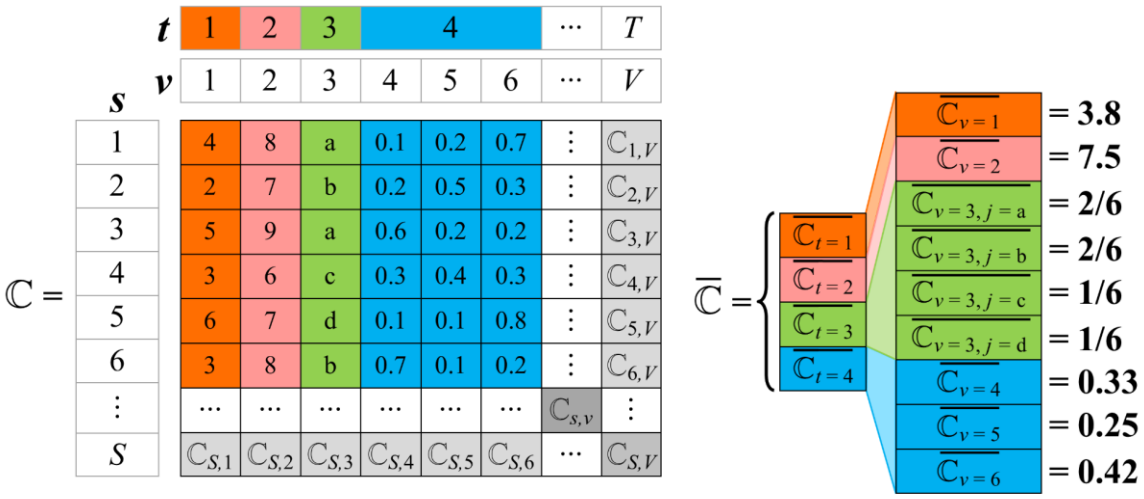

Fig. 7. A conceptual explanation of the calculations needed to derive a community centroid based on functional traits of different types: continuous (shades of red), categorical (green), and distributions (blue). Note that the first two elements of the centroid are mean values of corresponding continuous traits, the third element is a frequency distribution of a categorical trait, and the fourth element is a mean distribution

where $(\mathbb{S}_t)_{i,j}$ is a dissimilarity of the category value j observed for a species s and i is other possible category values, so that $(\mathbb{S}_t)_{i=j,j} = 0$.

Finally, in the case of distribution traits, trait-distinctiveness was an inverse function of an overlap between the respective distribution of a species and centroid. The overlap between the distributions was calculated as a sum of minimum percentage within each category,

$$O_{s,t} = \frac{1}{\sum_{v=f}^{F} \mathbb{C}_{s,v}} \sum_{v=f}^{F} \min\left(\mathbb{C}_{s,v}, \bar{\mathbb{C}}_{v}\right),$$

where f corresponds to the set of trait values $f = v \ldots F$ referring to a trait t. Since the overlap between distributions is inversely proportional to distinctiveness (i.e., it equals maximum possible overlap when species-specific distribution is identical to the centroid distribution, and it

equals zero when two distributions do not overlap in any of the discrete categories), the overlap was standardized for each trait as

$$\mathbb{D}_{s,t} = 1 - \frac{O_{s,t}}{\max(O_{s,t})}.$$

The resulting matrix $\mathbb{D}$ contained the estimates of distinctiveness for each species in a community by each trait. The columns of such a matrix needed to be standardized because they had different units of measurements depending on trait type and meaning. Therefore, each column referring to traits *t* was transformed into a vector of deviations within a community, using z-scores (i.e., $z = (x - \bar{x})/SD(x)$), and each value *z* was then transformed onto a scale between 0 and 1 under the assumption that $z \sim N(0, 1)$, i.e., as a probability of observation of a given deviation under the assumption that mean deviation approximated zero. The mean distinctiveness δ of a species was calculated as a mean deviation of trait-distinctiveness,

$$\delta_s = \sqrt{\frac{1}{T}\sum_{t=1}^{T}\left[P\{X \leq z_{s,t}\}\right]^2}.$$

Species functional distinctiveness δ then was normalized between 0 and 1, with a value of 0.5 denoting that a species was at the mean distance from a community centroid in a multidimensional trait space relative to all species within the community averaged by all possible functional traits considered.

Functional Divergence

Species functional distinctiveness within a community can be estimated both at local and regional levels (Violle et al. 2017). At a local scale, a community centroid would be constructed on a case-by-case basis for each observation separately. To study regional functional diversity, (which is more informative because regional functional diversity may indicate assembly mechanisms and habitat filtering of a regional pool, or metacommunity (Connor and Simberloff 1979, Mittelbach and Schemske 2015)), a community centroid was constructed based on the regional species list and estimated with Stanton's (2019) adjustment of species abundances within a given BCR in a given year. Regional functional distinctiveness of species was then

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drawn from the regional data for each observation to estimate the community's functional divergence.

Functional divergence represented the distribution of species' abundances along a functional trait axis within a community (Mason et al. 2005, Mouchet et al. 2010): low functional divergence was expected to indicate that abundant species exhibited functional traits close to centroid values. This metric allowed me to generalize the whole community matrix $\mathbb{D}$ into one integrative functional diversity metric. Functional divergence, denoted here as Δ, was calculated with a formula suggested by Villéger et al. (2008):

$$\Delta = \frac{\sum_{s=1}^{S}\left[w_s \times \left(\delta_S - \frac{1}{S}\sum_{s=1}^{S}\delta_s\right)\right] + \frac{1}{S}\sum_{s=1}^{S}\delta_s}{\sum_{s=1}^{S}\left[w_s \times \left|\delta_S - \frac{1}{S}\sum_{s=1}^{S}\delta_s\right|\right] + \frac{1}{S}\sum_{s=1}^{S}\delta_s},$$

where *w* is species abundance weight.

Potential Metrics of Functional Rarity

While Villéger's functional divergence Δ is related to the distribution of species' abundances within a multidimensional trait space, it is unclear if it can be used to quantify functional rarity in communities.

Functional rarity is a "feature of a species that integrates both functional distinctiveness and taxonomic scarcity at local scales, or both functional uniqueness and taxonomic restrictedness at the regional scale [...], functionally rare species possess the highest functional rarity value in the community (local scale) or in the regional pool (regional scale)" (Violle et al. 2017). However, in their paper, Violle et al. (2017) provide a vague definition for estimation of functional rarity, limiting their explanation to a statement that functional rarity is a function of species' functional distinctiveness and numerical rarity either at local or regional scales, without specifying the mathematical function itself. In a subsequent work, Violle's team provided the means to characterize functional rarity (Grenié et al. 2017), again, without any specifications of the mathematical transformations needed to estimate functional rarity, merely stating that "functional rarity [is] the average of functional uniqueness and taxon restrictedness per site" (Grenié et al. 2017, p. 1368) and leaving the definition of functional rarity open to interpretation.

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Functional rarity must reflect both species' rarity and functional distinctiveness, so that in this work, I suggest a sum of products of distinctiveness and rarity weight for each species (SFR) and their mean values (PFR) as potential metrics of functional rarity. To make these metrics independent of species richness, numerical rarity weights were transformed into relative numerical rarity weights, so that

$$\text{SFR} = \sum_{s=1}^{S}\left[\frac{w_s}{\sum_{s=1}^{S} w_s} \times \delta_s\right] \text{ and PFR} = \frac{1}{S}\sum_{s=1}^{S}[w_s \times \delta_s].$$

The objective of this study is to evaluate the relationship between rarity and functional distinctiveness by testing the performance of this metric and its interpretation. As an alternative to the SFR metric, Villéger's (2008) functional divergence Δ could be used with abundance weights substituted with numerical rarity weights. If so, the metric is expected to have an opposite meaning to the original Δ (i.e., high values of inverse functional divergence Δ_R are expected to indicate that rare taxa have more unique sets of traits relative to others in a community, which could be an indicator of communities consisting of more unique taxa). As mentioned earlier, Villéger's functional divergence indicates the distribution of weights rather than the composition of a community, so my goal was to test the use of such metric within the community context. Additionally, I also attempted to describe the relationship between numerical rarity and functional distinctiveness using Pearson correlation coefficients between these two descriptors of species within a community, which can potentially be used as a metric of functional rarity. Overall, the shape of the relationship between functional distinctiveness and numerical rarity was examined and discussed in Chapter 4.

Summary

Data analyses were conducted in a set of steps (Fig. 8): (1) I converted the raw data into matrices of observed counts of species according to unique taxonomic identities used in the study presented here (Appendix A); (2) species counts were summarized by BCRs and years; (3) regional species counts were extrapolated into species regional abundances and corrected for variability in species detection probabilities and sampling design; (4) data on 23 functional traits related to species' effects on ecosystem functioning (resource consumption, effects intensity, and biotic interactions) were determined for each species; (5) estimates of regional species

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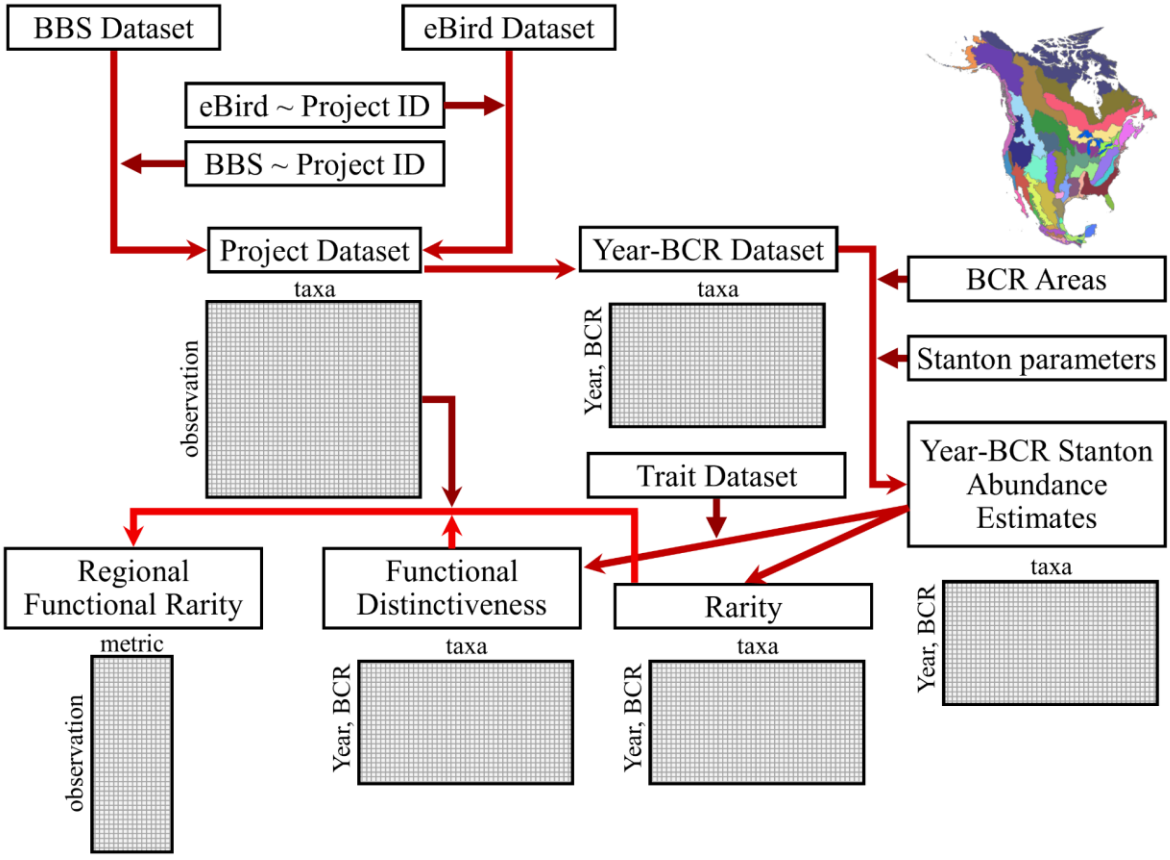

Fig. 8. An overview of steps in data analyses performed to transform raw datasets on species counts into functional rarity metrics

abundances were used to calculate regional rarity (as Leroy's estimator and log-rarity) and centroids of metacommunities in a multidimensional space of functional traits were constructed; (6) species functional distinctiveness was estimated relative to corresponding community centroids representing the uniqueness of sets of functional traits attributed to each species; (7) metrics of functional diversity were calculated based on functional distinctiveness and rarity/abundance values drawn from respective years and BCRs, such as functional distinctiveness, inverse functional distinctiveness (with numerical rarity weights substituting abundance weights), correlation between numerical rarity and functional distinctiveness of species within a community.

Throughout this process, data were screened and eliminated from the datasets when applicable. This included observations of species outside the breeding period, observations that were duplicated between datasets, and observations that were located outside of continental North America (including off-shore records). The metadata taken from the original datasets, such as longitude, latitude, date, duration and distance of sampling, were attached to the observed values of functional rarity metrics, so that the effect of environmental conditions could be tested. The overall resulting dataset contained 86,406 observations, among which 55,662 originated from the BBS and 30,744 — from eBird datasets, collected at 18,713 locations in Canada, Mexico, and the contiguous United States between January 2000 and October 2021.

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DIFFERENCES BETWEEN BREEDING BIRD SURVEY AND EBIRD DATASETS IN SAMPLING EFFORT, CIRCUMSTANCES, AND SPATIAL DISTRIBUTION

Introduction

The North American Breeding Bird Survey (BBS) and eBird are the most comprehensive, if not the only available, sources of data on bird occurrence over an entire continent for several decades. These projects are a joint effort of thousands of citizen scientists that yield data on species occurrence and local counts that would be impossible to collect independently or with a team of fieldworkers. Of course, there is a trade-off between quality of data and its availability, as inconsistent sampling and inaccurate records can make the data worthless while an overcomplicated sampling design needed for an adequate hypothesis-driven analysis would tend to discourage citizen scientists from participation in such a study (Bonney et al. 2009). There are three types of citizen-science projects: unstructured (i.e., open to everyone and aiming to collect as much data as possible, having few requirements for data collection), structured (i.e., having a rigorous protocol and survey design and clear objectives), and semistructured (gathering data on sampling to control for variation and bias during analysis) (Fink et al. 2010, Kelling et al. 2019). Yet, every dataset has its own limitations that sometimes can jeopardize scientific inference on research questions being asked. On the other hand, combining data from different sources may help obtain a broader perspective of the phenomenon being studied.

The Breeding Bird Survey (BBS) is an example of a structured project: the project team assigns survey routes to known and, usually, well prepared and experienced observers; the routes are predefined and are maintained from year to year; and there is a strict protocol on sampling (Sauer et al. 2003, 2017a, Sauer and Link 2011). The program started in 1966 and has been run every year since (except 2020 due to the global COVID-19 pandemic) on approximately 3,000 routes each year across the contiguous United States and Canada. The program was launched to monitor changes in avian populations, so that counts of each species can be independently used to detect changes among years. Since this ability to detect changes was the primary aim of the program, the routes are located at random among secondary routes of states and provinces, presumably biased towards the countryside and intact natural areas to reflect changes in wild populations. Each route connects 50 points 0.8 km apart, and the observers conduct a 3-min

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count of all birds within 400 m of each point starting 30 min before local sunrise (Boulinier et al. 1998b, 1998a, Sauer et al. 2003, 2017a, Link et al. 2017, Rosenberg et al. 2017).

eBird, on the other hand, is an example of a semistructured project. It collects data from birdwatchers, offering them a convenient way to keep track of their records on species observed (Sullivan et al. 2009, 2014, Johnston et al. 2021). Any eBird user can submit the observations anytime from any location with any sampling effort. There is some information that a user has to submit with every observation which can later be used to filter observations: along with obvious metadata like location, date, and time, a user has to indicate whether the checklist was completed (i.e., the checklist contains the observations of all species that could be identified), duration of sampling, sampling protocol (incidental, stationary, or traveling, with some additional special information), and distance sampled if the observer was traveling. All of these metadata can be used to limit observations to a particular sampling effort. eBird datasets consist of enormous amounts of data (>64 million observations as of March 2022 globally) due to user-friendly data collection, with the means to filter data for rigorous hypothesis testing (Fink et al. 2010, Hochachka et al. 2012, Kelling et al. 2019, Johnston et al. 2021). Overall, BBS and eBird have an impressive potential to complement each other in studying ecological patterns (e.g., effects of land use on bird ecology).

In this work, I intend to use both BBS and eBird data to study effects of urbanization on avian communities across the U.S., Canada, and Mexico. I first need to test whether sampling circumstances in these datasets are similar enough to combine them into one dataset. Here, I examine several issues that might arise: different spatial distributions, particularly along an urban gradient; different habitat composition and heterogeneity of locations sampled; variation in season and time of day; variation in weather conditions; relative sampling effort; and the overall effects of all of these components on the data obtained. This chapter attempts to justify combining datasets to examine continent-wide ecological processes.

Materials and Methods

BBS data were downloaded from the Patuxent Wildlife Research Center at the United States Geological Survey website (https://www.pwrc.usgs.gov/bbs/) on 01 Dec 2020. The dataset containing overall counts of species on a route were transformed into a matrix where rows represented sampling events and columns represented species counts. Only those observations

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were used that met BBS criteria on weather, date, time, and route completion in addition to approved sampling protocol and routes (i.e., observations coded with "RunType" = 1).

The eBird global dataset was downloaded in October of 2021 with data from all countries and all times. This dataset was filtered using the "auk" package for R that was developed specifically to work with eBird data (Strimas-Mackey et al. 2018). The following filters were applied to yield data similar to that of BBS: complete checklists only; collected in Canada, the U.S., and Mexico; from observers using the traveling sampling protocol; duration of sampling from 150 to 600 min (where 150 min was the smallest duration possible for consecutive 3-min sampling at 50 points and 600 min refers to 10 hours of continuous sampling); and sampling distance between 32.2 and 48.3 km (referring to a typical 39.4-km, or 24.5-mi BBS route).

BBS and eBird utilize different taxonomies — 60th update of the American Ornithological Society's checklist of North American birds (Chesser et al. 2019) and eBird/Clements' taxonomy (Clements 2007) respectively. Because there are some differences between them, both datasets were converged to an independent list of taxa compiling both taxonomies: the taxa counts were summarized if several species or subspecies entities of AOS's or Clements' taxonomy corresponded to a taxon identifier specific to the project presented.

The observations that were likely to be repeated both in BBS and eBird data were eliminated from the latter: such observations were defined as those occurring on the same day and within 0.1° from each other both by latitude and altitude. Also, all observations in the BBS data were assumed to correspond to breeding birds since the timing of surveys was chosen specifically within the framework of a structured project. However, eBird counts could have been conducted at any time, so that all counts of species collected outside the breeding season were ignored. The timing of the breeding season for each species was taken from the Cornell Laboratory of Ornithology Birds of the World platform (https://birdsoftheworld.org/bow/home).

I assumed that regions of North America varied in sampling effort within both datasets. While political boundaries of states and provinces are poor definitions of regions reflecting differences in avian community structures, bird conservation regions (BCRs) that have been defined by the North American Bird Conservation Initiative to reflect ecologically distinct regions in North America with similar bird communities, habitats, and resource management issues were used as definitions of ecologically meaningful regions in the study presented (Sauer et al. 2003).

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To test whether sampling locations in the datasets differed in their spatial distribution, I used Moran's I spatial autocorrelation test: the test statistic has a positive value if points with similar values are aggregated close to one another and a negative value if similar values tend to be distant from one another in a chess-board pattern. Test statistic close to zero means that there is random pattern in spatial distribution (Li et al. 2007). The source of an observation was coded as 1 for BBS and 0 for eBird to conduct Moran's I test using the R package "ape" (Paradis and Schliep 2019). To visualize the prevalence of a given data source, the proportion of BBS counts among both BBS and eBird observations within 40 km of each point across the continent was calculated.

To study the differences in habitat composition and level of urbanization across study sites, I used the Annual University of Maryland (UMD) classification of Terra and Aqua combined Moderate Resolution Imaging Spectroradiometer (MODIS) Land Cover Type (MCD12Q1, LC_Type2). This data product uses satellite imagery and supervised hierarchical classification to define habitat types of 500 m^2 pixels on a year-by-year basis. To derive the representation of habitat types by the two datasets, I constructed a 39.4-km buffer around each location sampled and calculated the ratio of area covered by each of 16 habitat types defined within a raster: water bodies, evergreen needleleaf forest, evergreen broadleaf forest, deciduous needleleaf forest, deciduous broadleaf forest, mixed forest, closed shrubland, open shrubland, woody savanna, savanna, grassland, permanent wetland, cropland, urban and built-up area, mosaic of croplands and natural vegetation, and non-vegetated area. The distribution of total counts of pixels assigned to different land cover types within the buffers was tested with a χ^2 test of homogeneity with simulated p-values based on 10,000 permutations.

Urbanization level at a sampling point was defined as a decimal logarithm of a ratio of urbanized areas defined in MCD12Q1 raster within a 40-km buffer around a point; the lower limit of this ratio was set to 500 m^2 (i.e., the smallest homogeneous patch of land cover that could be detected by the land cover classification algorithm). To compare the distribution of urbanization levels across the data to one expected if sampling locations were chosen at random across the continent, I created a set of random points within the limits of sampled areas of the continent and which were defined as ones that had at least one sampling point within 40 km. This was done to avoid a bias caused by unpopulated arctic and subarctic areas that lack sampling

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(Fig. 9). The number of random points (i.e., 18,713) corresponded to the number of unique sampling locations within the dataset analyzed.

To test whether the observed distribution of urbanization levels at sampling locations corresponded to that expected by chance, I tested the hypothesis that the true distribution was not less than a hypothesized one using a bootstrap single-sided Kolmogorov-Smirnov test with 1,000 Monte Carlo permutations (Abadie 2002). The data from different sources were tested using the same two-sided test.

Rarefaction curves were built for each observation using a non-hypergeometric formula based on species relative abundances within a community (Gotelli and Ellison 2013) to infer whether species detection varied between the two datasets. Distributions of numbers of detected individuals and species were compared using a bootstrap Kolmogorov-Smirnov test.

To test whether sampling duration or sampled distance affected the number of individuals observed or species in the eBird dataset, I used linear regression and compared it against a null intercept model using AIC. Unfortunately, the BBS program does not provide information on sampling duration, while distance sampled is assumed to equal 39.4 km (Boulinier et al. 1998b, Sauer and Link 2011).

Results

The spatial distribution of sampling locations with regards to their source was not random (Moran's I 0.046, $p < 0.001$). BBS counts were more evenly distributed across the continent (Fig. 9), and there are many locations where sampling by the BBS was more complete, although all observations in Mexico were taken from eBird — BBS surveys have not yet been conducted in Mexico. There were very few locations where the number of BBS counts was similar to the number of eBird counts (yellow color in Fig. 9B).

Despite some variation in area of land cover types from observations from different datasets (Fig. 10), their distributions did not differ significantly ($\chi^2 = 240.000$, df = 15, permutational $p = 1.000$).

Urbanization level at random locations had positively skewed distribution (i.e., towards less urbanized areas) both compared to BBS ($D = 0.301$, $p < 0.001$) and eBird ($D = 0.409$, $p < 0.001$) sampling locations, as well as when both datasets were combined ($D = 0.328$, $p < 0.001$) (Fig. 11). Distributions of urbanization levels also differed between the datasets ($D = 0.175$,

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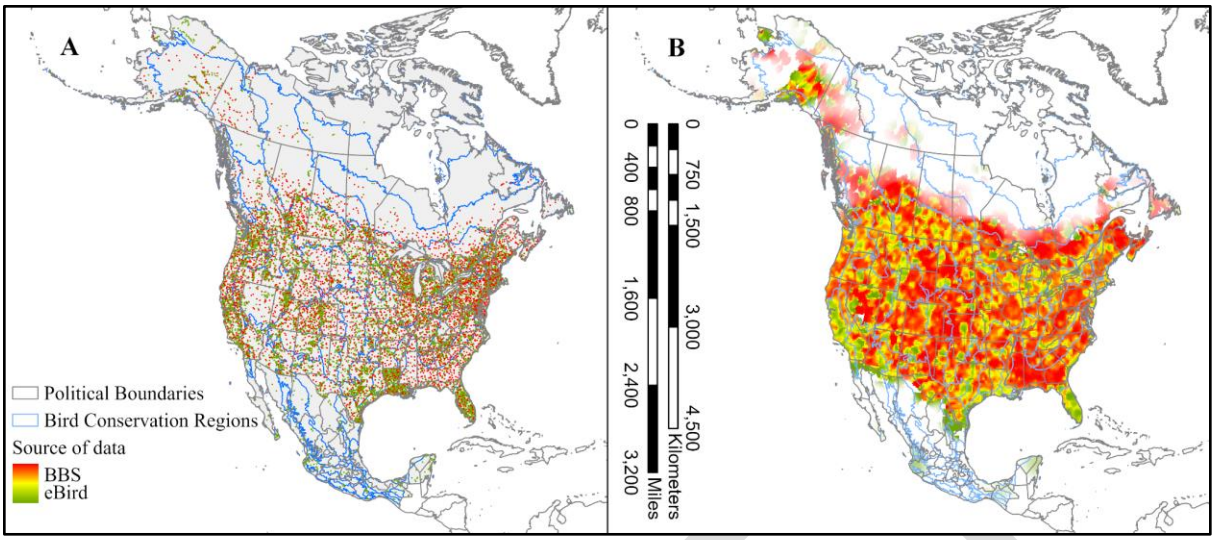

Fig. 9. Spatial distribution of sampling locations in Breeding Bird Survey and eBird datasets (A) and local prevalence of a given data source (B)

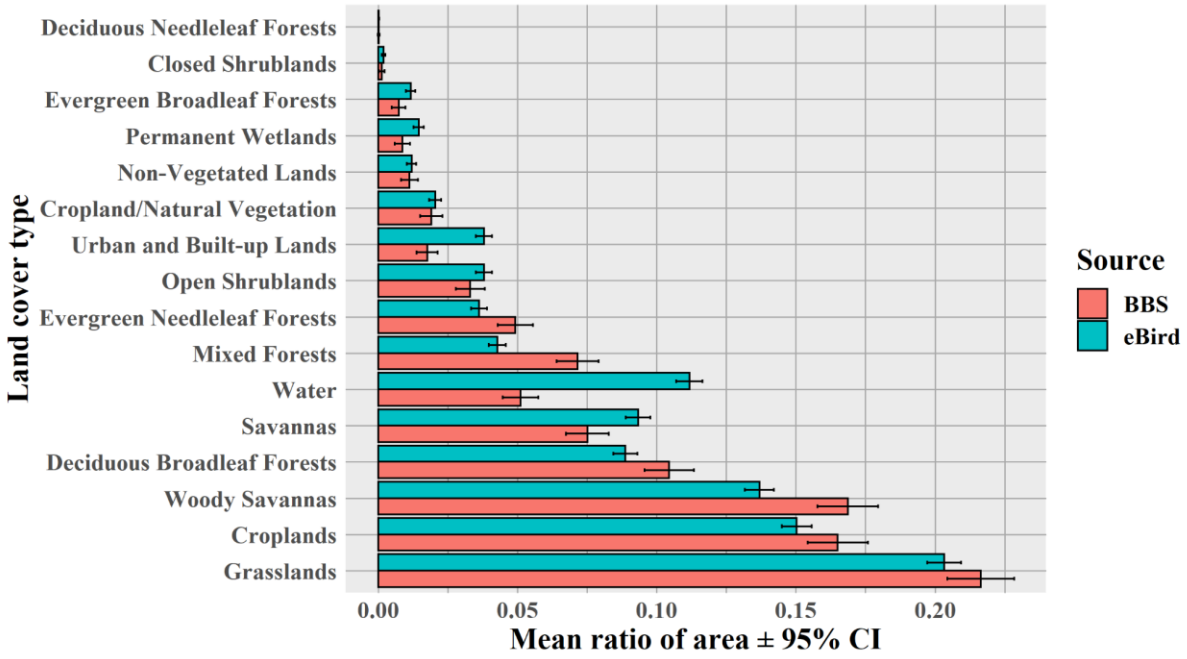

Fig. 10. Ratios of areas covered by different land cover types represented by Breeding Bird Survey and eBird observations

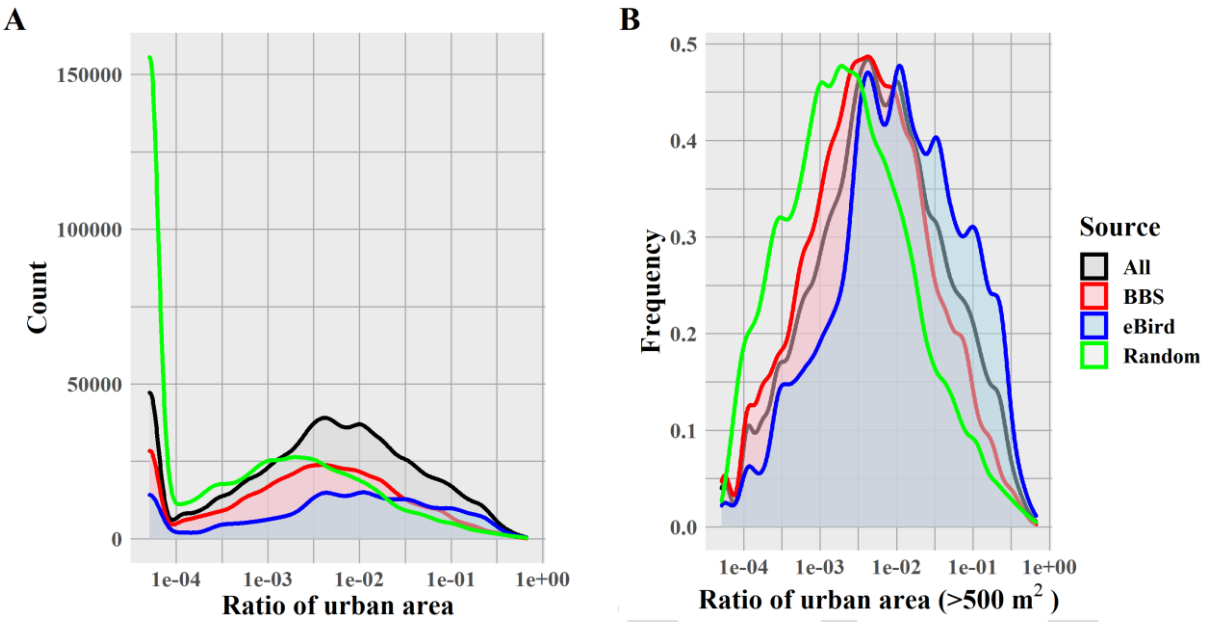

Fig. 11. Distribution of ratio of urban areas in the analyzed datasets and in randomly distributed locations with (A) and without (B) locations that did not have any urban area >500 m^2 within 39.4 km

$p < 0.001$) and neither BBS ($D = 0.069$, $p < 0.001$) nor eBird ($D = 0.106$, $p < 0.001$) had a similar distribution to their combined distribution.

The distributions of species observed differed between BBS and eBird datasets ($D = 0.683$, $p < 0.001$), with observations in eBird exhibiting, on average, lower numbers of species observed (Fig. 12). A similar pattern can be found for numbers of individuals observed ($D = 0.730$, $p < 0.001$), showing that the number of individuals observed is much less variable within the BBS dataset (Fig. 12). The distribution of both sampling distance and duration is not uniform within the eBird dataset (Fig. 13). The models implying a linear relationship between both sampling distance and duration combined and observed counts of individuals and species have the lowest AIC weights (Table 3).

Discussion

The data on observations of bird species is not distributed evenly across and within the countries of interest: there is a lack of observations in northern areas of Canada and Alaska,

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Table 3. Akaike information criterion ranks for linear models relating number of observed individuals and species in eBird counts with sampling effort

Model	K	AIC	ΔAIC	AIC Weight	Log-Likelihood
Number of individuals					
Distance + Duration	4	1,571,230	0.00	1.000	-785,610.8
Duration	3	1,571,241	11.56	0.000	-785,617.6
Distance	3	1,572,701	1,471.86	0.000	-786,347.7
Intercept	2	1,572,729	1,499.89	0.000	-786,362.7
Number of species					
Distance + Duration	4	787,838.7	0.00	1.000	-393,915.3
Duration	3	787,999.4	160.72	0.000	-393,996.7
Distance	3	830,285.9	4,2447.20	0.000	-415,139.9
Intercept	2	830,641.6	4,2802.96	0.000	-415,318.8

which can be explained by low population densities and hence low availability of potential observers, and in Mexico where there is a lack of comprehensive bird monitoring schemes (Ellis and Ramankutty 2008, Smith 2017). While the lack of data in northern Canada can be explained by the fact that these territories lack observers, scarcity of data in Mexico cannot be explained by this factor alone: although the three countries differ in their geographic scope of citizen-science programs (Devictor et al. 2010, Horns et al. 2018), Mexico along with the U.S. and Canada are within the top 10 countries relative to eBird data contribution (Zhang 2020). This suggests that although birdwatching community in Mexico is developed, there is a deficit of the data that would be similar in their sampling to BBS, rather than absence of eBird data itself. On the other hand, eBird seems to be the only option to supplement BBS in its spatial coverage outside of the U.S. and Canada.

