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Contact CEH NORA team at
noraceh@ceh.ac.uk

Butterfly abundance in a warming climate: patterns in space and time are not congruent

Nick J.B. Isaac[1], Marco Girardello[1], Tom M. Brereton[2] & David B. Roy[1]

[1]Centre for Ecology & Hydrology, Maclean Building, Benson Lane, Crowmarsh Gifford, Wallingford, Oxfordshire, OX10 8BB, UK

[2]Butterfly Conservation, Manor Yard, East Lulworth, Wareham, Dorset, BH20 5QP, UK

Abstract

We present a model of butterfly abundance on transects in England. The model indicates a significant role for climate, but the direction of association is counter to expectation: butterfly population density is higher on sites with a cooler climate. However, the effect is highly heterogeneous, with one in five species displaying a net positive association. We use this model to project the population-level effects of climate warming for the year 2080, using a medium emissions scenario. The results suggest that most populations and species will decline markedly, but that the total number of butterflies will increase as communities become dominated by a few common species. In particular, *Maniola jurtina* is predicted to make up nearly half of all butterflies on UK Butterfly Monitoring Scheme (UKBMS) transects by 2080. These results contradict the accepted wisdom that most insect populations will grow as the climate becomes warmer. Indeed, our predictions contrast strongly with those derived from inter-annual variation in abundance, emphasizing that we lack a mechanistic understanding about the factors driving butterfly population dynamics over large spatial and temporal scales. Our study underscores the difficulty of predicting future population trends and reveals the naivety of simple space-for-time substitutions, which our projections share with species distribution modelling.

Introduction

Climate change is now well-established as a major threat to biodiversity (Thomas et al. 2004) and species distributions are changing in a manner consistent with climate change (Hickling et al. 2006, Hitch and Leberg 2007). The most common way of predicting the effects of climate change is using species distribution modelling (also known as climate envelope or niche modelling, Guisan and Thuiller 2005, Araujo and Guisan 2006).

Distribution modelling works by mapping species patterns of spatial occurrence from a geographic to environmental space (the niche). The correlation between environmental gradients (especially temperature) is then used to predict the species distribution under some projected future combination of climate. The core assumption is that similar mechanisms operate across space and across time (the space-for-time substitution). Niche (bioclimate) models are increasingly the primary tool for identifying the risks of climate change and informing future conservation policy for biodiversity (Thomas et al. 2004), and specifically

butterflies (Settele et al. 2008), in spite of criticism that they generally ignore population biology or biotic interactions (Araujo and Luoto 2007).

Projections based on population time series are much less common (Roy et al. 2001), reflecting the limited taxonomic coverage of high-quality monitoring data. Time series projections make predictions about changes in population abundance (as opposed to species distributions), and therefore provide a more ecologically meaningful measure of biodiversity change. However, parameterization of such models is intensive and may be impractical for large numbers of species.

In this paper, we use the spatial pattern of population abundance to make predictions about the population-level effects of climate change. We employ a space-for-time substitution to project changes in abundance among nearly 10000 populations from sites in the UK Butterfly Monitoring Scheme (UKBMS). We compare our results with the time-based population model of Roy et al. (2001). The results allow us to test the robustness of the space-for-time substitution, and provide novel insights into the practice of using niche models to predict the effects of climate change.

Methods

Butterfly data

We measured butterfly population abundance as the geometric mean 'site index' for the years 2002-6, excluding sites that were surveyed only once during the 5-year period and also site-species combinations in which butterflies were never observed in more than one week of the year. We divided these abundance indices by the transect length, in order to derive an estimate of population density. The resulting dataset contains 9991 populations (site-by-species combinations) representing 46 species and 520 sites.

Model of butterfly abundance

Isaac et al. (in prep) infer a role for climate in butterfly abundance using multi-model inference (Burnham and Anderson 2002) and linear mixed effects models (Bolker et al. 2009). Their models describe the correlates of butterfly population density for these 9991 populations, and include site traits (climate, topography, site management), species traits (measures of life history and niche breadth) and population traits (position in range) as predictor variables. Isaac

et al. measured climatic conditions on UKBMS sites using two axes from a principal components analysis of 10 climate variables. The first principal component, which was not important in explaining butterfly abundance, was highly correlated with several rainfall measures. The second principal component of climatic variation was implicated as important in determining butterfly abundance: this axis was highly correlated with measures of site temperature (mean annual temperature, mean temperature of the coldest month, mean temperature of the warmest month, growing degree days).

