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To link to this article DOI: http://dx.doi.org/10.1111/ele.14362

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ECOLOGY LETTERS cnrs WILEY

Population links between an insectivorous bird and moths disentangled through national-scale monitoring data

Luke Christopher Evans[1] 🅞 | **Malcolm D. Burgess**[2] | **Simon G. Potts**[3] | **William E. Kunin**[4] | **Tom H. Oliver**[1]

[1]School of Biological Sciences, University of Reading, Reading, UK

[2]RSPB Centre for Conservation Science, Sandy, UK

[3]Centre for Agri-Environmental Research, School of Agriculture, Policy and Development, University of Reading, Reading, UK

[4]School of Biology, University of Leeds, Leeds, UK

Correspondence
Luke Christopher Evans, School of Biological Sciences, Health and Life Sciences Building, Whiteknights Campus University of Reading, Reading, RG6 6AS, UK.
Email: lukechristopher.evans@reading.ac.uk

Abstract

Insects are key components of food chains, and monitoring data provides new opportunities to identify trophic relationships at broad spatial and temporal scales. Here, combining two monitoring datasets from Great Britain, we reveal how the population dynamics of the blue tit *Cyanistes caeruleus* are influenced by the abundance of moths – a core component of their breeding diet. We find that years with increased population growth for blue tits correlate strongly with high moth abundance, but population growth in moths and birds is less well correlated; suggesting moth abundance directly affects bird population change. Next, we identify moths that are important components of blue tit diet, recovering associations to species previously identified as key food sources such as the winter moth *Operoptera brumata*. Our work provides new evidence that insect abundance impacts bird population dynamics in natural communities and provides insight into spatial diet turnover at a national-scale.

KEYWORDS

citizen science data, food webs, insect decline, monitoring data, population dynamics, trophic links

INTRODUCTION

Insects play important roles in ecosystems, performing various ecosystem functions, including supporting, as key food sources, the functions of higher trophic levels (Noriega et al., 2018; Prather & Laws, 2018; Schowalter, 2013). Recent concern over insect declines (Hallmann et al., 2017; Powney et al., 2019; Van Klink et al., 2020; Wagner et al., 2021) has focussed attention on how insect abundance may be impacting birds (Pearce-Higgins & Morris, 2023; Tallamy & Shriver, 2021) with several lines of evidence suggesting that declines in insectivorous birds may be driven, in part, by reductions in insect prey (Bowler et al., 2019; Hallmann et al., 2014; Narango et al., 2018; Nebel et al., 2010; Tallamy & Shriver, 2021). For example, declines in insect prey populations have been implicated in causing reductions in

breeding success in birds (Martay et al., 2023; Naef-Daenzer & Keller, 1999; Peach et al., 2015; Seress et al., 2018) and local-scale studies have found correlations between insect and bird population dynamics (Benton et al., 2002; Hart et al., 2006). Recent meta-analytic approaches similarly show that insects are often a limiting resource for birds with lower insect food provision reducing reproductive fitness (Grames et al., 2023). However, quantifying population-level impacts of insect abundance on birds remains challenging, particularly at broad spatial and temporal scales, as it requires concurrent information on the densities of both the birds and their insect prey and evidence of interactions between their populations (Buckner, 1966).

Two approaches have predominantly been used to link birds to their insect prey: diet and population

studies. Traditional diet studies have a long history in ecology (Betts, 1955; Poulton, 1929) and consist of some form of observation, or collection, of food taken, providing direct evidence of diet composition (Razeng & Watson, 2012; Vaughan, 1997). However, the need to identify the prey species, either before or after ingestion limits the scale of the analysis (Moreby & Stoate, 2000). Some limitations have been overcome by advances in molecular techniques that can provide greater taxonomic information (Jedlicka et al., 2011; Orłowski & Karg, 2013; Rytkönen et al., 2019; Whitby et al., 2020) and can be conducted at wider scales (Alberdi et al., 2020; Shutt et al., 2020). However, these approaches only provide a qualitative, or semi-quantitative, snapshot of dietary content at a given time and, without collecting additional information, do not provide conclusive insight into how changes in prey abundance impact predator populations. Similarly, population studies that measure both bird populations and prey abundance at a location (e.g. Martay et al., 2023; Visser et al., 2006) can link contemporaneous population dynamics but are typically limited to a handful of locations and time periods.

An alternative approach, which can be conducted at broader spatial and temporal scales, is to leverage national-scale monitoring data (Møller et al., 2021). The UK has several monitoring schemes that record abundance using standardized techniques (e.g. Breeding Bird Survey https://www.bto.org/our-science/projects/breeding-bird-survey, UK Butterfly Monitoring Scheme https://ukbms.org, Rothamsted Insect Survey https://insectsurvey.com/, National Bat Monitoring Program https://www.bats.org.uk/our-work/national-bat-monitoring-programme) that provide counts of abundance over multiple years at national-scales. These schemes offer the opportunity to link changing abundance of important insect prey to population change of higher trophic levels (Finch et al., 2022; Martay et al., 2023) at broad spatial and temporal scales. Here, we utilize two national monitoring schemes (the Breeding Bird Survey and Rothamsted Light Trap Network) to estimate the effect of moth abundance on population change in the blue tit *Cyanistes caeruleus*, an insectivorous bird that preys upon lepidopteran larvae, particularly during the breeding season (Betts, 1955; Cholewa & Wesołowski, 2011; Naef-Daenzer et al., 2000; Naef-Daenzer & Keller, 1999; Shutt et al., 2020). Our analysis covers the period 1995–2017 and most of Britain.

