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1 Butterfly abundance is determined by 2 food availability and is mediated by 3 species traits

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16

17 Running head:

18 Food availability determines butterfly abundance

19 Keywords: abundance, conservation, habitat quality, butterflies, macroecology, hostplant, nectar,
20 resources, species traits, UKBMS

21 Summary

- 22 1. Understanding the drivers of population abundance across species and sites is crucial
23 for effective conservation management. At present, we lack a framework for
24 predicting which sites are likely to support abundant butterfly communities.
- 25 2. We address this problem by exploring the determinants of abundance among 1111
26 populations of butterflies in the UK, spanning 27 species on 54 sites. Our general
27 hypothesis is that the availability of food resources is a strong predictor of
28 population abundance both within and between species, but that the relationship
29 varies systematically with species' traits.
- 30 3. We found strong positive correlations between butterfly abundance and the
31 availability of food resources. Our indices of hostplant and nectar are both significant
32 predictors of butterfly population density, but the relationship is strongest for
33 hostplants, which explain up to 36% of the intersite variance in abundance for some
34 species.
- 35 4. Among species, the hostplant–abundance relationship is mediated by butterfly
36 species traits. It is strongest among those species with narrow diet breadths, low
37 mobility and habitat specialists. Abundance for species with generalist diet and
38 habitat associations is uncorrelated with our hostplant index.
- 39 5. The hostplant–abundance relationship is more pronounced on sites with
40 predominantly north-facing slopes, suggesting a role for microclimate in mediating
41 resource availability.
- 42 6. *Synthesis and applications.* We have shown that simple measures can be used to
43 help understand patterns in abundance at large spatial scales. For some butterfly
44 species, population carrying capacity on occupied sites is predictable from
45 information about the vegetation composition. These results suggest that targeted
46 management to increase hostplant availability will translate into higher carrying
47 capacity. Among UK butterflies, the species that would benefit most from such
48 intervention have recently experienced steep declines in both abundance and
49 distribution. The hostplant–abundance relationship we have identified is likely to be
50 transferrable to other systems characterized by strong interspecific interactions
51 across trophic levels. This raises the possibility that the quality of habitat patches for
52 specialist species is estimable from rapid assessment of the hostplant resource.

53 **Introduction**

54 A key challenge for conservation biologists is to develop an evidence-based framework to
55 predict how species will respond to change in increasingly modified landscapes ([Sutherland](#)
56 [et al. 2004](#); [Evans et al. 2012](#)). To date, progress towards a predictive framework for
57 biodiversity has focussed on patterns at coarse spatial scales, such as how species
58 distributions might shift under climate change ([Thomas et al. 2004](#)) and the role of species'
59 traits in mediating response to change ([Webb et al. 2010](#)). Most applied conservation
60 management takes place on sites, i.e. at the population level, for which relatively little
61 evidence exists of predictable responses to change ([Cowlshaw et al. 2009](#); [Hanspach et al.](#)
62 [2012](#)). Even the factors driving large-scale variation in population abundance remain poorly
63 understood ([McGill 2008](#)). Thus, land managers and policymakers lack general rules for how
64 management interventions will impact on population sizes of target organisms ([Sutherland](#)
65 [& Freckleton 2012](#)).

66 Habitat quality has long been recognized as one of the fundamental determinants of
67 variation in abundance among populations of a single species ([Andrewartha & Birch 1954](#)),
68 yet quality has proven to be a difficult concept to define, especially across multiple species
69 ([Hodgson et al. 2009](#)). Quality might be defined in terms of food resources, since resource
70 supply sets an upper limit on carrying capacity ([Blackburn & Gaston 1999](#); [Brown et al.](#)
71 [2004](#)), and several studies on vertebrate populations have demonstrated strong
72 relationships between abundance and either edible biomass or habitat productivity ([Lack](#)
73 [1954](#); [Carbone & Gittleman 2002](#); [Pettoirelli et al. 2009](#)). For many invertebrates, eggs are
74 laid near to, directly on or inside the primary larval resource (the host). Thus, many studies
75 have shown strong correlations between the abundance of phytophagous insects and
76 biomass of the larval resource, the hostplant ([Dempster & Pollard 1981](#); [Strong et al. 1984](#);
77 [Marques et al. 2000](#)), although the strength of this relationship varies across both species
78 and sites ([New 2009](#)). The relationship between abundance and the availability of resources
79 for mobile life stages also varies, with strong positive relationships observed for some
80 insects ([Thomas 1991](#); [Holzschuh et al. 2013](#)), but with no consistent patterns across species
81 ([Thomas et al. 2011](#)).

82 Whilst the availability of resources is a necessary condition for a high-quality habitat ([Dennis](#)
83 [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-m² 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](https://doi.org/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*, *Satyrrium 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 ([Cowlshaw 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](#)).

219 **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 measurable, could therefore provide
359 useful information for the conservation management of any population where interactions
360 across trophic levels are strong.

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366 contributed data to the UKBMS.

367 **Data accessibility**

368 Vegetation abundance data is available from the NERC Environmental Information Data Centre:
369 [doi: 10.5285/ca34e25b-6138-4b72-b32c-778d762118f1](https://doi.org/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](https://doi.org/10.6084/m9.figshare.1494733).

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644 **Supporting Information**

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

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648 **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 <i>et al</i> (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 <i>et al</i> (2009)
Mobility	Degree of dispersal capabilities	Dispersal capabilities (1-9, low to high)	Dennis <i>et al</i> (2005)
Population structure	Measurement of colony structure	Defined as 'open' or 'closed' population (1-7, open to closed)	Warren <i>et al</i> (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