We first fitted a model containing the five most important predictor variables in the candidate set of models considered by Isaac et al (in prep). In addition to climate, these were butterfly species richness (of the site), larval growth rate and distributional extent (both species traits) and position in range (a population trait). We then refitted this model with site mean annual temperature instead of the principal component, which lead to a substantial improvement in model fit (∂AIC=9). Mean annual temperature estimates were derived from gridded data on long term monthly temperature records (New et al. 1999, Mitchell and Jones 2005) interpolated to 10km resolution (Oliver et al. 2009). Removing mean annual temperature from the model lead to a substantially worse fit (∂AIC=12.9, χ^2=14.9, df=1, p=0.0001), thus confirming the correlation between temperature and abundance.

We further adapted this model to test whether the response to temperature is heterogeneous among species by fitting a model in which temperature appears in the random part of the model (a random slopes model). In this model, the abundance-temperature relationship is different for each species and is assumed to follow a normal distribution: the estimated parameters are the mean and variance of this distribution. Standard model comparison was used to test whether the random slopes model is a significant improvement over the simple model, in which the temperature response is fixed across all species. Following Enders & Tofighi (2007), we used temperature data centred on zero for each species, in order to avoid spurious correlations. We extracted the species-specific slopes (i.e. the abundance-temperature relationships) from this model (following Isaac and Carbone 2010) and used them for further analyses.

We conducted all analyses using the *lme4* package (Bates et al. 2008) in *R* (R Development Core Team 2008).

Future climate

We used UK Climate Projections (Defra 2010) for mean annual temperature (median estimate) for the year 2080 based on a moderate emissions scenario SRES A1 B (IPCC 2007), which envisions a balance between fossil fuels and renewable energy sources. The A1 storyline and scenario family describe a world of rapid economic growth, with a peak in global population around 2050 and the rapid introduction of efficient new technologies. Major underlying themes are convergence among regions, capacity building and increased cultural and social interactions, with a substantial reduction in regional differences in per capita income. This scenario predicts that mean annual temperatures in 2080 will be up to 3.6°C warmer than present in southern England, and around 2.8°C warmer in northern England.

The data for climate projections is gridded with a resolution of 25km. We matched 477 UKBMS sites to the relevant grid cell in the climate projections dataset. We excluded 43 coastal sites that fell outside the grid extent for climate projections, including all five UKBMS sites of *Thymelicus acteon*. Our projected abundance dataset therefore covers 9075 populations representing 45 species and 477 sites.

Predicted abundance under climate change

We derived predicted abundance for each of our 9075 populations by using the species-specific temperature response, the site-specific temperature change and the current abundance (geometric mean for the years 2002-6). For each species, we summed both current and predicted future abundance across all sites; for each site, we summed across species. These values estimate the total number of butterflies for each species and each site, for both 2002-6 and 2080. We then expressed the difference between time periods as a percentage change in abundance.

Results

The overall relationship between mean annual temperature and butterfly density is weak but generally negative (figure 1). Before accounting for variation among species, the parameter estimate is –0.178, which means that a rise of 1°C in mean annual temperature is accompanied by a drop in abundance of ($1-e^{-0.178}=$) 16.3%.

After accounting for variation among species (the random slopes model), the mean effect of temperature is estimated to be slightly steeper, at –0.213, corresponding to a drop in

abundance of 19.2% for each degree rise in mean annual temperature. However, standard deviation in species' temperature responses (0.265) is large compared with the mean, indicating that a substantial proportion of species (20%) are more abundant at warmer sites (table 1). This random slopes model with species-specific temperature responses represents a substantial improvement in fit over the simpler model containing a single slope (∂AIC=102, χ^2=106, df=2, p<0.0001), supporting the hypothesis that species respond differently to temperature.