There are two main challenges when linking population data from different monitoring schemes; first, observations do not directly overlap in space, and second, the interactions between species are not observed (i.e. no observations of prey taken to the nest) increasing the chances of spurious associations. To address the first issue, we took only moth and bird survey sites within 5 km of one another and applied distance weighting when more than one moth site was included

in the radius. The second issue presents a greater challenge as correlations in population change and moth abundance may not be due to the direct effect of prey abundance, but rather that certain environmental conditions are beneficial to both taxa. For example, dry winter conditions may lead to increases in moth abundance by reducing the impact of pathogens (Conrad et al., 2002; McDermott Long et al., 2017) but also increase overwinter survival of birds. One approach to isolate direct effects is to search across a variety of possible environmental variables (including interactions and varying temporal windows) and then, after controlling for the appropriate variable(s), one can estimate direct effects. However, uncovering the important environmental variables impacting a single species is challenging and when multiple taxa are involved can become unwieldy. Choices between many variables can also invite brute force approaches, such as comparing all possible models, which while often suitable for prediction (Anderson & Burnham, 2004) does not guarantee the representation of causal relationships and correct estimation of effect sizes (McElreath, 2020b; Westreich & Greenland, 2013).

To address these issues, we apply a two-step procedure to evaluate different mechanisms that might explain associations between population change in the moths and blue tit. Our procedure aims to disentangle correlations in population dynamics derived from common environmental causes (mechanism two; see below) from the direct effects of moth abundance as food (mechanism one)—even though our approach is still ultimately correlational. We then build on these models to identify associations to moth species whose larvae are known to be in the diet of the blue tit and investigate spatial variation in their importance as food sources.

MATERIALS AND METHODS

Data

Population data for the blue tit were derived from the BTO/JNCC/RSPB Breeding Bird Survey (BBS). The scheme has been running since 1994 and has over 4000 survey squares currently monitored. The BBS uses stratified random sampling with skilled volunteers surveying 1 km transects twice during the breeding season. The first transect aligns with the early breeding season (April to early May) and the second with the late breeding season (late May to June). Volunteers record all birds seen or heard along the transects and separate observations into four distance categories (0–25, 25–100, >100 m and flying over). Transects are also split into sections which are coded for broad habitat categories (woodland, scrubland, semi-natural grassland/marsh, farmland, waterbodies, human sites, coastal, inland rock and miscellaneous;

Crick, 1992). We summed all observations across all distance categories and sections as our observed abundance for that site and year, and we used dominant transect habitat as our measure of the habitat of the site. To estimate the abundance from counts, we used an N-mixture framework (Royle, 2004; Supporting materials).

Moth data were derived from the Rothamsted light-trap network. This is a network of standardized light traps, currently operating at 84 sites, that are run throughout the year by volunteers. The samples are identified by volunteers, verified by an expert, and then the data are stored in a long-term database. The traps have been running since 1968, although records for a few species are only from a later period due to taxonomic uncertainty. As opposed to the bird data where we construct our site-level indices, for the moths we used a pre-constructed site-level index which was derived for calculating moth trends in the period 1968–2017 (Harrower et al., 2020). These indices were produced by applying the Generalized Abundance Index (GAI) method (Dennis et al., 2016) a widely used method to estimate site- and national-level indices from site-level monitoring data for butterflies and moths. To link moth populations to the bird populations, we identified all moth sites within a radius of 5 km of a bird sampling location. When there were multiple moth sites within the radii, we produced combined moth indices by inverse distance weighting.

Mechanisms

Our general approach for understanding how moths influenced the population dynamics of the birds derived from two observations when fitting a simpler a priori plausible model that linked population change in the blue tit to moth abundance. First, including yearly intercepts, to control for extraneous environmental influences on yearly population change, strongly influenced the estimate of the effect of moth abundance on population change in birds and caused high sampling inefficiency due to posterior correlations. Second, estimates of the yearly intercepts were highly correlated with annual moth abundance. Effectively, a good year for birds, in terms of population change, was a year when the abundance of moths was high. We considered three mechanisms that might explain these associations: mechanism one: high moth abundance provided ample food resources that supported increased population growth; mechanism two: moth and bird populations respond similarly to annual environmental variation; and mechanism three: a combination of the above two mechanisms. To disentangle these mechanisms, we developed a population change score model (Equation 1) to observe how the yearly intercepts (which we term the 'population change score') for the

birds correlated with average annual moth abundance (the annual average of the sum of moth abundances at each site) after accounting for average site effects and density dependence, that is, we asked regarding mechanism one, does a better than average year for birds correlate with high average moth abundance? We also repeated this for the Noctuidae (owlet moths) and the Geometridae (geometrid moths) where we expected a higher proportion of the species to be preyed upon (Cholewa & Wesołowski, 2011; Shutt et al., 2020) under the expectation of higher correlations for these groups (Note: we follow the taxonomic classifications for moth species provided in Harrower et al., 2020). Next, to test mechanism two we compared population change scores from the bird and moth groups, that is, did better-than-average years for birds correlate with better-than-average years for moths?