Although the distribution of land cover types sampled by both datasets was shown to be similar, there are still some differences (Fig. 10): evergreen conifers and deciduous broadleaf forests, woody savannas, croplands, and grasslands tend to be considerably more represented in BBS counts, and urban areas, water bodies, savannas are more covered by eBird, while other land cover types are sampled more or less similarly. Regarding coverage of urban areas, both datasets seem to represent different parts of the gradient in what would be expected if observers randomly sampled the continent. The study presented here shows that eBird is biased towards more urbanized areas and BBS covers more natural areas. Despite this fact, both BBS and eBird have a lower ratio of observations from non-urban areas than expected by chance. This finding

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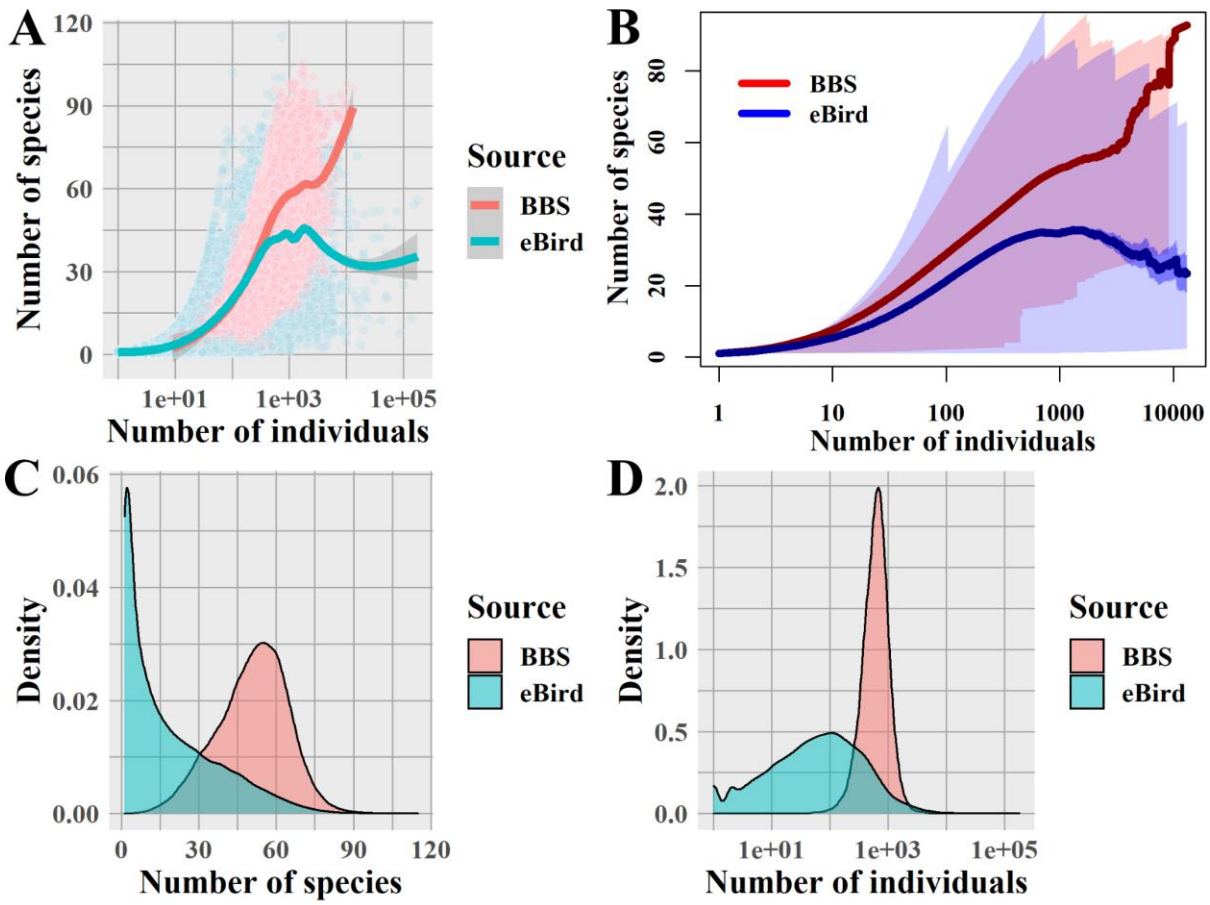

Fig. 12. Relationship between the numbers of observed individuals and species in Breeding Bird Survey and eBird datasets with 95% confidence intervals marked grey (A), mean, 95% confidence interval, and range of rarefaction curves (B), and distributions of the numbers of observed individuals (C) and species (D)

may be an artifact of the data analysis: the available land cover datasets have relatively low spatial resolution which means that small patches of urban areas are ignored by these data products. Indeed, it seems unrealistic that there are patches of land totally untouched by urbanization, especially in North America (Robinson 2002, Fahrig 2003, Halpern et al. 2008). The higher coverage of more urbanized areas by eBird can be explained by this source of the data being semistructured: a higher urbanization level implies that there are more cities around a sampled location, meaning its higher accessibility for the potential observer. It also means that

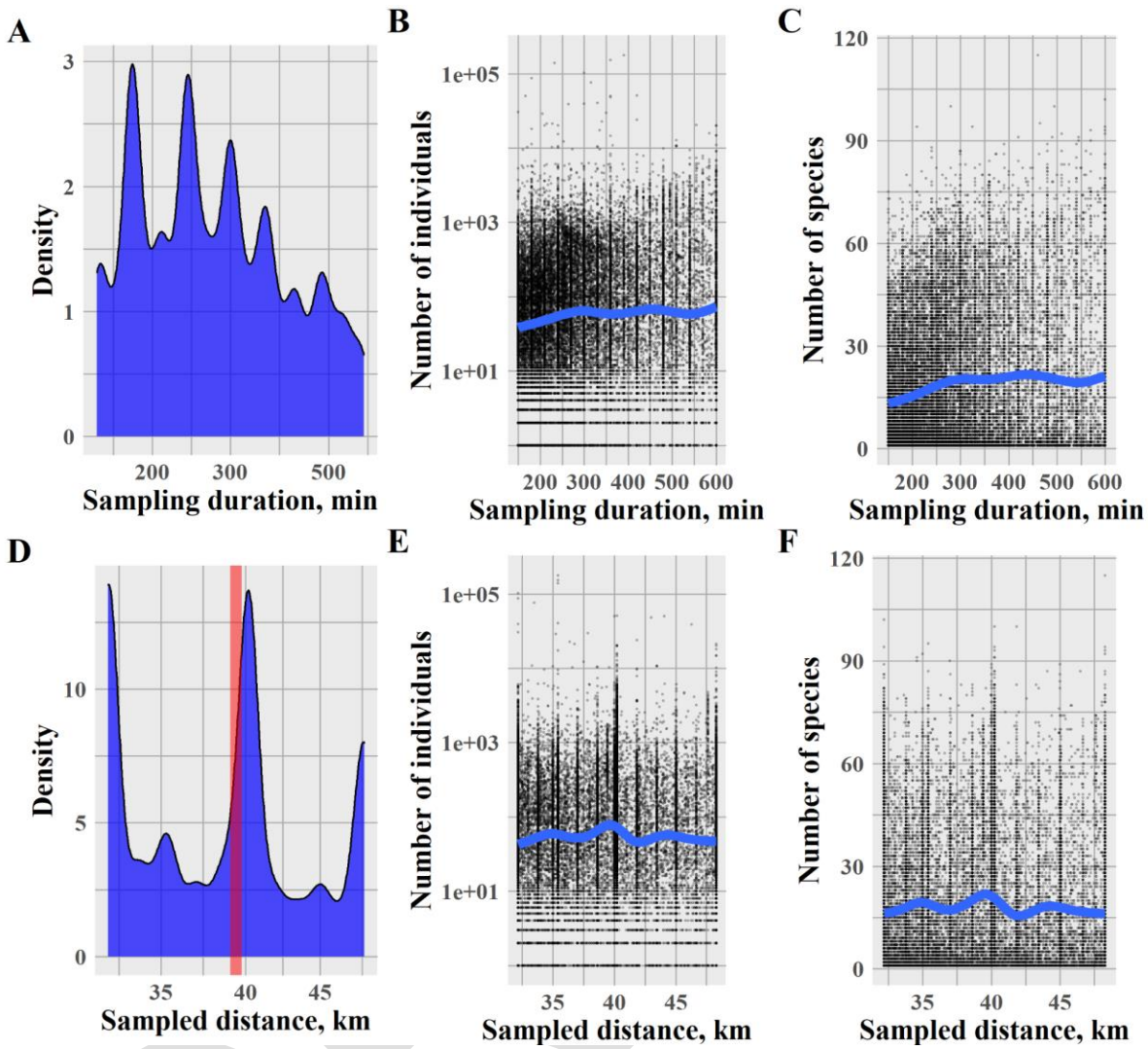

Fig. 13. Distribution of sampling duration (A) and distance sampled (D) (red line shows the assumed sampled distance in Breeding Bird Survey), their relationship with observed number of individuals (B, E), and species (C, F)

BBS and its rigorous sampling scheme succeed in representing more natural systems. In any case, the combination of the two datasets is beneficial from this perspective as it compensates for the biases of the separate datasets towards or against urbanized lands.

The most critical concern raised when combining the two datasets might be related to the differences in community structure described. Sampling effort is strictly standardized within the BBS protocol but is loosely defined within eBird. Sampling effort is important because a larger

effort leads to more data attributed to biases associated with species-area relationships (Hubbell 2001, Dengler 2009): a larger area contains more individuals, and the longer the duration of an observation, the greater the probability of detection is (Bibby et al. 2000). Thus, the area sampled, or distance as a proxy for this area, and duration of sampling should be good predictors of sampling effort. In the case of BBS data, sampling effort is controlled by the fixed amount of area sampled and duration of sampling: there are exactly 50 points, each of which is sampled for 3 minutes within a 400-m radius (Stanton et al. 2019). Whereas, in the case of eBird data, observations need to be filtered to minimize differences in sampling effort. It is, however, unclear whether both BBS and eBird approaches ultimately result in similar effort. For example, the peaks of sampling duration correspond to arbitrary values (180, 240, 300, 360, 420, 480 min) (Fig. 13A), as well as distance sampled (32, 40, 48 km) (Fig. 13D), which suggests that many values of distance and duration are not accurate but rather are just estimates provided by the observers.

There is also a difference in how one interprets spatial relationships between the two datasets: for BBS, it is assumed that each observation corresponds to a combined count of species from 50 similar point counts, whereas the eBird traveling protocol may denote a range of activities from a set of point counts to, presumably, continuous movement such as walking. On the other hand, eBird often collects the GPS-tracks of observers as they make observations during their travels. Using spatially explicit data, though, would add a level of complexity of data analysis beyond the scope of the present study.

These differences in sampling effort seem to be critical for the quality of data and corresponding patterns. Both distance sampled and duration of sampling are positively related to number of individuals and species. Even though the lower limit of sampling duration for eBird data was set to the assumed sampling duration of BBS data (i.e., 150 min), the number of individuals and the number of species observed as a function of the number of individuals was considerably lower in eBird counts compared to BBS. This pattern may be related to the data management applied to eBird data: while all observations in the BBS dataset were assumed to correspond to breeding birds, eBird data were additionally filtered to eliminate observations of species occurring outside of their breeding season, which resulted in a reduced set of data on species counts and detections. It might have also affected the shape of rarefaction curves: the observations of new species during a count were rarer in eBird data, compared with BBS.

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There are some other circumstantial factors that could affect the findings presented here. For example, time of day is an important bias that affects detection probability and any conclusions about species composition (Woodall 1997, Ohgushi et al. 2015). To maximize species detection, one would want to sample when there is peak detectability for the majority of species (Robbins 1981, Bibby et al. 2000). On the other hand, any protocol that attempts to maximize detections for all species will ultimately bias against other taxa that may be nocturnal or crepuscular since such species typically are inactive in the morning when most avian surveys are conducted (Amundson et al. 2014, La Sorte et al. 2018, Palacio et al. 2020). Thus, timing matters when comparing data from disparate sources, at least relative to studies that seek to measure taxonomic diversity. There is some evidence, though, that functional diversity metrics do not show considerable variation throughout the day due to the compensation of low detectability of some species by higher detectability of other species (unpublished data), which allows data collected at different times to be compared.

Another conventional rule is to conduct counts when weather conditions permit: bird activity drops significantly when there is precipitation or heavy winds (Elkins 2010, Anderson et al. 2015, Oliveira et al. 2018, Ellis and Taylor 2018). The BBS protocol is assumed to account for weather as there are established requirements when data can be collected. On the other hand, eBird does not impose such rigor and, thus, these two datasets cannot be compared relative to ambient conditions. For the purposes of the analyses presented here, I assumed that data from eBird were not collected under harsh weather conditions.

The data from BBS and, consequently, data from eBird that were filtered to emulate the BBS sampling protocol, have two more caveats that are related to the spatial extent of observations: first, long 39.4-km routes are unlikely to cover consistent habitat types throughout the route, which is highly undesired given that taxa differ in their habitat preferences and detectability in different habitats (Robbins et al. 1989, Thompson 2002, Glisson et al. 2017, MacLaren et al. 2018). Moreover, sampling distance determines the radius of buffer used to estimate the level of urbanization, but there is a high uncertainty about which part of a buffer corresponds to the area sampled. I assumed that area sampled by one count equaled, on average, 25.1 km^2, while the area of a 39.4-km-buffer is 4876.9 km^2 (i.e., only approximately 0.5 % of the area for which the urbanization level was estimated was sampled by the observer(s)).

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Second, 39.4 km is a long distance in which to sample. By definition, an ecological community is a set of species co-occurring in a given place and time and, presumably, connected via interspecific interactions (Magurran 2004). An interaction between individuals at a distance of nearly 40 km, even given their vagility, seems unlikely.

There are some reasons, though, that justify the use of such a large spatial extent. MCD12Q1 land cover classification with its spatial resolution of 500 m might be the only option for a continent-wide quantification of urbanization level. It means that making a scale of analysis finer would lead to a reduction in accuracy an estimate of level of urbanization — there would merely be a smaller number of pixels that would fall into a buffer around an observation point. If the buffer was too small, the urbanization level would approach a binary type of variable because a small area would either fall into an urbanized area or not rather than be covered by a gradient of urban land cover. Even with the size of buffers used here, there is a considerable amount of buffers that does not include urban areas at all (Fig. 11), and making the buffer size smaller would only result in making this distribution bimodal. Moreover, using a smaller spatial extent would end up reducing the amount of data available on community structure. In fact, the methodology associated with the BBS dataset already tends to underestimate species richness (Ankori-Karlinsky et al. 2022). Methodology that results in lower sampling effort would only increase the bias towards detection of common species and non-detection of rare ones (Watson 2003, Watson and Watson 2017), which would be in conflict with the goal of the present study.

Conclusions

Both the eBird and BBS datasets were combined so that eBird data could supplement BBS data in areas not covered by it. This potential bias affects both the geographic extent of the study to allow the inclusion of Mexico and accounts for the urban gradient whereby the BBS is assumed to sample primarily natural areas whereas eBird tends to be biased towards more urbanized areas. Having both urban and rural areas included allowed me to study the response of avian communities to urbanization. Even though eBird data were included, only those observations that were similar in sampling protocol to BBS were used. Likewise, only complete checklists that were collected while traveling at distance approximately equal to the length of a BBS route and with a similar sampling time were used.

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Even these efforts do not ensure either uniform spatial variation across the continent or the distribution across an urbanization gradient as one might expect under a null model of random sampling across the continent.

Observations from eBird, even after the appropriate filtering, exhibited considerably lower values of species richness and overall individual counts with higher variability, compared to BBS data. Rarefaction curves constructed for BBS observations were, on average, steeper, meaning that a similar sampling effort in BBS is expected to yield higher estimates of species richness.

All these facts must be considered when analyzing such data. One must ensure that diversity metrics used are insensitive to species richness. Also, one should account for the source of observations and analyze such data appropriately.

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FINDING A MEANINGFUL METRIC OF FUNCTIONAL RARITY: QUANTIFYING THE RELATIONSHIP BETWEEN REGIONAL NUMERICAL RARITY AND FUNCTIONAL DISTINCTIVENESS OF BREEDING BIRDS IN NORTH AMERICA

Introduction

Ongoing global mass extinction is widespread and is caused by global change leading to a rapid decrease in biodiversity manifested by habitat loss, climate change, pollution, invasive species, and overharvesting (Jackson 2001, Brooks et al. 2002, Geiger et al. 2010, Harley 2011, Galiana et al. 2014). The current average rate of vertebrate species loss is approximately two orders higher than natural background rates (Ceballos et al. 2015), the abundances of vertebrates and invertebrates has declined by 25% and 45%, respectively, since the pre-industrial era (Dirzo et al. 2014). There is a plethora of species currently threatened by extinction (Baillie et al. 2004), most of which are not likely to be preserved over the present century (Pimm et al. 1995) even despite conservation actions (Butchart et al. 2010). The scientific community, policy makers, and civil societies have been putting enormous effort towards mitigation of devastating species extinctions for decades and have attempted to develop efficient means to reach their targets (Wilson et al. 2006, Butchart et al. 2006, Rodrigues 2006). One of the valuable instruments for estimating extinction risk is an ability to quantify rarity (Rodrigues 2006). Species rarity, as estimated with data on abundance, occurrence, and range size, is commonly used as a proxy for species extinction risk, and provides managers with a means to prioritize conservation of the most rare species (Hartley and Kunin 2003).

Species threatened by extinction are a high priority of conservation biologists (Cardillo et al. 2006, Dulvy et al. 2014). The species that are thought to be the most vulnerable to extinctions are often rare due to a variety of reasons that include narrow geographic range (Grant and Grant 1997, Ricketts et al. 2005), having only one or a few distinct populations (Pinto et al. 2005), a small population size (Diamond et al. 1987), ongoing decline in population size (Peery et al. 2004), or being subject to overharvesting (Le Pape et al. 2017). Additionally, some taxa may not fall into these categories yet can remain threatened by extinction (Primack 2006). Such categories reflect different facets of rarity — namely low abundance, limited spatial distribution, and specialization (Rabinowitz 1981). Abundance and spatial distribution are used extensively

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by the International Union for the Conservation of Nature (IUCN) to assign conservation categories of vulnerability to extinction (Baillie et al. 2004, Rodrigues 2006, Mace et al. 2008).

Typically, the overall desired outcome of biological conservation is preservation of biodiversity (Humphries et al. 1995, Rands et al. 2010). Biodiversity in its broadest sense refers to the variety of genes, species, communities, and ecosystems (Heywood 1995, Purvis and Hector 2000), but often only corresponds to taxonomic diversity (i.e., diversity of artificially defined discrete species) (Hubbell 2001, Magurran 2004). Mitigation of the extinction crisis effectively means the preservation of taxonomic diversity as conservation actions are usually only applied to distinct species or populations (Chown et al. 2003, Primack 2006). Unfortunately, preservation of all threatened species does not seem realistic since the targets of modern conservation have not yet been met and decline in biodiversity continues. There are concerns that the amount of resources needed to preserve the whole range of biodiversity might not be feasible (Wilson et al. 2006, Rodrigues 2006, Butchart et al. 2010). When conservation goals cannot be met because of a lack of resources, a critical question is how to decide which species to prioritize for conservation activities.

Over the last few decades of research in ecology, investigators have demonstrated that ecosystems are complicated webs of interactions where a major disturbance, such as the extinction of a species, may result in a cascade of events that may lead to further extinctions (Säterberg et al. 2013) and, possibly, an overall collapse of the ecosystem (Miller 2005, Fowler 2010). Whether a collapse will occur often depends on the species entities (Donohue et al. 2017). For example, the effect of disturbances on keystone species is expected to have a disproportional outcome for ecosystems because such species have a unique position within food webs (Power et al. 1996, Simberloff 1998, Libralato et al. 2006, Harley 2011). Determining which species are keystone can be labor-intensive, and may often require controlled removal experiments that may or may not identify the most critical species (Power et al. 1996, Libralato et al. 2006). Yet, conservation efforts should not be limited to the keystone species exclusively (Gowdy 1997, Miller 2005). Ecosystem services is the construct that has been shown to be an effective instrument to illustrate the importance of natural biodiversity to human existence because of its role in providing food, clean air, water, and numerous other resources (Daily 1997, Costanza et al. 1997, Wallace 2007, Carpenter et al. 2009). Although ecosystem services is an anthropocentric term that focuses more on economic than ecology (Toman 1998), it is a function

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of ecosystem functioning (i.e., a sum of processes within an ecosystem (Scherer-Lorenzen et al. 2022)) which must be preserved to ensure stability and resilience of ecosystems to global changes (Schwartz et al. 2000, Srivastava and Vellend 2005, Cabello et al. 2012).

Taxonomic diversity is known to be one of the prerequisites for stable ecosystem functioning (Hooper et al. 2005, Balvanera et al. 2006, Brockerhoff et al. 2017), but it ignores the fact that different species have different functional roles and, more importantly, have different levels of redundancy in the functions they perform. The redundancy of species is important because it ensures ecosystem functioning when some species are removed from the ecosystem (i.e., through extinction), as well as highlights the importance of species with unique functional features — these species must be preserved since their extinction cannot be replaced by other species in a community (Yachi and Loreau 1999, Sanders et al. 2018).

Considering functional roles and redundancy of taxa is known as functional diversity: it views the species in a community as points or distributions within a multidimensional space of functional traits rather than merely discrete notions of species entities (Díaz and Cabido 2001, Diaz et al. 2007, Carmona et al. 2016). There are many metrics of functional diversity within biological communities, among which are functional richness, evenness, and divergence (Mason et al. 2005, Villéger et al. 2008, Cadotte et al. 2011, van der Plas et al. 2017). Functional richness refers to the whole range of functional traits inherent in species comprising a community; functional evenness corresponds to a distribution of such traits in multidimensional space; and functional divergence shows how far, on average, species are within a trait space from some community centroid (i.e., an abstract hypothetical species that represents the community niche), implying a range of ecological functions and environmental conditions under which a community can function effectively. Functional divergence is the metric that best captures unique characteristics of individual species based on quantitative assessment of species distinctiveness within a community (Villéger et al. 2008).

Functional rarity is a derivative of functional distinctiveness which is defined as a “feature of a species that integrates both functional distinctiveness and taxonomic scarcity at local scales, or both functional uniqueness and taxonomic restrictedness at the regional scale [...], functionally rare species possess the highest functional rarity value in the community (local scale) or in the regional pool (regional scale)” (Violle et al. 2017). However, Violle et al. (2017) provide a vague definition for estimation of functional rarity, limiting their explanation to a statement that

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functional rarity is some function of species' functional distinctiveness and numerical rarity either at local or regional scales, without specifying the mathematical function itself. In a subsequent work, Violle's team provides the means to characterize functional rarity (Grenié et al. 2017), again, without any specifications of the mathematical transformations needed to estimate functional rarity, merely stating that "functional rarity (is) the average of functional uniqueness and taxon restrictedness per site" (Grenié et al. 2017, p. 1368) and leaving the definition of functional rarity open to interpretation.

In the work presented here, I suggest prospective metrics of functional rarity that incorporate numerical rarity based on abundance and functional distinctiveness, which could be used to quantify how critical a species' conservation is for maintaining functional diversity and ecosystem functioning and would allow one to identify communities composed of functionally rare taxa. To do so, I hypothesize that (1) species functional distinctiveness is related to its numerical rarity, (2) a metric of functional rarity reflects numerical rarity and functional distinctiveness at species and community levels. My goal is to provide a means to quantify functional rarity in communities, which could help to find the communities that are most vulnerable to a loss of ecosystem functioning. The study's aim is to test whether protection of numerically rare species that are identified by modern conservation practices is expected to result in preservation of functional diversity.

Methods

Numerical rarity metric. Numerical rarity can be calculated based on different parameters such as, for example, absolute or relative abundance within a community that reflect population size (Gaston 1994). Numerical rarity must be inversely related to abundance within a community to reflect rarity. In fact, abundance itself is a metric of rarity, but some additional mathematical transformations are needed if one attempts to use rarity as a weight. Surprisingly, few methods have been proposed to estimate numerical rarity compared with an abundance of methods to determine diversity (Legendre and Legendre 1998). Most estimators of numerical rarity are binary (i.e., reflect whether a species is rare or common based on some arbitrary threshold (Gaston 1994, Magurran 2004, Balbuena et al. 2021)), others are difficult to interpret (Leroy et al. 2012). In this work, I estimated rarity in two ways. First, I used a metric that is the inverse of species abundance on a log-scale, which I term log-rarity:

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$$w_{log} = \frac{\log(N_i/N_{\max})}{\min[\log(N_i/N_{\max})]},$$

where *N* corresponds to species abundance, either absolute or relative.

I also used Leroy et al. (2012) rarity weight that assigns weights based on species absolute abundance with a rarity cut-off point that corresponds to some arbitrary percentile of abundance (set to 25th in the work presented here): weights of taxa with abundance lower than the cut-off level exponentially increase with distance between their abundance and the cut-off level rarity weight (Leroy et al. 2012, 2013).

Functional distinctiveness metric. Functional traits of species are traits that affect fitness to the environment and are assumed to determine the species influence on habitat, other species, and ecosystem functioning (Violle et al. 2007). Functional distinctiveness is a metric of uniqueness of species' functional traits compared to the collective set of traits exhibited by a community overall. Thus, functional distinctiveness is a characteristic of a species being dissimilar from other species within community (Violle et al. 2017). To quantify a species functional distinctiveness, one must calculate the distance between a species and a centroid (i.e., a set of mean species traits) from the community (Villéger et al. 2008). While it might seem rather straightforward, the determination of distinctiveness gets increasingly more difficult when the data on traits are stored as different types of variables.

In this work each species was described using three different types of variables: continuous (e.g., mean body mass, maximum lifespan, mean age of first breeding attempt, etc.), categorical (e.g., nest type, diet type, breeding system), and discrete distributions (e.g., food items, feeding method, nest substrate, etc.). The community centroid consisted of variety of data types rather than a vector of mean values of variables. Continuous variables and distributions were represented as mean values, but categorical variables were summarized as vectors of frequencies of each possible value possessed by a community. Thus, the community centroid was usually calculated as a combination of mean trait values weighted by species abundances (Villéger et al. 2008). However, since numerical rarity is also based on species abundances, the centroid was constructed as both weighted and unweighted.

Functional distinctiveness was calculated for each combination of species and traits (i.e., trait-distinctiveness), and represented how far each species was from the centroid on an axis of

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functional trait. Trait-distinctiveness was calculated as the absolute difference between species and centroid values for continuous variables, as mean similarity among different categories weighted by frequencies of these categories within a community for categorical variables, and as the inverse overlap of a distribution possessed by a species with a mean distribution within a community for discretely distributed traits. Trait-distinctiveness was then standardized using z-scores for each trait and species that corresponded to the divergence of each species trait-distinctiveness value. The z-score was transformed into a probability of observation of such a score or smaller being obtained by chance within a standard normal distribution. This process allowed the result to be more convenient to interpretation (scores were standardized between 0 and 1, where 0.5 would refer to a species that yields the mean community trait value). Functional distinctiveness of a species was then calculated as a mean deviation of trait-distinctiveness of a species. The detailed formulas are also provided in Chapter 2.

Potential functional rarity metrics. A set of potential metrics of functional rarity within communities was tested in the study presented here.

A probability of interspecific encounter (PIE) could be the most informative metric of taxonomic diversity because it can be inferred in a fashion that if there are more rare species in a community, then the probability of an interspecific encounter is lower (Hurlbert 1971). At the level of community-wide metrics, functional divergence and its product with PIE were tested as a metric of functional rarity.

At the level of different species, functional rarity was estimated as a mean functional distinctiveness weighted by rarity weight, either log-rarity or Leroy's rarity (Leroy et al. 2012). Also, modified functional divergence was used, where species abundance weights are substituted with weights of numerical rarity.

Assuming that there is a linear relationship between species functional distinctiveness and numerical rarity, a correlation coefficient between these two metrics of species comprising a community was suggested as a metric of functional rarity, where a positive value would assume that species rarity was related to functional distinctiveness and that such a community would be in need protection of rare species to preserve functional distinctiveness. To justify use of this metric, linearity of such relationship had to be confirmed, otherwise its use could lead to a misleading inference.

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The coefficient of correlation is a metric of association between two variables, but it does not correspond to values or the range of values. Metrics of functional rarity are expected to reflect both functional distinctiveness and numerical rarity of species that compose a community. Thus, I propose using the dimensionless mean value of products of functional distinctiveness and numerical rarity: such values are difficult to interpret, but this approach allows one to compare communities as this metric will be higher in communities composed of more numerically rare and functionally distinctive species.

Data. The relationship between numerical rarity and functional distinctiveness and performance of different metrics were tested using data on occurrence and local counts of 680 bird species across North America between 2000 and 2021. The data were taken from two comprehensive continent-wide open-access citizen-science datasets: North American Breeding Bird Survey (BBS) and eBird.

BBS is a joint effort led by the United States Geological Survey and Canadian Wildlife Service aimed to detect changes and trends in North American bird populations (Ziolkowski et al. 2010). BBS has been conducted every year since 1966 (except 2020 due to the global COVID-19 pandemic) on fixed 39.4 km routes that were selected at random among secondary roads of each state or province (Boulinier et al. 1998b); the data are collected from approximately 3000 separate routes in the contiguous United States and Canada each year. Typically, surveys are conducted during June, although late May is acceptable in southern regions and early July in northern regions (Sauer and Link 2011). Each BBS route consists of 50 points 800 m apart from each other: the observers are asked to conduct the survey of all birds seen and heard within a 400-m radius of each point for 3 min starting 30 min before local sunrise (Sauer and Link 2011).

eBird is a popular platform that allows birdwatchers around the world to keep track of their observations of bird species in exchange for eBird to collect data on species counts (Sullivan et al. 2009, 2014). Unlike BBS, which is an example of a structured citizen-science project with strict methodology dictated by targets of the program, eBird is a semistructured source of data (i.e., observers collect data on any suitable occasion, with any amount of effort, but are asked to report sampling effort) (Kelling et al. 2019). While this approach is data-driven, as opposed to hypothesis-driven when the collection of data is adjusted relative to question asked (Hochachka

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et al. 2012), it allows one to collect large volumes of data that can be later filtered relative to desired requirements of sampling (Johnston et al. 2021).

The observations from eBird were filtered in such a way that they would be similar in sampling effort to data collected by BBS: only complete checklists were used (i.e., all species observed were recorded) that were collected while traveling at distances between 32 and 48 km with a time of sampling between 150 and 600 minutes. Observations from Canada, U.S., and Mexico were used among countries available. All observations that likely overlapped with BBS observations (i.e., conducted on the same day and within 0.1° from each other both by latitude and altitude) and all off-shore observations were eliminated. Also, unlike the BBS dataset where all species were considered to be currently breeding, eBird data are continuously collected year-round. eBird datasets suffers from the limitation that timing of breeding varies among taxa and migrants can often co-occur with resident conspecifics, clouding a determination that birds being observed are actually breeding. To address some of these limitations, approximate breeding period was determined for each species using information provided by the Birds of the World project (https://birdsoftheworld.org/). This literature survey combines data from peer-reviewed sources that are edited by experts familiar with each particular taxon. Thus, all observations falling outside of the estimated breeding season were ignored.

Bird conservation regions (BCRs) were used as the operational definition of a region to avoid using ecologically meaningless political boundaries. BCRs were defined by the North American Bird Conservation Initiative to optimize the conservation efforts and reflect homogeneity of bird communities, habitats, and resource management issues (Sauer et al. 2003). The two datasets use different taxonomies so data were combined into a unified taxonomy. Overall, there were 86,406 observations accompanied by data on year, data source, and BCR. Analyses were conducted separately for each of 1,020 combinations of year and BCR to account for temporal population dynamics and differences in regional species pools. Local (i.e., at the level of separate observations) numerical rarity and functional distinctiveness were not analyzed because I did not expect it to be relevant for conservation purposes: even if a species is locally rare or functionally distinctive, it does not necessarily mean that this species was in a need of protection but rather that it is locally rare or might have been observed accidentally.

Variability in species detectability could significantly affect the observed results creating a bias towards more secretive species instead of species that have low abundances (Palacio et al.

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2020). To account for this issue, numerical rarity and a weighted centroid for calculations of functional distinctiveness were based on median estimates of regional species abundance that accounted for different sources of variability in detectability (Stanton et al. 2019).

To estimate functional distinctiveness, 23 functional traits were used. These traits were assumed to reflect resource requirements, intensity of species' effects on ecosystems, and biotic interactions, and included the following: diet type, diurnal and nocturnal feeding, diet items, feeding methods, feeding substrate, nest type, nest substrates, breeding system, chick development at hatching, nest aggregation, clutch size, first breeding age, number of clutches a year, breeding success, adult annual survival, mean biomass, maximum lifespan, hand-wing index, kleptoparasitism, nest parasitism, and the extent of dependency on other species for building a nest (Table 2). The data on these traits were compiled from a set of peer-reviewed resources describing biology and life history of North American birds (Ehrlich et al. 1988, Wilman et al. 2014, Sheard et al. 2020, Billerman et al. 2022). In a case when a trait value was unknown, it was assumed to be similar to its nearest relative taxa (e.g., a mean value for a genus).

Analysis. The relationship between regional numerical rarity and functional distinctiveness was visualized using values of regional species numerical rarity and functional distinctiveness only for those combinations of year and BCRs that had more than 5 observations (n = 950). Unique fitted lines were drawn using generalized additive models (GAMs) with cubic regression splines, assuming that the relationship might have non-linear humps. Overall trend was drawn using a GAM based on all observations with smoothed confidence intervals. Direction of a linear trend was tested using linear mixed-effect regression accounting for random effects of year and BCR.

Potential metrics of functional rarity were calculated separately for each observation of a community. Each of them needed two elements: a vector of numerical rarity values and a vector of functional distinctiveness values for each species comprising a local community. Since the regional scale was analyzed, these values were drawn from a respective combination of year and BCR (i.e., the parameters represented species at a regional level in a given year). To test whether a potential metric of functional rarity adequately related to both numerical rarity and functional distinctiveness and was higher for communities where regionally rare and distinctive species prevailed, its relationship was tested with the following: Hurlbert's PIE (which was assumed to

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reflect the overall rarity within a community (Magurran 2004)), mean rarity weight of a community, species richness (to test whether a metric was independent of it), mean and maximum functional distinctiveness within a community. Only unweighted functional distinctiveness was used in the calculations at this stage to avoid double accounting for species abundances, because species abundance was already accounted for when calculating its numerical rarity.

A suitable metric of functional rarity was expected to be negatively related to PIE, weakly related (or, ideally, not related at all) to species richness, and positively related with mean numerical rarity and functional distinctiveness of species comprising the community. These relationships were tested using linear mixed-effect regression accounting for a fixed effect of source of the data (BBS or eBird as a categorical variable with contrast coding system) and for random effects of year and BCR.

To visualize a correspondence of candidate functional rarity metric value assigned to a community to functional distinctiveness and numerical rarity of species comprising that community, the initial dataset was transformed to contain observations of individual species rather than communities, species' metrics of rarity and functional distinctiveness, and values of candidate functional rarity metrics of communities where that species occurred. The transformed dataset was used to test whether a candidate metric reflected the distribution of numerical rarity and functional distinctiveness of species occurring within that community using a linear mixed-effect model that accounted for a fixed effect of source of the data and random effects of year and BCR.

