

DATA ARTICLE OPEN ACCESS

AVONICHE: A Global Dataset of Dietary and Foraging Niches for Birds

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ABSTRACT

Motivation: The role of each animal species in an ecosystem is largely determined both by the resources it uses and the behaviours through which these resources are obtained. Even in well-studied vertebrate groups, like birds, quantitative data on the relative use of different food resources in the context of foraging strategies are generally lacking. Most analyses in macroecology, macroevolution and conservation biology are therefore limited to simplified dietary categories, ignoring the specific foraging behaviours and substrates used to access resources. Here we present AVONICHE, a dataset quantifying proportional membership in 32 foraging niches, representing a combination of dietary categories and associated foraging strategies used by all bird species.

Main Types of Variables Contained: Species-level information on the proportional use of foraging niches, each of which is defined as a particular foraging strategy within a specific dietary category (e.g., invertebrate feeding is subdivided into 7 foraging niches based on different foraging behaviors).

Spatial Location and Grain: Global.

Time Period and Grain: Present.

Major Taxa and Level of Measurement: All bird species (Class Aves). To allow integration with global phylogenies and other data resources published in future, we align species-level niche data with four different taxonomic treatments: BirdTree (9993 species), Clements/eBird (10,661 species), BirdLife International (10,999 species) and the new AviList taxonomy (10,981 species).

Software Format: Spreadsheet (.csv).

1 | Introduction

Many of the trophic processes at the heart of ecosystem functions and services are regulated by animals (Malhi et al. 2022; Schleuning et al. 2023; Stanworth et al. 2024). A wide array of research questions from evolutionary biology to community

ecology are centred on trophic interaction networks, including those connecting animals with their food plants, or predators with their prey. However, current information about animal diets and foraging behaviour is patchy and relatively simplistic, offering limited insight into eco-evolutionary processes or the structure and dynamics of ecosystems (Schleuning et al. 2023).

Alex L. Pigot and Joseph A. Tobias have contributed equally to this work.

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Mutualistic interactions between animal and plant species drive critical steps in the plant reproductive cycle, including pollination and seed dispersal, while antagonistic interactions such as herbivory constrain plant growth and productivity. Further top-down processes such as predation and scavenging play important roles in ecological functions such as regulating invertebrate populations and nutrient cycling (Sekercioglu 2006). Some progress has been made in quantifying the contribution of different animal species to these processes, yet standard classifications focus mainly on a single primary diet or habitat strata (Wilman et al. 2014; Tobias et al. 2022). Although grouping species into these broad diet or habitat categories is a useful step, this approach ignores the major differences in behavioural strategies and substrates that different species use for obtaining any particular food type, greatly over-simplifying the connection between animal diversity and ecosystem function (Ashmole 1971; Fitzpatrick 1980; Robinson and Holmes 1982; Prince and Morgan 1987; Remsen and Robinson 1990; Pigot et al. 2020).

The importance of considering differences in behavioural strategies is illustrated by predatory birds that have radiated into a striking variety of foraging niches involved in obtaining prey. For example, species feeding on invertebrates (i.e., invertivores) make use of different foraging strategies, with some species picking invertebrates from the ground or other hard surfaces, while others glean from foliage, or capture prey in flight (Alerstam et al. 1974; Fitzpatrick 1980; Robinson and Holmes 1982; Remsen and Robinson 1990). Similarly, birds feeding on aquatic prey use highly contrasting techniques, ranging from surface-feeding to diving or plunging below the water surface (Ashmole 1971; Prince and Morgan 1987; Shealer 2002). Such differences are not restricted to species feeding on animal prey at high trophic levels. For example, in nectivorous and frugivorous birds, different handling techniques include taking fruits from a perch or in hovering flight (Moermond and Denslow 1985). This diversity of foraging strategies has important implications for the structure and function of ecological communities. Species using different behaviours to exploit the same resources may exhibit distinct morphologies yet perform similar ecological roles (Luck et al. 2013). Conversely, contrasting foraging behaviours can drive differences in ecosystem processes like predation rates, highlighting the ecological importance of behavioural variation.

These hidden niche axes, involving not only *what* resources are consumed but *how* they are acquired, provide a more nuanced and comprehensive view of species' ecological functions. A healthy ecosystem requires a diversity of ecological roles to be filled, which can include a range of different behavioural foraging manoeuvres within the same substrate. In the case of predator-prey interactions, top-down control of prey may be disrupted if the functional diversity of predators declines within foraging strategies, since different behaviours often target distinct prey types. For instance, insectivores that capture prey by hover tend to consume flying insects such as dipterans and hymenopterans, whereas arboreal gleaners typically consume well-concealed or flightless prey, including larval lepidoptera (Robinson and Holmes 1982). These behavioural distinctions have important implications for community structure, as foraging strategies differ in resource-use efficiency and their contribution to ecosystem flow. Finally, incorporating the behavioural axes within

dietary niches can also shed new light on the response of populations to environmental change, given that some dietary specialists are behavioural generalists, while some dietary generalists are behavioural specialists (Tobias and Pigot 2019).

