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

5 Curtis, R.J.[1,2,3,4], Brereton, T.M.[5], Dennis, R.L.H.[1,6], Carbone, C.[3] & Isaac, N.J.B.[1]

7 [1]NERC Centre for Ecology & Hydrology, Maclean Building, Crowmarsh Gifford, Wallingford, OX10
8 8BB, UK

9 [2]University College London, Gower Street, London, WC1E 6BT, UK

10 [3]Institute of Zoology, Zoological Society of London, Regent's Park, London, NW1 4RY, UK

11 [4]Present address: Environment and Sustainability Institute, University of Exeter, Penryn Campus
12 Penryn, Cornwall TR10 9FE, UK

13 [5]Butterfly Conservation, Manor Yard, East Lulworth, Wareham, BH20 5QP, UK

14 [6]Institute for Environment, Sustainability and Regeneration, Room 113, The Science Centre,
15 Staffordshire University, Leek Road, Stoke-on-Trent ST4 2DF, UK.

17 Running head:

18 Food availability determines butterfly abundance

Summary

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

84   phytophagous insects (Thomas 1991; Ashton *et al.* 2009). Females of many butterfly species

85   display strong preferences for oviposition sites based on size and/or location (Thomas *et al.*

86   2001; Turlure *et al.* 2010). In temperate Europe, where many insects exist at the climatic

87   limits of their distribution, factors including aspect exert a strong influence on the

88   microclimatic suitability of individual hostplants in grassland systems (Bergman *et al.* 2008;

89   Dover *et al.* 2011a; Thomas *et al.* 2011), leading to measurable correlations between this

90   characteristic and population dynamic parameters (Lawson *et al.* 2012). Thus, the

91   relationship between resource availability and population abundance is expected to vary

92   among sites depending on aspect.

93   A complicating factor for land managers is that co-occurring species differ in their resource

94   requirements. The relationship between habitat quality and resource availability is likely to

95   vary, with traits of the consumer species playing a role in this variation. Diet breadth is likely

96   to be crucial, with monophagous species far more likely to be resource-limited than

97   polyphagous species (Dennis *et al.* 2005; Mattila *et al.* 2008), for whom the ability to feed on

98   multiple resources may act as a buffer against scarcity of preferred food plants. Similarly,

99   resource availability is likely to be a better reflection of habitat quality for philopatric

100   species than for highly mobile ones, which can sample the landscape more widely than the

101   area targeted by management (Dapporto & Dennis 2013). Whilst both niche breadth and

102   mobility have been linked to the conservation status of many insect species (Mattila *et al.*

103   2009; Poyry *et al.* 2009; Bommarco *et al.* 2010), the role of resource use in explaining these

104   patterns has yet to be demonstrated.

105   In this paper, we test the hypothesis that food availability is a good measure of habitat

106   quality in grassland butterflies of southern England. We focus on grasslands as they provide

107   breeding habitat for around 90% of butterflies found in this region (Brereton 2004).

108   Butterflies are an excellent model due to the large quantity of population data that has been

109   collected through the UK Butterfly Monitoring Scheme since 1976 (Pollard & Yates 1993),

110   and because the resource requirements of many of the species are well-known (Dennis

111   2010). Widespread declines in butterfly populations have been reported (Bonelli *et al.* 2011;

112   Dover *et al.* 2011b; Fox *et al.* 2011a), with deteriorating habitat quality due to land-use

113   change, inappropriate management and habitat fragmentation being strongly implicated

114   (Thomas 1995; Warren *et al.* 2001; Mortelliti *et al.* 2010). Thus, a predictive understanding

115   of habitat quality is crucial for the conservation of butterflies. The dependence of butterflies

116   on key plant species creates an ideal system for exploring functional links between trophic

117   levels (Pellissier *et al.* 2013).

118   Generally, correlations between food availability and adult abundance are weak, except

119   where the growth form of the hostplant is specified (Thomas *et al.* 2011), although

120   management for the hostplant of target butterfly species can lead to increases in population

121   abundance (Ellis *et al.* 2012). We test whether this relationship is generalizable across

122   species, using an unusually detailed data base on the abundance of 1111 butterfly

123   populations, the abundance of their foodplants, and the food preferences of the adults and

124   larvae of each species. Specifically, we test whether the availability of hostplants and nectar

125   has predictive power in explaining the observed variation in butterfly abundance, across

126   species and sites. We further test whether these relationships are contingent on butterfly

127   species' traits (mobility, diet breadth, and population structure) and aspect.

