



Taxonomy, habitat and conservation status explain the diet composition of insectivorous birds in Europe

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ABSTRACT

Populations of European birds and insects are declining, with consequences for trophic interactions. Insectivorous birds are particularly vulnerable to losses of arthropods, yet the factors shaping their diet composition remain insufficiently understood. We conducted a quantitative review of the arthropod diets of 94 European insectivorous bird species and assessed how diet richness and composition relate to taxonomy, developmental stage, climate, conservation status, habitat, migration status, sampling intensity, and methodological approach. Taxonomy, habitat and conservation status (both population trend over time and current status) were the primary predictors of diet richness and composition. Species of population concern in Europe relied more on Coleoptera and Orthoptera prey, while species with declining population trends and species in agricultural, artificial and semi-natural habitats showed strong dependence on Coleoptera prey. Species in forests and of global population concern had a higher percentage of Arachnida prey, while birds in inland water habitats relied on Diptera prey. Anthropogenic activities such as the use of insecticides and changes in land use in agricultural and forest habitats negatively impact the abundance and diversity of arthropods, including Coleoptera and Arachnida. These declines will cascade up the food chain, ultimately diminishing both common and threatened bird species by limiting their prey. Species of global conservation concern may be particularly at risk, as they exhibit the lowest prey taxonomic richness. It is therefore crucial that future legislation and policy interventions consider these indirect impacts on bird diets, as these vulnerable species are at high risk of further losses in arthropod prey.

1. Introduction

Several European bird species are declining (Inger et al., 2015; Burns et al., 2021), which is of concern for both ethical and functional reasons (Bibby, 2002; Gaston et al., 2018). At the same time, some insect groups are also declining in Europe (Cardoso et al., 2020), with up- and downstream consequences for trophic interactions. Because the majority of bird species are predominantly insectivorous and 75 % of all species at least occasionally consume arthropods (Whelan et al., 2015), declines in insectivorous birds may be a response to the loss of insects and their habitats (Møller, 2019; Newton, 2004; Bowler et al., 2019; Tallamy and

Shriver, 2021). Yet, the effects of arthropod declines on bird communities and species are not fully characterized.

Food resources and diet composition constitute a crucial link between the fitness of birds and their environment (Barnagaud et al., 2019; Grames et al., 2023), and studies on bird diets have been an important part of understanding their ecology, population dynamics, distribution and conservation (Newton, 1998; Hoenig et al., 2022; Jiménez-Albarral et al., 2025). Describing the preferences of insectivorous birds for different arthropod prey groups and how trophic interactions are affected by environmental change is key to better understanding both threats to bird populations and their future functional roles in food webs

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(Barnagaud et al., 2019; Hoenig et al., 2022). Food shortage has fundamental effects on individual fitness with consequences for population size and persistence (Newton, 1998; Grames et al., 2023). Thus, food limitation, partly resulting from insecticide use, has been proposed as a contributing factor to the decline of insectivorous birds in agricultural and forest ecosystems (Hallmann et al., 2014). In agriculture, this is also driven by increasing land use intensity and landscape simplification (Robinson and Sutherland, 2002; Newton, 2004; Reif and Hanzelka, 2020; Grames et al., 2023). In forests, it is driven by habitat loss, fragmentation and increasing pressure from invasive species (Razeng and Watson, 2015; Braby et al., 2023). However, we lack a comprehensive understanding of the importance of different arthropod taxa in the diet of insectivorous birds.

Insect declines do not appear to be random across insect orders, which have different ecological requirements and life histories (Wagner, 2020). The diet composition of birds that feed on insects and other arthropods may serve as an under-explored indicator of risks associated with global change by providing insight into the mechanisms driving population changes. Previous analyses of the diets of insectivorous bird species have focused on the energetic content of insect prey (Bell, 1990), the total biomass of prey consumed (Brooke 2004; Nyffeler et al., 2018), or their impact on tropical arthropod populations (Bael et al., 2008). The taxonomic composition of the diet of insectivorous species is an important additional aspect that can help to understand how environmental change affects trophic relationships (Hoenig et al., 2022). For example, Holland et al. (2006) showed for 22 farmland bird species in the UK that prey was dominated by only six insect orders and that diets were less diverse in the non-breeding season. Such studies can help to understand the manifold threats to insectivorous birds, but also their contribution to the provision of ecosystem functions and services (Sekercioglu, 2006; Whelan et al., 2008).

The aim of this quantitative review is to describe dietary variation among arthropod-feeding bird species across taxonomic groups with different conservation, development and migration status and in different habitats varying in climatic conditions (Table 1) – in order to understand the dietary needs of bird species of conservation concern at the European level.

2. Methods

2.1. Literature search & data processing

We used studies from a database originally obtained from a comprehensive literature search in Web of Science (Clarivate Analytics, US) using the search string: “TI=(diet* OR food OR predat* OR feed*) AND TS=((bird* OR avia*) AND (insect* OR arthro*))” in March 2017. The database contains 8518 articles published in English, excluding duplicates. We read the title and abstract and reviewed the full text of each identified article to determine whether the article met our inclusion criteria. We used the following inclusion criteria to select studies providing compositional data for arthropod diets of bird species relevant to our quantitative review: (i) studies investigating (at least in part) arthropod food consumption by individual bird species, (ii) studies with study sites in Europe (mainland, British Isles and Iceland), (iii) studies of wild birds and with known bird species, (iv) studies of birds studied/captured in the wild or in a setting where individuals could fly/walk in and out of the wild, (v) studies including at least in part arthropod food in the form in which it occurs in nature (dead or alive), (vi) studies that include empirical quantitative records of the arthropod prey items eaten or collected by a bird species per arthropod taxon and the total number of arthropod prey items recorded in the respective bird diet, and (vii) studies that include at least 24 arthropod prey items recorded per bird species (excluding studies that focus on and intentionally record only diet items from a single arthropod prey taxon). The inclusion threshold of 24 recorded prey items was based on the total number of arthropod taxa recorded in the diets of birds across the included studies (24 taxa in

Table 1
Predictor groups and predictor variables used in all three distance-based linear models (DistLM) for the a) rarefied taxonomic richness of prey in all birds, b) taxonomic composition of the diet in all birds and c) taxonomic composition of the diet in nestlings only.