Results

The relationship between regional numerical rarity and functional distinctiveness was significantly positive irrespective of a rarity metric used (Table 4). The analysis was also repeated for functional distinctiveness calculated for an unweighted-by-abundance centroid because constructing a centroid of functional traits implied weighting trait values by species abundances, which could distort the results and introduce correlation between numerical rarity and functional distinctiveness (i.e., both being a function of species abundances). It is notable that using unweighted centroids makes the relationship less steep (Fig. 14 C and F) compared to a weighted procedure (Fig. 14 B and E), and the relationship of these two metrics is more

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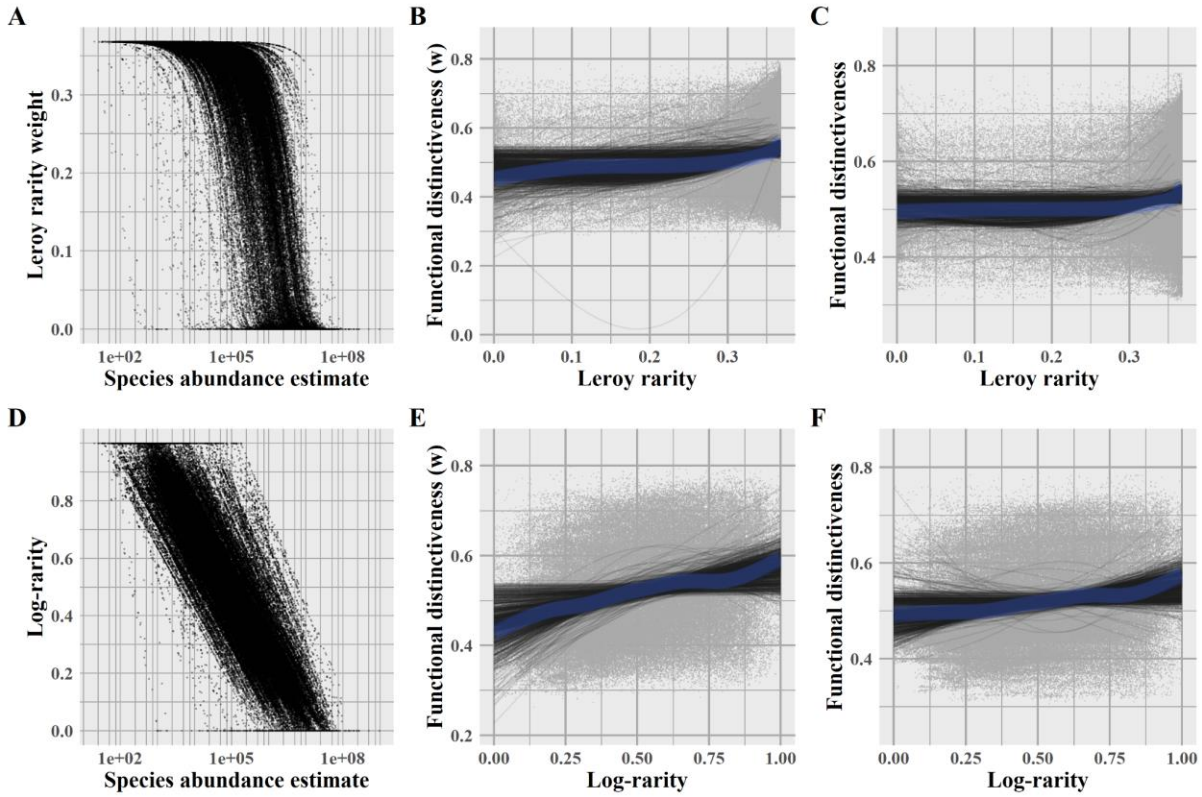

Fig. 14. Relationship between estimates of species regional abundance and rarity metrics (A, D), numerical rarity and functional distinctiveness, either based on weighted (B, E) or unweighted (C, F) community centroids

apparent when using log-rarity relative to Leroy's weight as a metric of numerical rarity (Fig. 14 E and F).

Among the candidates for a metric of functional rarity, the mean product of functional distinctiveness and log-rarity was consistent with the majority of presumed requirements: it was negatively associated with probability of interspecific encounter (as low values of PIE are assumed to reflect high overall rarity within a community), positively related to mean Leroy rarity weights and log-rarity, mean and maximum functional distinctiveness of species within a community. This metric was only not significantly related to species richness when all data were considered indiscriminately, but in a mixed-effect model with fixed effect of data source the

Table 4. Fixed effect estimates and variance of random effects in mixed-effect linear models fitted to explain weighted or unweighted functional distinctiveness as a function of metrics of numerical rarity

Model	Coefficient	Value	95% CI		p-value	Random effect variance	
			2.5% CI	97.5% CI		Year	BCR
Unweighted functional distinctiveness							
1	Intercept	0.498	0.489	0.507	<0.001	0.000	0.001
	Leroy rarity	0.074	0.045	0.103	<0.001	0.008	0.008
2	Intercept	0.494	0.485	0.502	<0.001	0.000	0.001
	Log-rarity	0.052	0.037	0.067	<0.001	0.000	0.002
Weighted functional distinctiveness							
3	Intercept	0.460	0.450	0.470	<0.001	0.000	0.001
	Leroy rarity	0.224	0.193	0.255	<0.001	0.002	0.009
4	Intercept	0.450	0.442	0.458	<0.001	0.000	0.001
	Log-rarity	0.135	0.120	0.150	<0.001	0.000	0.002

values for observations from eBird were not related to species richness, but the metric was positively associated with species richness in BBS observation (Appendix C). Another candidate metric meeting the presumed requirements was Pearson's correlation coefficient between functional distinctiveness and log-rarity: it was positively associated with mean log-rarity, mean and maximum functional distinctiveness of species within a community, and did not exhibit any significant relationship with species richness (Fig. 15, Appendix C). Yet, this metric showed no relationship with PIE (unless the data was limited to observations from eBird, in which case there was negative relationship), and the values of this metric of observations from BBS did not show any directional relationship with mean Leroy rarity weight of species within a community (Appendix C).

Other potential metrics met fewer of the assumed requirements for a good metric of functional rarity: a product of PIE and functional divergence failed to meet any of such requirements; mean functional distinctiveness weighted both by Leroy rarity weight and log-rarity exhibited desired relationship with PIE, mean log-rarity, mean and maximum functional distinctiveness, but not with mean Leroy rarity and species richness; functional divergence with species weights substituted with either Leroy rarity or log-rarity were negatively related to PIE

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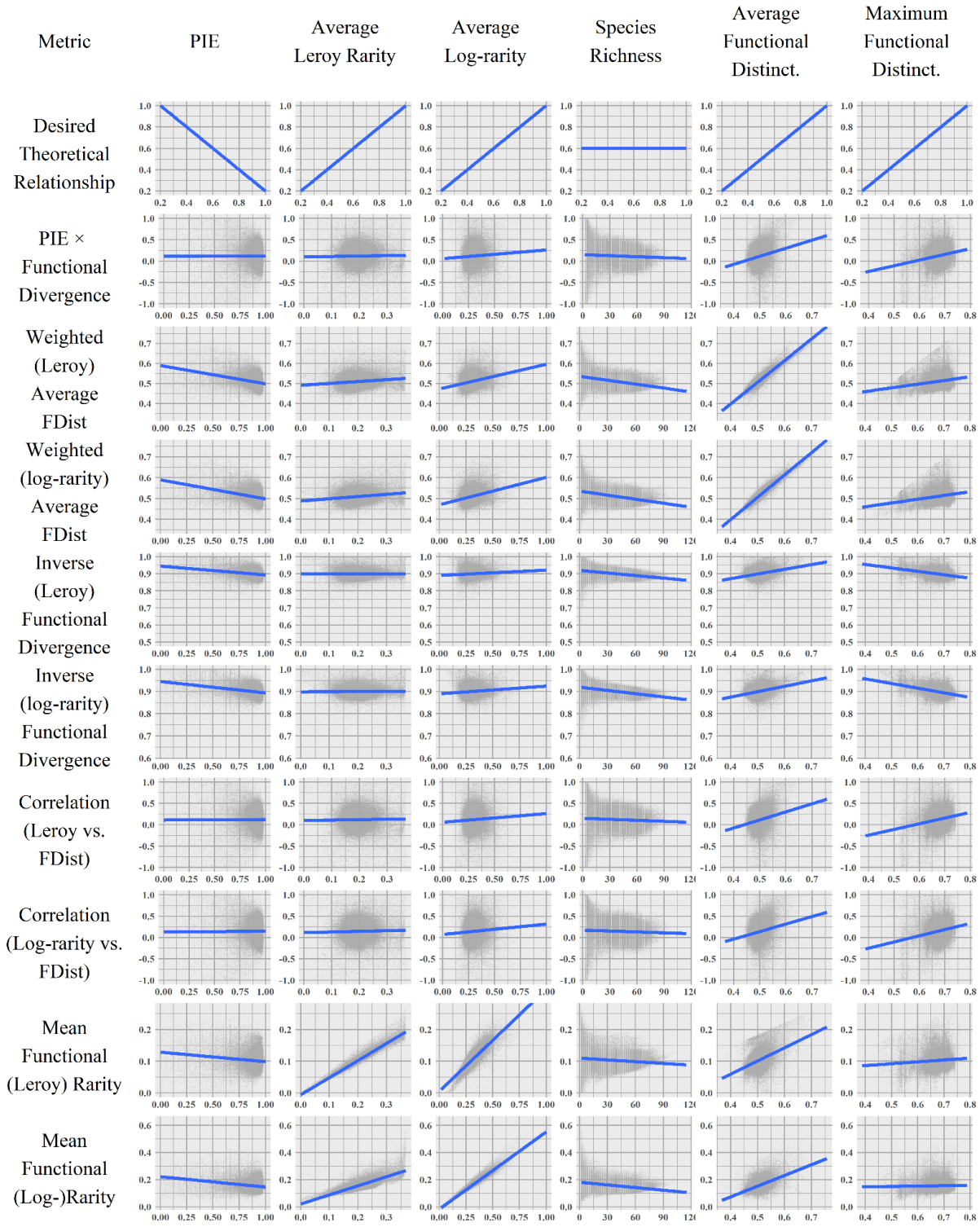

Fig. 15. Relationships between candidate metrics of functional rarity and community parameters

and positively related with mean functional distinctiveness, but failed to show required relationships with mean Leroy rarity and log-rarity, species richness, and maximum functional distinctiveness; Pearson's correlation between functional distinctiveness and Leroy rarity was not associated in a desirable fashion with PIE, mean Leroy rarity, and species richness; and mean product of functional distinctiveness and Leroy rarity failed to meet the requirements for a directional relationship with PIE and was positively associated with species richness (Appendix C).

Functional rarity is expected to reflect both functional distinctiveness and numerical rarity of species that constitute a community. Only mean product of functional distinctiveness and both Leroy rarity and log-rarity met this requirement (Fig. 16), although when the data was limited to BBS observations, this metric was not directionally related to unweighted functional distinctiveness of species within a community (Appendix C). Pearson's coefficients of correlation between functional distinctiveness and either Leroy rarity or log-rarity were positively associated with both weighted and unweighted by species abundance functional distinctiveness, but relationships of these metrics with Leroy rarity and log-rarity of species within a community were inconclusive (Appendix C). Same applies to mean functional distinctiveness weighted by either Leroy's rarity or log-rarity. The only exception among these four candidate metrics is coefficient of correlation between functional distinctiveness and log-rarity: when all data were considered indiscriminately from their sources, there was a positive relationship between this metric and log-rarity (Appendix C). Among other candidate metrics, the product of PIE and functional divergence was associated with neither numerical rarity metrics nor functional distinctiveness of species, while mean functional distinctiveness weighted by numerical rarity metrics were only positively associated with both weighted and unweighted functional distinctiveness, and inverse functional divergence was only positively associated with unweighted functional distinctiveness (Appendix C).

Discussion

Despite the fact that the quantification of functional rarity is complicated, this concept is of utmost importance in modern conservation. Rare taxa are under the greatest threat of extinction, since low abundance and/or limited spatial range of such taxa makes them most vulnerable to

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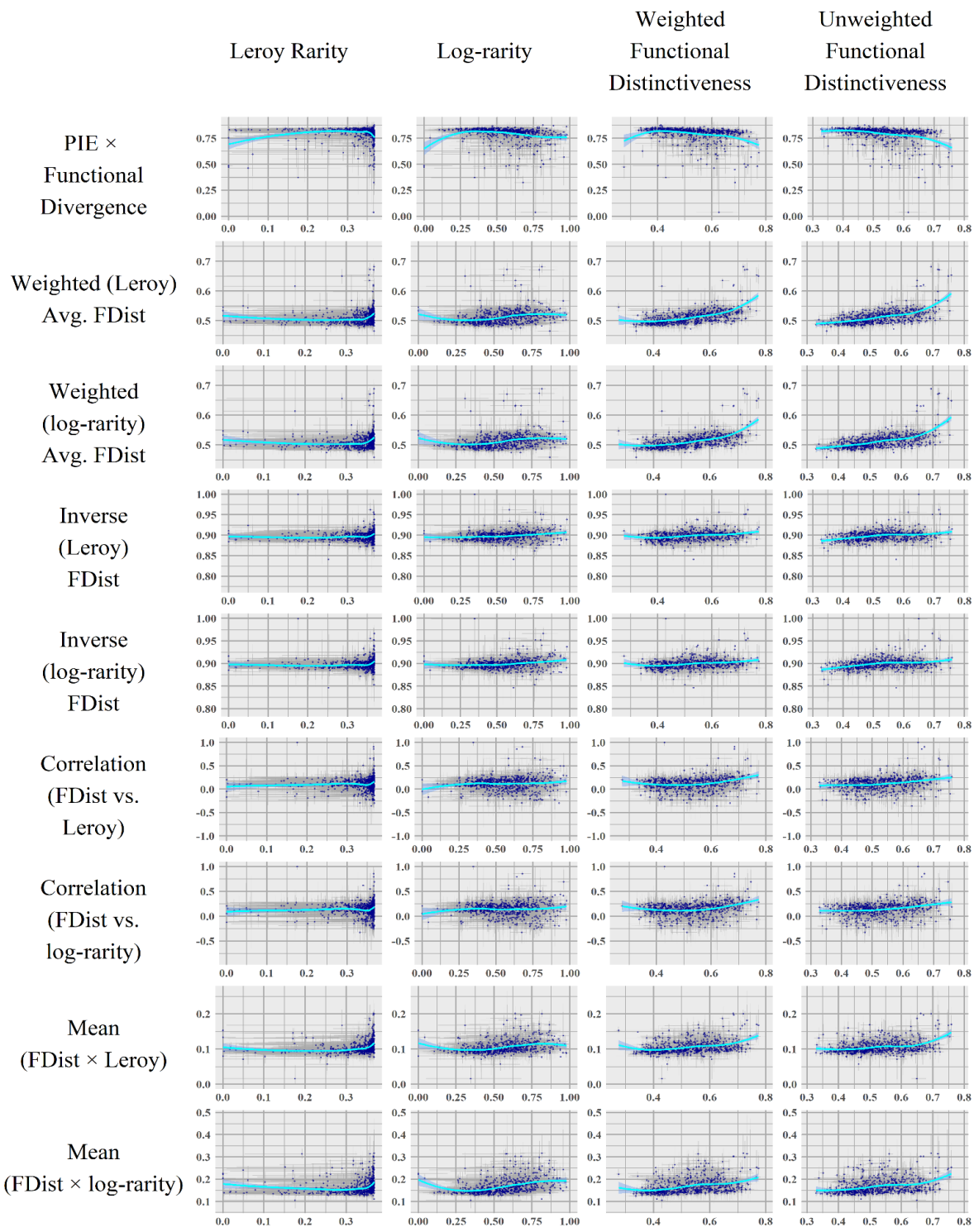

Fig. 16. Relationships between median (± quartile and range without the outliers) values of species' numerical rarity and functional distinctiveness, and median values of candidate functional rarity metrics of communities where these species occur

stochastic events that are expected to become more frequent due to global changes (Thorn et al. 2020). There is a wide theoretical support for a prediction that extinction of rare taxa may have devastating effects on ecosystem functioning. Both rare and common taxa are similarly important when ecosystems are in their native states (Chapman et al. 2018), but the admix of ongoing global changes will certainly affect such ecosystems, potentially shifting importance of rare and abundant taxa. Rare taxa are in high risk under such circumstances, and rare taxa often provide an insurance effect by supporting functional roles of common species (Petchey et al. 2007, Jousset et al. 2017), and can perform important ecological roles themselves (Loiseau et al. 2020). This fact should certainly be acknowledged in conservation policies given that the majority of North American birds can be considered rare (Valle et al. 2018).

This is a critical issue because species extinction will also put ecosystem functioning at risk, and hence ecosystem services as well (Leitão et al. 2016, Dee et al. 2019). The functional diversity framework helps connect the value of biological diversity for ecosystem functioning and estimates the importance of species with respect to functional traits and redundancy or uniqueness of a species within a community (Díaz and Cabido 2001, Carmona et al. 2016). There is much concern that species extinction will affect functional diversity in ecosystems (Toussaint et al. 2021), and that current conservation actions do not protect functional diversity to its full extent (Devictor et al. 2010, Grenié et al. 2017). There is, however, still a gap in our understanding of the relationship between rarity and functioning (Petchey and Gaston 2006, Mouillot et al. 2013), an area of modern ecology still being explored (Chao et al. 2014, Kondratyeva et al. 2019, Veron et al. 2021, Pavoine and Ricotta 2021).

The work presented here has demonstrated that there is indeed a positive relationship between numerical rarity and functional distinctiveness in avian taxa within North America, which is concordant with theoretical predictions (Mouillot et al. 2013, Dee et al. 2019). The simplest explanation for the patterns found would be that functional distinctiveness of a species is a function of its rarity, or even just an artifact of methodology of quantification of functional distinctiveness. Indeed, functional distinctiveness of a species was calculated as its distance to a community centroid within a multidimensional space of functional traits, corresponding to mean values of traits inherent to individuals within a community (i.e., weighted by species abundances, so that rare species are further from a centroid, assuming an association between species

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abundances and their functional traits). To account for this caveat, unweighted functional distinctiveness was also calculated for each species, weighting each species in a regional pool equally, and this did not affect the inference (i.e., there is a positive relationship between numerical rarity and functional distinctiveness). A more complicated explanation would be that functional distinctiveness itself predicts species rarity, and it is possible to find theoretical support for this assumption from the perspective of classic niche theory. Species functional traits are related to niches predicting resource consumption, biotic interactions, and, to some extent, habitat requirements (Dehling and Stouffer 2018). Environmental conditions might also act as environmental filters, allowing only those species that have appropriate traits to exist (Laughlin et al. 2012, Fowler et al. 2014). This would result not only in a non-random arrangement of functional traits within species, but also in variability in abundances because some species would find their environment to be more suitable than other species (McGill and Collins 2003, McGill et al. 2006, Mouillot et al. 2013, Baastrup-Spohr et al. 2015, Umaña et al. 2017). Moreover, there is a considerable body of literature suggesting that environmental filtering does predict the shape of avian communities (Kaisanlahti-Jokimäki et al. 2012, Stracey and Robinson 2012, Evans et al. 2018). Functional distinctiveness, by definition, is the uniqueness of species' traits, so that it seems plausible that functionally distinctive species are, to some extent, specialists — and specialists are known to have low abundances (Bock 1984).

Irrespective of the underlying mechanisms that relate species rarity and functional distinctiveness, there is an important implication to conservation. First, it implies that extinction is expected to threaten functional diversity disproportionately (Thorn et al. 2020, Toussaint et al. 2021): since rare species are more vulnerable to extinction and if they also happen to be functionally distinctive, their extinction will lead to a rapid loss of functional diversity leading to a loss in ecosystem functioning. It suggests that such communities should be prioritized where there is a strong relationship between rarity and distinctiveness, especially if some species are extremely rare (Fattorini 2011). It also means that numerical rarity of species may be used as an indicator of species distinctiveness: calculating functional distinctiveness is methodologically complicated and requires the data that might not be available for all taxa, but a relationship between numerical rarity and functional distinctiveness implies that protection of numerically rare species — as is typically prioritized — is expected to result in preservation of functional diversity, although such an assumption might be idiosyncratic (Toussaint et al. 2021).

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Quantification of the relationship between numerical rarity and functional distinctiveness might be of vital significance for conservation management: it would provide a means to optimize the effectiveness of conservation efforts that wish to prioritize particular communities where there are many regionally both functionally distinctive and numerically rare taxa. A metric that indicates co-occurrence of rare and distinctive species within a community would indicate functional rarity in these communities — a metric that has been concluded to be worthy of development for the sake of justified conservation efforts (Carmona et al. 2017). Yet, there is no consensus on which metric to use to quantify functional rarity of communities. The work presented here tested five candidate metrics: a product of PIE and functional divergence, where PIE was thought to be an optimal representation of the distribution of rarity within a community (Dorado et al. 2011) and functional divergence expected to represent functional distinctiveness of species (Petchey et al. 2004); weighted by rarity mean functional distinctiveness; inverse (i.e., weighted by rarity instead of abundance) functional divergence; Pearson's coefficient of correlation between species rarity and distinctiveness within a community; and mean product of numerical rarity and functional distinctiveness of species. Rarity was estimated with either Leroy's rarity weight and log-rarity despite Leroy's metric not being the most optimal since it tends to be clumped near extreme values (Fig. 14 B and C, 16), leading to a loss of information. Functional distinctiveness, in turn, was calculated for unweighted centroid to avoid the methodological bias (i.e., since abundance weights of species were already accounted for when estimating numerical rarity).

Among the candidate metrics tested, a correlation coefficient and mean product seem to be the most suitable compared to other potential metrics. First, they relate to both functional distinctiveness and numerical rarity of species in a community (Fig. 16), which is the most important assumption when quantifying functional rarity. Second, they show the desired relationships with community-level metrics of taxonomic and functional diversity (Fig. 15). Finally, a correlation coefficient is relatively easy to interpret, so that a positive value implies that there is a positive relationship between functional distinctiveness and rarity (i.e., preservation of the rarest taxa is expected to result in protection of functional diversity). Besides, both of these metrics are not related to species richness of communities analyzed, as was the case for other metrics. Even though rarity weights were standardized for calculations, there are some constraints related to calculations: when species richness is higher, standardized rarity weight

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will have more similar values leading to results that are difficult to interpret. In summary, a correlation coefficient and mean product of functional distinctiveness and numerical rarity might be the most convenient options for quantifying functional rarity.

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HOTSPOTS OF AVIAN FUNCTIONAL RARITY ACROSS NORTH AMERICA: EVIDENCE OF URBANIZATION AFFECTING UNIQUE SPECIES OVER TWO DECADES

Introduction

There are numerous ways by which human population growth affects natural ecosystems, and land use change might be the most direct and certainly one of the most significant facets of global change that put wildlife at risk (Newbold et al. 2015). Land use change has two main components: firstly, habitat fragmentation reduces connectivity among patches of suitable habitats, which leads to a slow decline in abundances and restricted gene flow within populations (Taylor et al. 1993); and, secondly, areas of suitable habitat shrink, thereby supporting fewer individuals — at some level there is eventually insufficient habitat for a species to persist (Bender et al. 1998). While there are ambiguous results on the effects of habitat fragmentation *per se* (Fahrig 1997, 2003), there is agreement on the negative effects of habitat loss such that is quantified and included in conservation policies (Brooks et al. 2002, Airoldi et al. 2008).

Urbanization represents the most profound degree of land use change — a process during which any previously existent habitat is substituted with dense urban infrastructure built-up and the creation of impervious areas (Antrop 2004, Alig et al. 2004, Aronson et al. 2014). When considered as an ecosystem, urbanized areas are not be fully sustainable since biodiversity is reduced and critical links missing from "healthy" food webs — primary resources are in short supply and disturbance is too great to maintain biodiversity (McKinney 2002, Palacio et al. 2018). Thus, urbanization, land use change, and overall global changes are the leading causes of mass species extinction that is currently occurring globally, increasing extinction rates far beyond natural background levels (Ceballos and Ehrlich 2002, Ceballos et al. 2015).

Extinction of local populations results in a rapid decrease in biological diversity and a decline in overall population size, making many taxa rare and more vulnerable to stochastic events and ultimate extinction (Diamond et al. 1987, Melbourne and Hastings 2008, Schreiber et al. 2019). Land use change that leads to extinction events causes a loss in ecosystem functioning, which ensures supply of clean water, food, and numerous ecosystem services (Cardinale et al. 2002, Hooper et al. 2005, Balvanera et al. 2006).

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Each species has a unique combination of life history traits that determine its habitat requirements, interactions with other species, and role in ecosystem functioning (Violle et al. 2007). Some species can possess a combination of traits that overlap with other species (i.e., functionally redundant), but this overlap is never 100% because of niche partitioning of coexisting species (Schoener 1974, Knowlton and Jackson 1994). Taken together, species or individuals that comprise a community form a convex hull within a multidimensional space of their functional traits, corresponding to a range of processes and resources that is being conducted and consumed by a community (Cardinale et al. 2011, Scherer-Lorenzen et al. 2022). This perspective is commonly referred to as "functional diversity", as it considers species as points or distributions within a space of functional traits at different distances among each other rather than discrete and equally different notions of species within a taxonomic diversity framework (Carmona et al. 2016). Under the functional diversity framework, one can quantify the functional uniqueness and/or redundancy of species in a community that correspond to the extent to which a species performs a functional role similar to other species in a community (Cadotte et al. 2011, Carmona et al. 2016, Dehling and Stouffer 2018). It provides a theoretical explanation of the relationship between species richness and ecosystem functioning and highlights the value of protecting biodiversity — at least, the most unique facets of it (Díaz and Cabido 2001, Díaz et al. 2003, Cardinale et al. 2011, Cabello et al. 2012, Brockerhoff et al. 2017).

Species that have small range and population sizes are the ones most threatened by extinction (Mace et al. 2008, Schreiber et al. 2019). Thus, it is possible to predict extinction risk based on numerical rarity — assuming that rare taxa are more vulnerable to stochastic disturbances that could lead to extinction, evaluation of rarity can be used to prioritize conservation efforts aimed at preserving rare taxa (Cardillo et al. 2006, Dulvy et al. 2014). On the other hand, current conservation efforts have been shown to be insufficient to mitigate the mass extinction across taxa (Butchart et al. 2010), and total preservation of all natural populations of all species might be unrealistic given lack of resources provided for conservation (Wilson et al. 2006, Rodrigues 2006). It is also unclear if numerically rare species tend to be functionally distinctive, meaning that extinction will certainly lead to functional eradication and jeopardize ecosystem functioning. There is some support that it will (Flynn et al. 2009, Barnagaud et al. 2017, Chapman et al. 2018), and in this case it is important to identify the

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communities that contain the most functionally rare species (Carmona et al. 2017). The concept of functional rarity unifies both numerical rarity and functional distinctiveness, so that a functionally rare species is expected to be most threatened by extinction and if it does go extinct, it will disproportionately affect functional diversity (Violle et al. 2017). Functional rarity has wide implications in conservation biology, and identifying functional rarity in ecological communities would help to optimize current efforts to preserve ecosystem functioning as much as possible (Grenié et al. 2017, Pavoine and Ricotta 2021), but it is still unclear how functional rarity responds to disturbances, particularly within a rapidly changing world.

Studying questions related to functional rarity requires large amounts of data. First, a databases is needed to include accurate information on species functional traits — morphological, physiological, phenological, or behavioral features of a species measurable at the level of individuals that are related to their fitness within the context of various environmental conditions (Petchey et al. 2007, Mouchet et al. 2010, Carmona et al. 2016). Information on these traits can typically only be obtained via a comprehensive review of available literature on the biology of each species and is especially scarce for rare taxa. Second, one needs access to data on community composition or, at least, species occurrence across disturbance gradient. Avian communities are a convenient study system for these types of questions as birds are widely distributed and readily detectable across different habitats, including urban areas, and they are common objects of observation providing ubiquitous data on their functional traits (Fernández-Juricic and Jokimäki 2001, Aronson et al. 2014, Marzluff 2016). Birdwatching is a popular hobby globally, which provides an opportunity for citizen-science approach that allows one to generalize trends across large area and helps to avoid idiosyncratic inferences (Fink et al. 2010).

Urban areas are known to act as environmental filters (Evans et al. 2018), resulting in selection for species that can persist in areas with relatively constant disturbance events (Kaisanlahti-Jokimäki et al. 2012, Stracey and Robinson 2012, Selva et al. 2014). One could predict a decrease in functional diversity across urbanized areas, as well as taxonomic diversity itself (McDonnell and Pickett 1990, Blair 1996, Clergeau et al. 1998, Grimm et al. 2008b), but the effects of urbanization on functional rarity cannot be generalized in the same fashion. Some investigators argue that the conservation potential of urbanized areas is underestimated: it is often assumed that natural habitats are of primary importance for rare taxa, but some rare species can also be found in urban areas, occasionally being more abundant than in protected areas

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(Goddard et al. 2010, Beresford et al. 2011, Dubovyk et al. 2020). Secondly, species can adapt to urban conditions and change their preferences towards urban areas (Partecke and Gwinner 2007, Nemeth and Brumm 2009, Francis and Chadwick 2012), which can be expected to become a more common phenomenon with growth of urban areas. It might be possible that functionally rare species are shifting towards urban areas, and if so, it could indicate that there is still hope for maintaining functional diversity despite rapid land cover changes across the continents.

In this work, I aim to study the spatial distribution of functional rarity on avian communities across North America and its changes between 2000 and 2021. There are two large citizen-science datasets on species occurrence that could be used to quantify change at such a large spatial extent: the North American Breeding Bird Survey has been conducted by the United States Geological Survey and Canadian Wildlife Service since 1966, and eBird, a platform developed by the Cornell Laboratory of Ornithology popular among the birding community worldwide. These datasets were used to estimate regional species rarity and combined with the literature on bird life histories to quantify their functional distinctiveness. There were two main tasks of this work: (1) to reveal spatial hotspots of functional rarity in avian communities across North America and their temporal changes, and (2) test whether functionally rare species shifted their distribution within the urban gradient over the last two decades. While the first part is more valuable for conservation management as it would highlight the areas and regions where urgent conservation efforts are of the highest importance, the second part would provide insight into the responses of functional diversity and functional rarity to disturbances and could help predict the future of functional diversity under constant and increasing anthropogenic stress.

Methods

Data on avian communities. The data on the occurrence of species of North American birds were obtained from the North American Breeding Bird Survey (BBS) and eBird. These two datasets were filtered to account for each other's sampling biases. BBS is conducted every breeding season (late May – early July) since 1966 on approximately 3000 39.4-km routes located on random secondary roads across the contiguous U.S. and southern Canada (Fig. 10) and each of these routes consists of 50 3-min stops during which all birds seen or heard within a 400-m radius being reported (Boulinier et al. 1998a, Sauer and Link 2011). An observation in the

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BBS dataset was assumed to represent overall species counts of all points within a route, so that the area sampled by one observation was equal to approximately 25.1 km^2 (Stanton et al. 2019).

While BBS is an example of a structured citizen-science project with a rigorous sampling protocol, eBird collects data from any user at any time, and varies in sampling design considerably: an observer can provide the data collected during a point count, accidentally, or traveling any distance and with any duration, ignoring some species or recording all species observed (Sullivan et al. 2009, 2014). All this information is being collected along with counts of observed species, which allows a user of the dataset to filter only those observations that meet certain sampling criteria — an approach that is called semi-structured (Kelling et al. 2019). To imitate the BBS sampling protocol, only full checklists were selected (meaning that these observations did not ignore any species) that have been collected across Canada, the U.S., and Canada while traveling from 32 to 48 km during 150–600 min. Since it was possible that BBS observers have also reported their results to eBird, all observations from eBird collected at BBS locations on the same date were ignored.

Sampling features of each dataset were also reasons to exclude the data from another dataset. For example, only BBS observations collected after 2000 were considered as the eBird enterprise started collecting sufficient amounts of data after this time. At the same time, BBS does not cover Mexico and aims for sampling more natural areas which leads to a bias against the urban areas, which means that eBird data is irreplaceable for a project studying effects of urbanization on avian communities. Another factor limiting the temporal framework of this study was the availability of high-resolution land cover data that was not available for most of the second half of the twentieth century. Besides that, eBird, unlike BBS, is conducted year round, so that counts of species observed outside of their breeding season were ignored.

Both BBS and eBird store the data as counts of taxonomic entities — species, subspecies, hybrids, etc., — but differ in taxonomic scheme. For this reason, the data from both datasets were converged to an independent project species-level taxonomy: all observations of subspecies were added to observations of respective species, and all higher than species taxa were ignored. The project taxonomy recognized 703 species, but since some observations fell out of breeding season and some were located off-shore, the actual species list was limited to 680 species of North American birds. Overall, there were 86,406 observations between 2000 and 2021 that met all requirements and were incorporated in this project.

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Functional rarity. Each observation was transformed to a value of functional rarity resulting from numerical rarity and functional distinctiveness of species comprising a community. Both of these facets were evaluated at the regional level, and Bird Conservation Regions (BCRs) were assumed to represent ecologically meaningful units. BCRs were originally defined to reflect similarity of bird faunas and their habitats, which could be used for optimized conservation efforts (Sauer et al. 2003). All species counts were summarized by unique combinations of BCR and year, so that functional distinctiveness and numerical rarity were estimated for each species within one of these year-BCRs, and then regional values of respective metrics for a species were drawn for each observation.

Regional species abundances were estimated for each BCR in a particular year using Stanton's formula (Stanton et al. 2019) that accounts for variability in species detection probabilities relative to time of the day, distance required to detect a bird, and ratio of individuals present to number of observed individuals. These estimates of regional abundance were meant to allow comparison between species relative abundances given heterogeneity in detectability, but their values should not be assumed to correspond to real abundances as this method has been shown to perform poorly for rare species (Stanton et al. 2019) and can be expected to have high uncertainty when there are few observations within a region. Besides that, the whole method was aimed to estimate confidence intervals of species abundances, but for the work presented here a median of the estimate after 500 iterations was used.

Regional abundance estimates were transformed into values of log-rarity, which is normalized by the minimal value of this metric logarithm of ratio of focal species abundance to the abundance of the most dominant species in a community. This metric equaled 1 for the rarest species in a community and 0 for the most abundant, and it forms a perfect line for a community on a logarithmic scale of species abundance distribution. Log-rarity was assumed to represent the regional numerical rarity of species.