128   ## Materials and methods

129   We selected 54 sites within southern England on which the predominant habitat is semi-

130   natural grassland (Figure S1 in Supporting Information). All the sites have been regularly

131   monitored as part of the UK Butterfly Monitoring Scheme (UKBMS), so data were already

132   available on the abundance of butterfly populations. We restricted our analysis to a single

133   habitat type in order to minimize unmeasured heterogeneity in our data set. We chose

134   grassland over other habitats (e.g. woodland, heathland) because of the large number of

135   butterfly species supported by grassland (Brereton 2004), and their relatively uniformity

136   (compared with woodland or heathland) across southern England.

137   *Estimates of vegetation abundance*

138   Vegetation surveys were conducted during the summer months of 2008 and 2009, with the

139   majority of surveys being conducted in August (Figure S2), i.e. after the summer peak in

140   plant biomass production. At each site, we used the structure and route of the UKBMS

141   transect in order to determine the number and location of quadrats. Most UKBMS transects

142   are divided into sections, reflecting discontinuities in the landscape: our sites contain 1–15

143   sections (mean = 7.5 per site, SD = 2.82). To adequately reflect the vegetation experienced

144   by butterfly populations, we placed four 1-m^2 quadrats in each section, for a total of 1624

145   quadrats (54 sites × 7.5 sections per site × 4 quadrats per section). The location of quadrats

146   were determined by selecting points at random from a 10-m wide polygon centred on the

147   transect route. Plant species were recorded as the percentage cover within each quadrat.

148   We recorded an average of 10.3 plant species per quadrat, for a total of 16 720 separate

149   estimates of plant abundance across all quadrats from 165 different plant species. When

150   aggregated to the site level, our data comprise 2934 plant : site combinations, with a mean

151   number of 54.3 plant species per site. The full data set is available from the NERC Data

152   Centre (Curtis & Isaac 2015, doi:10.5285/ca34e25b-6138-4b72-b32c-778d762118f1).

153   *Estimates of butterfly abundance*

154   We used the UKBMS to estimate the abundance of each butterfly species at each site.

155   Abundance on the UKBMS is estimated from regular (typically weekly) transect walks, on

156   which the numbers of adult butterflies of each species are counted. These individual counts

157   are aggregated into an annual index of abundance for each species : site combination

158   (Pollard & Yates 1993), and it is these 'site indices' that form the basis of our analyses.

159   Whilst the UKBMS methodology was not designed to estimate population abundance

160   (Pollard & Yates 1993), these indices are closely correlated with population density across

161   species and sites (Isaac *et al.* 2011a). We extracted index values spanning 2006–2010 for our

162   sites from the UKBMS data set and calculated the geometric mean for each species : site

163   combination. We then divided by the length of the transect to obtain an estimate of mean

164   population density.

165   A total of 45 butterfly species were recorded on our study sites. Of these, four wide-ranging

166   species were excluded because their hostplants were not detected within any of the study

167   sites (*Anthocharis cardamines, Pieris brassicae, Pieris napi* and *Pieris rapae*), such that our

168   models have no power to predict their abundance. We also excluded 11 species that

169   occurred on seven sites or fewer (*Euphydryas aurinia, Hamearis lucina, Hipparchia semele,*

170   *Limenitis camilla, Melitaea cinxia, Apatura iris, Satyrium w-album, Neozephyrus quercus,*

171   *Thecla betulae, Plebejus argus,* and *Leptidea sinapis*), and three migratory species (*Colias*

172   *croceus*, *Vanessa cardui* and *Vanessa atalanta*) for whom the abundance of adults

173   butterflies is clearly driven by factors other than the availability of hostplants on sites in the

174   UK. Across the remaining 27 species we were able to estimate abundance for 1111

175   populations (21 species per site; see Table S1).