For the population change score model, we used a linearized Ricker formulation (Ricker, 1954; Equation 1). The dependent variable is the log per capita population growth rate, and the model includes parameters estimating site-level modifiers on the growth rate, the population change score and density dependence.

$$
\begin{aligned}
\log\left(\frac{N_{t+1}}{N}\right) &= \text{site}_i + \text{year}_j + bN_t \\
b &\sim \text{Normal}(0, 1) \\
\text{site}_i &\sim \text{Normal}(0, 1) \\
\text{year}_j &\sim \text{Normal}(0, 1)
\end{aligned}
\tag{1}
$$

In Equation 1, N_t represents the population size and time t, b represents the coefficient on previous years' abundance (density dependence), site_i represent site offsets and year_j the population change score.

To test mechanism one, we extracted the population change scores from the blue tit model and then compared them with the annual abundances of moths and the annual abundance of species in the Noctuidae and Geometridae. This allowed us to see if good years for the blue tit population growth corresponded with high absolute moth abundance. For mechanism two, we fitted the same population change score model to the site-level moth abundances for all moths and the Noctuidae and Geometridae. We then extracted the population change scores from all models and compared them to see if years with higher population growth for the blue tit corresponded with years with higher population growth for each of the moth groups. Correlation coefficients and resultant contrasts between mechanisms one and two were estimated in a Bayesian framework by fitting a multivariate normal and extracting the correlation coefficients from the posterior variance–covariance matrices. All model variables were centred and scaled before fitting, and we used weakly regularizing standard normal priors for model parameters.

Estimating the effect of moth abundance and selected moth species

After establishing better support for mechanism one (high moth abundance leading to increased population sizes; *Results*), we aimed to estimate the effect of moth abundance on bird population change and identify moth species that may be particularly important food resources by adjusting Equation 1 to include the annual abundance of moths and the abundance of key moth species (Equation 2).

Here for the mean annual abundance of moths, we didn't sum moths at each site but instead took the average of the abundance index for every moth each year. This is perfectly correlated with the mean of the summed abundance but allows a simpler interpretation of the difference between the average moth abundance across all species and the abundance of a particular species (i.e. either + or – the average) which we apply to limit spurious correlations (below).

$$\log \left(\frac{N_{t+1}}{N} \right) = site_i + \overline{\beta X} + \gamma x_i + bN_t \quad (2)$$

In Equation 2, the dependent variable is bird population change, $\overline{\beta}$ is the coefficient for the mean annual moth abundance, $\overline{X}$ the annual mean moth abundance, γ the coefficient of the species abundance difference and x_i the species abundance difference at site I, and b represents the coefficient on previous years' bird abundance (density dependence).

Due to the relationship found in the first stage, we did not include a yearly intercept in these models, which means that shared environmental causes can influence our estimate of the effect of moth abundance (i.e. we do not rule out mechanism three; s*ee discussion*), though the results from the first test suggest that the more supported mechanism driving population change is moth abundance.

Identifying key species through this model also introduces potential confounding factors, as correlations between the population dynamics of different moth species might introduce spurious correlations between a non-target moth and population change in the blue tits. To limit this, we focussed only on species where we had some prior evidence that they are used as food resources for adult and nestling blue tits (Betts, 1955; Gibb & Betts, 1963; Shutt et al., 2020) and used the difference of the selected moths from the annual average moth abundance. Taking the difference decorrelates the abundance of a particular species from the mean annual abundance, providing a stronger test of whether a particular moth influences population change above and beyond the general abundance of all moths in that year. We also recognize our approach made multiple comparisons (models for 46 prey species) and even

with the above measures to limit spurious associations there are risks of errors of commission (i.e. false positives). On the other hand, we also recognized that identifying key diet species given the nature of these data (spatial and temporal separation across sampling sites) is challenging, and applying corrections for multiple testing, which do not fit straightforwardly into a Bayesian framework and are often overly conservative (Gelman et al., 2012), risking significant errors of omission. Therefore, our approach to identify possible key diet species and balance the errors of commission and omission was to describe only the results supported by our highest evidence boundary (95% CI) and to compare the number of species with evidence of a relationship to the number expected to show a relationship through chance, an approach termed informal calibration (Gelman et al., 2012).

When fitting, we found that the species abundances were often skewed with a few large abundance values that had high leverage on the regression fits. To account for this, we used the inverse hyperbolic sign transformation (Burbidge et al., 1988) which performs as a log transformation with larger values, but zero and negative values remain defined. To understand the effects of this transformation, we also re-ran the models without the transformation and further tested the impact of directly using species abundance by refitting all models with species abundance in place of the difference from mean abundance. In both cases, results were similar (Supporting information).

