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A multispecies perspective on ecological impacts of climatic forcing

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Summary

1. In the prevailing context of concerns over climate change and its potential impacts on ecosystems, evaluating ecological consequences of climatic forcing has become a critical issue.
2. Historical data on the abundance of organisms have been extensively used to characterize the ecological effects of climatic forcing through specific weather and/or climatic variables, with most of the studies confined to single population models.
3. However, population responses to environmental fluctuations typically depend upon positive and negative feedbacks induced by interactions with other species. It is therefore important to integrate the insights gained from single population approaches into a multispecies perspective.
4. Here we combine the hierarchical Bayesian modelling approach with the state-space formulation to extend the scope of previously proposed models of population dynamics under climatic forcing to multi-species systems.
5. We use our model to analyse long-term macro-moth (Lepidoptera) community data from the Rothamsted Insect Survey network in the UK, using winter rainfall and winter temperature as environmental covariates.
6. The effects of the two weather variables were consistent across species, being negative for winter rainfall and positive for winter temperature. The two weather variables jointly explained 15–40% of the total environmental variation affecting the dynamics of individual species, and could explain up to 90% of covariances in species dynamics.
7. The contribution of interspecific interactions to community-level variation was found to be weak compared to the contributions of environmental forcing and intraspecific interactions.

Key-words: Bayesian inference, biotic interactions, environmental forcing, Markov chain Monte Carlo

Introduction

Evaluating population dynamical consequences of climatic forcing has become a critical contemporary issue in ecology with the rising concerns over climate change progress and its potential ecological impacts (Woiwod 1997; Harrington, Woiwod & Sparks 1999; Hughes 2000; McCarthy 2001; Hill *et al.* 2002; Walther *et al.* 2002; Parmesan & Yohe 2003; Root *et al.* 2003). Historical data on the abundance of organisms have been extensively used for attempting to characterize the ecological impacts of climatic forcing through specific weather variables such as temperature, rainfall, snow cover etc., or large-scale climatic indices like the North Atlantic oscillation (NAO) or the El Niño/Southern Oscillation

(ENSO). For example, Saether *et al.* (2000) investigated population dynamical consequences of climate change for a small songbird, using winter temperature and precipitation as environmental covariates. Stenseth *et al.* (2004) examined the effects of fluctuations in the North Atlantic Oscillation (NAO) index on variation in Soay sheep counts. Henderson & Seaby (2005) analysed the role of fluctuations in winter NAO index and water temperature in determining temporal variation in abundance, recruitment and growth of *Solea solea* at Bridgwater Bay in the Bristol Channel, England. Westgarth-Smith *et al.* (2007) investigated the association between temporal variations in English populations of a forest insect pest, the green spruce aphid (*Elatobium abietinum*) and the NAO index.

However, most studies concerned with ecological impacts of climatic forcing have been confined to single population models, even though population responses to environmental

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fluctuations typically depend upon positive and negative feedbacks induced by interactions with other species (Ives 1995; Kilpatrick & Ives 2003). The next stage is to integrate the insights gained from single population approaches into a multispecies perspective so we can understand the mechanisms underlying fluctuations in species abundances and community structure.

In this paper we combine the hierarchical Bayesian modelling approach (Berlinier 1996; Gelman *et al.* 2003; Clark 2005; Wikle & Hooten 2006) with the state-space formulation (de Valpine & Hastings 2002; Buckland *et al.* 2004; Clark & Bjørnstad 2004; Rivot *et al.* 2004; Gimenez *et al.* 2007), to extend the scope of previously proposed models of population dynamics under climatic forcing to multi-species systems. We demonstrate the implementation of our model with long-term macro-moth (Lepidoptera) light-trapping data from the Rothamsted Insect Survey network in the UK, using two weather variables, namely winter (December–February) rainfall and winter temperature as environmental covariates. We also evaluate the proportion of variation attributable to different factors in the dynamics of individual species, as well as the proportion of environmental variance and covariance explained by the included environmental covariates.

