Spatial distribution of functionally rare landbird species in North America and its temporal changes relative to urbanized areas

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Abstract

Present-day conservation efforts are based on the rarity of species as a function of their abundance, trend in abundance, and range size. The ecological meaning of rarity, instead, is more complicated and should also include the functional importance for ecosystems and the phylogenetic uniqueness relative to genetic value. From this perspective, the functional role is the most utilitarian: if abundant species in the ecosystem fail to perform their functional roles, rare taxa provide a functional insurance effect, implying ecosystem resilience under changing environmental conditions and reducing the risk of extinction events.

The implementation of conservation efforts typically considers the areas essential for those rare species and the primary aim of those areas is to buffer the consequences of global changes. On the other hand, the effects of urbanization, as one of the most significant manifestations of current global change that is thought to be a major threat for biodiversity and can be considered as one of the main obstacles for nature conservation, on ecological communities remain unclear. Bird assemblages offer convenient systems to study large ecological processes driven by environmental change. One of the most remarkable datasets is the North American Breeding Bird Count, which has been conducted since 1966 and allows researchers to not only study large-scale processes in spatial dimensions but to also track temporal change without space-for-time substitution (i.e., an assumption that patterns of change in spatial gradients parallel changes through time for environmental gradients that have become more influential in contemporary times). Another valuable source of data is eBird, a citizen-science project that collects information on global bird observations.

In this study, I plan to investigate the relative value of North American breeding bird species to ecosystem functioning by assessing functional rarity at local and regional scales to allow comparison of conservation status with ecosystem importance. This analysis should reveal spatial hotspots of functional rarity. This work will also allow me to test whether functionally rare species are associated with areas of urbanization over the last 20 years. This study will allow me to assess the locations of most rapid change in functional rarity among bird communities, revealing ecosystems at greatest risk of overall functional decline.

Objectives

1. To define the avian taxa of highest conservation concern relative to functional rarity.

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 – some taxa can have high functional value yet be labeled as Least Concern or with non-evaluated status (Loiseau et al., 2020). An important caveat is that functional rarity is more related 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. I hypothesize that rare species designation likely does not fully represent functional rarity. Thus, re-evaluation of species is needed to determine the risks to ecosystems. This step is not fully independent or exhaustive but will be required as a prerequisite to the following objectives.

2. To identify the spatial hotspots of functionally rare species occurrence and abundance 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. Loiseau et al. (2020) has shown that functionally rare species are not distributed evenly but, instead, have distinct hotspots, areas with important conservation value. This implies that hotspots of functional rarity could serve as areas of more concentrated focus, given their limited scope and conservation importance. It follows, thus, that the distributional abundance across the urban gradient could be used to test if functionally rare taxa tend to avoid or exploit urban areas (Pennington & Blair, 2012).

3. To determine if the spatial distribution of hotspots of functionally rare bird species have changed relative to landcover changes associated with increasing urbanization during the last 20 years.

Some authors predict that more species, especially rare taxa, should associate with urbanized areas (Friedmann et al., 2016); it is, however, difficult to predict the direction of change because one might expect differential effects based on idiosyncrasies of particular cities or taxonomic groups (Harrison et al., 2019; Dubovyk et al., 2020). The relationship between rates of changes in land use and corresponding change in the structure of bird communities could be used to determine overall effect on functionally rare species.

Background

Rapid human population growth is one of the most significant factors that leads to global biodiversity losses manifested by habitat loss, invasion of exotic species, overharvesting, climate change, and pollution (Carpenter et al., 2009). An important facet of this growth is also an everincreasing demand for urban expansion, the main driver of land cover change and habitat loss in biodiversity hotspots (Seto et al., 2012). Urbanization, a term used to describe the process of ever-increasing city expansion related to changes in land use, is thought to negatively affect the properties of populations (Moll et al., 2019; Murray et al., 2019) and, consequently, ecological communities (McKinney, 2006; Brown, 2019) and ecosystems (Li et al., 2019). Ecological communities associated with urban areas are thought to be more novel than natural communities, leading to populations with altered behavioral, physiological, and morphological traits (Grimm et al., 2008). Such negative effects are likely the primary reason for the dramatic decrease in taxonomic and functional diversity associated with increasing urbanization (Aronson et al., 2014; La Sorte et al., 2018), and are related to increasing rates of species extinction (Czech et al., 2000; Fattorini, 2011; Shochat et al., 2010).