Pioneering studies from the 1970s to 1990s laid the foundations for incorporating the foraging dimension of birds into community ecology (Ashmole 1971; Fitzpatrick 1980; Robinson and Holmes 1982; Prince and Morgan 1987; Remsen and Robinson 1990). This early work was particularly important in developing classification systems for how the vast diversity of avian behaviours could be organised, as well a consistent terminology for how different components of foraging behaviour (e.g., search versus attack behaviours) could be described. This work mainly focused on individual clades (e.g., orders or families), habitats or locations and was often accompanied by incredibly fine-grained and detailed quantification of foraging behaviour based on extensive observations by experts in the field. For example, Remsen and Robinson's (1990) seminal classification system recognised 18 different manoeuvres that insectivorous birds could perform while perching on branches and foliage. However, scaling up such schemes remained a major challenge, resulting in multiple different categories for different clades, habitats and realms.

Despite these constraints on data availability, recent work on restricted samples of bird species has shown that information on this finer-scale behavioural aspect of species foraging niches can reveal new insights. For instance, previous studies indicate that quantification of avian foraging strategies reveals strong links with species-level variation in morphological traits (i.e., form-function relationships) that are obscured when species are simply lumped within coarse dietary categories (Felice et al. 2019; Sayol et al. 2025). In addition, finer ecological classifications can help to disentangle the underlying mechanisms shaping the assembly of species communities (Pigot et al. 2016), or to uncover different scaling laws associated with the diversity of trophic niches (Pawar et al. 2012). Some macroecological studies integrate foraging strategies into broad-scale models as an independent axis of dietary niches (Pellissier et al. 2018; Harmáčková et al. 2019). However, the different behaviours used by animal species to access food resources are perhaps better viewed within a hierarchical structure, as a finer-scale division of broader dietary groups (Pigot et al. 2016, 2020; Felice et al. 2019).

Here we present AVONICHE, a comprehensive species-level dataset of trophic niches for all extant bird species, combining general dietary information and behavioural foraging strategies. Our definition of niche extends beyond a purely resource-focused interpretation and includes a major behavioural axis of the broader ecological niche—complementing physiological tolerances and resource-use patterns (Schoener 2009; Tobias and Pigot 2019). Birds offer a unique opportunity for scaling up knowledge of trophic complexity in this way because they are widely studied and relatively well-known, with rich global datasets describing their geographic distribution, ecology, morphology and evolutionary relationships (Jetz et al. 2012; Wilman et al. 2014; Tobias et al. 2020, 2022), coupled with large collections of images for almost all species available online (Billerman et al. 2025). AVONICHE is designed in a hierarchical format, with a classification of distinct foraging behaviours overlaid

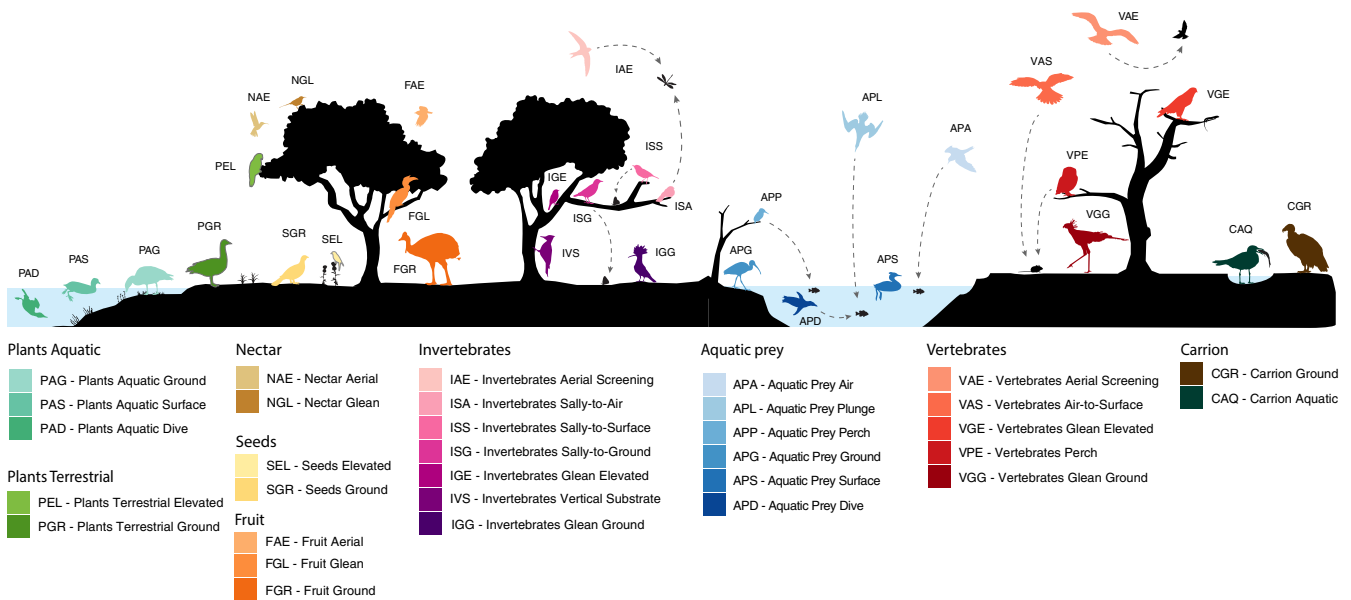


FIGURE 1 | Structure of the AVONICHE dataset partitioning the ecological role of all bird species into 32 foraging niches. The higher-level structure of the dataset is based on nine broad dietary categories, shown with different chromatic scales. Each of these primary diet categories is subdivided into different foraging strategies, resulting in 32 foraging niches. Silhouettes depict archetypal species belonging to each of the niches. Definitions for each category can be found in Table 1.

onto a set of nine dietary types, creating a matrix of 32 niche categories (Figure 1).

