

1 **Optimising trait and source selection for explaining occurrence**  
2 **and abundance changes: a case study using British Butterflies**

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14 Running head: Pitfalls of trait-based analyses

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## ABSTRACT

1. Functional traits that define the ecological role of an organism are increasingly being used to determine and predict responses to environmental change. Functional trait analyses of butterflies remain underexplored compared with other taxa, such as plants. Previous works using butterfly functional traits have not comprehensively addressed issues about the quality of trait data sets used and the relative predictive power of different trait types.
2. We compare the consistency of trait descriptions between six widely used trait sources for the British butterfly fauna. We analysed consistency of trait sources using Fleiss's kappa and ICC. PCA was used to produce species ordinations, comparing outputs to examine which trait sets were better at explaining recent species range and abundance changes within the UK.
3. There was a large range in congruence values for specific traits between sources. No single source can be relied upon to produce accurate trait information for British butterflies. Most trait sets are poor predictors of abundance and occurrence changes but are better at predicting current occurrence. An extensive trait set, supplementing biotope-related traits with explicit resource-based information recovers more informative ecological classifications and models than those primarily based on life-history traits or biotope descriptors. Smaller trait sets do, however, recover the specialist-generalist continuum.
4. We conclude that analyses of distribution and abundance changes that rely on traits are highly dependent on trait source and trait type. For butterflies, traits that are based on measures of biotope occupancy should be avoided in explaining changes of abundance and distribution. Including trait information that describes their resource requirements is essential for such analyses.

**Key-words:** butterfly biogeography, functional-traits, habitat, occurrence and abundance change, resource-use

## 40 INTRODUCTION

41 Functional traits are characteristics that define the ecological roles of organisms, including their  
42 interactions with other species (Díaz & Cabido, 2001). Functional trait-based studies of plant  
43 communities have revealed insights into plant strategies and tolerances of environmental conditions  
44 (e.g. Grime, 1977), invasion dynamics (e.g. Pyšek et al., 2015) and distribution changes (e.g. Powney,  
45 Giovanni, Preston, Purvis & Roy, 2014). Implicit to trait-based analyses is the understanding that  
46 identifying functional groups from shared traits will elucidate sets of species with shared responses to  
47 past, current and future climate and land-use changes and reveal the development of novel  
48 communities with environmental change. Trait-based analyses of animals are becoming common (e.g.  
49 Kotiaho, Kaitala, Komonin & Päivinen, 2005; Betzholtz, Pettersson, Ryrholm & Franzén, 2013; Luck,  
50 Carter & Smallbone, 2013), but tend to rely on small trait sets and do not consider intraspecific trait  
51 variation to the same extent as plant-based studies (e.g. Kichenin, Wardle, Peltzer, Morse, & Freschet,  
52 2013; Celis, Halpen & Jones, 2017). Theoretical work has suggested that including intraspecific  
53 variation is essential for addressing questions of community assembly (Siefert, et al., 2015) and such  
54 studies tend to use botanical systems as examples. The same theoretical framework is not applied to  
55 animal studies to the same extent, and not at all in those that use insects as model systems.

56 Butterflies respond rapidly to environmental change, being representative of wider trends in insect  
57 abundance (Thomas, 2005). Trait-based analyses of butterflies are relatively well established (e.g.  
58 Mattila, Kotiaho, Kaitala, Komonen & Päivinen, 2009) with commonly chosen traits including larval  
59 hostplant specificity, habitat/biotope breadth, flight period, body size and voltinism (e.g. Dennis et al.,  
60 2004; Kotiaho et al., 2005; Pöyry, Luoto, Heikkinen, Kuusaari & Saarinen, 2009; Betzholtz et al.,  
61 2013; Gallien, Altermatt, Wiemers, Schweiger & Zimmermann, 2017). Other analyses have used  
62 various measures of mobility as predictors of responses to environmental changes, such as mobility  
63 ranking based on mark-release-recapture studies (Warren et al., 2001) and expert opinion (Nilsson,  
64 Franzén, & Jönsson, 2008). Analyses that focus on resources and behaviours generally include many  
65 more parameters than those that focus on morphology, physiology or voltinism. For example,

66 Shreeve, Dennis, Roy and Moss (2001) used 145 character states (traits), independent of biotope  
67 occupancy, to identify relationships between trait sets and mobility, conservation status and  
68 distributions of UK butterflies; Pavlikova and Konvicka (2012) later expanded this approach to  
69 European macromoths.