Typically, in most ecological communities, the majority of species are thought to be rare (Kunin & Gaston, 1993; Gaston, 1994): this pattern was documented by Preston (1948) and forms the basis of classic theory in abundance distributions (Magurran, 2004). The rarity of species may suggest higher extinction risk (Mace & Kershaw, 1997; Courchamp et al., 2006; Marzluff & Rodewald, 2008), but the actual extinction risk is not necessarily directly related to the rarity itself and is related more to a defined dimension of rarity (*sensu* Rabinowitz, 1981) with geographic range size being more influential as a predictor of extinction than ecological niche breadth or population size (Harnik et al., 2012; Román-Palacios & Wiens, 2020). Numerically rare species are often the primary target for nature conservation (Scarano, 2009) although such taxa are not necessarily found within diversity hotspots (Prendergast et al., 1993) and are not as important at ecosystem scales as those of abundant and dominant species (Grime, 1998).

The importance of abundant and dominant species is more formally known as "the mass ratio hypothesis", that is the productivity of an ecosystem is mainly determined by the dominant taxa so that rare taxa are not required for stable ecosystem functioning; moreover, redundancy in taxa may even act to destabilize entire ecosystems (Putman, 1994). Of course, given the number of caveats in the mass ratio hypothesis (e.g., the fact that it was originally formulated in the context of plant communities, and the ecological roles of plants are more similar to each other than in animals of different trophic levels) it is impossible to ignore the importance of rare species. Indeed, as mentioned above, rare species are responsible for species richness in a community simply as a function of species number, which is not comprehensively informative per se. Moreover, rare species provide an insurance effect (Yachi & Loreau, 1999): in a moment in time or space, only a few species are in their ecological optimum while other – rare – species are in their zones of stress or intolerance but can be significantly valuable to ecosystem functioning when conditions change, and other species move away from their optimum, so that the community and, thus, ecosystem are expected to be more resilient towards disturbances. Why particular taxa may be rare under such fluctuating environments may thus be explained by both stochastic effects and a trade-off between stress resistance and low population growth. More resilient species tend to have a life history that predicts less probability of demographic explosion (Dee et al., 2019, Box 3). This can decrease the probability of establishment of new invasive taxa, increase the productivity of the overall community within fluctuating conditions, and enhance the productivity of dominant species (Fetzer et al., 2015; Jousset et al., 2017).

Thus, given the ubiquity of rare species in communities, it can be inferred that the functions of those taxa vary such that some species are redundant while others unique relative to ecosystem functioning (Jain et al., 2014). The original framework for the assessment of forms of rarity has been expanded from the basic description given by Rabinowitz (1981) based on the binary values of geographic range (small or large), habitat specificity (narrow or wide), and local population size (small or large). His well-established framework described the eight forms of rarity with the exception that one form (i.e., those with a large range, wide habitat specificity, and large local abundance) did not fit within our understanding of rarity (Rabinowitz, 1981). A more modern approach, in turn, is to view rarity from the perspective of functional value. In this way, the functional traits and abundance of taxa can be assessed at both local and regional scales, which in turn results in 12 types of functional rarity (Violle et al., 2017). This approach allows a more meaningful definition of rarity in the context of the functional uniqueness of taxa and their role in communities.

Avian communities are convenient subjects for the study of urbanization effects 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 & Jokimäki, 2001; Aronson et al., 2014). Generally high species diversity among climate zones and the ability to readily detect birds 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 changes in 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).

To describe changes in populations and communities of birds and potential mechanisms shaping the distribution of species as a response to rapid anthropogenic change, the concept of the urban gradient has been used. Urban gradient is an "abstract ordering of changes in land

cover, land use, and human activity" (Cadenasso et al., 2006), a popular and useful qualitative metric that is, unlike many other environmental gradients, difficult to quantify because there is no standard definition of urbanization as a factor (see Warren & Lepczyk, 2012; Moll et al., 2019).

