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Habitat associations of thermophilous butterflies are reduced despite climatic warming

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Running title: Habitat use under environmental change

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Habitat breadth, habitat specificity, niche breadth, range expansion, plant successional stages, climate change

Abstract

Climate warming threatens the survival of species at their warm, trailing-edge range boundaries, but also provides opportunities for the ecological release of populations at the cool, leading edges of their distributions. Thus, as the climate warms, leading-edge populations are expected to utilise an increased range of habitat types, leading to larger population sizes and range expansion. Here, we test the hypothesis that the habitat associations of British butterflies have expanded over three decades of climate warming. We characterise the habitat breadth of 27 southerly-distributed species from 77 monitoring transects between 1977 and 2007 by considering changes in densities of butterflies across 11 habitat types. Contrary to expectation, we find that 20 out of 27 (74%) butterfly species showed long term contractions in their habitat associations, despite some short-term expansions in habitat breadth in warmer-than-usual years. Thus, we conclude that climatic warming has ameliorated habitat contractions caused by other environmental drivers to some extent, but that habitat degradation continues to be a major driver of reductions in habitat breadth and population density of butterflies.

Introduction

The effects of climate change on the distributions of species at large spatial scales are increasingly well documented, showing shifts of species to higher latitudes and elevations (Chen *et al.*, 2011). In contrast, impacts of climate change on small-scale distribution patterns and habitat associations of species are less well understood. The latter is extremely important, however, because habitat availability is important to the persistence of populations, and insufficient habitat may prevent colonisations and large-scale climate-driven range expansions (Hill *et al.*, 1999, Hill *et al.*, 2001, Hodgson *et al.*, 2011). Furthermore, current species-specific conservation management practices may no longer be appropriate if species are shifting their distributions into different types of habitats (Oliver *et al.*, 2009).

Documenting and understanding these smaller-scale changes are essential to the development of conservation adaptation strategies that aim to facilitate the persistence and expansion of species under climate change.

The greatest changes to species' local distributions and habitat associations as a result of climate warming are expected to occur close to their geographic range limits. Populations of species at high-latitude 'leading-edge' range margins, living close to their cold thermal limits, generally occupy only a subset of the habitat types used elsewhere in their range (Thomas *et al.*, 1999, Lennon *et al.*, 2002, Oliver *et al.*, 2009). As the climate warms at these cold limits, a wider variety of habitats and sites would be expected to be warm enough for positive population growth. This would increase the range of habitats that could be exploited (Thomas, 1993, Thomas *et al.*, 2001, Davies *et al.*, 2006), especially for species for which physiological tolerances are important constraints on their distributions (Hutchinson, 1957, Frazier *et al.*, 2006, Deutsch *et al.*, 2008, Calosi *et al.*, 2010).

It is unclear how often climatic constraints are the primary determinant of habitat breadth for species, i.e. the degree to which certain broad land cover types or vegetation classes are

uninhabitable due to unsuitable microclimatic conditions. For thermophilous species that reach the northern edges of their geographic distributions within Britain, it is a reasonable assumption that temperature will be an important determinant. For example, the Adonis Blue butterfly *Polyommatus bellargus* shows variation in its associations with different grassland habitats according to seasonal variation in weather (Roy & Thomas, 2003). Another species, the Silver Spotted Skipper *Hesperia comma*, expands the range of locations where it lays its eggs in response to increased ambient temperatures, and colonises cooler north-facing slopes after a period of warm years (Thomas *et al.*, 2001, Davies *et al.*, 2005, Davies *et al.*, 2006). Climate is not the only constraint on distributions, however. For example, the northern distributional limits of the Brimstone butterfly *Gonepteryx rhamni* are largely delineated by its those of its larval host plants (Gutiérrez & Thomas, 2000), suggesting that for some species biotic interactions can be more important than the direct effects of climate (Settele *et al.*, 2008). Nonetheless, climate may exert an indirect effect if it determines host plant distributions, and habitat expansion by host plants may eventually result in parallel expansions in host-specific insects (Coope, 2004).

Climatic constraints are also thought to contribute to large-scale gradients of habitat use. For example, some butterflies that are restricted to grassland at the northern edges of their ranges in Britain occur at increased frequencies in scrub and deciduous woodland habitats towards the core of their ranges in mainland Europe (Settele *et al.*, 2009, Dennis, 2010). Within Britain, butterfly species exhibit increasingly constrained habitat associations at their cooler, high-latitude climatic range boundaries (Oliver *et al.*, 2009). Other taxonomic groups, such as coniferous trees, show similar trends (Lennon *et al.*, 2002). Because of these geographic gradients in habitat breadth and the observed behavioural responses of individuals to warmer conditions, increased temperatures at cool range boundaries are expected to result in increasingly broad habitat associations under recent climatic warming. Yet, to date,

temporal trends in species' habitat associations have not been explored, probably due to the scarcity of population data with sufficient spatial and temporal replication. However, understanding temporal dynamics in habitat use will be essential for managing species' populations under rapidly changing climates.

Here, we tested the hypothesis that populations of 27 British butterfly species have expanded their habitat associations between 1977 and 2007, a period in which the length of the growing season (accumulated growing day degrees above 5°C; GDD5) in Britain increased by 23%. We studied British butterflies because they comprise one of the longest-running and spatially-replicated datasets of population trends in the world, and one of very few suitable for a long-term analysis such as the one we present here. All of the species we analysed are at, or near, the northern edges of their European distributions within Britain (i.e. they are 'leading-edge' populations); hence, we predict that: a) species' populations will expand into more marginal (less frequently used) habitats in warmer years, and b) show an overall broadening of their habitat associations over three decades of regional warming (Thomas, 1993, Davies *et al.*, 2006, Oliver *et al.*, 2009). To test these predictions, we quantified the tendency for individuals to spread from primary into more marginal habitat types by relating changes in relative population density in different habitat types to total annual population sizes, annual weather (GDD5) and year. Total population size is often related to habitat breadth, so it was included in our statistical models as a control variable (Oliver *et al.*, 2009).

To demonstrate the importance of climate change versus trends in population density in affecting habitat associations of species, we modelled habitat associations of the 'average butterfly species' under three climate and population change scenarios: a) climatic warming but no long-term population decline, b) stable climate and population decline, and c) climate warming and long-term population decline (the actualised 'scenario' for British butterflies).

Relationships between climate, density and habitat were averaged across species to produce estimates for the ‘average species’ under the different scenarios. Necessarily, this simplification does not represent species with relationships that are exceptions to the rule, and these are addressed in a comparative analysis of trends between species. Our motivation in this particular analysis was to summarise the general trends across all species.

Our results suggested that British butterfly species have not exploited opportunities for habitat expansion under warmer climates; rather, total population sizes and habitat associations have declined. Considering relative trends across butterfly species, we observed that even those species traditionally associated with the warmest microclimates in Britain, and thus might be expected to benefit most from climatic warming (Thomas, 1993), have failed to expand their habitat associations. We conclude that climatic warming has ameliorated habitat contractions caused by other environmental drivers to some extent, but that, at least in Britain, habitat degradation continues to be a major driver of reductions in habitat breadth and population density of butterflies.

Methods

Sources of Climate and butterfly abundance data

We extracted climate data obtained from the Central England Temperature Series (Parker *et al.*, 1992) between 1977 and 2007. We used these data to calculate the annual growing day degrees above 5°C (GDD5) by summing mean daily temperatures above a 5°C threshold.

This measure of annual temperature is related to butterfly development (Warren *et al.*, 2001, Hill *et al.*, 2002). For the purposes of this study, the biological year was from October (year $t-1$) to September of the following year (year t). This period spanned the over-winter period between consecutive butterfly monitoring years, as well as the spring and summer weather during the flight (monitoring) period of year t . Accumulated day degrees, measured in this

way, increased by 23% over the study period, based on a linear regression (regression with 1977 starting as year zero: $GDD5 = 1776.1 + 13.6 \times \text{Year}$, $R^2 = 0.54$, $F_{1,29} = 36.8$, $n = 31$, $p < 0.001$).

Annual butterfly counts for all southerly distributed butterfly species across 77 monitoring transects were extracted from the United Kingdom Butterfly Monitoring Scheme (UKBMS) dataset. The UKBMS is a butterfly recording scheme comprising fixed transect routes walked by trained volunteers. Transects are 5m wide belts and typically between 1.5km and 3km in length. They are walked for up to 26 weeks of the year, encompassing the main flight periods of UK butterflies. Further details of the monitoring methodology can be found in Pollard and Yates (1993). For each year, an index of the annual abundance of each butterfly species at each transect is calculated allowing for missing counts (Rothery & Roy, 2001). In this study, transect routes were subdivided according to 11 broad land cover types (hereon referred to as ‘habitats’; Table S1). We assume that broad land cover types on transects remain unchanged during the sampling period. This assumption is based on anecdotal knowledge from UKBMS transect co-ordinators, and the fact that most transects occur on land under statutory protection (e.g. National Nature Reserves, Sites of Special Scientific Interest). In addition, if land cover type has changed within a small number of transects, there is little reason to expect the direction of changes to be consistent between transects; so any error should be random reducing the statistical power to detect trends, rather than introducing systematic bias.

Annual densities in each habitat were calculated as the total number of butterflies per year per km of 5m-wide transect route. Densities were natural log-transformed to improve normality of the data. To ensure data quality, for each species we only used data from transects that had been recorded for at least 10 consecutive years and that had a mean annual total abundance of more than 10 individuals. Following this filtering, only species occurring

at more than five transect sites were included in further analysis, because regressions with lower spatial replication would lead to less robust results.

Quantifying habitat breadth

Using UKBMS data from all transects and years combined, we identified the primary habitat of each species as the land cover type which most frequently had the highest density of butterflies (Table S2); ‘marginal’ habitat was classed as all other land cover types used by a species. For each year between 1977 and 2007, and for each transect, we calculated the proportional relative density of each species in marginal habitat, our index of ‘habitat breadth’, following the formula below:

$$P_{obs} = \frac{\frac{m}{a}}{\left(\frac{m}{a} + \frac{n}{b}\right)} \quad [1]$$

P_{obs} = proportional relative density of butterflies in marginal habitat

a = area of transect route containing the marginal habitat

b = area of transect route containing primary habitat

m = total number of butterflies in the marginal habitat

n = total number of butterflies in the primary habitat

Observed values for P_{obs} range from 0-1, with zero implying all individuals are found only in the species’ primary habitat. Note that this formula is similar to one used to calculate ‘habitat specificity’ in a previous study (Oliver *et al.*, 2009), but by focusing here upon proportional densities in marginal habitat we calculate ‘habitat breadth’, which is the inverse to ‘primary habitat specificity’ used previously. We present the index in this way because the hypotheses

we test concern increased habitat breadth of butterflies under climate warning and so presenting the index in this way made our results more easily interpretable.

