



Long-term declines of European insectivorous bird populations and potential causes

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Abstract: Evidence of declines in insect populations has recently received considerable scientific and societal attention. However, the lack of long-term insect monitoring makes it difficult to assess whether declines are geographically widespread. By contrast, bird populations are well monitored and often used as indicators of environmental change. We compared the population trends of European insectivorous birds with those of other birds to assess whether patterns in bird population trends were consistent with declines of insects. We further examined whether declines were evident for insectivores with different habitats, foraging strata, and other ecological preferences. Bird population trends were estimated for Europe (1990–2015) and Denmark (1990–2016). On average, insectivores declined over the study period (13% across Europe and 28% in Denmark), whereas omnivores had stable populations. Seedeaters also declined (28% across Europe; 34% in Denmark), but this assessment was based on fewer species than for other groups. The effects of insectivory were stronger for farmland species (especially grassland species), for ground feeders, and for cold-adapted species. Insectivory was associated with long-distance migration, which was also linked to population declines. However, many insectivores had stable populations, especially habitat generalists. Our findings suggest that the decline of insectivores is primarily associated with agricultural intensification and loss of grassland habitat. The loss of both seed and insect specialists indicates an overall trend toward bird communities dominated by diet generalists.

Keywords: agricultural intensification, bioindicators, climate change, insect declines, population trends

Declinaciones a Largo Plazo de Poblaciones de Aves Insectívoras en Europa y las Causas Probables

Resumen: La evidencia de las declinaciones poblacionales de insectos ha recibido recientemente una atención considerable por parte de la comunidad científica y la sociedad. Sin embargo, la falta de un monitoreo prolongado de los insectos complica valorar si estas declinaciones tienen una distribución extensa geográficamente. Como contraste, las poblaciones de aves tienen un monitoreo constante y con frecuencia se usan como indicadores del cambio climático. Comparamos las tendencias poblacionales de las aves insectívoras de Europa con las de otras aves para valorar si los patrones en las tendencias poblacionales de aves son consistentes con las declinaciones de insectos. Además examinamos si las declinaciones eran evidentes para aves insectívoras con diferentes hábitats, estratos de alimentación, y otras preferencias ecológicas. Las

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tendencias poblacionales de las aves se estimaron para Europa (1990 - 2015) y para Dinamarca (1990 - 2016). En promedio, las aves insectívoras declinaron a lo largo del periodo de estudio (13% en Europa y 28% en Dinamarca) mientras que las aves omnívoras tuvieron poblaciones estables. Las poblaciones de aves que se alimentan de semillas también declinaron (28% en Europa; 34% en Dinamarca), pero esta valoración se basó en menos especies que para los otros grupos. Los efectos de la insectivoría fueron más evidentes para las especies de tierras agrícolas (especialmente las especies de pastizales), para las especies que se alimentan sobre el suelo y para las especies adaptadas al frío. La insectivoría estuvo asociada con la migración de larga distancia, la cual también estuvo ligada a las declinaciones poblacionales. Sin embargo, muchas aves insectívoras tuvieron poblaciones estables, especialmente aquellas generalistas de hábitat. Nuestros hallazgos sugieren que la declinación de las aves insectívoras está asociada principalmente con la intensificación agrícola y la pérdida de pastizales. La pérdida de aves cuya alimentación es especialista en insectos o en semillas indica una tendencia general hacia comunidades de aves dominadas por aquellas con dietas generalistas.

Palabras Clave: bioindicadores, cambio climático, declinaciones de insectos, intensificación agrícola, tendencias poblacionales

Introduction

Declines in insect abundance have been reported in many locations within Europe (e.g., Thomas et al. 2004; Conrad et al. 2006; Hallmann et al. 2017; Valtonen et al. 2017) as well as in other parts of the world (Lister & Garcia 2018). If widespread, such declines would potentially affect many other species that, directly or indirectly, depend on insects in the ecosystem. A lack of large-scale, long-term insect monitoring hinders understanding of the dynamics of insect populations and ecosystem consequences. By contrast, birds have been the subject of the longest and most comprehensive terrestrial monitoring schemes and are often used as indicators of specific environmental changes (Donald et al. 2001; Jørgensen et al. 2016). However, it remains unclear whether monitoring data on bird populations, particularly of species that depend directly on insects, provide insight into changes within insect populations. We investigated whether changes in bird population abundances are consistent with widespread declines in insect abundance.

The populations of many different bird species, including insectivores, have been declining in many countries over recent decades (Newton 2004; Stanton et al. 2018). Few studies have directly linked insect and bird population dynamics due to a lack of matched long-term data. However, some local and regional studies show positive correlations between insect and bird abundance (Benton et al. 2002; Hart et al. 2006; Pearce-Higgins et al. 2010). Underlying drivers of large-scale bird population trends are often investigated using trait- or attribute-based approaches. Increases or decreases of species with specific attributes can reveal the main driver of change. For instance, impacts of land-use and climate change are manifest in declines of species with specific habitat (Jørgensen et al. 2016) and thermal (Jiguet et al. 2007) preferences. Based on similar reasoning, dietary preferences may affect species' responses to changes in insect populations.

