Assessing direct effects of insect change on insectivore populations in the United Kingdom

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Abstract

1. Declines in insect abundance are a cause for concern, with potential downstream impacts on the function of ecosystems. Insects are key food resources for insectivorous vertebrates, with evidence that declines in these species could be driven by changing insect abundance.
2. Quantifying the direct effect of insect abundance on vertebrate population dynamics is challenging especially at large spatial scales (e.g. regional-to-national scales) due to data limitations, and because correlations between population dynamics can result from shared responses to environmental variation.
3. We provide a comprehensive assessment of the role of insect abundance on the dynamics of 10 insectivores (five birds and five bats) within the United Kingdom, by assembling and pairing insect and vertebrate abundance data at three spatial resolutions (100, 50, 10km) utilising several citizen science monitoring programmes.
4. To address the challenges of quantifying direct effects, we use a multiple specification approach combining: 1) association, 2) prediction, and 3) causal inference.
5. We found evidence of overall declines for all bird species evaluated and for nearly all indices of insect food availability, though none of the bat species tested showed evidence of overall decline. Despite indices of both insect and bird abundance declining, declines did not always co-occur spatially. We also found limited decisive evidence that insect change was currently driving insectivore population change, identifying only moderate evidence of links between both blue tit and great tit and moth abundance, and grey partridge and Diptera abundance.
6. Our results suggest that for most insectivores assessed, reductions in insect food do not appear to be a primary cause of declines and that both insects and insectivores may be impacted by several (non-overlapping) factors associated with environmental

change. However, we discuss the challenges and limitations of assessing direct impacts of insect declines from observational monitoring data.

Introduction

There has been recent concern over insect declines (Hallmann et al., 2017; Wagner, Grames, et al., 2021; Warren et al., 2021). While measuring the extent of the declines is subject to methodological challenges (Didham et al., 2020; Müller et al., 2023), general surveys show sustained declines on average (Wagner, Grames, et al., 2021), though with variation between taxa and across different habitats (Hallmann et al., 2020; Powell et al., 2023; Wagner, Fox, et al., 2021). Loss of insect biodiversity is a concern in itself (Clayton, 2003; Wilson, 1986), but the necessity of understanding the causes and consequences of insect declines is underscored by the wide array of ecosystem functions and services insects provide (Forister et al., 2019; Goulson, 2019; van der Sluijs, 2020). One major issue relates to the importance of insects in food webs. As insects are important dietary components for many vertebrates, declines in insects could have knock-on repercussions on population dynamics and ecological function. There is some evidence insect decline may be impacting insectivorous birds (Bowler et al., 2019; Hallmann et al., 2014; Stanton et al., 2018) at least in specific habitats (e.g. farmland), but shared population responses to environmental pressures cannot be ruled out (Pearce-Higgins & Morris, 2023).

The role of insect change in insectivore population trends can be assessed through either indirect or direct approaches. Indirect approaches assess the impacts of drivers of change where the effects are expected to be partially or fully mediated through changes to insect abundance. Hallmann et al (2014), for example, found that the quantity of pesticide used in an area was negatively associated with bird population trends, suggesting a possible impact of insect abundance change on insectivores, assuming insects rather than birds are most affected by pesticides. Similarly, Rigal et al (2023) linked reduced European bird populations to agricultural intensification measured through pesticide and fertiliser use. Finally, comparisons of the trends of species more reliant on insects relative to those utilising a greater diversity of food sources, suggests declines in insectivorous species could be driven by insect abundance (Bowler et al., 2019). This indirect approach captures the ‘total’ effect of

such drivers, including impacts on insects, but we cannot easily separate shared responses to environmental challenges from direct effects of insect change. For example, changing insect abundance is just one of a suite of factors associated with agricultural intensification and a recent meta-analysis showed neonicotinoid pesticides have direct impacts on birds independent of their effects on insect abundance (Molenaar et al., 2024).

Another approach is to use insect population data to directly assess the effect of insect abundance change on insectivores. However, coextensive population data from insects and insectivores are limited, making links between insects and insectivore population changes challenging to test. One approach to tackle this constraint is to combine multiple smaller-scale studies through synthesis and meta-analysis (Grames et al., 2023), although here inference is necessarily limited to the species-interactions, locations, and times that have been relatively well studied. Alternatively, recent efforts show there is potential to estimate links between insects and insectivores by utilising citizen science monitoring data from standardised recording schemes (Evans et al., 2024; Martay et al., 2023; Yazdanian et al., 2024). While each such scheme targets different taxa, the substantial spatial and temporal replication of some schemes offers the potential to tie together local populations of insects and insectivores to assess direct effects of insect change at regional-to-national scales.

Utilizing national-scale monitoring data, however, brings additional challenges regarding measurement and inference. At the local scale, abundance will be measured with some error and this compounds when tying together monitoring schemes from different locations and when the most relevant life-stage is not recorded (e.g. if adult insects are recorded while the bird species in question mainly predates insect larvae). There are also several decision points when pairing and aggregating insect and insectivore data. One consideration is spatial scale, for example foraging behaviour may influence the scale at which effects are detected, as mobile insectivores may be able to overcome local reductions in insect abundance by foraging over greater distances (Oliver et al., 2010). This may result in correlations that are weaker at the local scale and stronger at a regional scale. However,

aggregating data across different scales can also have non-trivial impacts on signal-to-noise ratios and statistical power. Similarly, insectivores are likely to eat multiple insect species, therefore, there is a need to generate appropriate indices of overall food abundance from species-level data. Such indices could be aggregated under different weighting schemes (i.e. varying species importance) and with different units (e.g. abundance, biomass).

A major inferential challenge when using national-scale monitoring data is confounding effects, as correlated population fluctuations between insects and insectivores may result from shared responses to changing environmental variables (e.g. weather, habitat or land cover change). Omitting, or lacking control for such factors, can bias estimates of the role of insects, potentially either over or underestimating their impact. Additionally, even if direct effects are present, tightly coupled population dynamics between predators and prey can result in positive, negative, or zero correlations in abundances over time (Sugihara et al., 2012), resulting in shifting variable importance in a linear statistical analysis.

These issue around complex causal structures, confounding, data quality, and model specifications risk incurring both Type I and Type II errors, as, 1) we may falsely identify a link between insects and insectivore dynamics that could be due to noise or confounding variables, particularly shared responses to environmental variation; or, 2) we may fail to detect a link when there is one, due to measurement error (which will bias coefficients towards zero), improper controls, or model specifications that are unable to capture dynamic features.

Given the challenges both in terms of varying data quality and causal uncertainty, we think it is useful to analyse the role of insects on insectivore dynamics through a combination of approaches rather than any single analysis, especially given that researchers can generate different conclusions using the same data (Gould et al., 2023). We take inspiration from specification approaches (Simonsohn et al., 2019) by providing several tests evaluating links between insects and insectivores.

Our approach is to follow simple associative tests – which can help identify basic patterns in the data – to non-linear predictive approaches, useful for capturing associations that linear methods may be unable to identify, before using linear 'causal inference' models to help account for confounding.

The associative tests evaluate basic patterns between the dynamics of the insects and the insectivores i.e. are the directions of long-term population trends similar across space? While any correlations between the trends could obviously not be considered causal, they are still informative. For example, if on both insectivores and insects are declining, but the declines are in different locations then we can lower our confidence that insect declines are driving the insectivore declines. Therefore, while the below approaches provide better control for confounding, they might obscure these basic patterns (particularly after controlling for variation associated with site, year, or spatial factors).

Next, we use Empirical Dynamic Modeling (EDM) to test if insect abundances can predict insectivore dynamics (i.e. Granger Causality; Granger, 1969). This approach, while not free from spurious associations due to confounding, can capture temporal lags in associations and shifting correlations due to coupled dynamics that can be missed in linear statistical approaches. For example, if this approach showed that insects were highly predictive of insectivore dynamics, but linear approaches found no effect, then it may provide grounds to explore factors such as tightly coupled population dynamics (i.e. top-down and bottom-up controls), or lagged effects, rather than concluding there is no evidence for insect impacts and insectivore declines.

Finally, we apply several linear 'causal inference' approaches that, through different means, aim to robustly control for the cofounding effects of potential static (e.g. habitat quality) and dynamic factors (e.g. shared responses to weather) that can cause mirage associations between insect and insectivore dynamics. The fixed-effects panel estimator models used are designed to minimize the risk of Type I errors by accounting for unobserved heterogeneity and correlated external drivers. However, increased control comes with a trade-off in

interpretability and a potential increased risk for Type II errors for certain specifications of these models.