Modelling the effects of weather and population density on habitat breadth of species

We used a generalized linear mixed model GLMM (Bolker *et al.*, 2008) to model the effects of year, weather and local annual density upon habitat breadth of species. A mixed modelling approach was used to account for the repeated measures of population density at each transect. Separate models were fitted for each species because we were interested in differences in responses among species. Our response variable was proportion data (habitat breadth of the species at a given transect in a given year), and so we multiplied this value by the total number of butterflies recorded at any given transect in any given year, to give the expected number of butterflies in the marginal habitat had the marginal and primary habitats been of equal area. In order to model changes in habitat breadth, this value was then rounded to the nearest integer value and used to fit a logistic regression model with binomial error structure, with the total number of butterflies on the transect that year as the denominator. We used the package *lme4* (Bates *et al.*, 2008) in the program R (R Development Core Team, 2009).

For this analysis, we were interested in the effect of annual weather on habitat breadth of species, independent of species' local annual population density. For each species, we analysed habitat breadth as the response variable, and included GDD5, local annual density and year as fixed effects ("Habitat breadth- Weather and Density" model). All our fixed effect explanatory variables were continuous and therefore to improve model convergence we standardised them to zero mean and unit variance. *Transect* was included as a random effect to account for differences in the mean habitat breadth between transects. We also included a random slope within *Transect* for each of the fixed effects. This allowed the slope of each

fixed effect to vary at each transect (e.g. the trend in species' habitat breadth with year might differ between transects). We chose this model structure because comparisons of different model structures using AIC suggested such that model complexity was appropriate (i.e. the more complex models had consistently lower AIC scores). We tested for spatial autocorrelation in model residuals using the *ncf* package in R (Bjørnstad, 2009). There was no significant spatial autocorrelation in model residuals apparent for any species (Figure S2). Across all species, the significance of each fixed effect (i.e. GDD5, population density, year) was tested by comparing the pooled species' coefficients for a fixed effect to zero using a Wilcoxon Signed Ranks test. This test was used because the distribution of coefficients was not normal, precluding a Student's t-test. A full table of species' coefficients can be found in Table 1.

Assessing long-term changes in habitat breadth and population density

For each species, we quantified the long-term trend in habitat breadth over time, by including habitat breadth as the response and year as a fixed effect ("Habitat breadth - Year model"). We did not include local density or weather as fixed effects in these models because including these variables as covariates would mean that the coefficient for 'year' represented the expected change in habitat breadth after accounting for local density and weather for each year of the time series. Instead, for this analysis, we were interested solely in the observed long-term trend in habitat breadth over time (which might be driven by long-term changes in density, climate and other factors).

For each species, we also assessed changes in population density over the 31 year study period. For each species, we included log local annual density as the response variable, and year as a fixed effect ("Density -Year model"). In both these analyses, *Transect* was included as a random effect, along with a random slope for *Year* within *Transect*, which allowed for

temporal trends in habitat breadth and population density to differ between transects. In the case of population density, we specified a Gaussian error structure; for habitat breadth, we specified a binomial error structure. The species coefficients for these analyses can be found in Table 1. We tested for spatial autocorrelation in the residuals of both models and none was evident (Figure S2).

To examine whether population declines of species were associated with reductions in habitat breadth, we then regressed species' slope coefficients from the Density-Year model against coefficients from the Habitat breadth-Year model. We tested for phylogenetic autocorrelation in the species' slope coefficients and model residuals using a Moran's I test with Geary randomizations (1000 iterations; Paradis, 2006). We used a butterfly phylogeny from Cowley *et al.* (2001) with branch lengths assigned using Grafen's (1989) method. In the absence of phylogenetic autocorrelation (see below), we proceeded with a standard ordinary least squares regression (Kunin, 2008).

We found a positive association between population density and habitat breadth across species (see Results). To demonstrate this relationship, we used coefficients from the Habitat breadth - Year model to predict changes in habitat breadth between 1977 and 2007 for two example species: the Common Blue butterfly *Polyommatus icarus* and the Comma butterfly *Polygonia c-album*. These species were chosen because they have shown strong opposite trends in population density over time (see Results; Table 1).

Visualising the effects of climate and density on butterfly habitat associations

In order to examine how changes in climate (GDD5) and population density have affected butterfly habitat associations, and to explore the relative strength of these effects, we estimated changes in habitat breadth for the 'average' butterfly species under various scenarios of climate and population density change. To obtain relationships between weather,

density and year on habitat breadth for the ‘average species’ we took the geometric mean species’ coefficients for each of the explanatory variables: year, weather and density from the “Habitat breadth - Weather and Density” models. This approach summarises the relationships between habitat breadth and these explanatory variables across species, using the geometric mean to reduce the influence of outliers. It produces a hypothetical model for the ‘average’ species, which we then used to project the change in habitat breadth over time using empirical climate data between 1977 and 2007. The density of the ‘average’ species each year was calculated by setting its mean density between 1977 and 2007 to the geometric mean density across all species. This density then changed each year according to the geometric mean of density change across all species (i.e. there was an average decline in density of roughly 1% each year).

We then explored changes in habitat breadth under two alternative scenarios. Under a hypothetical scenario of no population decline between 1977 and 2007, we simply held the focal species’ density constant at the geometric mean density across all species. Under the hypothetical scenario of no climate warming, we detrended the climate time series using linear regression to produce a time series with the same inter-annual variation, but no average warming over time. Projections of changes in habitat breadth between 1977 and 2007 for our ‘average’ focal species were then repeated on these altered climate and density explanatory variables.

Interspecific patterns in habitat association and population trends

From the previous analyses, we noticed that species that traditionally occupy warmer microclimates in Britain have failed to expand their habitat associations, contrary to previous expectations. We tested this formally by relating the vegetation height association of species’ host plant(s) to trends in butterfly habitat breadth and population density between 1997 and

2007. Species' host plants were categorised by their primary occurrence in one of four vegetation classes of increasing height, ranging from short grassland to shrubs and trees. For example, Speckled Wood *Pararge aegeria* larvae primarily feed on grasses growing in woodlands and therefore this species has the tallest, most closed host vegetation association of shrubs and trees (Table 1). ANOVAs were used to test whether host plant vegetation associations were associated with differences in butterfly slope coefficients for habitat breadth on year (Habitat breadth-Year model) or density on year (Density-Year model). To find the minimum adequate model for each ANOVA, factor levels were grouped and significance of different models was tested using an F-test (Crawley, 2007). Phylogenetic autocorrelation in the response and explanatory variables and model residuals was tested for as above and found to be absent.

Results

Effects of annual weather and density on habitat breadth

We analysed a total of 27 butterfly species from 77 transects distributed throughout Britain (Figure S1). Information on each species' primary habitat type can be found in Oliver *et al.* (2009). As expected, we found that 19 out of the 27 species showed habitat expansion in warmer-than-usual years, spreading out from their primary habitat to occupy marginal habitat (Fig. 1a; species with a positive temperature coefficient, Table 1). However, only three species showed significant relationships between GDD5 and habitat breadth, although the overall trend across all 27 species suggested a slight effect of habitat expansion in warmer years (Wilcoxon test of species' slope coefficients: $V = 104$, $n = 27$ species, $p = 0.041$; Fig. 1a; Table 1). There was no evidence for consistent effects of annual local density on habitat breadth across species (Wilcoxon test of species' slope coefficients: $V = 139$, $n = 27$ species, $p = 0.23$; Fig. 1b; Table 1)

Long-term changes in habitat breadth

Contrary to expectation, we found that habitat breadth declined over the study period for 20 out of the 27 species, despite overall climate warming between 1977 and 2007 (Fig. 1c; species with a negative year coefficient, Table 1). Seven species had individually significant slopes for the effect of year on habitat breadth, all of which showed significant reduction in habitat breadth over the 31 year period. In addition, the overall trend across species suggested that habitat contraction has been a significant common trend (Wilcoxon test of species' slope coefficients for the effect of year on habitat breadth: $V = 14$, $n = 27$, $p = 0.0019$; Fig. 1c; Table 1). Therefore, the habitat associations of British butterflies have generally become more constrained over time, but in warmer years populations show brief, temporary habitat expansions.

Factors associated with contraction in habitat breadth

We tested for a relationship across species between population trends and changes in habitat associations between 1977 and 2007 and found that species that had the greatest rate of population decline also tended to show the greatest reduction in habitat breadth ($F_{1,25} = 8.92$, $p = 0.006$; Fig. 2). For example, populations of the Common Blue butterfly *P. icarus* were estimated to have declined by 42% between 1977 and 2007 and also showed a substantial reduction of habitat breadth; only 43% of *P. icarus* individuals were recorded in their primary (grassland) habitat in 1977, whereas 90% were confined to this primary habitat in 2007. In contrast, population density of the Comma butterfly *Polygonia c-album*, a common species which has expanded its distribution in the UK (Fox *et al.*, 2006), increased by 121%, and its habitat breadth also increased; the percentage of individuals in marginal habitat increased from 50 to 85% between 1977 and 2007.

We found that butterfly habitat breadth has declined most strongly for species that feed on host plants growing in open, short turf conditions (Fig. 3a), i.e. these species have withdrawn from using a wider variety of habitat types such as hedgerow, scrub and tall herb patches, and are now more concentrated in short turf grasslands. The same group of butterfly species have also declined most in population density (Fig 3b). In contrast, butterfly species that use host plants which grow in taller vegetation showed little overall change in habitat breadth or population density.

Visualising the effects of climate and density on butterfly habitat associations

We modelled the projected change in habitat breadth between 1977 and 2007 for an ‘average’ species, in order to demonstrate the relative importance of climate change versus trends in total population density for habitat associations. Under a scenario of stable butterfly populations and climate warming, we found that habitat breadth would be expected to increase over time because of increased GDD5. Under a scenario of a stable climate but with butterfly population decline, habitat breadth would be severely reduced (by 2007, the reduction in habitat breadth is 4.9 times larger than the increase expected from climate warming alone). Our model for the actual British situation over the past three decades (climate warming and butterfly population decline) shows an intermediate result - habitat breadth has declined overall, but climate warming appears to have acted to ameliorate the reduction in habitat breadth caused by other (non-temperature) drivers (Fig 4).