Predictor group	Explanation	Variables in each predictor group with variable type
Bird development stage	Diet exclusively for nestlings or not	1 variable (Categorical: binary coded): yes or no
Climate	Long-term climatic conditions in sampling region	4 variables (continuous): 1.) annual mean temperature, 2.) temperature seasonality, 3.) annual precipitation & 4.) precipitation seasonality
Conservation status	Bird population trend and population status	8 variables (Categorical: binary coded): population trend: 1.) increasing, 2.) stable, 3.) decreasing or 4.) uncertain population status: 5.) secure (S0), 6.) global concern and significant populations in Europe (S1), 7.) concern in Europe and population concentrated in Europe (S2) & 8.) concern in Europe and population not concentrated in Europe (S3)
Habitat	Major habitat type of study	6 variables (Categorical: binary coded): 1.) inland water, 2.) coastal & marine water, 3.) agricultural, 4.) artificial, 5.) forest & 6.) semi-natural
Migration status	Long-distance migratory bird species or not	1 variable (Categorical: binary coded): yes or no
Sampling intensity	Sum of identified arthropod prey items for each dataset	1 variable (Continuous): 62-57862 items
Sampling method	Sample method or combination of sample methods	2 variables (Categorical: binary coded): 1.) Top & 2.) bottom methods regarding the digestive system
Taxonomic identity	Order of each bird species	10 variables (Categorical: binary coded): 1.) Anseriformes, 2.) Apodiformes, 3.) Charadriiformes, 4.) Ciconiiformes, 5.) Coraciiformes, 6.) Falconiformes, 7.) Passeriformes, 8.) Pelecaniformes, 9.) Piciformes & 10.) Strigiformes

total). In theory, a bird species in a study with 24 recorded prey items could have consumed prey from all 24 arthropod taxa. The taxonomic classification of arthropods was based on Stork (2018), and taxonomy of arthropod prey groups was based on subphylum (for prey groups Crustacea, Myriapoda), class (for prey groups Arachnida, Collembola), or order level (for all insect prey groups) (see also Razeng and Watson, 2012 for a similar approach). Commonly used sampling methods included analysis of prey remains, observational studies (including videotaping), neck collars, analyses of pellets or regurgitates, digestive tract contents (e.g. stomach flushes) and faeces, and molecular methods such as DNA-based techniques.

We identified 307 studies that met the abovementioned criteria. Data, presented as relative contributions of arthropod taxa to bird diets, were entered directly into our database. Data provided as the total number of prey items in the diet per arthropod taxon were transformed to the relative contribution of each taxon to the total arthropod diet of bird species. WebPlotDigitizer version 4.1 (Marin et al., 2017) was used to extract data provided in figures only. Larval stages of arthropods were assigned to taxonomic groups according to the resolution provided in the respective study, and datasets were excluded if larval stages were not assigned to a specific taxonomic group in the original paper, e.g. “caterpillar” not assigned to Lepidoptera or Hymenoptera.

2.2. Predictor variables

In addition to the relative percentage of prey items per arthropod taxon among all arthropod prey items in the diet of each bird species dataset (dependent data), we extracted the following predictor groups from all identified studies (see also Table 1, and for further details supplementary methods): (1) “bird development status” of birds as exclusive or non-exclusive nestling diet; (2) “climate” in each study region as BIO1 = annual mean temperature, BIO4 = temperature seasonality (standard deviation * 100), BIO12 = annual precipitation, and BIO15 = precipitation seasonality (coefficient of variation) based on WorldClim version 2 (Fick and Hijmans, 2017); (3) “conservation status” as the trend of breeding populations for each bird species (stable, decreasing, increasing, uncertain/unknown/NA) and the population status (secure, global concern, concern in Europe and population concentrated in Europe and concern in Europe, but population not concentrated in Europe); (4) “habitat” from which data was collected in each study classified as inland water (marshes, pans, ponds, reed beds, rivers, wetlands), coastal and marine water (coastal waters, estuarine and deltaic areas, intertidal areas, lagoons, ocean, salt marshes), agricultural (arable crops, agricultural grasslands, orchards), artificial structures (buildings, built-up areas, infrastructure, urban parks, walls), forest (coniferous, deciduous, mixed) or semi-natural (abandoned farmland, alpine, cliffs, heathland, non-agricultural grassland, phrygana, sand pits & banks, shrub land, sub-alpine); (5) “migration status” of each species as long-distance migrant or not (Svensson et al., 2017, species factsheets provided by BirdLife International 2023); (6) “sampling intensity” as the total sum of arthropod prey items recorded; (7) “sampling method” classified as top (e.g. direct observation during feeding) or bottom (e.g. pellets), referring to the birds’ digestive system and (8) “taxonomic identity” of each bird species according to its order in Gill and Donsker (2019). Studies that did not provide sufficient detail to extract these predictors (or where predictors such as latitude and longitude could not be approximated by geographic names) were excluded. We then averaged the relative contribution of each arthropod taxon for all datasets of the same species from the same study if they were collected in the same country, with the same method, for the same development status, and in the same season. The final analysed dataset also included only those bird orders with at least three datasets (both for

analyses of diets of all birds and for analyses of exclusive nestling diets). Our final data included a total of 178 datasets from 121 studies for 94 bird species (in 10 orders) in Europe (24 countries; Fig. 1; Table S1), with data on the relative diet composition of 20 insect orders and 4 non-insect arthropod taxa (Table S2).

2.3. Data analyses

The resulting database of arthropod diets of European bird species is a multivariate matrix with 178 datasets (rows), relative dietary contributions for each of 24 taxonomic arthropod prey groups (columns), and 33 predictor variables in 8 predictor groups (Table 1). Distance-based linear models (DistLM; McArdle and Anderson, 2001) are permutational analogues of parametric multivariate multiple regression models developed to analyse community data (e.g., species or diet composition). These models fit predictors to a similarity matrix derived from a table of bird species (rows) and dietary contributions for arthropod prey taxa (columns). Using Bray-Curtis similarities, we calculated all pairwise similarities between datasets as a function of their arthropod diet, with values between 100 (identical diet in two datasets) and 0 (no diet overlap between two datasets). Information about a common absence of a prey taxon in the diet of two species was not used to characterize similarity. Distance-based linear models then partitioned the variation in similarity between pairs of species based on our predictor groups (Table 1). In DistLM, predictor variables are coded as either continuous (e.g. ‘sampling intensity’) or dummy (e.g. ‘migration status’). In DistLM, dummy coding involves converting each category of a categorical variable into a separate binary variable with binary coding (taking values of 0 or 1), representing the presence of a category by a value of 1 and its absence by a value of 0 in the regression analysis. Due to the logical connection between subsets of predictor variables, we did not use individual predictor variables in the DistLM models. Instead, we grouped the 33 predictor variables into eight predictor groups based on their relationships with one another (see Table 1). For example, the ten predictor variables providing dummy coding for the taxonomic order of bird species were grouped into the predictor group “taxonomic identity” to classify all the species in our dataset. These groups were then fitted to the similarity matrices in all DistLMs. First, the sampling method and sampling intensity were fitted in two multivariate DistLMs for the