Materials and methods

DESCRIPTION OF DATA

We use replicated time series of yearly light-trapping catches for 12 most abundant noctuid (*Noctuidae*) macro-moths (Lepidoptera) from the Rothamsted Insect Survey (RIS) network in the United Kingdom (Woiwod & Harrington 1994). The data involve replicates from two different sampling stations: Geescroft I and II, in woodland on Rothamsted Farm in Hertfordshire, UK (Woiwod & Gould 2008). The data cover the period 1973–2003 for Geescroft I and 1973–1998 for Geescroft II. The scientific and common names of the study species are given in Table 1, and time plots of observed species abundances (on a natural logarithmic scale) are shown in Fig. 1. Note that *Mesapamea secalis* is in fact a two species complex (*secalis/didyma*). These two species can only be separated on genitalia and were not recognized as separate when the sampling started so they are kept as one for consistency. We used winter (December–February) rainfall (F) in mm and winter temperature (T) in degrees Celsius as climatic covariates. The two variables were standardized to have zero-mean and unit variance. No significant correlation was observed between these two climatic variables ($\rho = 0.07$) at Rothamsted, in line with the suggestion of Westgarth-Smith *et al.* (2007). This implies that the two variables can enter the model additively without inducing multicollinearity issues which may lead to flawed inferences (Silvey 1969; Graham 2003). Time plots of standardized scores of the two environmental variables are shown in Fig. 2.

MODEL SPECIFICATION

The model is developed and fitted with a hierarchical Bayesian approach (Berlinier 1996; Gelman *et al.* 2003; Wikle & Hooten 2006). A state-space formulation (de Valpine & Hastings 2002; Buckland *et al.* 2004; Clark & Bjørnstad 2004; Rivot *et al.* 2004; Gimenez *et al.* 2007) is used to distinguish between the process model describing the actual dynamics of the study system by conditional Markovian

Table 1. Scientific and common names of the study moth species. All species belong to the noctuid (*Noctuidae*) family

Scientific name	Common name
<i>Agrostis exclamationis</i>	Heart & Dart
<i>Diarsia mendica</i>	Ingrailed Clay
<i>Xestia xanthographa</i>	Square-spot Rustic
<i>Noctua pronuba</i>	Large Yellow Underwing
<i>Orthosia gothica</i>	Hebrew Character
<i>Hoplodrina alsines</i>	The Uncertain
<i>Mesapamea secalis/didyma</i>	Common Rustic
<i>Cosmia trapezina</i>	The Dun-bar
<i>Agrochola macilenta</i>	Yellow-line Quaker
<i>Conistra vaccini</i>	The Chestnut
<i>Hypena proboscidalis</i>	The Snout
<i>Hermina grisealis</i>	Small Fan-foot

transitions between successive states, and the observation model intended to map the observed data to the actual states of the process.

The process model

We assume a Gompertz kernel for the underlying population dynamics. The Gompertz model has been widely used in modelling population and community dynamics (e.g. Saitoh, Stenseth & Bjørnstad 1997; Jacobson *et al.* 2004; Dennis *et al.* 2006; Mutshinda, O'Hara & Woiwod 2009), and has the advantage of being linear on a logarithmic scale. The model includes intra- and interspecific interactions, as well as linear terms measuring the dynamical effects of climatic variables on the growth rates of the study populations, and is designed to accommodate species covariations in response to latent environmental factors.

More specifically, let $N_{i,t}$ denote the actual number of individuals of species i in the community in year t (S species in total), and let F_t and T_t designate respectively the averaged winter (December–February) rainfall (in mm) and winter temperature (in degrees Celsius) in year t , standardized as indicated above. The number of individuals of species i at time t in the community is described by

$$N_{i,t} = N_{i,t-1} \exp \left\{ r_i \left(1 - \sum_{j=1}^S \alpha_{ij} \log N_{j,t-1} / k_i \right) + \beta_{i,1} F_t + \beta_{i,2} T_t + \varepsilon_{i,t} \right\}, \quad \text{eqn 1}$$