176   *Indices of resource availability*

177   We combined the vegetation survey data with existing knowledge about larval and adult

178   feeding preferences to generate simple indices of resource availability for each of the 1111

179   butterfly populations in our data set. The hostplant index for each species is simply the sum

180   of the percentage cover of all plant species listed as 'main' larval hostplants by Dennis

181   ([2010](#)), and ranged from 0 to 50. Similarly, the nectar index is the sum of the percentage

182   cover of all known nectar sources from Dennis ([2010](#)). Thus, we assume that plant cover in

183   late summer is a surrogate measure for nectar production across the growing season. Our

184   nectar indices ranged from 0 to 75 and were weakly correlated with matching hostplant

185   indices (r^2=0. 06, Figure S3). Eight of the 27 butterfly species use at least one plant species

186   as a hostplant and nectar source, so we repeated our nectar analyses using a second index

187   that ignored the contribution of hostplant species, but found qualitatively identical results

188   (Figure S4, Table S4).

189   *Species traits and site characteristics*

190   Aspect was recorded to the nearest five degrees for any quadrat where the ground surface

191   inclined in a consistent direction: a site-level aspect was calculated as the cosine of the

192   mean of the section means. Cosine transformation means that aspect varies from 1 (south-

193   facing) to -1 (north-facing).

194   We collected data on diet breadth, mobility and population structure from the literature

195   (Table 1).

196   *Statistical analysis*

197   Our data set contains 1111 estimates of population density for 27 butterfly species on 54

198   sites. Each estimate is accompanied by matching estimates of hostplant and nectar

199   availability. We modelled this variation using linear mixed-effects models with log (density)

200   as the response variable, species and site as random effects ([Cowlishaw *et al.* 2009](#); [Isaac *et*](#)

201   [*al.* 2011b](#)) and various combinations of food availability and traits as fixed effects (see

202   below). Using random effects, rather than fixed, allows us to make general statements

203   about how changes in resource availability might impact on the average species for the

204   average site. The fixed effects (including interaction terms) are thus used to test hypotheses

205   about the relationship between food availability and population abundance.

206   We first fitted models to explore the importance of food availability as a main effect, with a

207   single fixed effect each: first log (hostplant index) and log (nectar index). The nectar model

208   was repeated with the exclusion of nectar sources that are also hostplants.

209   We then tested whether the density–food relationship is mediated by species traits and site

210   characteristics. To do this, we added terms to the hostplant and nectar mixed effects

211   models: for the hypothesis that density–food relationships are mediated by adult diet

212   breadth, we added the number of 'core' hostplants (CHP) as a main effect and its interaction

213   with food availability (i.e. the hostplant and nectar indices). We conducted this exercise for

214   the five traits in Table 1 (5 traits × 2 measures of food availability = 10 models in total). The

215   null hypothesis, in each case, is that the interaction term has no effect.

216   Significance of fixed effects was assessed using Wald t-tests, as recommended by Bolker *et*

217   *al.* ([2009](#)), using the lme4 package in R ([Bates & Maechler 2010](#); [R Development Core Team](#)

218   [2010](#)).

Results

220   We found a strong positive relationship between butterfly population density and

221   abundance of their associated hostplants both within and between species (b=0.357,

222   SE=0.0415, t=8.61, *P*<0.001; Figure 1). This implies that, for the average species on an

223   average site, a doubling of hostplant availability leads to an increase in butterfly abundance

224   of 36%.

225   The nectar–abundance relationship (Figure 2) is also strongly positive (b=0.313,

226   SE=0.0599, t=5.23, *P*<0.001), implying that a doubling of nectar plant availability leads to an

227   increase in butterfly abundance of 31%. Qualitatively identical results are obtained when

228   the contribution of hostplant species is excluded from the nectar calculation (b=0.224,

229   SE=0.0557, t=4.036, *P*<0.001).

230   We found that interspecific variation in the hostplant–abundance relationship
231 between species (Figure 1) is indeed mediated by species traits (Table 2), including both
232 measures of diet breadth and mobility, but not population structure. The hostplant–
233 abundance relationship is almost twice as steep for the average monophagous species
234 (b=0.49) compared to species which use four main hostplants (b=0.25). Similarly, species
235 using fewer species of nectar plant show steeper relationships with the hostplant index than
236 species using many nectar sources. The hostplant–abundance relationship is much steeper
237 for sedentary species compared with highly mobile species (b=0.79 vs. 0.16).

