Links between an insectivorous bird and moths disentangled through national scale monitoring data

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Abstract

Insects play important roles in food chains, but quantifying how insect abundance affects population dynamics in natural communities is challenging. National scale monitoring data provides opportunities to identify trophic relationships at broad spatial and temporal scales but requires careful approaches to link data from different schemes. Here, using two monitoring datasets from Great Britain, we apply a two-step process to reveal how the population dynamics of the blue tit *Cyanistes caeruleus* is influenced by the abundance of moths - a core component of their breeding diet. We first find that at a national scale, years with increased population growth for blue tits strongly correlate with high average moth abundance, but population growth in moths and birds is less correlated; suggesting moth abundance affects bird population change rather than shared responses to environmental variation. Next, we identify moth species that are important components of the blue tits' diet, recovering associations to species previously identified as key food sources such as the winter moth *Operoptera brumata*. Our work provides rare evidence that insect abundance can impact bird population dynamics in natural communities and provides insight difficult to obtain from smaller-scale observations as we evaluate spatial diet turnover at a national scale.

Introduction

Insects play important roles in ecosystems, performing various ecosystem functions and, as key food sources, supporting the functions of higher trophic levels [1–3]. Recent concern over insect declines [4–7] has focussed attention on how insect abundance may be impacting birds [8,9] with several lines of evidence suggesting that declines in insectivorous birds may be driven by reductions of insect prey [9–12]. For example, declines in insect prey populations have been implicated in causing reductions in breeding success in birds [13–16] and local scale studies have found correlations between insect and bird population dynamics [17,18]. Recent meta-analytic approaches have also found that insects are often a limiting resource for birds with reduced insect food provision leading to lower reproductive fitness[19]. However, quantifying population-level impacts of insect abundance on birds remains a challenge, particularly at broad spatial and temporal scales, as it requires concurrent information on the densities of both the prey and the birds and evidence of a connection between their populations [20].

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[21,22] and consist of some form of observation, or collection, of food taken, providing direct evidence of diet composition [23–25]. However, the need to identifying the prey species, either before or after ingestion limits the scale of the analysis [26]. Some limitations have been overcome by advances in molecular techniques that can provide greater taxonomic information [27–30] and can be conducted at wider scales [31,32]. However, these approaches only provide a qualitative snapshot of dietary content at a given time and subset of locations and, without collecting additional information, do not provide insight into how changes in prey abundance impact population change. Similarly, population studies that measure both bird populations and prey abundance at a location (e.g. [16,33]) can link contemporaneous population dynamics but are typically limited to a handful of locations and time periods.

An alternative approach, that can be conducted at broader spatial and temporal scales, is to leverage national-scale monitoring data[34]. The UK has several monitoring schemes that record abundance using standardised techniques (e.g. Breeding Bird Survey, UK Butterfly Monitoring Scheme, Rothamsted Insect Survey, National Bat Monitoring Program) providing 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 [16,35] at broad spatial and temporal scales. Here we utilise two national monitoring schemes (the Bird Breeding Survey; https://www.bto.org/our-science/projects/breeding-bird-survey, and Rothamsted Light Trap Network; https://insectsurvey.com/) to estimate the effect of moth abundance on population change in the blue tit *Cyanistes caeruleus*, an insectivorous bird which preys upon Lepidopteran larvae, particularly during the breeding season [13,21,32,36,37]. Our analysis covers the period 1994-2017 and a region from southern England to northern Scotland.

There are two main challenges to linking population data from different monitoring schemes; first, observations do not directly overlap, 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 5km 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 [38,39] 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 correct 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 [40], does not guarantee the representation of causal relationships [41,42].

To address these issues, we apply a two-step procedure to evaluate the population effects of moth abundance on the blue tit. Our procedure aims to disentangle correlations in population dynamics derived from common environmental causes from the direct effects of moth abundance as food – even though our approach is still ultimately correlational. We then build on these models to identify key moth species in the diet of the blue tit and spatial variation in their importance as food sources.

Results

Moth abundance and bird population change

Our approach 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, that control for potential extraneous environmental influences on yearly population change, strongly influenced the estimate of the effect of moth abundance on population change and with model sampling efficiency subsequently low due to posterior correlations. Second, estimates of the intercepts were highly correlated with annual moth abundance. Effectively, a good year for birds in terms of population change was a year with lots of moths. Therefore, in the first step, to disentangle correlations derived from common environmental causes from the direct effects of moth abundance, we compared two multi-level models based on a linearized Ricker equation (*Methods*), fitted separately to site-level population growth in the birds and moths. In model one we observed, how the yearly intercepts (which we term the ‘population change score’) from the bird model correlated with total annual moth abundance (the annual average across all sites of the sum of all moths) after accounting for average site effects and density dependence, i.e. we asked, does a better than average year for birds correlate with high average moth abundance? We also repeated this for selected moth families where we expect a higher proportion of species to be preyed upon [32,37]. Next, we compared population change scores from the moth and bird model, i.e. did better than average years for birds correlate with better than average years for moths?