Spatial variability in trophic links

Finally, national monitoring data allow assessment of spatial variation in food sources at broad scales indicative of spatial diet turnover. To investigate these relationships, we used a Gaussian Process framework (Neal, 1998) which allowed the effects of moth abundance to vary smoothly across space. We fitted the model to annual mean moth abundance, and the abundance of *Operophtera brumata* (winter moth), *Operophtera fagata* (northern winter moth), *Erannis defoliaria* (mottled umber), *and Cosmia trapezina* (dun-bar). We selected these species as *O. brumata* and *O. fagata* are sister species but with different spatial distributions, and *O. brumata* is often recognized as a key food source (Betts, 1955), *E. defoliaria* as it is has also been reported as a relatively important food source (Betts, 1955), and *C. trapezina* as our analysis showed it to have the largest positive association at the national-scale.

To construct models, we adapted the model in Equation 2 to include a multivariate Gaussian on the site-level coefficient for the species-specific moth abundances (γ) with the covariance matrix between sites estimated using Euclidian distance and a squared exponential covariance function (L2 norm;

McElreath, 2020b). All variables were centred and scaled before fitting and site distances were max-scaled. We used weakly regularizing standard normal priors for linear model parameters.

$$\log\left(\frac{N_{t+1}}{N}\right) = \text{site}_i + \overline{\beta X} + \gamma_i x_i + bN_t$$

$$\begin{bmatrix} \gamma \\ \gamma_2 \\ \vdots \end{bmatrix} \sim MV\text{Normal}\left(\begin{bmatrix} 0 \\ 0 \\ \vdots \end{bmatrix}, R\right) \qquad (3)$$

$$R = \eta^2 e^{-p^2 D^{ij}} + \delta_{ij}\sigma^2$$

In Equation 3, i is an index for site, R is a covariance matrix, η^2 is the maximum covariance between any sites, ρ_{ij} is the correlation between site i and j, D_{ij} is the distance between sites i and j, and $\delta\sigma^2$ accounts for within-site variance in γ when $i=j$.

Fitting details

Analysis was conducted in R 4.1.2 (R Core Team, 2022), and the probabilistic programs for fitting the Bayesian models were written in Stan 2.21.0 (Stan Development Team, 2019). For most models, we used four chains with 2000 steps (1000 warm-up, 1000 samples). The spatially varying coefficient models and the index models had large numbers of parameters increasing memory usage; consequently, we used three chains. We used a cut-off of <1.1 for the $\hat{R}$ (Gelman et al., 2013) for indicating convergence. The R packages 'RStan' 2.26.11 (Stan Development Team, 2021) and 'rethinking' 2.13 (McElreath, 2020a) were used to analyse model outputs, and 'raster' 3.4–13 (Hijmans, 2021b) and 'geosphere' 1.5–14 (Hijmans, 2021a) were used for spatial processing and visualizations. Code and data in support of the results are archived at https://zenodo.org/doi/10.5281/zenodo.8021349.

RESULTS

Mechanisms

To describe all results, we use evidence language (Muff et al., 2022), with 'evidence' for an effect if the 95% posterior uncertainty intervals exclude zero, weak evidence if 80% uncertainty intervals exclude zero, and no evidence if 80% uncertainty intervals contain zero (Evans et al., 2023). We found evidence of positive correlations between the population change scores for blue tits and the mean abundance of all moth groups (Figure 1b,e,h; Tables S1–S11). However, when we compared population change scores for the blue tits and the moth groups, we found evidence (albeit marginal) of correlations for all moths and weak evidence for the Noctuidae and Geometridae (Figure 1a,d,g). The mean

posterior estimates of the correlation coefficients were uniformly lower in the comparisons of the population change scores (moth population change scores vs. bird population change scores) relative to the comparisons of the bird population change scores to moth abundance, and through posterior contrasts we found weak evidence that the correlation coefficients were higher in the Geometridae and the Noctuidae (Figure 1c,f,i Tables S1–S11). In combination, these results suggested that there was stronger support for mechanism one (high moth abundance leading to population increases) rather than mechanism two (shared responses to environmental variation) although the results do not rule out mechanism three (a combination of both these factors).

The importance of different moth species

We found evidence of a positive relationship between blue tit population change and the abundance of nine moth species and evidence of a negative relationship for one moth species (Figure 2a; Table S12). This is fourfold the number expected to occur by chance, with a notable bias towards positive effect sizes. Effect sizes for individual moth species were generally modest, with considerable additional unexplained variation (Figure 2c–f). We also found evidence for a strong effect of mean annual moth abundance (Figure 2b). Results from models included in the sensitivity analysis were broadly similar (Figure S1).

Spatial variation in diet

The spatial models outperformed the non-spatial versions in information criteria (lower WAIC; Watanabe & Opper, 2010) for all species apart from *O. fagata* where WAIC scores were practically indistinguishable (ΔWAIC 0.7; Table S14). This suggests relevant spatial variation in the effect of these moth abundances on population change in the blue tit (Figure 3a–d) although site-specific coefficients had high uncertainty (Tables S13–S16).