where r_i and k_i are the intrinsic growth rate and the natural logarithm of the carrying capacity of species i respectively; α_{ij} is the interaction coefficient quantifying the effect of species j on the growth of species i (interspecific interaction), with all coefficients of intraspecific interactions, $\alpha_{i,i}$, set to 1 (Loreau & de Mazancourt 2008; Mutshinda, O'Hara & Woiwod 2009); $\beta_{i,1}$ and $\beta_{i,2}$ quantify the effects of winter rainfall and winter temperature on the growth rate of species i , respectively. The random shocks, $\varepsilon_{i,t}$, representing the variability resulting from demographic stochasticity and un-modelled (latent) environmental factors are assumed to be serially independent and normally distributed with mean zero, but are allowed to covary across species at a specific time as discussed below. The normality assumption allows us to separately model the mean and covariance structures (Ripa & Ives 2003; Mutshinda, O'Hara & Woiwod 2009). On the natural logarithmic scale, equation 1 becomes

$$n_{i,t} = n_{i,t-1} + r_i \left(1 - \sum_{j=1}^S \alpha_{ij} n_{j,t-1} / k_i \right) + \beta_{i,1} F_t + \beta_{i,2} T_t + \varepsilon_{i,t}, \quad \text{eqn 2}$$

where $n_{i,t}$ denotes the natural logarithm of $N_{i,t}$. Equation 2 can be compactly written in matrix form as

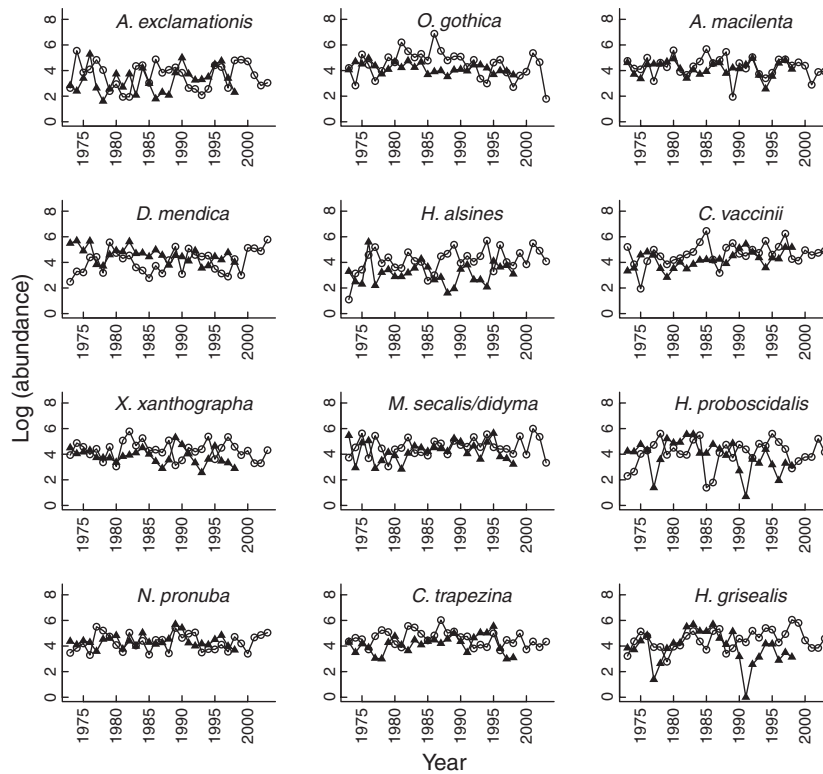


Fig. 1. Time plots of observed species abundances on the natural logarithmic scale. Open circles represent catches from Geescroft I over the period 1973–2003, and solid triangles represent catches from Geescroft II over the period 1973–1998.

$$\mathbf{n}_t = \mathbf{n}_{t-1} + \mathbf{R}(\mathbf{I}_S - \mathbf{A}\mathbf{n}_{t-1}) + \mathbf{B}\mathbf{W}_t + \boldsymbol{\varepsilon}_t, \quad \text{eqn 3}$$

