Butterfly abundance is determined by food availability and is mediated by species traits

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Running head:
Food availability determines butterfly abundance

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resources, species traits, UKBMS
1. Understanding the drivers of population abundance across species and sites is crucial for effective conservation management. At present, we lack a framework for predicting which sites are likely to support abundant butterfly communities.

2. We address this problem by exploring the determinants of abundance among 1111 populations of butterflies in the UK, spanning 27 species on 54 sites. Our general hypothesis is that the availability of food resources is a strong predictor of population abundance both within and between species, but that the relationship varies systematically with species’ traits.

3. We found strong positive correlations between butterfly abundance and the availability of food resources. Our indices of hostplant and nectar are both significant predictors of butterfly population density, but the relationship is strongest for hostplants, which explain up to 36% of the intersite variance in abundance for some species.

4. Among species, the hostplant–abundance relationship is mediated by butterfly species traits. It is strongest among those species with narrow diet breadths, low mobility and habitat specialists. Abundance for species with generalist diet and habitat associations is uncorrelated with our hostplant index.

5. The hostplant–abundance relationship is more pronounced on sites with predominantly north-facing slopes, suggesting a role for microclimate in mediating resource availability.

6. *Synthesis and applications.* We have shown that simple measures can be used to help understand patterns in abundance at large spatial scales. For some butterfly species, population carrying capacity on occupied sites is predictable from information about the vegetation composition. These results suggest that targeted management to increase hostplant availability will translate into higher carrying capacity. Among UK butterflies, the species that would benefit most from such intervention have recently experienced steep declines in both abundance and distribution. The hostplant–abundance relationship we have identified is likely to be transferrable to other systems characterized by strong interspecific interactions across trophic levels. This raises the possibility that the quality of habitat patches for specialist species is estimable from rapid assessment of the hostplant resource.
Introduction

A key challenge for conservation biologists is to develop an evidence-based framework to predict how species will respond to change in increasingly modified landscapes (Sutherland et al. 2004; Evans et al. 2012). To date, progress towards a predictive framework for biodiversity has focussed on patterns at coarse spatial scales, such as how species distributions might shift under climate change (Thomas et al. 2004) and the role of species’ traits in mediating response to change (Webb et al. 2010). Most applied conservation management takes place on sites, i.e. at the population level, for which relatively little evidence exists of predictable responses to change (Cowlishaw et al. 2009; Hanspach et al. 2012). Even the factors driving large-scale variation in population abundance remain poorly understood (McGill 2008). Thus, land managers and policymakers lack general rules for how management interventions will impact on population sizes of target organisms (Sutherland & Freckleton 2012).

Habitat quality has long been recognized as one of the fundamental determinants of variation in abundance among populations of a single species (Andrewartha & Birch 1954), yet quality has proven to be a difficult concept to define, especially across multiple species (Hodgson et al. 2009). Quality might be defined in terms of food resources, since resource supply sets an upper limit on carrying capacity (Blackburn & Gaston 1999; Brown et al. 2004), and several studies on vertebrate populations have demonstrated strong relationships between abundance and either edible biomass or habitat productivity (Lack 1954; Carbone & Gittleman 2002; Pettorelli et al. 2009). For many invertebrates, eggs are laid near to, directly on or inside the primary larval resource (the host). Thus, many studies have shown strong correlations between the abundance of phytophagous insects and biomass of the larval resource, the hostplant (Dempster & Pollard 1981; Strong et al. 1984; Marques et al. 2000), although the strength of this relationship varies across both species and sites (New 2009). The relationship between abundance and the availability of resources for mobile life stages also varies, with strong positive relationships observed for some insects (Thomas 1991; Holzschuh et al. 2013), but with no consistent patterns across species (Thomas et al. 2011).