Regional functional distinctiveness of a species was calculated as the distance between this species and community centroid in a multidimensional space of functional traits (Villéger et al. 2008, Mouchet et al. 2010). A community centroid represents the set of average values of functional traits carried by species that comprise that community. It normally utilizes weighted averages by species abundances (Villéger et al. 2008), but in this work centroid was calculated for regional pools of species irrespective of their abundances since abundances were accounted

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for when estimating species rarity. Functional trait space was constructed using 23 functional traits reflecting species biotic and abiotic interactions: diet category, diet items, diurnal and nocturnal activity, feeding method, feeding substrate, nest type, nest substrate, breeding system, chick development at hatching, spatial best aggregation, minimum and maximum clutch size, average age at first breeding, number of clutches per year, breeding success, annual survival of adults, mean biomass, maximum life expectancy in the wild, morphological hand-wing index (reflecting the shape of the wing and dispersal abilities), kleptoparasitism (stealing food from other individuals), dependency of nesting on other species, and nest parasitism. This information was obtained from the peer-reviewed literature for each species (Ehrlich et al. 1988, Wilman et al. 2014, Sheard et al. 2020, Billerman et al. 2022); in cases when some information was not available, a trait value was extrapolated based on sister taxa. Different traits had different types of data: some were coded as a continuous variable (e.g., body mass, annual survival, etc.), some as categorical variables (i.e., a species could have only one value of the nest type), and some as discrete distributions (i.e., different diet items or feeding methods were assumed to be more or less preferred by a species). Therefore, a community centroid had a more complicated structure than a typical vector of mean values: it contained mean values of continuous traits and mean distributions, but for categorical variables it was represented as a distribution of frequencies of possible values within a species pool. Species distinctiveness was then described as a set of distances between a centroid value and the species value of a trait, but these distances had different meanings for different types of traits: for continuous variables it was calculated as the difference between values, for categorical as a weighted by frequency of a category dissimilarity between categories, for distributions as an inverse overlap between the two. These distances were then rescaled to represent their deviations from the mean and the final species functional distinctiveness was then calculated as a probability of observation of a value of mean-across-traits rescaled distinctiveness being equal or less than zero in a standard normal distribution, so that a value 0.5 of species functional distinctiveness would mean that this species, on average (across traits), is moderately distinctive from a community centroid. A more detailed description of the calculations needed to estimate functional distinctiveness is provided in Chapter 2.

Functional rarity in communities was estimated in two ways to represent species uniqueness in dimensions of functional distinctiveness and numerical rarity (Grenié et al. 2017, Violle et al. 2017). Firstly, it was quantified as a Pearson's coefficient of correlation between

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regional functional distinctiveness and numerical rarity of species that constituted a community (hereafter, CFR). CFR could be useful as it describes the relationship between regional functional distinctiveness and numerical rarity of species and can be readily interpreted: when positively correlated, it means that rare taxa are the most functionally distinctive ones, so that communities with high positive values of CFR have the greatest need for conservation actions. When such actions are applied to the rarest taxa, it is expected to mitigate a decrease of functional diversity as a result of species extinction. Since CFR only quantifies the relationship irrespective of the values of both functional distinctiveness and numerical rarity (i.e., it can still have a high positive value even if all the taxa in a community do not have critically high values of rarity and/or distinctiveness), the second metric was used. It was calculated as an mean product of species functional distinctiveness and numerical rarity (PFR) and was expected to be high in communities that consist of rare and distinctive species.

Land cover data. To assess the levels of urbanization at each location sampled, the Terra and Aqua combined Moderate Resolution Imaging Spectroradiometer (MODIS) Land Cover Type (MCD12Q1) Version 6 data product was used — a popular dataset that is commonly used to estimate changes in land cover since 2001 (Zhao et al. 2018, Sulla-Menashe et al. 2019). This data product is based on satellite imagery classified by a supervised hierarchical classification model. The data provided have a spatial resolution of 500 m and each pixel has 13 bands: mostly technical information, such as classification confidence, but also 5 possible classifications, among which the Annual University of Maryland (UMD) classification was used (band "LC_Type2"). This band has one of 15 possible values representing land cover types. For this project, data were downloaded using Google Earth Engine (https://doi.org/10.5067/MODIS/MCD12Q1.006) and pixels with value "13" were isolated — they represent urban areas defined as at least 30% impervious surface area including buildings, asphalt, and vehicles. The isolated raster was then transformed into a shape feature in ArcGIS Pro and analyzed separately for each year (2001–2020). Year 2000 was assumed to have the same land cover distribution as 2001 and 2021 — as 2020.

The area of urban land cover was calculated for a 39.43-km buffer around each observation point to represent the length of a sampled route. The area was then transformed into a ratio of the urbanized area to the whole buffer area, i.e., $A_{urban}/(\pi \cdot 39.43^2)$. In cases where the area of urban land cover within a buffer was <0.25 km^2 (i.e., the minimum size of a certain land cover

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patch that could be identified by the MCD12Q1 algorithm (500 m^2)), this area was assumed to be 0.25 km^2. The ratio was then logarithmically transformed, so that the decimal logarithm of the ratio was denoted as the urbanization level in the work presented here.

Analysis. Spatial distribution was visualized using median values of CFR or PFR within arbitrary 80-km pixels using the "Points to Raster" ArcGIS tool. This tool counts only the spatial points that are located within a pixel, so it might be biased in undersampled cells. 80 km was chosen to represent an approximate double distance of one sampling. To account for that, kriging (Cressie 1990) was also applied, using a Gaussian semi-variogram model with a variable search radius within the closest 30 points. All data points from all years were used to show the spatial distribution of functional rarity. Temporal trends were estimated using a space-time cube analysis that utilizes Mann-Kendall statistic testing whether a variable is significantly changing at a given cell (Neeti and Eastman 2011). Again, since some areas of North America were undersampled, this analysis did not cover the whole continent. Hotspots of functional rarity were analyzed using Getis-Ord Gi* method (Songchitruksa and Zeng 2010) with distance parameter of 80 kilometers and visualized with kriging.

To test whether there were temporal changes in distribution of functional rarity across the urban gradient, a set of models was built implying different shapes of relationship between a functional rarity metric and urbanization level and complexity regarding a year of observation and random effects of BCR and fixed effect of data source (BBS or eBird as a categorical variable with contrast coding system). Three shapes were tested: intercept models, linear models, and quadratic models that implied a hump-shaped relationship. There were four types of models: (1) fitting all data indiscriminately, (2) accounting for year, (3) accounting for year and random effect of BCR, and (4) accounting for year, data source, and random effect of BCR. The ideal cases of these models are shown at Fig. 17. The data were fitted to each of these models explaining the distribution of both CFR and PFR, and the models were then weighted using corrected Akaike's information criterion (AICc).

To confirm the observed pattern, for each location where there were consecutive surveys in different years, a trend of functional rarity metric was built using a simple linear regression. A coefficient was considered to be either positive, negative, or stable (i.e., there was no significant relationship). The values of urbanization level over years were then used to test whether

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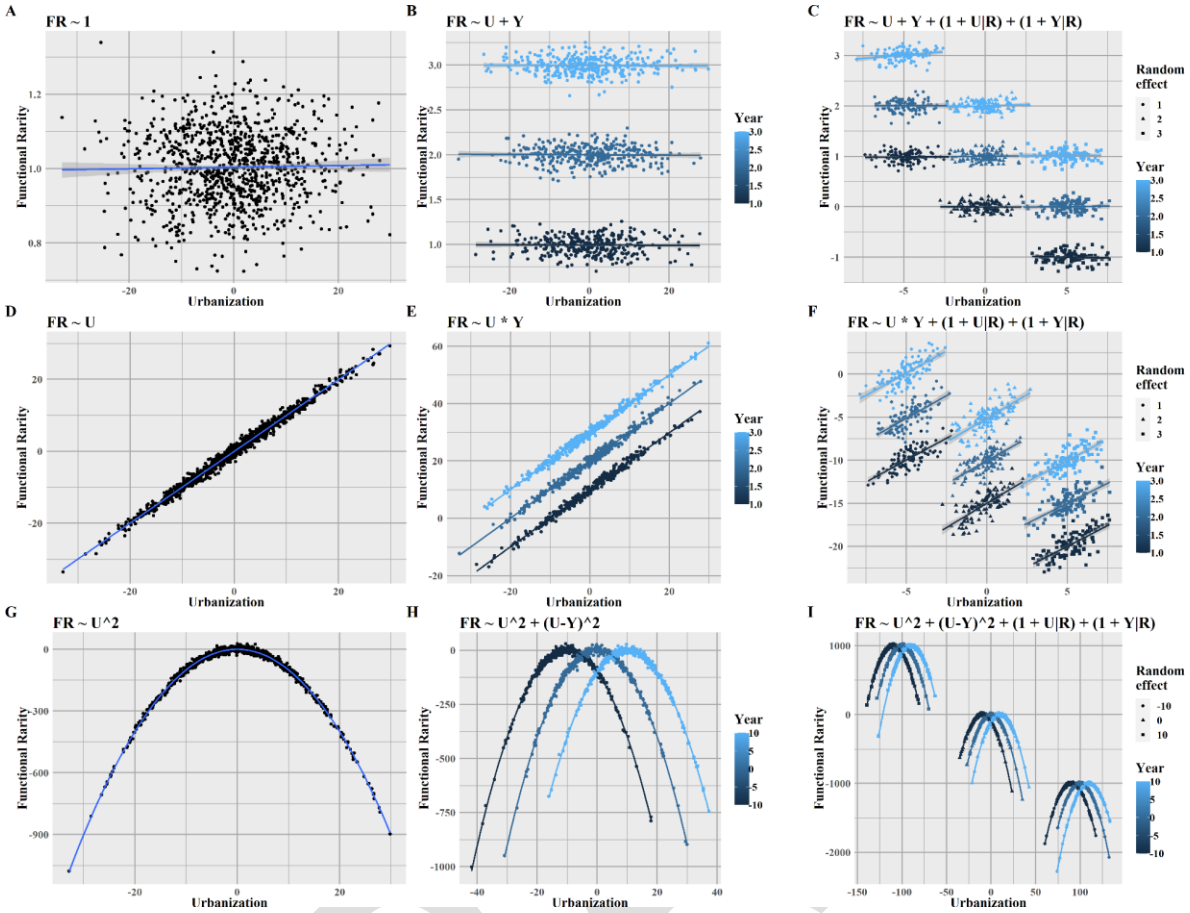

Fig. 17. Different hypothetical scenarios of relationship between functional rarity, urbanization level, and year of observation to which the linear models that were fitted to the data corresponded to

dispersion of urbanization level values within these three groups was greater than among them with a non-parametric Kruskal-Wallis test and post-hoc multiple comparisons after it.

Results

There was uneven distribution of both metrics of functional rarity across North America. CFR was higher in Northern and Northwestern Pacific forests, Northern Rocky mountains, Sierra Nevada, Western prairies, Boreal hardwoods and softwoods, Atlantic Northern forests, Central hardwoods, West gulf coastal plains, Appalachian mountains and Piedmont, Chihuahuan desert, and Tamaulipan brushlands (Fig. 18). At the same time, low values of CFR were observed in

Yucatan peninsula, Baja California and Pacific Mexico, Coastal California, Central and Eastern prairies. The pattern of the distribution of PFR was somewhat different: it was generally high across Mexico, Northwestern pacific forests, Hudson plains, Great basin, Rocky mountains, Sierra Nevada, Colorado plateau, West gulf coastal plains, Edwards plateau, Central hardwoods, and was clearly low in Prairie potholes, Eastern tallgrass prairies, Appalachian mountains, St. Lawrence plains (Fig. 18). Based on the results of hotspots analysis, it can be concluded that Northern Pacific rainforests, Northwestern interior forests, Boreal Taiga plains, Taiga shield and Hudson plains, Boreal softwood shield, Atlantic Northern forests, Boreal hardwood transition, Northern Rocky mountains, Great basin, Southern Rocky mountains and Colorado plateau, Badlands and Western prairies, Shortgrass prairies, Mid-Atlantic coast, Piedmont, Southeastern coastal plain, Northern peninsular Florida, Southern Planicie costera, and Sierra Madre Del Sur are the regions where hotspots of CFR tend to be located, whereas hotspots of PFR tended to be found in Western Alaska, Western and Southern parts of Northwestern interior forests, Taiga and Hudson plains, several parts of Boreal Taiga plains, Northern and Southern parts of Northern Pacific rainforests, Northern, Western, and Eastern parts of Great basin, Coastal California and Sierra Nevada, Baja California, Southern parts of Northern Rocky mountains and Badland prairies, Sonoran and Mojave deserts, on coasts of the Great lakes, Prairie hardwood transition, Central hardwoods, Coastal Southeastern plain and Northern Florida, West gulf coastal plains, Gulf coastal prairies, Southern shortgrass prairies, Edwards plateau, and across all BCRs located in Mexico (Fig. 19).

CFR appeared to increase over decades across Appalachian mountains, Central hardwoods, Piedmont, Southeastern coastal plain, Southern oakwoods and prairies, Northern mixed grass prairies, Tamaulipan brushlands, Southeastern Rocky mountains, but these patterns were inconsistent across the regions. CFR generally decreased across Northern prairies and in some more local places within the Southern tip of Florida, Alaska, California, and Northern Mexico. PFR has shown more increasing trends in multiple places across different regions, such as Central Alaska, and Northern Pacific coast, Sierra Nevada Great basin, Rocky mountains and Colorado plateau, western Sierra Madre, Central mixed grass prairie, Edwards plateau, Tamaulipan brushlands, Western and Eastern prairie potholes, prairie hardwood transition, whole Piedmont and numerous areas on the East coast, as well as several location on the Eastern Gulf coast (Fig. 19). Some negative trends in PFR could be found on the Western Gulf coast, Central

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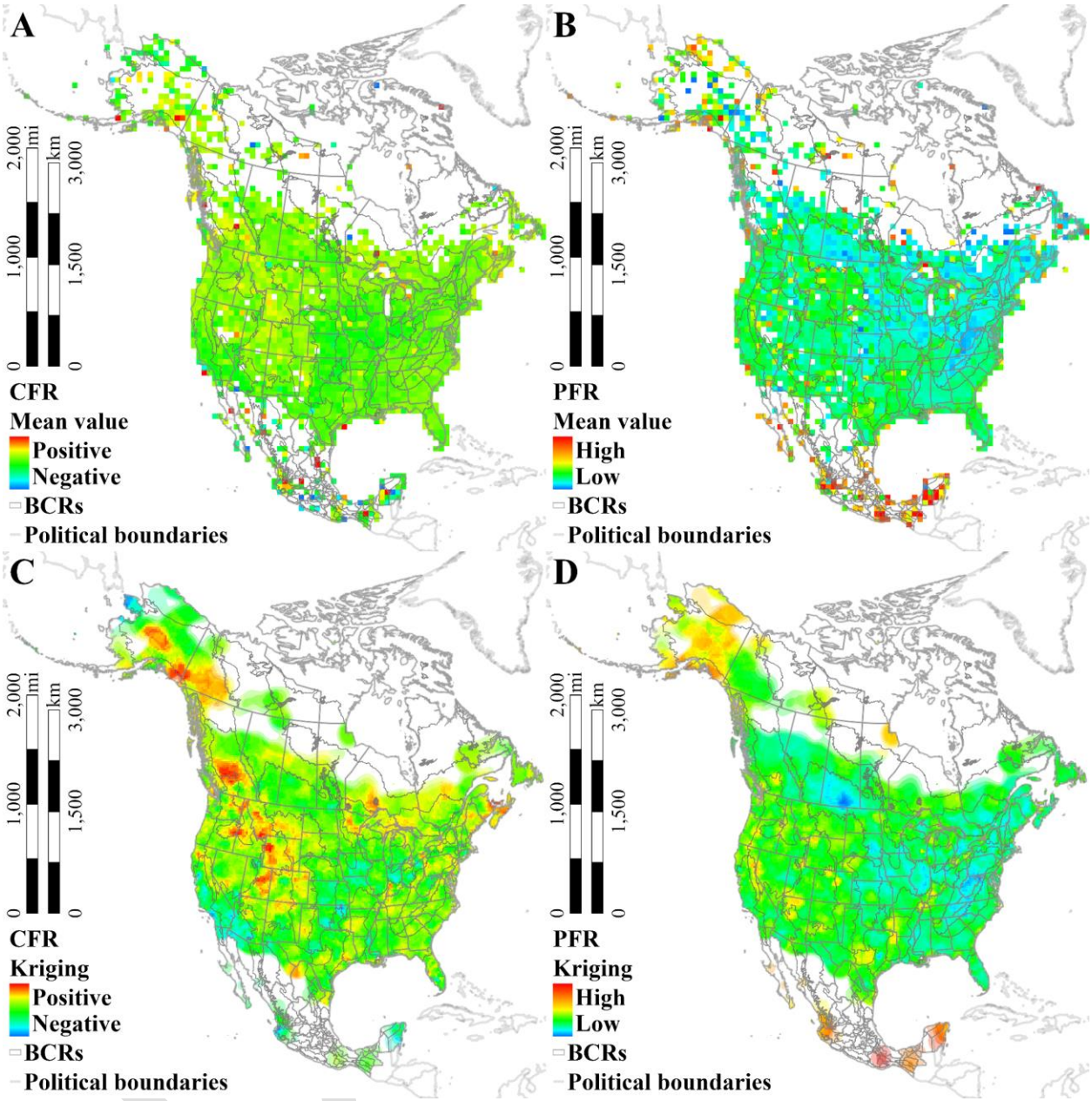

Fig. 18. Spatial distribution of Pearson's coefficient of correlation between regional numerical rarity and functional distinctiveness (A, C) and average product of numerical rarity and functional distinctiveness (B, D) shown as median values of points within 80-km cells (A, B) and using Kriging interpolation (C, D)

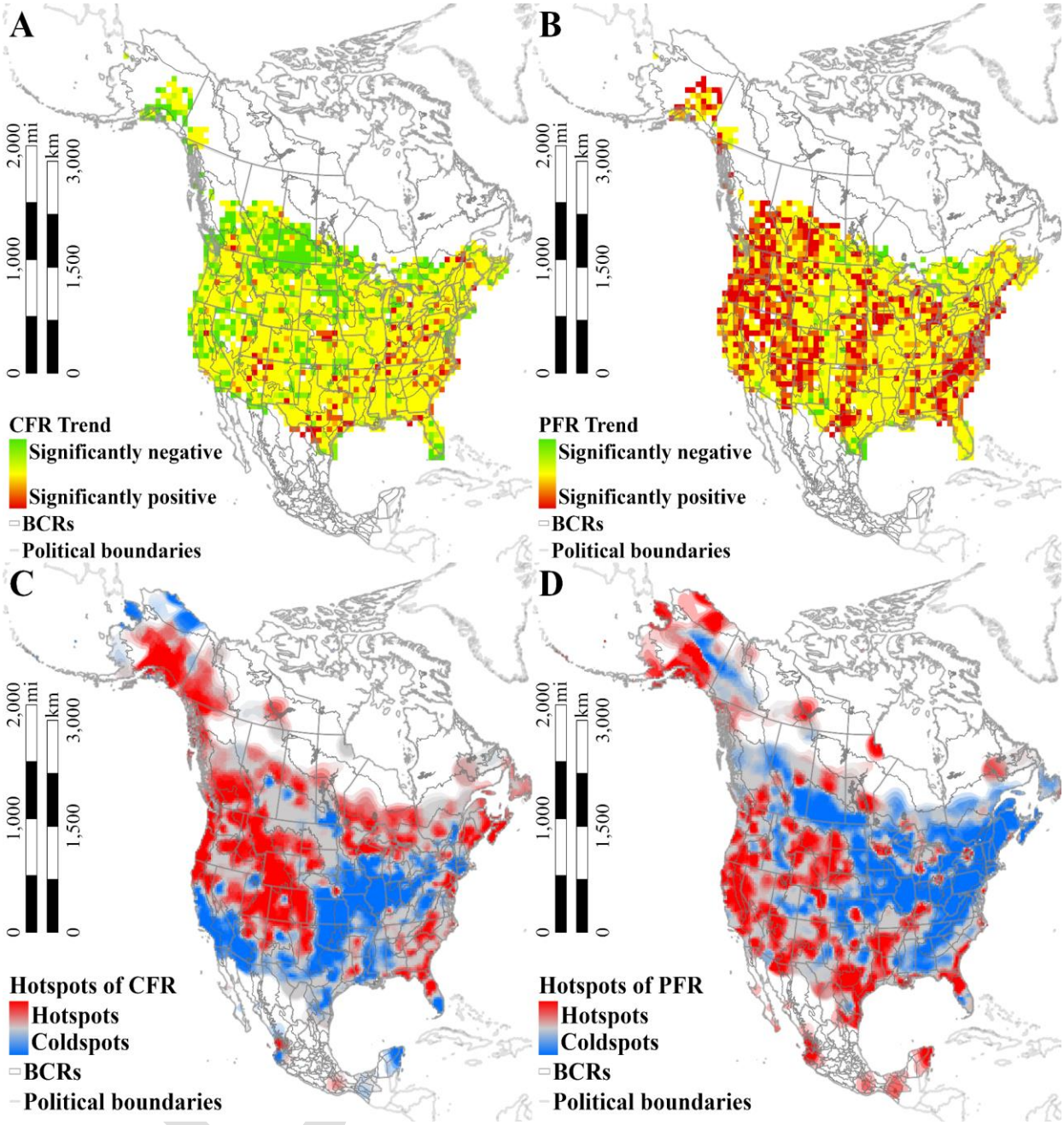

Fig. 19. Trends of changes between 2000 and 2021 (A, B) and spatial hotspots (C, D) of Pearson's coefficient of correlation between regional numerical rarity and functional distinctiveness (A, C) and average product of numerical rarity and functional distinctiveness (B, D)

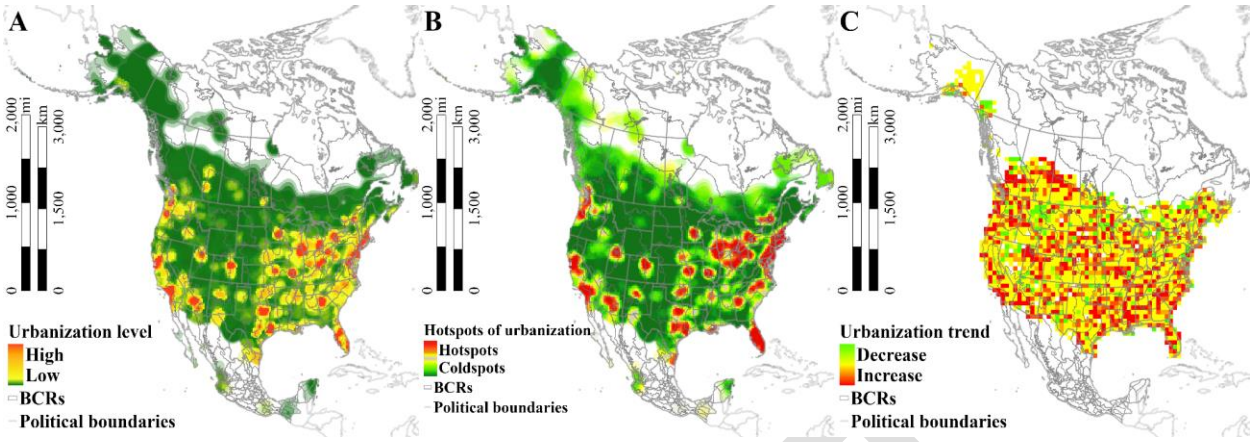

Fig. 20. Spatial distribution of urbanization levels (A), its hotspots (B), and trends between 2000 and 2021 (C) across North America

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prairies, and transition to Boreal forests.

There were clear hotspots of urbanization level across North America coinciding with the major cities: Anchorage in Northwestern interior forests; Vancouver, Seattle, Olympia, and Portland in Northern Pacific rainforests; San Francisco, San Jose, Los Angeles, San Diego, and Tijuana in Coastal California, Kennewick and Salt Lake City in the Great basin; Phoenix and Tucson in Sonoran desert, Albuquerque in Colorado plateau; Denver and Amarillo in shortgrass prairies; El Paso and Juárez in Chihuahuan desert; Brownsville and Moneterrey in Tamaulipan brushlands; Dallas, Oklahoma city, Austin and San Antonio in oaklands and prairies; Kansas city, Omaha, St. Louis, Chicago, Indianapolis, and Tulsa in Eastern shortgrass prairies; Minneapolis, Milwaukee, Detroit in prairie hardwood transition; Cleveland, Toronto, Ottawa, Montreal in St. Lawrence plain; Boston, Providence, New York, Philadelphia, Washington, Richmond, Norfolk on the Mid-Atlantic coast; Pittsburgh in Appalachian mountains; Philadelphia, Greensboro, Raleigh, Charlotte, Atlanta in Piedmont; Jacksonville and Mer in Southeastern coastal plain; Orlando, Tampa, and Miami in peninsular Florida; New Orleans in Mississippi alluvial valley; Houston in Gulf coastal prairies (Fig. 20).

Each of hypothetical models of relationship between urbanization level and functional rarity were fitted using (1) all data indiscriminately, (2) with an interaction with year of an observation, or (3) also accounting for random effects of BCR alone or (4) BCR and source of

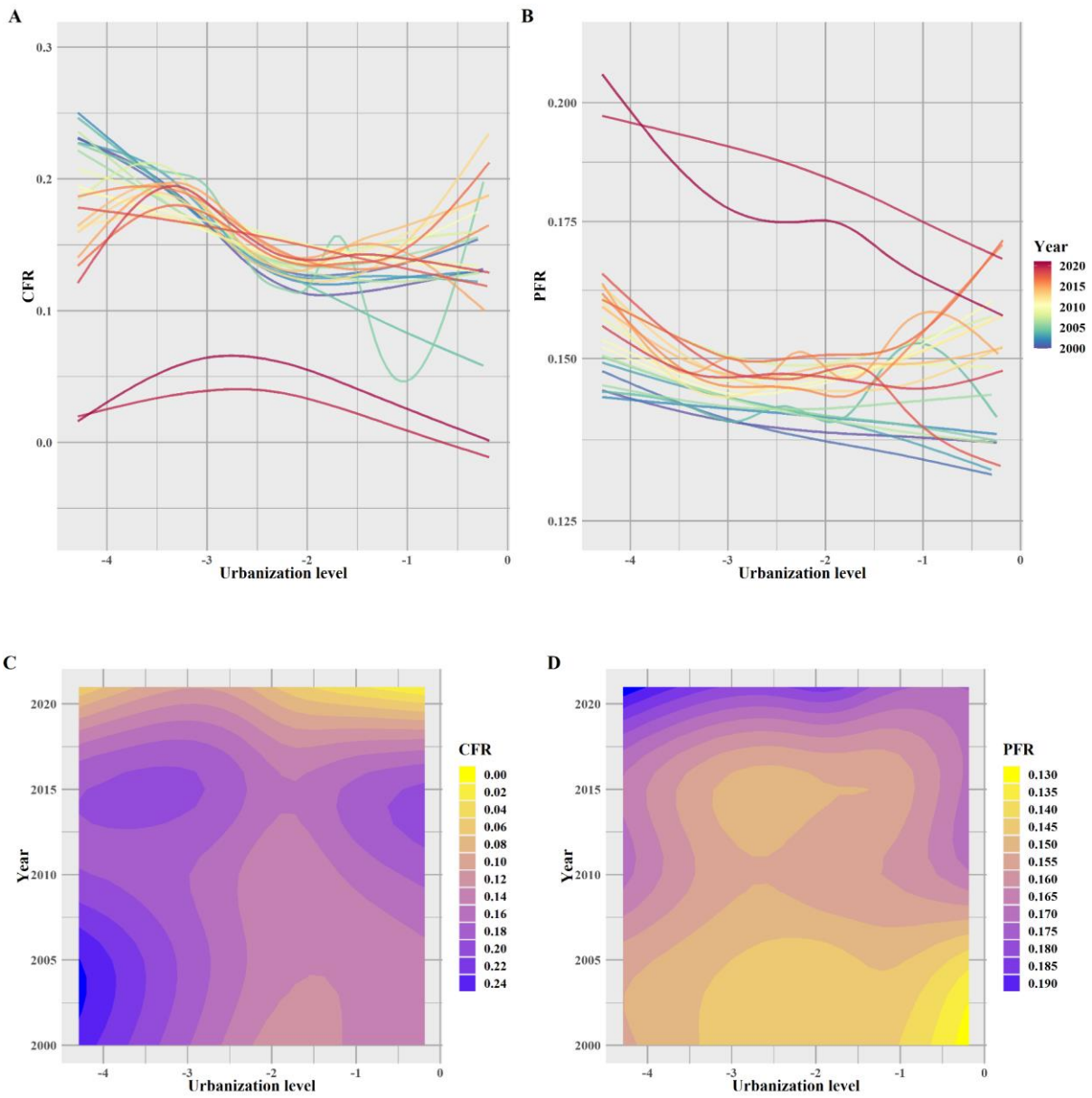

Fig. 21. Changes of overall distribution of functional rarity metrics across the urbanization gradient over the years

the data. For both CFR and PFR, the lowest AICc weight was assigned to a quadratic mixed-effect model (Appendix D) accounting for BCR and source of the data that implied that there were temporal changes in a position of a hump along the urbanization gradient, and the negative coefficients of the quadratic term of urbanization level and year suggested that the low peak of

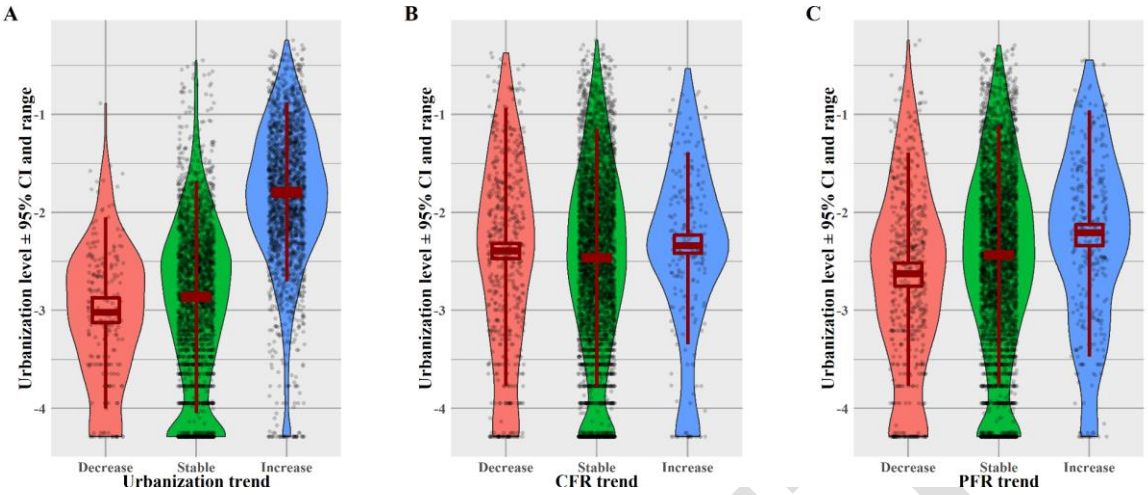

Fig. 22. Distribution of mean over years urbanization levels within the groups of locations where urbanization level (A), Pearson's coefficient of correlation (B), and average product (C) of species functional distinctiveness and numerical rarity are decreasing, increasing, or stable

this relationship was moving toward less urbanized areas (Fig. 21).

Among the total of 18,713 unique spatial points analyzed in this work, there were 4,860 points that were sampled in more than two different years and for which it was possible to assess trends of changes of urbanization level, CFR, and PFR. Thus, urbanization level was increasing over years at 1,961 locations, decreasing at 224 locations, and stable (i.e., coefficient of a linear regression included zero at $p = 0.05$) at 2,675 locations; CFR was increasing at 213 locations, decreasing at 561 locations, and stable at 4,086 locations; PFR was increasing at 331 locations, decreasing at 567 locations, and stable at the rest of 3,962 locations. The mean urbanization level over time was significantly higher at these locations where the trend of urbanization was positive (Fig. 22, Table 5). Regarding functional rarity metrics, urbanization level seemed not to vary considerably relative to trend of CFR, but it was different at the locations that showed different trends in PFR.

Discussion

The results of this work indicate that there is uneven spatial distribution of CFR and PFR across North America that have been consistently changing over the last two decades, and land

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use transition into urbanized areas may be related to this process. Spatial-wise, it seems that functional rarity metrics were higher in natural areas. Both metrics of functional rarity seemed to have a hump-shaped relationship with urbanization level, with functional rarity being higher at intermediate levels of urbanization level, as per the intermediate disturbance hypothesis (Grime 1973, Connell 1978, Townsend et al. 1997, Shea et al. 2004).

The central question of my work was whether the relationship between urbanization level and functional rarity undergoes any temporal changes, and what it means to bird conservation. There is some temporal pattern of a general increase of functional rarity (Fig. 21) in terms of both CFR (i.e., functionally distinctive species tend to become more and more rare) and PFR (i.e., functional rarity of taxa comprising avian communities was increasing). CFR was generally lower in 2020–2021 and PFR was higher over the same period, corresponding to an absence of data from the BBS (2020 was the only year since 1966 when BBS surveys were not conducted due to the COVID-19 pandemic, and the dataset has not yet been updated to contain the data from 2021). This fact reflects the importance of accounting for data source when analyzing functional diversity: it can be assumed that more consistent coverage of BBS than in eBird provides more accurate and lower values of numerical rarity — hence, lower CFR and higher PFR. Still, changes in CFR do not seem to respond to urbanization as strongly as in PFR: the fact that urbanization level is related to a trend of PFR means that communities in urbanized areas are more likely to undergo such species turnover that favors more regionally unique species. It seems that areas that were already urbanized were more likely to undergo a development of urban areas, and that an increase in PFR was more likely to occur at urbanized areas over the last two decades (Fig. 22, Table 5).

There are some caveats in this work that should be taken into account. First, as has already been mentioned, the study presented here combines two different datasets to address questions on dynamics of functional rarity, but the inference seems to be strongly dependent on the source of the data. To deal with potential biases based on source, linear mixed-effect models were deployed so that the data source could be included as a random effect and give insight into the general pattern in the data within combinations of these random effects. Effectively it means that while BBS and eBird datasets were combined to compensate for each other's biases across the urban gradient, these data should not be analyzed as a whole.