2 | Materials and Methods

2.1 | Rationale and Data Acquisition

As the initial framework for our dataset, we used the dietary niche categories and scores published in EltonTraits (Wilman et al. 2014), including extensive updates and re-organisation implemented by subsequent studies (Pigot et al. 2016, 2020; Tobias and Pigot 2019; Tobias et al. 2022). EltonTraits provides scores of the % contribution to a species diet of different food types in 10% intervals. This scoring is based on the largely qualitative descriptions of diets provided for each species in The Handbook of the Birds of the World (HBW) series (Del Hoyo et al. 1992). We found that in some cases, these descriptions can overemphasise rarely used food items that are highlighted precisely because of their novelty. To avoid overinflating rarely used food items, we reviewed species scores based on the text describing typical diets for each family in HBW as well as consulting numerous other sources on avian ecology (See details below). Our dietary categories also differ from EltonTraits in that we subdivided some animal and plant-based resource types into separate aquatic and terrestrial categories. This helps us to avoid highly heterogeneous categories such as invertivores, which in EltonTraits spans a wide variety of species from insectivorous warblers to squid-eating albatrosses. Another difference from EltonTraits is that we lump together fish (Diet.Vfish) and aquatic invertebrates (part of Diet.Inv) into a single category (Ap; Aquatic prey) because there is strong functional overlap between predators of fish and invertebrates such as molluscs and crustacea, with many aquatic birds targeting a combination of these food sources depending on their availability. For similar reasons, we

also pool together predators consuming vertebrate endotherms (Diet.Vend) and ectotherms (Diet.Vect) into a single category (Ve; Vertebrates).

After rescaling in this way, our schema contains nine different dietary niches: five targeted by primary consumers (aquatic plant matter, terrestrial plant matter, nectar, seeds, fruit) and four targeted by secondary consumers, tertiary consumers and scavengers (terrestrial invertebrates, terrestrial vertebrates, aquatic prey, carrion). Terrestrial plant matter includes roots, stems, leaves and buds, but not exudates or morphological features directly associated with plant reproduction; these are separated into nectar/sap, seeds and fruit. Aquatic prey includes both vertebrates and invertebrates. Carrion includes any dead animal matter across terrestrial and aquatic systems. We compared the diet scores between the two datasets, using the most equivalent diets as follows: (EltonTraits = Avoniche): PlantO = Pa + Pt; Nectar = Ne; Seed = Se; Fruit = Fr; Inv = In; Vfish = Ap; Vect + Vend = Vt; Scav = Ca. Between the two datasets, 18.4% of species ($n = 1842$) changed their primary diet (i.e., the category constituting $\geq 60\%$, See Figure S1), and 29.5% of species ($n = 2849$) had a change in the percentage contribution of at least one of the diet categories (Figure S2).

2.2 | Foraging Strategies

To provide finer-scale information beyond species dietary niches, we included subcategories for each diet based on foraging strategies, thus creating a total of 32 foraging niches representing combinations of diet and foraging behaviour (Figure 1). For terrestrial environments, these categories were defined with reference to different search and attack strategies as well as the substrates from which the food is obtained. For example, species feeding on invertebrates can forage by gleaning insects from

TABLE 1 | Codes and definitions of all 32 foraging niches within the 9 main dietary types.

Code	Description of 32 foraging niches within each of the 9 broader diet types
Plants aquatic	species obtaining food resources from plant materials in aquatic systems, including algae and aquatic plant leaves.
PAG	Plants Aquatic Ground—species foraging on aquatic vegetation (including seeds) either below or above the water surface (algae, pondweed, waterside vegetation). The species collects vegetation while under water, sitting on the water surface or wading.
PAS	Plants Aquatic Surface—species foraging on aquatic vegetation (including seeds) on/under water whilst swimming on the water surface. The species may dip under the water but, in contrast to PAD, contact with the surface is maintained.
PAD	Plants Aquatic Dive—species foraging on aquatic vegetation (including seeds) under water by diving from the surface.
Plants terrestrial	species obtaining food resources from other plant materials in non-aquatic systems, including leaves, buds, whole flowers, etc.
PEL	Plants Elevated—species foraging on leaves, buds, blossom or other vegetation (except fruit, seeds and nectar). The food is taken from above ground, often perching on branches or other stems. Generally, a small part of diet, except for hoatzin, plant cutters.
PGR	Plants Ground—species foraging on grass, leaves, buds, blossom or other vegetation (not fruit or seeds) taken while the species is on the ground (e.g., geese). The vegetation may itself be off the ground.
Nectar	species obtaining food resources from nectar.
NAE	Nectar Aerial—species feeding on nectar or other plant exudates (e.g., sap) while in flight (e.g., hummingbirds).
NGL	Nectar Glean—species feeding on nectar or other plant exudates (e.g., sap) while perched, including nectar predators that pierce corollas (e.g., sunbirds, flowerpiercers). Species feeding on honey (e.g., honeyguides) included under IVS.
Seeds	Species obtaining food resources from seeds or nuts.
SEL	Seeds Elevated—species foraging on seeds, grains and nuts taken from vegetation (e.g., trees, grass stems) while perched (e.g., seedeaters, finches).
SGR	Seeds Ground—species foraging on fallen seeds, grains and nuts collected from the ground (e.g., partridges, pheasants, finches).