Using our specification approach, and assessing evidence holistically across different methods, we evaluate evidence for the role of changing insect abundance in insectivore decline for several insect groups and 10 insectivorous vertebrate species. Specifically, we ask three main questions: 1) are insect and insectivores long-term trends and interannual changes correlated across space? 2) Does information on insect abundance predict insectivore abundance change? 3) After controlling for shared environmental factors, is there evidence for a direct effect of insects on insectivore dynamics?

Methods

Insectivore data

Data for insectivores were derived from the National Bat Monitoring Programme (NBMP; https://www.bats.org.uk/our-work/national-bat-monitoring-programme, Barlow et al., 2015) and the Breeding Bird Survey (BBS; https://www.bto.org/our-science/projects/breeding-bird-survey, Massimino et al., 2025).

For the BBS, volunteers walk two transects across a 1km square twice a year during the bird breeding season with observations organised into four distance categories (0–25, 25–100, >100 m and flying over). To generate indices of relative local abundance, we summed observations from all categories (other than those 'flying over', as these birds may not be members of the local breeding population) and took the maximum number observed as the index of abundance. We targeted five insectivorous species that occupy a range of habitats and which specialise on different insect groups: great tit (*Parus major*), blue tit (*Cyanistes caeruleus*), grey partridge (*Perdix perdix*), skylark (*Alauda arvensis*), and corn bunting

(*Emberiza calandra*). For the skylark, we retained 'flying over' counts as skylarks sing directly over their breeding territories.

For bats we used relative abundance data from the NBMP Field and Waterway Surveys. The Field Survey captures the number of 'passes' by common and soprano pipistrelle (*Pipistrellus pipistrellus, P. pygmaeus*) at point counts along a field transect, and by noctule (*Nyctalus noctule*), and serotine (*Eptesicus serotinus*) along the walked section between each point. The Waterway Survey captures the number of Daubenton's bat (*Myotis daubentonii*) passes at point counts along a transect adjacent to a waterway. For both schemes, we generated relative indices of site-level abundance by taking the maximum number of passes for a given visit (summed across transect section). We additionally only used data from completed transects and removed sites with only zero counts (i.e. the species never occurred). One additional challenge with these data is over-dispersion in passes due to the potential for counting the same individuals more than once. Previous approaches have circumvented such issues by using alternative measures of abundance such as the number of transect sections the bats were found to occupy (Barlow et al., 2015). However, this approach removes information and adds an upper bound to the index. As we were interested in indices of relative abundance, we treated the potential for over-dispersion as a source of additional noise that we expected to be consistent across years, but we note that the bat indices are likely to have more noise relative to our bird and insect indices.

Insect data

We assembled data from four insect monitoring programmes that provide indices of relative abundance for moths, butterflies, freshwater invertebrates, and carabid beetles. Schemes for butterflies, moths, and freshwater invertebrates provide a relatively high spatial coverage at either the country or national level (England), whereas data for the beetles were available for 12 sites. We derived indices at the order level for all groups except carabids which are necessarily at the family level, and we kept moths and butterflies separate as they are

recorded in different schemes. We choose to use combined indices at the order and family level to constrain the already extensive analysis, but also because insectivores are expected to eat a variety of insect prey within an order and previous research indicates a signal of insect abundance on insectivore dynamics at the order level (Evans et al., 2024) or with combined insect indices (Martay et al., 2023). A combined index might be biased towards more detectable rather than abundant species, but there was not sufficient information on inter-specific variation in detectability to control for such effects across our insect taxa.

Data on moth abundance were derived from the Rothamsted Insect Survey light-trap network (https://www.rothamsted.ac.uk/national-capability/the-insect-survey). The traps currently operate nightly at approximately 80 sites. For a local index of population abundance we used the site-level indices produced by Harrower et al (2020) covering the period 1968–2017. These data comprise species-level indices of abundance that we subsequently converted into order level indices by summing the relevant species level indices for each site and year.

The butterfly indices were derived from the UKBMS 2019 site level indices (Botham et al., 2020). These indices are measures of relative abundance calculated using standardised methods from the data collected in the UK Butterfly Monitoring Scheme (https://ukbms.org/; Dennis et al., 2016) spanning the period 1976-2019.

Abundance data for freshwater invertebrates were extracted from the Environment Agency's ecological monitoring database which covers rivers in England (Environment Agency, 2020a). We used the pre-processing applied by Powell et al (2023) to derive indices of local abundance by summing the abundances derived from 3-min kick-samples.

Data for carabid beetles were derived from carabid beetle surveys undertaken at the terrestrial sites of the Environmental Change Network (Rennie, 2017). The surveys consist of standardised deployment of pitfall traps at twelve sites undertaken throughout the year across the period 1992-2015. Unlike the other insect data here we derived our own indices

by estimating fixed effects of yearly annual abundance. Details of our approach are presented in the supplementary materials.

Weather data

For comparisons of the predictive role of insects relative to weather, we used the HadUK gridded 5km observations (Met Office et al., 2023) which provide observations of annual and seasonal mean temperatures and total precipitation at the 5km scale (https://www.metoffice.gov.uk/research/climate/maps-and-data/data/haduk-grid/overview). We averaged these values to scale to relevant grid sizes (see below).

Pairing insects and insectivores

To select the candidate insect food source(s) we used a combination of expert opinion and literature review. Our approach was to fill matrices of potential food sources (insectivores-by-insect) using three categories: 1) insect taxon is a primary food source, 2) insect taxon is a secondary food source, or, 3) limited or no evidence of the insect taxon as a food source. The matrices were at the level of insect families nested within orders. The categorisation for the birds were undertaken by a taxon expert (*anonymised*) supported by the relevant literature. For the bats, the importance categories were conducted by *anonymised* informed by a rapid review of the diet literature for bats. The matrices and references supporting the assessments are presented in the code and data supplement (10.5281/zenodo.15037980).

After categorising food importance for our 10 species, we cross-referenced the selections with the insect data aiming to identify one or two primary candidates for the analysis. Occasionally, a key resource was not tested due to data limitations. For example, diet studies for noctule and serotine bats in the UK highlight *Scarabaeoidea* as a key resource, however, we did not have data for this beetle family. Similarly, carabid beetles are taken by grey partridge, however we had insufficient overlap between the data sets to test associations. For Diptera (true flies), we only utilised data for aquatic species (i.e. aquatic larvae), though we note most species will be primarily feeding on the adults.

Our selections are as follows, we paired blue tit and great tit with moths, corn bunting with moths and butterflies, skylark with *Carabidae,* and grey partridge with aquatic Diptera. For bats, we tested common and soprano pipistrelle with aquatic Diptera*,* noctule with aquatic Diptera and moths, serotine with aquatic Diptera and moths, and Daubenton's bat with aquatic Diptera.

Aggregating and pairing by grid squares

To combine and pair insect, insectivore, and weather data, we used a grid-based approach using the Ordnance Survey national grid reference system. To generate grid level indices, we averaged, for each year, the data for each insect, insectivore, and weather index at three scales 100km, 50km and 10km grid squares. This resulted in time series of relative abundance for each taxon at the different spatial aggregations. Insect-insectivore time series where then paired within each grid square to test for an impact of insect abundance on insectivore dynamics (Figure 1).

Our grid-based approach is one of several potential methods for linking proximate surveying sites from the different monitoring schemes. We favoured this approach for several reasons. First, it provides a simple and objective method to tie together indices at fixed levels of aggregation without concern for utilising the same data in multiple comparisons. Second, it's a well-utilised reference system that situates the trends and dynamics of the target species within a recognisable spatial context. Finally, we take advantage of the nesting structure of the national grid system with smaller spatial units within larger ones to correlate standard errors in the fixed effects panel estimators (see below). A downside of the grid-based approach is that there might be sites near the edges of grids that are closer in geographic space, but which are nevertheless assessed in different pairings, however we view this as a reasonable trade-off given the described advantages.