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Table 5. Kruskal-Wallis test and multiple post-hoc comparison (significant difference in bold) of mean urbanization levels in groups corresponding to trend of urbanization level, Pearson's coefficient of correlation, and average product of species functional distinctiveness and numerical rarity

Kruskal-Wallis χ^2 (df = 2)	p-value	Comparison	Difference	Critical value (p = 0.05)
Urbanization level				
		Decrease Stable	202.495	233.641
1698.000	**<0.001**	Decrease Increase	**1874.611**	**236.905**
		Stable Increase	**1672.116**	**99.858**
Pearson's coefficient of correlation between functional distinctiveness and numerical rarity				
		Decrease Stable	66.961	151.240
4.203	0.122	Decrease Increase	113.577	270.339
		Stable Increase	180.539	236.078
Average product of species functional distinctiveness and numerical rarity				
		Decrease Stable	**286.781**	**150.822**
37.847	**<0.001**	Decrease Increase	**581.226**	**232.351**
		Stable Increase	**294.445**	**192.185**

Secondly, functional rarity was analyzed at regional scale (i.e., regions were accounted for as a random effect). Moreover, the spatial extent of one observation is considerable (i.e., a 40-km radius corresponding to a BBS route length), and likely includes a variety of habitats, including different levels of urbanization. Because the spatial extent was so large, individual birds that were encountered were unlikely to interact with each other. Yet, some authors have suggested that even areas sampled that are considerably larger than a typical defended territory of a pair are still valuable for conservation and ecological studies (Rodewald 2012). The effects of urbanization can be addressed at large spatial scales as well since habitat modification affects large areas around cities (Clergeau et al. 1998). This observation is particularly relevant since it was not feasible to evaluate levels of urbanization at a continental scale with a high precision but using accessible datasets on land cover with relatively low (500 m) resolution. Similarly, the large spatial extent of a BBS observation does not reflect small-scale community structure, but allows one to observe more general patterns in avian communities and populations (Catano et al. 2020).

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Some of the most frequently reported patterns of avian communities along urban gradients are increases in overall abundance and biomass and decreases in species richness in more urbanized habitats. These patterns are typically explained by an increase in availability of specific resource, allowing certain taxa to reach high abundances (Leston and Rodewald 2006, Stracey and Robinson 2012). In contrast, increased fragmentation, homogenization, and a decrease in habitat availability are often used to explain reductions in taxonomic diversity (Beissinger and Osborne 1982, Rodewald and Yahner 2001, MacGregor-Fors et al. 2012, Aronson et al. 2014, Newbold et al. 2015, Saura 2020, Garizábal-Carmona and Mancera-Rodríguez 2021). Moreover, there is evidence that urbanization also results in reduced phylogenetic diversity, so that urban species are less unique and more clustered phylogenetically (Aronson et al. 2014, La Sorte et al. 2018, Morelli et al. 2018, Vaccaro et al. 2019).

There is much evidence that shows that urban habitats perform as habitat filters and affect avian community assembly (Laughlin et al. 2012, Mouillot et al. 2013). Observations suggest that species that succeed in establishing a population within an urban environment bear similar traits, which have led some researchers to propose an "ecological portrait" of an urban bird (Croci et al. 2008, Evans et al. 2011). It is clear that species respond to urbanization differently (Pennington and Blair 2012), and those that adapt to life in cities are usually similar in their functional traits (MacGregor-Fors et al. 2012): they are often omnivores or granivores (Clergeau et al. 1998, Lim and Sodhi 2004, Rodewald 2012, Evans et al. 2018), cavity-nesters or are able to defend their nest from increased predator abundances (Kaisanlahti-Jokimäki et al. 2012, Stracey and Robinson 2012), and, moreover, some species can also change their behavior to adapt to anthropogenic disturbances, suggesting that ecological plasticity helps some taxa adapt to land cover change (Sol et al. 2013). At local scales, urbanization can be expected to determine some decline in functional diversity due to strong environmental filters, which could lead to more apparent declines in phylogenetic and taxonomic diversity — and these effects have indeed been observed across the world (Flynn et al. 2009, Thuiller et al. 2014, Schütz and Schulze 2015, Oliveira et al. 2018, Chapman et al. 2018, La Sorte et al. 2018, Palacio et al. 2018, Matuoka et al. 2020). Urban environmental filters may also select for species from regional pools that are functionally dissimilar from other native species — and urban habitats may be a better match for some taxa. Effectively it would mean that urbanization results in a decrease in functional diversity, but those species that manage to adapt are functionally distinctive at a regional scale.

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The regional functional uniqueness of a species could be related to their restricted distribution — especially considering that urban areas are a relatively scarce land cover type, — and given the relationship between numerical rarity and functional distinctiveness (Chapter 4), it is possible that species able to adapt to an urban setting may be functionally rare species within regional pools.

Approximately 30% of threatened species occur in cities (Aronson et al. 2014). Rare taxa are expected to be more sensitive to temporal changes of disturbance because they are often associated with vulnerable habitats that disappear due to disturbance (Harrison et al. 2019). Urban areas can be similar to such habitats (e.g., early successional ones) and therefore provide a refuge for some rare taxa (Knapp et al. 2009). Urban habitats exhibit high spatial heterogeneity which may be preferred by some bird species (Pennington and Blair 2012), and some habitats within an urban matrix can provide islands of natural-like habitats attracting rare species (MacGregor-Fors et al. 2012, Palacio et al. 2018).

Unlike a decrease in species diversity, changes in functional rarity are not always evidence of a negative process or need for mitigative efforts. A positive trend in functional rarity is not a positive process in terms of conservation, but rather is opposite: it means that taxa in communities tend to become more numerically rare and functionally distinctive, so that there is a higher chance of an extinction and if it happens, it disproportionally affects functional diversity. Therefore, an increase in functional rarity is a warning call, and should be incorporated into conservation practice to preserve ecosystem functioning. There is some evidence that functional diversity in avian communities have changed over decades across the United States (Barnagaud et al. 2017): many communities have shifted towards more distinctive species that are evenly distributed within a functional space, which could be a result of land cover change, and could be misinterpreted as a positive sign for ecosystem functioning. My work, however, has demonstrated that these increases in distinctiveness might be sensitive to the global change and extinction events.

Prioritizing conservation hotspots is important for conservation management (Myers et al. 2000), but areas currently protected do not always align with such hotspots (Devictor et al. 2010). Functional diversity, among other useful metrics, also exhibits spatial hotspots (Cooke et al. 2019), which is especially valuable given that functional extinctions, when taxa are so scarce that they effectively do not contribute to ecosystem functioning, can happen long before the

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actual extinction of the taxa (Säterberg et al. 2013). Decreases in functional diversity can indicate future decreases in taxonomic diversity (Mouillot et al. 2013).

The present work argues that spatial hotspots are in an urgent need of conservation since they show the locations where an extinction is likely and expected to result in functional eradication. But what is more important, and somewhat surprising, is that functional rarity seems to increase more rapidly in urban environments. Conservation efforts within urban ecosystems has not been considered seriously (Leston and Rodewald 2006, Marzluff and Rodewald 2008, Miller 2012), but the pattern of functional rarity dynamics within an urbanization gradient strongly suggests that there is a potential for urban bird conservation.

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SUMMARY

The framework of functional diversity offers important insights into community assembly rules and directly relates the value of biological diversity to ecosystem functioning and ecosystem services. Contemporary global change challenges the resilience of natural systems via a variety of effects, such as pollution, overharvesting, invasive species, and land cover change. The loss of natural habitats as a result of urbanization and related processes can impair ecosystem functioning because of the decline in species abundance, ultimately leading to extinction. The perspective of functional diversity implies that the effect of species extinction depends on the entity of these species, specifically, on what functional role they play within an ecosystem and whether this role is redundant or unique within the context of overall ecological communities.

Species and communities can be described with various metrics within this framework, but the overall philosophy of using the functional approach is to compare species comprising a community between each other in terms of their functional traits. Such traits can be used to examine how species interact with their environment and overall effect on the ecosystem. This approach acknowledges that species are not discrete categories of organisms, but are objects within a multidimensional trait space, so that some species are more similar to each other than others. While functional diversity of communities can be described in terms of the distribution of species within this space, species can also be weighted based on their distinctiveness within a community.

Obviously, analysis of functional diversity requires a considerable amount of data — not only on the occurrence of particular species, but, more importantly, an accurate quantitative description of a species' biology to evaluate the functional traits. Birds are widespread and generate a disproportionately high amount of research interest, attracting numerous citizen-science projects with the data that are freely available. The present work has combined two comprehensive datasets on species occurrence across North America for more than two last decades, and a review of the literature on species biology, to reveal the effects of ongoing urbanization processes on functional diversity.

First, I showed that functional distinctiveness and numerical rarity were related to each other in such a way that functionally distinctive species tend to be rare. Conservation efforts

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based on prioritization of rare species are expected to result in the preservation of not only taxonomic diversity, but also functional diversity, reinforcing the expectation that nature conservation will help to ensure a stable supply of vital ecosystem services. Second, I found that rare species should be protected, because their decline and extinction would result in a decline in ecosystem functioning, and communities that contained more functionally distinctive and numerically rare species were the highest priority for conservation measures.

Quantifying the relationship between functional distinctiveness and numerical rarity was a central question of the work presented here — choosing the most suitable metric was the most critical task since using the wrong metric could lead to erroneous inferences. In fact, quantifying such relationships would be justified when attempting to quantify functional rarity — a concept that currently lacks rigorous methodology. Functionally rare species are expected to be both functionally distinctive and numerically rare, meaning that the value of its preservation for community functioning is greatest, as well as extinction risk. Functional rarity of communities is more vague, but in general reflects how fragile a community is and weights it based on importance of the species within. A community that has a high value of such a metric is expected to consist of both numerically rare and functionally distinctive taxa, but this metric should be independent of species richness to ensure an unbiased estimate. In this work, I tested a set of candidate metrics and found that two of them met such requirements: Pearson's coefficient of correlation between functional distinctiveness and numerical rarity of species that constitute a community, and average product of functional distinctiveness and numerical rarity. These two metrics reflect different facets of functional rarity: while average product shows the average functional rarity of a species within a community, correlation coefficient reflects the shape of the relationship between distinctiveness and rarity. Both of these metrics indicate the communities where conservation efforts are most urgent to preserve functional diversity.

I did not find a strong evidence that a correlation between functional distinctiveness and numerical rarity shifts its distribution along the urbanization gradient over time, but there was evidence that an increase in average product of functional distinctiveness and numerical rarity was more likely to occur in urbanized areas. This finding implies that urbanization contributes to an increase in functional rarity of avian communities in North America. It might be related to the fact that urbanization acts as an environmental filter so that species that succeed in adapting to urban environments carry a unique suite of regional species pool traits, but it also indicates that a

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decrease in functional diversity is more likely to happen in urbanized areas. In fact, it means that conservation in urban areas is needed to preserve functional diversity of birds and ecosystem functioning in general.

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APPENDICES

Appendix A. Correspondence of taxonomy of North American birds used in the project to American Ornithological Society (60th version) check list identifiers used in Breeding Bird Survey dataset and Clements check list identifiers used in eBird dataset

Project ID	Scientific name	English name	BBS ID	BBS subspecies ID	eBird ID	eBird subspecies ID
10	*Dendrocygna autumnalis*	Black-bellied Whistling-Duck	1770		221	
20	*Dendrocygna bicolor*	Fulvous Whistling-Duck	1780		226	
30	*Anser canagicus*	Emperor Goose	1760		241	
40	*Anser caerulescens*	Snow Goose	1690	1691	242	243, 244
50	*Anser rossii*	Ross's Goose	1700		245	
60	*Anser albifrons*	Greater White-fronted Goose	1710		255	259, 260
70	*Branta bernicla*	Brant	1730	1740	279	
80	*Branta canadensis*	Canada Goose	1720		303	305, 306, 308, 309, 311, 312, 313
85	*Branta hutchinsii*	Cackling Goose	1725		292	
90	*Cygnus olor*	Mute Swan	1782		337	
100	*Cygnus buccinator*	Trumpeter Swan	1810		341	
110	*Cygnus columbianus*	Tundra Swan	1800		343	
115	*Alopochen aegyptiaca*	Egyptian Goose	20630		373	
116	*Cairina moschata*	Muscovy Duck	10210		397	
120	*Aix sponsa*	Wood Duck	1440		406	
130	*Spatula discors*	Blue-winged Teal	1400		431	
140	*Spatula cyanoptera*	Cinnamon Teal	1410		432	433, 434, 435, 436, 437
150	*Spatula clypeata*	Northern Shoveler	1420		443	
160	*Mareca strepera*	Gadwall	1350		447	
170	*Mareca americana*	American Wigeon	1370		456	
175	*Mareca penelope*	Eurasian Wigeon	1360		454	
180	*Anas platyrhynchos*	Mallard	1320	1331	483	484, 485
190	*Anas rubripes*	American Black Duck	1330		505	
200	*Anas fulvigula*	Mottled Duck	1340		509	
210	*Anas acuta*	Northern Pintail	1430		526	
220	*Anas crecca*	Green-winged Teal	1390		541	
230	*Aythya valisineria*	Canvasback	1470		591	
240	*Aythya americana*	Redhead	1460		592	
250	*Aythya collaris*	Ring-necked Duck	1500		597	
260	*Aythya marila*	Greater Scaup	1480		616	617, 618
270	*Aythya affinis*	Lesser Scaup	1490		622	
271	*Aythya fuligula*	Tufted Duck	1491		609	

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Project ID	Scientific name	English name	BBS ID	BBS subspecies ID	eBird ID	eBird subspecies ID
280	*Polysticta stelleri*	Steller's Eider			632	
290	*Somateria fischeri*	Spectacled Eider			633	
300	*Somateria spectabilis*	King Eider	1620		634	
310	*Somateria mollissima*	Common Eider	1590		636	
320	*Histrionicus histrionicus*	Harlequin Duck	1550		647	
330	*Melanitta perspicillata*	Surf Scoter	1660		649	
340	*Melanitta fusca*	Velvet Scoter	1650		650	
350	*Melanitta nigra*	Common Scoter	1630		656	
360	*Clangula hyemalis*	Long-tailed Duck	1540		661	
370	*Bucephala albeola*	Bufflehead	1530		662	
380	*Bucephala clangula*	Common Goldeneye	1510		663	664, 665
390	*Bucephala islandica*	Barrow's Goldeneye	1520		668	
400	*Lophodytes cucullatus*	Hooded Merganser	1310		673	
410	*Mergus merganser*	Common Merganser	1290		681	683, 684
420	*Mergus serrator*	Red-breasted Merganser	1300		689	
430	*Nomonyx dominicus*	Masked Duck			696	
440	*Oxyura jamaicensis*	Ruddy Duck	1670		697	
450	*Ortalis vetula*	Plain Chachalaca	3110		769	770, 771, 772, 773
460	*Oreortyx pictus*	Mountain Quail	2920		920	
470	*Colinus virginianus*	Northern Bobwhite	2890		933	935, 936, 937, 938, 939, 940, 941, 942, 943, 945, 946, 948, 949, 950, 951, 953, 954, 955, 956, 957, 958
480	*Callipepla squamata*	Scaled Quail	2930		987	988, 989, 990, 991
490	*Callipepla californica*	California Quail	2940		999	1000, 1001, 1002, 1003, 1004, 1005, 1006, 1007
500	*Callipepla gambelii*	Gambel's Quail	2950		1009	1010, 1012, 1013, 1014, 1015
510	*Cyrtonyx montezumae*	Montezuma Quail	2960		1020	1022, 1023, 1024, 1026, 1027
520	*Alectoris chukar*	Chukar	2882		1659	1660, 1661, 1662, 1663, 1664, 1665, 1666, 1667, 1668, 1669, 1670, 1671, 1672, 1673
530	*Phasianus colchicus*	Ring-necked Pheasant	3091		1375	1377, 1378, 1379, 1380, 1382, 1383, 1384, 1385, 1386,

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Project ID	Scientific name	English name	BBS ID	BBS subspecies ID	eBird ID	eBird subspecies ID
						1387, 1388, 1389, 1390, 1391, 1392, 1393, 1394, 1395, 1396, 1397, 1398, 1399, 1400, 1401, 1402, 1403, 1404, 1405, 1406, 1407, 1409, 1410, 1411
535	*Pavo cristatus*	Indian Peafowl	3095		1471	
540	*Perdix perdix*	Gray Partridge	2881		1350	1351, 1352, 1353, 1354, 1355, 1356, 1357
550	*Bonasa umbellus*	Ruffed Grouse	3000		1189	1190, 1191, 1192, 1193, 1194, 1195, 1196, 1197, 1198, 1199, 1200, 1201, 1202, 1203
560	*Centrocercus urophasianus*	Greater Sage-Grouse	3090		1218	
565	*Centrocercus minimus*	Gunnison Sage-Grouse	3089		1219	
570	*Canachites canadensis*	Spruce Grouse	2980		1309	1311, 1312, 1313, 1314, 1315
580	*Lagopus lagopus*	Willow Ptarmigan	3010		1255	1258, 1259, 1260, 1261, 1262, 1263, 1264, 1265, 1266, 1267, 1268, 1269, 1270, 1271, 1272, 1273, 1274, 1275
590	*Lagopus muta*	Rock Ptarmigan	3020		1276	1277, 1278, 1279, 1280, 1281, 1282, 1283, 1284, 1285, 1286, 1287, 1288, 1289, 1290, 1291, 1292, 1293, 1294, 1295, 1296, 1297, 1298, 1299, 1300, 1301, 1302, 1303, 1304, 1305, 1306
600	*Lagopus leucura*	White-tailed Ptarmigan	3040		1249	1250, 1251, 1252, 1253, 1254
610	*Dendragapus obscurus*	Dusky Grouse	2970		1221	1222, 1223, 1224, 1225
615	*Dendragapus fuliginosus*	Sooty Grouse	2971		1226	1227, 1228, 1229, 1230
620	*Tympanuchus phasianellus*	Sharp-tailed Grouse	3080		1232	1233, 1234, 1235, 1236, 1237, 1238
630	*Tympanuchus cupido*	Greater Prairie-Chicken	3050		1241	
640	*Tympanuchus pallidicinctus*	Lesser Prairie-Chicken	3070		1246	

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Project ID	Scientific name	English name	BBS ID	BBS subspecies ID	eBird ID	eBird subspecies ID
650	*Meleagris gallopavo*	Wild Turkey	3100		1180	1181, 1182, 1183, 1184, 1185, 1186
660	*Phoenicopterus ruber*	American Flamingo			1744	
670	*Tachybaptus dominicus*	Least Grebe	50		1779	1780, 1781, 1782, 1783, 1784
680	*Podilymbus podiceps*	Pied-billed Grebe	60		1785	1786, 1787, 1788
690	*Podiceps auritus*	Horned Grebe	30		1796	1797, 1798
700	*Podiceps grisegena*	Red-necked Grebe	20		1799	1800, 1801
710	*Podiceps nigricollis*	Eared Grebe	40		1806	1807, 1808, 1809
720	*Aechmophorus occidentalis*	Western Grebe	10		1818	1819, 1820
730	*Aechmophorus clarkii*	Clark's Grebe	11		1821	1822, 1823
740	*Columba livia*	Rock Pigeon	3131		1827	1829, 1830, 1831, 1832, 1833, 1834, 1835, 1836, 1837, 1838, 1839, 1840, 1841
750	*Patagioenas leucocephala*	White-crowned Pigeon	3140		1929	
760	*Patagioenas flavirostris*	Red-billed Pigeon	3130		1930	1931, 1932, 1933, 1934
770	*Patagioenas fasciata*	Band-tailed Pigeon	3120		1939	1941, 1942, 1943, 1946, 1947, 1948
780	*Streptopelia decaocto*	Eurasian Collared-Dove	22860		1997	
781	*Streptopelia chinensis*	Spotted Dove	3151		2034	2037, 2038
782	*Streptopelia roseogrisea*	African Collared-Dove	3152		2001	2002, 2003
790	*Columbina inca*	Inca Dove	3210		2205	
800	*Columbina passerina*	Common Ground Dove	3200		2206	
810	*Columbina talpacoti*	Ruddy Ground Dove	3201		2230	2231, 2232, 2233, 2234
820	*Leptotila verreauxi*	White-tipped Dove	3180		2282	2284, 2285, 2286, 2287, 2288, 2289, 2290, 2291, 2292, 2295, 2296, 2297, 2298
830	*Zenaida asiatica*	White-winged Dove	3190		2346	2347, 2348, 2349
840	*Zenaida macroura*	Mourning Dove	3160		2369	2370, 2371, 2372, 2373, 2374
850	*Crotophaga ani*	Smooth-billed Ani	3830		2964	
860	*Crotophaga sulcirostris*	Groove-billed Ani	3840		2965	
870	*Geococcyx californianus*	Greater Roadrunner	3850		2976	

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Project ID	Scientific name	English name	BBS ID	BBS subspecies ID	eBird ID	eBird subspecies ID
880	*Coccyzus americanus*	Yellow-billed Cuckoo	3870		3169	
890	*Coccyzus minor*	Mangrove Cuckoo	3860		3172	
900	*Coccyzus erythropthalmus*	Black-billed Cuckoo	3880		3174	
910	*Centronyx bairdii*	Baird's Sparrow	5450		32180	
920	*Chordeiles acutipennis*	Lesser Nighthawk	4210		3433	3434, 3435, 3436, 3437, 3438, 3439, 3440
930	*Chordeiles minor*	Common Nighthawk	4200		3441	3442, 3443, 3444, 3445, 3446, 3447, 3448, 3449, 3450
940	*Chordeiles gundlachii*	Antillean Nighthawk	4201		3451	3452, 3453
950	*Nyctidromus albicollis*	Common Pauraque	4190		3486	3487, 3488, 3489, 3490, 3491, 3492, 3493
960	*Phalaenoptilus nuttallii*	Common Poorwill	4180		3537	3538, 3539, 3540, 3541, 3542
970	*Antrostomus carolinensis*	Chuck-will's-widow	4160		3543	
980	*Antrostomus ridgwayi*	Buff-collared Nightjar			3561	3562, 3563
990	*Antrostomus vociferus*	Eastern Whip-poor-will	4171		3564	
1000	*Antrostomus arizonae*	Mexican Whip-poor-will	4172		3566	3567, 3568, 3569, 3570, 3571
1010	*Cypseloides niger*	Black Swift	4220		3735	
1020	*Chaetura pelagica*	Chimney Swift	4230		3788	
1030	*Chaetura vauxi*	Vaux's Swift	4240		3789	3793, 3794, 3795
1040	*Aeronautes saxatalis*	White-throated Swift	4250		4063	4064, 4065
1050	*Eugenes fulgens*	Rivoli's Hummingbird	4260		4612	
1060	*Lampornis clemenciae*	Blue-throated Mountain-gem	4270		4640	4641, 4642
1070	*Calothorax lucifer*	Lucifer Hummingbird	4370		4685	
1080	*Archilochus colubris*	Ruby-throated Hummingbird	4280		4688	
1090	*Archilochus alexandri*	Black-chinned Hummingbird	4290		4689	
1100	*Calypte anna*	Anna's Hummingbird	4310		4699	
1110	*Calypte costae*	Costa's Hummingbird	4300		4702	
1120	*Selasphorus platycercus*	Broad-tailed Hummingbird	4320		4720	
1130	*Selasphorus rufus*	Rufous Hummingbird	4330		4710	
1140	*Selasphorus sasin*	Allen's Hummingbird	4340		4714	4715, 4716

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Project ID	Scientific name	English name	BBS ID	BBS subspecies ID	eBird ID	eBird subspecies ID
1150	*Selasphorus calliope*	Calliope Hummingbird	4360		4707	
1160	*Cynanthus latirostris*	Broad-billed Hummingbird	4410		4745	4747, 4748, 4749
1170	*Saucerottia beryllina*	Berylline Hummingbird			4927	4929, 4930, 4932, 4933, 4934
1180	*Amazilia yucatanensis*	Buff-bellied Hummingbird	4390		4976	4979, 4980
1190	*Leucolia violiceps*	Violet-crowned Hummingbird	4391		4915	4916, 4917
1200	*Basilinna leucotis*	White-eared Hummingbird			4794	4795, 4796, 4797
1210	*Rallus elegans*	King Rail	2080		5130	
1220	*Rallus crepitans*	Clapper Rail	2110		5134	5136, 5137, 5139, 5140, 5142, 5143, 5144, 5145, 5147, 5148, 5149
1225	*Rallus obsoletus*	Ridgway's Rail	2111		5115	
1230	*Rallus limicola*	Virginia Rail	2120		5155	5157, 5158
1240	*Porzana carolina*	Sora	2140		5313	
1250	*Gallinula galeata*	Common Gallinule	2190		5327	5329, 5330, 5331, 5332, 5333
1260	*Fulica americana*	American Coot	2210		5359	5360, 5361
1270	*Porphyrio martinica*	Purple Gallinule	2180		5372	
1275	*Porphyrio porphyrio*	Western Swamphen	21930		5377	
1280	*Larus marinus*	Great Black-backed Gull	470		6397	
1290	*Coturnicops noveboracensis*	Yellow Rail	2150		5491	
1300	*Laterallus jamaicensis*	Black Rail	2160		5515	5517, 5518, 5520, 5521
1310	*Aramus guarauna*	Limpkin	2070		5534	5536, 5537, 5538
1320	*Antigone canadensis*	Sandhill Crane	2060		5561	5564, 5565
1330	*Grus americana*	Whooping Crane	2040		5580	
1340	*Himantopus mexicanus*	Black-necked Stilt	2260		5626	
1350	*Recurvirostra americana*	American Avocet	2250		5636	
1360	*Haematopus palliatus*	American Oystercatcher	2860		5653	5654, 5655
1370	*Haematopus bachmani*	Black Oystercatcher	2870		5660	
1380	*Pluvialis squatarola*	Black-bellied Plover	2700		5664	
1390	*Pluvialis dominica*	American Golden-Plover	2720		5668	
1390	*Pluvialis dominica*	American Golden-Plover	2721		5668	
1400	*Charadrius nivosus*	Snowy Plover	2780		5757	

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Project ID	Scientific name	English name	BBS ID	BBS subspecies ID	eBird ID	eBird subspecies ID
1410	*Charadrius wilsonia*	Wilson's Plover	2800		5762	5763, 5764, 5765, 5766
1420	*Charadrius semipalmatus*	Semipalmated Plover	2740		5770	
1425	*Charadrius hiaticula*	Common Ringed Plover	2750		5767	5768, 5769
1430	*Charadrius melodus*	Piping Plover	2770		5773	
1440	*Charadrius vociferus*	Killdeer	2730		5793	5794, 5795, 5796
1450	*Charadrius montanus*	Mountain Plover	2810		5797	
1460	*Jacana spinosa*	Northern Jacana			5837	5838, 5839, 5840
1470	*Bartramia longicauda*	Upland Sandpiper	2610		5852	
1480	*Numenius tahitiensis*	Bristle-thighed Curlew	2680		5853	
1490	*Numenius phaeopus*	Whimbrel	2650		5854	
1500	*Numenius borealis*	Eskimo Curlew			5863	
1510	*Numenius americanus*	Long-billed Curlew	2640		5864	5865, 5866
1520	*Limosa lapponica*	Bar-tailed Godwit	2500		5875	5878, 5879
1520	*Limosa limosa*	Black-tailed Godwit	2500		5880	5878, 5879
1530	*Limosa haemastica*	Hudsonian Godwit	2510		5885	
1540	*Limosa fedoa*	Marbled Godwit	2490		5886	5887, 5888
1550	*Arenaria interpres*	Ruddy Turnstone	2830		5891	5892, 5893
1560	*Arenaria melanocephala*	Black Turnstone	2840		5894	
1570	*Calidris canutus*	Red Knot	2340		5900	5901, 5902, 5903, 5904, 5905, 5906
1580	*Calidris virgata*	Surfbird	2820		5908	
1590	*Calidris himantopus*	Stilt Sandpiper	2330		5916	
1600	*Calidris alba*	Sanderling	2480		5922	
1610	*Calidris alpina*	Dunlin	2430		5923	5925, 5926, 5932, 5933, 5934
1620	*Calidris ptilocnemis*	Rock Sandpiper	2356		5936	
1630	*Calidris maritima*	Purple Sandpiper	2350		5942	
1640	*Calidris bairdii*	Baird's Sandpiper	2410		5945	
1650	*Calidris minutilla*	Least Sandpiper	2420		5948	
1660	*Calidris fuscicollis*	White-rumped Sandpiper	2400		5949	
1670	*Calidris subruficollis*	Buff-breasted Sandpiper	2620		5951	
1680	*Calidris melanotos*	Pectoral Sandpiper	2390		5953	
1690	*Calidris pusilla*	Semipalmated Sandpiper	2460		5956	
1700	*Calidris mauri*	Western Sandpiper	2470		5957	

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Project ID	Scientific name	English name	BBS ID	BBS subspecies ID	eBird ID	eBird subspecies ID
1705	*Calidris acuminata*	Sharp-tailed Sandpiper	2380		5915	
1705	*Calidris ruficollis*	Red-necked Stint	2422		5921	
1706	*Calidris pugnax*	Ruff	2600		5911	
1710	*Limnodromus griseus*	Short-billed Dowitcher	2310		5962	
1720	*Limnodromus scolopaceus*	Long-billed Dowitcher	2320		5966	
1730	*Scolopax minor*	American Woodcock	2280		5976	
1740	*Gallinago gallinago*	Common Snipe	2300		5994	5995, 5996
1740	*Gallinago delicata*	Wilson's Snipe	2300		5998	5995, 5996
1750	*Phalaropus tricolor*	Wilson's Phalarope	2240		6020	
1760	*Phalaropus lobatus*	Red-necked Phalarope	2230		6021	
1770	*Phalaropus fulicarius*	Red Phalarope			6022	
1780	*Actitis macularius*	Spotted Sandpiper	2630		6026	
1780	*Actitis macularius*	Spotted Sandpiper	2631		6026	
1790	*Tringa solitaria*	Solitary Sandpiper	2560		6029	
1795	*Tringa nebularia*	Common Greenshank	2530		6037	
1800	*Tringa incana*	Wandering Tattler	2590		6033	
1810	*Tringa melanoleuca*	Greater Yellowlegs	2540		6036	
1820	*Tringa semipalmata*	Willet	2580		6040	
1830	*Tringa flavipes*	Lesser Yellowlegs	2550		6043	
1840	*Tringa glareola*	Wood Sandpiper			6046	
1850	*Stercorarius pomarinus*	Pomarine Jaeger	360		6176	
1860	*Stercorarius parasiticus*	Parasitic Jaeger	370		6177	
1870	*Stercorarius longicaudus*	Long-tailed Jaeger	380		6179	6180, 6181
1880	*Alle alle*	Dovekie			6186	6187, 6188
1890	*Uria aalge*	Common Murre	300		6189	6190, 6191, 6192, 6193
1900	*Uria lomvia*	Thick-billed Murre	310		6194	6195, 6196, 6197, 6198
1910	*Alca torda*	Razorbill	320		6201	6202, 6203
1920	*Cepphus grylle*	Black Guillemot	270		6206	6209, 6210, 6211, 6212
1930	*Cepphus columba*	Pigeon Guillemot	290		6213	6216, 6217, 6218, 6219
1940	*Brachyramphus marmoratus*	Marbled Murrelet	230		6223	
1950	*Brachyramphus brevirostris*	Kittlitz's Murrelet	240		6224	
1960	*Synthliboramphus hypoleucus*	Guadalupe Murrelet			6226	

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Project ID	Scientific name	English name	BBS ID	BBS subspecies ID	eBird ID	eBird subspecies ID
1970	*Synthliboramphus antiquus*	Ancient Murrelet	210		6231	6232, 6233
1980	*Ptychoramphus aleuticus*	Cassin's Auklet	160		6236	6237, 6238
1990	*Aethia psittacula*	Parakeet Auklet			6239	
2000	*Aethia pusilla*	Least Auklet			6240	
2010	*Aethia pygmaea*	Whiskered Auklet			6241	
2020	*Aethia cristatella*	Crested Auklet			6242	
2030	*Cerorhinca monocerata*	Rhinoceros Auklet	150		6243	
2040	*Fratercula arctica*	Atlantic Puffin			6245	6246, 6247, 6248
2050	*Fratercula corniculata*	Horned Puffin	140		6249	
2060	*Fratercula cirrhata*	Tufted Puffin	120		6250	
2070	*Rissa tridactyla*	Black-legged Kittiwake	400		6254	
2080	*Rissa brevirostris*	Red-legged Kittiwake			6257	
2090	*Pagophila eburnea*	Ivory Gull			6259	
2100	*Xema sabini*	Sabine's Gull	620		6260	6261, 6262, 6263, 6264
2110	*Chroicocephalus philadelphia*	Bonaparte's Gull	600		6267	
2120	*Chroicocephalus ridibundus*	Black-headed Gull	551		6285	
2130	*Hydrocoloeus minutus*	Little Gull	601		6291	
2140	*Rhodostethia rosea*	Ross's Gull	610		6292	
2150	*Leucophaeus atricilla*	Laughing Gull	580		6295	6296, 6297
2160	*Leucophaeus pipixcan*	Franklin's Gull	590		6299	
2170	*Larus heermanni*	Heermann's Gull	570		6317	
2180	*Larus canus*	Common Gull	550		6318	
2190	*Larus delawarensis*	Ring-billed Gull	540		6326	
2200	*Larus occidentalis*	Western Gull	490		6331	6332, 6333
2205	*Larus schistisagus*	Slaty-backed Gull	480		6380	
2206	*Larus fuscus*	Lesser Black-backed Gull	500		6368	
2210	*Larus californicus*	California Gull	530		6336	
2220	*Larus argentatus*	Herring Gull	510		6339	6344, 6345
2230	*Larus glaucoides*	Iceland Gull	430		6359	
2240	*Larus glaucescens*	Glaucous-winged Gull	440		6382	
2250	*Larus hyperboreus*	Glaucous Gull	420		6388	6389, 6390, 6391, 6392
2260	*Anous stolidus*	Brown Noddy			6410	6412, 6413, 6414, 6415
2270	*Onychoprion fuscatus*	Sooty Tern			6446	6447, 6448, 6450, 6451, 6452, 6453, 6454