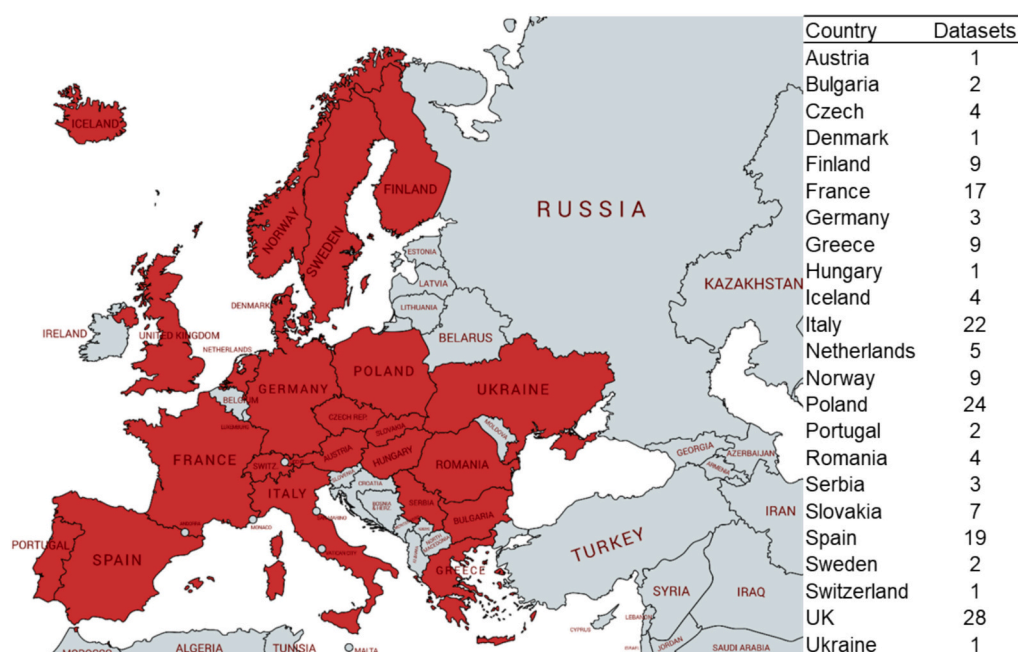


Fig. 1. Map of countries with datasets that fit the selection criteria and number of datasets per country included in the statistical analyses.

taxonomic composition of prey for 1) all birds and 2) nestlings only, in order to account for potential bias caused by differences between studies. The DistLM routine then combined all the other predictor groups into a single global model. This was done alongside the results of the marginal tests, which fitted each predictor group to the resemblance matrix independently of the others. We also used a univariate DistLM to test for relationships between the predictor groups and the rarefied taxonomic richness of prey in the diets of all birds, treating this as a single dependent variable. We used the rarefied taxonomic richness, comparing richness at the lowest number of prey items ($N = 62$) among all datasets to account for sampling bias through differences in sampling intensity. In this model, we used Euclidean distances to characterize similarities between datasets. We did not fit for sampling intensity or method first, as compared to the models for taxonomic composition, as we already accounted for intensity by rarefying taxonomic richness across datasets.

We used distance-based linear models for both univariate and multivariate models to ensure a consistent methodological framework across our analyses, particularly with regard to the interpretation of environmental gradients. This has the advantage that the coding of the predictor variables and the structure of the predictor groups are identical in the univariate and multivariate DistLMs and have the same statistical power. Distance-based linear models are very flexible and powerful statistical techniques, that are not restricted to multivariate analyses (Bakker, 2024). Three DistLMs were calculated, testing for the effects of the predictor groups on either 1) the rarefied taxonomic richness of prey in all birds (univariate) or the taxonomic composition of the diet (multivariate) in either 2) all birds or 3) only nestlings.

To illustrate model results in detail in the DistLM for community composition, distance-based redundancy analysis (dbRDA) ordination was used for the two most important predictor groups, and all predictor variables are shown in box and jitter plots of the raw data to illustrate effects of individual levels on selected prey taxa. Prey taxa for these plots were selected from vectors for all 24 prey taxa in the dbRDA ordinations based on prey taxa with a multiple correlation coefficient >0.2 . All models and ordinations were calculated using the PERMANOVA+ add-on in PRIMER-7 (Anderson, 2008). Box and jitter plots were created using the ggplot2 package in R (version 4.4.1; Wickham, 2016).

3. Results

3.1. Taxonomic richness of prey

The global model for rarefied taxonomic richness in the diets of all birds explained 40.1 % of the variation. Marginal tests revealed that the predictor groups explained decreasing percentages of variation in the following order: taxonomic identity, conservation status, habitat, migration status, developmental stage, climate, sampling method and sampling intensity (see Table 2a). Five bird orders had a relatively high rarefied taxonomic richness of prey: Apodiformes, Coraciiformes, Passeriformes, Pelecaniformes and Piciformes, while Anseriformes had a very low prey richness (Fig. 2a). Species with different population trends did not differ in rarefied taxonomic richness (Fig. 2b), but species with populations of global conservation concern (S1, Fig. 2c) had a lower rarefied taxonomic richness than species with secure populations (S0). Species that were sampled in agricultural habitats had a higher rarefied taxonomic richness than those that were sampled in artificial habitats (Fig. 2d).

3.2. Diet composition

On average across all bird datasets, three prey taxa accounted for more than 50 % of all arthropod prey items (Coleoptera, Diptera and Orthoptera; Table 3), but Orthoptera was replaced by Lepidoptera as the third most important prey taxon when considering the diets of nestlings only (Table 3). Five other prey taxa were still frequently observed in the

Table 2

Results of distance-based linear models (DistLM) for the rarefied taxonomic richness of prey in a) all birds and for the taxonomic composition of prey in b) all birds or c) only nestlings with pseudo-F values and the percentage of explained variation for each predictor group in marginal tests. Note that the subset of nestlings in DistLM c) was not tested for the predictor group development stage as only nestling data was used in this model.

Predictor group	Taxonomic richness		Taxonomic composition			
	a) All birds		b) All birds		c) Nestlings	
	Pseudo-F	Expl. var.	Pseudo-F	Expl. var.	Pseudo-F	Expl. var.
Bird development stage	9.01	4.87	11.86	6.31	NA	NA
Climate	1.53	3.41	5.56	11.39	3.24	13.78
Conservation status	2.46	7.95	4.65	14.03	2.96	18.38
Habitat	2.93	7.85	6.76	16.43	3.81	19.25
Migration status	9.65	5.20	4.79	2.65	7.99	8.68
Sampling intensity	0.07	0.04	0.60	0.34	2.07	2.41
Sampling method	2.36	2.62	8.28	8.64	2.79	6.29
Taxonomic identity	8.70	31.78	8.36	30.94	4.81	30.16

diets of all birds, with individual contributions between 5 and 10 %: Arachnida, Crustacea, Lepidoptera, Hymenoptera, and Hemiptera. Nestling diets contained the same taxa, but not always in the same order (Table 3).

The global model for the diet composition of all birds was first adjusted for sampling bias by fitting the sampling method and intensity. Together, these two variables explained 9.0 % of the variation in diet composition (Table 2b). The full model, incorporating all predictor groups, then explained 51.5 %. Marginal tests revealed that the predictor groups explained decreasing proportions of variation in the following order: taxonomic identity, habitat, conservation status, climate, bird development stage, and migration status (Table 2b). Results for taxonomic identity, habitat and conservation status are provided in the following sections, results for climate, bird development stage, migration status and sampling method are provided in the supplementary (Figs. S1–4).

3.2.1. Diet composition & taxonomic identity

The taxonomic identity (order) of the bird species alone explained 30.9 % of the variation in diet composition (Table 2b). Species from the bird orders Ciconiiformes, Falconiformes, Piciformes and Strigiformes cluster in the top right quadrant of the dbRDA, based on their high contribution of Coleoptera and Orthoptera prey. The single species of Ciconiiformes was represented with only three datasets, but the white stork *Ciconia ciconia* had relatively high contributions of Orthoptera and Coleoptera prey to its diet (Fig. 3). The arthropod diet of four species of Falconiformes was dominated by Coleoptera prey and, to a lesser extent, Orthoptera prey in the 11 datasets (Fig. 3). The datasets for Strigiformes species suggest an arthropod diet composition similar to the diet composition of Falconiformes species (Figs. 3 & 4). The three Piciformes datasets (all *Picoides tridactylus*) showed a high contribution of Coleoptera and Arachnida prey (Fig. 3).