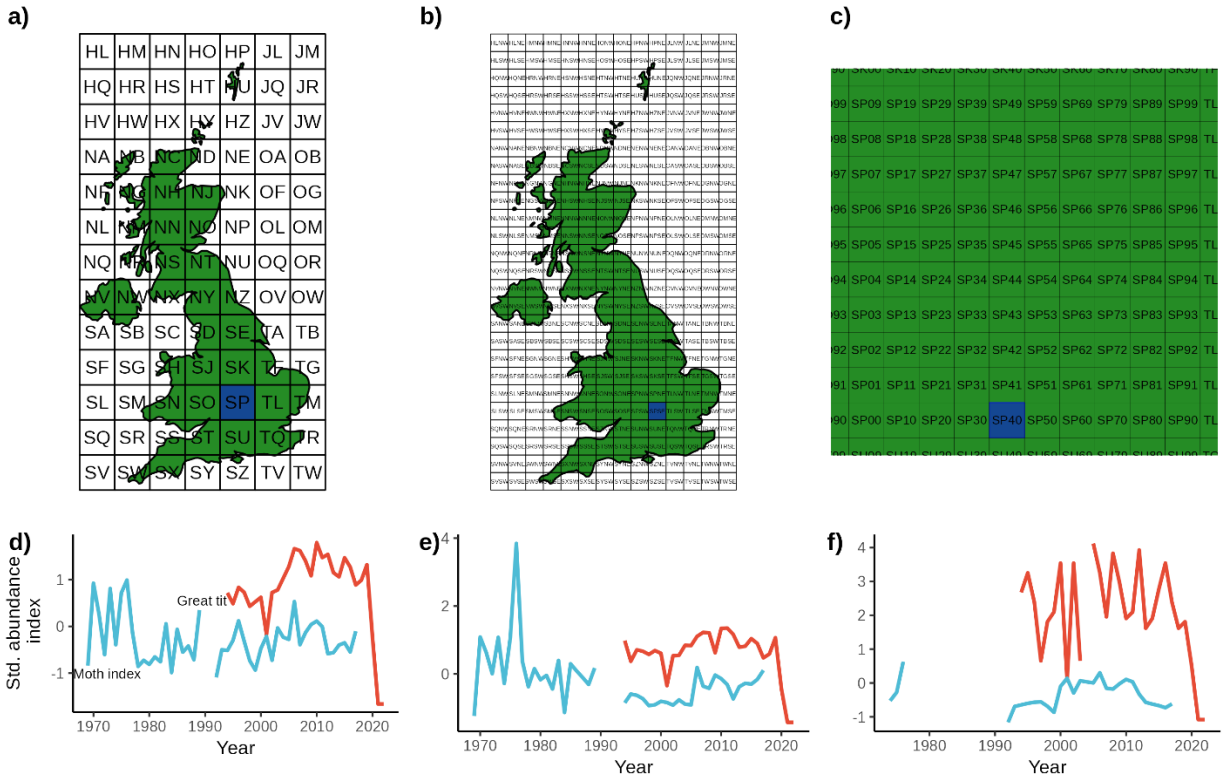


Figure 1. Demonstration of the grid-based strategy a) 100km, b) 50km, and c) 10km grid squares. d), e), and f) show the generated standardised abundances for the great tit (red line) and moth index (blue line) for a selected (and nested) grid square at each scale. Grid squares vary in coverage across space and time with the indices becoming sparser at higher spatial resolutions.

Overall analytic strategy

We used three approaches 1) *association*, 2) *prediction*, and 3) *causal inference* to test the main hypotheses. For *association,* we used Seasonal and Trend decomposition using Loess (STL; Cleveland et al., 1990) which partitions a time series into a trend and remainder. The trend captures the long-term trajectory of the population, and the remainder captures inter-annual fluctuations. For *prediction*, we used Empirical Dynamic Modelling (specifically Gaussian process regression EDM; Munch & Rogers, 2024). This method can assess potential links (including non-linear and time-varying interactions) between insects and insectivores by demonstrating how prediction accuracy increases with the inclusion of

certain variables (i.e. Granger causality, Granger, 1969; Shojaie & Fox, 2022). Finally for *causal inference,* we used a panel of fixed effects estimators (Wooldridge, 2010). These tested for linear interactions after controlling for static grid-level average differences in population growth and shared dynamic effects (i.e. shared yearly environmental effects), while utilising clustered standard errors to capture correlated errors within regions (i.e. 100km squares).

Association: STL decomposition

We decomposed each time series into a long-term trend and remainder (interannual change beyond the trend) by applying STL at all three spatial scales for time series with five or more years of consecutive abundance data. We used STL as it splits time-series' into trends and remainders which allows us to separately evaluate if the trends in insectivores and insects are correlated across space or if interannual changes beyond the trend is correlated (suggestive of either direct effect or shared environmental responses). As STL cannot incorporate missing data we took the longest consecutive run of data at each spatial scale keeping only those grids where there were at least ten years of data, excluding sites where >50% of the time-series was zero as they provide little information on trend. After decomposing the time series, we assessed the correlation in both trend and remainder for each insect-insectivore pairing. For the remainder, we calculated the Pearson correlation for each grid pairing and then calculated the average and standard error to assess if there was evidence of a positive (or negative) association. For the trend, we initially fitted a mixed linear model for each species with abundance as the dependent variable and year fitted as a continuous variable, and with random correlated slopes and intercepts for each grid square. We then took the values of these slopes for insect and insectivore and split them into two categories: increasing or decreasing. We then assessed if there was more agreement in the direction of these slopes than expected by chance through a binomial test.

Prediction: Gaussian process regression empirical dynamic modelling

Our framework for EDM was gaussian-process empirical dynamic modelling with automatic relevance determination, applied through the GPEDM package (Munch & Rogers, 2024) . This hierarchical approach utilises time-delay embedding and shared information across spatial replicates to construct approximations of the state-space manifold, thereby capturing the system dynamics alongside estimating the underlying dynamic correlation i.e. the similarity in the underlying dynamics across sites. An accessible overview of the EDM approaches are provided by Chang et al. (2017) and Edwards et al. (2024).

We used a time-delay of one year, and to constrain the complexity of the models a maximum embedding dimension of three years. To assess the role of insect abundance in insectivore dynamics we fitted 10 GPEDM models for each insectivore-insect pairing at each scale. This consisted of five direct comparisons: 1) insectivore only vs insectivore and insect; 2) insectivore and spring weather variables vs insectivore, insect, and spring weather variables; 3) insectivore and summer weather variables vs insectivore, insect, and summer weather variables; 4) insectivore and winter weather variables vs insectivore, insect, and winter weather variables; and 5) insectivore and annual weather variables vs insectivore, insect, and annual weather variables.

Out-of-sample predictive performance was estimated through leave-one-timepoint-out validation (Munch & Rogers, 2024). To handle missing data, we identified the longest consecutive run of time series data for each grid square and utilised that in the analysis.

Causal inference: Fixed effects panel estimator

The fixed effects panel estimator is a regression-based approach that attempts to estimate ‘causal’ effects by controlling for static (site-level) and dynamic confounding (year-level) effects. These approaches can be preferable to random effects models for causal inference as they make no distributional assumptions about variation across units and induce no shrinkage; they also make no assumptions of independence between the site-level

characteristics and independent variables and are unbiased when the independent variables are correlated with unobserved heterogeneity – factors expected to be common in observational data (Byrnes & Dee, 2025). However, estimation differs, as rather than modelling site and year-level variation as draws from a normal distribution, the static and dynamic effects are eliminated through de-meaning the independent and dependent variables prior to the regression, e.g. centering the independent and dependent variable at each site. When only site (unit-level) fixed effects are included, we estimate how within-unit deviations from the site mean are influenced by the independent variables. When only time effects are included, the coefficients for the independent variables represent the average (across all years) of how differences in the independent variables between sites within a given year are associated with differences in the dependent variable across sites in that same year. But when both site and time level effects are included, the coefficient of interest represents a complex combination of within-year and across unit contrasts which is both challenging to interpret and can generate bias under certain circumstances (De Chaisemartin & d'Haultfoeuille, 2020; Goodman-Bacon, 2021; Kropko & Kubinec, 2020). However, including both site and year fixed effects provides robust control for shared 'shocks' (insectivores and insects responding similarly in a given year due to unmeasured confounding factors e.g. a drought). Therefore, in line with our overall specification approach, we specify a set of different models that vary in controls generating results that can be interpreted holistically.