Discussion

Our results show that the majority of UK butterfly species that we studied have exhibited long term reduction in habitat breadth over three decades, despite modest expansions in habitat associations in warmer-than-usual years. The positive effect of accumulated annual

temperature on habitat breadth fits expectations that warmer weather increases the number of land cover types that can provide suitable microclimates for insect survival and development (Thomas, 1993, Davies *et al.*, 2006). An additional explanation is that warmer temperatures promote flight initiation in these heliothermic insects (Shreeve *et al.*, 2009). Although increased flight movement *per se* might not be expected to alter the observed relative density of individuals in different habitat types (because detectability would be similarly increased in both marginal and primary habitat types), it may do if such movement is targeted (i.e. an increased propensity to travel across unfavourable habitat types; Dyck & Baguette, 2005). For example, certain longer distance dispersal modes may have minimum temperature thresholds, thereby increasing the number of ‘vagrant’ individuals observed across a wide range of habitat types and the perceived habitat breadth under warmer temperatures. Such temperature-limitation to movements could be due to physiological constraints, but might also be adaptive, allowing dispersing individuals to access the increased range of resources and microclimates available under warmer temperatures (Thomas, 1993, Davies *et al.*, 2006).

For all the reasons above, under three decades of warming in Britain, we had expected an overall expansion of habitat associations; yet, in fact, habitat breadth declined for most species. On average across British butterfly species we demonstrated that climatic warming over the last three decades has probably ameliorated the declines caused by other factors, which have driven declines in both population size and habitat breadth (Fig. 4). For example, declines in habitat breadth over time were strongly correlated with population declines across species (Fig. 2) and were more marked for butterfly species feeding on host plants in open short turf vegetation (Fig 3).

There are a number of reasons why, despite climatic warming, the habitat breadth of these thermophilous insects has declined in the last three decades. Firstly, a non-climatic anthropogenic driver of change such as habitat loss and degradation might be driving

population declines with consequent (indirect) effects on habitat use. In recent decades, habitat loss and degradation are thought to have the greatest negative impacts on British biodiversity, compared with climate change and other drivers (UK NEA, 2011), and butterflies are no exception (Warren *et al.*, 2001). Habitat breadth might be linked to population density through density-dependent mechanisms. In higher density populations, survivorship and fecundity are often reduced (e.g. through host plant limitation or natural enemy aggregation; Yamamura & Yano, 1999, Gibbs *et al.*, 2004, Baguette & Schtickzelle, 2006), and when population density is higher individuals may spread into marginal habitats as they become more favourable relative to fitness in the 'primary' habitat. Hence, overall declines in butterfly population density in Britain between 1977 and 2007 (Botham *et al.*, 2009), may have resulted in reduced density-dependent costs, thereby concentrating individuals in the best possible habitats.

An additional density-related explanation for declines in habitat breadth over time is that populations exhibit density-dependent emigration and immigration, with individuals being more likely to emigrate from marginal habitat patches which have low population density (Roland *et al.*, 2000). Hence, as population density declines, this process could provide a positive feedback, further depleting numbers in marginal habitats.

Changes in butterfly habitat associations over time, however, are unlikely to be mediated solely through indirect effects on population density. Non-climatic anthropogenic drivers of change, such as habitat loss and degradation, may have direct effects on butterfly habitat use. Indeed, the lack of a consistent relationship between annual density and habitat breadth across species (Fig 1b), suggests that other factors are important in driving species' habitat associations. Underlying factors appear to drive simultaneous declines in population density and habitat breadth, leading these trends to covary across species (Fig 2). One possible such underlying driver is habitat degradation. Reductions in habitat quality as a consequence of

habitat degradation, are known to have a strong effects on population change in butterflies (Dennis, 2010, Thomas *et al.*, 2011), and, although the broad habitat types on the UKBMS transects are unlikely to have changed substantially over the monitoring period, habitat quality may well have done so. Comparing temporal trends in habitat breadth across species, we found that butterfly species feeding on host plants in open short turf vegetation (i.e. hotter microclimates) have suffered the greatest habitat contractions, mirrored also by declines in population density. Note that this is the opposite pattern predicted under an assumption that climate is the primary factor limiting habitat associations, i.e. where species occupying the warmest microclimates in Britain would show the greatest expansions in habitat breadth and population density (Thomas, 1993). Hence, the observed pattern suggests that some other non-climatic driver appears to be responsible for most of the changes in habitat associations of British butterflies over the last three decades.

There is reason to believe that the driver responsible might be changes in habitat quality. However, we present this as a hypothesis and stress that more detailed experimental studies would be needed to confirm mechanistic relationships. Nevertheless, a number of other studies support the contention that changes in habitat quality may be driving habitat changes in British butterflies. Firstly, butterfly population declines in the past century have been primarily driven by habitat destruction and degradation, particularly in relation to agricultural intensification and abandonment (Asher *et al.*, 2001, Warren *et al.*, 2001). In Britain, evidence from a countrywide survey, spanning the same three decades as this study, shows that many natural habitats have become more shady over time through changes in management practices (Countryside Survey, 2008). Secondly, countries with high levels of nitrogen deposition and experiencing climate warming may experience increased plant growth in spring, which can actually lead to microclimatic cooling. Hence, warmth-loving insect species associated with open and short vegetation may find many fewer habitat types

suitable (Wallisdevries & Van Swaay, 2006). Therefore, one possibility is that, although the macroclimate in Britain over the last three decades has warmed, the availability of warmer microclimates (and their associated plants) in British landscapes may have declined due changes in land management and vegetation architecture. Further work is needed exploring the relationship between changes in macroclimate (i.e. climatic warming) and land management to changes in microclimate (i.e. the availability of warmer and cooler microsites).

To conclude, from previous research on climate and species' habitat associations (Thomas, 1993, Thomas *et al.*, 2001, Lennon *et al.*, 2002, Davies *et al.*, 2006, Oliver *et al.*, 2009), we expected climatic warming over the past three decades to lead to the expansion of habitat breadth for high-latitude leading-edge populations of species. We did find a signal of such 'ecological release' in warmer years, but the long-term trend was one of reduced habitat associations. Other constraints appear to be outweighing the positive effects of a warming climate on habitat breadth. Across species, the gradual shrinking in butterfly habitat breadth over the past three decades was correlated with population declines. Population density may influence habitat associations through density-dependent mechanisms. A non-mutually exclusive explanation is that the ultimate drivers of butterfly population declines, such as reductions in habitat quality, may also directly influence habitat associations. Whatever, the exact driver(s), many species appear to have been unable to exploit opportunities for ecological release provided by climate change. This prompts the concern that, in addition to limited dispersal abilities, a reduced habitat breadth may additionally hinder the ability of high-latitude leading-edge populations to expand their ranges northwards even though macro-climatic conditions have become more favourable (Hill *et al.*, 1999, Warren *et al.*, 2001). The ecological release and range expansion of leading edge populations has probably been key in

allowing species to survive past periods of climatic warming (Coope, 2004). In contrast, the persistence of species may now be threatened by their failure to expand in situations where present-day climatic amelioration should allow it. Instead, smaller more ecologically constrained populations will be more susceptible to environmental stochasticity (Oliver *et al.*, 2010) and are likely to have a limited ability for expansion (Hill *et al.*, 1999, Warren *et al.*, 2001). Our results suggest that only if other non-climatic drivers can be reduced or reversed will species be able to fully exploit any emerging opportunities provided by climate warming.

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Tables

Table 1. Species' coefficients for models of habitat breadth and population density

Species' coefficients from: model 1- relationship between habitat breadth (HB) and annual accumulated temperature, annual density and year; model 2- relationship between habitat breadth and year; model 3- relationship between density and year. Individually significant species slopes ($p < 0.05$) are indicated by an asterisk. Also listed are the number of transects analysed for each species, and the species' host plant vegetation association: 1- short grassland, 2- medium grassland, 3- tall grassland, 4- shrubs/trees.

Species	Number of transects analysed	Model 1	Model 1	Model 1	Model 2	Model 3	Host vegetation association
		Temperature on HB coefficient	Density on HB coefficient	Year on HB coefficient	Year on HB coefficient	Year on density coefficient	
<i>Aglais urticae</i>	50	0.061	-0.031	-0.358*	-0.364*	-0.339*	3
<i>Anthocaris cardamines</i>	18	0.051	0.022	-0.12	0.006	0.015	2
<i>Aphantopus hyperantus</i>	43	0.083	-0.19	-0.283*	-0.171	0.058	3
<i>Argynnis paphia</i>	8	0.194*	-0.064	-0.013	0.31	0.261*	4
<i>Aricia agestis</i>	14	0.275	0.792	0.069	0.059	-0.019	2
<i>Callophrys rubi</i>	6	-0.17	0.333	0.113	-0.09	-0.133	4
<i>Celastrina argiolus</i>	7	0.122	-0.13	-0.198	-0.133	-0.113	4
<i>Coenonympha pamphilus</i>	31	-0.230*	-0.121	0.072	-0.148	-0.224*	1
<i>Erynnis tages</i>	9	-0.025	0.474	-0.372	-0.452	-0.207	1
<i>Gonepteryx rhamni</i>	27	0.007	0.025	-0.126	-0.121	0.002	4
<i>Inachis io</i>	54	0.026	0.032	-0.222*	-0.153*	-0.076	3
<i>Lasiommata megara</i>	13	-0.007	-0.048	-0.128	-0.091	-0.262*	1
<i>Lycaena phlaeas</i>	24	0.023	-0.048	-0.149	-0.176	-0.254*	2
<i>Maniola jurtina</i>	62	0.039	-0.210*	-0.095	-0.089	0.076	3
<i>Melanargia galathea</i>	29	0.09	0.191	-0.429*	-0.430*	0.110*	3
<i>Ochlodes venata</i>	48	0.079	0.143	-0.261*	-0.185	-0.264	3
<i>Pararge aegeria</i>	44	-0.135*	0.183	0.215*	0.082	0.026	4