To describe the results we use evidence-language[43], 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[44]. We found evidence of strong correlations between the population change scores estimated in the blue tit population change model and the mean abundance of all moths, as well as with the mean abundance of the Noctuidae (owlet moths) and the Geometridae (geometrid moths) (Figure 1c&d, g&h, k&l). 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 the Noctuidae, and weak evidence for the Geometridae. Mean posterior correlation coefficients were uniformly lower when comparing population change scores for the birds and moths relative to those comparing bird population change score to moth abundance. The results suggest that increased population growth for blue tits is most associated with years of high moth abundance rather than moths and blue tits having synchronised dynamics due to shared responses to environmental variation. The mean posterior estimate for the correlation coefficients between bird population change score and moth abundance were higher for Noctuidae and Geometridae than for all moths combined as anticipated given these groups make up a large component of the diet of blue tits [32,37], although there was substantial overlap in posterior correlation coefficients. We also find evidence of site-level variation and density dependence for both birds and moths (*supplementary materials*).

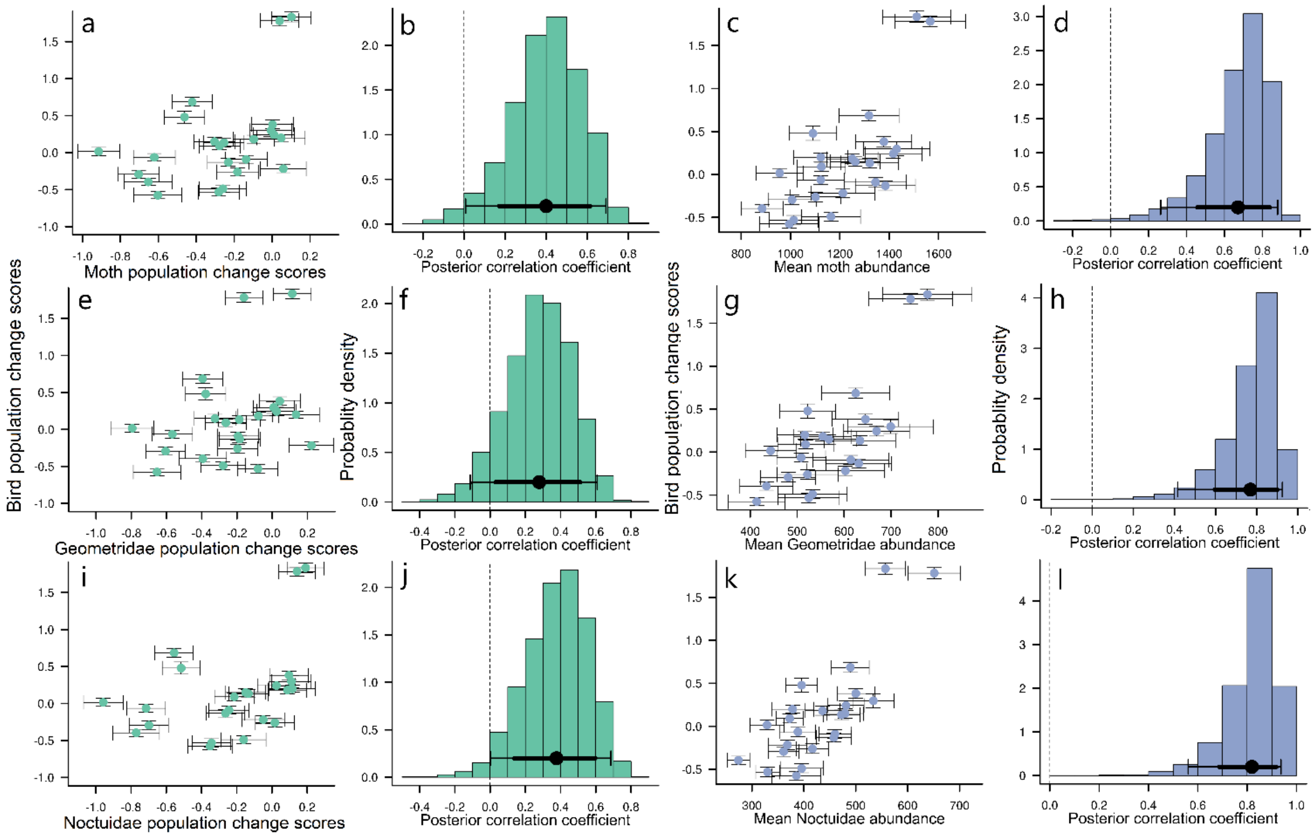

Figure 1. Comparisons between population change scores (average annual population change) for the blue tit and population change scores for different moth groupings, alongside comparisons for population change scores for the blue tit and the annual abundance of moth groups. Each scatterplot is paired with a posterior estimate of the correlation coefficient to its right. Each point in the scatterplots refers to a single year. Comparisons are a and b) population change scores for the blue tit and yearly offset in total moth abundance; e and f) population change scores for the blue tit and yearly offset for the Geometridae; I and j) population change scores for the blue tit and yearly offset for the Noctuidae; c and d) population change scores for the blue tit and mean total moth abundance; g and h) population change scores for the blue tit and mean abundance of Geometridae; and k and l) population change scores for the blue tits and mean abundance of Noctuidae. In a, e and i uncertainty intervals on the x-axis and y-axis show standard deviations of posterior estimates for the offsets. For c, g, and k, uncertainty intervals on y-axis show standard deviations of posterior estimates and on the x-axis show standard error of the mean.