The first model was a one-way fixed effect model, with a fixed effect at the unit level (each grid square at a given scale). This model aims to control for unmeasured time-invariant unit-level confounds (e.g. habitat) and estimates the within unit effect of insect abundance on insectivore growth rate. However, this model provides limited control for possible time-varying factors/shocks (such as shared responses of insects and insectivores to extreme weather). For the 10km and 50km scales, we included some control for time varying factors through clustered standard errors at the regional level (100km) which account for spatially

structured environmental shocks that may induce correlations in the residuals of nearby units. The second model was a two-way fixed effects model including an additional fixed effect at each year that aimed to additionally control for time-varying shocks. But as stated above, we are asking an unusual question: *in a given year, do sites with more insect abundance than other sites experience higher population growth relative to the average at these sites?* The final two models had the same fixed effect structures as the above two models, but additionally include covariates for annual temperature and precipitation. Here for the one-way fixed effect, this attempts to adjust for the shared responses to climate, which, if a main determinant of shared annual responses across sites, should provide better estimates of the impact of changing insect abundance on insectivores. However, these models will not control for all unmeasured temporal factors, especially those uncorrelated with the climatic variables. And finally, the two-way fixed effect has the same benefits and limitations as above, but additionally controls for the effect of shared climate.

The models were instantiated within a linearized Gompertz equation (Equation 1) predicting the log growth rate – the log ratio of the current and previous years population size.

Equation 1:

$$log(\Delta insectivore_{it}) = \log\left(Insectivore\right)_{i(t-1)} + Site_i + Year_t + Insect_{it} + Insect_{i(t-1)} + \epsilon_{ir}$$

With *i* relating to each unit (10km/50km/100km grid square) and *t* to each year. In the panel estimator standard errors were clustered by the unit (*i)* at 100km and region (*r*) and unit for the 50 and 10km models*.* In this equation, we show the framework for the 50 or 10km model including the fixed effects for year ($Year_t$) - though this fixed effect is not present in models 1 and 3. As we were working with log growth rates, we needed to deal with zeros indices as they result in undefined growth rates. We first removed sites for the insectivores that contained more than 50% zeros as they induce considerable dilution in assessing relationships to insect abundance. For the remaining sites, we computed growth as the change in log(y+1) between consecutive years. This transformation prevents the undefined growth rates and retains observations where populations crash to, or recover from, zero,

which are ecologically meaningful events. However, we recognise adding one alters the scale of the growth rate and may disproportionately affect low counts, but we accepted this trade-off to capture important losses and gains in the abundance indices. All models were fitted using the *feols* function in the *fixest* package (Bergé, 2018).

All analysis was undertaken in R 4.2 with the code and data in support of the results available at 10.5281/zenodo.15037980.

Results

As there are several results from each of insect-insectivore pairing, we present detailed results for great tits and moths and provide full results in the supplementary materials and code supplement.

Association: Correlations between trends and dynamics

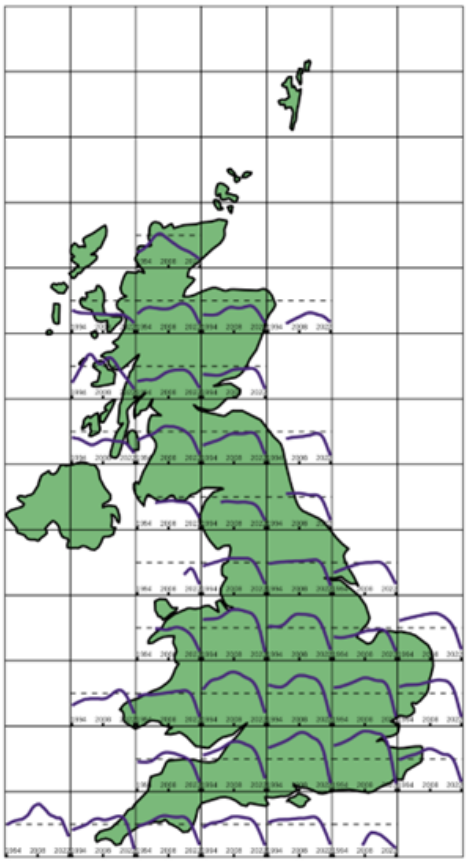
All birds showed evidence of decline across all scales, but none of the bat species showed evidence of overall decline (Figure 2).

For indices of insect abundance, we found consistent negatives trends across all scales with only the moth index showing no change at 100km and 50km, but negative trends at the 10km scale.

a

Taxa	100km	50km	10km
Blue tit	↘	↘	↘
Great tit	↘	↘	↘
Corn bunting	↘	↘	↘
Grey partridge	↘	↘	↘
Skylark	↘	↘	↘
Common pipistrelle	→	→	→
Soprano pipistrelle	→	→	↗
Noctule	→	→	→
Serotine	→	→	→
Daubenton's bat	→	→	→
Moth index	→	→	↘
Butterfly index	↘	↘	↘
Diptera index	↘	↘	↘
Beetle index	↘	-	-

b



441

442 Figure 2. a) Summary of average linear trends for insectivores and insect indices at different
443 grid aggregations. Positive trends are indicated by ↗, negative trends are indicated by ↘, and
444 no change is shown by →. Scales without data presented are indicated by -. b) Trends
445 across space for the great tit at 100km.

446 There were few simple associations between the trends in insects and insectivores, though
447 both the great tit and blue tit showed positive correlations with moths at the 50 and 10km
448 scales and there was a positive association between butterflies and the corn bunting at the
449 100km scale (Figure 3). For inter-annual change, we found positive associations for blue tit
450 and moths, and noctule and Diptera at the 10km scale, and negative associations between,
451 Daubenton's bat and Diptera at the 100 and 50 km scale.

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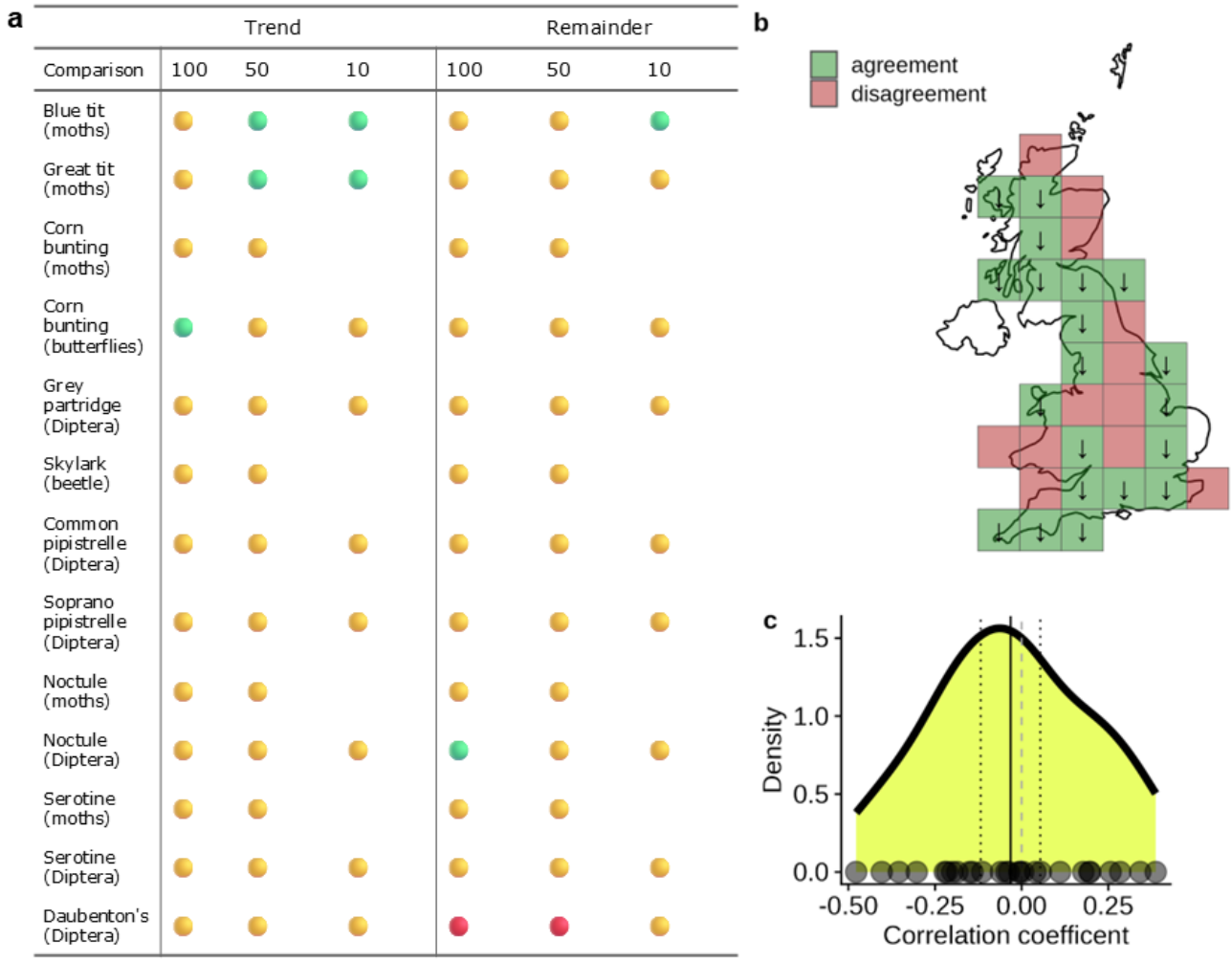