<i>Pieris brassicae</i>	46	-0.001	0.015	0.081	0.058	-0.124*	2
<i>Pieris napi</i>	45	-0.009	0.023	0.018	0.019	-0.040*	2
<i>Pieris rapae</i>	57	0.051	-0.053	-0.176*	-0.161*	-0.182	2
<i>Polygonum c-album</i>	13	0.076	0.354	0.291	0.421	0.194*	3
<i>Polyommatus icarus</i>	47	0.043	-0.008	-0.422*	-0.600*	-0.132*	1
<i>Pyrgus malvae</i>	7	0.14	0.178	-0.24	-0.167	-0.137	1
<i>Pyronia tithonus</i>	53	0.005	-0.042	-0.175*	-0.183*	0.062	3
<i>Thymelicus sylvestris</i>	37	0.05	0.285*	-0.188	-0.234*	-0.353*	3
<i>Vanessa atalanta</i>	23	0.037	-0.021	-0.161	-0.123	0.191*	3
<i>Vanessa cardui</i>	14	-0.065	0.077	0.021	-0.024	0.035	3

Figures

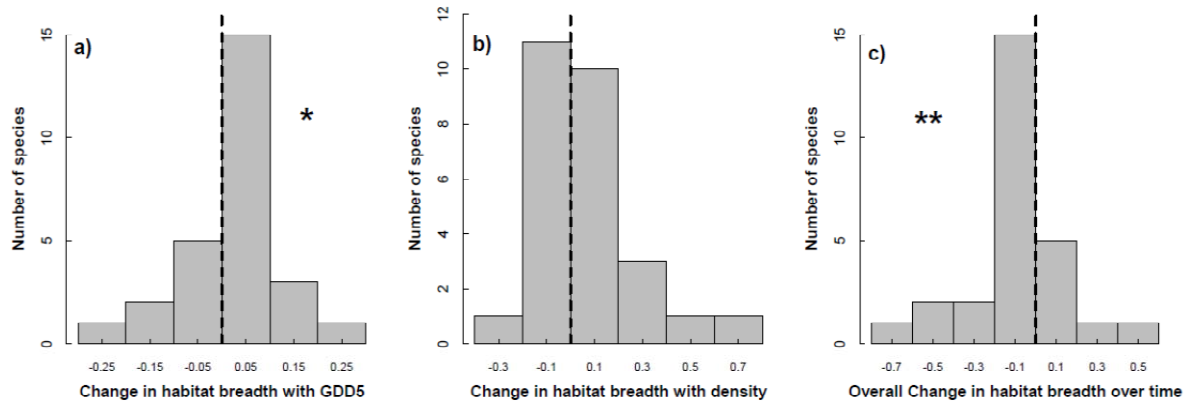


Fig. 1, Effects of weather, density and year on habitat breadth

Histograms of species' slope coefficients for the relationships between habitat breadth and a) annual weather (measured by growing day degrees above 5°C), and b) local annual butterfly density. Panel c shows the overall trend in habitat breadth between 1977 and 2007. For all panels, positive coefficients indicate expansion of habitat associations and negative coefficients contraction of habitat associations. Asterisks indicate significance level of multispecies trends (* $p < 0.05$, ** $0.001 < p < 0.01$).

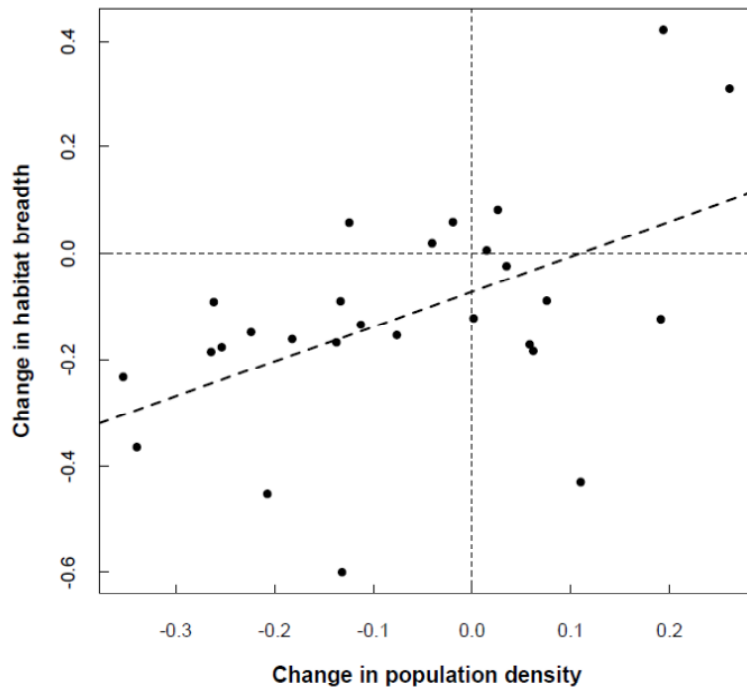


Fig. 2, Long-term changes in habitat breadth and population density

Butterfly species that have shown the greatest population declines have also shown the greatest decline in habitat breadth. Population change is measured as the average change in the density of a species across all transects. Habitat breadth is measured as the average change in proportional relative density in marginal habitats across all transects.

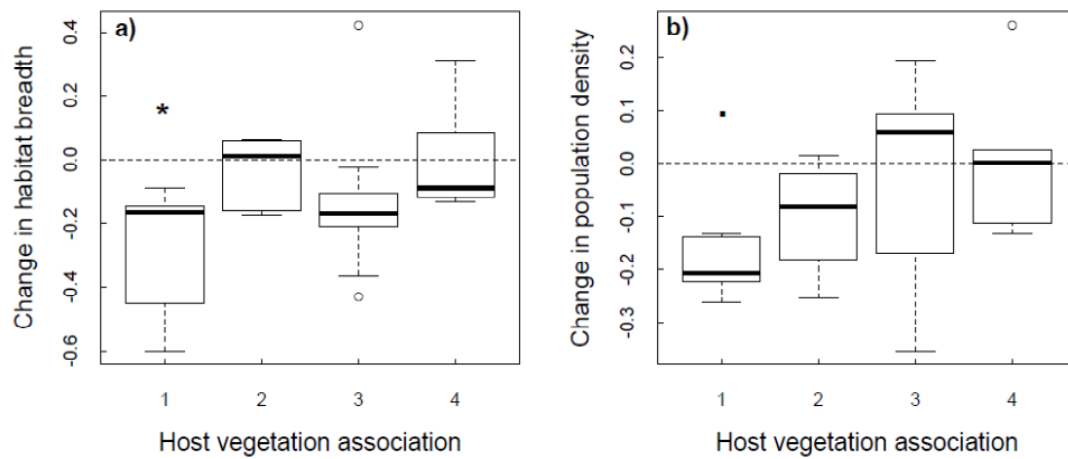


Fig. 3, Host plant vegetation association and changes in habitat breadth and population density

Relationships between the host plants used by butterfly species and changes in butterfly a) habitat breadth, and b) population density, between 1977 and 2007. Positive coefficients indicate expansion of habitat associations or population increase, and negative coefficients declines in habitat breadth or population density. Host plant vegetation associations are: 1- short grassland, 2- medium grassland, 3- tall grassland, 4- shrubs/trees. Species feeding on host plants associated with open, short grassland suffered significantly greater contraction of habitat associations ($F_{1,25} = 4.86, p = 0.037$) and marginally greater population decline ($F_{1,25} = 3.91, p = 0.059$) between 1977 and 2007.

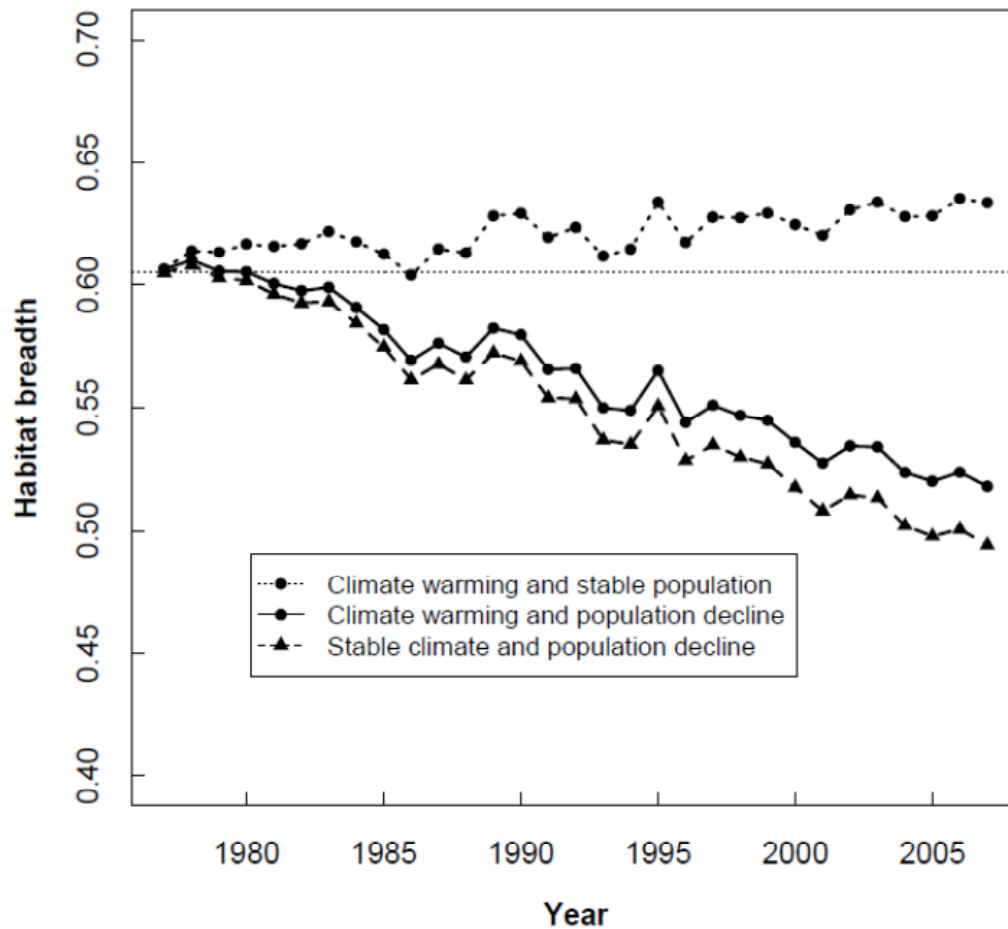


Fig. 4, Changes in habitat breadth between 1977 and 2007

The estimated average trend in habitat breadth for butterflies under three different scenarios of climate and population change. Increasing values on the y-axis indicate expansion of habitat associations. The solid line with circles depicts the actual scenario where the climate in Britain has warmed over time, but any effects habitat breadth have been offset by other environmental drivers associated with butterfly population decline. The other lines depict hypothetical scenarios. The dashed line with triangles shows that observed decline in habitat breadth would be more severe were it not for climate warming. The dashed line with circles shows that expansion of habitat associations might have occurred in Britain were populations not declining so rapidly.