Biological communities, as an array of populations within urban ecosystems, are in a state of constant flux that is thought to reflect changing conditions within such ecosystems (Clergeau et al., 1998). The changes in basic community parameters such as species richness, abundance (Blair, 1996; Clergeau et al., 1998), and species turnover are likely caused by urbanization processes through time: urbanization is thought to act as an environmental filter that selects for particular ecological traits or taxa of certain guilds (Evans et al., 2018). Urbanization processes are slow and may have begun centuries ago (Zhang & Seto, 2011). Understanding how urbanization has manifested itself over time is complicated with long-term data and the ability to examine spatially how sites at different temporal stages have effects on communities or other ecological units is known as space-for-time substitution analyses (Pickett, 1989). This substitution implies that patterns of change in spatial urban gradients are similar to changes through time because urbanization intensity is considered as a function of time (Pickett, 1989; França et al., 2016). A space-for-time substitution approach has been verified as reliable in studies which attempt to assess the effects of land use and global climate change (La Sorte et al., 2009; Bonthoux et al., 2013), but many consider the approach to result in misleading conclusions based on differences in spatial and temporal variability (La Sorte et al., 2018; Damgaard, 2019). Since this criticism considers the general use of the space-for-time substitution, long-term data are preferable to draw conclusions about temporal change in community structure that includes features such as species and functional group abundance and distribution, species richness and overall density, and diversity and rarity. Moreover, the ability to track spatial change through time is not possible if one focuses solely on the spatial dimension.

Some of the features associated with increasing urbanization in bird 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). Unfortunately, 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 & Osborne, 1982). For example, the presence of additional resources in urban ecosystems can explain the abundance of avian and mammal predators, which also shapes the abundance of prey, especially species vulnerable to nest predation (Stracey & Robinson, 2012). Some studies have demonstrated that such nest predation favors larger taxa that can defend their nests or smaller taxa that have more cryptic nests. But, of course, many such findings tend to be idiosyncratic and have not resulted in an overarching consensus among studies (Kaisanlahti-Jokimäki et al., 2012; Stracey & Robinson, 2012). Besides influencing predator numbers, urbanization also alters the ratio of functional groups of birds (Petchey et al., 2007; Marzluff & Rodewald, 2008; Rodewald, 2012; Aronson et al., 2014; Galewski & Devictor, 2016; Marzluff, 2016) and that some species associated with increasing urbanization have increased in abundance during the last few decades (Sauer & Link, 2011), implying that an investigation into changes in functional rarity could reveal underlying mechanisms responsible for changes in bird community structure that are driven by increasing urbanization.

A better alternative to the use of idiosyncratic cases of particular urban areas would be an approach to test assumptions using big datasets from large areas. For example, the Breeding Bird

Survey (BBS) program is a comprehensive long-term dataset that chronicles breeding bird communities in North America. The BBS was established by Patuxent Wildlife Research Center of the U.S. Geological Survey in partnership with the Canadian Wildlife Service in 1966 in reaction to the publication of Rachel Carson's "Silent Spring" (Ziolkowski et al., 2010; Sauer et al., 2017). The BBS data describe the abundances of more than 400 bird species for more than half of which trends of abundance changes can be derived with a high level of reliability (Rosenberg et al., 2017).

Given that some caveats can be related to the use of BBS data (e.g., BBS routes are typically established within natural ecosystem and avoid urbanized habitats), these data can be supplemented with other comprehensive sources of data, such as eBird (Hochachka et al., 2012; Kelling et al., 2019). This platform collects the information on observation of birds from birdwatchers around the world, and a thoughtful process of data sorting allows researchers to make ecological inferences based on, for example, occurrence data.

The main use of such long-term datasets is to examine population trends and to guide conservation efforts (Sauer & Link, 2011). In addition, such datasets allow researchers to test general theoretical assumptions and methodological approaches in ecology (Boulinier et al., 1998; Galewski & Devictor, 2016; Valle et al., 2018; Catano et al., 2020; Chiffard et al., 2020), In particular, the citizen-science data collected in the British Trust for Ornithology's programs has been shown to be useful in functional ecology (Petchey et al., 2007), but, to the best of my knowledge, data from Northern America has not been used for such purposes.

Overview of the Study Design

I will use a combination of BBS and eBird datasets for an even distribution of sampling effort throughout urban gradients. The BBS dataset contains data on the abundance of more than 400 breeding bird species on more than 4,600 routes across North America from 1966 to present. These data are available from the BBS program. According to the BBS methodology, experienced participants move through a 39.4 km (24.5 mi) route and make 3-min stops every 800 m (0.5 mi) to count all of the individuals observed in a 400-m (0.25-mi) radius around the stopping point. I will convert such data into both a spatial dimension (the coordinates of a stop point) and a temporal dimension (the year of the count), along with the abundance of each species. From the eBird data, I will extract the observations of comparable sampling effort, i.e., 2–4 min point counts with full checklists of observed species. The consistent collection of the eBird data started between 2000 and 2005 so that this research will be limited in temporal scope by the availability of eBird data.