Figure 3. Associations between trends and the remainder (interannual change) for insectivore-insect pairs. a) Correlations between insectivores and food indices for trends and remainders across scales. The green points represent positive associations, the red points negative associations, and the yellow points uncertain associations. b) shows how trends for the great tit and the moth index compare at the 100km scale with locations where the trends have the same sign shown in green and locations where trends have the opposite sign in red. The arrows within each grid-square indicate the trend direction where there is agreement. c) Distribution of correlations between the remainders within 100km grid squares for the great tit and moth index. The solid black line shows the mean correlation, dotted lines show 95% confidence intervals, and a grey dashed line indicates zero.

Prediction: Empirical dynamic modelling

Predictive skill generally increased when including insect indices, although with considerable variability across scales and controls (Figure 4). Improvements in predictive skill were also typically small and overall performance degraded at smaller scales. For six insectivore species (great tit, grey partridge, skylark, common pipistrelle, noctule and Daubenton's bat) the majority of the best models across different scales included the insect data. The only species where none of the best models included the insect variable was corn bunting regarding butterflies.

a

Scale	Comparison	Blue tit (moths)	Great tit (moths)	Corn bunting (moths)	Corn bunting (butterflies)	Grey partridge (diptera)	Skylark (beetle)	Common pipistrelle (Diptera)	Soprano pipistrelle (Diptera)	Noctule (moths)	Noctule (Diptera)	Serotine (moths)	Serotine (Diptera)	Daubenton's (Diptera)
	Insect	(✓)	✓	(✓)	✓	✓	✓	✗	✓	✗	✓	(✗)	✗	✓
	Spring	✓	✓	✗	(✗)	(✓)	✓	✓	(✓)	✗	✓	✓	✗	(✓)
100	Summer	✓	(✓)	✗	✗	✓	✓	✓	✓	✗	(✗)	✗	✗	✗
	Winter	✓	✓	✓	✗	✓	✗	✓	✓	(✗)	✓	✗	(✓)	✓
	Annual	✓	✗	✗	✗	✓	(✓)	(✓)	✗	✗	✓	✗	✓	✗
	Insect	✗	✗	✓	✓	(✓)	✗	✗	✓	✗	✗	(✓)	✓	(✗)
	Spring	✗	✗	✓	✗	✓	✗	(✓)	✓	✓	(✓)	✗	✓	✗
50	Summer	(✗)	(✓)	✓	✓	✗	✓	✗	✓	✗	✓	✓	(✗)	✓
	Winter	✗	✗	✓	✗	✓	(✓)	✓	(✗)	(✓)	✓	✗	✗	✓
	Annual	✗	✗	(✗)	(✗)	✓	✓	✗	✓	✓	✓	✓	✓	✗
	Insect	(✗)	✓		✗	(✓)		✓	✓		✗		✓	(✓)
	Spring	✓	✗		✗	✗		(✓)	✓		✓		(✗)	✓
10	Summer	✗	✗		✗	✗		✓	✗		✗		✓	✓
	Winter	✗	(✗)		✓	✓		✓	(✓)		✗		✓	✗
	Annual	✗	✓		(✗)	✗		✗	✓		(✓)		✓	✗

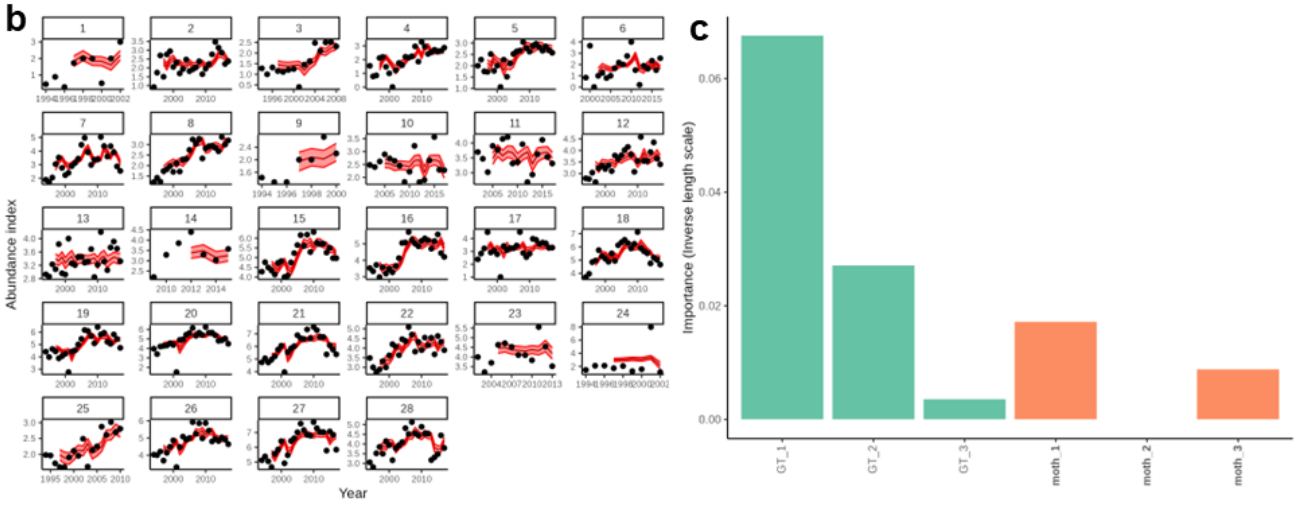

Figure 4. a) Model comparisons for EDM, for each comparison ✗ indicates that the model without insects had highest R^2, ✓ the insect model had highest R^2 and the symbol in brackets was the single best model at that scale. Results for great tit at 100km scale for the insect and insectivore model with b) time series of abundance for a selection of 100km grid-squares with the EDM predictions shown in red and, c) inverse-length scale from the auto relevance determination reflecting the inferred importance of each time-lagged input for predictive performance. GT 1:3 refers to lags of great tit abundance while moth 1:3 refers to lags of moth abundance.

Causal links: Fixed effects panel estimator

For the fixed effects panel estimators, evidence for direct effects of insects on insectivores was mixed (Figure 5). Positive links included those for great tit, blue tit, common pipistrelle, grey partridge and noctule, but this varied between model specification and scale – with sometimes the lag or sometimes the concurrent measure of insect abundance showing the effect (e.g. for the blue tit). We also identified negative links for the serotine, soprano pipistrelle and blue and great tit for the concurrent index abundance at some scales. In general, where effects were detected, they were for model specifications 1 and 3 that included only unit level fixed effects and climate controls.