where $\mathbf{n}_t = (n_{1,t}, \dots, n_{S,t})^T$ is the S -dimensional vector of log-transformed abundances of the S species at time t , \mathbf{R} is a S -by- S diagonal matrix with $\mathbf{R}_{i,i} = r_i$, and \mathbf{I}_S is the S -dimensional vector with all elements equal to 1; $\mathbf{A}_{i,j} = \alpha_{i,j}/k_i$, $\mathbf{W}_t = (F_t, T_t)^T$, \mathbf{B} is a $n \times 2$ matrix with (β_{i1}, β_{i2}) as i^{th} row, and $\boldsymbol{\varepsilon}_t = (\varepsilon_{1,t}, \dots, \varepsilon_{S,t})^T$ is the vector of process disturbances affecting the community dynamics at time t , with one element by species. The serially independent vectors $\boldsymbol{\varepsilon}_t$ are assumed to be multivariate normally distributed around the zero-vector, with a covariance matrix denoted by $\boldsymbol{\Sigma}_t$ i.e. $\boldsymbol{\varepsilon}_t \sim \text{MN}(\mathbf{0}, \boldsymbol{\Sigma}_t)$. The covariance matrix $\boldsymbol{\Sigma}_t$ is further decomposed into its environmental and demographic components as

$$\boldsymbol{\Sigma}_t = \mathbf{C} + \mathbf{D}_t. \quad \text{eqn 4}$$

The covariance matrix \mathbf{C} represents the variability not explained by intrinsic dynamics or by the included environmental covariates, including the effect of interactions with un-modelled species at the same trophic level as well as species at other trophic levels. The matrix \mathbf{C} is henceforth referred to as the environmental covariance matrix. Species are also allowed to covary in their response to latent (un-modelled) environmental factors by assuming that the elements, $C_{i,i}$, on the main diagonal of \mathbf{C} and the off-diagonal elements, $C_{i,j}$ ($i \neq j$), represent species-specific and joint responses to latent environmental factors, respectively. $\mathbf{D}_t = \text{diag}(\delta_t^2/N_{i,t-1})$, where $\delta_t^2/N_{i,t-1}$ denotes the (population-level) demographic variance affecting the dynamics of species i from time $t-1$ to t , which is scaled inversely with the population size (Saether *et al.* 2000; Bjørnstad & Grinell 2001; Lande, Engen & Saether 2003). It is in fact the dependence of demo-

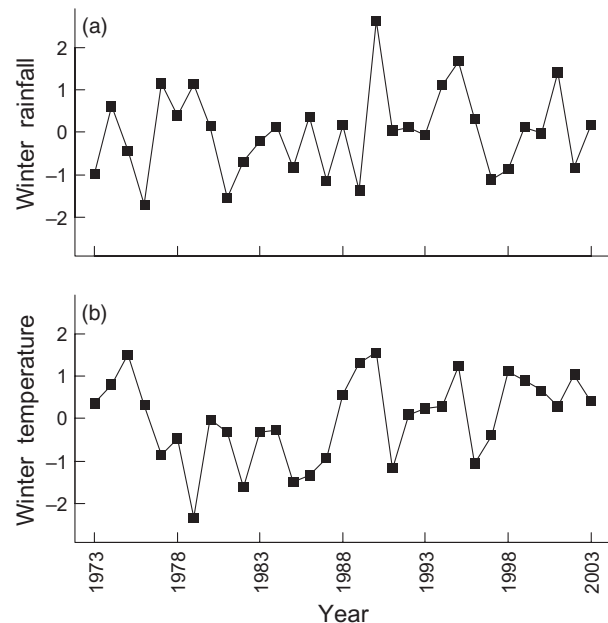


Fig. 2. Time plots of (a) mean winter rainfall (in mm) and (b) mean winter temperatures (in degrees Celsius) over the period 1978–2003 in Hertfordshire UK, standardized to have zero mean and unit variance.

graphic variance on the population size that makes the demographic and environmental components of the process variance involved in equation 4 statistically identifiable.

Following Saether *et al.* (2000), the total environmental variance, E_i , affecting the dynamics of species i can be split into a component, $\beta_{i,1}^2 \text{var}(F) + \beta_{i,2}^2 \text{var}(T)$, attributable to the included environmental variables, and a residual environmental variance, $C_{i,i}$, quantifying the variability not accounted for by the included variables. That is,

$$E_i = C_{i,i} + \beta_{i,1}^2 \text{var}(F) + \beta_{i,2}^2 \text{var}(T). \quad \text{eqn 5}$$