The orders Anseriformes, Charadriiformes and Pelecaniformes are separated at the bottom of the dbRDA based on a high consumption of Crustacea (Fig. 3). The arthropod diet of Anseriformes species in our database consisted almost exclusively of Crustacea (3 bird species) or Diptera (3 species) prey (98.4 % of all arthropod prey items in the six datasets (Fig. 4). The 14 Charadriiformes species had a very heterogeneous diet, and all prey taxa had median contributions of less than 15 %

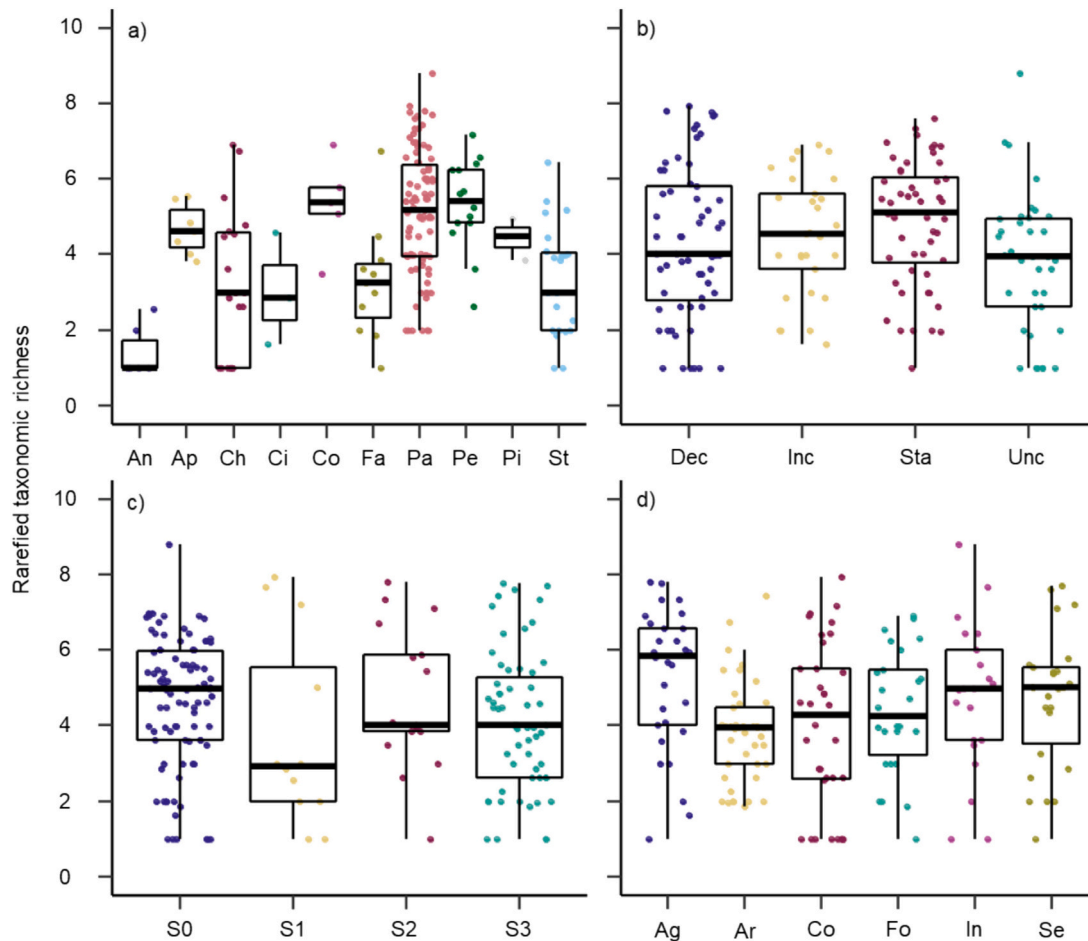


Fig. 2. Rarefied taxonomic richness of prey by a) bird order: Anseriformes (●, $N = 6$), Apodiformes (●, 8), Charadriiformes (●, 24), Ciconiiformes (●, 3), Coraciiformes (●, 7), Falconiformes (●, 11), Passeriformes (●, 94), Pelecaniformes (●, 14), Piciformes (●, 3) and Strigiformes (●, 28); b) conservation status based on population trend: Decreasing (●, $N = 60$), Increasing (●, 29), Stable (●, 52), Uncertain (●, 37); c) conservation status based on population status: secure (S0 ●, $N = 90$), global concern (S1 ●, 12), concern in Europe and population concentrated in Europe (S2, ●, 17) and concern in Europe, but population not concentrated in Europe (S3, ●, 59) and d) habitat: Agricultural (●, $N = 30$), Artificial (●, 41), Coastal & marine (●, 34), Forest (●, 26), Inland water (●, 21) and Semi-natural (●, 26). Taxonomic richness was rarefied to 62 prey items, as the lowest number in any dataset. Box plot show medians, 25th and 75th percentiles and outlier range ($1.5 \times$ interquartile range) for each bird order.

of the diet of these species, with the exception of relatively high contributions of Crustacea prey in the 19 datasets (Fig. 4). The eight species of Pelecaniformes frequently consumed Crustacea prey, but also used Coleoptera and Orthoptera prey (Fig. 4). Passeriformes cluster in the top left quadrant of the dbrDA based on a relatively high consumption of Arachnida and Lepidoptera (Figs. 3 & 4). The 49 species of Passeriformes dominate the database ($N = 87$), and the diets show relatively high contributions of Arachnida and Diptera prey (Fig. 4). Passeriformes represent the only bird order in our data with significant contributions of Lepidoptera prey (Fig. 4). The four Apodiformes species had relatively high contributions of Diptera prey, but a relatively low percentage of Coleoptera prey in the seven datasets. (Fig. 4). One of the two Coraciiformes species - the European bee-eater (*Merops apiaster*) - consumed predominantly Hymenoptera prey (68.6 %). Patterns for the diet composition of all birds (Fig. 4) and exclusive diets of nestlings did not differ (Fig. S5).

3.2.2. Diet composition & habitat

The major habitat in which the diets were sampled accounted for

16.4 % of the variation in diet composition. The species sampled in artificial, semi-natural and forest habitats, as well as in agricultural habitats (all of which are terrestrial), which cluster at the top of the dbrDA (Fig. 3) had a low consumption of Crustacea prey (Fig. 5). This is in contrast with the majority of species sampled in coastal and marine habitats in the bottom of the dbrDA (Fig. 3), which consumed high proportions of Crustacea prey (Fig. 5). Several passerine species sampled in inland water and coastal/marine habitats cluster with other passerine species sampled in terrestrial habitats in the top left quadrant of the dbrDA (Fig. 3). This pattern results from their relatively high consumption of Arachnida and Lepidoptera prey (Fig. 5). Terrestrial non-passerine species cluster in the top right quadrant of the dbrDA (Fig. 3), because of their relatively high consumption of Coleoptera and Orthoptera prey (Fig. 5). Arachnida and Lepidoptera prey were most important for species in forests, while Diptera prey were most important for species in inland water habitats (Fig. 5). Coleoptera were an important prey for species sampled in artificial habitats, and to a lesser extent for species sampled in agricultural and semi-natural terrestrial habitats (Fig. 5). Coleoptera were a more important source of prey for

Table 3

List of 24 prey taxa with the average relative percentage of arthropod prey items among the total sum of arthropod prey items (all arthropods = 100 %) and percentage of datasets with the respective arthropod prey taxa across all 178 datasets.