DISCUSSION

We provide compelling evidence that the abundance of moths influences population change in the blue tit, and we find associations to several moth species expected to influence population dynamics. This is one of only a handful of demonstrations that annual insect abundance influences population change in birds at broad spatial and temporal scales. Further, applying national monitoring scheme data allowed us to uncover large-scale spatial variation in the importance of these species in the diet of the blue tit suggestive of spatial diet turnover. However, our approach also shows that these
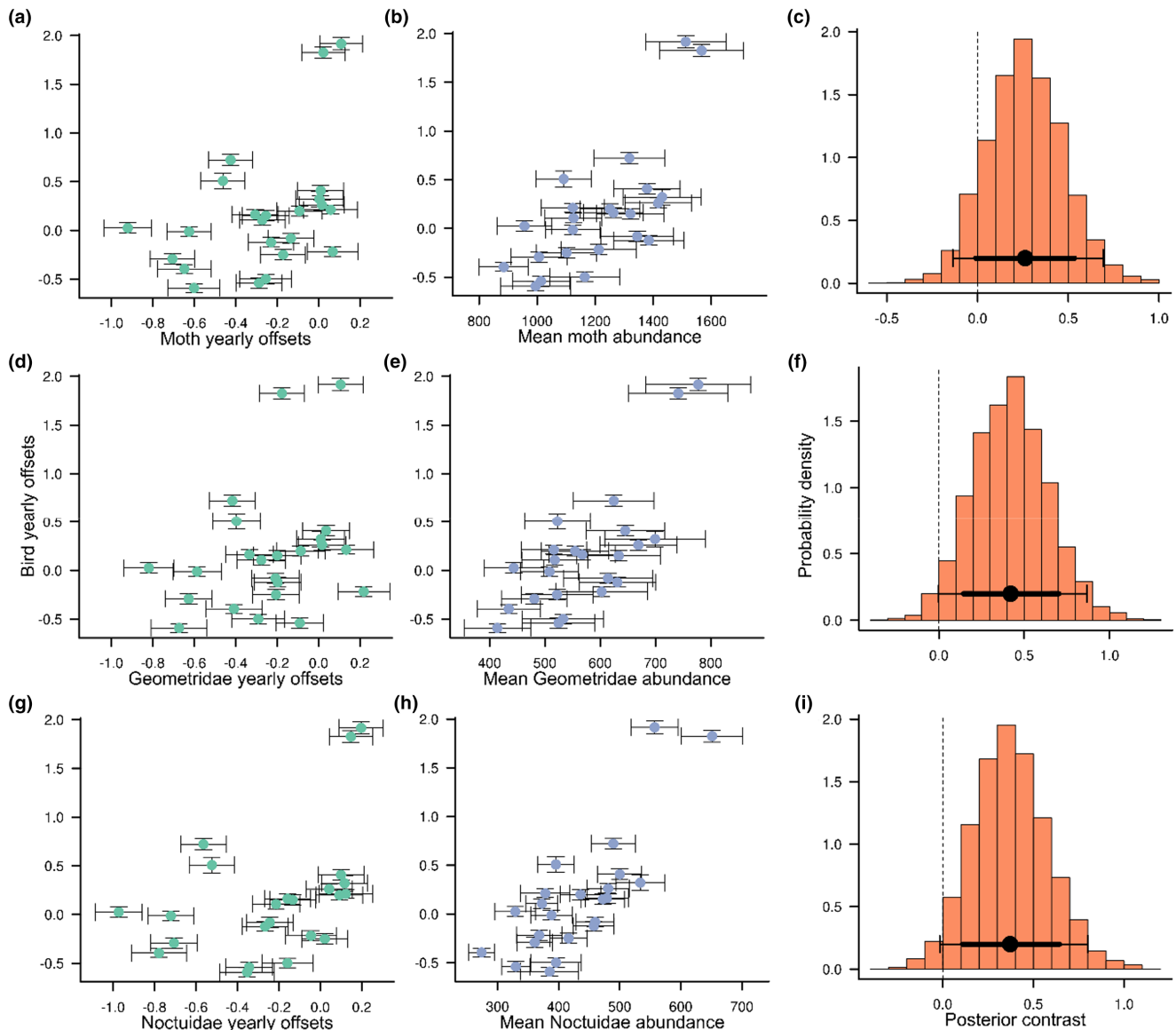
FIGURE 1 Comparisons between population change scores (average annual population change) for the blue tit and population change scores for different moth groupings (i.e. mechanism two), alongside comparisons for population change scores for the blue tit and the annual abundance of moth groups (i.e. mechanism one). Each point in the scatterplots refers to a single year. Comparisons are matched across rows: (a) and (b) represent comparisons of population change scores for all moths and the birds and the population change scores for birds against mean moth abundance, respectively, and c) shows the contrast of the posterior correlation coefficients (correlation for mechanism one—correlation for mechanism two). (d–e) show comparisons for the Geometridae, and (g–i) show comparisons for the Noctuidae. In a, d and g uncertainty intervals on the x-axis and y-axis show standard deviations of posterior estimates. For b, e, and h, uncertainty intervals on the y-axis show standard deviations of posterior estimates and on the x-axis show standard error of the mean.

analyses must be undertaken cautiously and with consideration of different mechanisms that may drive associations between the population changes of species across trophic levels. We first provide our interpretation of the key results and then suggest approaches to enhance the use of national monitoring data to understand trophic relationships.