In particular, if the covariates F and T are standardized to unit variance as is the case here, then equation 5 takes the simple form $C_{i,i} + \beta_{i,1}^2 + \beta_{i,2}^2$ so that $(\beta_{i,1}^2 + \beta_{i,2}^2)/E_i$ represents the proportion of environmental variation attributable to the included weather variables. Additionally, the environmental covariance between the dynamics of species i and j is given by

$$(\beta_{i,1}\beta_{j,1})\text{var}(F) + (\beta_{i,2}\beta_{j,2})\text{var}(T) + C_{i,j}, \quad \text{eqn 6}$$

which is simply $\beta_{i,1}\beta_{j,1} + \beta_{i,2}\beta_{j,2} + C_{i,j}$ with standardized covariates. Moreover, if $C_{i,j} > 0$ and the effects of the two covariates on the dynamics of species i and j turn out to be of identical signs, then the proportion of environmental covariance between species i and j that is explained by the covariates is given by

$$(\beta_{i,1}\beta_{j,1} + \beta_{i,2}\beta_{j,2})/(\beta_{i,1}\beta_{j,1} + \beta_{i,2}\beta_{j,2} + C_{i,j}).$$

We used the Bayesian variable selection method known as stochastic search variable selection (SSVS) (George & McCulloch 1993; Mutshinda, O'Hara & Woivod 2009) to constrain the coefficients of spurious inter-species interactions to be close to zero so that they do not affect the model results. The rationale of SSVS is to embed a multiple regression set-up in a hierarchical normal mixture model, and use latent indicators to identify promising sets of predictors. For each coefficient of interspecific interaction, $\alpha_{i,j}$ ($i \neq j$), we introduced an auxiliary indicator $\gamma_{i,j} \sim \text{Bern}(p_{i,j})$, $0 < p_{i,j} < 1$, such that $\gamma_{i,j} = 1$ when species j is included in the dynamics of species i , and $\gamma_{i,j} = 0$ otherwise. Conditionally on $\gamma_{i,j}$, we defined the prior distribution of $\alpha_{i,j}$ as a mixture of two Gaussians i.e. $\alpha_{i,j}|\gamma_{i,j} \sim (1 - \gamma_{i,j}) \times N(0, c_1) + \gamma_{i,j} \times N(0, c_2)$. The positive constant c_1 was selected to be small and c_2 to be large. This prior specification constrains $\alpha_{i,j}$ to be concentrated around zero when $\gamma_{i,j} = 0$ since the ensuing prior corresponds to the spike part of the Gaussian mixture prior placed on $\alpha_{i,j}$, which is confined around zero. On the other hand, $\alpha_{i,j}$ is freely estimated from the data when $\gamma_{i,j} = 1$ since the corresponding prior, the slab part of the Gaussian mixture priors placed on $\alpha_{i,j}$, is diffuse (flat).

A Gibbs sampling methodology is used to generate samples from the joint posterior of all unknowns, including the inclusion indicators $\gamma_{i,j}$. The relevance of a single interaction effect, $\alpha_{i,j}$, is evaluated through the Bayes factor $B_{i,j} = \frac{P(\gamma_{i,j}=1|\text{Data})}{1 - P(\gamma_{i,j}=1|\text{Data})} \times \frac{1 - P(\gamma_{i,j}=1)}{P(\gamma_{i,j}=1)}$, which quantifies the amount by which the prior odds of including vs. not including $\alpha_{i,j}$ into the model are changed into posterior odds by the data. If $B_{i,j}$ is larger than 1, we say that the data provide more support in favour of including $\alpha_{i,j}$ into the model than assumed *a priori*, and *vice-versa*. Bayes factors for comparing two hypotheses (or models) H_1 and H_2 are usually interpreted on the following scale due to Jeffreys (1961). $B_{1,2} < 1$: 'Negative support for H_1 (i.e. support for H_2)'; $1 \leq B_{1,2} < 3$: 'Barely worth mentioning evidence in favour of H_1 '; $3 \leq B_{1,2} < 10$: 'Substantial support for H_1 '; $10 \leq B_{1,2} < 100$: 'Strong support for H_1 '; $B_{1,2} > 100$: 'Decisive support for H_1 '. For us here H_1 and H_2 represent the inclusion and exclusion of individual interaction coefficients into the model, respectively.