Neither the mean temperature response nor the variance among species is substantially altered by removing the other non-species traits (richness and position in range) from the model. We also repeated our model comparison after excluding the five extreme sites with mean annual temperature below 8°C and found the results were qualitatively unchanged.

Combining the species-specific temperature responses with site-specific predictions for climate warming by 2080 yielded projected changes in abundance for 9075 butterfly populations. These ranged from –93% to +71%, with a mean of –26% and median of –36%. However, the predicted change in total abundance (i.e. weighting each population by present abundance) is +21%. In other words, although most populations are predicted to decline, the total number of butterflies on UKBMS sites in England is predicted to rise.

Projected change in species abundance under climate change varies from –92% (*Argynnis aglaja*) to +68% (*Maniola jurtina*). However, species are distributed bimodally through this range (figure 2), with a median projected change of –50%. Sites cover a similar range, but a small majority are predicted to gain butterflies (figure 2): the median change is +0.5%. There is no obvious pattern to the spatial distribution of predicted change among sites: many sites predicted to suffer heavy losses are in close proximity to others that we predict will gain butterflies (figure 3). The variation in space reflects both turnover in community composition and local variation in the (current) abundance of individual species. The apparent contradiction between site and species projections is explained by the response of just two species, Gatekeeper *Pyronia tithonus* and Meadow Brown *Maniola jurtina*. These are the two commonest species on UKBMS transects in England, and both are projected to increase in abundance by over 50% (table 1). Our model suggests that *Maniola jurtina*, which currently makes up 29% of butterflies on UKBMS sites in England, will make up 48% of the total by 2080. Comparable figures for *Pyronia tithonus* are 12% and 15%. The 50% rarest species

currently contribute 1 in 21 observations on the UKBMS: by 2080 this rate is projected to fall to 1 in 41 (data from table 1).

Discussion

Our results suggest substantial future declines in the abundance of most UK butterfly species due to climate change. Our models predict that climate warming will lead to the increased domination of butterfly communities by a few generalist species, providing another example of biotic homogenisation (Keith et al. 2009, Pino et al. 2009, Ekroos et al. 2010). Taken at face value, these findings present a worrying picture for butterfly conservation and imply that conservation priorities should be reassessed urgently.

There are several reasons to suspect the predictions of our models are at best incomplete, or at worst misleading. First and foremost, our model describes patterns of population density in narrow strips on occupied sites, completely ignoring patterns of site occupancy and changes therein. Measuring density over larger spatial scales, incorporating unoccupied sites, might lead to a different set of conclusions (see Cowley et al. 2001a). Changes in occupancy over time are equally important: most UK butterflies are continuing to decline in their distributions (Warren et al. 2001, Fox et al. 2006), and future population extinctions would be in addition to the losses predicted here. However, 29% of species are increasing (Fox et al. 2006), and for these species any losses in abundance predicted here might be offset by colonization of previously unoccupied sites. A second important caveat is that our predictions are based solely on changes in temperature, ignoring other variables in the model that might conceivably change, notably position in range and species richness. Both of these traits would be affected by changes in species' distributions and both had much larger effects on butterfly abundance than did temperature. Moreover, seasonal shifts and changes in site management are probably more important than the crude index of mean annual temperature used here. We were also unable to model changes in microclimatic availability, which may show quite different patterns to mean annual temperature (Wallisdevries and Van Swaay 2006). Finally, we must question the correlation from which our predictions were generated. The negative relationship between abundance and temperature is highly counter-intuitive: climate warming is generally assumed to benefit ectotherms such as butterflies (Warren et al. 2001). UK butterflies are reported to be expanding their range margins northwards in response to climate change (Hickling et al. 2006) and most species are more abundant in warmer years

(Roy et al. 2001). Why then, for most species, are there more butterflies in sites where it's colder?