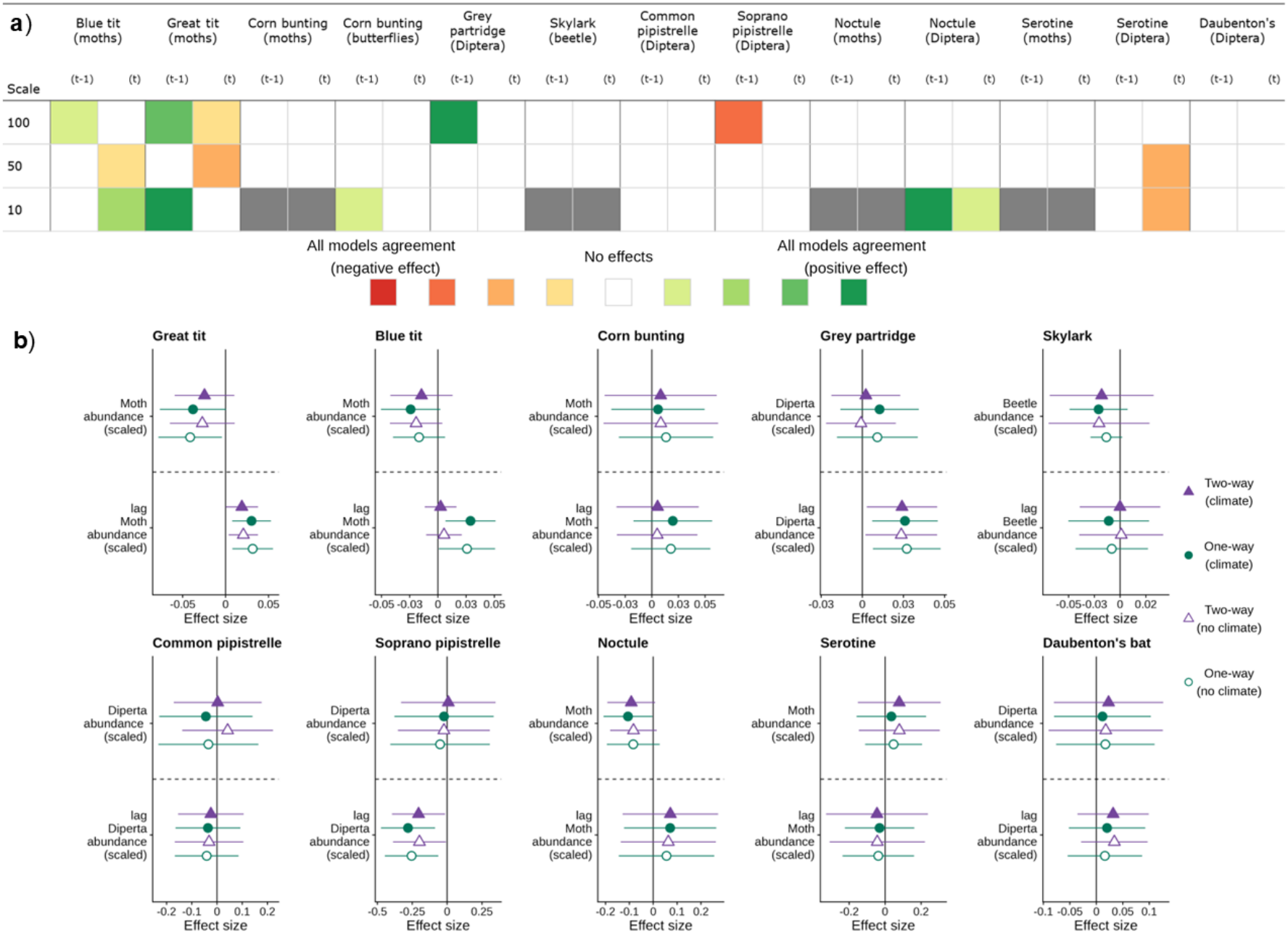
a)
Blue tit (moths)
Great tit (moths)
Corn bunting (moths)
Corn bunting (butterflies)
Grey partridge (Diptera)
Skylark (beetle)
Common pipistrelle (Diptera)
Soprano pipistrelle (Diptera)
Noctule (moths)
Noctule (Diptera)
Serotine (moths)
Serotine (Diptera)
Daubenton's (Diptera)
(t-1)
(t)
Scale
100
50
10
All models agreement (negative effect)
No effects
All models agreement (positive effect)
b)
Great tit
Blue tit
Corn bunting
Grey partridge
Skylark
Common pipistrelle
Soprano pipistrelle
Noctule
Serotine
Daubenton's bat
Moth abundance (scaled)
lag Moth abundance (scaled)
Diperta abundance (scaled)
lag Diperta abundance (scaled)
Beetle abundance (scaled)
lag Beetle abundance (scaled)
Effect size
Two-way (climate)
One-way (climate)
Two-way (no climate)
One-way (no climate)

Figure 5. a) Summary of results from the fixed effects panel estimators. The colours (red or green hues) represent the direction of the effect while the strength of the hue shows the number of models where a significant effect was detected, a grey square indicates the analysis was not conducted at this scale. b) Forest plots of the effect of concurrent and lagged insect abundances on population change for comparisons at the 100km scale.

Discussion

We have provided a holistic assessment of evidence for impacts of insect abundance on the dynamics and trends of 10 vertebrate insectivore species in the UK. We explored three key questions: 1) are long-term trends and interannual variation between insect and insectivore pairings correlated over space? 2) Does information on insect abundance predict insectivore abundance change? 3) After controlling for shared static and dynamic environmental factors, is there evidence for a direct effect of insects on insectivore dynamics?

Firstly, we found few spatial associations in trends between insects and insectivores. This despite all bird species and almost all indices of insect abundance showing evidence of declines (this being consistent with other analyses for these taxa; Bell et al., 2020; Brooks et al., 2012, though also dependent time-series length and analytic method e.g. Woodward et al., 2020). The only positive associations between trends across space were for the blue tit, great tit, and corn bunting. This suggests that, though the populations of these insectivore species and insects are declining on average, they are not necessarily declining in the same locations. No bat species were declining on average and, consequently, it is reasonable to assume that, so far and for the specific species groups we investigated, declines in the insect groups tested are not leading to declines in UK bat abundance (although they may still impact population growth rates).

Overall, this first level of associative testing, though lacking control for possible confounds, provides a high-level overview of spatial patterns, and suggests that declines in the insect groups tested are unlikely to be a primary cause of decline for most of the insectivores we assessed. This is plausible as there is evidence that declines to both insects and insectivores result from a combination of several drivers including land use change, agricultural intensification, and changing climate (Pearce-Higgins & Morris, 2023; Wagner, Grames, et al., 2021). The contrast in spatial patterning in insect and insectivores suggests that some of these drivers of change may be non-overlapping, or at least, the importance of

the drivers may vary between the insects and insectivores. Further evaluation of the underlying causes of regional variation in trends for both insects and insectivores, and the generality of such patterns, would therefore be highly valuable.

For those species where we found associations with insect indices, it was necessary to assess if insect abundance was impacting dynamics after controlling for possible confounds. Similarly, even for those species where there were no associations in trends, it is possible that low insect abundance could cause reduced population numbers in particular years and, for the bats, where we found limited evidence of populations declining, it may still be the case that populations may have been higher, and trends more positive, had insect abundance not decreased.

We found that inclusion of information on insects generally improved the predictive skill of the EDMs, but by only small amounts. Model performance also declined at finer spatial scales, suggesting either increased noise or reduced time-series lengths, reduced our ability to capture dynamics. Generally, when assessing both predictive and statistical criteria, results were mixed and demonstrated scale dependency. Handling variation across scales is challenging as it influences signal-noise relationships alongside coverage of the data across time and space. These issues are also related to the challenge of generating site-level or regional trends given a particular scheme. For example, for butterflies, local trends and abundance indices have been utilised frequently to understand local drivers of population dynamics, but it remains challenging to estimate robust bat population trends at scales smaller than country-level, due to smaller sample sizes.

We next applied panel estimators to robustly handle shared dynamic and static factors influencing populations and isolate the direct (linear) effect of insects on insectivores. As with the EDMs, we found limited conclusive evidence of a direct effect of insect abundance on insectivore populations. Positive links across the majority of scales tested (but not for all model specifications) were only found for blue tit, and great tit. We also found evidence of positive links for grey partridge, corn bunting, and noctule but only at one scale. However,

we also found a handful of negative links in either the lag or concurrent insect abundance at at least one scale for blue tit, great tit, soprano pipistrelle and serotine. Ignoring data limitations, the occurrence of negative links and the disconnect between the EDM and the panel estimators could suggest that links between insects and insectivores are not simply bottom-up linear effects (insects influence insectivore abundance) but may include a variety of processes. For example, top-down effects, which have been observed to operate in both bird- and bat-insect systems (Beilke & O'Keefe, 2023; Holmes et al., 1979), could generate apparent reverse causation that complicates interpretation, and lagged responses from insectivores combined with density dependence in the insect populations might generate apparent negative relationships. While not feasible given this broad survey, close examination of non-linear approaches like EDM, against a variety of plausible top-down and bottom-up causal structures assessed through linear statistical approaches may help to identify any complex or non-linear associations.