The observation model

We took advantage of the replicated feature of our data (time series from two light-traps: Geescroft I and Geescroft II on the same site) to explicitly accommodate potential discrepancies in capture efficiency across traps for different species. Our observation model was also specified with Gaussian errors.

More specifically, let $Y_{i,t,k}$ denote the observed number of individuals of species i at time t from trap k , and let $y_{i,t,k} = \log(Y_{i,t,k})$. We assume that

$$y_{i,t,k}|n_{i,t} \sim N(n_{i,t} + b_{i,k}, \tau_i^2), \quad \text{eqn 7}$$

where the random variable $b_{i,k}$, intended to correct for differences in capture efficiency between species across traps, is set to zero for one of the traps (Geescroft I) to force identifiability. So we only estimate $b_{i,2}$, and consider negative values of it as implying lower capture efficiency for Geescroft II compared to Geescroft I and *vice-versa*.

PRIOR SPECIFICATION

Fitting a Bayesian model to the data requires explicit statements of prior distributions for all unknown quantities. We placed on the covariance matrix \mathbf{C} an inverse Wishart prior with scale matrix $\mathbf{\Omega}$ and a number, q , of degrees of freedom set to the smallest possible number, i.e. the rank of $\mathbf{\Omega}$, to convey vague prior information. We then set $\mathbf{\Omega}$ to the S -dimensional identity matrix, \mathbf{I}_S . For all species, we independently placed diffuse $N(0, 15)\mathbf{I}(0, \infty)$ on the log-carrying capacities and $N(0, \sigma_r^2)\mathbf{I}(0, +\infty)$ on the intrinsic growth rate, where $\mathbf{I}(\cdot)$ denotes the indicator function. The parameters $\beta_{i,1}$ and $\beta_{i,2}$ representing the effects of winter rainfall and winter temperature were independently assigned diffuse $N(0, 100)$ priors, and all $p_{i,j}$ (the *a priori* inclusion probability of interspecific interactions) were set to 0.2. Finally, we placed *Unif*(0, 10) priors on the standard deviations δ_i , τ_i and σ_r . Gelman (2006) gives a justification for this approach to prior specification for variance parameters.

MODEL FITTING

We used Markov chain Monte Carlo (MCMC) simulation methods (Gilks, Richardson & Spiegelhalter 1996) through OpenBUGS (Thomas *et al.* 2006) to sample from the joint posterior of the model parameters. We ran 80 000 iterations of three Markov chains starting from dispersed parameter values, and discarded the first 20 000 samples of each chain as burn-in, thinning the remainder to every 25th sample. The convergence was assessed visually through the mixing of the chains and the behaviour of the sample autocorrelation plots. The BUGS code for the model fitting is provided in the Appendix S1 (Supporting information).

We used posterior predictive cross-validation to check the model adequacy by omitting the last five observations from the Geescroft I data set for each species, and forecasting them from the model to determine how well the model predictions would approximate the omitted data. In all cases, the model predictions were consistent with the discarded data as illustrated by Fig. 3 where *M. secalis/didyma* and *H. proboscidalis* are used for illustration.

Results

The multivariate normality assumption on the residuals $\boldsymbol{\varepsilon}_t = (\varepsilon_{1,t}, \dots, \varepsilon_{S,t})^T$, was corroborated by the Shapiro–Wilks multivariate normality test through the function `mshapiro()`

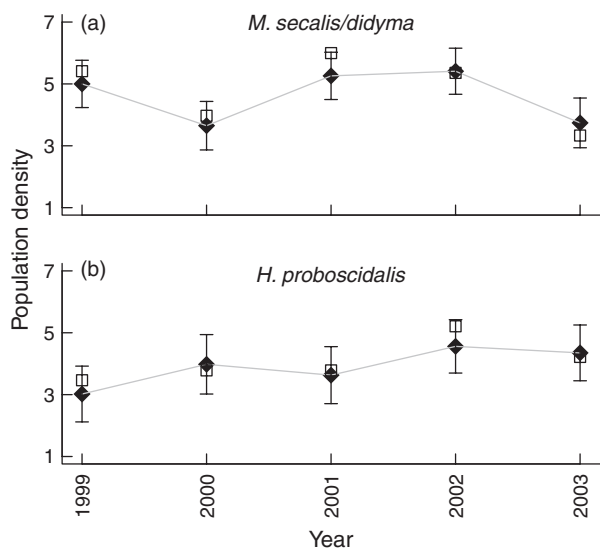


Fig. 3. Posterior predictive distributions of observed population densities of *Mesapamea secalis/didyma* and *Hypena proboscidalis* over the period 1998–2003 for Geescroft I. The black diamonds represent posterior means, the error-bars show the 95% central predictive intervals, and the open squares plotted on top represent the observed values. The two species were selected to illustrate the full set of our results.

from the `mvnormtest` R package (the R Development Core Team 2009), ruling out concerns about model misspecification.