The importance of different moth species

In the second step of our analysis, after establishing that moth abundance was the likely cause of increased average yearly population growth, we aimed to estimate this effect in a multi-level model and identify moth species that may be particularly important food sources (*Methods*). Due to the relationship found in the first stage, we did not include a yearly offset in these models, which means shared environmental causes may confound our estimate of the effect of moth abundance, though our results suggest that these influences are likely weak. Isolating the importance of a single species also introduces other potential confounding factors, as correlations between the population dynamics of different moths 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 sources for the adult and nestlings of blue tits [21,32,45] and used a model where we controlled for the effect of mean annual moth abundance (the mean abundance of all moths across all sites) before regressing the difference of the selected moth from this average. 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 abundance above and beyond the general abundance of all moths in that year. If the moth is an important component of the diet, we expected a positive relationship (note: models including abundances rather than differences, and varying transformations on differences, are provided in a sensitivity analysis in the supplementary materials). Our approach also made multiple comparisons (models for 46 prey species). Corrections for multiple testing do not fit simply into the Bayesian paradigm and corrections are often overly conservative [46]. Consequently, we compare the number of species with evidence for a relationship to the number expected to show a relationship through chance (i.e. informal calibration).

We found evidence for a positive relationship between blue tit population change and the abundance of ten moth species and evidence of a negative relationship for one moth species (Figure 2a). This is greater than four-fold the number expected to occur by chance. Effect sizes for individual moth species were generally modest, with considerable additional unexplained variation (Figure 2b). We also found evidence for a strong effect of mean annual moth abundance (Figure 2a and 2d). Results from models included in the sensitivity analysis were broadly similar (supplementary materials).