Most directly, insectivorous species may be more immediately affected by insect declines than species with other diets.

There are 2 main ways diet may affect species responses to environmental change. First, declines in insect prey may directly affect birds by reducing their ability to meet energetic requirements. Several food supplementation quasi experiments show that food availability is a limiting factor of bird demographic rates and population abundances (Siriwardena et al. 2007; Seward et al. 2013). Insects, with generally short generation times, may respond more quickly to environmental change than other organisms (Thomas et al. 2004), which may render insectivorous birds more sensitive to environmental change than other birds. Declines of farmland birds, many of which are insectivorous (at least during the breeding season), are associated with adverse impacts of pesticide use on insects (Benton et al. 2002; Hallmann et al. 2014). Second, diet may indirectly affect species trends due to covariation between diet and other attributes that affect responses to environmental change (Barnagaud et al. 2012). For instance, diet preferences may be linked with habitat and temperature preferences. Thus, declines of species with certain temperature or habitat preferences would also lead to declines of species with a specific diet type.

The effect of species' dietary preferences on population trends has been less studied compared with the effects of species' habitat and temperature preferences. Diet explains some interspecific variation in long-term trends for some European populations (Van Turnhout et al. 2010; Reif et al. 2011) but not others (Jiguet et al. 2007). In North America, aerial insectivores are declining (Nebel et al. 2010), whereas in Central America, understory tropical forest insectivores (Sekercioglu et al. 2002; Sigel et al. 2006; Michel et al. 2015) are declining. However, it remains to be determined whether insectivorous birds in Europe are declining more than other birds across

different habitats. Moreover, the effect of covariation between diet and other species' attributes has not been considered.

We used 2 long-term bird monitoring data sets (the Pan-European Common Bird Monitoring Scheme [PECBMS] and Denmark's national data set) to examine population changes of species with different diets. The Danish populations of species largely spatially overlap and hence were mostly exposed to the same environmental change, unlike in the larger European data set in which species' distributions only partly overlap. We used *insectivore* to describe birds feeding on insects and, in some cases, other invertebrates. We examined population trends of species with different diets to test whether insectivorous birds have declined more than other birds. We reasoned that if insect declines were associated with a specific vegetation stratum or habitat, insectivorous birds foraging in this stratum or habitat would show greater declines. Hence, we examined whether insectivore declines were greater for those using farmland. We also tested whether temperature preference was more important for insectivores than omnivores due to climate-change-related trophic mismatches between birds and their resources. Finally, we examined whether patterns were more pronounced in Denmark than in Europe due to greater land-use change and land-use intensity.

Methods

Population Data

Europe-wide population indices were obtained from the PECBMS of the European Bird Census Council from their website. Data are collected in 27 countries with a standardized counting method (e.g., territory mapping, line transect, or point counts). Each country estimates TRIM indices (trends and indices for monitoring data) (Panekoek & Van Strien 2004), which are abundance population indices for each species and year obtained by fitting log-linear regression models to count data with Poisson error terms. National totals per species are combined across countries to produce supranational indices (see <https://pecbms.info/methods/pecbms-methods/> for methodological details). Data were available from 1980 onward, but the indices for early years are less likely to be representative because surveys began in different years in different countries, so we used data for 1990–2015. We excluded 7 marine species because one of our main environmental drivers of interest was related to land use. This left 130 species for analysis (Supporting Information).

Danish population indices were based on annual point count surveys at approximately 370 routes across the country (see Nyegaard et al. [2015] for more details). The annual national abundance indices for each species are calculated by DOF-BirdLife Denmark with the TRIM method. We used data for 1990–2016 from the DOF web-

site, excluding marine species. This left 95 species for analysis, 86 of which were also in the PECBMS data set. The Danish data are included in the PECBMS data set; hence, the 2 data sets are not completely independent. However, because Denmark is a small part of the European land area, this nonindependence is weak.

Diet and Foraging Stratum

Diet data were taken from the EltonTraits 1.0 bird traits database (Wilman et al. 2014). This database provides categorical diet data (insectivores; plant and seedeaters; omnivores; and vertebrate, scavengers, and fish eaters) and continuous data on the proportion of each food type in each species diet. Using these data, we created diet categories of insectivore, seedeater, and omnivore. Seedeaters were separated from the original plant-and-seed category if seeds constituted 40% or more of their diet. Because there were some discrepancies between diet descriptions in the EltonTraits database and other literature resources (Snow & Perrins 1998; del Hoyo et al. 2014), we changed the diet classification for some species. The Common Raven (*Corvus corax*), Carrion Crow (*Corvus corone*), and European Magpie (*Pica pica*) were included in the vertebrate, scavenger, and fish diet category of the EltonTraits database, but we categorized them as omnivores based on these literature sources. We dropped the few species with other diets (plants, fish, or other vertebrates) from our analysis because of their low number (European and Danish data sets, 13 and 15 species, respectively). The EltonTraits 1.0 database provides percent use of different foraging strata, which we used to define species as water feeders (water stratum use >0%), ground feeders (ground stratum use >40%), canopy feeders (canopy use >20%), or midstratum feeders (remaining species). We used the literature sources to identify species that commonly feed aerially.