Taxon	Level	Percentage, % all birds	% Datasets	Percentage, % nestlings only	% Datasets
1. Coleoptera	Order	31.88	88.8	22.72	87.2
2. Diptera	Order	12.02	59.6	17.22	76.7
3. Orthoptera	Order	10.05	43.8	7.30	37.2
4. Arachnida	Class	9.45	60.7	15.19	74.4
5. Crustacea	Subphylum	8.57	22.5	4.04	18.6
6. Lepidoptera	Order	8.46	47.2	15.79	64.0
7. Hymenoptera	Order	8.19	65.7	7.52	64.0
8. Hemiptera	Order	6.78	58.4	6.07	66.3
9. Odonata	Order	1.40	23.6	2.38	22.1
10. Dermaptera	Order	1.21	19.1	0.06	11.6
11. Trichoptera	Order	0.86	8.4	0.65	9.3
12. Ephemeroptera	Order	0.45	6.2	0.14	5.8
13. Neuroptera	Order	0.15	12.4	0.16	16.3
14. Myriapoda	Subphylum	0.15	12.4	0.13	12.8
15. Collembola	Class	0.12	3.9	0.21	4.7
16. Mecoptera	Order	0.11	4.5	0.23	8.1
17. Plecoptera	Order	0.06	2.2	0.08	2.3
18. Mantodea	Order	0.04	5.6	0.00	1.2
19. Psocoptera	Order	0.03	3.4	0.07	5.8
20. Blattodea	Order	0.01	1.7	0.02	1.2
21. Embioptera	Order	0.01	1.1	0.01	2.3
22. Thysanoptera	Order	<0.01	1.1	0.01	2.3
23. Raphidioptera	Order	<0.01	0.6	<0.01	1.2
24. Thysanura	Order	<0.01	0.6	<0.01	1.2

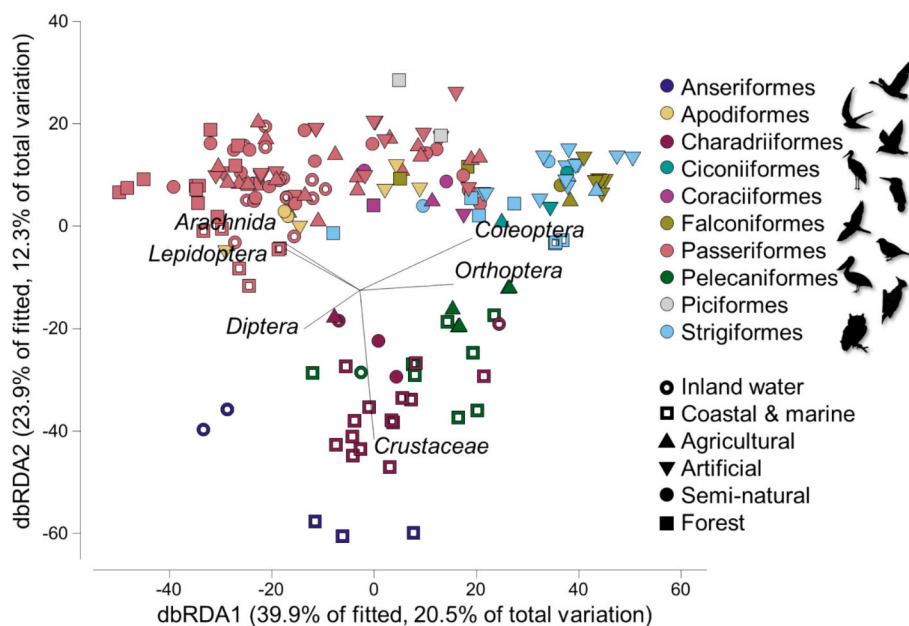


Fig. 3. Distance-based redundancy analysis (dbRDA) ordination based on the percentage of prey items from 24 prey taxa in 178 datasets of 94 bird species in Europe. The plot shows individual datasets coded for the bird order (colours) and sampled habitat (symbol). Vectors are superimposed based on multiple correlation coefficients >0.2 for prey groups and axis scores of all datasets. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

nestlings in coastal and marine habitats than for all birds (Fig. 5), and a less important source of prey for nestlings than for all birds in semi-natural habitats (Fig. S6).

3.2.3. Diet composition & conservation status

The conservation status of bird species alone explained 14.0 % of the variation in diet composition. Bird species with decreasing population trends in Europe were characterized by a relatively high contribution of Coleoptera prey to the diet compared to species with increasing population trends (Fig. 6). In contrast, Coleoptera prey was less important in the arthropod diet of bird species with an increasing population trend, as

these species were characterized by diets with a relatively higher contribution of Arachnida and Lepidoptera prey. Patterns for the diet composition of all birds (Fig. 6) and exclusive diets of nestlings did not differ (Fig. S7) in response to conservation status.

Bird species with population status of concern that are either concentrated in Europe (S2) or not concentrated in Europe (S3) have arthropod diets that are relatively more dominated by Coleoptera and Orthoptera prey compared to European species with populations that are classified as secure (S0) or of global concern (S1) (Fig. 7). The opposite pattern, but to a lesser extent, is observed for Arachnida and Lepidoptera prey, which are more characteristic of European species