Overall, our analysis of trends and links between insectivores and insect food indices provides some evidence that populations of great tit, blue tit, and grey partridge, may be influenced by the abundance of their insect prey. For the blue tit, this link is also consistent with results from Evans et al (2024) albeit using different methods and different aggregations of the underlying data. For the remaining bird species, we provide limited evidence that the abundance of the insect prey assessed is driving dynamics or declines. These results may be surprising as there is considerable circumstantial evidence that insectivorous birds are impacted by changing insect abundance (Tallamy & Shriver, 2021). Evidence from synthesis (Grames et al., 2023) and studies utilising monitoring data (Martay et al., 2023; Yazdanian et al., 2024) also strongly suggest a link between insect abundance and either insectivore vital rates or distributions. None of these studies, however, evaluate, or find, a direct link between insect abundance and population changes in insectivores per se. Consequently, it may be that limitations with the data (see below) or the complex influence of multiple drivers acting

584 on both insect and insectivore populations makes it challenging to detect direct links
585 between insect and insectivores population change at large scales.

586 None of the bat species were declining on average, and although we found some evidence
587 (using EDM) that insect abundance provided some predictive information for bats, there was
588 only one positive link using the panel estimators (noctule and Diptera). It is challenging to
589 link bat populations trends to trends in their insect prey (though see Langton et al., 2010;
590 Vaughan et al., 1996). Bat populations in the UK are at historic lows likely due to habitat
591 change (Razgour et al., 2024) and, therefore, changes to insect abundance may not be a
592 main factor limiting populations. Bats are also highly mobile foragers allowing them to exploit
593 ephemeral concentrations of aerial insects, which might mitigate the effects of reductions in
594 local insect abundances. In sum, this analysis does not provide evidence that bat
595 populations are limited by changing abundance of the insect groups tested here, though we
596 identify that generating more robust regional trends for bats and assessing both the potential
597 for top-down bottom-up dynamics could better clarify links between bat populations and their
598 prey in the UK.

599 Although we covered several methodological possibilities in our specification approach, we
600 recognise limitations in our analyses. Principally, the data used to make comparisons
601 between insects and insectivores are not from the same locations and the underlying indices
602 were not designed with the analysis undertaken here in mind. Additionally, the coarseness of
603 the population aggregations and insect food indices might introduce considerable noise, and
604 targeted analyses using data collected from key insect species (or a combination of key
605 species) in the same location as insectivore populations might reveal stronger effects. More
606 sophisticated approaches to generating such insect food indices, such as weighting by
607 insect food preference, or using biomass, might similarly identify stronger effects of changing
608 insect abundance. Nevertheless, we hope this research has identified plausible avenues for
609 further research into trophic links between populations at large scales and identified
610 considerations regarding scale and method when conducting such analyses.

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Code and Data

Code and data in support of the manuscript is available at 10.5281/zenodo.15037980

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References

Barlow, K., Briggs, P., Haysom, K., Hutson, A., Lechiara, N., Racey, P., Walsh, A., & Langton, S. (2015). Citizen science reveals trends in bat populations: The National Bat Monitoring Programme in Great Britain. *Biological Conservation*, *182*, 14–26.

Beilke, E. A., & O'Keefe, J. M. (2023). Bats reduce insect density and defoliation in temperate forests: An exclusion experiment. *Ecology*, *104*(2), e3903.

Bell, J. R., Blumgart, D., & Shortall, C. R. (2020). Are insects declining and at what rate? An analysis of standardised, systematic catches of aphid and moth abundances across Great Britain. *Insect Conservation and Diversity*, *13*(2), 115–126. https://doi.org/10.1111/icad.12412

Bergé, L. (2018). Efficient estimation of maximum likelihood models with multiple fixed-effects: The R package FENmlm. *CREA Discussion Papers*, *13*.

Botham, M., Brereton, T., Harrower, C., Middlebrook, I., & Roy, D. B. (2020). *United Kingdom Butterfly Monitoring Scheme: Site indices 2019*. NERC Environmental Information Data Centre. https://doi.org/10.5285/180a1c76-bceb-4264-872b-deddfe67b3de

Bowler, D. E., Heldbjerg, H., Fox, A. D., de Jong, M., & Böhning-Gaese, K. (2019). Long-term declines of European insectivorous bird populations and potential causes. *Conservation Biology*, *33*(5), 1120–1130. https://doi.org/10.1111/cobi.13307

Brooks, D. R., Bater, J. E., Clark, S. J., Monteith, D. T., Andrews, C., Corbett, S. J., Beaumont, D. A., & Chapman, J. W. (2012). Large carabid beetle declines in a United Kingdom monitoring network increases evidence for a widespread loss in insect biodiversity. *Journal of Applied Ecology*, *49*(5), 1009–1019. https://doi.org/10.1111/j.1365-2664.2012.02194.x

Byrnes, J. E., & Dee, L. E. (2025). Causal inference with observational data and unobserved confounding variables. *Ecology Letters*, *28*(1), e70023.

Chang, C.-W., Ushio, M., & Hsieh, C. (2017). Empirical dynamic modeling for beginners. *Ecological Research*, *32*(6), 785–796. https://doi.org/10.1007/s11284-017-1469-9

Clayton, S. (2003). Environmental identity: A conceptual and an operational definition. *Identity and the Natural Environment: The Psychological Significance of Nature/The MIT Press*.

Cleveland, R. B., Cleveland, W. S., McRae, J. E., & Terpenning, I. (1990). STL: A seasonal-trend decomposition. *J. off. Stat*, *6*(1), 3–73.

De Chaisemartin, C., & d'Haultfoeuille, X. (2020). Two-way fixed effects estimators with heterogeneous treatment effects. *American Economic Review*, *110*(9), 2964–2996.

Dennis, E. B., Morgan, B. J. T., Freeman, S. N., Brereton, T. M., & Roy, D. B. (2016). A generalized abundance index for seasonal invertebrates. *Biometrics*, *72*(4), 1305–1314. https://doi.org/10.1111/biom.12506

Didham, R. K., Basset, Y., Collins, C. M., Leather, S. R., Littlewood, N. A., Menz, M. H. M., Müller, J., Packer, L., Saunders, M. E., Schönrogge, K., Stewart, A. J. A., Yanoviak, S. P., & Hassall, C. (2020). Interpreting insect declines: Seven challenges and a way forward. *Insect Conservation and Diversity*, *13*(2), 103–114. https://doi.org/10.1111/icad.12408

Edwards, A. M., Rogers, L. A., & Holt, C. A. (2024). Explaining empirical dynamic modelling using verbal, graphical and mathematical approaches. *Ecology and Evolution*, *14*(5), e10903. https://doi.org/10.1002/ece3.10903

Evans, L. C., Burgess, M. D., Potts, S. G., Kunin, W. E., & Oliver, T. H. (2024). Population links between an insectivorous bird and moths disentangled through national-scale monitoring data. *Ecology Letters*, *27*(1), e14362.

Forister, M. L., Pelton, E. M., & Black, S. H. (2019). Declines in insect abundance and diversity: We know enough to act now. *Conservation Science and Practice*, *1*(8), e80.

Goodman-Bacon, A. (2021). Difference-in-differences with variation in treatment timing. *Journal of Econometrics*, *225*(2), 254–277.

Gould, E., Fraser, H. S., Parker, T. H., Nakagawa, S., Griffith, S. C., Vesk, P. A., Fidler, F., Hamilton, D. G., Abbey-Lee, R. N., & Abbott, J. K. (2023). *Same data, different analysts: Variation in effect sizes due to analytical decisions in ecology and evolutionary biology*. *BMC Biology, 23*(1), 35.

Goulson, D. (2019). The insect apocalypse, and why it matters. *Current Biology*, *29*(19), R967–R971.

Grames, E. M., Montgomery, G. A., Youngflesh, C., Tingley, M. W., & Elphick, C. S. (2023). The effect of insect food availability on songbird reproductive success and chick body condition: Evidence from a systematic review and meta-analysis. *Ecology Letters*, *26*(4), 658–673.

Hallmann, C. A., Foppen, R. P., Van Turnhout, C. A., De Kroon, H., & Jongejans, E. (2014). Declines in insectivorous birds are associated with high neonicotinoid concentrations. *Nature*, *511*(7509), 341–343.