(Continues)

TABLE 1 | (Continued)

Code	Description of 32 foraging niches within each of the 9 broader diet types
Fruit —Species obtaining food resources from fruit.	
FAE	Fruit Aerial—species foraging on fruits in flight, including those that hover to pluck fruit from bushes and trees (e.g., oilbird, some manakins).
FGL	Fruit Glean—species foraging on fruits while perched (not in flight) above ground and plucking fruits from vegetation (e.g., toucans, hornbills).
FGR	Fruit Ground—species foraging on fruits lying on the ground (e.g., trumpeters).
Invertebrates —Species obtaining food resources from invertebrates in terrestrial systems, including insects, worms, arachnids, etc.	
IAE	Invertebrates Aerial Screening—species capturing flying invertebrates on the wing (e.g., swallows, swifts). Often described as ‘screening’ or ‘hawking’. In contrast to ISA, characterised by continuous and extended flight with multiple items captured before landing.
ISA	Invertebrates Sally-to-Air—species capturing flying invertebrates in mid-air, with the attack starting from a perch (i.e., branch, rock, fence post, telegraph wire, etc.) and then returning to a perch (e.g., jacamars, kingbirds, etc.). ‘Hawking’ will sometimes refer to this category, but the key distinguishing feature is that only a single prey item is captured before returning to a perch.
ISS	Invertebrates Sally-to-Surface—species capturing invertebrates (including arachnids, worms, molluscs, etc.) attached to the substrate (e.g., leaves, twigs, branches, rock faces, etc.) following an aerial attack manoeuvre (e.g., flight, pounce, jump, hover).
ISG	Invertebrates Sally-to-Ground—species capturing invertebrates on the ground following an aerial attack manoeuvre (e.g., flying, gliding, dropping or pouncing) (e.g., chats, shrikes, kiskadee, etc.). The aerial manoeuvre may be followed by brief hopping toward prey (e.g., terns).

(Continues)

Code	Description of 32 foraging niches within each of the 9 broader diet types
IVS	<p>Invertebrates Vertical Substrate—species capturing invertebrates attached to or concealed within large branches and trunks (e.g., woodpeckers, treecreepers, woodcreepers, wallcreepers, nuthatches, sittelas, nuthatches, vangas, etc., including honeyguides). This is distinguished from IGE by at least one criterion. First, the species employs specialised methods for moving over surfaces which are often, but not always vertical and too large to be gripped by the closed foot (including creeping, climbing or scaling). Second, the species extracts prey from in/under the bark using specialised methods (including hammering, probing or chiselling). Also includes species capturing insects from rock and cliff-faces (though not just on boulders), habitually perching on or clinging to large mammals and species that feed on honey and beeswax.</p>
IGE	<p>Invertebrates Glean Elevated—species capturing invertebrates attached to the substrate (e.g., leaves, twigs, branches, grass, bamboo, stems, hanging dead-leaves [not dead leaves on the ground] etc.). No aerial attack manoeuvre is involved.</p>
IGG	<p>Invertebrates Glean Ground—species capturing invertebrates on the ground. In contrast to ISG, the search and attack manoeuvres take place on the ground (e.g., thrushes). This includes species standing on the ground and gleaning insects from vegetation (e.g., tinamous or larks) but excludes species that jump or sally upwards to capture prey from vegetation (ISS) or the air (ISA). The ground is dry and thus excludes aquatic habitats (e.g., beaches, estuaries, wetlands, marshes [APG]).</p>
Aquatic prey	<p>—species obtaining food resources from vertebrate and invertebrate animals in aquatic systems, including fish, crustacea, molluscs, etc.</p>
APA	<p>Aquatic Prey Air—species capturing invertebrates or vertebrates on/under water during continuous flight (including dipping, hovering, pattering, snatching). In contrast to APP, prey item is identified while flying (not from perch). The predator's body may partially submerge but does not plunge beneath the surface (see APL). Includes kleptoparasitic species capturing fish by chasing other piscivores and forcing them to regurgitate (e.g., skuas, frigatebirds).</p>
APL	<p>Aquatic Prey Plunge—species capturing invertebrates or vertebrates by plunging under water following continuous flight. The predators body submerges entirely beneath the surface, with the prey captured either by the momentum of the plunge or following propelled swimming.</p>

(Continues)

TABLE 1 | (Continued)