Supporting Information

Additional supporting Information is available for this article:

Table S1- Broad habitat classes used in the analysis

Table S2- Average density and habitat breadth of butterfly species

Figure S1- Locations of the UKBMS transects used in the analysis

Figure S2- Spline correlograms to test for spatial autocorrelation in model residuals

Supporting Information

This supporting information contains the following:

Table S1- Broad habitat classes used in the analysis

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Figure S1- Locations of the UKBMS transects used in the analysis

Figure S2- Spline correlograms to test for spatial autocorrelation in model residuals

Table S1- Broad habitat classes used in the analysis

Broad Habitat	Description	EUNIS codes
Arable	Intensive arable crops; bare ground/weeds of arable field margins or fallow/recently abandoned arable crops (e.g. set-aside)	I1.1/1.5
Bracken	Bracken dominated glades or hillsides	E5.3
Coniferous woodland	Mature coniferous woodland	G3
Coastal	Marine saltmarshes/estuaries/saline reedbeds; coastal dune grassland; coastal dune and sand heath; coastal dune and sand scrub; coastal dune slacks; coastal shingle	A2, B1.4/1.5/1.6/1.8/2.
Deciduous woodland	Mature broadleaved woodland; mature mixed broadleaved and coniferous woodland; lines of trees or scattered trees of parkland; small man-made woodlands; recently felled areas/early-stage woodland and coppice; orchards, hop gardens and vineyards	G1/4/5.1/5.2/5.6/5.7/5.8, G1.D
Fen/ Bog	Fen/swamp/marsh vegetation of inland freshwater edges; bare ground/sparse vegetation of inland freshwater edges; acid bog/mire habitats; flushes; inland swamp/fen stands without open water (e.g. reed and sedgebeds)	C3.1/3.2/3.3/3.4/3.5/3.6/3.7/3.8, D1/2/4/5
Grassland	Dry semi/unimproved (flower-rich) chalk/limestone grassland; dry semi/unimproved acid grassland; dry semi/unimproved (flower-rich) neutral grassland; agriculturally improved/re-seeded/ heavily fertilised grassland; seasonally wet and wet marshy grasslands	E1.2/1.7/2.1/2.2/2.6/3
Heathland	Wet and dry heathland/ dry heather moorland	F4
Hedgerow/ Mosaic habitats	Stands of tall herbs (e.g. nettle and willow-herb beds); dry scrub/shrub thickets; Hedgerows; bare ground/woodland herb/grass mosaics of woodland rides, hedgebanks and green lanes	F3.1, FA, E5.2
Urban/ suburban	Ornamental shrubs/trees/lawns of churches/parks/domestic gardens etc; bare ground/weed communities of post-industrial sites e.g. quarries/pits/road/rail/landfill sites	I2, J3/4/6
Waterside scrub	Wet willow scrub of fen, river and lake-side	F9

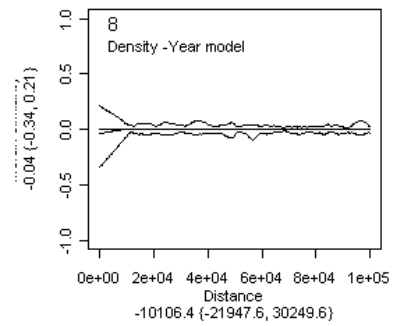
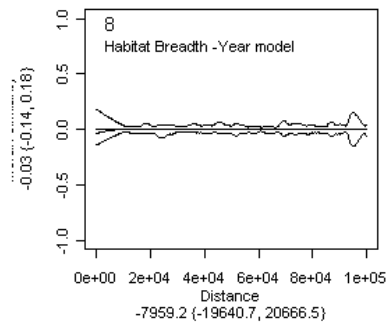
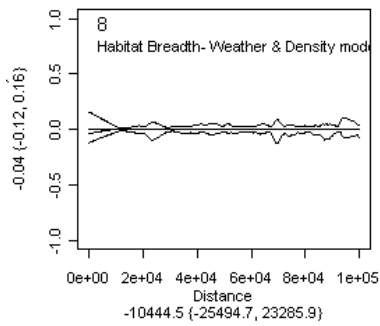
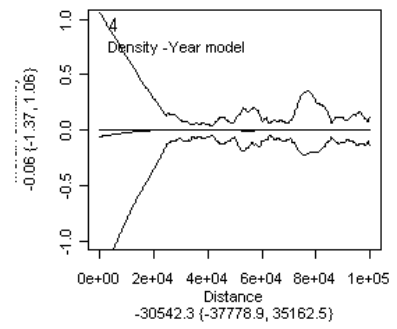
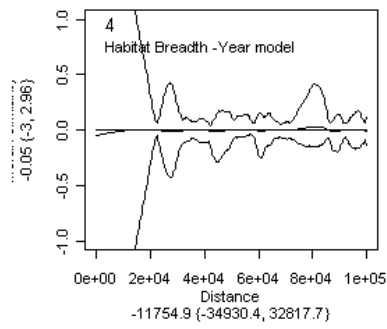
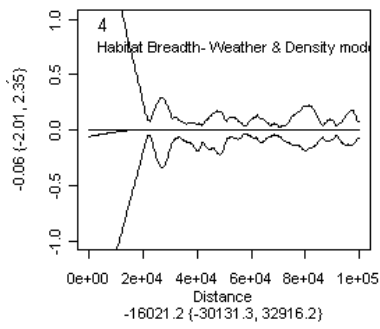
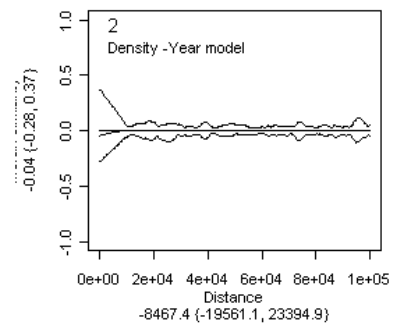
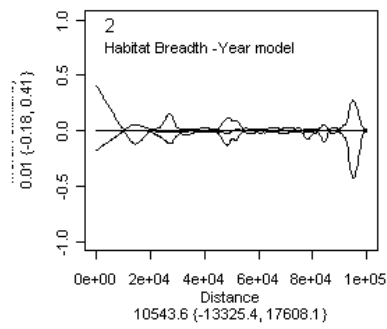
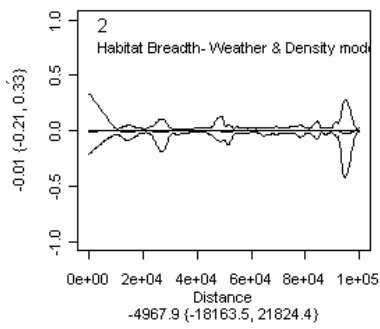
Table S2- Average density and habitat breadth of butterfly species

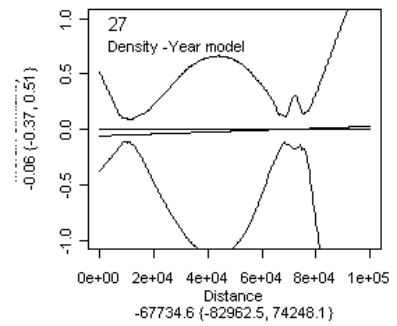
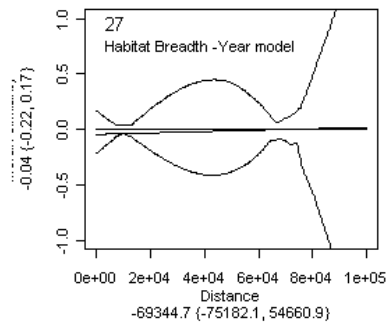
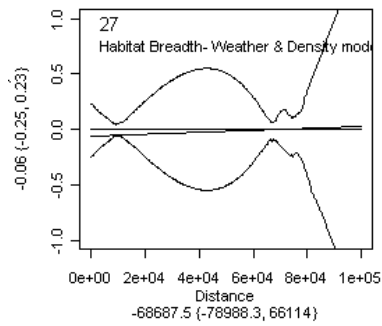
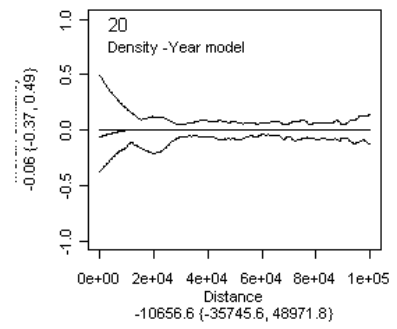
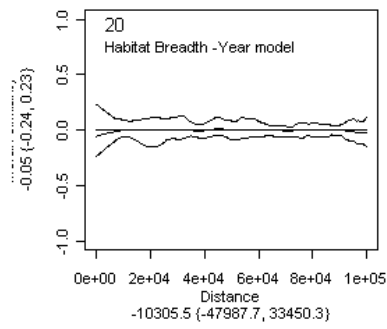
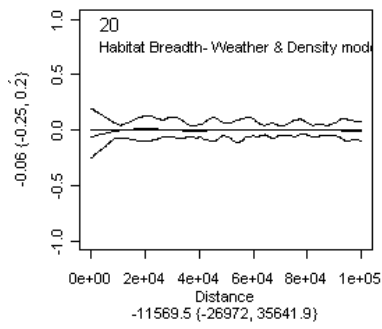
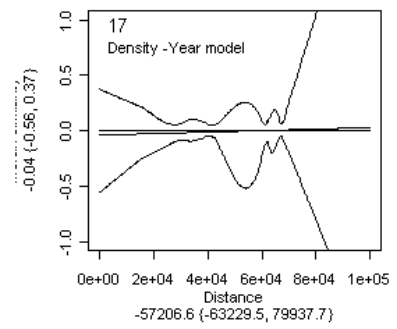
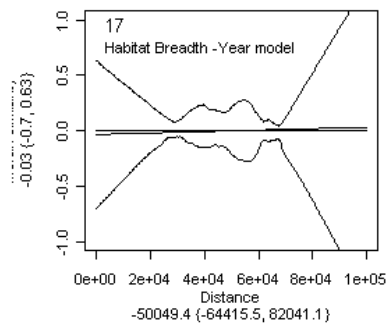
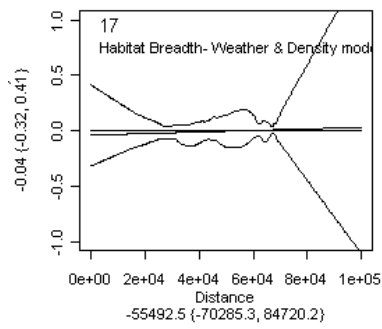
Median density and habitat breadth of butterfly species across all transects and years. Habitat breadth is calculated as the proportional relative density of butterflies *outside* of the primary habitat type. The top two marginal habitat types for each species are also listed. Habitat category codes are as follows: DW- deciduous woodland, G- grassland, H- heathland, HeMo- hedgerow and mosaic habitats.