Although species' diets can vary seasonally, this database classifies only the main diet of each species (Wilman et al. 2014). Moreover, almost all the species use insects in the breeding season to feed chicks. We regarded insectivores as more dependent on insects throughout their life than other species whose dependence is more variable.

Habitat Preference, Migratory Behavior, and Temperature Preference

In the European data set, habitat preference was first defined according to the PECBMS classification, which designated each species as farmland, forest, or other. Because this classification meant many species were placed into the other category, we also used information from a database (Storchová et al. 2018; Storchová & Hořák 2018) with binary data on habitat use of deciduous forest, coniferous forest, woodland, shrub, savanna, tundra,

grassland, mountain meadows, reed, swamps, desert, freshwater, marine and rocks, and human settlements. We used these 2 sources to classify the main breeding habitat for each species as farmland, forest, freshwater, habitat specialist (of a different habitat from these aforementioned), or habitat generalist. Farmland birds were defined directly according to the PECBMS classification (<https://pecbms.info/methods/pecbms-methods>). Forest birds were defined according to the PECBMS classification and those using forest or woodland and not any open habitat. Freshwater species were those that used freshwater or reed habitats but not terrestrial habitat. Of the remaining species, habitat generalists were those using >2 habitat types, and habitat specialist used 1-2 open habitat types. Because farmland comprises grassland and pastures and cultivated arable land, we also created a grassland-use category, defined as grassland use and not forest or woodland use. Grassland use partially overlapped with farmland use (55% overlap). Habitat breadth was assessed as the number of different habitat classes used (Storchová et al. 2018). We also classified long-distance migration (trans-Saharan or Asian) by combining data from the literature (del Hoyo et al. 2014) and distribution maps (BirdLife International & NatureServe 2012).

In the Danish data set, species' relative habitat uses (coniferous forest, deciduous forest, arable land, meadow, bog or marsh, heath, dunes or shore, lake and urban) were taken from Larsen et al. (2011). These data were compiled from national observations of species within Denmark and comprise continuous variables reflecting how much each species uses each habitat relative to other habitats available (Larsen et al. 2011). These data were regarded as a better source of habitat information for the Danish data set than the more general bird-trait database used for the European data set. We focused on species' uses of grassland, farmland, forest, and freshwater. Each variable was log transformed to reduce skew. We identified grassland specialists as those with a relative habitat use of grassland (vs. other habitats) >2 (Eskildsen et al. 2013). As a measure of habitat breadth, we used the coefficient of variation of species' relative uses across all habitats multiplied by -1 (Julliard et al. 2006). Finally, species were classified as long-distance migrants (trans-Saharan) based on ringing recovery data (Bønløkke et al. 2006).

Species' temperature preferences were calculated by overlaying species distribution data (BirdLife International & NatureServe 2012) with average (1969-1990) daily mean temperature maps (from E-OBS) delimited to Europe on a 25 × 25 km equal area grid (Eckert IV projection) (Jiguet et al. 2007). Because some species were migrants, we used only the breeding distribution and spring (March-May) temperature data. We calculated the mean and range of temperatures at occupied grid cells to create a variable that organized species on a gradient from cool to warm temperature preference.

Statistical Analyses

The abundance indices were standardized to 100 in the first census year to facilitate comparison. Because the abundance data were indices and not true counts, we used the log-transformed annual indices as the response variable. We used mixed-effects linear models in which the population trends of each species were treated as random effects around an average trend, which accounted for temporal autocorrelation (AR1). Random variation among species was included for the intercept, trend, and AR1 correlation. We considered an alternative method that uses the associated sampling error of the TRIM indices (Soldaat et al. 2017); however, similar were results (Supporting Information), and this approach had the disadvantage of being less flexible and not accounting for temporal autocorrelation.

We tested whether species with different diets showed different long-term population trends. To examine trends, we tested the effect of year (as a continuous variable) in a mixed-effects linear model. We also fitted the model with year as a categorical explanatory variable, removing the model intercept so that the coefficients were the predicted indices for each year for visualization of the time series.

For each species attribute (habitat preferences, migratory strategy, and temperature preferences), we examined their covariation with diet. We used chi-squared tests when the attribute was categorical and a linear model when the attribute was continuous. We further examined population trends for each diet group split by the attributes. We focused on the diet-attribute subsets in which there were over 5 species and estimated the mean trends following the modeling procedure described above. For simplicity, continuous attributes were split at the median to create a categorical variable of 2 groups. Finally, we fitted multiple regression models on species' abundances that tested interactions between year and each attribute and, after backward stepwise deletion of significant variables, extracted the effect size of each attribute for each diet group. Grassland use and farmland use were tested in separate multiple regression models because they covaried. We also considered the effects of genus, family, and order as random intercepts to account for phylogeny, but they had little effect. Pearson's correlation coefficient was used to compare the trends of species between the Danish and European data sets.