Hallmann, C. A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., Stenmans, W., Müller, A., Sumser, H., Hörren, T., Goulson, D., & de Kroon, H. (2017). More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLOS ONE*, *12*(10), e0185809–e0185809. https://doi.org/10.1371/journal.pone.0185809

Hallmann, C. A., Zeegers, T., van Klink, R., Vermeulen, R., van Wielink, P., Spijkers, H., van Deijk, J., van Steenis, W., & Jongejans, E. (2020). Declining abundance of beetles, moths and caddisflies in the Netherlands. *Insect Conservation and Diversity*, *13*(2), 127–139. https://doi.org/10.1111/icad.12377

Harrower, C. A., Bell, J. R., Blumgart, D., Botham, M. S., Fox, R., Isaac, N. J. B., Roy, D. B., & Shortall, C. R. (2020). *Moth trends for Britain and Ireland from the Rothamsted Insect Survey light-trap network (1968 to 2016)*. NERC Environmental Information Data Centre. https://doi.org/10.5285/0a7d65e8-8bc8-46e5-ab72-ee64ed851583

Holmes, R. T., Schultz, J. C., & Nothnagle, P. (1979). Bird predation on forest insects: An exclosure experiment. *Science*, *206*(4417), 462–463.

Kropko, J., & Kubinec, R. (2020). Interpretation and identification of within-unit and cross-sectional variation in panel data models. *PLOS ONE*, *15*(4), e0231349. https://doi.org/10.1371/journal.pone.0231349

731 Martay, B., Leech, D. I., Shortall, C. R., Bell, J. R., Thackeray, S. J., Hemming, D. L., & Pearce-Higgins, J.
732 W. (2023). Aerial insect biomass, but not phenological mismatch, is associated with chick
733 survival of an insectivorous bird. *Ibis, 165*(3), 790-807.
734 Massimino, D., Baillie, S. R., Balmer, D. E., Bashford, R. I., Gregory, R. D., Harris, S. J., Heywood, J. J.
735 N., Kelly, L. A., Noble, D. G., Pearce-Higgins, J. W., …, & Gillings, S. (2025). The Breeding Bird
736 Survey of the United Kingdom. *Global Ecology and Biogeography*, *34*(1), e13943.
737 https://doi.org/10.1111/geb.13943
738 Met Office, D Hollis, McCarthy, M., Kendon, M., & Legg, T. (2023). *HadUK-Grid Gridded Climate*
739 *Observations on a 5km grid over the UK, v1.2.0.ceda (1836-2022).* [Dataset]. NERC EDS
740 Centre for Environmental Information Data Centre Analysis.
741 https://doi.org/10.5285/abf1a6cf830b4f5385c5d73609df8423
742 Molenaar, E., Viechtbauer, W., van de Crommenacker, J., & Kingma, S. A. (2024). Neonicotinoids
743 Impact All Aspects of Bird Life: A Meta-Analysis. *Ecology Letters*, *27*(10), e14534.
744 https://doi.org/10.1111/ele.14534
745 Müller, J., Hothorn, T., Yuan, Y., Seibold, S., Mitesser, O., Rothacher, J., Freund, J., Wild, C., Wolz, M.,
746 & Menzel, A. (2023). Weather explains the decline and rise of insect biomass over 34 years.
747 *Nature*, *628*(8007), 349-35. https://doi.org/10.1038/s41586-023-06402-z
748 Munch, S., & Rogers, T. (2024). *GPEDM: Gaussian Process regression for Empirical Dynamic Modeling*
749 (Version R package version 0.0.0.9008) [Computer software].
750 https://tanyalrogers.github.io/GPEDM
751 Oliver, T., Roy, D. B., Hill, J. K., Brereton, T., & Thomas, C. D. (2010). Heterogeneous landscapes
752 promote population stability. *Ecology Letters*, *13*(4), 473–484.
753 https://doi.org/10.1111/j.1461-0248.2010.01441.x
754 Pearce-Higgins, J. W., & Morris, R. K. (2023). Declines in invertebrates and birds–could they be linked
755 by climate change? *Bird Study*, *69*(3-4), 59-71.

Powell, K. E., Oliver, T. H., Johns, T., González-Suárez, M., England, J., & Roy, D. B. (2023). Abundance trends for river macroinvertebrates vary across taxa, trophic group and river typology. *Global Change Biology*, *29*(5), 1282–1295. https://doi.org/10.1111/gcb.16549

Razgour, O., Montauban, C., Festa, F., Whitby, D., Juste, J., Ibáñez, C., Rebelo, H., Afonso, S., Bekaert, M., & Jones, G. (2024). Applying genomic approaches to identify historic population declines in European forest bats. *Journal of Applied Ecology*, *61*(1), 160–172.

Rennie, C., S. ;Adamson, J. ;Anderson, R. ;Andrews, C. ;Bater, J. ;Bayfield, N. ;Beaton, K. ;Beaumont, D. ;Benham, S. ;Bowmaker,… M. ;Wood. (2017). *UK Environmental Change Network (ECN) carabid beetle data: 1992-2015*. NERC Environmental Information Data Centre. https://doi.org/10.5285/8385f864-dd41-410f-b248-028f923cb281

Rigal, S., Dakos, V., Alonso, H., Auniņš, A., Benkő, Z., Brotons, L., Chodkiewicz, T., Chylarecki, P., de Carli, E., del Moral, J. C., … Devictor, V. (2023). Farmland practices are driving bird population decline across Europe. *Proceedings of the National Academy of Sciences*, *120*(21), e2216573120. https://doi.org/10.1073/pnas.2216573120

Simonsohn, U., Simmons, J. P., & Nelson, L. D. (2019). Specification curve: Descriptive and inferential statistics on all reasonable specifications. *Available at SSRN 2694998*.

Stanton, R., Morrissey, C., & Clark, R. (2018). Analysis of trends and agricultural drivers of farmland bird declines in North America: A review. *Agriculture, Ecosystems & Environment*, *254*, 244–254.

Sugihara, G., May, R., Ye, H., Hsieh, C., Deyle, E., Fogarty, M., & Munch, S. (2012). Detecting causality in complex ecosystems. *Science*, *338*(6106), 496–500.

Tallamy, D. W., & Shriver, W. G. (2021). Are declines in insects and insectivorous birds related? *Ornithological Applications*, *123*(1), duaa059. https://doi.org/10.1093/ornithapp/duaa059

van der Sluijs, J. P. (2020). Insect decline, an emerging global environmental risk. *Current Opinion in Environmental Sustainability*, *46*, 39–42.

781 Wagner, D. L., Fox, R., Salcido, D. M., & Dyer, L. A. (2021). A window to the world of global insect
782 declines: Moth biodiversity trends are complex and heterogeneous. *Proceedings of the*
783 *National Academy of Sciences*, *118*(2), e2002549117.
784 https://doi.org/10.1073/pnas.2002549117
785 Wagner, D. L., Grames, E. M., Forister, M. L., Berenbaum, M. R., & Stopak, D. (2021). Insect decline in
786 the Anthropocene: Death by a thousand cuts. *Proceedings of the National Academy of*
787 *Sciences*, *118*(2), e2023989118.
788 Warren, M. S., Maes, D., van Swaay, C. A. M., Goffart, P., Van Dyck, H., Bourn, N. A. D., Wynhoff, I.,
789 Hoare, D., & Ellis, S. (2021). The decline of butterflies in Europe: Problems, significance, and
790 possible solutions. *Proceedings of the National Academy of Sciences*, *118*(2), e2002551117.
791 https://doi.org/10.1073/pnas.2002551117
792 Wilson, E. O. (1986). *Biophilia*. Harvard university press.
793 Woodward, I., Massimino, D., Hammond, M., Barber, L., Barimore, C., Harris, S., Leech, D., Noble, D.,
794 Walker, R., & Baillie, S. (2020). BirdTrends 2020: Trends in numbers, breeding success and
795 survival for UK breeding birds. *BTO Research Report*, *732*.
796 Wooldridge, J. M. (2010). *Econometric analysis of cross section and panel data*. MIT press.
797 Yazdanian, M., Kankaanpää, T., Merckx, T., Huikkonen, I.-M., Itämies, J., Jokimäki, J., Lehikoinen, A.,
798 Leinonen, R., Pöyry, J., Sihvonen, P.,… Kivelä, S. M. (2024). Evidence for bottom-up effects of
799 moth abundance on forest birds in the north-boreal zone alone. *Ecology Letters*, *27*(12),
800 e14467. https://doi.org/10.1111/ele.14467
801