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

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

244 **Discussion**
245 Our analyses reveal the extent to which butterfly population abundance is predictable from
246 resource availability; at least within the selection of sites in our data set (Table 2, and
247 Figures 1, 2, and Tables S2, S3 for species specific results). Our results confirm the
248 importance of resource availability in determining population abundance and help define a
249 predictive basis for habitat quality. By characterizing the functional space (Butler & Norris
250 2013) of multiple butterfly species, our results inform the management options for declining
251 butterfly species.

252   In particular, we find that hostplant quantity explains a substantial portion of the
253 intersite variation in population abundance for species that are dietary and habitat
254 specialists. For species with these traits (notably *Cupido minimus, Aricia agestis,*
255 *Polyommatus bellargus*) the hostplant index explains more than one third of the intersite
256 variation in population density, but for others (e.g. *Maniola jurtina, Ochlodes sylvanus*) the
257 two are uncorrelated (Figure 1, Table S2). The findings have direct implications for the
258 management of butterflies sharing these traits, many of which are of conservation concern.

259 That our results were broadly in line with predictions highlights the value of ecological
260 theory in applied conservation management (Doak & Mills 1994; see also Dapporto &
261 Dennis 2013).

262   Principally, our results underscore the importance of maximizing hostplant
263 abundance within occupied sites. This evidence is based on a large sample size along two
264 axes of variation – both between and within species – and spans a large range of values for
265 both butterfly population density and hostplant abundance. Indeed, it is possible that these
266 results contrast with fine-scale studies (Thomas 1983; Kelly & Debinski 1998; Rabasa *et al.*
267 2008) because of differences in the range of variation in hostplant abundance. However,
268 many of the sites are managed specifically for butterflies and so a high percentage of
269 hostplants are likely to be in suitable condition, such that simple measures like percentage
270 cover more accurately reflect the food resources available to butterfly larvae. A priority for
271 future research is to establish whether our findings are generalizable across habitat types
272 without explicit consideration of hostplant suitability (Dennis 2010).

273   The strength of the relationship between the nectar index and butterfly abundance,
274 although weaker than the matching hostplant relationship, is surprisingly strong on several
275 grounds. For one thing, associations between butterflies and nectar sources are recorded
276 far less reliably than hostplants: the former are mostly casual observations, biased towards
277 gardens, whereas the latter have been validated using rearing experiments (Hardy *et al.*
278 2007). Second, our nectar index is a crude sum of the percentage cover across plant species
279 recorded as nectar sources: a better measure would have been the number of florets
280 produced during the adult flight period. Thirdly, most butterflies reproduce within a few
281 days of emerging as adults (Cushman *et al.* 1994; Wahlberg 1995), such that abundant
282 nectar is likely to be of limited benefit to fecundity and recruitment. Fourth, previous work
283 on butterfly population dynamics has suggested that survival is primarily determined by
284 nutrients acquired during larval development (i.e. hostplants) (Labine 1968; Baylis & Pierce
285 1991; Hughes 2000), but that adult diet (i.e. nectar) can influence fecundity (Boggs &
286 Freeman 2005). For these reasons we are cautious about overstating the role of nectar
287 availability in butterfly carrying capacity. However, our results emphasize that the
288 possibility of nectar availability should remain a key area of research in butterfly
289 conservation biology (Tudor *et al.* 2004; Wallisdevries *et al.* 2012).

290   Furthermore, we recognize more general limitations to this study. Our vegetation

291   surveys recorded only a snapshot of the resource availability, and do not account for

292   seasonal variation. Our conversion of plant cover scores into indices of nectar and hostplant

293   availability do not consider feeding preferences when multiple food sources are available,

294   highlighting the complexities of managing for generalist species (Finlay-Doney & Walter

295   2012). Incorporating this sort of information would improve the predictive power of our

296   models. However, these limitations reflect the trade-off between macroecological

297   generalization and microecological detail: our study is unusual in combining a broad spatial

298   extent and large number of species with fine-grained information about individual

299   populations (Beck et al. 2012). Given the uncertainties in our data set, it is perhaps

300   surprising that we were able to make such clear inferences about the food–abundance

301   relationship.