70 Recently Moretti et al. (2016) provided a list of traits for terrestrial invertebrates applicable across  
71 taxa and measurable in a standardized way for individuals. In fact, it has been suggested that  
72 functional traits should be measured at the individual rather than population, community or ecosystem  
73 levels to avoid ambiguity about the mechanisms underlying community structure and ecosystem  
74 functioning (Violle et al., 2007). From this perspective, a series of traits commonly used for butterflies  
75 obtained from their distribution (e.g. range size, climatic niche characteristics; see Schweiger, Harpke,  
76 Wiemers & Settele, 2014)) or by defining the biotope(s) in which the species occur, cannot be  
77 considered as functional traits.

78 Reliable trait-based analyses require two main assumptions to be met. The first is that trait  
79 information is accurate and fully encompasses variation, both within and among species. Dennis,  
80 Hardy & Dapporto (2012) argued that trait data should be explicitly labelled temporally and spatially  
81 in order to account for variation; despite this, such explicit labelling is not common. Fitzsimmons  
82 (2013), working on Canadian butterfly species, showed that commonly used traits were not reported  
83 consistently across different literature sources. Traits with a generally low level of congruence  
84 between sources included overall habitat breadth, presence/absence in different habitat types and  
85 behavioural traits. This may indicate that individual trait sources do not report the full range of  
86 variation for these traits. European Lepidoptera are comparatively better studied than those of Canada;  
87 the UK in particular has an especially long history of field guides, reference works and, more recently,  
88 online resources for Lepidoptera (e.g. South, 1906; Frohawk, 193; Emmet & Heath, 1989; Asher et  
89 al., 2001, Eeles, 2016). Recent trait-based analyses (Curtis, Brereton, Dennis, Carbone & Isaacs,  
90 2015) conducted on the UK butterfly fauna have used works such as Dennis (2010) but consistency  
91 between trait sources, and thus the reliability of trait-based conclusions, remains unclear.

92 The second assumption of reliable trait-based analyses is that the adaptive response of species' traits  
93 to land-use and climate changes are fully understood. This depends on the relative plasticity of each  
94 trait, which is not commonly considered in trait-based studies. This second assumption is more  
95 intractable than the first, carrying a risk of circular reasoning. In Lepidopteran trait-based analyses of  
96 distribution changes, the main traits used are some measure of dispersal (often approximated by  
97 wingspan or more rarely by ratio of thorax width to forewing length) (Sekar, 2012; Gallien et al.,  
98 2017), larval hostplant specificity or number of hostplants used (Öckinger et al., 2010) and  
99 overwintering stage (Mattila et al., 2009). Some traits are logical descriptors of occurrence; Dennis et  
100 al. (2005) found a positive correlation between larval hostplant breadth and overall distribution for  
101 UK butterflies. Other traits can be more problematic. 'Habitat' is also a commonly used trait in many  
102 analyses; despite often lacking a precise definition in many studies (cf., Dennis, Shreeve & Van Dyck,  
103 2003; Dennis, Dapporto & Dover, 2014); there is a tendency to associate 'habitat' with loosely  
104 defined biotopes. If defined as a vegetation association, 'habitat' is not consistent with resource  
105 requirements, which are frequently more precise (e.g. woodland vegetation structures could include  
106 several overlapping resources). The association of species with habitats/biotopes becomes  
107 increasingly uncertain the more structurally complex the biotope and the greater the range of  
108 resources a species uses (Shreeve et al., 2001; Dennis et al., 2005; Vanreusel & Van Dyck, 2007).  
109 Resource distributions are not fixed in time and any measure of habitat used in trait-based studies  
110 should take this into account as species are expected to shift their vegetation associations in response  
111 to climate warming (Oliver, Hill, Thomas & Roy, 2009). Observed dietary breadth has also been  
112 known to shift in response to climate warming (Pateman, Hill, Roy, Fox, & Thomas, 2012) and  
113 mobility has equally been shown to be a variable trait. For instance, measured mobility potential has  
114 rapidly shifted in response to habitat fragmentation (Dennis, 1993; Shreeve, 1995; Hill, Thomas &  
115 Lewis, 1999) and is a selected response to previous and current landscape configurations (Dennis,  
116 1977; Shreeve & Dennis 2011; Dennis, Dapporto, Dover & Shreeve, 2013) rather than being  
117 invariant. As these traits have been used as predictors of responses to environmental change, whilst

118 also being affected by these changes, circular reasoning is a legitimate concern at least when trait  
119 plasticity is not considered.

120 To address these issues of trait reliability and their resulting predictive power we (i) examine the  
121 variability in trait information for British butterflies, (ii) determine the sensitivity of relationships  
122 between species occurrence and abundance and traits to the source of trait data, (iii) compare these  
123 relationships with those generated by randomly selected trait sets (iv) compare the sensitivity of trait-  
124 based analyses to the inclusion of different trait types, and (v) recommend how trait-based analyses of  
125 Lepidoptera could be improved to predict community responses more reliably to current and predicted  
126 environmental changes.