We focused interpretation on the effect sizes (standardized regression model coefficients) and inferred statistical significance when 95% CIs did not overlap 0. Because the abundance indices were log transformed, the coefficients and 95% CIs were back transformed by the exponential. Trend estimates represented the average multiplicative change in population abundance between consecutive years (1 indicated no change). All statistical analyses

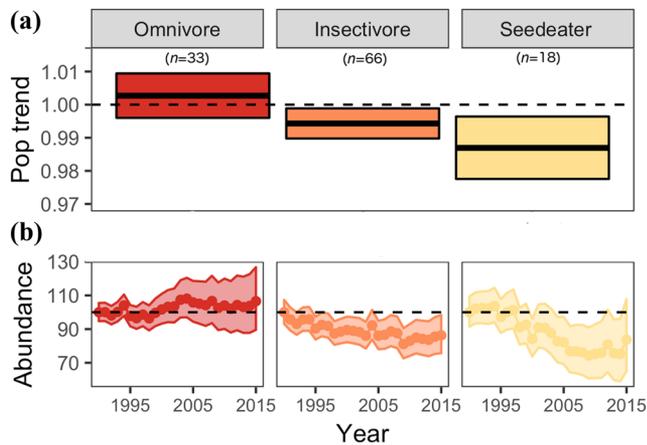


Figure 1. Mean (95% CI) of (a) population trends (multiplicative annual change in abundance) (1, no change; n, number of species in each group) and (b) annual abundance indices across Europe of bird species in 3 diet groups (dashed lines, no change).

were run in R version 3.4.1, and models were fitted using R-INLA (Rue et al. 2009).

Results

European Community Composition and Population Trends

Insectivory was the most common diet (66 of 130 species). Insectivores included warblers, some tits, woodpeckers, flycatchers, wagtails, and waders. The mean abundance of insectivore species declined by 13% (95% CI 3–23%) over the 25-year study period (Fig. 1). Omnivory was the next most common diet (33 species). Omnivores included some tits, corvids, thrushes, and a broad range of other species. Omnivore species showed no significant average change in abundance (–10% to 26%). Seed eaters (18 species) included finches, buntings, and sparrows. Abundance of seed eating species declined on average by 28% (9–43%).

Effects of Species Attributes

Foraging stratum and diet were significantly associated ($\chi^2 = 28.6$, $df = 12$, $p = 0.004$). This was driven by a greater than expected number of insectivores feeding aerially and a lower than expected number of seed eaters in the canopy. Within insectivores, ground feeders and canopy feeders showed the most negative population trends. Within seed eaters, midstratum feeders had the most negative population trends (Fig. 2a). On average, insectivore species that commonly feed aerially were not declining. However, the most characteristic aerial feeders (*Apus apus*, *Delichon urbicum*, *Hirundo rustica*, *Merops*

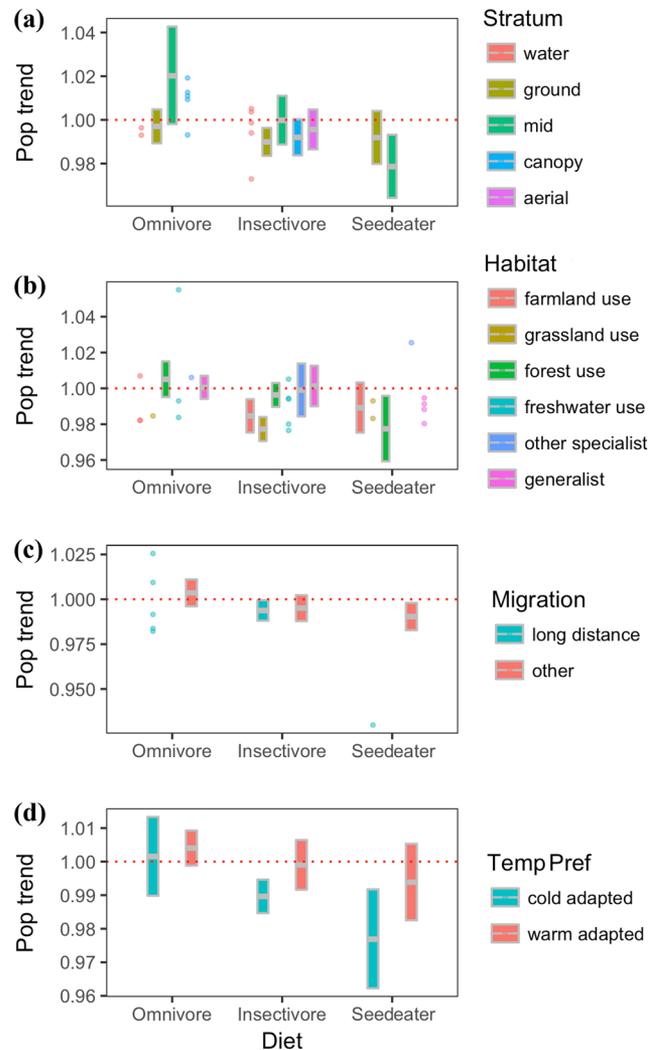


Figure 2. Population trends (multiplicative annual abundance change) of birds in 3 diet groups by (a) foraging stratum, (b) habitat preference, (c) migratory strategy, and (d) temperature preference (dashed line, no change). For groups with fewer than 5 species, the trend for each species is a separate point; otherwise, the mean (95% CI) of the trends is shown. Supporting Information contains number of species in each subset and the mean and 95% CI for all subsets.

apiaster, and *Muscicapa striata*) were significantly declining (average trend: 0.990, 95% CI 0.981–0.999). Neither omnivorous ground feeders nor omnivorous midstratum feeders were, on average, declining.