Whilst the availability of resources is a necessary condition for a high-quality habitat (Dennis 2010), the microclimatic conditions of hostplants are crucial to the development of many
phytophagous insects (Thomas 1991; Ashton et al. 2009). Females of many butterfly species
display strong preferences for oviposition sites based on size and/or location (Thomas et al.
2001; Turlure et al. 2010). In temperate Europe, where many insects exist at the climatic
limits of their distribution, factors including aspect exert a strong influence on the
microclimatic suitability of individual hostplants in grassland systems (Bergman et al. 2008;
Dover et al. 2011a; Thomas et al. 2011), leading to measurable correlations between this
characteristic and population dynamic parameters (Lawson et al. 2012). Thus, the
relationship between resource availability and population abundance is expected to vary
among sites depending on aspect.

A complicating factor for land managers is that co-occurring species differ in their resource
requirements. The relationship between habitat quality and resource availability is likely to
vary, with traits of the consumer species playing a role in this variation. Diet breadth is likely
to be crucial, with monophagous species far more likely to be resource-limited than
polyphagous species (Dennis et al. 2005; Mattila et al. 2008), for whom the ability to feed on
multiple resources may act as a buffer against scarcity of preferred food plants. Similarly,
resource availability is likely to be a better reflection of habitat quality for philopatric
species than for highly mobile ones, which can sample the landscape more widely than the
area targeted by management (Dapporto & Dennis 2013). Whilst both niche breadth and
mobility have been linked to the conservation status of many insect species (Mattila et al.
2009; Poyry et al. 2009; Bommarco et al. 2010), the role of resource use in explaining these
patterns has yet to be demonstrated.

In this paper, we test the hypothesis that food availability is a good measure of habitat
quality in grassland butterflies of southern England. We focus on grasslands as they provide
breeding habitat for around 90% of butterflies found in this region (Brereton 2004).
Butterflies are an excellent model due to the large quantity of population data that has been
collected through the UK Butterfly Monitoring Scheme since 1976 (Pollard & Yates 1993),
and because the resource requirements of many of the species are well-known (Dennis
2010). Widespread declines in butterfly populations have been reported (Bonelli et al. 2011;
Dover et al. 2011b; Fox et al. 2011a), with deteriorating habitat quality due to land-use
change, inappropriate management and habitat fragmentation being strongly implicated
(Thomas 1995; Warren et al. 2001; Mortelliti et al. 2010). Thus, a predictive understanding
of habitat quality is crucial for the conservation of butterflies. The dependence of butterflies on key plant species creates an ideal system for exploring functional links between trophic levels (Pellissier et al. 2013).

Generally, correlations between food availability and adult abundance are weak, except where the growth form of the hostplant is specified (Thomas et al. 2011), although management for the hostplant of target butterfly species can lead to increases in population abundance (Ellis et al. 2012). We test whether this relationship is generalizable across species, using an unusually detailed data base on the abundance of 1111 butterfly populations, the abundance of their foodplants, and the food preferences of the adults and larvae of each species. Specifically, we test whether the availability of hostplants and nectar has predictive power in explaining the observed variation in butterfly abundance, across species and sites. We further test whether these relationships are contingent on butterfly species’ traits (mobility, diet breadth, and population structure) and aspect.

**Materials and methods**

We selected 54 sites within southern England on which the predominant habitat is semi-natural grassland (Figure S1 in Supporting Information). All the sites have been regularly monitored as part of the UK Butterfly Monitoring Scheme (UKBMS), so data were already available on the abundance of butterfly populations. We restricted our analysis to a single habitat type in order to minimize unmeasured heterogeneity in our data set. We chose grassland over other habitats (e.g. woodland, heathland) because of the large number of butterfly species supported by grassland (Brereton 2004), and their relatively uniformity (compared with woodland or heathland) across southern England.

**Estimates of vegetation abundance**

Vegetation surveys were conducted during the summer months of 2008 and 2009, with the majority of surveys being conducted in August (Figure S2), i.e. after the summer peak in plant biomass production. At each site, we used the structure and route of the UKBMS transect in order to determine the number and location of quadrats. Most UKBMS transects are divided into sections, reflecting discontinuities in the landscape: our sites contain 1–15 sections (mean = 7.5 per site, SD = 2.82). To adequately reflect the vegetation experienced
by butterfly populations, we placed four 1-m² quadrats in each section, for a total of 1624 quadrats (54 sites × 7.5 sections per site × 4 quadrats per section). The location of quadrats were determined by selecting points at random from a 10-m wide polygon centred on the transect route. Plant species were recorded as the percentage cover within each quadrat. We recorded an average of 10.3 plant species per quadrat, for a total of 16 720 separate estimates of plant abundance across all quadrats from 165 different plant species. When aggregated to the site level, our data comprise 2934 plant : site combinations, with a mean number of 54.3 plant species per site. The full data set is available from the NERC Data Centre (Curtis & Isaac 2015, doi:10.5285/ca34e25b-6138-4b72-b32c-778d762118f1).