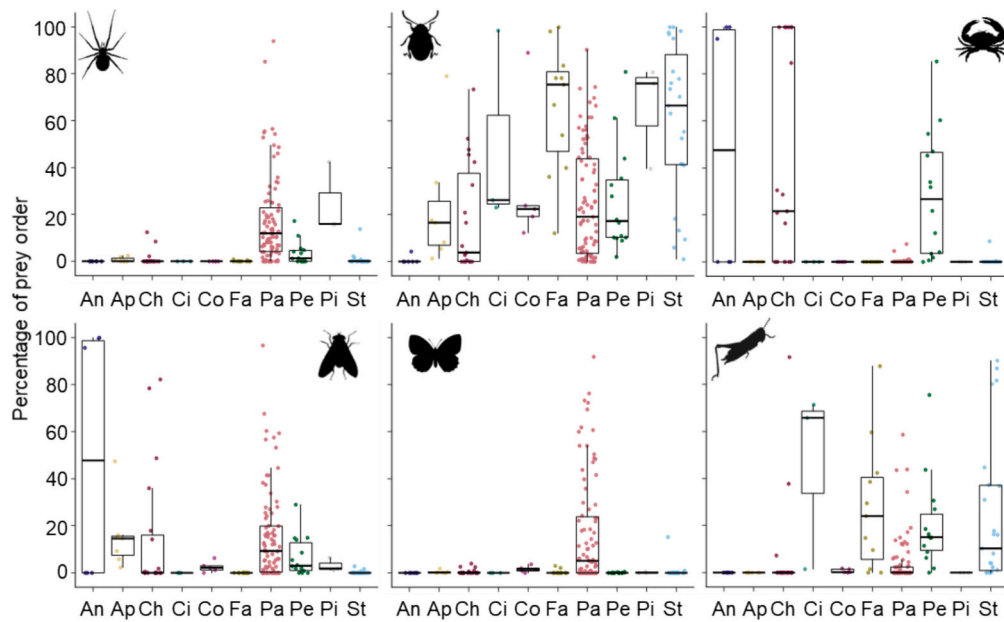


Fig. 4. Percentage of prey items from different prey taxa that contribute to the dissimilarity between bird species from different taxonomic orders with: **Anseriformes** (●, $N = 6$), **Apodiformes** (●, 8), **Charadriiformes** (●, 24), **Ciconiiformes** (●, 3), **Coraciiformes** (●, 7), **Falconiformes** (●, 11), **Passeriformes** (●, 94), **Pelecaniformes** (●, 14), **Piciformes** (●, 3) and **Strigiformes** (●, 28). Box plot show medians, 25th and 75th percentiles and outlier range ($1.5 \times$ interquartile range) for each bird order and prey taxon. Prey taxonomic groups are from top to bottom and left to right: Arachnida, Coleoptera, Crustacea, Diptera, Lepidoptera and Orthoptera.

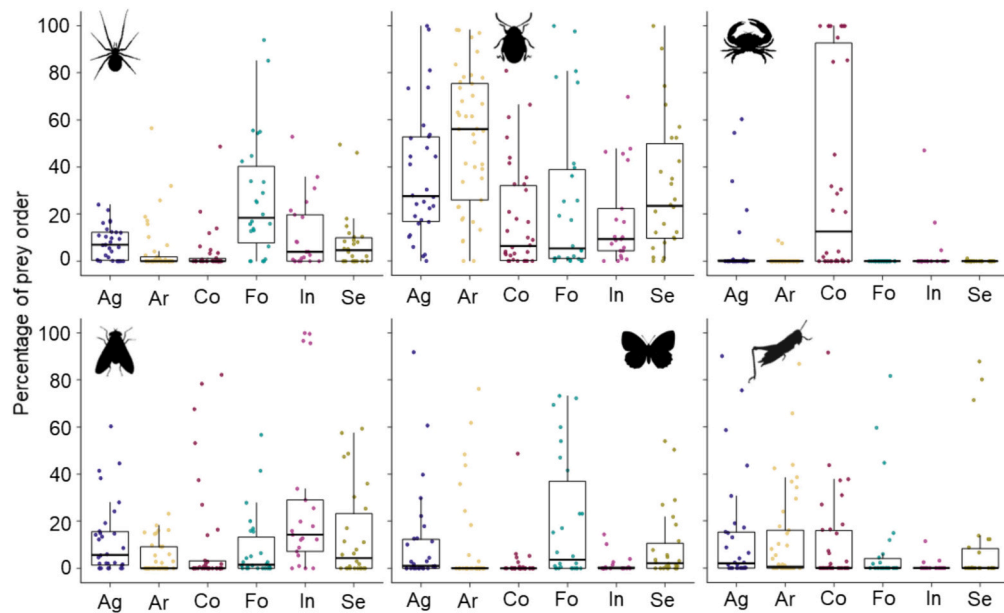


Fig. 5. Percentage of prey items from different prey taxa that contribute to the dissimilarity between bird species in different habitats with: **Agricultural** (●, $N = 30$), **Artificial** (●, 41), **Coastal & marine** (●, 34), **Forest** (●, 26), **Inland water** (●, 21) and **Semi-natural** (●, 26). Box plot show medians, 25th and 75th percentiles and outlier range ($1.5 \times$ interquartile range) for each bird order and prey taxon. Prey taxonomic groups are from top to bottom and left to right: Arachnida, Coleoptera, Crustacea, Diptera, Lepidoptera and Orthoptera.

with populations that are secure or of global concern (Fig. 7). Arachnida and Lepidoptera were a more important prey for nestlings in species of global conservation concern (Fig. S8) than for all birds (Fig. 7).

4. Discussion

We provide a comprehensive, quantitative review of the taxonomic richness and composition of arthropod diets in European bird species in

relation to their taxonomic identity, habitat, conservation status, developmental stage, migration status, and the climatic conditions in the study locations. Our data focuses exclusively on the arthropod diet of birds, and for many bird species other animal or plant resources may be the dominant component that is neglected here, such as small mammals in the diets of owls and birds of prey. The investigated bird species consumed a wide range of 24 arthropod taxa, but three arthropod taxa (Coleoptera, Diptera and Orthoptera) accounted for more than 50 % of

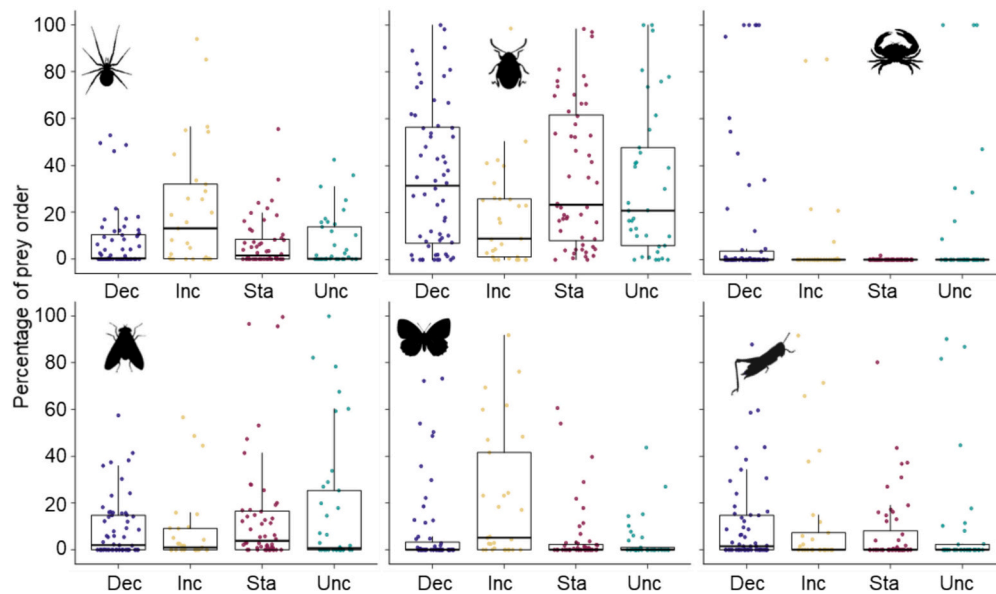


Fig. 6. Percentage of prey items from different prey taxa that contribute to the dissimilarity between bird species in different conservation status categories according to population trends: **Decreasing** (●, $N = 60$), **Increasing** (●, 29), **Stable** (●, 52), **Uncertain** (●, 37). Box plot show medians, 25th and 75th percentiles and outlier range ($1.5 \times$ interquartile range) for each bird order and prey taxon. Prey taxonomic groups are from top to bottom and left to right: Arachnida, Coleoptera, Crustacea, Diptera, Lepidoptera and Orthoptera.