Environmental variation was the most important driver of population dynamics in the focal community, accounting for between 45 and 75% of variation in the dynamics of individual moth species. Intraspecific interactions (i.e. the effects of density dependence) were found to be the second most important source of variation in species abundances and explained roughly 10–30% of temporal variation in species abundances. However, the contribution of interspecific inter-

actions was minor, broadly explaining less than 10% of variation in the dynamics of individual species (Fig. 4c).

Effects of the two weather variables were consistent across species, being negative for winter rainfall and positive for winter temperature (Fig. 4a). When the environmental variance was split into contributions from the two environmental covariates and the residual (unexplained) variance, the two weather variables jointly explained 15–40% of the total environmental variation. Individually, the two variables explained 10–20% of the total environmental variation (Fig. 4d). Moreover, the two environmental variables explained up to 90% of environmental covariances between species. The highest environmental covariances are given in Table 2.

The coefficients of interspecific interactions were mainly far lower than one, with Bayes factors in favour of their inclusion providing no more than a barely worth mentioning support.

The contribution of demographic stochasticity to the temporal variation in species abundances was estimated to be weak, with posterior means of δ_i^2 lying between 1.5 and 3, implying much lower population-level demographic variances, given that our data sets are limited to species occurring in high numbers.

Figure 4b shows posterior means and 68% central credible intervals for the variable b , implying slightly higher capture efficiency for the Geescroft I trap for most species.

Discussion

In this paper we developed a hierarchical Bayesian model to investigate the ecological impacts of climatic forcing from a multispecies perspective. We applied the methodology to macro-moth (Lepidoptera) light-trapping data from the Rothamsted Insect Survey network in the UK, using winter (December–February) rainfall and winter temperature as environmental covariates. The results agree with our previous

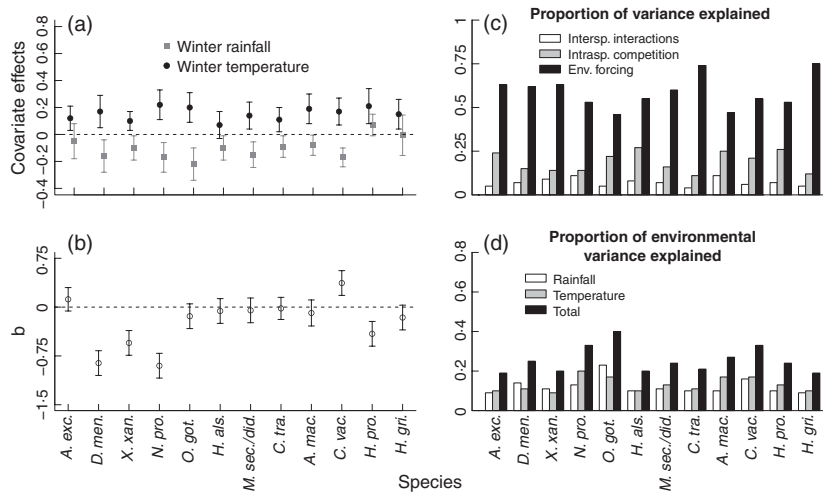


Fig. 4. (a) Posterior means and 68% credible intervals for the parameters representing the effects of winter rainfall (grey squares) and winter temperature (black circles) on the growth of individual species; (b) Posterior means and 68% credible intervals for the variable b representing the efficiency of the Geescroft II trap relative to Geescroft I for each species, with all values corresponding to Geescroft I set to zero. Panel (c) shows barplots for the proportions of environmental variance attributable to environmental stochasticity, as well as intra-/interspecific interactions in the dynamics of individual species, whereas panel (d) shows barplots for the proportions of environmental variance explained by winter rainfall and winter temperature, both individually and collectively.