Estimates of butterfly abundance

We used the UKBMS to estimate the abundance of each butterfly species at each site. Abundance on the UKBMS is estimated from regular (typically weekly) transect walks, on which the numbers of adult butterflies of each species are counted. These individual counts are aggregated into an annual index of abundance for each species : site combination (Pollard & Yates 1993), and it is these ‘site indices’ that form the basis of our analyses. Whilst the UKBMS methodology was not designed to estimate population abundance (Pollard & Yates 1993), these indices are closely correlated with population density across species and sites (Isaac et al. 2011a). We extracted index values spanning 2006–2010 for our sites from the UKBMS data set and calculated the geometric mean for each species : site combination. We then divided by the length of the transect to obtain an estimate of mean population density.

A total of 45 butterfly species were recorded on our study sites. Of these, four wide-ranging species were excluded because their hostplants were not detected within any of the study sites (Anthocharis cardamines, Pieris brassicae, Pieris napi and Pieris rapae), such that our models have no power to predict their abundance. We also excluded 11 species that occurred on seven sites or fewer (Euphydryas aurinia, Hamearis lucina, Hipparchia semele, Limenitis camilla, Melitaea cinxia, Apatura iris, Satyrium w-album, Neozephyrus quercus, Thecla betulae, Plebejus argus, and Leptidea sinapis), and three migratory species (Colias croceus, Vanessa cardui and Vanessa atalanta) for whom the abundance of adults butterflies is clearly driven by factors other than the availability of hostplants on sites in the
UK. Across the remaining 27 species we were able to estimate abundance for 1111 populations (21 species per site; see Table S1).

Indices of resource availability

We combined the vegetation survey data with existing knowledge about larval and adult feeding preferences to generate simple indices of resource availability for each of the 1111 butterfly populations in our data set. The hostplant index for each species is simply the sum of the percentage cover of all plant species listed as ‘main’ larval hostplants by Dennis (2010), and ranged from 0 to 50. Similarly, the nectar index is the sum of the percentage cover of all known nectar sources from Dennis (2010). Thus, we assume that plant cover in late summer is a surrogate measure for nectar production across the growing season. Our nectar indices ranged from 0 to 75 and were weakly correlated with matching hostplant indices ($r^2=0.06$, Figure S3). Eight of the 27 butterfly species use at least one plant species as a hostplant and nectar source, so we repeated our nectar analyses using a second index that ignored the contribution of hostplant species, but found qualitatively identical results (Figure S4, Table S4).

Species traits and site characteristics

Aspect was recorded to the nearest five degrees for any quadrat where the ground surface inclined in a consistent direction: a site-level aspect was calculated as the cosine of the mean of the section means. Cosine transformation means that aspect varies from 1 (south-facing) to -1 (north-facing).

We collected data on diet breadth, mobility and population structure from the literature (Table 1).

Statistical analysis

Our data set contains 1111 estimates of population density for 27 butterfly species on 54 sites. Each estimate is accompanied by matching estimates of hostplant and nectar availability. We modelled this variation using linear mixed-effects models with log (density) as the response variable, species and site as random effects (Cowlishaw et al. 2009; Isaac et al. 2011b) and various combinations of food availability and traits as fixed effects (see below). Using random effects, rather than fixed, allows us to make general statements...
about how changes in resource availability might impact on the average species for the average site. The fixed effects (including interaction terms) are thus used to test hypotheses about the relationship between food availability and population abundance.

We first fitted models to explore the importance of food availability as a main effect, with a single fixed effect each: first log (hostplant index) and log (nectar index). The nectar model was repeated with the exclusion of nectar sources that are also hostplants.