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2280	*Onychoprion aleuticus*	Aleutian Tern	730		6464	
2290	*Sternula antillarum*	Least Tern	740		6472	6473, 6474, 6475
2300	*Gelochelidon nilotica*	Gull-billed Tern	630		6493	6495, 6496, 6497, 6498, 6499
2310	*Hydroprogne caspia*	Caspian Tern	640		6501	
2320	*Chlidonias niger*	Black Tern	770		6503	
2330	*Sterna dougallii*	Roseate Tern	720		6513	6514, 6515, 6516, 6517, 6518
2340	*Sterna hirundo*	Common Tern	700		6526	6528, 6529
2350	*Sterna paradisaea*	Arctic Tern	710		6533	
2360	*Sterna forsteri*	Forster's Tern	690		6546	
2370	*Thalasseus maximus*	Royal Tern	650		6555	
2380	*Thalasseus sandvicensis*	Sandwich Tern	670		6561	
2390	*Thalasseus elegans*	Elegant Tern	660		6566	
2400	*Rynchops niger*	Black Skimmer	800		6580	
2410	*Gavia stellata*	Red-throated Loon	110		6610	
2420	*Gavia arctica*	Arctic Loon	90		6611	6612, 6613
2430	*Gavia pacifica*	Pacific Loon	100		6614	
2440	*Gavia immer*	Common Loon	70		6616	
2450	*Gavia adamsii*	Yellow-billed Loon	80		6617	
2460	*Hydrobates furcatus*	Fork-tailed Storm-Petrel			6719	6720, 6721
2470	*Hydrobates leucorhous*	Leach's Storm-Petrel	1060		6723	
2480	*Hydrobates homochroa*	Ashy Storm-Petrel			6733	
2490	*Hydrobates melania*	Black Storm-Petrel			6744	
2491	*Sula dactylatra*	Masked Booby	1140		6987	6988, 6989, 6990, 6991
2492	*Sula nebouxii*	Blue-footed Booby	1141		6994	6995, 6996
2493	*Sula leucogaster*	Brown Booby	1150		6998	
2500	*Fulmarus glacialis*	Northern Fulmar	860		6758	6760, 6761
2505	*Calonectris diomedea*	Cory's Shearwater	880		6863	
2510	*Puffinus puffinus*	Manx Shearwater	900		6881	
2520	*Mycteria americana*	Wood Stork	1880		6963	
2530	*Fregata magnificens*	Magnificent Frigatebird	1280		6976	
2540	*Morus bassanus*	Northern Gannet	1170		7011	
2550	*Anhinga anhinga*	Anhinga	1180		7015	7016, 7017
2560	*Urile penicillatus*	Brandt's Cormorant	1220		7034	
2570	*Urile urile*	Red-faced Cormorant			7035	
2580	*Urile pelagicus*	Pelagic Cormorant	1230		7036	7037, 7038

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2590	*Phalacrocorax carbo*	Great Cormorant	1190		7042	7047, 7048
2600	*Nannopterum brasilianum*	Neotropic Cormorant	1210		7077	7078, 7079
2610	*Nannopterum auritum*	Double-crested Cormorant	1200		7071	7072, 7073, 7074, 7075
2620	*Pelecanus erythrorhynchos*	American White Pelican	1250		7104	
2630	*Pelecanus occidentalis*	Brown Pelican	1260		7105	7109, 7110
2640	*Botaurus lentiginosus*	American Bittern	1900		7127	
2650	*Ardea herodias*	Great Blue Heron	1940	1920	7168	7170, 7171, 7172, 7173
2660	*Ardea alba*	Great Egret	1960		7200	
2670	*Egretta thula*	Snowy Egret	1970		7229	7230, 7231
2675	*Egretta garzetta*	Little Egret	1961		7217	
2680	*Egretta caerulea*	Little Blue Heron	2000		7233	
2690	*Egretta tricolor*	Tricolored Heron	1990		7235	7236, 7237
2700	*Egretta rufescens*	Reddish Egret	1980		7240	7241, 7242
2710	*Bubulcus ibis*	Cattle Egret	2001		7247	
2720	*Butorides striata*	Striated Heron			7267	7271, 7272, 7273, 7274, 7275, 7276, 7277, 7278, 7279, 7281, 7282, 7283, 7284, 7285, 7286, 7287, 7288, 7289, 7290, 7291, 7292, 7293, 7294
2720	*Agamia agami*	Agami Heron			7297	7271, 7272, 7273, 7274, 7275, 7276, 7277, 7278, 7279, 7281, 7282, 7283, 7284, 7285, 7286, 7287, 7288, 7289, 7290, 7291, 7292, 7293, 7294
2725	*Butorides virescens*	Green Heron	2010		7261	7263, 7264
2730	*Nycticorax nycticorax*	Black-crowned Night-Heron	2020		7305	
2740	*Nyctanassa violacea*	Yellow-crowned Night-Heron	2030		7318	7320
2750	*Eudocimus albus*	White Ibis	1840		7343	
2760	*Plegadis falcinellus*	Glossy Ibis	1860		7346	
2770	*Plegadis chihi*	White-faced Ibis	1870		7347	
2780	*Platalea ajaja*	Roseate Spoonbill	1830		7407	
2790	*Gymnogyps californianus*	California Condor	3240		7409	
2800	*Coragyps atratus*	Black Vulture	3260		7412	7413, 7414, 7415
2810	*Cathartes aura*	Turkey Vulture	3250		7416	7418, 7419
2820	*Pandion haliaetus*	Osprey	3640		7429	
2830	*Elanus leucurus*	White-tailed Kite	3280		7445	7446, 7447

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2840	*Chondrohierax uncinatus*	Hook-billed Kite	3271		7463	
2850	*Elanoides forficatus*	Swallow-tailed Kite	3270		7486	7487, 7488
2860	*Aquila chrysaetos*	Golden Eagle	3490		7662	7663, 7664, 7665, 7666, 7667, 7668
2870	*Rostrhamus sociabilis*	Snail Kite	3300		7700	7701, 7702, 7703
2880	*Ictinia mississippiensis*	Mississippi Kite	3290		7709	
2890	*Circus hudsonius*	Northern Harrier	3310		7732	
2900	*Accipiter striatus*	Sharp-shinned Hawk	3320		7896	7898, 7899, 7900, 7902, 7903, 7904
2910	*Accipiter cooperii*	Cooper's Hawk	3330		7909	
2920	*Accipiter gentilis*	Northern Goshawk	3340		7926	7928, 7929, 7930, 7931, 7932, 7933, 7935, 7936
2930	*Haliaeetus leucocephalus*	Bald Eagle	3520		7967	7968, 7969
2940	*Buteogallus anthracinus*	Common Black Hawk	3450		7995	7997, 7998, 8000, 8001, 8002
2950	*Parabuteo unicinctus*	Harris's Hawk	3350		8032	
2960	*Geranoaetus albicaudatus*	White-tailed Hawk	3410		8036	8037, 8038, 8039
2970	*Ixobrychus exilis*	Least Bittern	1910		7149	7150, 7151, 7152, 7153, 7154
2980	*Buteo plagiatus*	Gray Hawk	3460		8060	8062, 8063, 8064
2980	*Buteo nitidus*	Gray-lined Hawk	3460		8061	8062, 8063, 8064
2990	*Buteo lineatus*	Red-shouldered Hawk	3390		8066	8068, 8069, 8070
3000	*Buteo platypterus*	Broad-winged Hawk	3430		8075	8078, 8079, 8080, 8081, 8082
3010	*Buteo brachyurus*	Short-tailed Hawk	3440		8086	8087, 8088
3020	*Buteo swainsoni*	Swainson's Hawk	3420		8090	
3030	*Buteo albonotatus*	Zone-tailed Hawk	3400		8092	
3040	*Buteo jamaicensis*	Red-tailed Hawk	3370	3380	8094	8096, 8097, 8105, 8106
3050	*Buteo lagopus*	Rough-legged Hawk	3470		8114	8115, 8116, 8117, 8118
3060	*Buteo regalis*	Ferruginous Hawk	3480		8121	
3070	*Tyto alba*	Barn Owl	3650		8193	8195, 8196, 8197, 8198, 8207, 8208, 8209, 8210, 8211, 8212, 8214, 8215, 8216, 8217, 8218, 8219, 8223, 8224
3080	*Psiloscops flammeolus*	Flammulated Owl	3740		8370	
3090	*Megascops trichopsis*	Whiskered Screech-Owl	3731		8375	8376, 8377, 8378

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3100	*Megascops kennicottii*	Western Screech-Owl	3732		8430	8432, 8433, 8434, 8435, 8436, 8437
3110	*Megascops asio*	Eastern Screech-Owl	3730		8440	
3120	*Bubo virginianus*	Great Horned Owl	3750		8481	8483, 8484, 8485, 8486, 8487, 8488, 8489, 8490, 8491, 8492, 8493, 8494
3130	*Bubo scandiacus*	Snowy Owl	3760		8542	
3140	*Surnia ulula*	Northern Hawk Owl	3770		8565	8568, 8569
3150	*Glaucidium gnoma*	Northern Pygmy-Owl	3790		8576	8579, 8580, 8581
3160	*Glaucidium brasilianum*	Ferruginous Pygmy-Owl	3800		8602	8604, 8605, 8606, 8607, 8608, 8609, 8610, 8611, 8612, 8613, 8614, 8615
3170	*Micrathene whitneyi*	Elf Owl	3810		8659	8660, 8661, 8662, 8663
3180	*Athene cunicularia*	Burrowing Owl	3780		8688	8690, 8691, 8694, 8695, 8696, 8697, 8698, 8699, 8701, 8702, 8703, 8705, 8706, 8709, 8710, 8711
3190	*Strix occidentalis*	Spotted Owl	3690		8769	
3200	*Strix varia*	Barred Owl	3680		8773	8774, 8775, 8776
3210	*Strix nebulosa*	Great Gray Owl	3700		8796	
3220	*Asio otus*	Long-eared Owl	3660		8806	8808, 8809, 8811, 8812
3230	*Asio flammeus*	Short-eared Owl	3670		8829	8834, 8835, 8838, 8839, 8840, 8841
3240	*Aegolius funereus*	Boreal Owl	3710		8849	8851, 8852, 8853, 8854, 8855
3250	*Aegolius acadicus*	Northern Saw-whet Owl	3720		8857	
3251	*Melopsittacus undulatus*	Budgerigar	3822		12003	
3252	*Psittacula krameri*	Rose-ringed Parakeet	3823		11807	11808, 11809, 11810, 11811
3253	*Myiopsitta monachus*	Monk Parakeet	3824		12258	12260, 12261, 12262
3254	*Amazona viridigenalis*	Red-crowned Parrot	3826		12344	
3255	*Brotogeris chiriri*	Yellow-chevroned Parakeet	52021		12269	12270, 12271
3256	*Trogon elegans*	Elegant Trogon	3890		9071	9073, 9074, 9075, 9077, 9078
3257	*Aratinga nenday*	Nanday Parakeet	51830		12555	
3260	*Megaceryle torquata*	Ringed Kingfisher	3901		9777	9779, 9780
3270	*Megaceryle alcyon*	Belted Kingfisher	3900		9782	

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3280	*Chloroceryle americana*	Green Kingfisher	3910		9792	9793, 9794, 9795, 9796, 9797
3290	*Sphyrapicus thyroideus*	Williamson's Sapsucker	4040		10633	10634, 10635
3300	*Sphyrapicus varius*	Yellow-bellied Sapsucker	4020		10636	
3310	*Sphyrapicus nuchalis*	Red-naped Sapsucker	4021		10637	
3320	*Sphyrapicus ruber*	Red-breasted Sapsucker	4030		10640	
3330	*Melanerpes lewis*	Lewis's Woodpecker	4080		10651	
3340	*Melanerpes erythrocephalus*	Red-headed Woodpecker	4060		10654	
3350	*Melanerpes formicivorus*	Acorn Woodpecker	4070		10655	10657, 10658, 10659, 10660, 10661, 10662
3360	*Melanerpes uropygialis*	Gila Woodpecker	4110		10685	10686, 10687, 10688
3370	*Melanerpes aurifrons*	Golden-fronted Woodpecker	4100		10691	10694, 10695, 10696, 10697, 10698, 10699, 10700, 10701, 10702, 10703
3380	*Melanerpes carolinus*	Red-bellied Woodpecker	4090		10707	
3390	*Picoides dorsalis*	American Three-toed Woodpecker	4010		10724	
3400	*Picoides arcticus*	Black-backed Woodpecker	4000		10728	
3410	*Dryobates pubescens*	Downy Woodpecker	3940		10892	10894, 10895, 10897, 10898, 10900, 10901
3420	*Dryobates nuttallii*	Nuttall's Woodpecker	3970		10902	
3430	*Dryobates scalaris*	Ladder-backed Woodpecker	3960		10904	10905, 10906, 10907, 10908, 10909, 10910, 10911, 10912
3440	*Dryobates borealis*	Red-cockaded Woodpecker	3950		10917	
3450	*Dryobates villosus*	Hairy Woodpecker	3930		10918	10920, 10921, 10922, 10923, 10924, 10925, 10927, 10928, 10929, 10930, 10932, 10933, 10935, 10936
3460	*Dryobates albolarvatus*	White-headed Woodpecker	3990		10942	10943, 10944
3470	*Dryobates stricklandi*	Strickland's Woodpecker	3975		10951	

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3480	*Campephilus principalis*	Ivory-billed Woodpecker			11053	
3490	*Dryocopus pileatus*	Pileated Woodpecker	4050		11237	11238, 11239
3500	*Colaptes auratus*	Northern Flicker	4123	4120, 4130, 4125	11371	11375, 11376, 11378, 11379, 11380, 11381
3505	*Colaptes chrysoides*	Gilded Flicker	4140		11384	11385, 11386, 11387, 11388
3520	*Falco sparverius*	American Kestrel	3600		11494	11496, 11497, 11498, 11499, 11505, 11506, 11507, 11508, 11509, 11510, 11511, 11512
3530	*Falco columbarius*	Merlin	3570		11528	11530, 11531, 11532, 11533, 11534
3540	*Falco femoralis*	Aplomado Falcon	3590		11555	11556, 11557, 11558
3550	*Falco rusticolus*	Gyrfalcon	3540		11574	
3560	*Falco peregrinus*	Peregrine Falcon	3560		11575	11578, 11579, 11583, 11584, 11585, 11594, 11595
3570	*Falco mexicanus*	Prairie Falcon	3550		11599	
3580	*Pachyramphus aglaiae*	Rose-throated Becard	4411		15422	15423, 15424, 15425, 15426, 15427, 15428, 15429, 15430
3590	*Camptostoma imberbe*	Northern Beardless-Tyrannulet	4720		15889	
3600	*Contopus cooperi*	Olive-sided Flycatcher	4590		16223	
3610	*Contopus pertinax*	Greater Pewee	4600		16224	
3620	*Contopus sordidulus*	Western Wood-Pewee	4620		16236	16237, 16238, 16239, 16240
3630	*Contopus virens*	Eastern Wood-Pewee	4610		16241	
3640	*Empidonax flaviventris*	Yellow-bellied Flycatcher	4630		16282	
3650	*Empidonax virescens*	Acadian Flycatcher	4650		16283	
3660	*Empidonax alnorum*	Alder Flycatcher	4661		16284	
3670	*Empidonax traillii*	Willow Flycatcher	4660		16285	16288, 16289
3680	*Empidonax minimus*	Least Flycatcher	4670		16296	
3690	*Empidonax hammondii*	Hammond's Flycatcher	4680		16297	
3700	*Empidonax wrightii*	Gray Flycatcher	4691		16298	
3710	*Empidonax oberholseri*	Dusky Flycatcher	4690		16299	

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3720	*Empidonax difficilis*	Pacific-slope Flycatcher	4641		16308	16309, 16310, 16311
3730	*Empidonax occidentalis*	Cordilleran Flycatcher	4640		16312	16313, 16314
3740	*Empidonax fulvifrons*	Buff-breasted Flycatcher	4700		16321	16322, 16323, 16324, 16325, 16326, 16327
3750	*Sayornis nigricans*	Black Phoebe	4580		16330	16332, 16333, 16334, 16335, 16337, 16338
3760	*Sayornis phoebe*	Eastern Phoebe	4560		16339	
3770	*Sayornis saya*	Say's Phoebe	4570		16341	16342, 16343
3780	*Pyrocephalus rubinus*	Vermilion Flycatcher	4710		16360	16362, 16363, 16364, 16365, 16368, 16369, 16370, 16371, 16372
3790	*Myiarchus tuberculifer*	Dusky-capped Flycatcher	4550		16617	16620, 16621, 16622, 16623, 16624, 16625, 16626, 16627, 16629, 16630, 16632, 16633
3800	*Myiarchus cinerascens*	Ash-throated Flycatcher	4540		16656	16657, 16658
3810	*Myiarchus crinitus*	Great Crested Flycatcher	4520		16665	
3820	*Myiarchus tyrannulus*	Brown-crested Flycatcher	4530		16666	16669, 16670, 16671, 16674, 16675
3830	*Pitangus sulphuratus*	Great Kiskadee	4490		16699	16700, 16701, 16702, 16703, 16704, 16705, 16706, 16707, 16708, 16709
3840	*Myiodynastes luteiventris*	Sulphur-bellied Flycatcher	4510		16769	
3850	*Tyrannus melancholicus*	Tropical Kingbird	4460		16783	16784, 16785, 16786
3860	*Tyrannus couchii*	Couch's Kingbird	4461		16788	
3870	*Tyrannus vociferans*	Cassin's Kingbird	4480		16790	16791, 16792
3880	*Tyrannus crassirostris*	Thick-billed Kingbird	4451		16793	16794, 16795
3890	*Tyrannus verticalis*	Western Kingbird	4470		16796	
3900	*Tyrannus tyrannus*	Eastern Kingbird	4440		16800	
3910	*Tyrannus dominicensis*	Gray Kingbird	4450		16802	16803, 16804
3920	*Tyrannus forficatus*	Scissor-tailed Flycatcher	4430		16816	
3925	*Tyrannus savana*	Fork-tailed Flycatcher	4420		16819	
3930	*Vireo atricapilla*	Black-capped Vireo	6300		18437	

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3940	*Vireo griseus*	White-eyed Vireo	6310		18439	18441, 18442, 18443, 18444, 18445
3950	*Vireo bellii*	Bell's Vireo	6330		18466	18468, 18469
3960	*Vireo vicinior*	Gray Vireo	6340		18472	
3970	*Vireo huttoni*	Hutton's Vireo	6320		18473	18475, 18476, 18477, 18478, 18479, 18480, 18481, 18482, 18484, 18485, 18486, 18487, 18488
3980	*Vireo flavifrons*	Yellow-throated Vireo	6280		18489	
3990	*Vireo cassinii*	Cassin's Vireo	6291		18492	
4000	*Vireo solitarius*	Blue-headed Vireo	6290		18495	18496, 18497
4010	*Vireo plumbeus*	Plumbeous Vireo	6292		18500	18502, 18503, 18504, 18506, 18507
4020	*Vireo philadelphicus*	Philadelphia Vireo	6260		18512	
4030	*Vireo gilvus*	Warbling Vireo	6270		18513	18516, 18517, 18518, 18519
4040	*Vireo olivaceus*	Red-eyed Vireo	6240		18533	
4050	*Vireo altiloquus*	Black-whiskered Vireo	6230		18556	18557, 18558, 18559, 18560, 18561, 18562
4055	*Vidua macroura*	Pin-tailed Whydah	19510		30406	
4060	*Lanius ludovicianus*	Loggerhead Shrike	6220		20282	20283, 20284, 20285, 20286, 20287, 20288, 20289, 20290, 20291, 20292, 20293
4070	*Lanius borealis*	Northern Shrike	6210		20294	20296, 20297, 20298, 20299
4070	*Lanius excubitor*	Great Gray Shrike	6210		20303	20296, 20297, 20298, 20299
4080	*Perisoreus canadensis*	Canada Jay	4840		20384	20386, 20387, 20388, 20389, 20391, 20392, 20394, 20395
4090	*Psilorhinus morio*	Brown Jay			20425	20426, 20427, 20428, 20429
4100	*Cyanocorax yncas*	Green Jay	4830		20434	20436, 20437, 20438, 20439, 20440, 20442, 20443, 20444, 20445, 20446, 20447
4110	*Gymnorhinus cyanocephalus*	Pinyon Jay	4920		20475	
4120	*Cyanocitta stelleri*	Steller's Jay	4780		20476	20478, 20479, 20480, 20481, 20483, 20484, 20485, 20486, 20488, 20489,

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						20490, 20491, 20492, 20493, 20494, 20495
4130	*Cyanocitta cristata*	Blue Jay	4770		20496	20497, 20498, 20499, 20500
4140	*Aphelocoma coerulescens*	Florida Scrub-Jay	4790		20503	
4150	*Aphelocoma insularis*	Island Scrub-Jay	4811		20504	
4160	*Aphelocoma californica*	California Scrub-Jay	4812		20505	20506, 20507, 20508, 20509, 20510, 20511, 20512, 20513
4170	*Aphelocoma californica*	California Scrub-Jay	4813		20505	20506, 20507, 20508, 20509, 20510, 20511, 20512, 20513
4180	*Aphelocoma wollweberi*	Mexican Jay	4820		20527	20529, 20530, 20531, 20535, 20536
4180	*Aphelocoma ultramarina*	Transvolcanic Jay	4820		20534	20529, 20530, 20531, 20535, 20536
4190	*Pica hudsonia*	Black-billed Magpie	4750		20682	
4200	*Pica nuttalli*	Yellow-billed Magpie	4760		20683	
4210	*Nucifraga columbiana*	Clark's Nutcracker	4910		20690	
4220	*Corvus brachyrhynchos*	American Crow	4880		20762	20764, 20765, 20766, 20767
4240	*Corvus ossifragus*	Fish Crow	4900		20776	
4250	*Corvus cryptoleucus*	Chihuahuan Raven	4870		20780	
4260	*Corvus corax*	Common Raven	4860		20829	20830, 20831, 20832, 20833, 20834, 20835, 20836, 20837
4270	*Poecile carolinensis*	Carolina Chickadee	7360		21254	21255, 21256, 21257, 21258
4280	*Poecile atricapillus*	Black-capped Chickadee	7350		21259	21260, 21261, 21262, 21263, 21264, 21265, 21266, 21267, 21268
4290	*Poecile gambeli*	Mountain Chickadee	7380		21271	21273, 21274, 21275, 21277, 21278, 21279
4300	*Poecile sclateri*	Mexican Chickadee	7370		21282	21283, 21284, 21285, 21286
4310	*Poecile rufescens*	Chestnut-backed Chickadee	7410		21287	21288, 21289, 21290
4320	*Poecile hudsonicus*	Boreal Chickadee	7400		21291	21292, 21293, 21294, 21295, 21296

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4330	*Poecile cinctus*	Gray-headed Chickadee			21299	21300, 21301, 21302, 21303
4340	*Baeolophus wollweberi*	Bridled Titmouse	7340		21337	21338, 21339, 21340, 21341
4350	*Baeolophus inornatus*	Oak Titmouse	7330		21342	21343, 21344, 21345, 21346
4360	*Baeolophus ridgwayi*	Juniper Titmouse	7331		21347	21348, 21349
4370	*Baeolophus bicolor*	Tufted Titmouse	7310		21352	
4380	*Baeolophus atricristatus*	Black-crested Titmouse	7320		21355	21356, 21357, 21358
4390	*Auriparus flaviceps*	Verdin	7460		21456	21457, 21458, 21459, 21460, 21461, 21462
4400	*Eremophila alpestris*	Horned Lark	4740		21754	21757, 21758, 21759, 21760, 21761, 21763, 21764, 21765, 21766, 21767, 21768, 21769, 21773, 21774, 21775, 21776, 21778, 21779, 21780, 21781, 21782, 21783, 21784, 21785, 21786, 21787, 21789, 21790, 21791, 21792, 21793, 21794, 21797, 21798, 21799, 21800, 21801
4410	*Alauda arvensis*	Eurasian Skylark	4730		21905	21907, 21908, 21909, 21910, 21911, 21912, 21913, 21915, 21916, 21917, 21918, 21920, 21921
4420	*Stelgidopteryx serripennis*	Northern Rough-winged Swallow	6170		23172	23174, 23175, 23176, 23177, 23179, 23180
4430	*Progne subis*	Purple Martin	6110		23187	23189, 23190
4440	*Tachycineta bicolor*	Tree Swallow	6140		23211	
4450	*Tachycineta thalassina*	Violet-green Swallow	6150		23221	23222, 23223
4460	*Riparia riparia*	Bank Swallow	6160		23242	23243, 23244, 23245, 23246
4470	*Hirundo rustica*	Barn Swallow	6130		23291	23297, 23298
4480	*Petrochelidon pyrrhonota*	Cliff Swallow	6120		23383	23385, 23386, 23387
4490	*Petrochelidon fulva*	Cave Swallow	6121		23391	23393, 23394, 23395, 23396

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4500	*Phylloscopus borealis*	Arctic Warbler	7470		24077	
4510	*Psaltriparus minimus*	Bushtit	7430		24372	24374, 24375, 24376, 24377, 24378, 24381, 24382, 24383, 24384
4520	*Chamaea fasciata*	Wrentit	7420		24546	24547, 24548, 24549, 24550, 24551
4530	*Regulus satrapa*	Golden-crowned Kinglet	7480		25946	25947, 25948, 25949, 25950, 25951, 25952
4540	*Corthylio calendula*	Ruby-crowned Kinglet	7490		25942	25943, 25944, 25945
4550	*Sitta canadensis*	Red-breasted Nuthatch	7280		26022	
4560	*Sitta carolinensis*	White-breasted Nuthatch	7270		26025	26028, 26029, 26030, 26031, 26032, 26033, 26035, 26036
4570	*Sitta pygmaea*	Pygmy Nuthatch	7300		26037	26038, 26039, 26040, 26041, 26042, 26043, 26044
4580	*Sitta pusilla*	Brown-headed Nuthatch	7290		26045	
4590	*Certhia americana*	Brown Creeper	7260		26109	26111, 26112, 26113, 26114, 26115, 26117, 26118, 26120, 26121, 26123, 26124
4600	*Polioptila caerulea*	Blue-gray Gnatcatcher	7510		26211	26213, 26214, 26215, 26216, 26217, 26218
4610	*Polioptila californica*	California Gnatcatcher	7530		26225	26226, 26227, 26228
4620	*Polioptila melanura*	Black-tailed Gnatcatcher	7520		26221	26222, 26223, 26224
4630	*Salpinctes obsoletus*	Rock Wren	7150		26237	26239, 26240, 26241, 26242, 26243, 26245, 26246, 26247
4640	*Catherpes mexicanus*	Canyon Wren	7170		26271	26272, 26273, 26274
4650	*Troglodytes aedon*	House Wren	7210		26278	26280, 26281, 26282, 26291, 26292, 26293, 26294, 26296, 26297, 26298, 26299, 26300, 26301, 26302, 26303, 26304, 26305, 26306, 26307, 26308,

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						26309, 26310, 26311, 26312, 26313
4660	*Troglodytes troglodytes*	Eurasian Wren			26339	26348, 26349, 26350, 26351, 26352, 26353, 26354, 26355, 26356, 26357, 26358, 26359, 26360, 26361, 26362, 26363, 26364, 26365, 26366, 26367, 26368
4670	*Troglodytes pacificus*	Pacific Wren	7221		26369	26371, 26372, 26373, 26374, 26375, 26376, 26377, 26378, 26380, 26381, 26382, 26383, 26384
4680	*Troglodytes hiemalis*	Winter Wren	7222		26385	26386, 26387
4690	*Cistothorus platensis*	Grass Wren	7240		26394	26396, 26397, 26398, 26399, 26400, 26401, 26402, 26403, 26410, 26411, 26413, 26414
4700	*Cistothorus palustris*	Marsh Wren	7250		26419	26421, 26422, 26423, 26424, 26426, 26427, 26428, 26430, 26431, 26432, 26433, 26434
4710	*Thryothorus ludovicianus*	Carolina Wren	7180		26438	26440, 26441, 26442, 26443, 26445, 26446, 26447, 26449, 26450
4720	*Thryomanes bewickii*	Bewick's Wren	7190		26451	26454, 26455, 26456, 26457, 26458, 26460, 26461, 26462, 26463, 26464, 26465, 26466, 26467, 26468
4730	*Campylorhynchus brunneicapillus*	Cactus Wren	7130		26497	26499, 26500, 26501, 26502, 26504, 26505, 26506
4740	*Thryophilus sinaloa*	Sinaloa Wren	16600		26595	26596, 26597, 26598
4750	*Cinclus mexicanus*	American Dipper	7010		26751	26753, 26754, 26755
4760	*Sturnus vulgaris*	European Starling	4930		26890	26891, 26892, 26893, 26894, 26895, 26896, 26897, 26898,

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						26899, 26900, 26901, 26902
4770	*Acridotheres tristis*	Common Myna	4932		26935	26936, 26937, 26960, 26961, 26962
4770	*Acridotheres cristatellus*	Crested Myna	4932		26959	26936, 26937, 26960, 26961, 26962
4780	*Toxostoma lecontei*	LeConte's Thrasher	7110		27123	27125, 27126
4790	*Dumetella carolinensis*	Gray Catbird	7040		27065	
4800	*Toxostoma curvirostre*	Curve-billed Thrasher	7070		27090	27092, 27093, 27094, 27096, 27097, 27098, 27099
4810	*Toxostoma rufum*	Brown Thrasher	7050		27103	27104, 27105
4820	*Toxostoma longirostre*	Long-billed Thrasher	7060		27106	27107, 27108
4830	*Toxostoma bendirei*	Bendire's Thrasher	7080		27112	27113, 27114, 27115
4840	*Toxostoma redivivum*	California Thrasher	7100		27120	27121, 27122
4850	*Toxostoma crissale*	Crissal Thrasher	7120		27128	27129, 27130, 27131, 27132
4860	*Oreoscoptes montanus*	Sage Thrasher	7020		27135	
4870	*Mimus gundlachii*	Bahama Mockingbird	7031		27145	27146, 27147
4880	*Mimus polyglottos*	Northern Mockingbird	7030		27176	27177, 27178, 27179
4890	*Sialia sialis*	Eastern Bluebird	7660		27185	27187, 27188, 27190, 27191, 27192, 27193, 27194
4900	*Sialia mexicana*	Western Bluebird	7670		27195	27196, 27197, 27198, 27199, 27200, 27201
4910	*Sialia currucoides*	Mountain Bluebird	7680		27203	
4920	*Myadestes townsendi*	Townsend's Solitaire	7540		27221	27222, 27223
4930	*Ixoreus naevius*	Varied Thrush	7630		27311	27312, 27313, 27314
4940	*Catharus fuscescens*	Veery	7560		27369	27370, 27371, 27372, 27373
4950	*Catharus minimus*	Gray-cheeked Thrush	7570		27374	27375, 27376
4960	*Catharus bicknelli*	Bicknell's Thrush	7571		27377	
4970	*Catharus ustulatus*	Swainson's Thrush	7580		27380	27382, 27383, 27384, 27386, 27387, 27388
4980	*Catharus guttatus*	Hermit Thrush	7590		27389	27391, 27392, 27393, 27394, 27396, 27397, 27398, 27400, 27401
4990	*Hylocichla mustelina*	Wood Thrush	7550		27403	
5000	*Turdus migratorius*	American Robin	7610		27616	27619, 27620, 27621, 27622, 27623

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5005	*Lonchura punctulata*	Scaly-breasted Munia	8110		30045	30048, 30049, 30050, 30051, 30052, 30053, 30054, 30055, 30056, 30057, 30058
5010	*Luscinia svecica*	Bluethroat	7640		28419	28421, 28422, 28423, 28424, 28425, 28426, 28427, 28428, 28431, 28432
5020	*Oenanthe oenanthe*	Northern Wheatear	7650		28785	28788, 28789
5030	*Bombycilla garrulus*	Bohemian Waxwing	6180		28886	28887, 28888, 28889
5040	*Bombycilla cedrorum*	Cedar Waxwing	6190		28890	
5050	*Phainopepla nitens*	Phainopepla	6200		28908	28909, 28910
5060	*Peucedramus taeniatus*	Olive Warbler	6510		29673	29674, 29675, 29676, 29677, 29678
5065	*Euplectes franciscanus*	Northern Red Bishop	19500		29916	
5070	*Passer domesticus*	House Sparrow	6882		30494	30495, 30496, 30497, 30498, 30499, 30500, 30501, 30502, 30503, 30504, 30505, 30506
5080	*Passer montanus*	Eurasian Tree Sparrow	6883		30560	30561, 30562, 30563, 30564, 30565, 30566, 30567, 30568, 30569
5090	*Motacilla flava*	Western Yellow Wagtail	6960		30637	30657, 30658
5090	*Motacilla tschutschensis*	Eastern Yellow Wagtail	6960		30655	30657, 30658
5100	*Motacilla alba*	White Wagtail	6940		30675	30677, 30678
5110	*Anthus cervinus*	Red-throated Pipit	6990		30824	
5120	*Anthus rubescens*	American Pipit	6970		30836	30839, 30840, 30841
5130	*Anthus spragueii*	Sprague's Pipit	7000		30843	
5140	*Coccothraustes vespertinus*	Evening Grosbeak	5140		31032	31033, 31034, 31035
5150	*Pinicola enucleator*	Pine Grosbeak	5150		31167	31169, 31170, 31171, 31172
5160	*Leucosticte arctoa*	Asian Rosy-Finch			31234	31235, 31236, 31237, 31238, 31239
5170	*Leucosticte tephrocotis*	Gray-crowned Rosy-Finch	5240		31240	31245, 31246, 31247, 31248
5180	*Leucosticte atrata*	Black Rosy-Finch	5250		31250	
5190	*Leucosticte australis*	Brown-capped Rosy-Finch	5260		31251	
5200	*Haemorhous mexicanus*	House Finch	5190		31253	31255, 31256, 31257, 31258, 31259, 31260,