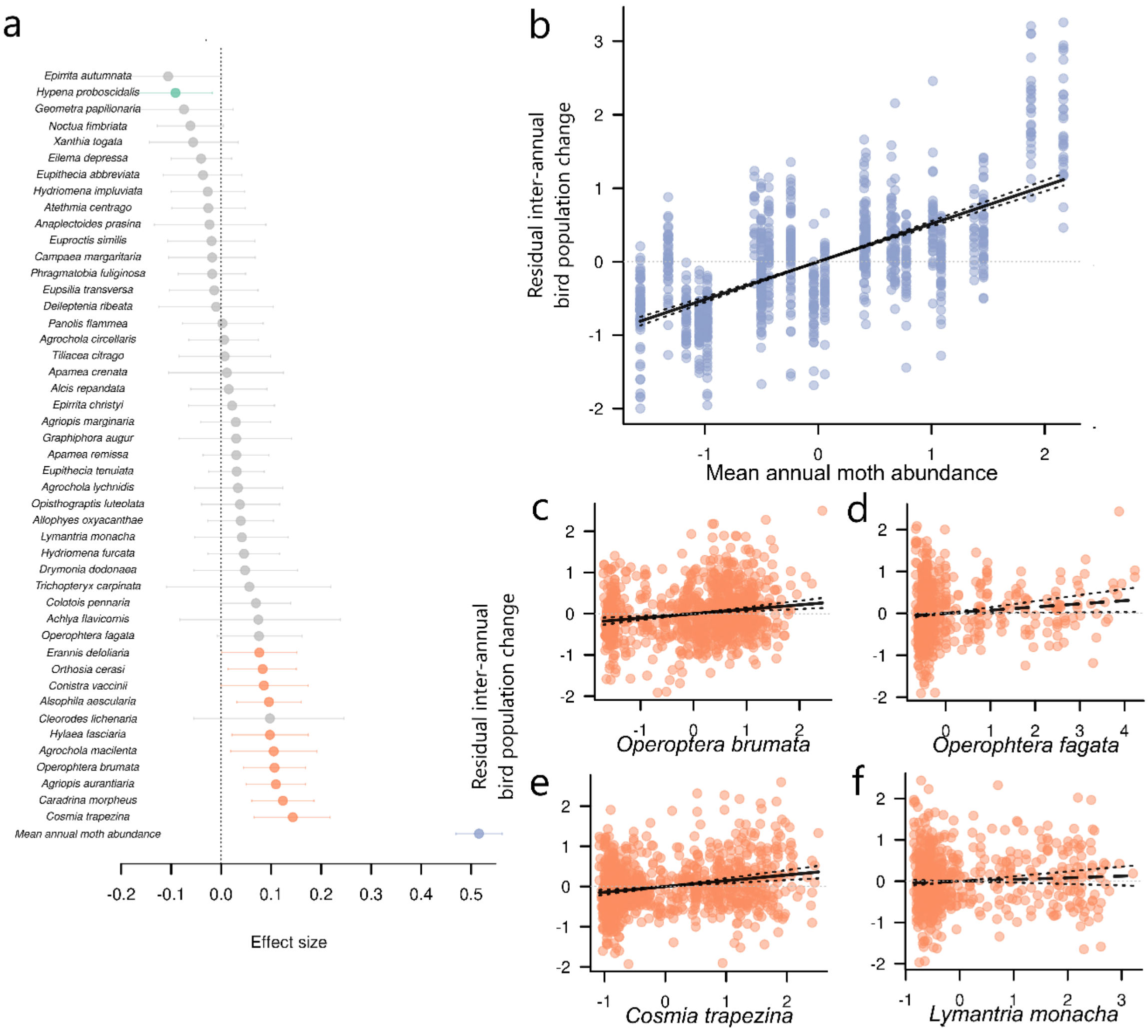

Figure 2. Influence of moth species and mean annual moth abundance on population change in the blue tit*:* a) effect sizes for moths species from all models and for the mean annual moth abundance (as an example we present the fit for mean annual abundance from the *Operoptera brumata* model) b) marginal fit of mean annual moth abundance against residual inter-annual change and, c-f) marginal fits of abundance against residual inter-annual change for c) *Operoptera brumata* d) *Operophtera fagata*, e) *Cosmia trapezina*, f) *Lymantria monacha*. Reasons for the selection of these species are explained below. Bars represent 95% uncertainty intervals on slope coefficient posteriors and in scatterplots dashed lines represent fits with weak or no evidence of a relationship and solid lines represent those where we have evidence of a relationship, variables are presented on a standardised scale.

Spatial variation in diet

Finally, national monitoring data allows assessment of spatial variation in food sources at broad scales indicative of spatial diet turnover. To investigate these relationships, we used a Gaussian Process model that allowed the effects of moth abundance to vary through space. We fitted the model to annual mean moth abundance, and the abundance of *Operophetra brumata* (winter moth), *Operophetra fagata* (northern winter moth)**,** *Erannis defoliaria* (mottled umber), *Cosmia trapezina* (dun-bar), and *Lymantria monachal* (black arches). We selected these species as *O. brumata* and *O. fagata* are sister species but with different spatial distributions and *O.brumata* is often recognised as a key food source [21], *E. defoliaria* as it is has also been reported as a relatively important food source [21], *C. trapezina* as our analysis showed it to have the largest positive association at the national scale and *L. monacha* as a representative of one of the species where we found no evidence of an association at a national scale, but where there could be regional variation in its importance due to variation in regional diets. Our spatial models outperformed the non-spatial versions in information criteria (lower WAIC[47]) for all species apart from *O. fagata* where WAIC scores were practically indistinguishable (ΔWAIC 0.3). This suggests relevant spatial variation in the effect of mean annual moth abundance on population change in the blue tit (Figure 3a), along with spatial variation for individual species (Figure 3 b-f).