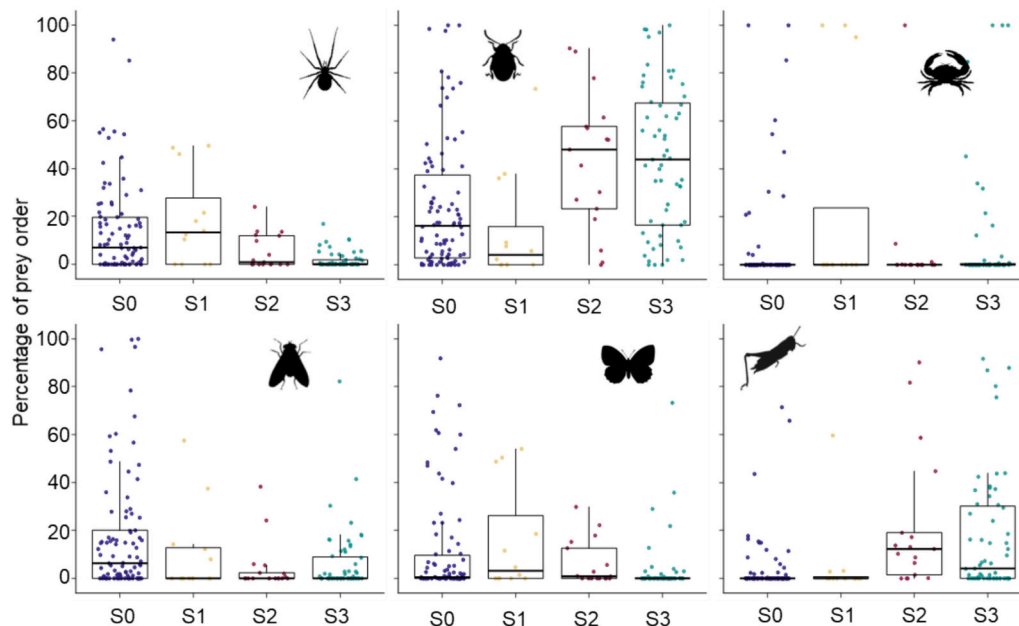


Fig. 7. Percentage of prey items from different prey taxa that contribute to the dissimilarity between bird species in different conservation status categories according to population status: secure (S0, ●, $N = 90$), global concern (S1, ●, 12), concern in Europe and population concentrated in Europe (S2, ●, 17) and concern in Europe, but population not concentrated in Europe (S3, ●, 59). Box plot show medians, 25th and 75th percentiles and outlier range ($1.5 \times$ interquartile range) for each bird order and prey taxon. Prey taxonomic groups are from top to bottom and left to right: Arachnida, Coleoptera, Crustacea, Diptera, Lepidoptera and Orthoptera.

all prey items. As expected, the strongest predictor of arthropod diet richness and composition was the bird species' taxonomic identity, but our results also show that prey composition is related to the habitat and conservation status of bird species. Climatic conditions, bird developmental stage and migration status were relatively minor predictors of the total variation in arthropod prey composition.

4.1. Diet and taxonomic identity

Taxonomic identity was the most important factor in determining

bird diet. This result suggests that, similar to gross dietary choices (carnivory, omnivory and herbivory) in animals in general (Roman-Palacios et al., 2019), dietary choices in birds are subject to evolutionary conservatism. The dietary choices of birds are determined by morphological and physiological adaptations that influence habitat selection (Battley and Piersma, 2005), the capture and handling of prey (Grosch, 2003), and the processing of prey with different defences and nutritional qualities (Duke, 1997). Although there is ample evidence of links between foraging adaptations and diets in birds, both between and within species (Morse, 1971), dietary shifts between some arthropod taxa

might involve significant changes in foraging adaptations, which will be constrained by evolution. For instance, it is unsurprising that water-adapted birds from the orders Anseriformes, Charadriiformes, and Pelecaniformes are distinct from other orders due to their high consumption of Crustacea prey, or that the predation skills of the orders Falconiformes and Strigiformes have enabled individuals of these species to opportunistically capture Coleoptera and Orthoptera. However, it is interesting that despite forming a distinct group, passerines exhibit significant dietary variation. This pattern reflects the adaptive radiation and success of the group (Miles et al., 2023). As both diet and ecological traits are influenced by bird taxonomy and evolutionary history, there is a risk of phylogenetic non-independence in our study — closely related species may have similar diets due to shared ancestry rather than adaptation. This study does not focus on these aspects; however, incorporating trait-based approaches, such as analysing foraging morphology or body size, would help to distinguish the effects of evolutionary history from functional adaptation in future studies.

In our study, Anseriformes species exhibited generally low prey taxonomic richness, whereas the bird orders with the highest prey taxonomic richness were Apodiformes, Coraciiformes, Passeriformes, Pelecaniformes and Piciformes. Regional studies have previously shown that insectivorous birds primarily consume arthropod prey from six to seven arthropod taxa: Coleoptera, Lepidoptera, Orthoptera, Diptera, Hemiptera, Hymenoptera, and Araneae (Gajdos and K., 1997; Wilson et al., 1999; Devey and Peres, 2000; Holland et al., 2006; Gámez-Virués et al., 2007; Razeng and Watson, 2012; Sam et al., 2017; Nyffeler et al., 2018). Our results underscore the dominant importance of Coleoptera as prey for insectivorous bird species across Europe. Beetles (Coleoptera) are highly diverse, comprising 27 % of all insect species worldwide (Stork et al., 2015). They also contribute significantly to ecosystem services (e.g. biological control of pests, dung removal, pollination) and disservices (pests in agriculture and forestry, threats to museum collections) worldwide (Bouchard et al., 2017). Diptera and Orthoptera were the second and third most important prey taxa in our study, which contrasts with findings from Australia, where Coleoptera, Hymenoptera (Formicidae), and Lepidoptera were the most important prey taxa in 12 adult forest bird species (Razeng and Watson, 2012), and the UK, where Coleoptera, Hemiptera and Lepidoptera dominated insect prey among 22 farmland bird species (Holland et al., 2006). However, the review by Holland et al. (2006) identified Diptera as the most important prey order for chicks. We argue that the inclusion of a large number of non-Passeriformes species in our quantitative review, including species dependent on aquatic habitats and birds of prey, may at least partially explain the observed differences in the importance of prey taxa between studies. The importance of Diptera (partly due to the inclusion of Apodiformes) and Orthoptera (due to the inclusion of Ciconiiformes, Falconiformes, Pelecaniformes and Strigiformes) prey for non-Passeriformes species and the fact that Lepidoptera were preyed on almost exclusively by Passeriformes in our data, support this interpretation. Bird orders with relatively low taxonomic richness of prey (e.g. Anseriformes) and those with high contributions of single prey taxa (e.g. >60 % Coleoptera for Piciformes, and Orthoptera for Ciconiiformes) are particularly at risk if these prey groups are disproportionately negatively affected by human-induced change (see next section). However, even less commonly consumed prey groups such as Dermaptera or Odonata may be important for the diets of some bird species to meet specific nutritional needs, such as amino acid supply (Ramsay and Houston, 2003) or calcium requirements (Graveland, 1996).