Habitat use and diet were also significantly associated ($\chi^2 = 22.22$, $df = 12$, $p = 0.035$). Seed eaters were more common than expected in farmland. Insectivores were the only species common in grassland, and these species declined the most consistently, more so than farmland insectivores (Fig. 2b). Some forest insectivores were also declining, but their mean trend did not significantly

differ from 0. Insectivores that were habitat generalists or specialists of other habitats were not declining. Seedeating forest birds had significantly negative trends, whereas omnivorous forest birds did not (Fig. 2b).

Long-distance migrants were overwhelmingly insectivores (82%, $\chi^2 = 32.72$, $df = 3$, $p < 0.001$). Insectivore migrants had significantly negative mean trends; however, other insectivores were also declining, albeit, more marginally significantly (Fig. 2c). Temperature preferences did not significantly differ among diet groups; however, cold-adapted insectivores and seedeaters were declining, whereas warm-adapted species were not (Fig. 2d).

Multiple Regression Modeling of Species Attributes

Grassland use remained the only significant predictor (negative effect) of population trends for insectivores, but farmland use approached significance (Fig. 3). For seedeaters, temperature preference was the only significant predictor and was positively related to population trends (Fig. 3), a tendency also seen for insectivores. After we removed 1 outlier species, there was no significant negative effect of temperature range for omnivores, and none of the other predictors were significant. The time-series data suggest that insectivores using grassland have declined consistently since 1990 (Fig. 4a), whereas cold-adapted seedeaters have declined since the 2000s (Fig. 4b).

Comparison at National Scale

Patterns in Denmark were similar to those in Europe (Fig. 5): declines of insectivores (on average by 28%) and seedeaters (by 34%) and mostly stable trends of omnivores. Trends of the 86 species that overlapped both data sets were moderately correlated ($r = 0.5$, $p < 0.01$), but omnivores and insectivores were declining more in Denmark than in Europe (95% of trend difference = 0.002–0.009 and 0.0007–0.006, respectively). Grassland use, as a continuous variable, was not significantly related to insectivore population trends (Supporting Information); however, specialist grassland birds were declining more than other insectivores (Fig. 6a). The best predictor of population trends for insectivores was habitat specialization (negative effect) (Fig. 6b & Supporting Information). For seedeaters, the best predictor of population trend was temperature preference (Supporting Information); cold-adapted species declined (Fig. 6c).

Discussion

We found that variation in bird population trends since 1990 at the European scale and at a national scale was partly associated with dietary preference, further

modified by habitat, foraging stratum, and temperature preference. Insectivores, including species feeding on insects and other invertebrates, were the most common diet group and declined consistently by 13% across Europe over the 25-year period. Declines were also seen among seedeaters, but the sample size was much lower. By contrast, the populations of omnivorous birds remained more or less stable.

Insectivores were present in all habitats, but the strongest declines were among those using farmland, and especially grassland, including the Common Grasshopper Warbler (*Locustella naevia*), Northern Wheatear (*Oenanthe oenanthe*), and Meadow Pipit (*Anthus pratensis*). Recent agricultural change encompasses a suite of changes that have adversely affected farmland birds (Newton 2004; Jørgensen et al. 2016; Stanton et al. 2018). Some of these changes are thought to directly affect the availability of food resources. Dutch insectivorous bird populations declined to a greater extent in areas with relatively high amounts of neonicotinoid insecticides, suggesting impacts mediated via insect abundance (Hallmann et al. 2014). Farmland comprises different habitat types that can be broadly split into grassland (including pastures) and cultivated arable land for crop production. Our findings demonstrated the specific adverse effect of grassland use on insectivore population trends. Grasslands have been affected by intensification of management, including increased fertilization, mowing frequencies and, livestock densities, and by abandonment and afforestation. These changes have likely decreased the extent and quality of grassland as both feeding and breeding habitat for birds (Vickery et al. 2001; Strebel et al. 2015).

Insect taxa vary in their response to landscape change; hence, while some insect groups may be declining, others are probably not (Ockinger et al. 2012; Schuch et al. 2012). We found that ground-feeding insectivores declined the most; however, this was probably rather related to ground feeders being common in grassland instead of a specific decline of ground-dwelling insects. Like studies in North America (Nebel et al. 2010), we also found that the most characteristic aerial insectivore feeders declined, which could reflect lower availability of flying insects. However, insectivores that were habitat generalists or specialists of other habitats, beyond farmland and grassland, including Western Orphean Warbler (*Sylvia hortensis*), Middle Spotted Woodpecker (*Dendrocopos medius*), and Golden Plover (*Pluvialis apricaria*), had stable or even positive trends. This suggests that insects are sufficiently abundant in the landscape for some bird species to meet their resource requirements.