Code	Description of 32 foraging niches within each of the 9 broader diet types
APP	Aquatic Prey Perch—species capturing invertebrates or vertebrates on/under water following a direct attack flight from a perch (e.g., kingfisher).
APG	Aquatic Prey Ground—species capturing invertebrates or vertebrates while standing in aquatic habitats (including beaches, estuaries, wetlands and marshes) (e.g., storks, herons, shorebirds). Prey may be captured on the ground or on/under water. This category includes species capturing aquatic prey (e.g., fish) or terrestrial prey in aquatic habitats (e.g., grasshopper).
APS	Aquatic Prey Surface—species capturing invertebrates or vertebrates on/under water whilst swimming on the water surface. In contrast to APP or APA there is no direct attack flight. The species may dip under the water but, in contrast to APD, contact with the surface is maintained.
APD	Aquatic Prey Dive—species capturing invertebrates or vertebrates under water by diving from the surface (not the air, see APL and APP).
Vertebrates	—species obtaining food resources from vertebrate animals in terrestrial systems, including mammals, birds, reptiles etc.
VAE	Vertebrates Aerial Screening—species captures Vertebrates prey during flight. Both predator and prey are in flight (e.g., bat hawk, some falcons).
VAS	Vertebrates Air-to-Surface—species captures prey on branches or the ground by diving from the air, usually after circling or hovering in flight. Includes quartering flight (e.g., kestrels, kites, some owls).
VSS	Vertebrates Perch—species captures prey on branches or the ground by diving from a perch (e.g., many owls, eagles).
VGE	Vertebrates Glean Elevated—species capturing prey from foliage, branches, epiphytes, cavities, bark or other arboreal substrate while perched on the substrate. There is no flight attack involved. This includes predating bird chicks from arboreal nests and drinking blood while perched on animals.
VGG	Vertebrates Glean Ground—species capturing prey on the ground, including eggs in ground nests, while they themselves are also walking or running on the ground (e.g., secretary bird, seriemas, ground hornbills).
Carrion	—species obtaining food resources from carrion, offal or refuse.
CAA	Carrion Aquatic—species eating carrion (dead animal remains) from water or adjacent to marine shorelines and freshwater wetlands (e.g., sheathbills, some storks)
CAG	Carrion Ground—species eating carrion (dead animal remains) on the ground (e.g., vultures).

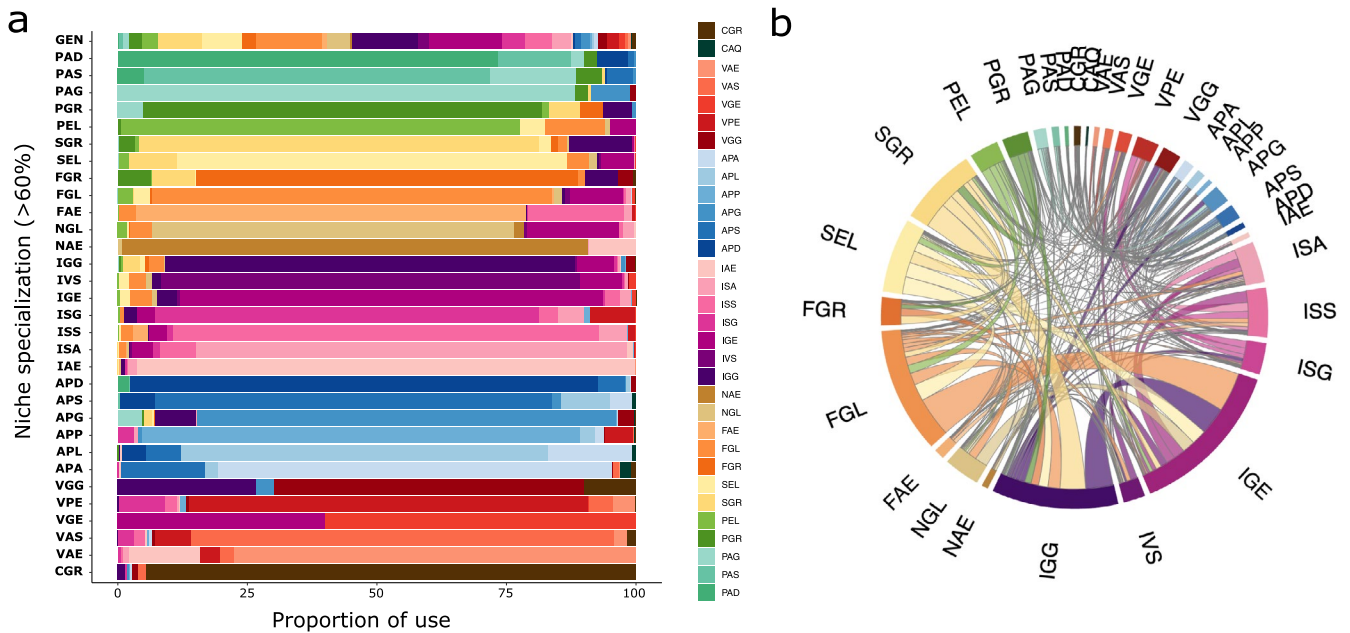


FIGURE 2 | Combinations of foraging niches occupied by foraging specialists and generalists. (a) Diversity of foraging niches occupied within major foraging specialisations. Coloured bars represent the average proportional use of different foraging niches for the species within each foraging specialisation (See acronyms in Figure 1), as well as for generalists. Species are classified as foraging specialists if they obtain more than 60% of their food from a single foraging niche (i.e., diet by foraging strategy combination). Species occupying multiple foraging niches, each contributing < 60% of their food, are classified as generalists (indicated as ‘GEN’ in the top row). (b) Co-occupancy of pairs of foraging niches across bird species. The width of the connections between pairs of foraging niches indicates the number of species occupying both of those foraging niches. Only foraging niches that constitute > 10% of a species overall diet are considered when calculating the degree of niche co-occupancy.

foliage and branches while perched, or by ‘sallying’, an attack manoeuvre that involves flight from a perch. Species that employ sallying can use this manoeuvre in combination with different substrates, capturing prey from the ground or the air, each of which represents a distinct foraging strategy. Other species can feed from the air but in continuous flight, while others feed while walking on the ground or climbing bark or other vertical surfaces. For invertivores, which represent the bulk of avian species richness, we recognised seven foraging subcategories. We subdivided other dietary niches into foraging subcategories in similar ways, resulting in 2–7 foraging niches per diet reflecting the degree of behavioural variation exhibited and the level of information available. The resulting 32 foraging niches are illustrated in Figure 1, with further definitions and examples in Table 1.