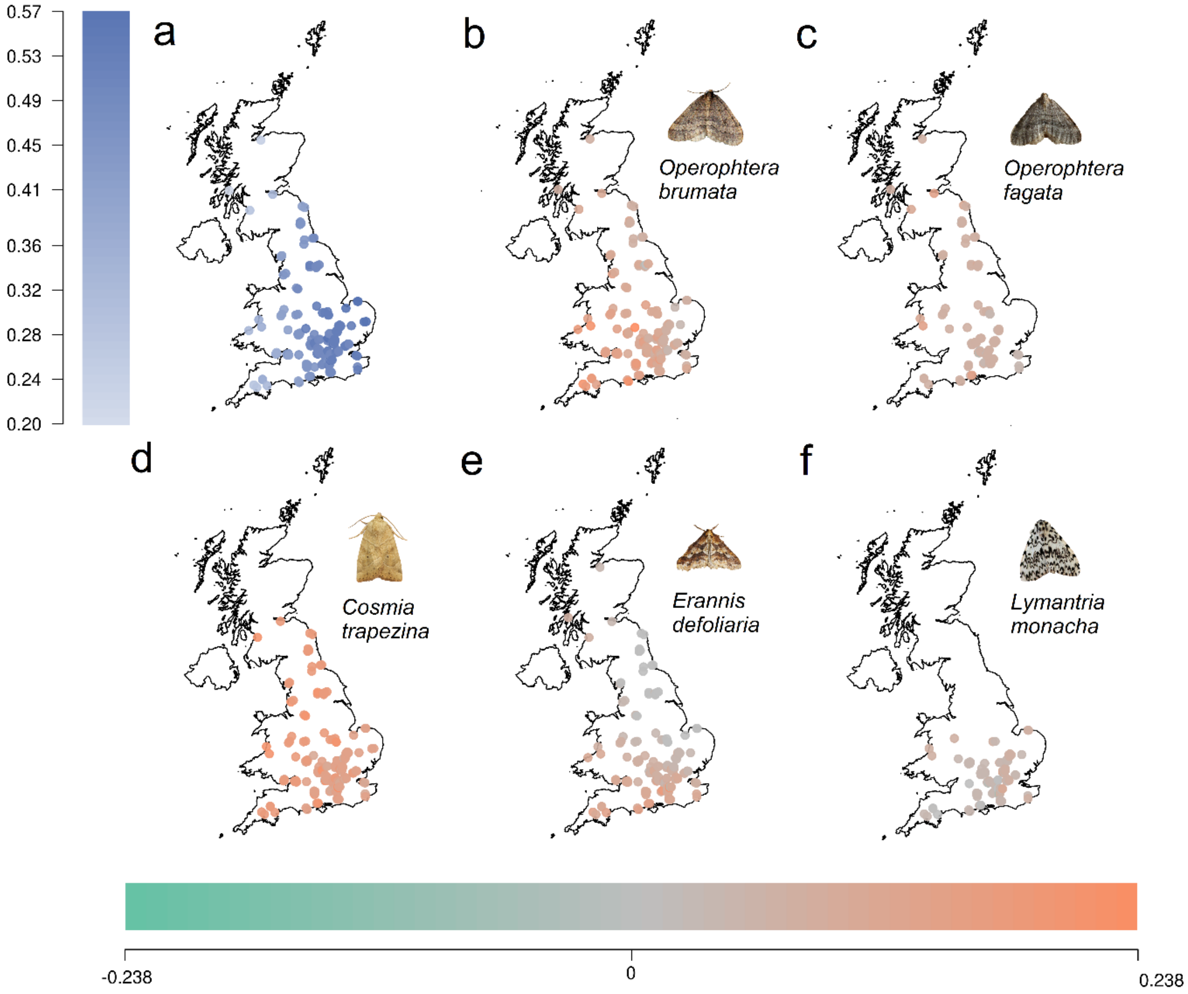

Figure 3. Spatial variation in the relationship between a) mean annual moth abundance and interannual population change in the blue tit and b-f) species-specific abundances and population change in the blue tit. Darker blue colours show larger (positive) regression coefficients for mean annual moth abundance, with effect sizes presented in the adjacent colour bar. For species-specific abundances, 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, the values of the standardised regression coefficient are indicated on the lower colour bar. Moth indices are b)

Operophetra brumata, c) *Operophtera fagata*, d) *Cosmia trapezina*, e) *Erannis defoliaria* , f) *Lymantria monacha.* Photo credits are provided in the acknowledgements.

Discussion

We provide compelling evidence that the abundance of moths influences population change in the blue tit and identify several moth species that may be important enough in the diet of the blue tit 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, our approach of using national monitoring scheme data uncovers possible spatial variation in how important these species are in the diet of the blue tit suggesting diet turnover. However, our approach also shows that these analyses must be conducted with caution. 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.

We found a strong correlation between bird population growth and annual total moth abundance, indicating that years with high moth abundances resulted in increased population growth for the blue tit (Figure 1, 2). Our results suggest that blue tits prey on a variety of Geometridae and Noctuidae, consistent with faecal/gut content analysis and field observations [21,32,37,45,48]. The weaker effects we observed for individual species, compared with that of total moth abundance suggest that the blue tit's diet is diverse and not strongly dependent on any single species. However, we recover evidence for relationships between *O. brumata* and *E. defoliaria* consistent with previous research highlighting the relative importance of these species in the blue tits diet. We also found evidence of spatial variation in the strength of association for several moth species, indicating that the composition of the blue tits' diet likely varies across space (Figure 3), consistent with other research on diet turnover [32]. Reasons for this could include the changing abundance and distribution of moth species, as we 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 optimise energy intake [49–53]. We note that the spatial variation in the effect size of total moth abundance may not represent changing importance of moths in the diet, but rather reflect the fact that the annual mean we calculate is most informed by south-eastern sites, which make up a larger proportion of the sample, and so the index better represents moth abundance in these regions. However, this factor does not influence our results from the individual moth species, as their abundance is based on the abundance of the moth at each site (Figure 2, 3).

In our study, we applied a sequence of models 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 likely requires careful consideration of the causal factors driving population changes for both trophic levels. Rather, our results suggest that including variables in an exploratory approach could hinder inference. For example, including weather variables without clear mechanistic interpretations in an attempt to control for extraneous sources of population variability in the birds, may include, but are not limited to estimating 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 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 [54] and other insectivorous birds [19]. 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 [9,55,56] for predation rates), then years when they had been successful (e.g. through optimal phenology[57]) 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.

Our results and approach open further avenues for enquiry. Plausibly, national monitoring data could be used to identify the collection of prey species that best predict population change for predators. This would be a challenging model selection problem, but generating a reliable combined index could further resolve the importance of insects for higher trophic levels and be used as a general index of insect food that could 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 [32], or semi-quantitative [21,37] and these data only representing a snapshot of diet for a few timepoints. Informally our results are plausible, given we identify key species (e.g. *O. brumata)* often highlighted as crucial resources [21,58].