302   Despite the obvious theoretical link between food and abundance, there have been

303   few other studies providing spatially-explicit quantitative evidence of a correlation. The

304   food–abundance relationship has been previously demonstrated in birds (Lack 1954) and

305   mammals (Carbone & Gittleman 2002; Prevedello et al. 2013). The relationship has

306   previously been tested in butterflies, with mixed results (Gutierrez & Menendez 1995;

307   Hughes 2000; Kuussaari et al. 2000; Cowley et al. 2001). Our finding that the hostplant–

308   abundance relationship is mediated by species traits (and site aspect) could explain why

309   single-species studies often find weak or nonsignificant correlations (Thomas et al. 2011).

310   The development of a trait-based framework allows us to predict how species will

311   respond to changes in food availability. Although some of these traits are intercorrelated,

312   the patterns that emerge give some insights into the ecological mechanisms linking resource

313   availability with population abundance (Ockinger et al. 2010; Sekar 2011). In this study,

314   species which have narrower dietary niche breadth (as both larvae and adults) and low

315   mobility are more sensitive to changes in hostplant abundance (Dapporto & Dennis 2013).

316   These traits are all indicative of a strong ecological interaction between the butterfly and

317   hostplant, with individual butterflies completing their entire life cycle in a restricted area,

318   hence the strength of the statistical relationship linking plant and butterfly abundance. By

319   contrast, individual butterflies in species with the opposite set of traits (polyphagy and

320   mobility) experience only weak interactions with the plant population on which they fed as

321 larvae (Dennis *et al.* 2014). Polyphagy allows adult butterflies to select oviposition sites from

322 a range of hostplant species; mobility allows butterflies to travel between habitat patches in

323 order to reproduce. The importance of these mechanisms implies that tight correlations

324 between the abundance of species at different trophic levels are likely to be found in other

325 systems where interspecific interactions are strong (e.g. host–parasitoid interactions).

326   A trait-based framework also has important ramifications for conservation (Daily

327 2001), as it allows land managers to predict how different species will respond to alternative

328 management strategies. Species with few hostplants and low mobility could benefit from

329 targeted management to increase carrying capacity by managing for the abundance of their

330 hostplants (Dennis *et al.* 2013). Given that some of the most rapidly declining butterfly

331 species possess several of these traits (Fox *et al.* 2011b), our results are positive for

332 conservation: the species that will benefit most from targeted management are also the

333 ones for which intervention is most needed. Indeed, increasing the resource base within

334 sites has been observed to have a positive impact on many of the UK's rarest butterflies at

335 the landscape scale (Ellis *et al.* 2012).

336   Aspect has a strong negative interaction with hostplants suggesting that populations

337 inhabiting sites with cooler aspects (e.g. more north-facing), are more sensitive to variation

338 in hostplant abundance. This does not mean that north-facing slopes harbour more

339 abundant butterfly populations, but rather that a unit change in our hostplant index has a

340 larger effect on butterfly abundance on a north-facing slope than on a south-facing one,

341 with other slopes intermediate. Temperature is a key driver of whether a hostplant is in a

342 suitable condition (Thomas 1983; Renwick & Chew 1994), and aspect is an important factor

343 determining temperature (Bennie *et al.* 2008). Therefore aspect is a strong determinant of

344 the thermal microclimate: on south-facing slopes the majority of plants are likely to be

345 within a suitable microclimate for the development of butterfly larvae. Our result implies

346 that management of hostplants is likely to have a greater impact on carrying capacity in

347 cooler microclimates (north-facing slopes). However, our data set contains relatively few

348 north-facing sites, so further research is required to explore whether this is a general

349 phenomenon, or whether it is specific to a small number of highly thermophilous butterfly

350 species on a small number of sites.

351　Our key finding has been that abundance is predictable for species with strong interactions

352　with their hostplant e.g. monophagous species. This predictability makes it possible, for

353　some species, to estimate carrying capacity without counting the organisms. Vegetation

354　surveys can be conducted within a single day to provide estimates for multiple species with

355　different characteristic phenology, rather than repeated surveys over several months. One

356　might envisage a hostplant count being used to supplement low-effort insect surveys

357　(Brereton *et al.* 2011), or in situations where a dedicated workforce of volunteer surveyors

358　is not available. Data on resource availability, where measureable, could therefore provide

359　useful information for the conservation management of any population where interactions

360　across trophic levels are strong.