We note that in addition to diet, EltonTraits provides scores on the overall use of different foraging strata, which gives some indication of the height above ground at which the species moves or forages. Our foraging niche categories were scored independently of EltonTraits foraging strata data and resolve some key ambiguities. In particular, our 32 foraging niche categories represent combinations of diet and foraging behaviour, recognising that species may utilise different behaviours and substrates for different resources. Our schema also recognises that a single substrate can be utilised in multiple ways. For example, invertivores can attack prey on the ground either while walking (i.e., Invertebrates Glean Ground) or by sallying from an elevated perch (i.e., Invertebrates Sally to Ground).

AVONICHE data have been used previously to characterise foraging niche estimates for birds at a global scale (Tobias and

Pigot 2019; Pigot et al. 2020). The names and definitions of categories have been updated for clarity but are roughly equivalent. However, the data have only been previously published in the form of the primary foraging strategy utilised by each species, defined as the category with a proportional use of at least 60%. Some of the 32 strategies do not appear in previous treatments (Tobias and Pigot 2019; Pigot et al. 2020) because they do not exceed 60% usage in any bird species. The AVONICHE dataset contains all the underlying data on the proportional use of all 32 diet and foraging niche categories for each species, providing access to more detailed and quantitative information about foraging strategies. It can be used to create foraging niche categories by setting any threshold from 10% to 100%, allowing exploration of both generalist and specialist categories, as well as the relative composition of different strategies adopted by each species (Figure 2). To help clarify the link with previous datasets and to facilitate comparisons across studies, we have included the primary diet category using a 60% threshold, along with a table showing how the names of AVONICHE categories map onto those used by Pigot et al. (2020).

2.3 | Data Sources

Quantitative data on the proportional use of different resources or foraging strategies are generally lacking, so we follow previous studies (Wilman et al. 2014) in using expert descriptions in the literature and translating them into scores for the proportional use of each niche category. While this scoring should not be interpreted as a precise estimate, it represents the best available summary of current knowledge at this scale, capturing major differences in diets and behaviours for use in broad-scale analyses.

A major source of information was The Handbook of the Birds of the World (HBW) series (Del Hoyo et al. 1992), comprising species and family accounts for all extant bird species. Where clarifications were necessary, we checked updated texts in the online version of Birds of the World (BOW) (Billerman et al. 2025). We also consulted numerous additional books and papers that described the foraging ecology of particular clades or habitats and in some cases provided quantitative data on the use of different foraging behaviours (included in the [Supporting Information](#)). We also scanned for relevant photographs and videos to better assess the precise foraging techniques used by poorly known species, making extensive use of online archives at Macaulay Library (<https://www.macaulaylibrary.org/>) and BOW (Billerman et al. 2025).

In cases where no direct dietary or foraging information was available for the target species, we based our scoring on the available information for the most relevant species or group of species. To maximise relevance, we generally selected the closest phylogenetic relative, either a sister species or congener. In some cases, we used morphological and behavioural information to ensure that we were selecting a species with the closest matching dietary and foraging niches, based on the assumption that species with very similar morphologies and behaviours are likely to use similar foraging strategies. Given that dietary niches and foraging strategies have strong phylogenetic signal in birds (Tobias et al. 2022), inferring foraging niches from closely related species in a small minority of cases is likely to introduce only small amounts of error.

2.4 | Translating Textual Descriptions to Proportional Scores

We used a standardised protocol to translate qualitative descriptions into semi-quantitative scores, following established methods (Wilman et al. 2014). First, for each dietary niche (i.e., the nine broad food categories) we scored the % use of each foraging behaviour. Second, we calculated the % of total resources obtained through each of the 32 niches by taking the product of the percentage of the species' diet made up of a given resource type and the proportion of that resource type obtained through a particular foraging behaviour. To translate descriptions in HBW (Del Hoyo et al. 1992) and BOW (Billerman et al. 2025) into quantitative contributions of each dietary niche or foraging behaviour, we used general terms describing relative frequency as a starting point when multiple foraging behaviours were mentioned (e.g., 'mostly' > 6, 'sometimes' = 2, 'occasionally' = 1). Categories stated earlier in the description were given a higher weight than those listed at the end if there was no indication of the relative use of different behaviours. Species scores were adjusted based on the remaining content of the species account, family-level summaries and extensive additional literature searches. Species scores across the 32 niche categories sum to 100%, but we also report the aggregated % for each of the 9 dietary niches.

To illustrate the scoring approach, the diet of the Great Hornbill (*Buceros bicornis*) is described in BOW (Billerman et al. 2025) as: 'Mainly fruit; also, insects and other arthropods, besides various small reptiles, birds and mammals'. On this basis, we score the diet out of 10 as Fruit (6), Invertebrates (2) and

Vertebrates (2). For the foraging strategy, BOW (Billerman et al. 2025) describes the species as feeding 'Mainly in canopy, but will descend to ground for fallen fruit', leading to classification as predominantly Fruit Glean (FGL) (9), with a small proportion of Fruit Ground (FGR) (1). The rest of the diet, composed of animal prey, is assumed to be consumed in the canopy (i.e., Invertebrate Glean Elevated [IGE] and Vertebrate Glean Elevated [VGE] strategies). When we multiply diets by strategies, the resulting scores for this species are FGL (54%), FGR (6%), IGE (20%) and VGE (20%).