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						31261, 31262, 31263, 31264, 31265
5210	*Haemorhous purpureus*	Purple Finch	5170		31267	
5220	*Haemorhous cassinii*	Cassin's Finch	5180		31271	
5230	*Acanthis flammea*	Common Redpoll	5280		31423	31426, 31427
5240	*Acanthis hornemanni*	Hoary Redpoll	5270		31430	
5250	*Loxia curvirostra*	Red Crossbill	5210		31438	31450, 31458, 31459, 31460, 31461, 31462, 31463, 31464, 31465
5260	*Loxia leucoptera*	White-winged Crossbill	5220		31480	
5270	*Spinus pinus*	Pine Siskin	5330		31530	31532, 31533
5280	*Spinus psaltria*	Lesser Goldfinch	5300		31544	31545, 31546, 31547, 31548, 31549
5290	*Spinus lawrencei*	Lawrence's Goldfinch	5310		31550	
5300	*Spinus tristis*	American Goldfinch	5290		31551	31552, 31553, 31554, 31555
5305	*Carduelis carduelis*	European Goldfinch	5261		31491	31493, 31494, 31495, 31496, 31497, 31498, 31499, 31500, 31501, 31503, 31504, 31505
5310	*Calcarius ornatus*	Chestnut-collared Longspur	5380		31596	
5320	*Calcarius pictus*	Smith's Longspur	5370		31597	
5330	*Rhynchophanes mccownii*	Thick-billed Longspur	5390		31598	
5340	*Calcarius lapponicus*	Lapland Longspur	5360		31592	31593, 31594, 31595
5350	*Plectrophenax nivalis*	Snow Bunting	5340		31600	31601, 31602, 31603, 31604
5360	*Plectrophenax hyperboreus*	McKay's Bunting			31606	
5370	*Peucaea carpalis*	Rufous-winged Sparrow	5790		31823	31824, 31825, 31826
5380	*Peucaea botterii*	Botteri's Sparrow	5760		31836	31838, 31839, 31840, 31841, 31842, 31844, 31845, 31846, 31847
5390	*Peucaea cassinii*	Cassin's Sparrow	5780		31848	
5400	*Peucaea aestivalis*	Bachman's Sparrow	5750		31850	31851, 31852, 31853
5410	*Ammodramus savannarum*	Grasshopper Sparrow	5460		31855	31856, 31857, 31858, 31859, 31860, 31861, 31862, 31863, 31864, 31865, 31866

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5420	*Arremonops rufivirgatus*	Olive Sparrow	5860		31878	31880, 31881, 31882, 31883, 31884, 31886, 31887, 31888, 31889
5430	*Spizella passerina*	Chipping Sparrow	5600		31905	31906, 31907, 31908, 31909, 31910
5440	*Spizella pallida*	Clay-colored Sparrow	5610		31911	
5450	*Spizella atrogularis*	Black-chinned Sparrow	5650		31913	31914, 31915, 31916, 31917
5460	*Spizella pusilla*	Field Sparrow	5630		31918	31919, 31920
5470	*Spizella breweri*	Brewer's Sparrow	5620		31923	
5480	*Amphispiza bilineata*	Black-throated Sparrow	5730		31930	31931, 31932, 31933, 31934, 31935, 31936, 31937, 31938, 31939, 31940
5490	*Amphispizopsis quinquestriata*	Five-striped Sparrow			31902	31903, 31904
5500	*Chondestes grammacus*	Lark Sparrow	5520		31941	31942, 31943
5510	*Calamospiza melanocorys*	Lark Bunting	6050		31944	
5520	*Spizelloides arborea*	American Tree Sparrow	5590		32008	32009, 32010
5530	*Passerella iliaca*	Fox Sparrow	5850		32012	32014, 32015, 32016, 32017, 32018, 32019, 32020, 32022, 32023, 32024, 32025, 32026, 32028, 32029, 32030, 32031, 32032, 32034, 32035
5540	*Junco hyemalis*	Dark-eyed Junco	5677	5670, 5671, 5680, 5660, 5690	32036	32039, 32040, 32043, 32044, 32045, 32046, 32047, 32048, 32049
5550	*Junco phaeonotus*	Yellow-eyed Junco	5700		32060	32062, 32063
5560	*Zonotrichia leucophrys*	White-crowned Sparrow	5540		32099	
5570	*Zonotrichia atricapilla*	Golden-crowned Sparrow	5570		32107	
5580	*Zonotrichia querula*	Harris's Sparrow	5530		32109	
5590	*Zonotrichia albicollis*	White-throated Sparrow	5580		32112	
5600	*Artemisiospiza nevadensis*	Sagebrush Sparrow	5738		32118	
5610	*Artemisiospiza belli*	Bell's Sparrow	5739		32119	
5620	*Pooecetes gramineus*	Vesper Sparrow	5400		32128	32129, 32130, 32131

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5630	*Ammospiza leconteii*	LeConte's Sparrow	5480		32132	
5640	*Ammospiza maritima*	Seaside Sparrow	5500		32133	32135, 32136, 32139, 32140, 32141
5650	*Ammospiza nelsoni*	Nelson's Sparrow	5491		32143	32145, 32146
5660	*Ammospiza caudacuta*	Saltmarsh Sparrow	5490		32149	32150, 32151
5670	*Passerculus sandwichensis*	Savannah Sparrow	5420		32155	32157, 32158, 32159, 32160, 32161, 32162, 32163, 32164, 32165, 32166, 32167, 32168, 32169, 32172, 32173, 32174, 32175, 32178, 32179
5680	*Centronyx henslowii*	Henslow's Sparrow	5470		32181	32182, 32183
5690	*Melospiza melodia*	Song Sparrow	5810		32187	32189, 32190, 32192, 32193, 32195, 32196, 32197, 32198, 32199, 32201, 32202, 32204, 32205, 32206, 32207, 32208, 32212, 32213, 32214, 32216, 32217, 32218, 32219
5700	*Melospiza lincolnii*	Lincoln's Sparrow	5830		32220	32221, 32222, 32223
5710	*Melospiza georgiana*	Swamp Sparrow	5840		32225	32226, 32227, 32228
5720	*Melozone fusca*	Canyon Towhee	5910		32240	32241, 32242, 32243, 32244, 32245, 32246, 32247, 32248, 32249, 32250
5725	*Melozone crissalis*	California Towhee	5911		32260	32261, 32262, 32263, 32264, 32265, 32266, 32267, 32268
5730	*Melozone aberti*	Abert's Towhee	5920		32254	32255, 32256, 32257
5740	*Aimophila ruficeps*	Rufous-crowned Sparrow	5800		32284	32285, 32286, 32287, 32288, 32289, 32290, 32291, 32292, 32293, 32294, 32295, 32296
5750	*Pipilo chlorurus*	Green-tailed Towhee	5900		32298	
5760	*Pipilo maculatus*	Spotted Towhee	5880		32299	32301, 32302, 32303, 32304,

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						32305, 32306, 32307, 32310, 32311, 32312, 32313, 32314, 32315, 32316, 32317, 32318, 32319, 32320, 32321
5770	*Pipilo erythrophthalmus*	Eastern Towhee	5870		32327	32329, 32330, 32332, 32333
5780	*Icteria virens*	Yellow-breasted Chat	6830		32466	
5790	*Xanthocephalus xanthocephalus*	Yellow-headed Blackbird	4970		32469	
5800	*Dolichonyx oryzivorus*	Bobolink	4940		32470	
5810	*Sturnella neglecta*	Western Meadowlark	5011		32471	32472, 32473
5820	*Sturnella magna*	Eastern Meadowlark	5010		32474	32477, 32478, 32479, 32480, 32481, 32482, 32483, 32484, 32485, 32486, 32487, 32488, 32489, 32491, 32492, 32493
5830	*Icterus spurius*	Orchard Oriole	5060		32578	
5840	*Icterus cucullatus*	Hooded Oriole	5050		32581	32583, 32584, 32586, 32587, 32588
5850	*Icterus bullockii*	Bullock's Oriole	5080		32635	32636, 32637
5860	*Icterus pectoralis*	Spot-breasted Oriole	5032		32648	32649, 32650
5870	*Icterus gularis*	Altamira Oriole	5031		32651	32652, 32653, 32654, 32655, 32656, 32657
5880	*Icterus graduacauda*	Audubon's Oriole	5030		32658	32660, 32661, 32663, 32664
5890	*Icterus galbula*	Baltimore Oriole	5070		32666	
5900	*Icterus parisorum*	Scott's Oriole	5040		32672	
5910	*Agelaius phoeniceus*	Red-winged Blackbird	4980		32676	32678, 32679, 32680, 32681, 32682, 32683, 32684, 32685, 32686, 32687, 32688, 32689, 32690, 32691, 32692, 32693, 32694, 32695, 32696, 32697, 32698, 32700, 32701
5920	*Agelaius tricolor*	Tricolored Blackbird	5000		32706	
5930	*Molothrus aeneus*	Bronzed Cowbird	4960		32725	32727, 32728, 32729

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Project ID	Scientific name	English name	BBS ID	BBS subspecies ID	eBird ID	eBird subspecies ID
5940	*Molothrus ater*	Brown-headed Cowbird	4950		32732	32733, 32734, 32735, 32736
5945	*Molothrus bonariensis*	Shiny Cowbird	4961		32716	32717, 32718, 32719, 32720, 32721, 32722, 32723
5950	*Euphagus carolinus*	Rusty Blackbird	5090		32747	32748, 32749
5960	*Euphagus cyanocephalus*	Brewer's Blackbird	5100		32750	
5970	*Quiscalus quiscula*	Common Grackle	5110		32752	32754, 32755
5980	*Quiscalus major*	Boat-tailed Grackle	5130		32757	32760, 32761
5990	*Quiscalus mexicanus*	Great-tailed Grackle	5120		32763	32765, 32766, 32767, 32769, 32770, 32771, 32772, 32773
6000	*Seiurus aurocapilla*	Ovenbird	6740		32843	32844, 32845, 32846
6010	*Helmitheros vermivorum*	Worm-eating Warbler	6390		32847	
6020	*Parkesia motacilla*	Louisiana Waterthrush	6760		32849	
6030	*Parkesia noveboracensis*	Northern Waterthrush	6750		32850	
6040	*Vermivora bachmanii*	Bachman's Warbler			32852	
6050	*Vermivora chrysoptera*	Golden-winged Warbler	6420		32853	
6060	*Vermivora cyanoptera*	Blue-winged Warbler	6410		32854	
6070	*Mniotilta varia*	Black-and-white Warbler	6360		32859	
6080	*Protonotaria citrea*	Prothonotary Warbler	6370		32860	
6090	*Limnothlypis swainsonii*	Swainson's Warbler	6380		32861	
6100	*Leiothlypis peregrina*	Tennessee Warbler	6470		32869	
6110	*Leiothlypis celata*	Orange-crowned Warbler	6460		32870	
6120	*Leiothlypis crissalis*	Colima Warbler			32876	
6130	*Leiothlypis luciae*	Lucy's Warbler	6430		32877	
6140	*Leiothlypis ruficapilla*	Nashville Warbler	6450		32878	
6150	*Leiothlypis virginiae*	Virginia's Warbler	6440		32882	
6160	*Oporornis agilis*	Connecticut Warbler	6780		32886	
6170	*Geothlypis tolmiei*	MacGillivray's Warbler	6800		32900	
6180	*Geothlypis philadelphia*	Mourning Warbler	6790		32901	
6190	*Geothlypis formosa*	Kentucky Warbler	6770		32906	
6200	*Geothlypis trichas*	Common Yellowthroat	6810		32921	32923, 32924, 32925, 32927,

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Project ID	Scientific name	English name	BBS ID	BBS subspecies ID	eBird ID	eBird subspecies ID
						32928, 32929, 32930, 32931, 32933, 32934, 32935
6210	*Setophaga citrina*	Hooded Warbler	6840		32949	
6220	*Setophaga ruticilla*	American Redstart	6870		32950	
6230	*Setophaga kirtlandii*	Kirtland's Warbler	6700		32951	
6240	*Setophaga tigrina*	Cape May Warbler	6500		32952	
6250	*Setophaga cerulea*	Cerulean Warbler	6580		32953	
6260	*Setophaga americana*	Northern Parula	6480		32955	
6270	*Setophaga pitiayumi*	Tropical Parula	6490		32958	32966, 32967, 32968
6280	*Setophaga magnolia*	Magnolia Warbler	6570		32971	
6290	*Setophaga castanea*	Bay-breasted Warbler	6600		32973	
6300	*Setophaga fusca*	Blackburnian Warbler	6620		32974	
6310	*Setophaga petechia*	Yellow Warbler	6520		32976	32978, 32979, 32980, 32981, 32982, 32983, 32985, 32986, 32987, 32988, 32989, 32990, 32991, 32992, 32993, 32994, 32995, 32998, 32999, 33000, 33001, 33002, 33003, 33004, 33005, 33006, 33007, 33008, 33009, 33010, 33011, 33012, 33013
6320	*Setophaga pensylvanica*	Chestnut-sided Warbler	6590		33018	
6330	*Setophaga striata*	Blackpoll Warbler	6610		33020	
6340	*Setophaga caerulescens*	Black-throated Blue Warbler	6540		33023	33024, 33025
6350	*Setophaga palmarum*	Palm Warbler	6720		33029	
6360	*Setophaga pinus*	Pine Warbler	6710		33034	33035, 33036, 33037, 33038
6370	*Setophaga coronata*	Yellow-rumped Warbler	6556	6550, 6560	33040	
6380	*Setophaga dominica*	Yellow-throated Warbler	6630		33049	33052, 33053
6390	*Setophaga discolor*	Prairie Warbler	6730		33061	33062, 33063
6400	*Setophaga graciae*	Grace's Warbler	6640		33069	33070, 33071, 33072, 33073

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Project ID	Scientific name	English name	BBS ID	BBS subspecies ID	eBird ID	eBird subspecies ID
6410	*Setophaga nigrescens*	Black-throated Gray Warbler	6650		33075	33076, 33077
6420	*Setophaga townsendi*	Townsend's Warbler	6680		33080	
6430	*Setophaga occidentalis*	Hermit Warbler	6690		33084	
6440	*Setophaga chrysoparia*	Golden-cheeked Warbler	6660		33089	
6450	*Setophaga virens*	Black-throated Green Warbler	6670		33090	
6460	*Basileuterus rufifrons*	Rufous-capped Warbler			33095	33097, 33098, 33099, 33100, 33104, 33105, 33106
6470	*Cardellina canadensis*	Canada Warbler	6860		33215	
6480	*Cardellina pusilla*	Wilson's Warbler	6850		33216	
6490	*Cardellina rubrifrons*	Red-faced Warbler	6900		33220	
6500	*Myioborus pictus*	Painted Redstart	6880		33227	33228, 33229
6510	*Piranga flava*	Hepatic Tanager	6090		33281	33283, 33284, 33285, 33286, 33287, 33289, 33290, 33291, 33292, 33293, 33294, 33296, 33297, 33298, 33299
6520	*Piranga rubra*	Summer Tanager	6100		33300	33301, 33302
6530	*Piranga olivacea*	Scarlet Tanager	6080		33304	
6540	*Piranga ludoviciana*	Western Tanager	6070		33306	
6550	*Cardinalis cardinalis*	Northern Cardinal	5930		33382	33384, 33385, 33386, 33387, 33388, 33389, 33390, 33391, 33392, 33393, 33394, 33395, 33396, 33397, 33398, 33399, 33400
6560	*Cardinalis sinuatus*	Pyrrhuloxia	5940		33402	33403, 33404, 33405
6570	*Pheucticus ludovicianus*	Rose-breasted Grosbeak	5950		33424	
6580	*Pheucticus melanocephalus*	Black-headed Grosbeak	5960		33425	33426, 33427
6590	*Passerina caerulea*	Blue Grosbeak	5970		33465	33466, 33467, 33468, 33469, 33470, 33471, 33472
6600	*Passerina amoena*	Lazuli Bunting	5990		33473	
6610	*Passerina cyanea*	Indigo Bunting	5980		33474	
6620	*Passerina versicolor*	Varied Bunting	6000		33482	33483, 33484, 33485, 33486
6630	*Passerina ciris*	Painted Bunting	6010		33487	33488, 33489
6640	*Spiza americana*	Dickcissel	6040		33493	

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Appendix B. Matrices of dissimilarity for categories of categorical functional traits

Table B1. Dissimilarities between the categories of nest type

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	0	0.1	0.2	0.4	0.45	0.5	0.55	0.6	0.65	0.75	0.8	0.85	0.9	0.95
2		0	0.25	0.35	0.4	0.45	0.55	0.6	0.65	0.75	0.8	0.85	0.9	0.95
3			0	0.5	0.55	0.55	0.3	0.5	0.6	0.7	0.75	0.8	0.85	0.9
4				0	0.15	0.25	0.6	0.6	0.6	0.8	0.8	0.9	0.9	0.9
5					0	0.3	0.6	0.6	0.6	0.8	0.8	0.8	0.9	0.9
6						0	0.6	0.5	0.4	0.4	0.35	0.35	0.7	0.7
7							0	0.2	0.3	0.6	0.6	0.7	0.8	0.9
8								0	0.15	0.5	0.7	0.8	0.8	0.9
9									0	0.4	0.5	0.6	0.7	0.8
10										0	0.5	0.5	0.6	0.6
11											0	0.2	0.15	0.6
12												0	0.1	0.6
13													0	0.6
14														0

Note. categories are coded as following: no = 1, parasitic = 2, scrape = 3, crevice = 4, burrow = 5, cavity = 6, platform = 7, saucer = 8, cup = 9, sphere = 10, chamber = 11, oven = 12, gourd = 13, pendant = 14.

Table B2. Dissimilarities between the categories of chick development at hatching

	pre2	pre3	pre4	semipre	semialt1	semialt2	alt
pre2	0	0.1	0.2	0.4	0.6	0.8	1
pre3		0	0.1	0.3	0.5	0.7	0.9
pre4			0	0.2	0.4	0.6	0.8
semipre				0	0.2	0.4	0.6
semialt1					0	0.2	0.4
semialt2						0	0.2
alt							0

Note. categories are coded as following: precocial 2 = pre2, precocial 3 = pre3, precocial 4 = pre4, semiprecocial = semipre, semialtricial 1 = semi1, semialtricial 2 = semi2, altricial = alt.

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Table B3. Dissimilarities between the categories of breeding system

	coop	polygam	promisc	lek	polyand	polygyn	monog
coop	0	0.25	0.4	0.6	0.8	0.8	0.7
polygam		0	0.3	0.3	0.5	0.5	0.9
promisc			0	0.25	0.4	0.4	1
lek				0	0.5	0.5	0.9
polyand					0	0.25	0.6
polygyn						0	0.6
monog							0

Note. categories are coded as following: cooperative = coop, polygamous = polygam, promiscuous = promisc, lekking = lek, polyandry = polyand, polygyny = polygyn, monogamy = monog.

Table B4. Dissimilarities between the categories of diet category

	FruiNect	Invertebrate	Omnivore	PlantSeed	VertFishScav
FruiNect	0	0.6	0.4	0.2	0.8
Invertebrate		0	0.5	0.7	0.2
Omnivore			0	0.5	0.4
PlantSeed				0	0.3
VertFishScav					0

Note. categories are coded as following: fruits and nectar = FruiNect, invertebrates = Invertebrate, omnivore = Omnivore, green parts of plants and seeds = PlantSeed, vertebrates, fish, and carcasses = VertFishScav.

Table B5. Dissimilarities between the categories of nest aggregation

	Solitary	Loosely colonial	Strongly colonial
Solitary	0	0.5	1
Loosely colonial		0	0.5
Strongly colonial			0

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Appendix C. Fixed effect estimates and variance of random effects in mixed-effect linear models fitted to relate candidate metrics of functional rarity and community or species parameters that are assumed to determine them

Table C1. Fixed effect estimates and variance of random effects in mixed-effect linear models fitted to relate candidate metrics of functional rarity and community parameters that are assumed to determine them

Model	Coefficient	Value	95% CI		p-value	Random effects variance	
			2.5% CI	97.5% CI		BCR	Year
PIE × Functional divergence							
1	Intercept	-0.194	**-0.309**	**-0.078**	**0.002**	0.131	0.021
	PIE:bbs	0.613	**0.575**	**0.651**	**<0.001**	0.006	0.003
	PIE:ebd	0.635	**0.600**	**0.670**	**<0.001**		
2	Intercept	-0.196	**-0.311**	**-0.082**	**0.001**	0.130	0.021
	PIE	0.631	**0.596**	**0.666**	**<0.001**	0.006	0.004
3	Intercept	-0.523	**-0.747**	**-0.299**	**<0.001**	0.570	0.064
	Avg Leroy:bbs	-0.022	-0.095	0.052	0.567	0.051	0.009
	Avg Leroy:ebd	-0.245	**-0.318**	**-0.172**	**<0.001**		
4	Intercept	-0.523	**-0.744**	**-0.302**	**<0.001**	0.553	0.063
	Avg Leroy	-0.171	**-0.235**	**-0.107**	**<0.001**	0.044	0.005
5	Intercept	-0.368	**-0.599**	**-0.138**	**0.003**	0.594	0.057
	Avg log:bbs	-0.127	**-0.201**	**-0.053**	**0.001**	0.048	0.009
	Avg log:ebd	-0.299	**-0.372**	**-0.226**	**<0.001**		
6	Intercept	-0.376	**-0.605**	**-0.147**	**0.002**	0.590	0.056
	Avg log	-0.252	**-0.320**	**-0.183**	**<0.001**	0.044	0.007
7	Intercept	0.632	**0.460**	**0.805**	**<0.001**	0.368	0.005
	Species richness:bbs	0.478	**0.335**	**0.620**	**<0.001**	0.273	0.001
	Species richness:ebd	1.402	**1.260**	**1.545**	**<0.001**		
8	Intercept	0.579	**0.372**	**0.785**	**<0.001**	0.513	0.023
	Species richness	1.122	**0.929**	**1.314**	**<0.001**	0.427	0.037
9	Intercept	-0.360	**-0.549**	**-0.171**	**<0.001**	0.423	0.035
	Avg FDist:bbs	-0.405	**-0.472**	**-0.337**	**<0.001**	0.041	0.006
	Avg FDist:ebd	-0.442	**-0.509**	**-0.376**	**<0.001**		
10	Intercept	-0.364	**-0.552**	**-0.176**	**<0.001**	0.422	0.034
	Avg FDist	-0.432	**-0.498**	**-0.366**	**<0.001**	0.041	0.006
11	Intercept	-0.341	**-0.528**	**-0.153**	**0.001**	0.394	0.046
	Max FDist:bbs	0.045	-0.002	0.092	0.068	0.021	0.002
	Max FDist:ebd	0.454	**0.407**	**0.500**	**<0.001**		
12	Intercept	-0.369	**-0.551**	**-0.186**	**<0.001**	0.376	0.042
	Max FDist	0.309	**0.242**	**0.377**	**<0.001**	0.028	0.012

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Model	Coefficient	Value	95% CI		p-value	Random effects variance	
			2.5% CI	97.5% CI		BCR	Year
Weighted by Leroy rarity functional distinctiveness							
13	Intercept	0.190	**0.109**	**0.271**	**<0.001**	0.064	0.007
	PIE:bbs	-0.587	**-0.667**	**-0.506**	**<0.001**	0.071	0.005
	PIE:ebd	-0.266	**-0.344**	**-0.187**	**<0.001**		
14	Intercept	0.155	**0.068**	**0.243**	**0.001**	0.074	0.009
	PIE	-0.325	**-0.404**	**-0.246**	**<0.001**	0.078	0.003
15	Intercept	0.168	**0.048**	**0.287**	**0.008**	0.124	0.028
	Avg Leroy:bbs	-0.012	-0.100	0.076	0.791	0.091	0.008
	Avg Leroy:ebd	0.163	**0.076**	**0.251**	**<0.001**		
16	Intercept	0.172	**0.052**	**0.292**	**0.006**	0.126	0.027
	Avg Leroy	0.106	**0.024**	**0.188**	**0.014**	0.085	0.005
17	Intercept	0.251	**0.055**	**0.448**	**0.017**	0.462	0.022
	Avg log:bbs	0.133	**0.037**	**0.228**	**0.008**	0.104	0.008
	Avg log:ebd	0.199	**0.104**	**0.294**	**<0.001**		
18	Intercept	0.252	**0.056**	**0.448**	**0.016**	0.460	0.022
	Avg log	0.182	**0.089**	**0.275**	**<0.001**	0.102	0.007
19	Intercept	-0.051	-0.133	0.030	0.225	0.065	0.002
	Species richness:bbs	-0.029	-0.124	0.067	0.557	0.106	0.004
	Species richness:ebd	-0.533	**-0.628**	**-0.438**	**<0.001**		
20	Intercept	0.028	-0.045	0.100	0.455	0.052	0.001
	Species richness	-0.345	**-0.429**	**-0.261**	**<0.001**	0.074	0.007
21	Intercept	-0.114	-0.235	0.008	0.074	0.212	0.004
	Avg FDist:bbs	1.134	**1.099**	**1.170**	**<0.001**	0.016	<0.001
	Avg FDist:ebd	0.944	**0.909**	**0.980**	**<0.001**		
22	Intercept	-0.131	**-0.248**	**-0.015**	**0.033**	0.195	0.004
	Avg FDist	0.994	**0.955**	**1.034**	**<0.001**	0.015	0.002
23	Intercept	0.290	**0.115**	**0.464**	**0.002**	0.249	0.072
	Max FDist:bbs	0.321	**0.267**	**0.374**	**<0.001**	0.028	0.002
	Max FDist:ebd	0.385	**0.333**	**0.438**	**<0.001**		
24	Intercept	0.285	**0.109**	**0.461**	**0.002**	0.255	0.073
	Max FDist	0.363	**0.312**	**0.415**	**<0.001**	0.027	0.002
Weighted by log-rarity functional distinctiveness							
25	Intercept	0.194	**0.119**	**0.269**	**<0.001**	0.052	0.007
	PIE:bbs	-0.635	**-0.715**	**-0.555**	**<0.001**	0.069	0.006
	PIE:ebd	-0.285	**-0.363**	**-0.207**	**<0.001**		
26	Intercept	0.156	**0.073**	**0.239**	**0.001**	0.063	0.009
	PIE	-0.350	**-0.427**	**-0.273**	**<0.001**	0.074	0.003
27	Intercept	0.184	**0.065**	**0.303**	**0.003**	0.125	0.027
	Avg Leroy:bbs	-0.010	-0.105	0.084	0.829	0.104	0.010
	Avg Leroy:ebd	0.182	**0.088**	**0.276**	**<0.001**		
28	Intercept	0.189	**0.070**	**0.308**	**0.003**	0.127	0.026

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Model	Coefficient	Value	95% CI		p-value	Random effects variance	
			2.5% CI	97.5% CI		BCR	Year
29	Avg Leroy	0.120	**0.033**	**0.206**	**0.009**	0.096	0.006
	Intercept	0.272	**0.075**	**0.469**	**0.010**	0.469	0.021
	Avg log:bbs	0.156	**0.056**	**0.256**	**0.003**	0.114	0.009
	Avg log:ebd	0.225	**0.125**	**0.324**	**<0.001**		
30	Intercept	0.273	**0.076**	**0.470**	**0.010**	0.469	0.021
	Avg log	0.207	**0.110**	**0.304**	**<0.001**	0.112	0.008
31	Intercept	-0.061	-0.141	0.019	0.143	0.062	0.002
	Species richness:bbs	-0.039	-0.132	0.054	0.415	0.097	0.005
	Species richness:ebd	-0.565	**-0.657**	**-0.473**	**<0.001**		
32	Intercept	0.024	-0.048	0.096	0.516	0.050	0.001
	Species richness	-0.366	**-0.450**	**-0.282**	**<0.001**	0.070	0.009
33	Intercept	-0.081	-0.168	0.005	0.071	0.098	0.005
	Avg FDist:bbs	1.159	**1.127**	**1.191**	**<0.001**	0.013	<0.001
	Avg FDist:ebd	0.973	**0.942**	**1.005**	**<0.001**		
34	Intercept	-0.100	**-0.181**	**-0.018**	**0.020**	0.088	0.004
	Avg FDist	1.023	**0.987**	**1.059**	**<0.001**	0.013	0.002
35	Intercept	0.326	**0.149**	**0.503**	**0.001**	0.258	0.073
	Max FDist:bbs	0.337	**0.282**	**0.392**	**<0.001**	0.030	0.002
	Max FDist:ebd	0.406	**0.352**	**0.460**	**<0.001**		
36	Intercept	0.321	**0.143**	**0.499**	**0.001**	0.262	0.074
	Max FDist	0.382	**0.329**	**0.436**	**<0.001**	0.029	0.002
Functional divergence weighted by Leroy rarity							
37	Intercept	0.027	-0.075	0.128	0.608	0.116	0.007
	PIE:bbs	-0.322	**-0.425**	**-0.218**	**<0.001**	0.141	0.002
	PIE:ebd	-0.102	**-0.204**	**-0.001**	0.059		
38	Intercept	0.003	-0.099	0.105	0.953	0.115	0.008
	PIE	-0.142	**-0.248**	**-0.035**	**0.015**	0.156	0.002
39	Intercept	-0.062	-0.212	0.087	0.417	0.259	0.022
	Avg Leroy:bbs	-0.067	-0.147	0.012	0.103	0.085	0.002
	Avg Leroy:ebd	-0.010	-0.089	0.069	0.809		
40	Intercept	-0.062	-0.211	0.088	0.422	0.260	0.022
	Avg Leroy	-0.029	-0.109	0.050	0.474	0.086	0.002
41	Intercept	-0.043	-0.406	0.321	0.821	1.870	0.022
	Avg log:bbs	0.029	-0.066	0.125	0.557	0.119	0.002
	Avg log:ebd	0.032	-0.063	0.127	0.519		
42	Intercept	-0.042	-0.406	0.321	0.822	1.869	0.022
	Avg log	0.031	-0.063	0.126	0.529	0.119	0.002
43	Intercept	-0.212	**-0.355**	**-0.070**	**0.011**	0.217	0.005
	Species richness:bbs	-0.219	**-0.366**	**-0.071**	**0.015**	0.293	0.001
	Species richness:ebd	-0.394	**-0.541**	**-0.247**	**<0.001**		
44	Intercept	-0.194	**-0.344**	**-0.043**	**0.025**	0.238	0.008

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Model	Coefficient	Value	95% CI		p-value	Random effects variance	
			2.5% CI	97.5% CI		BCR	Year
	Species richness	-0.338	**-0.490**	**-0.186**	**0.001**	0.306	0.003
	Intercept	-0.228	-0.456	0.001	0.061	0.740	0.006
45	Avg FDist:bbs	0.403	**0.312**	**0.493**	**<0.001**	0.101	0.002
	Avg FDist:ebd	0.349	**0.259**	**0.438**	**<0.001**		
46	Intercept	-0.233	**-0.461**	**-0.005**	0.055	0.739	0.006
	Avg FDist	0.364	**0.275**	**0.453**	**<0.001**	0.099	0.002
	Intercept	-0.207	**-0.412**	**-0.002**	0.058	0.594	0.007
47	Max FDist:bbs	-0.331	**-0.424**	**-0.238**	**<0.001**	0.110	0.002
	Max FDist:ebd	-0.360	**-0.453**	**-0.268**	**<0.001**		
48	Intercept	-0.206	**-0.411**	**-0.001**	0.059	0.594	0.007
	Max FDist	-0.351	**-0.445**	**-0.257**	**<0.001**	0.113	0.002
Functional divergence weighted by log-rarity							
	Intercept	0.016	-0.079	0.112	0.738	0.096	0.009
49	PIE:bbs	-0.432	**-0.526**	**-0.338**	**<0.001**	0.112	0.003
	PIE:ebd	-0.143	**-0.235**	**-0.050**	**0.005**		
50	Intercept	-0.018	-0.114	0.077	0.709	0.093	0.009
	PIE	-0.197	**-0.292**	**-0.101**	**<0.001**	0.124	0.002
	Intercept	-0.062	-0.211	0.087	0.418	0.245	0.026
51	Avg Leroy:bbs	-0.082	**-0.158**	**-0.007**	**0.037**	0.073	0.003
	Avg Leroy:ebd	0.006	-0.069	0.081	0.872		
52	Intercept	-0.061	-0.210	0.088	0.426	0.247	0.025
	Avg Leroy	-0.024	-0.099	0.051	0.532	0.074	0.002
	Intercept	0.010	-0.271	0.290	0.947	1.052	0.026
53	Avg log:bbs	0.039	-0.036	0.113	0.314	0.063	0.004
	Avg log:ebd	0.048	-0.025	0.122	0.208		
54	Intercept	0.010	-0.270	0.291	0.943	1.052	0.026
	Avg log	0.046	-0.028	0.119	0.232	0.063	0.004
	Intercept	-0.275	**-0.433**	**-0.117**	**0.005**	0.265	0.010
55	Species richness:bbs	-0.300	**-0.445**	**-0.155**	**0.001**	0.276	0.001
	Species richness:ebd	-0.494	**-0.639**	**-0.350**	**<0.001**		
56	Intercept	-0.261	**-0.432**	**-0.091**	**0.010**	0.305	0.014
	Species richness	-0.433	**-0.586**	**-0.281**	**<0.001**	0.298	0.005
	Intercept	-0.224	**-0.434**	**-0.014**	**0.043**	0.605	0.009
57	Avg FDist:bbs	0.415	**0.318**	**0.512**	**<0.001**	0.114	0.003
	Avg FDist:ebd	0.386	**0.290**	**0.482**	**<0.001**		
58	Intercept	-0.227	**-0.438**	**-0.017**	**0.040**	0.606	0.009
	Avg FDist	0.394	**0.298**	**0.490**	**<0.001**	0.113	0.003
	Intercept	-0.146	-0.295	0.004	0.065	0.295	0.008
59	Max FDist:bbs	-0.344	**-0.424**	**-0.264**	**<0.001**	0.074	0.003
	Max FDist:ebd	-0.376	**-0.455**	**-0.296**	**<0.001**		
60	Intercept	-0.144	-0.295	0.006	0.068	0.296	0.008