Land cover data provided by the Multi-Resolution Land Characteristics consortium (MLRC) (https://www.mrlc.gov/national-land-cover-database-nlcd-2016) or MODIS/Terra+Aqua Land Cover Type (https://lpdaac.usgs.gov/products/mcd12q1v006/) will be used to identify and quantify large urbanized areas and impervious area. The coordinates of BBS/eBird counts will be used to calculate the distance to the nearest urbanized area by year.

The functional rarity of each species will be calculated using diet, foraging strategy, substrate, timing, nesting strategy and other ecologically meaningful species traits known from literature sources in conjunction with abundance data provided by BBS/eBird. The local abundance rarity (i.e., calculated for the groups of spatially close counts, which will denote aggregated species-abundance data from several stopping points and/or routes) and local functional distinctiveness (extended to the same groups of counts), which is a metric of

distinctiveness of species as a point in functional trait space, will be used to calculate the functional rarity species. Such functional rarity will be weighted by the abundance of species, resulting in a functional value of the entire community.

This analysis will create a matrix of weighted abundances of functionally rare species by the distance to the closest urbanized area year by year. It will be possible to compare those matrices and to determine the trends in abundance.

Methods and Materials

BBS data will be transformed using Python. I will not use data prior to 2000 because of the lack of land cover data for the second half of the 20^{th} century. The existing data layout provides only the coordinates of a start point of each route and thus one needs to map the entire route to determine the data associated with each stop. Groups by ten closest points will be considered as one observation of a "community" (Boulinier et al., 1998) so that the data will be transformed into abundances of observed species anchored to mean coordinates of 10 points. This will also slightly reduce the sample size of approx. 6×10^6 (5,757 routes \times 20 years \times 50 stops) observations expected.

To assess local rarity, I will consider every point as a focal point in a local group of communities that are located no more than some manually defined distance (Fig. 1; I plan to use 1th-percentile distance between all the count points within the dataset as this distance). Thus, I will receive a subset of communities for every focal point and will sum the abundances of every species; the further local numerical rarity (i.e., calculated based on species abundances) and functional distinctiveness assessment will be conducted relative to the full subset of species-abundance/species-trait data on a local group of points. Regional rarity will be assessed to the extent of the given bird conservation region (BCRs were established for the management of conservation of North American birds, were based on the Commission for Environmental Cooperation's ecoregions and are expected to represent different types of avifauna; see https://nabci-us.org/resources/bird-conservation-regions-map/ and Sauer et al., 2003).

There are several possible approaches to calculate the value of relative abundance rarity. In general, this value should be inverse to the abundance: maximal (1) for the rarest species and minimal (0) for the most dominant species. These approaches are different from more common, and easier to interpret, statuses of species so that the rarity value is categorical (e.g., IUCN statuses) or even can be reduced to binary (rare [species that fall into some part of a distribution; e.g., lower quartile of abundance, biomass or frequency] or not rare; Gaston, 1994; Magurran, 2004). I will use the continual values of rarity, which implies the possibility of considering the degree of importance of species: thus, species will be not considered as rare or not rare, but rarity will be a relative value. To assess the rarity, one may use the ranks of abundance (Magurran & Henderson, 2011) or ratio of a maximal abundance to focal species abundance (Canard & Ysnel, 2002; Leroy et al., 2012), but these methods are not biased towards the importance of rare species (Leroy et al., 2012). Instead, two metrics can be used. The first one is based on logarithmic transformation of ratios of maximal and focal species abundances and was proposed independently:

$$RR_{log,i} = \frac{log(n_i/n_{max})}{min(log(n_i/n_{max}))},$$

where n_i is an abundance of *i*-th species so that dividend is a logarithm of this ratio and the divisor is a minimal such logarithm among the community.

Also, another useful metric is described by Leroy et al. (2012):

$$RR_{e,i} = e^{-(\frac{n_i}{n_{max}}\eta + 1)^2},$$

where η is an adjustment coefficient that regulates the threshold of rarity (25% as in Gaston, 1994) – it influences the number of species that will be considered as more rare by this assessment.

Functional distinctiveness of every species will be assessed as a mean Gower distance between a focal species and all other species considered in a multidimensional space of species functional traits (Petchey et al., 2007). Also, regional functional uniqueness will be considered as a minimal distance between a focal species and other species comprising the regional species pool (Violle et al., 2017). The ecological traits that are planned to be used are described in Table 1, the data for populating the values of traits will be obtained from the Cornell Lab of Ornithology Birds of the World database (https://birdsoftheworld.org/), or other sources if needed.