Insectivory and trans-Saharan migration are strongly associated (Hockey 2000; Jiguet et al. 2007). Declines of long-distance migrants are well documented (Sanderson et al. 2006; Kramer et al. 2018) and have been explained by different hypotheses, including climate and habitat

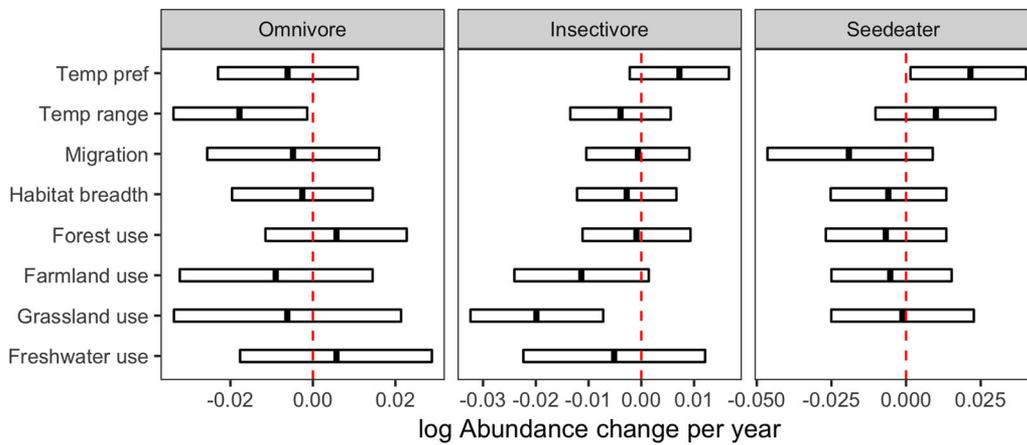


Figure 3. Standardized effect (95% CI) of species' attributes on log abundance change per year for European bird populations in 3 diet groups.

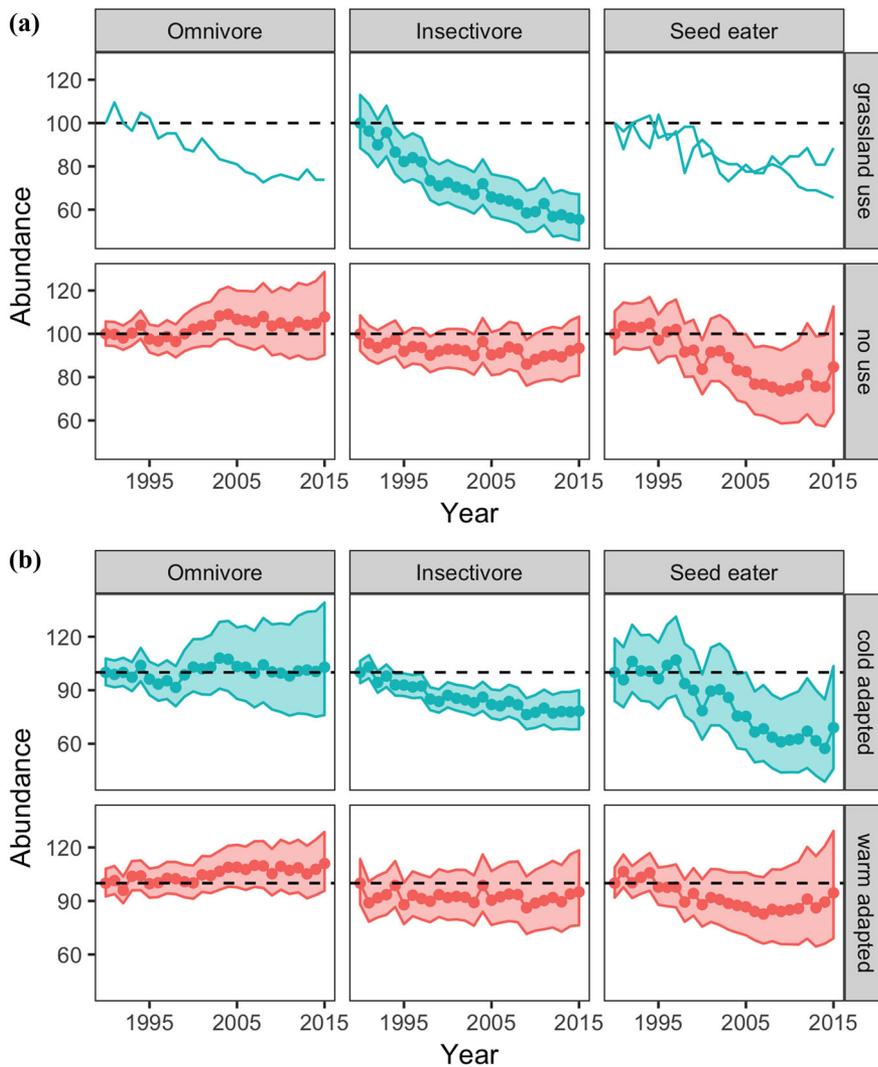


Figure 4. Mean (95% CI) annual abundance indices for European birds in 3 diet groups by (a) grassland use and (b) temperature preference. Because seedeaters and omnivores using grassland had fewer than 5 species in their groups, the individual time series for each species is shown.