To ensure consistency in scoring, all observers were trained and provided with detailed guidelines to standardise the evaluation criteria. When there was conflict between sources, or ambiguity in textual descriptions, cases were flagged and reviewed to maintain accuracy and consistency in interpretation.

2.5 | Taxonomic Matching

We present our data according to four different taxonomic treatments, totalling 9993 species in the BirdTree phylogeny (Jetz et al. 2012), 10,661 species under eBird taxonomy (Clements et al. 2021), 10,999 species under BirdLife International (2020) taxonomy and 10,981 in the unified Global Checklist of the World's Birds (AviList Core Team 2025). To facilitate incorporation into previous phylogenetic analyses, the initial data collection and scoring followed BirdTree species limits. For newly described species in BirdLife, eBird and AviList taxonomies, we scored their niche data directly from published descriptions. For the remaining taxonomic mismatches, we used the crosswalk published with the AVONET dataset (Tobias et al. 2022) to convert scores from BirdTree to BirdLife and eBird taxonomic treatments. For the AviList taxonomy, we combined these crosswalks with manual verification to ensure inclusion of all species listed in AviList.

The simplest taxonomic transitions were one-to-one matches between datasets. This direct matching applied to most species (e.g., 81% of BirdTree to BirdLife transitions) and involved direct transfer of identical niche data. For transitions representing splits (one-to-many matches), we extrapolated data from the nominal parent species to all daughter species. For transitions representing lumps (many-to-one matches), we copied the data from the nominate subspecies because these are the oldest (first-named) and often the most familiar subspecies in each taxon, and therefore likely to have the highest quality data. Nonetheless, when ecological information was available, we manually checked split or lumped species to score them directly from published descriptions (Billerman et al. 2025). In the case of splits, we assessed whether different daughter species have contrasting foraging niches, adjusting data as necessary. In the case of lumped species, we either (a) retained data for the nominate form when it seemed to reflect niche traits across the expanded taxon, (b) selected data from a different parent taxon that provided better information, or (c) aggregated data from the complete set of parent species if they occupy different trophic niches. Niche scores for all taxonomic treatments, and information on whether data are directly scored or inferred, are presented in the AVONICHE datasets. For each dataset, we indicate whether species traits were scored directly from literature (0), were fully

or partially obtained from a close relative (1), or were inferred from a taxonomic split or merger across taxonomic crosswalks (2). Overall, the proportion of data points imputed from close relatives was 4%–4.5% across datasets, whereas between 12.6% and 17% of species were scored from splits or lumps, depending on taxonomy.

3 | Results

Viewing avian niches through the lens of broad dietary niches, there is a high degree of redundancy. For example, most birds consume at least some invertebrates in their diet ($n = 8796$, 83%) while around half of all bird species could be considered as specialist invertivores, meaning that this resource constitutes at least 60% of their diet ($n = 5161$, 48%). Previous analyses tend to treat this component of avian diversity as a homogenous ecological niche. However, disaggregating this group using our finer-scale information on foraging behaviour and identifying species specialised (i.e., at least 60%) on a single foraging niche (i.e., diet \times foraging strategy combination) reveals a more complex picture with much lower niche redundancy. We found that the most speciose niche was the Invertivore Gleaning Elevated (IGE) niche, accounting for 16% of bird species ($n = 1654$) including orioles (family Oriolidae), warblers (Phylloscopidae) and vireos (Vireonidae). Other invertivorous birds are partitioned among six other specialised niches: Invertebrates Glean Ground (IGG, $n = 901$, 9%), Invertebrates Sally-to-Air (ISA, $n = 302$, 3%), Invertebrates Vertical Substrate (IVS, $n = 300$, 3%), Invertebrates Aerial Screening (IAE, $n = 289$, 3%), Invertebrates Sally-to-Surface (ISS, $n = 283$, 3%) and Invertebrates Sally-to-Ground (ISG, $n = 180$, 2%). Viewed across avian diversity as a whole, the number of species that can be considered specialists (i.e., using a single niche $\geq 60\%$) is 83% ($n = 8806$ species) when considering the 9 broad dietary categories, but drops to 65% ($n = 6889$ species) when using the 32 foraging niches. The level of redundancy drops further when we consider extreme levels of specialisation. There are 3826 (38%) species that use a single dietary category, whereas only 1837 (18%) species use a single foraging niche. At the other end of the scale, some species (e.g., black-faced cuckoo-shrike *Coracina novaehollandiae*) utilise 12 different foraging niches. Between the two extremes, the majority of bird species ($n = 6806$, 68%) use 2–4 niches, while smaller subsets use 5–7 niches (12%) or 8–14 niches (14%). This level of behavioural plasticity and flexibility results in a complex web of trophic interactions that are overlooked by standard diet categories, and which often span multiple major food types (Figure 2).