We then tested whether the density–food relationship is mediated by species traits and site characteristics. To do this, we added terms to the hostplant and nectar mixed effects models: for the hypothesis that density–food relationships are mediated by adult diet breadth, we added the number of ‘core’ hostplants (CHP) as a main effect and its interaction with food availability (i.e. the hostplant and nectar indices). We conducted this exercise for the five traits in Table 1 (5 traits × 2 measures of food availability = 10 models in total). The null hypothesis, in each case, is that the interaction term has no effect.

Significance of fixed effects was assessed using Wald t-tests, as recommended by Bolker et al. (2009), using the lme4 package in R (Bates & Maechler 2010; R Development Core Team 2010).

**Results**

We found a strong positive relationship between butterfly population density and abundance of their associated hostplants both within and between species (b=0.357, SE=0.0415, t=8.61, P<0.001; Figure 1). This implies that, for the average species on an average site, a doubling of hostplant availability leads to an increase in butterfly abundance of 36%.

The nectar–abundance relationship (Figure 2) is also strongly positive (b=0.313, SE=0.0599, t=5.23, P<0.001), implying that a doubling of nectar plant availability leads to an increase in butterfly abundance of 31%. Qualitatively identical results are obtained when the contribution of hostplant species is excluded from the nectar calculation (b=0.224, SE=0.0557, t=4.036, P<0.001).
We found that interspecific variation in the hostplant–abundance relationship between species (Figure 1) is indeed mediated by species traits (Table 2), including both measures of diet breadth and mobility, but not population structure. The hostplant–abundance relationship is almost twice as steep for the average monophagous species (b=0.49) compared to species which use four main hostplants (b=0.25). Similarly, species using fewer species of nectar plant show steeper relationships with the hostplant index than species using many nectar sources. The hostplant–abundance relationship is much steeper for sedentary species compared with highly mobile species (b=0.79 vs. 0.16).

We also found a significant interaction between aspect and hostplant abundance (Table 2), with butterfly populations on sites with northerly aspects apparently more than twice as sensitive to changes in hostplant abundance than on sites with southerly aspects (b=0.61 vs. 0.28).

We found no evidence that the nectar–abundance relationship is mediated by any of the species traits or site characteristics (Table 2).

Discussion
Our analyses reveal the extent to which butterfly population abundance is predictable from resource availability; at least within the selection of sites in our data set (Table 2, and Figures 1, 2, and Tables S2, S3 for species specific results). Our results confirm the importance of resource availability in determining population abundance and help define a predictive basis for habitat quality. By characterizing the functional space (Butler & Norris 2013) of multiple butterfly species, our results inform the management options for declining butterfly species.

In particular, we find that hostplant quantity explains a substantial portion of the intersite variation in population abundance for species that are dietary and habitat specialists. For species with these traits (notably Cupido minimus, Aricia agestis, Polyommatinus bellargus) the hostplant index explains more than one third of the intersite variation in population density, but for others (e.g. Maniola jurtina, Ochlodes sylvanus) the two are uncorrelated (Figure 1, Table S2). The findings have direct implications for the management of butterflies sharing these traits, many of which are of conservation concern.
That our results were broadly in line with predictions highlights the value of ecological theory in applied conservation management (Doak & Mills 1994; see also Dapporto & Dennis 2013).

Principally, our results underscore the importance of maximizing hostplant abundance within occupied sites. This evidence is based on a large sample size along two axes of variation – both between and within species – and spans a large range of values for both butterfly population density and hostplant abundance. Indeed, it is possible that these results contrast with fine-scale studies (Thomas 1983; Kelly & Debinski 1998; Rabasa et al. 2008) because of differences in the range of variation in hostplant abundance. However, many of the sites are managed specifically for butterflies and so a high percentage of hostplants are likely to be in suitable condition, such that simple measures like percentage cover more accurately reflect the food resources available to butterfly larvae. A priority for future research is to establish whether our findings are generalizable across habitat types without explicit consideration of hostplant suitability (Dennis 2010).