Our results suggest that a strong component of increased population growth in blue tits is high moth abundance (mechanism one) rather than moths and blue tits having synchronized dynamics due to shared responses to environmental variation (mechanism two). The mean

of the posterior for the correlation coefficients between the bird population change scores and moth abundance fit the expected pattern being higher for the Noctuidae and the Geometridae than for all moths combined with these groups expected to make up a larger component of the diet of blue tits (Cholewa & Wesołowski, 2011; Shutt et al., 2020). Similarly, through posterior correlation contrasts, we found weak evidence for a higher correlation between bird population change score and abundance of the Noctuidae and the Geometridae versus correlations of moth and bird population change scores, supporting mechanism one over mechanism two. However, even
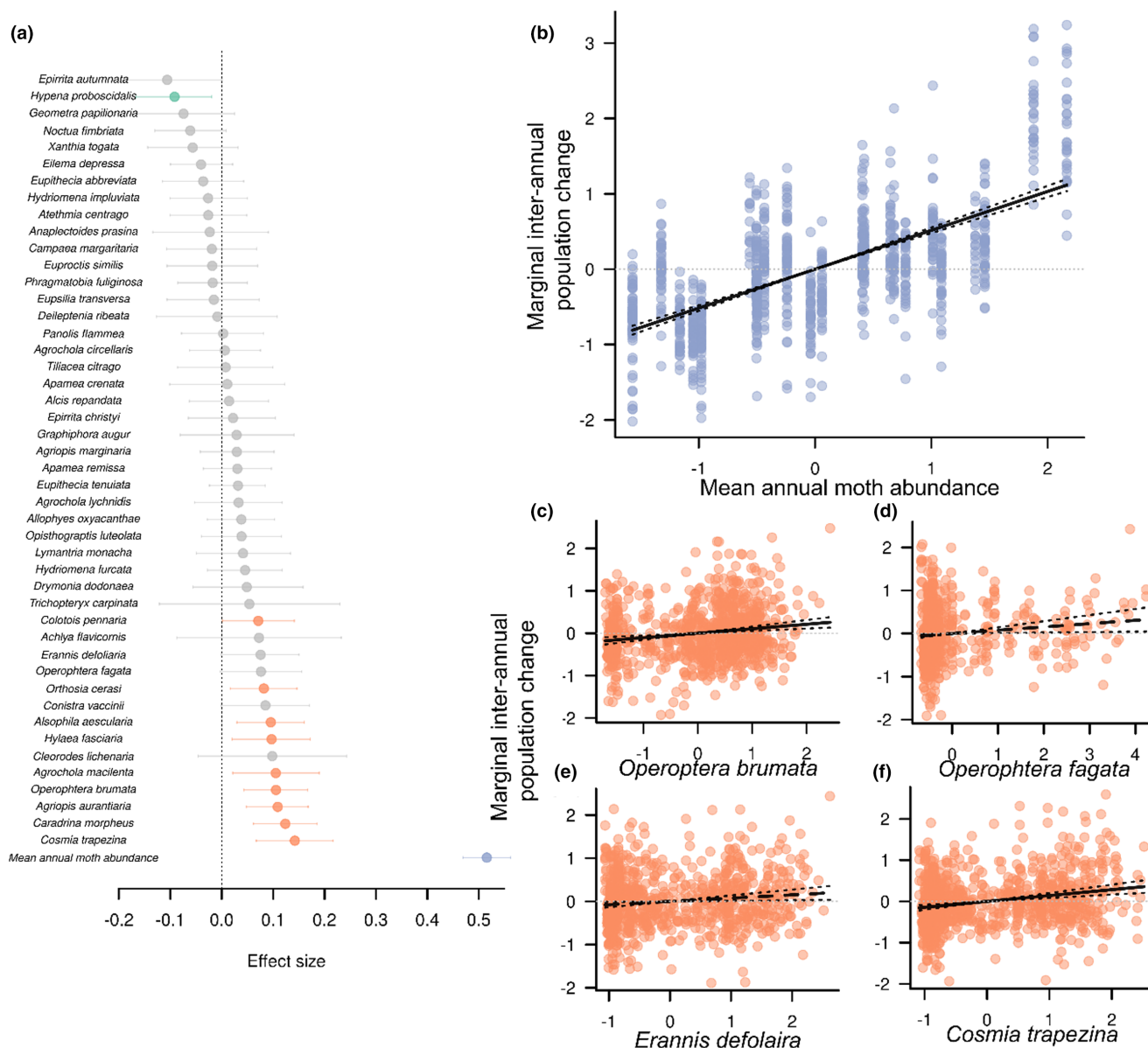
FIGURE 2 Influence of moth species and mean annual moth abundance on population change in the blue tit: (a) effect sizes for moths species from all models and for the mean annual moth abundance (as an example we present the fit for mean annual abundance from the *Operoptera brumata* model), orange points show species with evidence for a positive association, green points evidence of a negative association; (b) marginal fit of mean annual moth abundance against inter-annual change; and (c–f) marginal fits of abundance against inter-annual change for (c) *Operoptera brumata*, (d) *Operophtera fagata*, (e) *Erannis defoliaria*, (f) *Cosmia trapezina*. Bars represent 95% uncertainty intervals on slope coefficient posteriors, and in scatterplots dashed lines represent fits with weak evidence of a relationship and solid lines represent those where we have evidence of a relationship, variables are presented on a standardized scale.

though the correlations were lower, we cannot entirely rule out that shared responses to environmental variation may lead to some synchronization in the dynamics of moths and birds and that a combination of these two mechanisms may generate associations between moth and bird population dynamics. Additionally, as expected, we found evidence of site-level variation in population change and density dependence for both birds and moths (Tables S1–S11).