National monitoring data also opens opportunities to better resolve the importance of drivers of population change at large scales. Reliable inference for the effects of multiple drivers may 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, and also provide clearer mechanistic insight than utilising monitoring data alone. 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 [57] and similar methods could investigate factors such as food choice and inter-specific competition on population change in birds. Similarly, developing transparent causal relationships and applying the tools of causal inference [59] 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 that we do not consider here, such as varying habitat types and qualities, predation rates, or the impact of supplementary feeding. Summarising current evidence either through meta-analytic approaches, or expert elicitation, and then testing a variety of graphical causal model structures [60] will likely produce more reliable estimands and also summarise the major factors influencing population growth in an accessible manner for a variety of stakeholders.

Online 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 1km 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 (0-25m, 25-100m, >100m 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[61]). 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.

Moth data were derived from the Rothamsted light-trap network. This is a network of standardised 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, though 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 [62]. These indices were produced by applying the Generalised Abundance Index (GAI) method [63] a widely used method to estimate site and national-level indices from site-level monitoring data for butterflies and moths.

Generating site-level indices for the blue tit

Site level counts are taken only a few times a year, most often twice a year, introducing two sources of error, error due to only encountering only a subsample of the population during a visit and error from detecting only a proportion of those that were encountered.

N-mixture models [64] explicitly account for these processes to estimate a latent local population abundance from repeated count data. To produce site-level indices for the blue tit we used a hierarchical GAM N-mixture framework. The N-mixture model, models count data as a mixture of an ecological process and an observational process. An observer first encounters at visit *i*, a fraction, $N_{i,}$ of the individuals from the unobserved latent population abundance λ. Though the N-mixture model is estimating a latent abundance we use it only here to estimate a relative yearly site level index rather than an estimate of absolute local population size.

$$(1)\ N_i \sim Poisson(\lambda) \text{ where } \lambda >= N_i$$

Factors affecting changes in λ over time are ecological processes and are estimated in a log-linear model e.g.

$$(2)\ Log(\lambda) = \alpha + \beta X$$

Where α is an intercept, X is a matrix of variables, and β a vector of parameters. We use a hierarchical GAM to estimate log(λ) which we describe in more detail below.

For the observational process, the model estimates out of those encountered individuals, N_i, how many, $y_{i,}$ are detected (y_i is the actual count data recorded) with the probability of detection given by parameter p.

$$(3)\quad yi \mid N_i \sim Binom(N_{i,}p)$$

Similarly, to the ecological process, factors affecting the observation process can be modelled in a logit-linear model e.g.

$$(4)\quad Logit(p) = \alpha + \delta X$$

$$Logit(\delta) \sim N(0,1.6)$$

Here we use the notation δ to indicate coefficients on the observational model which can, and do here, include different variables from the ecological model. The parameter *p* varies between visits to represent detection probability varying throughout the year varying, but λ is considered a fixed estimate of abundance for a site each year.

Our model for the ecological component was a hierarchical GAM. The hierarchical approach strikes a balance between using information contained across all sampling locations and the information at a particular site (a variety of similar model structures were considered using pilot data from similar datasets *10.5281/zenodo.8026915*).

$$(5)\quad Log(\lambda_j) = \alpha_j + \sum_1^K \beta_{jk} b_{jk}$$

$$Log(\beta_{jk}) \sim N(\hat{\beta}_k, \sigma)$$

$$Log(\hat{\beta}_{1:k}) \sim N(0, 0.05)$$

$$\sigma \sim Exponential(1)$$

$$Log(\alpha_j) \sim N(2, 1)$$

Where K is the number of splines covering the sampling years, β_k a vector of coefficients, and b_k basis functions (here we use B spline basis functions). The optimal number of splines for fitting the trends were estimated around Fewster's [65] recommendation of 0.3 x the number of years for bird trends, however, we tested models ± 1 and 2 splines on a subset of the data and selected splines for the final model using WAIC [47].

In the observational process models, we considered all the variables recorded in the survey that may influence bird detection. Due to relatively large dataset and the complexity of the model, the model runtime was slow putting a priority on minimising unnecessary model complexity and precluding exhaustive testing of model structures. Therefore, we first used a subset of the data and tested a model containing all potentially relevant variables and only retained those for the full model run where there was any evidence they influenced detection probability, this included visit time (early, late), detection band, and dominant habitat type.

Models linking across trophic levels

To link moth populations to the bird populations, we identified all moth sites within a radius of 5km of a bird sampling location. When there were multiple moth sites within the radii, we produced a combined moth index through inverse distance weighting. We use two main summed moth indices in the analysis, total annual moth abundance and mean annual abundance. For total annual moth abundance, we first summed all moths at the site before applying distance weighting to estimate the average total abundance at a location. This process was then repeated to provide summed indices for species in the Noctuidae and the Geometridae. For mean annual abundance, we simply took the yearly average abundance across every moth. During analysis, we also considered the previous year's moth abundances but found stronger correlations with the current moth generation and bird population change in the models constructed below and so preceded with only the current year indices.