Three broad classes of explanation exist for the generally negative relationship between abundance and temperature. One is that basal metabolic rates of ectothermic animals increase exponentially with temperature (Gillooly et al. 2001), so that more energy is required for each individual to remain alive. This means that energy supply (i.e. food availability) must rise with increasing temperature in order to sustain the same number of individuals (Brown et al. 2004). All other things being equal, metabolic theory therefore predicts the negative correlation between population density and temperature that we have observed (Storch 2003). For the range of mean annual temperatures across England, each degree rise in temperature raises individual metabolic rates by 9% (Gillooly et al. 2001), thus accounting for much of the 16-19% drop in abundance suggested by our models. However, the rise in temperature (in space or in time) is likely accompanied by longer growing seasons and greater primary productivity, thus offsetting the increase in individual metabolic requirements.

A second explanation is that abundance is mediated by natural enemies. It seems likely that most insects experience high rates of parasitism and disease (Roy et al. 2009), although few specific case studies for butterflies have been described (Revels 2006). The abundance and species richness of natural enemies probably declines with latitude (Rosenzweig 1995), such that butterflies on colder sites in northern England experience much lower exposure to natural enemies than those in the south (Menendez et al. 2008, Gaston 2009). If abundance in the absence of natural enemies (i.e. carrying capacity) is independent of temperature then a negative relationship would be observed with mean abundance, on account of including sites and years with high mortality. However, this would imply smaller inter-annual fluctuations in population size at colder sites, which is the opposite to that reported for the majority of species on the UKBMS (Thomas et al. 1994). However, the role of natural enemies on mean butterfly population size would be testable with comparative data on parasite load at multiple sites.

Finally, it is possible that the apparent correlation between abundance and temperature is an artefact of changes in occupancy and niche breadth with latitude. Most UK butterflies approach their northern range boundaries in the UK, and occupancy (measured as proportion of grid cells) is typically lower near the margins than in the centre of the species range (Gaston 2003, Fox et al. 2006). We also know that niche breadth in UK butterflies declines towards

species' range margins (Oliver et al. 2009). These two observations suggest that butterfly populations near range margins are restricted to favoured biotopes: sites that would be suitable in warmer climates are unoccupied (see also Cowley et al. 2001b, Paivinen et al. 2005). If notional carrying capacity is biotope-specific but unrelated to climate then the relationship between mean density and temperature would be triangular, with both high- and low-density populations in the warmer south but only high-density populations in the colder north. Such heterogeneity is evident in the residual distribution for four species *Aglais urticae, Coenonympha pamphilus, Vanessa atalanta* and *V. cardui*, but does not appear to be a general phenomenon. Further investigation into the relationship between occupancy, temperature, niche breadth and density, at a range of spatial scales, is therefore to be encouraged.

Our predictions contrast strongly with those of Roy et al. (2001), who found that most butterfly species increased in abundance (measured as the national index) during warm years. These correlations had low power to predict subsequent population trends for most species, but for eight species the correlations were sufficiently strong to permit projections for abundance trends under climate warming up to the year 2080. Six species were predicted to increase, one decrease (*Pieris brassicae*) and one to remain approximately stable (*Lasiommata megera*). Of these species, we predict two species to increase (*Pieris brassicae* and *Pyronia tithonus*) and six to decline: i.e. seven out of eight predictions are in the opposite direction! The results of Roy et al. (2001) are quite intuitive: butterflies are more abundant in warm years because of lower winter mortality, rapid development and higher plant biomass. Moreover, Roy & Sparks (2000) reported rapid changes in butterfly life cycles in response to recent climate warming (e.g. advanced eclosion of adult butterflies, extended flight seasons, increased propensity for multivoltinism), all suggesting generally positive population responses to warming. The time-based population model of Roy et al (2001) was based on fine-scale climatic data (e.g. specific months related to the butterfly life cycle), that would be difficult to generalise to large numbers of species. The approach described here, whilst lacking certain subtleties of butterfly ecology, has the advantage that it could be applied to any situation where there is spatial data on population density.

Although the explanation for our negative temperature-abundance relationship remains elusive, our results demonstrate clearly that different processes operate across space and over time. Put bluntly, we lack a mechanistic understanding about the drivers of butterfly population dynamics over large spatial and temporal scales. Without such knowledge, it is speculative to

extrapolate from current patterns into the future. This message is profoundly important for interpreting the climate projections of niche models (Guisan and Thuiller 2005, Araujo and Guisan 2006), which share with our study the simple assumption that patterns in space are static, and can be used as a substitute for patterns in time. In this case we are fortunate that time-series information is available to verify our projections. Unfortunately, such reality checks are unavailable for the vast majority of modelling exercises.