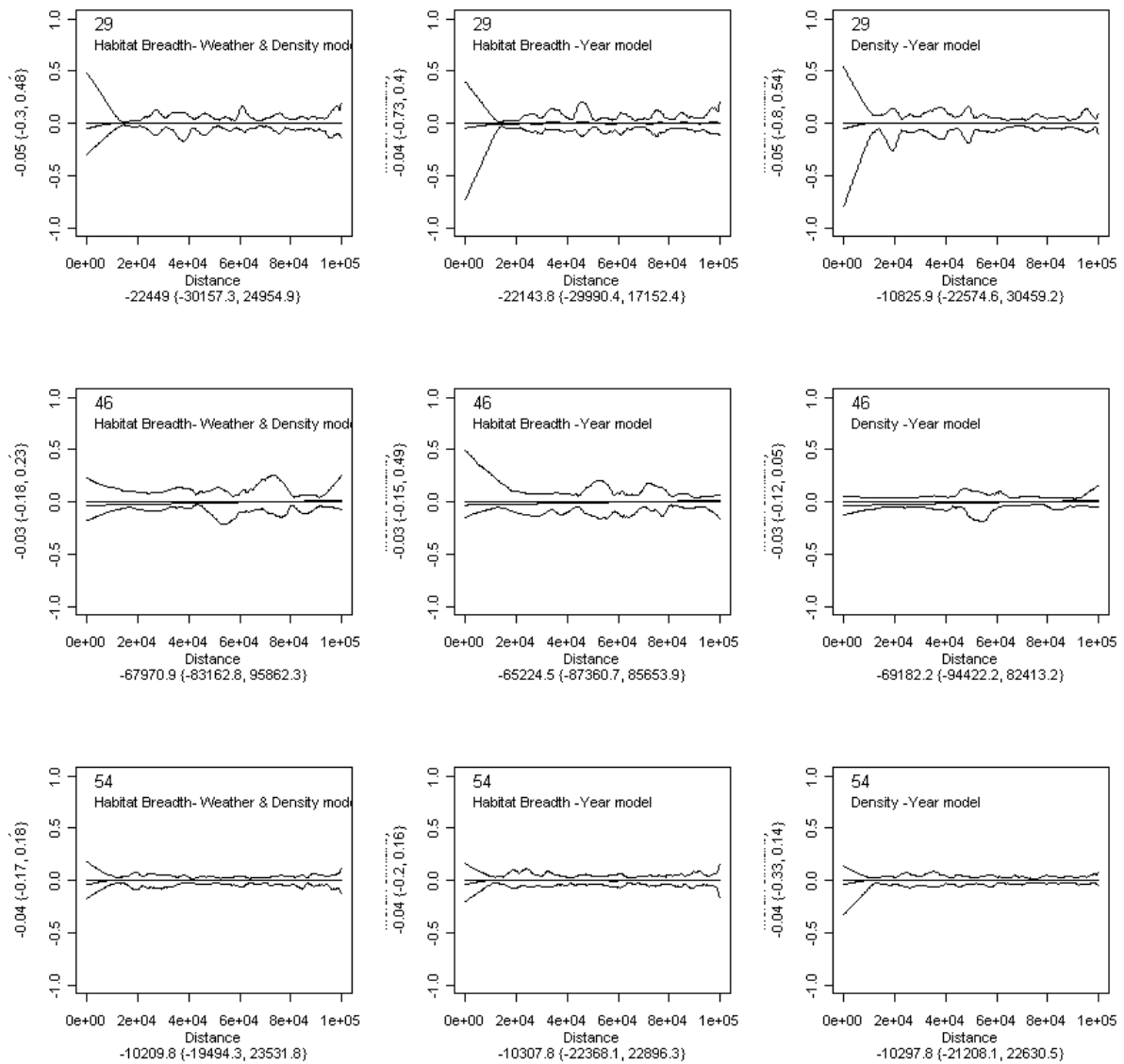
Species	Number of transects analysed	Primary habitat type	Marginal habitat types	Median habitat breadth	Median Density
<i>Aglais urticae</i>	50	G	HeMo, DW	0.56	0.53
<i>Anthocaris cardamines</i>	18	HeMo	G, DW	0.75	0.29
<i>Aphantopus hyperantus</i>	43	G	HeMo, DW	0.61	1.95
<i>Argynnis paphia</i>	8	G	DW, HeMo	0.71	1.17
<i>Aricia agestis</i>	14	G	DW, HeMo	0.33	0.45
<i>Callophrys rubi</i>	6	G	HeMo, DW	0.39	0.26
<i>Celastrina argiolus</i>	7	HeMo	G, DW	0.87	0.26
<i>Coenonympha pamphilus</i>	31	G	HeMo, H	0.30	1.42
<i>Erynnis tages</i>	9	G	HeMo, DW	0.17	0.50
<i>Gonepteryx rhamni</i>	27	HeMo	G, DW	0.62	0.62
<i>Inachis io</i>	54	G	HeMo, DW	0.68	0.66
<i>Lasiommata megara</i>	13	G	HeMo, DW	0.49	0.24
<i>Lycaena phlaeas</i>	24	G	HeMo, DW	0.41	0.36
<i>Maniola jurtina</i>	62	G	HeMo, DW	0.47	7.01
<i>Melanargia galathea</i>	29	G	HeMo, DW	0.35	2.08
<i>Ochlodes venata</i>	48	G	HeMo, DW	0.52	0.55
<i>Pararge aegeria</i>	44	DW	HeMo, G	0.55	1.46
<i>Pieris brassicae</i>	46	HeMo	G, DW	0.63	0.48
<i>Pieris napi</i>	45	HeMo	G, DW	0.65	0.73
<i>Pieris rapae</i>	57	G	HeMo, DW	0.65	0.76
<i>Polygonum c-album</i>	13	HeMo	DW, G	0.68	0.29
<i>Polyommatus icarus</i>	47	G	HeMo, DW	0.28	1.09
<i>Pyrgus malvae</i>	7	G	HeMo, DW	0.56	0.49
<i>Pyronia tithonus</i>	53	G	HeMo, DW	0.59	2.18
<i>Thymelicus sylvestris</i>	37	G	HeMo, DW	0.43	0.98
<i>Vanessa atalanta</i>	23	HeMo	G, DW	0.74	0.24
<i>Vanessa cardui</i>	14	G	HeMo, UG	0.50	0.14

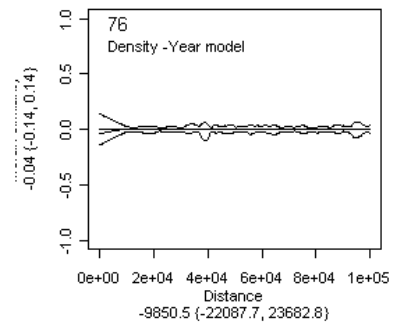
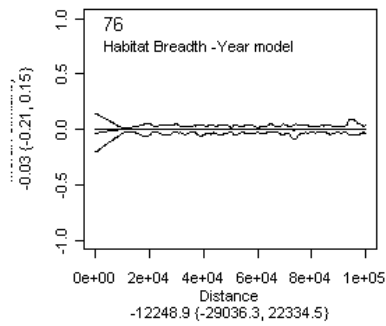
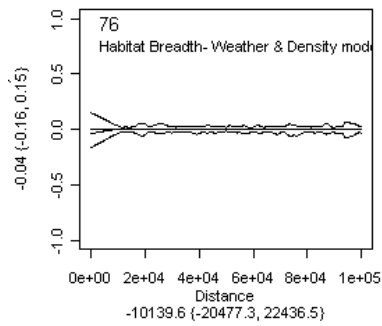
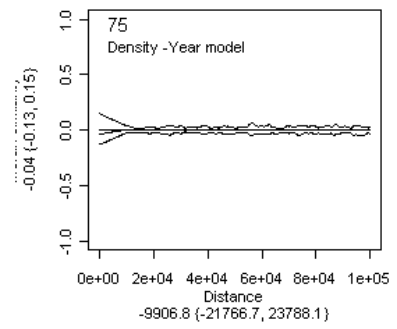
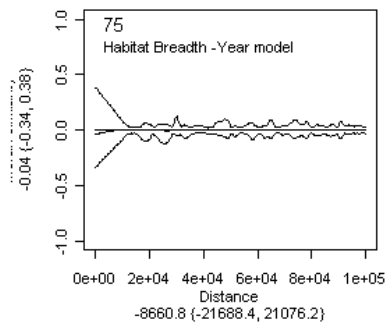
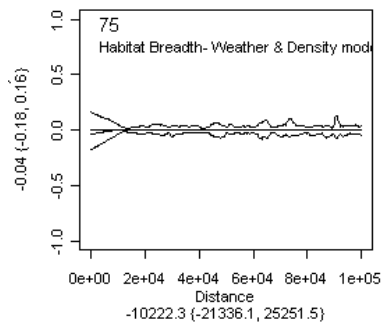
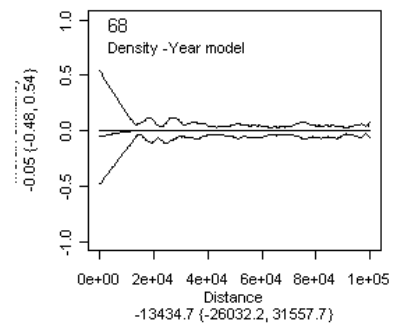
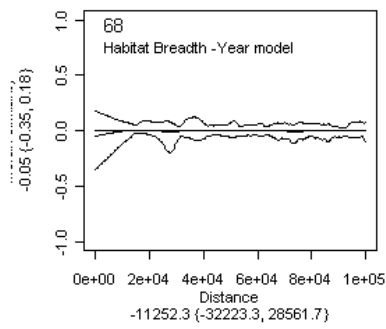
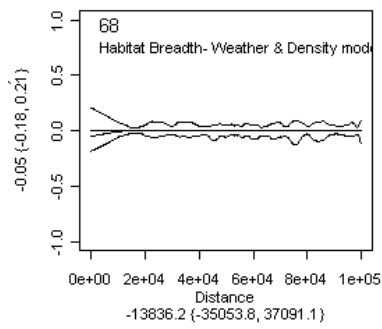