It is important to note that there are many facets of rarity and none of them can be considered as true rarity (Kondratyeva et al., 2019). This means that I will obviously receive a number of metrics for every focal species (e.g., local and regional abundance rarity, functional distinctiveness, and regional uniqueness) and every focal community (means and weighted abundances by species-specific metrics mentioned above), and those variables will likely show high multicollinearity and any attempt to look for patterns with ordination methods would be fruitless given the arbitrary nature of their ecological constructs.

One potential method of unifying local rarity estimates for every species with functional distinctiveness would be to take the product of those parameters to express an index of relative community importance by species. I could then compare the results within the context of designations under IUCN, Endangered Species Act, and Convention on International Trade in Endangered Species of Wild Fauna and Flora and local (state/province-level) classifications to determine the extent of accordance of formal statuses with actual value of species in ecosystems.

Land cover data will be taken to assess the areas of urbanized. All polygons with an area less than 4 km² (which is the 5th percentile of urban areas in the U.S. according to the 2019 TIGER/LineTM Shapefiles data, https://www.census.gov/geographies/mapping-files/timeseries/geo/tiger-line-file.html) will be eliminated as non-urban cores. This step will be done using Google Earth Engine, QGIS and R.

I will calculate two distances from every point: one will be to the centroid of the closest urban area polygon, and the other will be to the closest point of the closest polygon (its edge), which will be negative if a point is located inside of a polygon (Fig. 1). I presume that those two distances will be a function of the level of urbanization. Also, the total area of urbanized areas (with patches <4 km²) and percentage of impervious surface inside of each circle around a focal point will be calculated to assess the local level of urban development.

For every spatial point, I will determine the abundance of birds and species richness, the abundance weighted by local rarity and regional rarity, the abundances weighted by products of those rarities and local functional distinctiveness and regional functional uniqueness, distances to the nearest urban polygon centroid and nearest point of such polygon, and the area covered by urbanized landscapes/impervious area. I will use values of these metrics for every year.

The approach outlined will allow me to map the weighted abundances on local and regional rarity, then to assess the rates of change on distinct 100×100 km quadrats across North America. This will help to determine the locations of hotspots of functional rarity. The visualization at this step will be an animation of maps of functional rarity among bird communities by year.

The consequent analysis will use a model (I expect that a nonlinear mixed effects model will be the most appropriate) with products of local and regional abundance rarity and functional local distinctiveness and regional uniqueness as dependent variables and the predictors of distances to centroid and the nearest point of polygons of urbanized areas, the area covered by urban habitats, and year. This will allow me to check if the functionally valuable bird communities are positively or negatively associated with urban habitats and if these patterns have changed over the last 20 years.

Significance

As a general rule, the need for conservation efforts is assessed using abundance data, its trends, and spatial occurrence (e.g., IUCN Red List Categories and Criteria, 2012). The focus of conservation efforts is typically on threatened or endangered species. Given the possible functional importance of particular species, some common species may play an important functional role but be overlooked when simply conserving the abundantly rare but functionally redundant species, creating a need for reevaluating functionally rare taxa (Kondratyeva et al., 2019). The extinction of functionally rare species may be extremely harmful to ecosystems, which would also affect species of current special conservation concern. It is important to mention one more facet of rarity, namely phylogenetic, which is known to be used for evaluation of regional conservation importance relative to phylogenetic and colonizing history (Pollock et al., 2017): the same approach could be used with the notion of functional rarity.

The conservation of species is normally applied to areas that are particularly vulnerable relative to populations and/or species. Areas of conservation concern are likely biased towards abundance and little effort has been awarded to functional roles or evolutionary histories (Veron et al., 2017).

The larger areas likely support very few functionally rare species and the areas that contain such rare species are thought to contain more functionally rare taxa than expected by chance (Grenié et al., 2018; Loiseau et al., 2020). Given the possible effects of global environmental change, which could lead to a functional extinction crisis (Gardner et al., 2019), there is an urgent need to identify hotspots of functional rarity, particularly as it relates to the development of conservation policies.

Budget

No specific funds for field or laboratory work are thought to be needed to implement this research project.

For computations, an external hard drive will be needed to store land cover data (less than \$150). This expense will be covered by an IdeaWild small grant.