To construct the population models, we used a linearized Ricker formulation (Equation 6). This is a log-linear Ricker growth model [66] with the dependent variable the log per capita population growth rate and parameters estimating intrinsic growth, environmental modifiers on growth rate (e.g. moth abundance, site random intercept, year random intercept), and density dependence. All model variables were centred and scaled before fitting and we used weakly regularizing standard normal priors for the linear model parameters, and exponential priors with λ =1 for the standard deviations.

$$(6)\ \log\left(\frac{N_{t+1}}{N}\right) = site_i + year_j + \beta X + bN_t$$

$$b \sim Normal(0\,,1)$$

$$B_i \sim Normal(0\,,1)$$

$$site \sim Normal(0,1)$$

$$year \sim Normal(0,1)$$

In Equation 6 N_t represents the population size and time *t*, b represents the coefficient on previous years' abundance (density dependence), $site_i$ and $year_j$ represent site and year offsets, β the coefficient on the moth index and *X* the moth index.

We fitted this model to population data of the blue tit and then to the yearly estimates of total moth abundance and abundances of the Noctuidae and the Geometridae at each site. We then extracted the year coefficients from both models and compared them to see if good years for the blue tit corresponded with a good year for moths. We next extracted the year coefficients from the blue tit model and compared this with the mean total annual abundance (i.e. averages of total abundance across all sites) for each group of moths. This allowed us to see if good years for the blue tit corresponded with high moth abundance. Correlations for the comparisons were estimated in a Bayesian framework by fitting a multivariate normal and extracting the correlation coefficient from the posterior variance-covariance matrix.

In the next stage, we aimed to estimate the effect of mean annual moth abundance and the effect of selected species on bird population change. To do this we removed the yearly intercept due to the aforementioned correlations with mean annual abundance and included the mean annual moth abundance and the difference between this average and the candidate moth species at each (Equation 7). The model was then rerun for each candidate. Here for the mean annual abundance, we didn’t sum moths and instead took the average abundance of all moths at a site and year. This is essentially perfectly correlated with the mean of the summed total abundance, but makes the difference measure a similar scale and therefore more interpretable (i.e. either + or – the average).

$$(7)\ \log\left(\frac{N_{t+1}}{N}\right) = site_i + \bar{\beta}\bar{X} + \gamma x_i + bN_t$$

In Equation 7 symbols are as before but $\bar{\beta}\bar{X}$ represent the coefficient on the mean annual abundance and the annual mean abundance respectively, γx_i represents the coefficient on the species abundance difference and the species abundance difference at site i respectively.

When fitting, we found that the species abundances were often skewed with a few large values that had high leverage on the regression fits. To account for this we used the inverse hyperbolic sign transformation [67] 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 using the difference rather than directly using species abundance by refitting all models with species abundance in place of the difference. In both cases, results were similar (Supplementary materials).

Spatial variability trophic-link models

To construct models that accounted for spatial variation in the importance of different food sources, we adapted the model in Eq. 7 to include a Gaussian Process [68] on γ the response to the species-specific moth abundance and in the model in Eq. 6 to include spatial variation on β (again excluding the year random intercept). In the Gaussian Process, parameters were drawn from a multivariate normal with the covariance matrix between sites estimated using Euclidian distance and a squared exponential covariance function (L2 norm)[42]. 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, and an exponential prior with λ =1 for the standard deviations, η, and *p.*

$$(8)\ \log\left(\frac{N_{t+1}}{N}\right) = site_i + \beta_i X + b\,N_t$$

$$b \sim Normal(\bar{b}\,, \sigma_b)$$

$$\begin{bmatrix}\beta_1\\ \beta_2\\ \vdots\end{bmatrix} \sim MVNormal\left(\begin{bmatrix}0\\ 0\\ \vdots\end{bmatrix}, R\right)$$

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

In Equation 8, *i* is an index for site, *R* is a covariance matrix, η^2 is the maximum covariance between any sites, ρ_{ij} the correlation between site *i* and *j,* D_{ij} the distance between sites *i* and *j,* and $\delta\sigma^2$ accounts for within-site variance in β when $i = j$.

The spatial models were fitted to the mean annual abundance and to a representative panel of five selected individual species (*Operoptera brumata, Erannis defolaria, Operoptera fagata, Cosmia trapezina, Lymantria monacha).* We selected *O. brumata* and *E. defolaria* as they are often cited as key species in the diet of blue tit*; O. fagata* as it is a sister species to

O. brumata but there was less evidence for an effect overall (see *Results*); *C. trapezina* as it had the largest effect size; and *L. monacha* as a species representative of a national scale effect that was estimated close to zero.