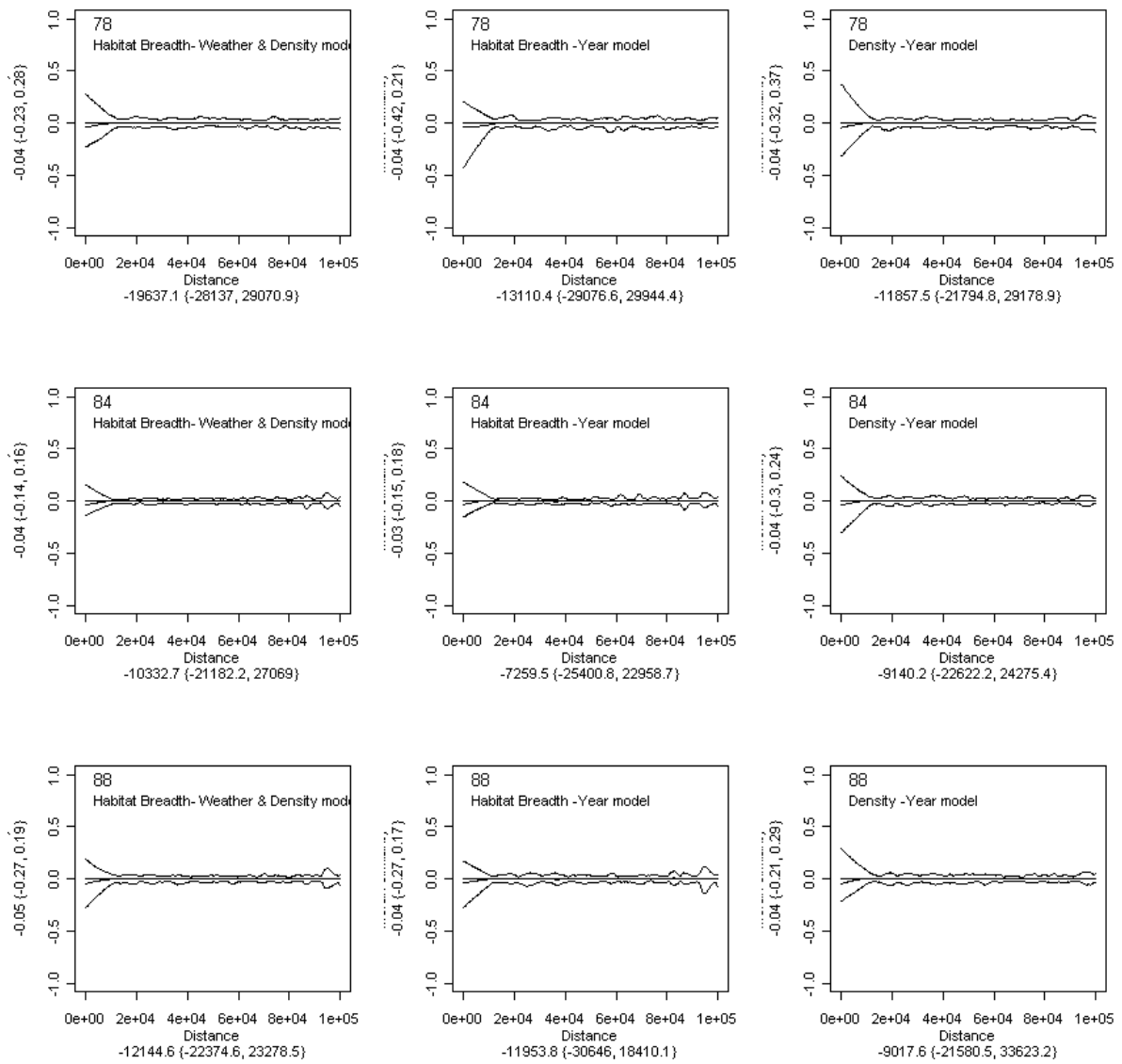
Figure S1- Locations of the UKBMS transects used in the analysis

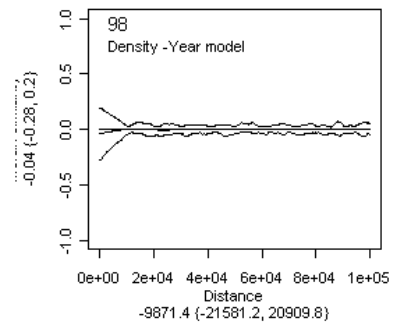
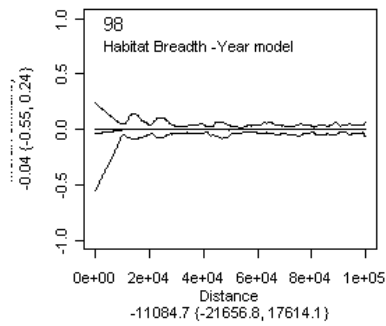
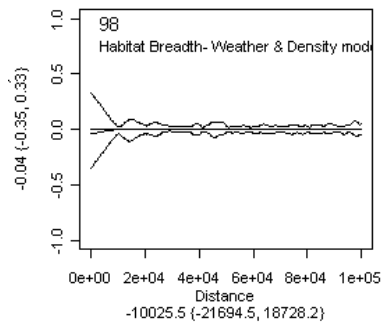
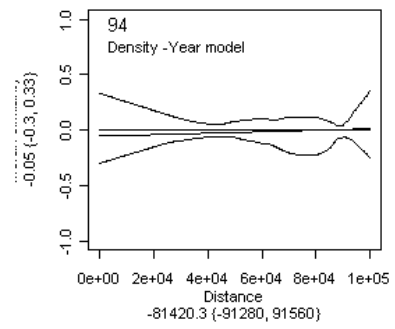
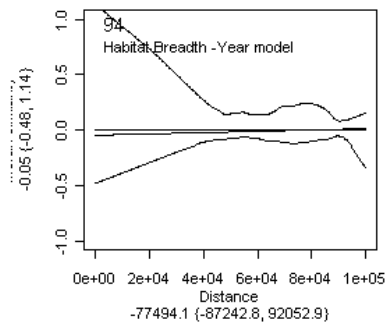
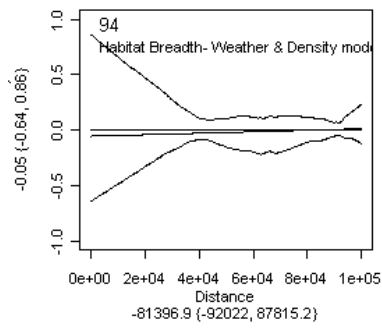
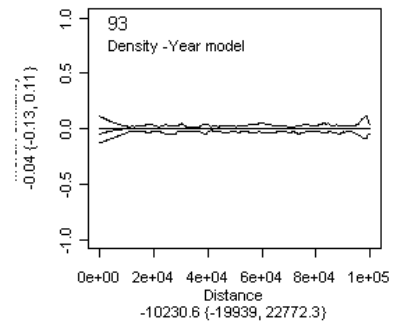
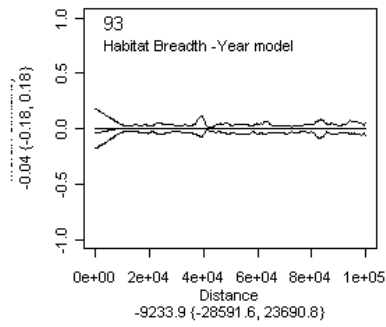
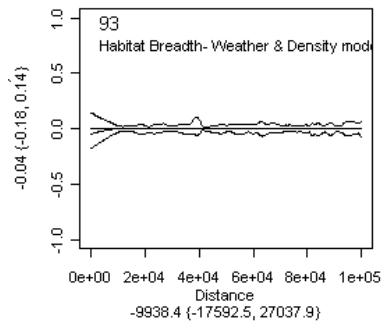