Niche (bioclimate) models assume phenotypic plasticity of populations and constant responses across a species' entire range (Berry et al. 2002). However, evidence of widespread adaptation of butterfly populations to local climates is accumulating (Van Dyck and Wilding 2009) and gradients in butterfly biology along climatic gradients are well known (Nylin 2009). Many butterflies occurring towards their cooler range limit shift to inhabit warmer, narrower niches, whereas with core populations sample the landscape more widely (Thomas 1993, Thomas et al. 1999, Cowley et al. 2001b, Roy and Thomas 2003, Oliver et al. 2009). Other studies report gradients in size or melanism in butterflies across latitudes (Dennis and Shreeve 1989, Nylin and Svard 1991, Ayres and Scriber 1994). A fuller assessment of the extent of local adaptations within populations is therefore essential for more accurate predictions of the impacts of climate warming on biodiversity and the ecosystem services they support (Visser 2008), particularly for species with low dispersal ability.

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Table 1. Species abundance changes in response to a warming climate. Species are sorted in decreasing order of temperature response. beta$_T$ is the species-specific temperature response, measured as the change in log(density) for each degree of temperature increase. Current abundance is the sum of population density (per linear meter of transect) across 477 English UKBMS sites for 2002-6; Future is the comparable value under climate warming in 2080. Change and %change are the simple differences between current and future abundance estimates, in absolute and percentage terms respectively.

Species	beta$_T$	current	future	change	%change
Maniola jurtina	0.149	111.76	187.72	75.96	68.0
Celastrina argiolus	0.114	1.27	1.89	0.62	49.1
Cupido minimus	0.112	1.07	1.59	0.52	48.6
Pyronia tithonus	0.079	45.78	60.44	14.66	32.0
Pararge aegeria	0.076	18.62	24.20	5.58	30.0
Pieris rapae	0.074	19.07	24.69	5.62	29.5
Polygonia c-album	0.067	3.92	4.94	1.02	26.1
Pieris brassicae	0.042	10.29	11.92	1.63	15.8
Vanessa atalanta	0.007	4.01	4.11	0.10	2.5
Euphydryas aurinia	-0.068	0.86	0.68	-0.18	-21.1
Lycaena phlaeas	-0.073	2.98	2.31	-0.67	-22.4
Colias croceus	-0.081	0.60	0.45	-0.15	-24.7
Polyommatus coridon	-0.097	11.43	8.11	-3.32	-29.0
Hesperia comma	-0.098	1.16	0.82	-0.34	-29.2
Polyommatus icarus	-0.111	20.54	13.94	-6.60	-32.1
Coenonympha tullia	-0.132	0.08	0.05	-0.03	-35.2
Ochlodes sylvanus	-0.127	6.34	4.08	-2.27	-35.7
Argynnis adippe	-0.157	0.67	0.41	-0.26	-39.0
Limenitis camilla	-0.157	0.52	0.30	-0.22	-42.3
Melitaea athalia	-0.167	0.30	0.17	-0.13	-43.2
Vanessa cardui	-0.188	2.96	1.56	-1.41	-47.5
Leptidea sinapis	-0.194	0.42	0.21	-0.21	-49.3
Plebejus argus	-0.196	0.63	0.31	-0.32	-50.2
Hamearis lucina	-0.207	0.27	0.13	-0.14	-51.5
Gonepteryx rhamni	-0.219	8.64	4.02	-4.62	-53.5
Aricia artaxerxes	-0.248	0.47	0.22	-0.25	-54.1
Anthocharis cardamines	-0.244	3.01	1.30	-1.71	-56.8
Argynnis paphia	-0.250	3.39	1.41	-1.98	-58.4
Hipparchia semele	-0.262	1.15	0.47	-0.69	-59.4
Polyommatus bellargus	-0.257	2.82	1.14	-1.68	-59.7
Pieris napi	-0.303	12.80	4.52	-8.28	-64.7
Boloria euphrosyne	-0.342	0.78	0.25	-0.53	-68.2
Erynnis tages	-0.335	2.09	0.66	-1.43	-68.3
Aglais urticae	-0.336	8.40	2.64	-5.76	-68.6