Data accessibility

368　Vegetation abundance data is available from the NERC Environmental Information Data Centre:

369　doi: 10.5285/ca34e25b-6138-4b72-b32c-778d762118f1. The derived dataset used for statistical

370　analysis is available from Figshare: doi: 10.6084/m9.figshare.1494733.

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

646

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Figures

649

650   Figure 1. A scatterplot of population density against the hostplant index for 27 butterfly species on 54

651   UKBMS sites. Population density was estimated as the average during 2006–2010; the hostplant data was

652   collected from the same sites recorded during 2008–2009.

653

654   Figure 2. A scatterplot of population density against the nectar index for 27 butterfly species on 54

655   UKBMS sites. Population density was estimated as the average during 2006–2010; the nectar data was

656   collected from the same sites recorded during 2008–2009.

657

658   Table 1. Description of diet breadth, life-history and site traits

659

Trait	Measure	Definition	Source
Diet breadth			
Larval niche breadth	Number of larval Core Host Plants (CHP)	Records of only main host plants including prominent regional ones	Dennis (2010)
Adult niche breadth	Degree of adult nectar specialism (RanS)	Monte Carlo estimated number of nectar sources (from mean number of nectar sources per 100 records)	Hardy *et al* (2007)
Life history traits			
Habitat specialist	Degree of adult habitat specialism	Habitat preferences as wider countryside species and migrants or specialists restricted to specific habitats	Botham *et al* (2009)
Mobility	Degree of dispersal capabilities	Dispersal capabilities (1-9, low to high)	Dennis *et al* (2005)
Population structure	Measurement of colony structure	Defined as 'open' or 'closed' population (1-7, open to closed)	Warren *et al* (2001)
Larval duration	Duration of larval stage calculated from life history tables	Average number of days spent feeding on hostplant during March - October	Frowhawk (1934)
Site Traits			
Aspect	Aspect (to nearest five degrees)	A measure of ground orientation	This study

660

661   Table 2. Results of separate linear mixed models between the logarithmic geometric mean of density for

662   all 27 butterfly species recorded across 54 UKBMS sites during 2006–2010, against site and species traits

663   as: i) an interaction with hostplants and ii) an interaction with nectar. The results in the table are

664   therefore obtained from 10 separate models (5 for both nectar and hostplants) and the results of the

665   main effect have been omitted

666

Independent variable	i) Interaction with host plants				ii) Interaction with nectar plants			
	Estimate	Std. Error	t value	p value	Estimate	Std. Error	t value	p value
Diet breadth								
Larval niche breadth	-0.171	0.070	-2.463	0.014	-0.022	0.029	-0.766	0.444
Adult niche breadth	-0.010	0.003	-3.017	0.003	-0.003	0.004	-0.733	0.463
Life history traits								
Mobility	-0.315	0.081	-3.914	<0.001	-0.179	0.092	-1.945	0.052
Population structure	-0.004	0.018	-0.242	0.809	-0.055	0.061	-0.915	0.360
Site traits								
Aspect	-0.165	0.072	-2.273	0.023	-0.082	0.077	-1.066	0.286

667

Figure: Population Density (y-axis, log scale) versus Hostplant index (x-axis, log scale) for multiple butterfly species. Panels: Aglais urticae, Aphantopus hyperantus, Argynnis aglaja, Argynnis paphia, Aricia agestis, Callophrys rubi, Celastrina argiolus, Coenonympha pamphilus, Cupido minimus, Erynnis tages, Gonepteryx rhamni, Hesperia comma, Inachis io, Lasiommata megera, Lycaena phlaeas, Maniola jurtina, Melanargia galathea, Ochlodes sylvanus, Pararge aegeria, Polygonia c-album, Polyommatus bellargus, Polyommatus coridon, Polyommatus icarus, Pyrgus malvae, Pyronia tithonus, Thymelicus lineola, Thymelicus sylvestris.