Fitting details

Analysis was conducted in R 4.1.2 [69], and the probabilistic programs for fitting the Bayesian models were written in Stan 2.21.0 [70]. We used a cut-off of <1.1 for the $\hat{R}$ [71] for indicating convergence. The R packages 'RStan' 2.26.11 [72] and 'rethinking' 2.13 [73] were used to analyse model outputs, and 'raster' 3.4-13 [74] and 'geosphere' 1.5-14 [75] were used for spatial processing and visualisations. Code and data in support of the results are available at 10.5281/zenodo.8021350

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Supplementary materials

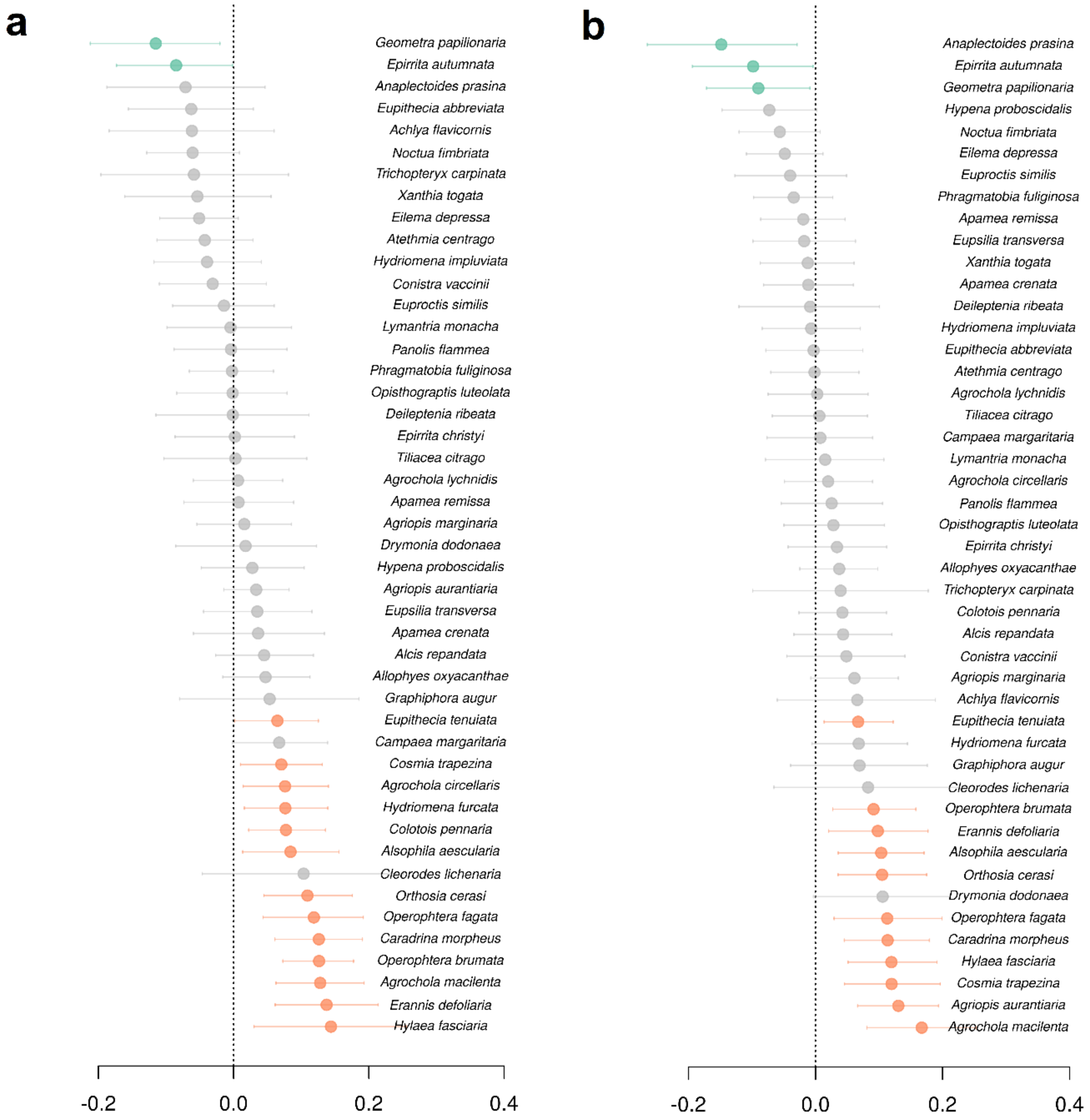

Figure S1. Species-specific coefficients when a) fitting without using the inverse hyperbolic sine transformation, and b) when using raw abundance rather than differences from the mean moth abundance.

Table S1. Coefficients of density dependence from the population change models, columns show posterior means and boundaries of the 95% credible intervals.

	Mean	2.5%	97.5%
blue tit	-0.09	-0.13	-0.06
Total moth abundance	-0.71	-0.76	-0.66
Noctuidae	-0.50	-0.54	-0.46
Geometridae	-0.63	-0.69	-0.57