We found a strong correlation between bird population growth and annual moth abundance, indicating that years with high moth abundances resulted in

increased population growth for the blue tit (Figures 1 and 2). Our results suggest that blue tits benefit over broad spatial scales when Geometridae and Noctuidae numbers are elevated, consistent with faecal/gut content analysis and field observations (Betts, 1955; Cholewa & Wesołowski, 2011; Gibb & Betts, 1963; Royama, 1970; Shutt et al., 2020). The weaker effects we observed for individual species, compared with that of total moth abundance, suggest that blue tit diet is diverse and not strongly dependent on any single species. However, we recover evidence for relationships between blue tit population growth and abundance of *O. brumata*, consistent
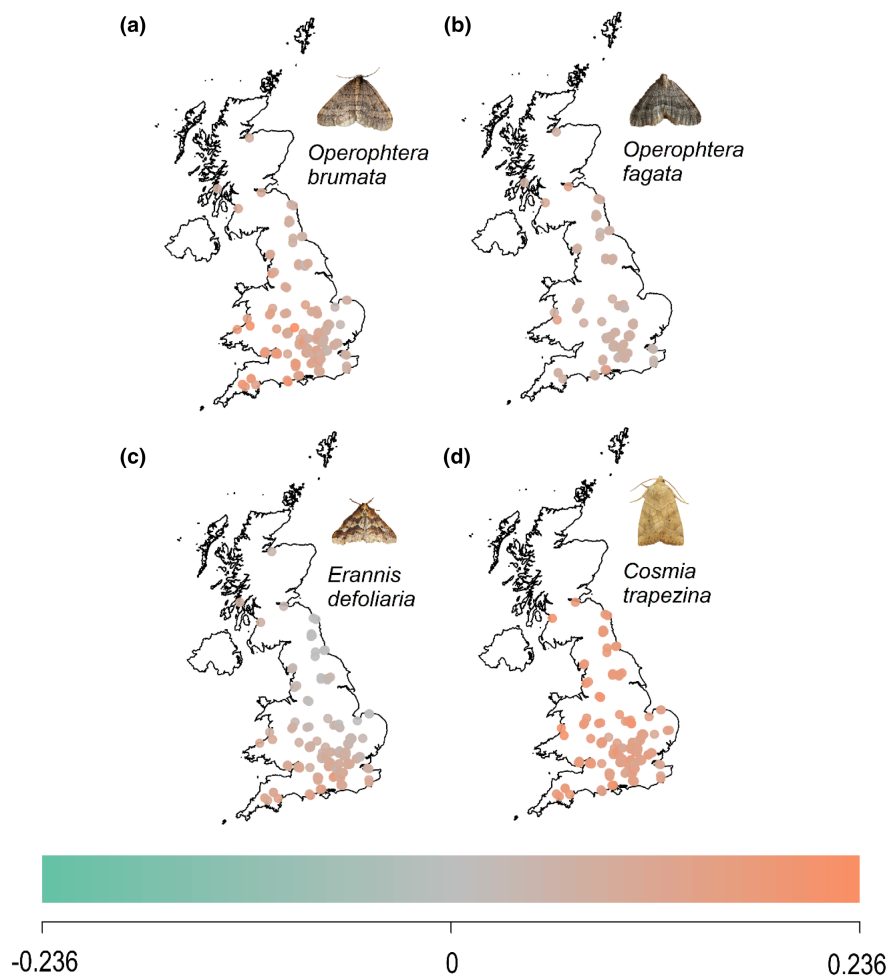
FIGURE 3 Spatial variation in the relationships between moth species abundances and population change in the blue tit. Effect sizes are presented in the adjacent colour bar, stronger orange colours show larger (positive) regression coefficients indicating a greater influence on bird population dynamics, grey shows little to no correlation, and green shows negative correlations. Moth indices are (a) *Operophtera brumata*, (b) *Operophtera fagata*, (c) *Erannis defoliaria*, (d) *Cosmia trapezina*. Photo credits are provided in the acknowledgements.

with previous research highlighting the importance of this species in blue tit diet. Other species such as *E. defoliaria* and *O. fagata*, also recognized as key food sources, did not quite pass the higher evidence threshold we set, though their effects were essentially on the evidence boundary, and we found evidence for both these species in different model formulations presented in the sensitivity analysis (Figure S1). That we find the families and species expected to play a role in blue tit diet with the strongest positive associations provides us with some confidence that national monitoring data can be used to detect genuine signals in trophic interactions. We also found evidence of spatial variation in the strength of association for several moth species (Figure 3), consistent with other research on spatial diet turnover (Shutt et al., 2020). Reasons for this could include the changing abundance and distribution of moth species, as well as varying phenology. Moth species becoming more important components of diet in sites where they are more abundant is qualitatively consistent with blue tits selecting prey simply opportunistically or prey switching to

optimize energy intake (Allen et al., 1997; García-Navas & Sanz, 2010; Greenwood & Elton, 1979; Murdoch, 1969; van Leeuwen et al., 2013).