## 127 METHODS

### 128 *Species selection and data sources*

129 Fifty-six species of habitual current resident UK butterflies were selected for analysis. Following  
130 Fitzsimmons (2013), rare migrants and species described as ‘migrant’ were excluded; these latter  
131 comprise *Vanessa atalanta* (but see: Fox & Dennis, 2010), *Vanessa cardui* and *Colias* species.  
132 Species that may have a substantial migratory portion, but are generally considered to overwinter and  
133 breed in the UK (*Aglais* and *Pieris* species) were included. Trait sources were selected based on the  
134 following criteria: 1) containing information on all 56 resident UK species, and 2) were published  
135 recently or are currently in wide use. Five sources of non-resource-based trait information (four  
136 books: Emmet and Heath (1989); Asher et al. (2001); Thomas (2010); Newland, Still, Swash &  
137 Tomlinson (2015) and one online resource: Eeles (2016)) and one resource-based trait source (Dennis,  
138 2010) were selected.

139 The recent splitting of *Leptidea sinapsis* into a species pair (*Leptidea sinapis/juvernica* (Dincă,  
140 Lukhtanov, Talavera & Vila, 2011), is not reflected in all the sources used. In this case, where trait  
141 differences were noted by locality, only traits related to locations matching the currently known  
142 locality of *Leptidea sinapis* were used for coding. Species nomenclature used in this study follows

143 that used in Fauna Europaea (Karsholt & van Nieuwerkerken, 2016), except *Leptidea sinapis*, where we  
144 have followed Dincă et al. (2011).

#### 145 *Trait coding*

146 Data were collected and coded for 23 trait types, following Fitzsimmons (2013) and containing  
147 information on: biotope usage, behaviour, resource use, ecological niche and wingspan (Table 1).  
148 Biotope usage was coded using the European Nature Information System (EUNIS) habitat codes  
149 (Davies, Moss & Hill, 2004). When information on a trait was not provided by a source it was left  
150 blank. To minimise interpersonal bias, all coding was carried out by one author (JMW). Our species  
151 trait databases are available from the Dryad Digital Repository (Middleton Welling et al, 2018).

#### 152 *Data analyses*

153 Ordinal and categorical trait agreement between sources was measured using Fleiss's kappa and  
154 continuous trait agreement was measured using a two-way intraclass correlation coefficient (ICC).  
155 Kappa and ICC scores vary from -1 (complete disagreement) to 1 (complete agreement) with 0 being  
156 equivalent to the amount of agreement expected by chance. Kappa and ICC scores were generated  
157 using the 'irr' package (Gamer, Lemon, Fellows & Singh, 2012) in R (R Core Development team,  
158 2017)

159 In order to assess how trait source affected predictions of species responses to changing  
160 environmental conditions we performed PCA ordinations on data from the different trait sources ,  
161 with and then without biotope information, using the 'dudi.mix' function of 'Ade4' (Dray & Dufour,  
162 2007). Each PCA was performed on a correlation matrix scaled to unit variance. *Leptidea juvernica*  
163 was removed from the datasets (where present) so that all data sources were comparable. The number  
164 of components extracted in each PCA was determined by extracting those components with  
165 eigenvalues > 1. The 'protest' function in the 'vegan' package (Oksanen et al., 2016), returning a  
166 statistic which measured the level of correlation between two matrices, was used to test the degree of  
167 concordance between all the PCA outputs, both with and without biotope information.

168 Trait codings for the PCA analyses were the same as for the Kappa statistics, except when missing  
169 data would lead to biologically nonsensical results. Mate-locating method was coded as two separate  
170 traits - perching and patrolling. Myrmecophily was removed from the trait list because this  
171 information was absent in most sources, including for those species known to have some association  
172 with ants. Hilltopping, flight month information and wingspan were also removed as these variables  
173 are not present in all trait sources. Any remaining missing data within sources were assigned the  
174 average values of particular traits for that source.

175 Fifty random datasets (null models) were generated in R in order to compare the explanatory power of  
176 the different trait sources to randomly assembled trait sets. We first calculated the number of  
177 occurrences of each trait state using all the data sets. We then randomly sampled from these trait  
178 distributions to generate each random species x trait matrix. Random datasets were used to generate  
179 PCAs using the methods described for the source data.