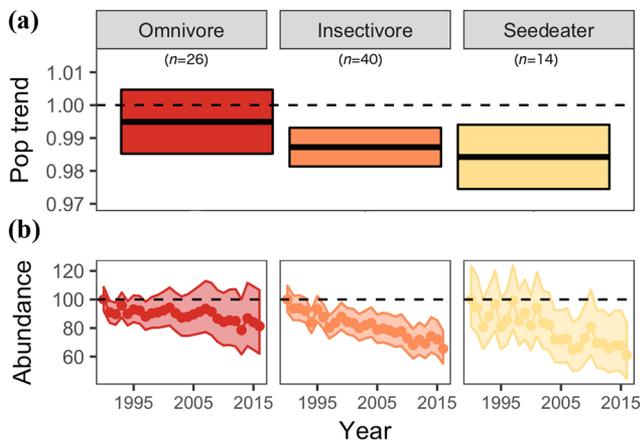


Figure 5. Mean (95% CI) (a) population trends (multiplicative annual change in abundance) (1, no change; *n*, number of species in each group) and (b) annual abundance indices in Denmark of bird species in 3 diet groups (dashed lines, no change).

change in breeding or wintering grounds (Vickery et al. 2014). One hypothesis is that long-distance migrants are vulnerable to phenological advances of insect populations because they are less able to adaptively match their breeding time to the timing of peak insect availability on breeding grounds (Both et al. 2010). Long-distance migratory insectivores tended to decline more than other insectivores in the European data set; however, many short-distance migratory or sedentary insectivores were also declining. Hence, pressures associated with trans-Saharan migration did not fully explain the decline of insectivores.

Because only 18 seedeaters were included in the European data set, we can only speculate about general patterns. Seedeaters were most consistently declining among forest species. Some of these species, such as the Rustic Bunting (*Emberiza rustica*), the only long-distance migratory seedeater in the data set (Edenius et al. 2017), and the Nutcracker (*Nucifraga caryocatactes*), a pine nut specialist (del Hoyo et al. 2014), are probably declining for rather species-specific reasons. Several seedeating farmland species were also declining, including the Yellowhammer (*Emberiza citronella*). Seedeating was positively associated with farmland use, but few seedeaters used grassland. Hence, declines among farmland seedeaters may be linked with different land-use changes than those affecting farmland and grassland insectivores. Seedeaters have been adversely affected by changes in sowing practices and loss of winter stubble (Newton 2004; Siriwardena et al. 2007). Also, almost all of the seedeaters feed on invertebrates during the breeding season, especially to feed their offspring, which means their populations may also be influenced by insect availability (Benton et al. 2002; Hart et al. 2006).

Temperature preference was the best predictor of the declines of seedeaters, and it was also marginally important for insectivores. Cold-adapted species declined, whereas warm-adapted species remained stable or declined less. This association may explain why forest seedeaters had negative trends; forest species tend to have cooler temperature preferences (Barnagaud et al. 2012). Temperature preferences were based on species' distributions within Europe (Jiguet et al. 2007); hence, cold-adapted species were those occupying colder regions of Europe, usually at more northerly latitudes that are especially subject to climate-change effects. Warming temperatures are predicted to cause advances in the phenology of organisms, which may lead to trophic mismatches between organisms and their resources (Visser et al. 2015). Hence, cold-adapted seedeaters and insectivores may be more affected by trophic mismatches than warm-adapted species. Diet specialists may be generally more sensitive than omnivores to temperature-related changes in resource availability and long-term climate change.

We focused our analysis on patterns at the European scale; however, we also analyzed data from Denmark to test whether the same patterns were seen at a smaller scale within which populations were exposed to the same combination of environmental change. We expected any patterns to be stronger in Denmark because of the intensity of land-use there (Donald et al. 2001). This prediction was generally supported. Insectivores in Denmark declined more than across Europe (28% vs. 13%), especially habitat specialists. These insectivorous habitat specialists exploited a range of habitats, and their declines may suggest more widespread insect declines in Denmark. Although beyond the scope of our present study, the evidence for geographic variation in the role of diet (Jiguet et al. 2007; Van Turnhout et al. 2010; Reif et al. 2011) supports further investigation based on spatial variation in the underlying drivers, such as the extent and type of land-use change (Donald et al. 2001). Beyond Europe, in the tropical forests of Central America, declines in insectivorous birds are associated with changes in habitat structure rather than reduced food availability (Sekercioglu et al. 2002; Michel et al. 2015).

A core component of current policy frameworks, such as IPBES (Diaz et al. 2015), is not only the impact of environmental change on biodiversity, but also its impact on the functioning of ecosystems and the provision of ecosystem services. Species' dietary preferences have strong implications for their ecological roles in communities because diet determines which and how species interact (Sekercioglu 2006). Because insectivory was the most common diet, insectivore declines would tend to increase the functional evenness of the bird community. However, the decline of diet specialists (insectivores and seedeaters) could decrease functional richness. Many studies suggest a general increase of generalist species,