4 | Discussion

Global datasets of trophic niche—consisting of approximate scores for the use of major resource types or classifications of a species' primary diet—have been available for over a decade (Wilman et al. 2014; Tobias et al. 2022). Given the relevance of trophic ecology to a wide range of research questions, these datasets have been widely used in evolutionary biology, community ecology, macroecology and ecosystem science (e.g., Germain et al. 2023; Barber et al. 2024). However, such broad dietary classifications mask the enormous variation in species foraging niches, and in particular the diverse foraging behaviours used

to obtain these resources. AVONICHE attempts to illuminate this hidden diversity by classifying each dietary niche into 2–7 finer-scale categories, offering a more comprehensive characterisation of avian foraging niches.

By partitioning species with similar food preferences into distinct foraging strategies, AVONICHE data adds a crucial behavioural dimension absent from broad dietary categories. Integrating this dimension into niche classifications shows that gleaning from elevated substrates is by far the most species-rich foraging strategy across both invertivores (IGE) and frugivores (FGL). In contrast, other major dietary groups are associated with different predominant strategies: ground foraging in granivores (SGR), aerial nectar feeding in nectarivores (NAE) and attacking prey from a perch in vertivores (VPE). These differences highlight the behavioural diversity embedded within dietary groups and suggest that foraging behaviour should be incorporated into assessments of trophic niches to provide a more detailed estimate of avian resource use and specialisation. For example, AVONICHE data can be used to improve estimates of niche partitioning and complementarity within species assemblages (e.g., Sol et al. 2022).

Different behavioural foraging strategies may influence the sensitivity of species to anthropogenic pressures, with important implications for ecological processes in disturbed or modified habitats. For example, previous studies have shown that ground-feeding invertivores are more sensitive than other invertivores to tropical forest loss and fragmentation (Stratford and Stouffer 2015). In addition, a species may appear functionally redundant at a given locality when classified by their primary diet, and yet locally unique in terms of the combination of diet and foraging behaviour. Estimates of the relative use of different foraging manoeuvres used by species can offer a different perspective on ecological redundancy and complementarity at a range of spatial scales. AVONICHE contains this type of standardised data in an accessible format, providing a library of response and effect traits for quantifying and predicting impacts of environmental pressures, including climate change, land-use change and biological invasions (Hordley et al. 2021).

As with many other trait datasets generated from literature, AVONICHE may be sensitive to biases in knowledge. Trophic niches and interactions are poorly described for many species of plants and animals—part of the Eltonian shortfall proposed by Hortal et al. (2015). Given that the depth and quality of niche-related information varies widely across bird species, users should be alert to potential biases and circularity. A frequent example is that common or familiar species tend to have wider niches based on published observations, which may reflect greater niche breadth or simply more research attention leading to more comprehensive published information (Vázquez and Stevens 2004). Despite these limitations, AVONICHE represents the best available information on foraging niches and can serve as a valuable template for directing future research toward lesser-known species.

In addition to possible biases, we note that diets and foraging behaviours vary in a continuous way and that our classification system is just one way of splitting this variation into discrete units. While our classification system is similar to earlier

attempts to classify foraging behaviours for particular avian clades or habitats, it is inevitably coarser and constrained by data availability at a global scale. More detailed information exists for some species to recognise even finer scale variation in their foraging behaviour, such as the subtle differences in body posture or methods for handling prey, but incorporating this information would result in a much sparser matrix with many missing values. Our approach therefore reflects a practical compromise between granularity and coverage of data across species. AVONICHE is a comprehensive, standardised resource designed for use in global or regional comparative analyses and macroecological studies. The information can also be used at smaller scales, for example to quantify basic shifts in niche specialisation or ecological structure of assemblages distributed across local vegetation or land-use gradients. However, the data presented here are less suitable for inferring fine-scale ecological processes in local communities, where direct field observations of foraging behaviour at high resolution are more appropriate (Kohli and Jarzyna 2021).

5 | Conclusions

The trophic interactions and foraging strategies summarised in AVONICHE reveal that most bird species, including many ecological specialists, supplement their diet in a variety of alternative niches—typically within their broader dietary group but often extending across major dietary categories (Figure 2). Capturing this full spectrum of niche flexibility is essential for understanding trophic interaction networks, ecological plasticity and the functional resilience of species assemblages. By releasing these trait data for unrestricted use in line with Open Science principles (Gallagher et al. 2020), we hope to stimulate further research in macroecology, macroevolution and conservation science (Tobias and Pigot 2019; Tobias et al. 2025). To these ends, AVONICHE is harmonised across major taxonomic frameworks, permitting integration with AVONET (Tobias et al. 2022), BOW/eBird (Sullivan et al. 2014; Billerman et al. 2025), the unified global species checklist (AviList Core Team 2025) and current global phylogenies (McTavish et al. 2024; Claramunt et al. 2025). Together, these resources offer a framework for testing key hypotheses about the structure and function of biodiversity (Pigot et al. 2020; Sayol et al. 2025). In addition, given the importance of behavioural specialisation and plasticity in predicting species responses to environmental change (Tobias et al. 2025), future studies should explore the use of AVONICHE data in metrics of ecosystem integrity and resilience.

Author Contributions

J.A.T. and A.L.P. conceived and designed the study. A.L.P., C.S., M.N.-C. and J.A.T. compiled the original dataset. F.S. prepared the different taxonomic versions of the dataset, conducted the analyses and created the visualisations. F.S. and J.A.T. wrote the manuscript. All authors contributed to the critical revision of the manuscript and approved the final version.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data is available on Dryad at <https://doi.org/10.5061/dryad.1zcrjdg56>.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** geb70197-sup-0001-DataS1.docx.