The strength of the relationship between the nectar index and butterfly abundance, although weaker than the matching hostplant relationship, is surprisingly strong on several grounds. For one thing, associations between butterflies and nectar sources are recorded far less reliably than hostplants: the former are mostly casual observations, biased towards gardens, whereas the latter have been validated using rearing experiments (Hardy et al. 2007). Second, our nectar index is a crude sum of the percentage cover across plant species recorded as nectar sources: a better measure would have been the number of florets produced during the adult flight period. Thirdly, most butterflies reproduce within a few days of emerging as adults (Cushman et al. 1994; Wahlberg 1995), such that abundant nectar is likely to be of limited benefit to fecundity and recruitment. Fourth, previous work on butterfly population dynamics has suggested that survival is primarily determined by nutrients acquired during larval development (i.e. hostplants) (Labine 1968; Baylis & Pierce 1991; Hughes 2000), but that adult diet (i.e. nectar) can influence fecundity (Boggs & Freeman 2005). For these reasons we are cautious about overstating the role of nectar availability in butterfly carrying capacity. However, our results emphasize that the possibility of nectar availability should remain a key area of research in butterfly conservation biology (Tudor et al. 2004; Wallisdevries et al. 2012).
Furthermore, we recognize more general limitations to this study. Our vegetation surveys recorded only a snapshot of the resource availability, and do not account for seasonal variation. Our conversion of plant cover scores into indices of nectar and hostplant availability do not consider feeding preferences when multiple food sources are available, highlighting the complexities of managing for generalist species (Finlay-Doney & Walter 2012). Incorporating this sort of information would improve the predictive power of our models. However, these limitations reflect the trade-off between macroecological generalization and microecological detail: our study is unusual in combining a broad spatial extent and large number of species with fine-grained information about individual populations (Beck et al. 2012). Given the uncertainties in our data set, it is perhaps surprising that we were able to make such clear inferences about the food–abundance relationship.

Despite the obvious theoretical link between food and abundance, there have been few other studies providing spatially-explicit quantitative evidence of a correlation. The food–abundance relationship has been previously demonstrated in birds (Lack 1954) and mammals (Carbone & Gittleman 2002; Prevedello et al. 2013). The relationship has previously been tested in butterflies, with mixed results (Gutierrez & Menendez 1995; Hughes 2000; Kuussaari et al. 2000; Cowley et al. 2001). Our finding that the hostplant–abundance relationship is mediated by species traits (and site aspect) could explain why single-species studies often find weak or nonsignificant correlations (Thomas et al. 2011).

The development of a trait-based framework allows us to predict how species will respond to changes in food availability. Although some of these traits are intercorrelated, the patterns that emerge give some insights into the ecological mechanisms linking resource availability with population abundance (Ockinger et al. 2010; Sekar 2011). In this study, species which have narrower dietary niche breadth (as both larvae and adults) and low mobility are more sensitive to changes in hostplant abundance (Dapporto & Dennis 2013). These traits are all indicative of a strong ecological interaction between the butterfly and hostplant, with individual butterflies completing their entire life cycle in a restricted area, hence the strength of the statistical relationship linking plant and butterfly abundance. By contrast, individual butterflies in species with the opposite set of traits (polyphagy and mobility) experience only weak interactions with the plant population on which they fed as
larvae (Dennis et al. 2014). Polyphagy allows adult butterflies to select oviposition sites from a range of hostplant species; mobility allows butterflies to travel between habitat patches in order to reproduce. The importance of these mechanisms implies that tight correlations between the abundance of species at different trophic levels are likely to be found in other systems where interspecific interactions are strong (e.g. host–parasitoid interactions).

A trait-based framework also has important ramifications for conservation (Daily 2001), as it allows land managers to predict how different species will respond to alternative management strategies. Species with few hostplants and low mobility could benefit from targeted management to increase carrying capacity by managing for the abundance of their hostplants (Dennis et al. 2013). Given that some of the most rapidly declining butterfly species possess several of these traits (Fox et al. 2011b), our results are positive for conservation: the species that will benefit most from targeted management are also the ones for which intervention is most needed. Indeed, increasing the resource base within sites has been observed to have a positive impact on many of the UK’s rarest butterflies at the landscape scale (Ellis et al. 2012).