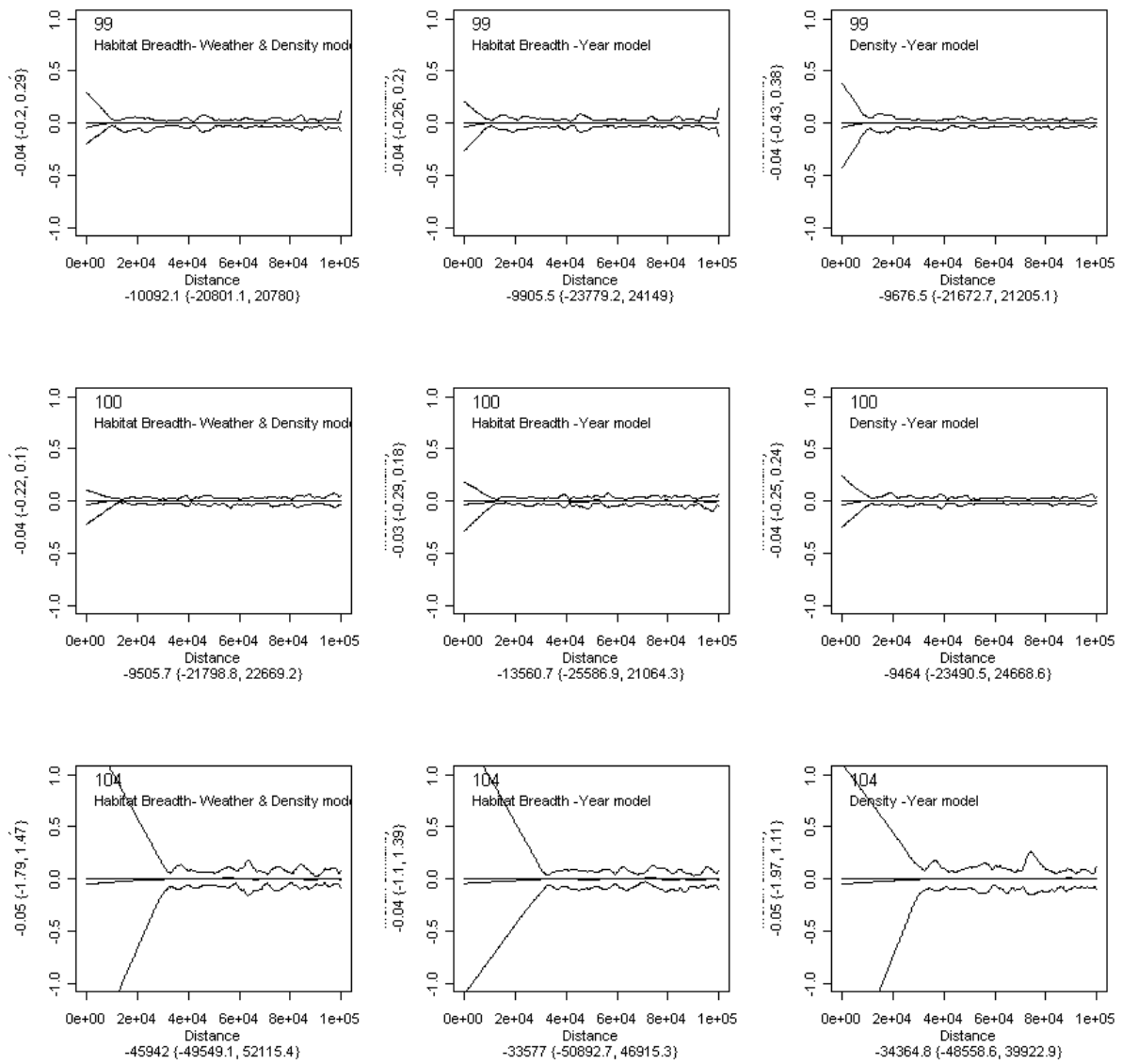


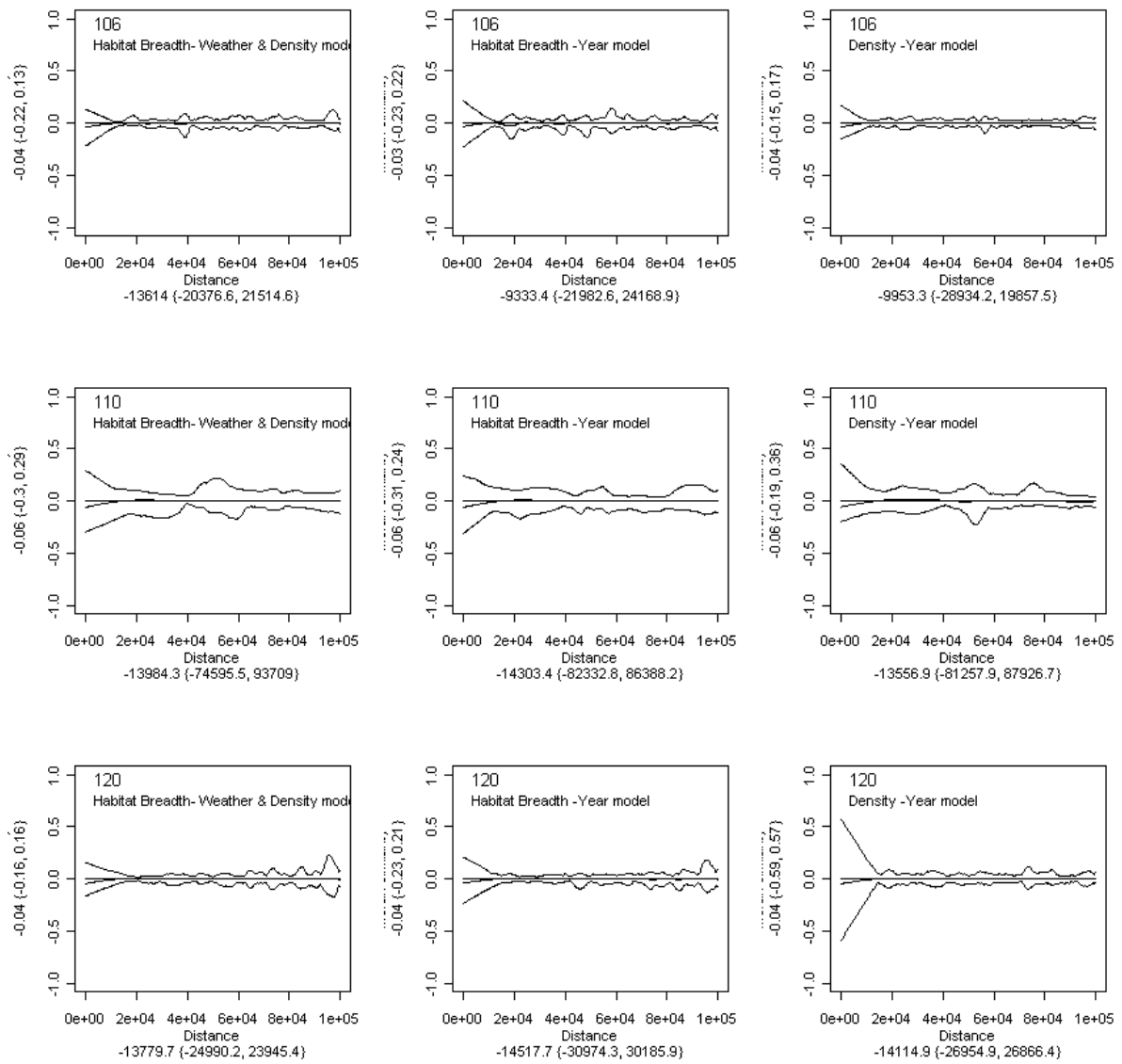


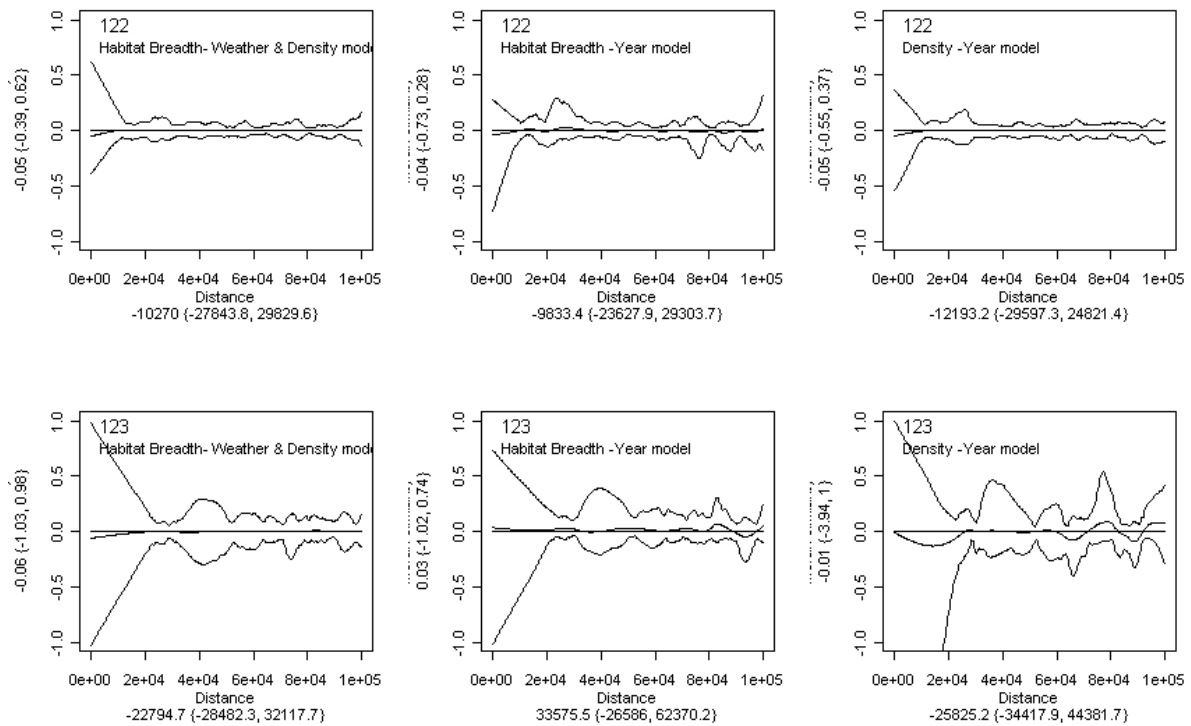












Species code	Common name	Latin name
2	Small tortoiseshell	<i>Aglais urticae</i>
4	Orange tip	<i>Anthocaris cardamines</i>
8	Ringlet	<i>Aphantopus hyperantus</i>
17	Silver-washed fritillary	<i>Argynnis paphia</i>
20	Brown argus	<i>Aricia agestis</i>
27	Holly blue	<i>Celastrina argiolus</i>
29	Small heath	<i>Coenonympha pamphilus</i>
46	Dingy skipper	<i>Erynnis tages</i>
54	Brimstone	<i>Gonepteryx rhamni</i>
68	Small copper	<i>Lycaena phlaeas</i>
75	Meadow brown	<i>Maniola jurtina</i>
76	Gatekeeper	<i>Pyronia tithonus</i>
78	Marbled white	<i>Melanargia galathea</i>
84	Peacock	<i>Inachis io</i>
88	Large skipper	<i>Ochlodes venata</i>
93	Speckled wood	<i>Pararge aegeria</i>
94	Wall brown	<i>Lasiommata megara</i>
98	Large white	<i>Pieris brassicae</i>
99	Green-veined white	<i>Pieris napi</i>
100	Small white	<i>Pieris rapae</i>
104	Comma	<i>Polygonum c-album</i>
106	Common blue	<i>Polyommatus icarus</i>
110	Grizzled skipper	<i>Pyrgus malvae</i>
120	Small skipper	<i>Thymelicus sylvestris</i>
122	Red admiral	<i>Vanessa atalanta</i>
123	Painted lady	<i>Vanessa cardui</i>

Figure S2- Spline correlograms to test for spatial autocorrelation in model residuals

We tested for spatial autocorrelation in the three statistical models fitted to data for each species using the *ncf* package in the program *R* (Bjornstad, 2009, R Development Core Team, 2009). See main text for statistical model explanations. Species' codes are given in the table beneath the panels. For one species, the Green Hairstreak *Callophrys rubi*, only six sites were included in the analysis and so a test for spatial autocorrelation for this species was not possible.

REFERENCES

- Bjornstad ON (2009) *ncf: spatial nonparametric covariance functions*, R package version 1.1-3. <http://CRAN.R-project.org/package=ncf>.
- R Development Core Team (2009) *R: A language and environment for statistical computing.* (ed Computing RfS) pp Page, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org>.