Table 2. Proportions of covariance in species abundances explained by the environmental covariates

	<i>X. xanthographa</i>	<i>N. pronuba</i>	<i>M. secalis/didyma</i>	<i>C. trapezina</i>	<i>C. vaccini</i>
<i>N. pronuba</i>	30%		32%	58%	65%
<i>O. gothica</i>	48%	67%	90%	80%	85%
<i>M. secalis/didyma</i>	26%	32%		37%	72%

analysis of the same community (Mutshinda, O'Hara & Woiwod 2009), although there are some small differences, as this analysis included two replicate sampling stations.

The model was based on a loglinear (Gompertz) kernel and included intra- and interspecific interactions, along with linear terms measuring the effects of environmental variables, and was designed to accommodate species covariation in response to latent environmental factors.

The effects of winter rainfall and winter temperature on the dynamics of the study species were consistently negative for the former and positive for the latter (Fig. 4a). These results are in line with the suggestions of previous studies of the ecological impacts of weather on Lepidoptera (Beirne 1955; Pollard 1988; Crozier 2004).

Plausible explanations for negative effects of winter rainfall on Lepidoptera include the fact that heavy rains are usually accompanied by strong winds which might dislodge larvae from their host plants, thereby disrupting their feeding behaviour. In addition, wet weather might favour the incidence and the spread of moth fungal pathogens which may drastically affect larval and pupal survival.

The positive association between winter temperature and the growth rate of the study species agrees with the generally accepted view that warm conditions are favourable to larval survival for many Lepidoptera species (e.g. Crozier 2004).

Environmental stochasticity (not including the variation due to interspecific interactions between the included species) was the most important source of variation in species abundances as it accounted for between 45 and 75% of the total variance in the dynamics of individual species. Intra-specific interactions were of secondary relative importance and accounted between 10 and 30% of the total variance in the dynamics of individual species. The influence of interspecific interactions on community-level variation was found to be minor with contributions to total variance in the dynamics of individual species broadly less than 10%. This result corroborates the previously suggested weak contribution of interspecific interactions to explaining community-level variation (Ives, Gross & Klug 1999; Kokkoris, Troumbis & Lawton 1999; Houlahan *et al.* 2007; Mutshinda, O'Hara & Woiwod 2009). Moreover, the Bayes factors in favour of including inter-species interactions into the model were found to be broadly less than one, except a few of them whose values lay between 1 and 3, implying a support that is not worth more than a bare mention on the Jeffreys' scale.

We further partitioned the total environmental variance affecting the dynamics of individual species into the contribu-

tions from the included weather variables and the unexplained (residual) variance. Winter rainfall and temperature jointly explained up to 40% of the total environmental variation in the dynamics of individual species.

The environmental covariances between species were broadly positive, and the two environmental covariates accounted for up to 90% of covariances between species. We chose environmental covariates that we suspected, *a priori*, would influence the community, and there are many other covariates that might also have an effect. It is thus promising that we can start to untangle the causes of these environmental correlations. The excess environmental covariation may be ascribed to other factors not included in the model such as extra-trophic interactions (e.g. predation pressure from insectivorous birds or generalists parasitoids), or indirect climatic effects. It is also well known that if two populations have the same density-dependent structure, then correlated density-independent factors can bring the population fluctuations into synchrony, the 'Moran effect' (Moran 1953; Royama 1992).

Synchrony in population fluctuations has implications for the community viability, with positive correlations increasing the probability of local and even global extinction. Palmquist & Lundberg (1998) pointed out that synchronously fluctuating populations face a greater risk of global extinction than do independently fluctuating populations. We have shown that we can find some of the causes of these environmental correlations, which then suggests that we can start to estimate the effects of changes in these variables (e.g. due to anthropogenic climate change) on real communities, and assess their viability.

The population-level signature of demographic variances was found to be weak. This is not surprising given the inverse scaling of the demographic variance with the population size (Lande, Engen & Saether 2003) and the fact that the data sets used here are confined to species occurring in high numbers.

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Appendix S1. OpenBUGS code.

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