Aspect has a strong negative interaction with hostplants suggesting that populations inhabiting sites with cooler aspects (e.g. more north-facing), are more sensitive to variation in hostplant abundance. This does not mean that north-facing slopes harbour more abundant butterfly populations, but rather that a unit change in our hostplant index has a larger effect on butterfly abundance on a north-facing slope than on a south-facing one, with other slopes intermediate. Temperature is a key driver of whether a hostplant is in a suitable condition (Thomas 1983; Renwick & Chew 1994), and aspect is an important factor determining temperature (Bennie et al. 2008). Therefore aspect is a strong determinant of the thermal microclimate: on south-facing slopes the majority of plants are likely to be within a suitable microclimate for the development of butterfly larvae. Our result implies that management of hostplants is likely to have a greater impact on carrying capacity in cooler microclimates (north-facing slopes). However, our data set contains relatively few north-facing sites, so further research is required to explore whether this is a general phenomenon, or whether it is specific to a small number of highly thermophilous butterfly species on a small number of sites.
Our key finding has been that abundance is predictable for species with strong interactions with their hostplant e.g. monophagous species. This predictability makes it possible, for some species, to estimate carrying capacity without counting the organisms. Vegetation surveys can be conducted within a single day to provide estimates for multiple species with different characteristic phenology, rather than repeated surveys over several months. One might envisage a hostplant count being used to supplement low-effort insect surveys (Brereton et al. 2011), or in situations where a dedicated workforce of volunteer surveyors is not available. Data on resource availability, where measureable, could therefore provide useful information for the conservation management of any population where interactions across trophic levels are strong.

Acknowledgments
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Data accessibility
Vegetation abundance data is available from the NERC Environmental Information Data Centre: doi: 10.5285/ca34e25b-6138-4b72-b32c-778d762118f1. The derived dataset used for statistical analysis is available from Figshare: doi: 10.6084/m9.figshare.1494733.

References
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**Supporting Information**

Additional Supporting Information may be found in the online version of this article:

**Figures**

Figure 1. A scatterplot of population density against the hostplant index for 27 butterfly species on 54 UKBMS sites. Population density was estimated as the average during 2006–2010; the hostplant data was collected from the same sites recorded during 2008–2009.

Figure 2. A scatterplot of population density against the nectar index for 27 butterfly species on 54 UKBMS sites. Population density was estimated as the average during 2006–2010; the nectar data was collected from the same sites recorded during 2008–2009.
Table 1. Description of diet breadth, life-history and site traits

<table>
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<th>Definition</th>
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<td><strong>Diet breadth</strong></td>
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<tr>
<td>Larval niche breadth</td>
<td>Number of larval Core Host Plants (CHP)</td>
<td>Records of only main host plants including prominent regional ones</td>
<td>Dennis (2010)</td>
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<tr>
<td>Adult niche breadth</td>
<td>Degree of adult nectar specialism (RanS)</td>
<td>Monte Carlo estimated number of nectar sources (from mean number of nectar sources per 100 records)</td>
<td>Hardy et al (2007)</td>
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<td><strong>Life history traits</strong></td>
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<td>Habitat specialist</td>
<td>Degree of adult habitat specialism</td>
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<td>Mobility</td>
<td>Degree of dispersal capabilities</td>
<td>Dispersal capabilities (1-9, low to high)</td>
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<td>Population structure</td>
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<td>Larval duration</td>
<td>Duration of larval stage calculated from life history tables</td>
<td>Average number of days spent feeding on hostplant during March - October</td>
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<td><strong>Site Traits</strong></td>
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<td>Aspect</td>
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<td>A measure of ground orientation</td>
<td>This study</td>
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Table 2. Results of separate linear mixed models between the logarithmic geometric mean of density for all 27 butterfly species recorded across 54 UKBMS sites during 2006–2010, against site and species traits as: i) an interaction with hostplants and ii) an interaction with nectar. The results in the table are therefore obtained from 10 separate models (5 for both nectar and hostplants) and the results of the main effect have been omitted.

<table>
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<th>Site traits</th>
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<td>ii) Interaction with nectar plants</td>
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