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Model	Coefficient	Value	95% CI		p-value	Random effects variance	
			2.5% CI	97.5% CI		BCR	Year
	Max FDist	-0.365	**-0.446**	**-0.284**	**<0.001**	0.077	0.003
Pearson correlation between functional distinctiveness and Leroy rarity							
61	Intercept	-0.072	-0.195	0.052	0.259	0.168	0.014
	PIE:bbs	-0.258	**-0.326**	**-0.190**	**<0.001**	0.047	0.003
	PIE:ebd	0.027	-0.038	0.092	0.416		
62	Intercept	-0.108	-0.225	0.009	0.077	0.156	0.010
	PIE	-0.024	-0.091	0.044	0.493	0.051	0.003
63	Intercept	-0.134	-0.274	0.005	0.065	0.256	0.008
	Avg Leroy:bbs	0.036	-0.016	0.087	0.178	0.031	0.001
	Avg Leroy:ebd	0.038	-0.012	0.089	0.144		
64	Intercept	-0.134	-0.274	0.006	0.065	0.256	0.008
	Avg Leroy	0.037	-0.013	0.088	0.150	0.031	0.001
65	Intercept	-0.179	-0.360	0.001	0.058	0.419	0.010
	Avg log:bbs	0.120	**0.075**	**0.165**	**<0.001**	0.019	0.001
	Avg log:ebd	0.071	**0.027**	**0.115**	**0.002**		
66	Intercept	-0.184	**-0.364**	**-0.004**	0.052	0.419	0.010
	Avg log	0.084	**0.041**	**0.128**	**<0.001**	0.019	0.002
67	Intercept	-0.126	-0.262	0.009	0.074	0.191	0.017
	Species richness:bbs	-0.068	-0.136	0.001	0.062	0.048	0.001
	Species richness:ebd	-0.069	**-0.137**	**-0.001**	0.055		
68	Intercept	-0.126	-0.262	0.009	0.074	0.191	0.017
	Species richness	-0.069	**-0.136**	**-0.001**	0.055	0.048	0.001
69	Intercept	-0.137	-0.320	0.047	0.150	0.387	0.035
	Avg FDist:bbs	0.555	**0.467**	**0.642**	**<0.001**	0.094	0.001
	Avg FDist:ebd	0.195	**0.109**	**0.282**	**<0.001**		
70	Intercept	-0.172	**-0.344**	**-0.001**	0.054	0.338	0.029
	Avg FDist	0.293	**0.200**	**0.385**	**<0.001**	0.097	0.007
71	Intercept	-0.147	**-0.276**	**-0.018**	**0.030**	0.214	0.005
	Max FDist:bbs	0.114	**0.037**	**0.191**	**0.007**	0.072	0.001
	Max FDist:ebd	0.155	**0.079**	**0.232**	**<0.001**		
72	Intercept	-0.149	**-0.278**	**-0.020**	**0.028**	0.215	0.005
	Max FDist	0.142	**0.067**	**0.217**	**0.001**	0.069	0.001
Pearson correlation between functional distinctiveness and log-rarity							
73	Intercept	-0.070	-0.194	0.054	0.272	0.162	0.017
	PIE:bbs	-0.290	**-0.357**	**-0.223**	**<0.001**	0.044	0.003
	PIE:ebd	0.041	-0.023	0.105	0.215		
74	Intercept	-0.113	-0.229	0.004	0.063	0.148	0.012
	PIE	-0.019	-0.085	0.047	0.571	0.048	0.004
75	Intercept	-0.135	-0.272	0.003	0.059	0.240	0.011
	Avg Leroy:bbs	0.046	-0.003	0.095	0.070	0.027	0.001
	Avg Leroy:ebd	0.053	**0.005**	**0.100**	**0.036**		

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Model	Coefficient	Value	95% CI		p-value	Random effects variance	
			2.5% CI	97.5% CI		BCR	Year
76	Intercept	-0.135	-0.272	0.003	0.059	0.240	0.011
	Avg Leroy	0.051	**0.003**	**0.098**	**0.043**	0.027	0.001
77	Intercept	-0.199	**-0.386**	**-0.012**	**0.044**	0.447	0.013
	Avg log:bbs	0.155	**0.110**	**0.200**	**<0.001**	0.019	0.001
	Avg log:ebd	0.083	**0.040**	**0.126**	**<0.001**		
78	Intercept	-0.205	**-0.391**	**-0.019**	**0.037**	0.446	0.013
	Avg log	0.102	**0.059**	**0.146**	**<0.001**	0.018	0.002
79	Intercept	-0.112	-0.240	0.016	0.092	0.158	0.019
	Species richness:bbs	-0.065	-0.137	0.007	0.089	0.055	0.002
	Species richness:ebd	-0.042	-0.113	0.030	0.260		
80	Intercept	-0.116	-0.243	0.011	0.081	0.157	0.019
	Species richness	-0.050	-0.121	0.021	0.180	0.056	0.002
81	Intercept	-0.151	-0.335	0.034	0.115	0.383	0.039
	Avg FDist:bbs	0.584	**0.498**	**0.670**	**<0.001**	0.090	0.001
	Avg FDist:ebd	0.200	**0.115**	**0.285**	**<0.001**		
82	Intercept	-0.190	**-0.362**	**-0.018**	**0.034**	0.331	0.033
	Avg FDist	0.304	**0.214**	**0.394**	**<0.001**	0.091	0.006
83	Intercept	-0.144	**-0.273**	**-0.015**	**0.034**	0.214	0.006
	Max FDist:bbs	0.150	**0.078**	**0.221**	**<0.001**	0.059	0.002
	Max FDist:ebd	0.183	**0.112**	**0.254**	**<0.001**		
84	Intercept	-0.145	**-0.274**	**-0.017**	**0.032**	0.214	0.006
	Max FDist	0.172	**0.102**	**0.242**	**<0.001**	0.058	0.001
Average product of functional distinctiveness and Leroy rarity							
85	Intercept	-0.344	**-0.580**	**-0.108**	**0.006**	0.730	0.035
	PIE:bbs	-0.031	-0.115	0.052	0.464	0.077	0.005
	PIE:ebd	-0.030	-0.111	0.051	0.475		
86	Intercept	-0.344	**-0.580**	**-0.109**	**0.006**	0.729	0.035
	PIE	-0.030	-0.111	0.051	0.471	0.077	0.005
87	Intercept	0.035	**0.006**	**0.063**	**0.019**	0.006	0.002
	Avg Leroy:bbs	0.895	**0.873**	**0.917**	**<0.001**	0.004	0.001
	Avg Leroy:ebd	1.010	**0.988**	**1.031**	**<0.001**		
88	Intercept	0.038	**0.009**	**0.067**	**0.012**	0.007	0.002
	Avg Leroy	0.972	**0.954**	**0.990**	**<0.001**	0.003	<0.001
89	Intercept	-1.064	**-1.397**	**-0.731**	**<0.001**	1.698	0.017
	Avg log:bbs	0.721	**0.652**	**0.791**	**<0.001**	0.061	0.005
	Avg log:ebd	0.698	**0.628**	**0.767**	**<0.001**		
90	Intercept	-1.064	**-1.397**	**-0.731**	**<0.001**	1.694	0.016
	Avg log	0.703	**0.634**	**0.773**	**<0.001**	0.063	0.004
91	Intercept	0.200	-0.026	0.426	0.092	0.464	0.071
	Species richness:bbs	0.929	**0.689**	**1.168**	**<0.001**	0.770	0.022
	Species richness:ebd	0.279	**0.040**	**0.519**	**0.028**		

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Model	Coefficient	Value	95% CI		p-value	Random effects variance	
			2.5% CI	97.5% CI		BCR	Year
92	Intercept	0.198	-0.004	0.401	0.063	0.348	0.062
	Species richness	0.441	**0.235**	**0.648**	**<0.001**	0.559	0.018
93	Intercept	-0.402	**-0.617**	**-0.187**	**0.001**	0.653	0.017
	Avg FDist:bbs	0.156	**0.053**	**0.259**	**0.005**	0.137	0.006
	Avg FDist:ebd	0.288	**0.186**	**0.391**	**<0.001**		
94	Intercept	-0.391	**-0.608**	**-0.175**	**0.001**	0.665	0.017
	Avg FDist	0.255	**0.157**	**0.353**	**<0.001**	0.127	0.005
95	Intercept	-0.401	**-0.656**	**-0.147**	**0.003**	0.801	0.063
	Max FDist:bbs	0.220	**0.169**	**0.271**	**<0.001**	0.025	0.002
	Max FDist:ebd	0.181	**0.130**	**0.232**	**<0.001**		
96	Intercept	-0.398	**-0.652**	**-0.143**	**0.003**	0.804	0.063
	Max FDist	0.196	**0.145**	**0.247**	**<0.001**	0.024	0.003
Average product of functional distinctiveness and log-rarity							
97	Intercept	0.998	**0.705**	**1.290**	**<0.001**	1.130	0.054
	PIE:bbs	-0.206	**-0.289**	**-0.123**	**<0.001**	0.071	0.006
	PIE:ebd	-0.104	**-0.184**	**-0.023**	**0.014**		
98	Intercept	0.986	**0.691**	**1.281**	**<0.001**	1.146	0.057
	PIE	-0.121	**-0.204**	**-0.039**	**0.005**	0.073	0.007
99	Intercept	1.313	**0.919**	**1.707**	**<0.001**	2.348	0.028
	Avg Leroy:bbs	0.659	**0.582**	**0.736**	**<0.001**	0.060	0.010
	Avg Leroy:ebd	0.909	**0.833**	**0.986**	**<0.001**		
100	Intercept	1.323	**0.930**	**1.717**	**<0.001**	2.343	0.027
	Avg Leroy	0.830	**0.765**	**0.894**	**<0.001**	0.050	0.004
101	Intercept	0.029	-0.008	0.067	0.138	0.016	0.001
	Avg log:bbs	0.888	**0.860**	**0.916**	**<0.001**	0.008	0.001
	Avg log:ebd	0.985	**0.957**	**1.012**	**<0.001**		
102	Intercept	0.031	-0.008	0.069	0.126	0.017	0.001
	Avg log	0.959	**0.935**	**0.984**	**<0.001**	0.007	0.001
103	Intercept	1.073	**0.659**	**1.487**	**<0.001**	2.154	0.097
	Species richness:bbs	0.541	**0.360**	**0.723**	**<0.001**	0.353	0.026
	Species richness:ebd	-0.143	-0.324	0.039	0.132		
104	Intercept	1.125	**0.741**	**1.508**	**<0.001**	1.880	0.074
	Species richness	0.065	-0.090	0.220	0.417	0.260	0.014
105	Intercept	0.905	**0.627**	**1.183**	**<0.001**	1.062	0.034
	Avg FDist:bbs	0.308	**0.193**	**0.422**	**<0.001**	0.145	0.013
	Avg FDist:ebd	0.483	**0.369**	**0.597**	**<0.001**		
106	Intercept	0.922	**0.648**	**1.196**	**<0.001**	1.040	0.032
	Avg FDist	0.438	**0.330**	**0.545**	**<0.001**	0.137	0.008
107	Intercept	0.975	**0.658**	**1.292**	**<0.001**	1.279	0.093
	Max FDist:bbs	0.224	**0.165**	**0.282**	**<0.001**	0.036	0.002
	Max FDist:ebd	0.213	**0.155**	**0.271**	**<0.001**		

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Model	Coefficient	Value	95% CI		p-value	Random effects variance	
			2.5% CI	97.5% CI		BCR	Year
108	Intercept	0.976	**0.659**	**1.292**	**<0.001**	1.279	0.093
	Max FDist	0.217	**0.159**	**0.275**	**<0.001**	0.036	0.002

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Table C2. Fixed effect estimates and variance of random effects in mixed-effect linear models fitted to relate candidate metrics of functional rarity and numerical rarity and functional distinctiveness of species constituting these communities

Model	Coefficient	Value	95% CI		p-value	Random effects variance	
			2.5% CI	97.5% CI		BCR	Year
PIE × Functional Divergence							
1	Intercept	0.747	**0.721**	**0.773**	**0.000**	0.010	0.000
	Leroy:bbs	0.102	**0.052**	**0.152**	**0.000**	0.029	0.003
	Leroy:ebd	-0.151	**-0.202**	**-0.101**	**0.000**		
2	Intercept	0.747	**0.721**	**0.774**	**0.000**	0.010	0.000
	Leroy	-0.025	-0.062	0.013	0.202	0.019	0.000
3	Intercept	0.750	**0.724**	**0.777**	**0.000**	0.011	0.000
	Log-rarity:bbs	0.071	**0.045**	**0.096**	**0.000**	0.005	0.002
	Log-rarity:ebd	-0.109	**-0.134**	**-0.084**	**0.000**		
4	Intercept	0.751	**0.724**	**0.778**	**0.000**	0.011	0.000
	Log-rarity	-0.022	**-0.034**	**-0.010**	**0.001**	0.002	0.000
5	Intercept	0.756	**0.724**	**0.789**	**0.000**	0.016	0.000
	FDist W:bbs	0.041	**0.012**	**0.070**	**0.008**	0.012	0.000
	FDist W:ebd	-0.097	**-0.126**	**-0.068**	**0.000**		
6	Intercept	0.757	**0.723**	**0.791**	**0.000**	0.018	0.000
	FDist W	-0.029	**-0.056**	**-0.002**	**0.036**	0.008	0.001
7	Intercept	0.794	**0.769**	**0.819**	**0.000**	0.009	0.000
	FDist U:bbs	-0.030	**-0.058**	**-0.002**	**0.040**	0.010	0.000
	FDist U:ebd	-0.167	**-0.195**	**-0.139**	**0.000**		
8	Intercept	0.796	**0.770**	**0.822**	**0.000**	0.010	0.000
	FDist U	-0.101	**-0.131**	**-0.071**	**0.000**	0.010	0.001
Weighted by Leroy rarity mean functional distinctiveness							
9	Intercept	0.514	**0.509**	**0.520**	**0.000**	0.000	0.000
	Leroy:bbs	-0.042	**-0.057**	**-0.026**	**0.000**	0.002	0.000
	Leroy:ebd	0.034	**0.019**	**0.050**	**0.000**		
10	Intercept	0.514	**0.509**	**0.520**	**0.000**	0.000	0.000
	Leroy	-0.006	-0.015	0.003	0.187	0.001	0.000
11	Intercept	0.513	**0.508**	**0.519**	**0.000**	0.000	0.000
	Log-rarity:bbs	-0.025	**-0.034**	**-0.016**	**0.000**	0.001	0.000
	Log-rarity:ebd	0.029	**0.020**	**0.038**	**0.000**		
12	Intercept	0.513	**0.508**	**0.519**	**0.000**	0.000	0.000
	Log-rarity	0.002	-0.003	0.006	0.408	0.000	0.000
13	Intercept	0.493	**0.486**	**0.499**	**0.000**	0.001	0.000
	FDist W:bbs	0.021	**0.013**	**0.030**	**0.000**	0.001	0.000
	FDist W:ebd	0.062	**0.054**	**0.071**	**0.000**		
14	Intercept	0.493	**0.486**	**0.500**	**0.000**	0.001	0.000
	FDist W	0.041	**0.031**	**0.052**	**0.000**	0.001	0.000

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Model	Coefficient	Value	95% CI		p-value	Random effects variance	
			2.5% CI	97.5% CI		BCR	Year
15	Intercept	0.478	**0.471**	**0.485**	**0.000**	0.001	0.000
	FDist U:bbs	0.049	**0.037**	**0.061**	**0.000**	0.002	0.000
	FDist U:ebd	0.090	**0.078**	**0.102**	**0.000**		
16	Intercept	0.477	**0.470**	**0.484**	**0.000**	0.001	0.000
	FDist U	0.071	**0.056**	**0.086**	**0.000**	0.002	0.001
Weighted by log-rarity mean functional distinctiveness							
17	Intercept	0.515	**0.510**	**0.520**	**0.000**	0.000	0.000
	Leroy:bbs	-0.044	**-0.059**	**-0.028**	**0.000**	0.002	0.001
	Leroy:ebd	0.035	**0.020**	**0.050**	**0.000**		
18	Intercept	0.515	**0.510**	**0.520**	**0.000**	0.000	0.000
	Leroy	-0.005	-0.013	0.002	0.182	0.001	0.000
19	Intercept	0.514	**0.509**	**0.519**	**0.000**	0.000	0.000
	Log-rarity:bbs	-0.025	**-0.034**	**-0.016**	**0.000**	0.001	0.000
	Log-rarity:ebd	0.030	**0.021**	**0.040**	**0.000**		
20	Intercept	0.514	**0.509**	**0.519**	**0.000**	0.000	0.000
	Log-rarity	0.002	-0.002	0.007	0.278	0.000	0.000
21	Intercept	0.494	**0.488**	**0.500**	**0.000**	0.001	0.000
	FDist W:bbs	0.020	**0.011**	**0.029**	**0.000**	0.001	0.000
	FDist W:ebd	0.063	**0.054**	**0.071**	**0.000**		
22	Intercept	0.494	**0.487**	**0.501**	**0.000**	0.001	0.000
	FDist W	0.041	**0.030**	**0.051**	**0.000**	0.001	0.000
23	Intercept	0.478	**0.472**	**0.485**	**0.000**	0.000	0.000
	FDist U:bbs	0.049	**0.037**	**0.061**	**0.000**	0.001	0.000
	FDist U:ebd	0.091	**0.079**	**0.103**	**0.000**		
24	Intercept	0.477	**0.470**	**0.484**	**0.000**	0.000	0.000
	FDist U	0.072	**0.057**	**0.087**	**0.000**	0.002	0.001
Inversed (Leroy weights) functional divergence							
25	Intercept	0.896	**0.889**	**0.903**	**0.000**	0.001	0.000
	Leroy:bbs	-0.021	**-0.039**	**-0.002**	**0.035**	0.005	0.000
	Leroy:ebd	0.008	-0.010	0.027	0.401		
26	Intercept	0.896	**0.889**	**0.903**	**0.000**	0.001	0.000
	Leroy	-0.007	-0.025	0.011	0.442	0.005	0.000
27	Intercept	0.896	**0.888**	**0.903**	**0.000**	0.001	0.000
	Log-rarity:bbs	-0.012	**-0.017**	**-0.007**	**0.000**	0.000	0.000
	Log-rarity:ebd	0.008	**0.004**	**0.013**	**0.001**		
28	Intercept	0.896	**0.888**	**0.903**	**0.000**	0.001	0.000
	Log-rarity	-0.002	-0.006	0.002	0.347	0.000	0.000
29	Intercept	0.889	**0.880**	**0.898**	**0.000**	0.001	0.000
	FDist W:bbs	0.003	-0.005	0.010	0.512	0.001	0.000
	FDist W:ebd	0.020	**0.012**	**0.027**	**0.000**		
30	Intercept	0.889	**0.880**	**0.898**	**0.000**	0.001	0.000

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Model	Coefficient	Value	95% CI		p-value	Random effects variance	
			2.5% CI	97.5% CI		BCR	Year
31	FDist W	0.011	**0.003**	**0.019**	**0.011**	0.001	0.000
	Intercept	0.885	**0.875**	**0.894**	**0.000**	0.001	0.000
	FDist U:bbs	0.011	**0.000**	**0.022**	0.052	0.002	0.000
	FDist U:ebd	0.028	**0.017**	**0.039**	**0.000**		
32	Intercept	0.885	**0.875**	**0.894**	**0.000**	0.001	0.000
	FDist U	0.019	**0.008**	**0.030**	**0.001**	0.002	0.000
Inversed (log-weights) functional divergence							
33	Intercept	0.898	**0.893**	**0.903**	**0.000**	0.000	0.000
	Leroy:bbs	-0.023	**-0.035**	**-0.010**	**0.001**	0.002	0.000
	Leroy:ebd	0.010	-0.003	0.022	0.144		
34	Intercept	0.898	**0.893**	**0.903**	**0.000**	0.000	0.000
	Leroy	-0.007	-0.019	0.004	0.211	0.002	0.000
35	Intercept	0.897	**0.892**	**0.902**	**0.000**	0.000	0.000
	Log-rarity:bbs	-0.012	**-0.017**	**-0.008**	**0.000**	0.000	0.000
	Log-rarity:ebd	0.011	**0.006**	**0.015**	**0.000**		
36	Intercept	0.897	**0.892**	**0.903**	**0.000**	0.000	0.000
	Log-rarity	-0.001	-0.004	0.002	0.504	0.000	0.000
37	Intercept	0.891	**0.884**	**0.899**	**0.000**	0.001	0.000
	FDist W:bbs	0.001	-0.006	0.009	0.724	0.001	0.000
	FDist W:ebd	0.020	**0.012**	**0.028**	**0.000**		
38	Intercept	0.892	**0.884**	**0.899**	**0.000**	0.001	0.000
	FDist W	0.010	**0.002**	**0.019**	**0.015**	0.001	0.000
39	Intercept	0.887	**0.879**	**0.895**	**0.000**	0.001	0.000
	FDist U:bbs	0.010	-0.001	0.020	0.070	0.001	0.000
	FDist U:ebd	0.028	**0.018**	**0.038**	**0.000**		
40	Intercept	0.887	**0.879**	**0.895**	**0.000**	0.001	0.000
	FDist U	0.019	**0.008**	**0.029**	**0.001**	0.001	0.000
Pearson correlation coefficient between functional distinctiveness and Leroy rarity weight							
41	Intercept	0.063	**0.006**	**0.120**	**0.035**	0.050	0.000
	Leroy:bbs	-0.173	**-0.258**	**-0.089**	**0.000**	0.065	0.014
	Leroy:ebd	0.092	**0.007**	**0.176**	**0.037**		
42	Intercept	0.063	**0.006**	**0.120**	**0.035**	0.050	0.000
	Leroy	-0.043	-0.109	0.023	0.206	0.052	0.003
43	Intercept	0.052	-0.005	0.109	0.078	0.050	0.000
	Log-rarity:bbs	-0.079	**-0.118**	**-0.041**	**0.000**	0.007	0.005
	Log-rarity:ebd	0.108	**0.070**	**0.147**	**0.000**		
44	Intercept	0.053	-0.004	0.111	0.076	0.051	0.000
	Log-rarity	0.014	-0.009	0.037	0.250	0.005	0.001
45	Intercept	-0.016	-0.084	0.051	0.637	0.066	0.001
	FDist W:bbs	0.074	**0.026**	**0.122**	**0.004**	0.027	0.001
	FDist W:ebd	0.221	**0.172**	**0.269**	**0.000**		

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Model	Coefficient	Value	95% CI		p-value	Random effects variance	
			2.5% CI	97.5% CI		BCR	Year
46	Intercept	-0.018	-0.086	0.050	0.607	0.068	0.001
	FDist W	0.150	**0.105**	**0.196**	**0.000**	0.026	0.000
47	Intercept	-0.026	-0.092	0.041	0.453	0.062	0.002
	FDist U:bbs	0.091	**0.033**	**0.148**	**0.004**	0.041	0.001
	FDist U:ebd	0.236	**0.179**	**0.294**	**0.000**		
48	Intercept	-0.028	-0.095	0.038	0.408	0.063	0.002
	FDist U	0.168	**0.116**	**0.220**	**0.000**	0.033	0.001
Pearson correlation coefficient between functional distinctiveness and log-rarity weight							
49	Intercept	0.085	**0.029**	**0.141**	**0.005**	0.048	0.001
	Leroy:bbs	-0.154	**-0.231**	**-0.077**	**0.000**	0.047	0.014
	Leroy:ebd	0.159	**0.083**	**0.236**	**0.000**		
50	Intercept	0.085	**0.029**	**0.141**	**0.005**	0.048	0.001
	Leroy	-0.004	-0.060	0.051	0.886	0.037	0.002
51	Intercept	0.074	**0.017**	**0.130**	**0.013**	0.048	0.001
	Log-rarity:bbs	-0.078	**-0.117**	**-0.038**	**0.000**	0.007	0.006
	Log-rarity:ebd	0.141	**0.101**	**0.180**	**0.000**		
52	Intercept	0.075	**0.018**	**0.133**	**0.012**	0.049	0.001
	Log-rarity	0.029	**0.008**	**0.050**	**0.008**	0.004	0.001
53	Intercept	0.001	-0.063	0.066	0.964	0.060	0.002
	FDist W:bbs	0.083	**0.039**	**0.127**	**0.001**	0.021	0.001
	FDist W:ebd	0.255	**0.211**	**0.299**	**0.000**		
54	Intercept	0.000	-0.065	0.066	0.993	0.061	0.002
	FDist W	0.171	**0.130**	**0.212**	**0.000**	0.020	0.000
55	Intercept	-0.007	-0.071	0.057	0.837	0.056	0.002
	FDist U:bbs	0.097	**0.042**	**0.152**	**0.002**	0.037	0.001
	FDist U:ebd	0.268	**0.212**	**0.323**	**0.000**		
56	Intercept	-0.009	-0.073	0.055	0.776	0.056	0.002
	FDist U	0.187	**0.138**	**0.236**	**0.000**	0.028	0.001
Mean product of functional distinctiveness and Leroy rarity weight							
57	Intercept	0.077	**0.070**	**0.084**	**0.000**	0.001	0.000
	Leroy:bbs	0.063	**0.047**	**0.080**	**0.000**	0.004	0.000
	Leroy:ebd	0.112	**0.095**	**0.128**	**0.000**		
58	Intercept	0.077	**0.070**	**0.084**	**0.000**	0.001	0.000
	Leroy	0.088	**0.067**	**0.109**	**0.000**	0.005	0.001
59	Intercept	0.081	**0.074**	**0.087**	**0.000**	0.001	0.000
	Log-rarity:bbs	0.010	**0.004**	**0.017**	**0.004**	0.001	0.000
	Log-rarity:ebd	0.043	**0.036**	**0.050**	**0.000**		
60	Intercept	0.080	**0.074**	**0.087**	**0.000**	0.001	0.000
	Log-rarity	0.027	**0.020**	**0.035**	**0.000**	0.000	0.000
61	Intercept	0.079	**0.073**	**0.085**	**0.000**	0.001	0.000
	FDist W:bbs	0.012	**0.002**	**0.022**	**0.026**	0.001	0.000

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Model	Coefficient	Value	95% CI		p-value	Random effects variance	
			2.5% CI	97.5% CI		BCR	Year
62	FDist W:ebd	0.037	**0.027**	**0.047**	**0.000**		
	Intercept	0.079	**0.072**	**0.085**	**0.000**	0.001	0.000
	FDist W	0.025	**0.014**	**0.037**	**0.000**	0.001	0.000
63	Intercept	0.089	**0.083**	**0.096**	**0.000**	0.001	0.000
	FDist U:bbs	-0.008	-0.018	0.002	0.123	0.001	0.000
	FDist U:ebd	0.017	**0.007**	**0.027**	**0.002**		
64	Intercept	0.088	**0.081**	**0.095**	**0.000**	0.001	0.000
	FDist U	0.007	-0.003	0.016	0.181	0.001	0.000
Mean product of functional distinctiveness and log-rarity							
65	Intercept	0.182	**0.170**	**0.194**	**0.000**	0.002	0.000
	Leroy:bbs	0.051	**0.034**	**0.068**	**0.000**	0.004	0.000
	Leroy:ebd	0.144	**0.127**	**0.161**	**0.000**		
66	Intercept	0.182	**0.170**	**0.194**	**0.000**	0.002	0.000
	Leroy	0.099	**0.076**	**0.122**	**0.000**	0.006	0.001
67	Intercept	0.178	**0.166**	**0.189**	**0.000**	0.002	0.000
	Log-rarity:bbs	0.019	**0.010**	**0.029**	**0.000**	0.001	0.000
	Log-rarity:ebd	0.083	**0.074**	**0.092**	**0.000**		
68	Intercept	0.177	**0.165**	**0.189**	**0.000**	0.002	0.000
	Log-rarity	0.053	**0.042**	**0.064**	**0.000**	0.001	0.000
69	Intercept	0.172	**0.158**	**0.185**	**0.000**	0.003	0.000
	FDist W:bbs	0.029	**0.013**	**0.045**	**0.001**	0.003	0.000
	FDist W:ebd	0.077	**0.061**	**0.093**	**0.000**		
70	Intercept	0.171	**0.157**	**0.185**	**0.000**	0.003	0.000
	FDist W	0.055	**0.037**	**0.073**	**0.000**	0.003	0.000
71	Intercept	0.191	**0.173**	**0.208**	**0.000**	0.004	0.000
	FDist U:bbs	-0.007	-0.026	0.012	0.457	0.005	0.000
	FDist U:ebd	0.040	**0.022**	**0.059**	**0.000**		
72	Intercept	0.190	**0.172**	**0.208**	**0.000**	0.005	0.000
	FDist U	0.018	-0.001	0.036	0.063	0.004	0.000

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Appendix D. Linear and mixed-effect models fitted to describe relationship between functional rarity metrics, urbanization level, year, and random effects of bird conservation region and source of the data

Table D1. Linear and mixed-effect models fitted to describe relationship between z-scaled Pearson's coefficient of correlation between regional functional distinctiveness and log-rarity, urbanization level (U), Year, source of the data (BBS or eBird), and random effects of bird conservation region (BCR)

Coefficient	Value	p-value	AICc	ΔAICc	df	logL
CFR ~ 1						
(Intercept)	0.000	1.000	245212.6	8937.1	2	-122604.3
CFR ~ log(U) + Year						
(Intercept)	13.805	**0.000**				
log(U)	-0.066	**0.000**	244633.7	8358.2	4	-122312.9
Year	-0.007	**0.000**				
CFR ~ log(U) + Year + (1 + log(U) | BCR)						
(Intercept)	10.198	**0.000**				
log(U)	0.037	0.133	237251.1	975.7	7	-118618.6
Year	-0.005	**0.000**				
CFR ~ log(U):Source + Year:Source + (1 + log(U) | BCR)						
(Intercept)	26.092	**0.000**				
log(U):BBS	-0.017	0.498				
log(U):eBird	0.065	**0.013**	236369.2	93.8	9	-118175.6
BBS:Year	-0.013	**0.000**				
eBird:Year	-0.013	**0.000**				
CFR ~ log(U)						
(Intercept)	-0.170	**0.000**	244783.7	8508.2	3	-122388.8
log(U)	-0.069	**0.000**				
CFR ~ log(U) × Year						
(Intercept)	-5.620	0.057				
log(U)	-7.960	**0.000**	244585.2	8309.7	5	-122287.6
Year	0.003	0.065				
log(U):Year	0.004	**0.000**				
CFR ~ log(U) × Year + (1 + log(U) | BCR)						
(Intercept)	4.483	0.122				
log(U)	-2.283	**0.036**	237261.8	986.3	8	-118622.9
Year	-0.002	0.119				
log(U):Year	0.001	**0.033**				
CFR ~ log(U):Year:Source + (1 + log(U) | BCR)						

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Coefficient	Value	p-value	AICc	ΔAICc	df	logL
(Intercept)	0.004	0.962				
log(U):Year:BBS	0.000	**0.008**	237149.6	874.2	7	-118567.8
log(U):Year:eBird	0.000	**0.179**				
CFR ~ I[log(U)^2]						
(Intercept)	-0.091	**0.000**	244794.1	8518.6	3	-122394
I(log(U)^2)	0.013	**0.000**				
CFR ~ I[log(U)^2] + I[(log(U) - Year)^2]						
(Intercept)	7.060	**0.000**				
I(log(U)^2)	0.014	**0.000**	244637.5	8362.0	4	-122314.7
I((log(U) - Year)^2)	0.000	**0.000**				
CFR ~ I[log(U)^2] + I[(log(U) - Year)^2] + (1 + log(U) | BCR)						
(Intercept)	5.063	**0.000**				
I(log(U)^2)	-0.018	**0.000**	237243.8	968.3	7	-118614.9
I((log(U) - Year)^2)	0.000	**0.000**				
CFR ~ I[log(U)^2]:Source + I[(log(U) - Year)^2]^Source + (1 + log(U) | BCR)						
(Intercept)	13.336	**0.000**				
I(log(U)^2):BBS	-0.028	**0.000**				
I(log(U)^2):eBird	-0.049	**0.000**	236275.5	**0.0**	9	-118128.7
I((log(U) - Year)^2):BBS	0.000	**0.000**				
I((log(U) - Year)^2):eBird	0.000	**0.000**				

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Table D2. Linear and mixed-effect models fitted to describe relationship between average product of functional distinctiveness and log-rarity, urbanization level (U), Year, source of the data (BBS or eBird), and random effects of bird conservation region (BCR)

Coefficient	Value	p-value	AICc	ΔAICc	df	logL
PFR ~ 1						
(Intercept)	0.000	0.994	245208.00	29608.95	2	-122602.00
PFR ~ log(U) + Year						
(Intercept)	-59.281	**0.000**				
log(U)	-0.061	**0.000**	242232.10	26633.09	4	-121112.10
Year	0.029	**0.000**				
PFR ~ log(U) + Year + (1 + log(U) | BCR)						
(Intercept)	-46.507	**0.000**				
log(U)	0.076	**0.006**	227629.30	12030.29	7	-113807.70
Year	0.024	**0.000**				
PFR ~ log(U):Source + Year:Source + (1 + log(U) | BCR)						
(Intercept)	9.044	**0.000**				
log(U):BBS	0.088	**0.006**				
log(U):eBird	-0.010	0.737	215601.40	2.38	9	-107791.70
BBS:Year	-0.004	**0.000**				
eBird:Year	-0.004	**0.000**				
PFR ~ log(U)						
(Intercept)	-0.122	**0.000**	244988.00	29389.00	3	-122491.00
log(U)	-0.049	**0.000**				
PFR ~ log(U) × Year						
(Intercept)	-60.532	**0.000**				
log(U)	-0.569	0.603	242233.90	26634.88	5	-121111.90
Year	0.030	**0.000**				
log(U):Year	0.000	0.643				
PFR ~ log(U) × Year + (1 + log(U) | BCR)						
(Intercept)	-57.012	**0.000**				
log(U)	-4.188	**0.000**	227627.40	12028.42	8	-113805.70
Year	0.029	**0.000**				
log(U):Year	0.002	**0.000**				
PFR ~ log(U):Year:Source + (1 + log(U) | BCR)						
(Intercept)	1.131	**0.000**				
log(U):Year:BBS	0.000	**0.000**	216797.20	1198.16	7	-108391.60
log(U):Year:eBird	0.000	**0.044**				
PFR ~ I[log(U)^2]						
(Intercept)	-0.089	**0.000**	244811.60	29212.61	3	-122402.80
I(log(U)^2)	0.012	**0.000**				
PFR ~ I[log(U)^2] + I[(log(U) - Year)^2]						
(Intercept)	-29.339	**0.000**	242121.70	26522.66	4	-121056.80

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I(log(U)^2)	0.009	**0.000**				
I((log(U) - Year)^2)	0.000	**0.000**				
PFR ~ I[log(U)^2] + I[(log(U) - Year)^2] + (1 + log(U) | BCR)						
(Intercept)	-22.969	**0.000**				
I(log(U)^2)	0.042	**0.000**	227555.60	11956.61	7	-113770.80
I((log(U) - Year)^2)	0.000	**0.000**				
PFR ~ I[log(U)^2]:Source + I[(log(U) - Year)^2]^Source + (1 + log(U) | BCR)						
(Intercept)	4.533	**0.000**				
I(log(U)^2):BBS	0.015	**0.000**				
I(log(U)^2):eBird	0.035	**0.000**	215599.00	**0.00**	9	-107790.50
I((log(U) - Year)^2):BBS	0.000	**0.000**				
I((log(U) - Year)^2):eBird	0.000	**0.000**				

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Dubovyk, O. 2019. Annual dynamics of bird communities in urban parks in Lviv, Ukraine: preliminary analysis of diversity and composition variability. Studia Biologica 13:79–98.

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