Melanargia galathea	-0.355	18.19	5.22	-12.96	-71.3
Aphantopus hyperantus	-0.383	32.13	8.52	-23.61	-73.5
Aricia agestis	-0.397	2.88	0.71	-2.17	-75.3
Boloria selene	-0.441	0.93	0.22	-0.71	-76.5
Pyrgus malvae	-0.444	0.82	0.17	-0.65	-78.8
Erebia aethiops	-0.496	0.52	0.11	-0.41	-79.0
Inachis io	-0.473	9.10	1.83	-7.26	-79.8
Coenonympha pamphilus	-0.495	13.15	2.36	-10.78	-82.0
Lasiommata megera	-0.596	1.01	0.15	-0.86	-85.4
Callophrys rubi	-0.566	0.82	0.12	-0.70	-85.8
Argynnis aglaja	-0.756	1.76	0.14	-1.62	-92.1

Figure 1. Scatter plot of butterfly population density (log$_e$ transformed) against mean annual temperature (MATEMP) for 35 UK butterfly species. Population density is measured as the geometric mean 'site index' using 2002-6, divided by transect length. Species found on fewer than 30 sites are not displayed but were included in the model.
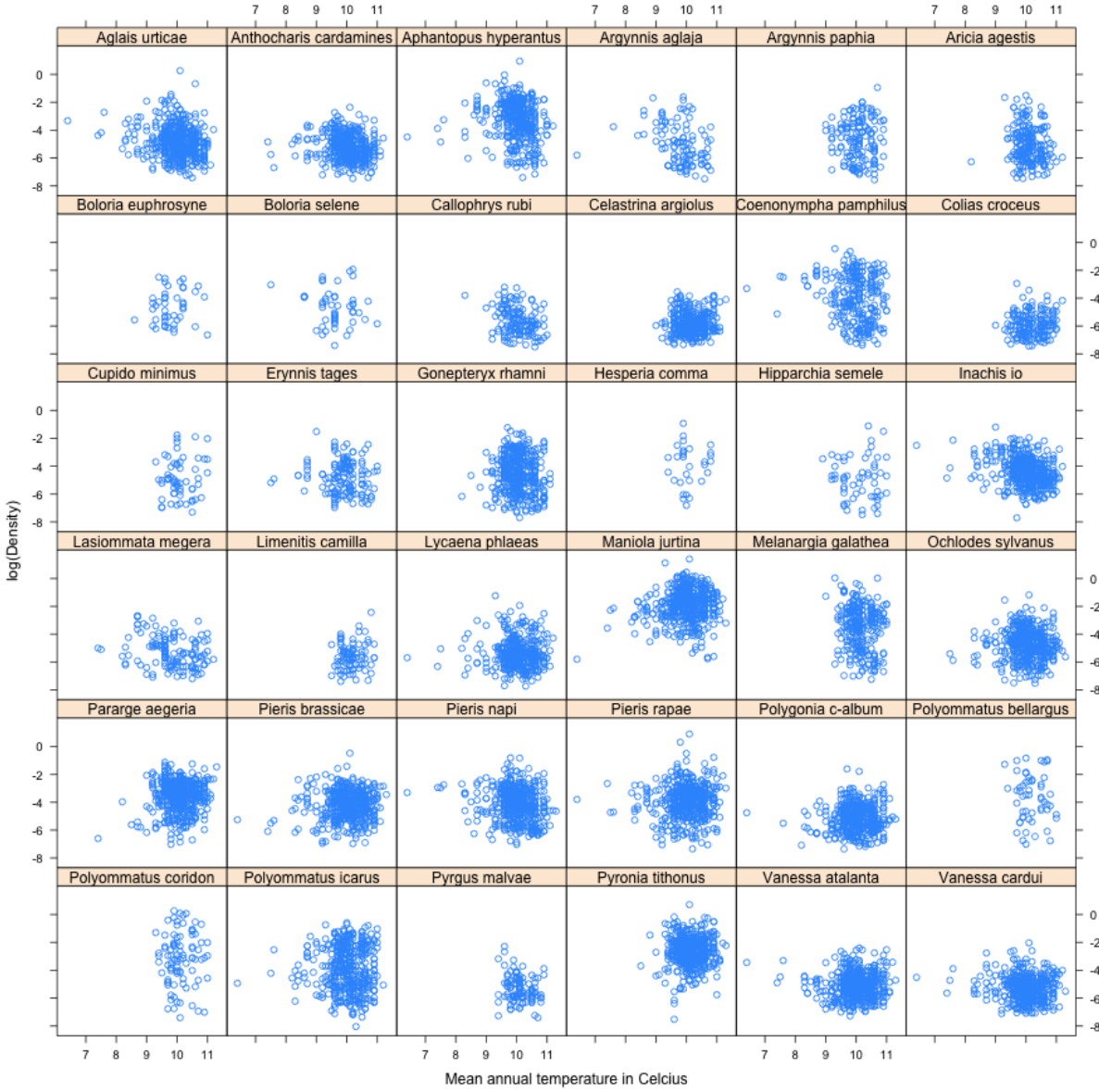
Figure 2. Histogram of projected change in abundance due to climate change, expressed as a percentage. These data were generated from model predictions for 9075 populations, summed across species (n=45) and sites (n=477).
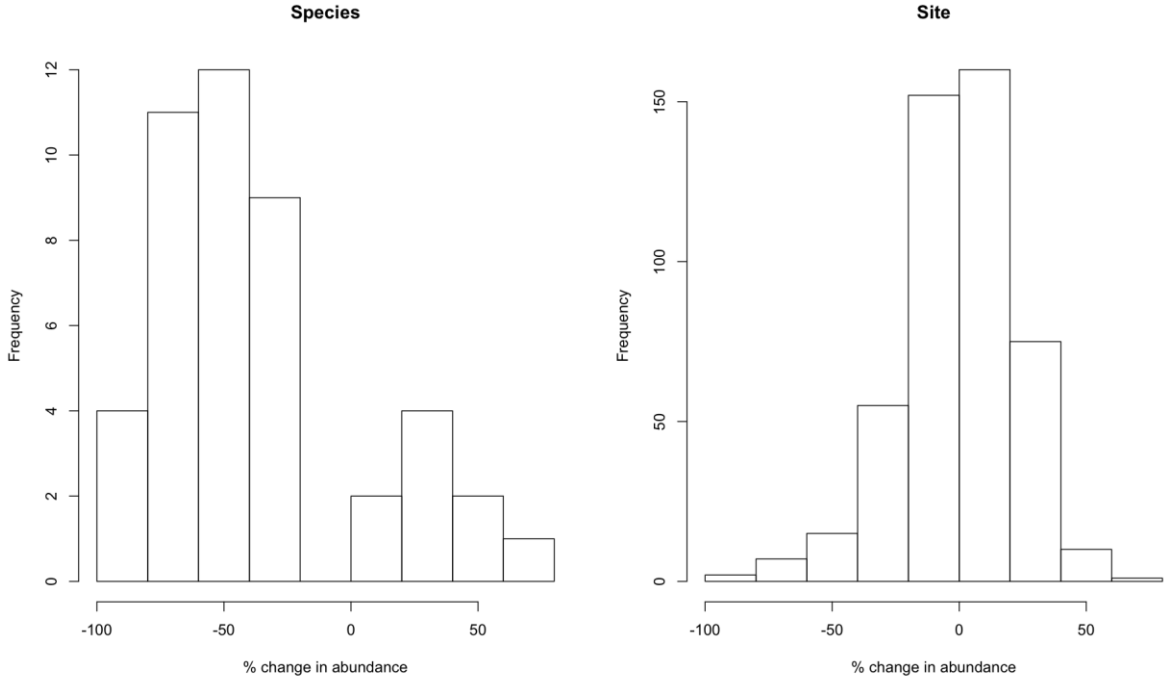
Figure 3. Map of 477 UKBMS sites showing projected change in abundance due to warming (expressed as a percentage), summed across species (n=45).