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Figures and tables

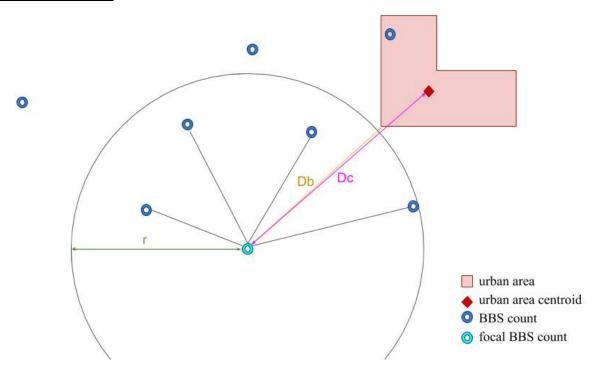


Fig. 1. The algorithm used to calculate local abundance rarity of species in a focal count. The "localitiness" is determined by a distance r: all the counts farther than r from the focal point are ignored. The distance to an urbanized area is derived from both the distance to centroid Dc and the distance to the closest point of an urbanized area Db (this number will be negative if the count is located inside of an urban polygon)

Table 1. Species-specific ecological traits to be used for assessment of functional diversity, rationale for their use, and alternatives

Trait	Rationale	Variable
Lifespan	essential for conservation efforts because those species that need several years to mature or those that have a	continuous (years)
Maturity age	short lifespan are expected to be more threatened	continuous (years)
Seasonal productivity	species that produce fewer offspring per season are expected to be more vulnerable to changes in population size	continuous (offspring/ season)
Body mass	ecologically meaningful because bigger organisms need higher consumed biomass per unit of time to persist; despite the expected correlation with other traits (Brawn et al., 1995), some physiological peculiarities that have not been considered in any other trait can be related to body mass (e.g., torpor capability)	continuous (g)
Nesting aggregation • solitary • families • colonies	the species that form colonies or colony-like structures might be more influential on the ecosystem and community structure because they are usually abundant when present	categorical
Nesting strategy	nesting strategy is one of the main determinants of species occupancy within a certain habitat during the breeding season, thus affecting the community composition and, to some extent, the ecosystem in general	binary
Foraging period	nocturnal activity is limited among bird taxa and can be associated with specific adaptations that should be conserved (high divergence)	binary (diurnal)
Hand wing index	morphology-based index calculated as $HWI = 100 \times \frac{wing \ length-secondary \ length}{wing \ length}$ (see Claramunt et al., 2011; Kennedy et al., 2016) is expected to covary with different diet-related traits, but it has also been shown to be related with dispersal ability which is an important functional role in an ecosystem (Sheard et al., 2020)	continuous
Foraging substrate • mud • water • timber • ground	these functional traits are expected to be related with ecological mechanisms of community assemblage through competition for foraging resources: niche partitioning to happen due to different diet sources, methods and substrates of collection; these three groups	binary

Trait	Rationale	Variable
• vegetation	of functional traits have been used in other works related	
• air	to functional diversity in birds (e.g., Petchey et al., 2007)	
• dump		
Foraging	•	
components		
• vertebrates		
invertebrates		
• seeds		
• fruits		
• nectar		
• green parts of		
plants		
• leftovers		
Foraging methods		
• pursuit		
• gleaning		
• pouncing		
• grazing		
• digging		
• scavenging		
• probing		
1 8	Considered but not to be used	
		continuous
Effective clutch		(hatchlings/
size	and almost in a surrounded in accessed and dissipativity which	breeding
	are already incorporated in seasonal productivity which is, in fact, a product of these two values and is more	attempt)
	ecologically meaningful	continuous
Breeding attempts	ecologically incamingful	(breeding
		attempts/
		season)
	the fact that other species dependent on the presence of	
	this species (for making cavities, finding a meal, etc.) can	
Interspecific	be vital in shaping community and, thus, its diversity, but	1.
dependency	this description is opaque; besides, this trait is expected to	binary
,	correlate with others, e.g., the woodpeckers that make	
	cavities that can be used by other taxa are related by their	
	foraging techniques and nesting strategy	
Feeding	may explain the amount of biomass needed to persist in	continuous
frequency	an ecosystem along with body mass, but is redundant	(meals/day)
	expected to be a driver of shaping of a community:	
Aggression	expected to be a driver of shaping of a community: interspecific aggression (e.g., as a mechanism of	binary
interspecificintraspecific	competition) may lower a probability of establishment of	
	ecologically similar species while intraspecific aggression	
	coologically similar species with muaspecific aggression	

Trait	Rationale	Variable
	may lower abundance of a species, but both can be	
	difficult to measure and might be variable under different	
	circumstances (e.g., Duckworth & Badyaev, 2007)	