4.2. Diet, habitat and conservation status

The negative effects of land use change on the availability of arthropod prey have long been suggested as a key factor in the local decline of insectivorous bird populations (see references in Holland et al., 2006). Concerns that consumers such as Passeriformes may suffer from dietary constraints driven by losses of arthropod prey have recently

been reignited by reports of a global decline in insect biomass (Cardoso et al., 2020; Møller et al., 2021; Grames et al., 2022).

Our results suggest that prey from the orders Coleoptera and Orthoptera are particularly important for bird species of conservation concern in Europe, and for those with declining population trends. Coleoptera were also a particularly important source of prey for birds in agricultural, artificial, and semi-natural habitats, as well as for nestlings in coastal and marine habitats. These insectivorous bird species in Europe depend heavily on beetle prey, and there is increasing evidence of declining population trends in major Coleoptera families (e.g. water beetles: Roth et al., 2020; ground beetles: Brooks et al., 2012; rove beetles: Méndez-Rojas et al., 2021). These findings highlight the serious threat that biodiversity loss in one taxonomic group can pose to bird species of conservation concern in different habitats. Intensified agricultural practices resulting in a loss of Coleoptera will not only have direct negative consequences for these already threatened species (Rigal et al., 2023), but will also affect their populations by causing food shortages. Bird species of conservation concern in Europe also had higher contributions of Orthoptera prey. Orthoptera benefit from the presence of extensively managed permanent grasslands (Chisté et al., 2016), so bird species relying on this prey taxon would be expected to suffer from the conversion of grasslands to arable land in Europe.

Bird species that are of global conservation concern and have increasing population trends are more dependent on prey from the order Arachnida, particularly spiders. Some spider genera, especially those in the Linyphiidae family, benefit more from conventional than organic farming practices in Europe. They are less affected by the intensification of agricultural practices than other invertebrate taxa, such as granivorous or omnivorous ground beetles (Birkhofer et al., 2014). Such agrobiont species can reach high numbers in intensively cultivated farmland (Birkhofer et al., 2013), meaning bird species that rely on spiders as prey can still find sufficient food in these habitats. However, Arachnida are particularly important prey for forest birds, and insecticides used to control forestry pests in Europe (e.g. diflubenzuron) negatively affect non-target arthropods, including spiders (see Brunk et al., 2019, for a review). Broad-spectrum insecticide applications are therefore problematic not only in agriculture (see previous paragraph), but also in forests, where they reduce the availability of important prey. Equally concerning is the significant role of Diptera prey for birds in inland water habitats. Diptera were particularly important prey, for nestlings in inland water habitats in the order Anseriformes. Anthropogenic eutrophication may change the composition of Diptera communities leading to increases or decreases in the abundance depending on species (Keiper et al., 2002). It is unclear how such effects on Diptera prey alter the populations of Anseriformes species, but it is possible that a will negatively impact the reproductive success of these and other insectivorous bird species associated with freshwater (Marteau et al., 2025).

Like quantitative reviews and meta-analyses in general, our study has several limitations. First, and most obviously, our literature review potentially suffers from the file drawer problem. In meta-analysis, the file drawer problem refers to the bias that occurs when studies with non-significant results are less likely to be published. This leads to an over-estimation of effect sizes in the published meta-analytic results. However, we argue that many of the studies considered here are purely descriptive and do not rely on significant results from statistical models for publication. Of course, differences in sampling intensity between studies may have biased our results, but the sum of arthropod prey items recorded in each dataset was by far the weakest predictor in our models. This suggests that there is no significant numerical bias in terms of taxonomic richness or composition arising from the different sample sizes. This result is probably at least partly explained by the coarse level of prey classification, and stronger biases would be expected if richness and composition were assessed at the species level. Furthermore, the primary studies in our data only represent temporal snapshots, so ontogenetic differences and seasonal changes are only marginally approximated by including nestling diet as a predictor. Adult and chick

diets are known to differ in many species (Holland et al., 2006), but the majority of studies included in the analysis did not allow a detailed classification of bird developmental stages. Many studies reported combined results for chicks and adults or did not report the developmental stage of prey that the birds consumed. Finally, bird species on average were represented by two datasets per species in our database, but several species were represented by more datasets, the most extreme case being the little owl *Athene noctua* (12 datasets). To partly deal with the unbalanced number of datasets per bird species, we always pooled data for the same species sampled with the same method and from the same location to produce independent estimates of diet composition for the same species for use in our model. Finally, our correlational study, while informative about the degree of association between variables, cannot establish causal relationships.

4.3. Conclusions and outlook

The importance of different arthropod orders in the diet of birds varied greatly depending on the taxonomic identity, conservation status and habitat of insectivorous birds in Europe. Nevertheless, Coleoptera, Diptera, Orthoptera, and Arachnida were the most significant prey groups among arthropods, accounting for over 60 % of the diets of bird species. Importantly, the conservation status and habitat of the birds were closely linked to the composition of their diets: species experiencing population declines and those of conservation concern in Europe consumed high percentages of Coleoptera and Orthoptera prey. In contrast, forest species and species of global concern consumed higher percentages of Arachnida prey. Anthropogenic impacts affecting Coleoptera in open land (such as agricultural, artificial, and semi-natural habitats) and Arachnida in forest habitats have a negative effect, for example through insecticide applications. This reduces insect abundance and diversity and has a negative effect on common and threatened bird species by cascading up the food chain. The indirect links between human actions — particularly impacts such as insecticide applications, fertilisation, pollution and land use change — and bird diets cannot be ignored or underestimated and must be considered in future legislation and policies (see Lees et al., 2022, for a review). This recommendation is particularly important given that birds of global conservation concern in Europe exhibited the lowest prey taxonomic richness in our study. These species therefore seem particularly vulnerable to the decline or loss of individual prey orders from their habitats. Novel techniques such as metabarcoding have become essential tools for studying the diets of insectivorous bird species, offering high taxonomic resolution that uncovers detailed prey composition critical for conservation planning (Arazmi et al., 2025). By revealing habitat-linked dietary diversity, molecular approaches will enhance our ability to develop informed habitat management strategies that support bird populations and the ecosystem services they provide in the future (da Silva et al., 2024; Arazmi et al., 2025).

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CRediT authorship contribution statement

Klaus Birkhofer: Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Formal analysis, Conceptualization. **Johan Ekroos:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis. **Viktoria Mader:** Writing – review & editing, Methodology, Data curation. **Matthias Tschumi:** Writing – review & editing, Methodology, Conceptualization. **Ai-ping Wu:** Writing – review & editing, Methodology, Data curation. **Henrik G. Smith:** Writing – original draft, Visualization, Investigation, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Matthias Tschumi reports financial support was provided by Swiss National Science Foundation. Klaus Birkhofer reports financial support was provided by Swedish Research Council Formas. Johan Ekroos reports financial support was provided by Swedish Research Council Formas. Johan Ekroos reports financial support was provided by Biodiversity and Ecosystem Services in a Changing Climate (BECC). If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data is available as supplementary to this article (Table S2).

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