In our study, we applied a sequence of tests to attempt to disentangle the effects of common environmental causes from the effects of moth abundance on bird population change. However, fully maximizing the use of national monitoring data to understand trophic relationships requires careful consideration of the causal factors driving population changes across both trophic levels. Our results show that separating environmental confounds from the main effect of interest is challenging when analysing monitoring data and including variables in an ad hoc exploratory approach could mask relationships. For example, including weather variables without clear mechanistic interpretations in an attempt to control for extraneous sources of bird population variability could, in practice, control for an indirect relationship mediated through insect abundance, a combination of its effects on insect abundance and foraging suitability, or a direct influence on

bird mortality. The correlations we found between population change scores and moth abundance in our first models suggest these relationships may be difficult to separate. This issue may be particularly prevalent for national monitoring schemes where abundance observations are only an approximate estimate of the true local abundance and could be outperformed, in terms of measures such as information criteria, by models based on predictors with uncertain mechanisms.

Additional considerations when using national monitoring data are both the ecological relationships and the data-generating process. Our results suggest that populations of blue tits are controlled bottom-up, as a lower abundance of moths was correlated with reduced population growth, consistent with other studies conducted on blue tit populations (Pollock et al., 2017) and other insectivorous birds. However, greater top-down control in combination with different sampling regimes could reverse the directions of the correlations. For example, if birds varied in their effectiveness of finding prey between years and consumed a substantial proportion of the local prey population (see for predation rates Brewer, 1961; Stewart, 1973; Tallamy & Shriver, 2021), then years when the birds had been successful (e.g. through optimal phenology Burgess et al., 2018) may correlate with both increased blue tit population growth and a lower than expected abundance of adult moths caught in the traps later in the year. That both positive and negative relationships could plausibly provide evidence of prey–predator interactions is challenging from a falsification standpoint and can likely only be resolved through careful consideration of both ecological and observational processes. These relationships will vary with the life stage at which the prey is preyed upon relative to the life stage when it is observed in the monitoring scheme.

In the case here, we expect the limitations of the monitoring data to weaken correlations between moth abundance and bird population change. First, as moths are recorded as adults, but the blue tit is predominantly reliant on the larvae during breeding, there is noise introduced through variability in the number of larvae surviving to adulthood along with the noise introduced when estimating the abundance of the adult population from limited samples. Second, only using annual indices of abundance does not account for factors such as variations in phenology that may disrupt the link between moth abundance and bird population change (Burgess et al., 2018). Plausibly monitoring data could be used to investigate the impacts of varying moth phenology on bird population dynamics at large scales by extrapolating larval emergence from the times adults are caught in traps, or utilizing tools such as degree-day models to predict life stage transitions (e.g. Jones et al., 2013).

Our results open further avenues for enquiry. National monitoring data could be used to identify the collection of prey species that best predict population change for higher trophic levels. This would be a challenging model selection problem, but generating a reliable combined index could better resolve the importance of insects for higher trophic levels and be used as an index of insect food to identify regions or times of shortfalls. Our results also described spatial variation in insect food and could lead to new hypotheses about how diet varies at broad scales. Validating the spatial patterns is currently challenging as diet studies for the blue tit have been qualitative (Shutt et al., 2020) or semi-quantitative (Betts, 1955; Cholewa & Wesołowski, 2011), and these data only represent a snapshot of diet for a few timepoints and locations.

National monitoring data also open opportunities to better resolve the importance of multiple drivers of population change, and their interactions, at large scales. Reliable inference of these relationships will be challenging using only monitoring data, but combined approaches may overcome some of these limitations. For example, combining monitoring data and field studies may allow a broadening of the scale of the analysis relative to a typical field study, while also providing clearer mechanistic insight into relationship between a driver and population change. Approaches combining smaller-scale studies and national monitoring data have been applied to investigate the effects of trophic asynchrony on population change in the blue tit (Burgess et al., 2018), and similar methods could investigate factors such as foraging choices and inter-specific competition on population change in birds. Similarly, developing transparent causal relationships and applying the tools of causal inference (Arif & MacNeil, 2023) could provide a useful route to reliable estimates of drivers of population change. For example, several factors likely impact annual population growth in blue tits, such as varying habitat types and qualities, predation rates, or the impact of supplementary feeding that we do not consider. Summarizing current evidence either through meta-analytic approaches (Grames et al., 2023), or expert elicitation, and then testing a variety of graphical causal model structures (Pearl, 2009) will likely produce more reliable estimates of effect sizes and also summarize the major factors influencing population growth in a manner accessible for a variety of stakeholders. Such results would add to the growing evidence that insect losses may have profound consequences for higher trophic groups and whole ecosystems.

AUTHOR CONTRIBUTIONS

LCE designed and undertook the analysis with support from TH, LCE wrote with first draft and all authors contributed substantially to revisions.

ACKNOWLEDGEMENTS

PEER REVIEW
The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ele.14362.

DATA AVAILABILITY STATEMENT
Code and data in support of the results are archived at https://zenodo.org/doi/10.5281/zenodo.8021349.

ORCID
Luke Christopher Evans https://orcid.org/0000-0001-8649-0589

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SUPPORTING INFORMATION

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