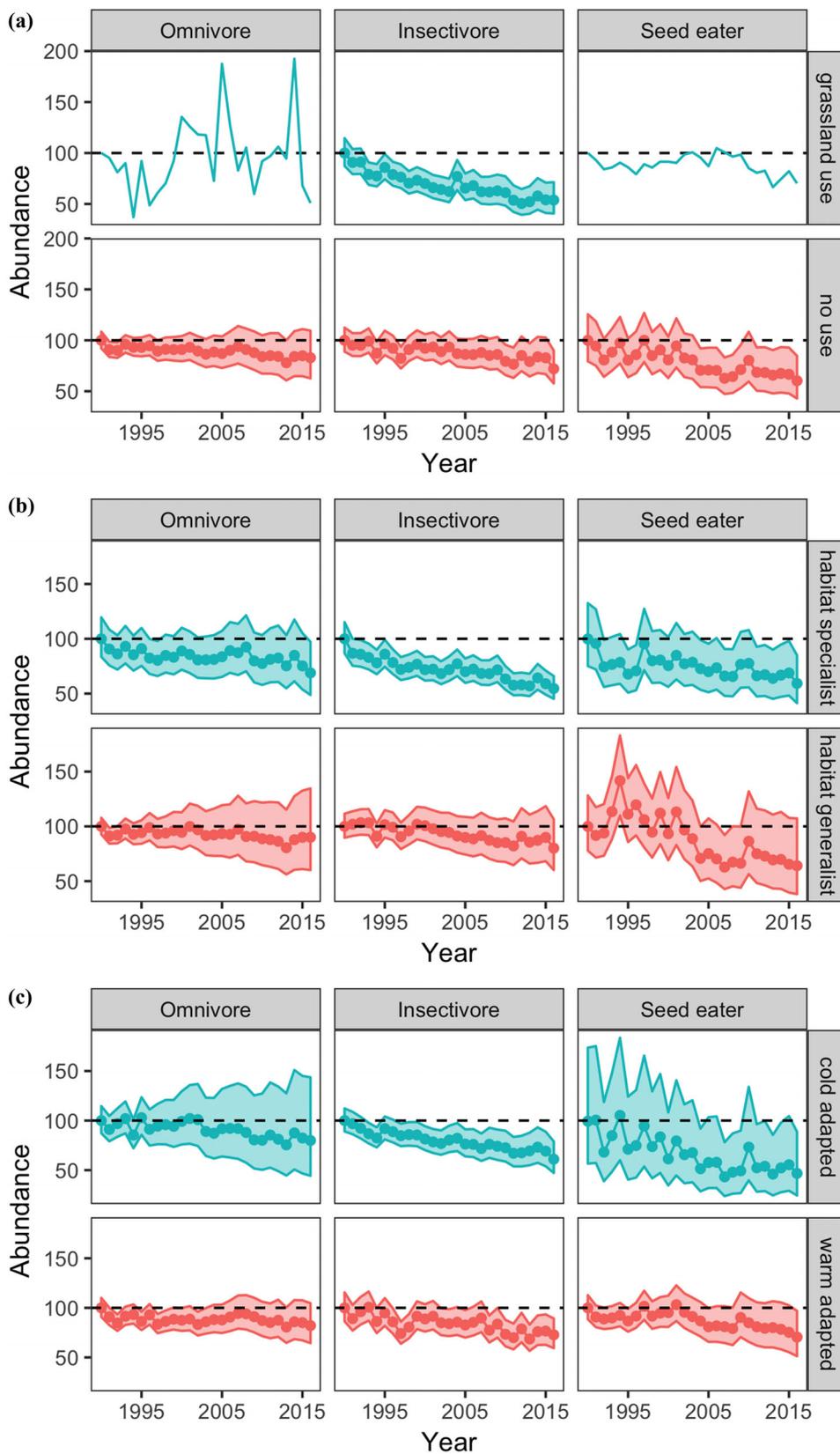


Figure 6. Mean (95% CI) annual abundance indices for Danish birds in 3 diet groups by (a) grassland use, (b) habitat specialism, and (c) temperature preference. Because seedeaters and omnivores using grassland had fewer than 5 species in their groups, the individual time series for each species is shown.

which are tolerant of different sorts of environmental change (Clavel et al. 2011). Our findings add to the body of evidence that shows communities are becoming more dominated by generalists, specifically omnivores.

At the same time that insect declines are being reported in many European countries, we found that insectivorous bird populations are declining at both a European scale and at a national scale in Denmark, which raises the question of whether bird declines are related to changes in insect populations. The decline of avian insectivores was most strongly related to farmland use, and especially grassland use, hinting that agricultural practices are the main driver of change. Climate change may also play a role because cold-adapted species also tended to be declining to a greater extent than warm-adapted species. However, many other insectivores were not declining, suggesting that insect declines have not had widespread impacts on bird populations. Long-term insect monitoring within farmland and in other habitats is essential to better understand the association with agricultural practices. Moreover, simultaneous monitoring of birds and insects would improve understanding of the consequences of insect declines for the functioning of communities and determine the information on insects that may be accessible from data on bird monitoring.

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Supporting Information

Species in the analysis (Appendix S1), species attribute table (Appendix S2), analysis with the MSI tool (Appendix S3), number of species in each diet subgroup (Appendix S4), 95% CIs of trends for all diet subgroups (Appendix S5), and effect of species attributes on trends in Denmark (Appendix S6) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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