180 To determine the explanatory power of each trait set the PCA case scores produced for each trait  
181 source were regressed against the seven metrics provided in the State of the UK's Butterflies 2015  
182 (Fox et al. 2015). These were: the number of 10km, 1km squares and UKBMS sites occupied in 2014,  
183 and long-term (1976-2014) and short term (2005-2014) percentage occurrence and percentage  
184 abundance changes. This information is the most recent publically available assessment of short term  
185 and long term butterfly trends for the whole UK butterfly fauna. The PCA case scores were also  
186 regressed against 'colonfac', a commonly used measure of generalism (Dapporto & Dennis, 2013),  
187 for all trait sources that exclude biotope associations. The colonfac scores for all species were taken  
188 from Dapporto and Dennis (2013: Table A1). Colonfac measures species generalism by quantifying  
189 resource breadth; a higher value indicates an increased ability to exploit a hypothetical vacant patch.  
190 Dependent variables were normalised using min-max normalisation. Regressions were conducted  
191 using a generalized linear model (GLM) with quasibinomial error function and a logit link function.  
192 Model assumptions were assessed by examining the normality of the residuals and the linearity of the  
193 Q-Q plots. The first six components extracted using the PCA were initially all included as co-



194 predictors. Two sets of models were built, one set with biotope information included and one set  
195 where it was excluded. Models were compared using log-likelihood values and the best models were  
196 retained. Factor scores underlying the principal components were compared in order to see whether  
197 the variables that were correlated with particular principle components were analogous between  
198 sources.

199 To test which trait types correlate most strongly with abundance and occurrence change we repeated  
200 the analysis using the dataset from Dennis (2010). We split traits into three types; ‘life-history traits’,  
201 ‘biotope traits’ and ‘resource-specific traits’. Life-history traits are those that define the life-history  
202 strategy of a particular species, by either affecting the reproductive output or relative investment in  
203 particular life-history stages. Biotope traits describe the biotope in which a species is commonly  
204 found. Resource-specific traits define consumables that a species uses either as a larva or adult, or a  
205 utility that a species uses as part of a behaviour but does not consume. We carried out the same  
206 analysis as on the more restricted trait sets; we produced PCAs for each trait set and then correlated  
207 the components with the measures of conservation status given in Fox et al. (2015). We then used the  
208 same model structure and simplification procedure as with the more restricted trait sets. The analyses  
209 were carried out on life-history traits alone, with life-history traits in combination with either biotope  
210 or resource specific traits and with the full trait set. We compared the ordinations produced by the  
211 different trait combinations using the ‘protest’ function in the ‘vegan’ package (Oksanen et al., 2016).

## 212 RESULTS

### 213 *Intra-source trait consistency*

214 Inconsistencies were found between sources for all traits. In particular, these may be caused by the  
215 lack of coverage of behavioural data in some sources and difficulty in applying EUNIS habitat criteria  
216 to sources that used unclear habitat terminology. These behavioural and habitat traits were therefore  
217 often the most inconsistent (Table 2). In comparison, basic life-history information (viz., number of

218 generations, overwintering stage and size) was available for all species and was the most consistently  
219 described. In general the extent of agreement varied widely between both sources and traits.

#### 220 *Multivariate analysis*

221 When biotope type and breadth were included in the analyses, the first component consistently  
222 explained 20-28% of the variation (see Table S1A in Supporting Information) and represented a  
223 continuum from biotope specialism to generalism; biotope total (i.e. the total number of EUNIS  
224 biotope categories that a species was recorded as utilising) was a contributing trait for all datasets. The  
225 contributions of other trait types to the first and other components were inconsistent between trait  
226 sources (see Table S2A). With biotope excluded, the first component explained 26-30% of the  
227 variation (see Table S1B) with overwintering stage, hostplant specialism and number and generation  
228 number being the most important traits. Overall, the contributions of all the underlying variables  
229 (identified from the factor scores) differed between datasets, especially for the more minor  
230 components (see Table S2B).

231 The Protest analysis indicates that the PCAs of each source are significantly correlated with each  
232 other, but there is evidence that each ordination is marginally different (Table 3). The random datasets  
233 were more different from the real datasets than the real datasets were from each other. Principal  
234 component analysis of data from Dennis (2010) produces an ordination that is primarily explained by  
235 resources used by all life cycle stages and adult behaviour (Table S4).

#### 236 *Does biotope improve correlation with change of status?*

237 With biotope included, the best models produced by all six trait sources were highly correlated (p  
238 <0.001) with all three of the measures of current occurrence from Fox et al. (2015). This is largely due  
239 to the first component being highly correlated with current occurrence (see Table S3A). Half of the  
240 sources also produced a model that was significantly correlated with long term occurrence change (p  
241 <0.05 ) although the components that were included in the best model varied (see Table S3A) and  
242 there are differences in the contributing traits (see Table S3A). With biotope occupancy included, four

243 sources: Emmet and Heath (1989), Asher (2001) Thomas (2010), Newland et al. (2015) and Eeles  
244 (2016) produced models that were significantly correlated with long term abundance change ( $p$   
245  $<0.05$ ). These models all included the first component as a significant predictor but otherwise varied  
246 in their composition (see Table S3B) and explanatory power (see Table 4). No trait source produced  
247 models that were significantly correlated with short-term occurrence changes. Most of the  
248 relationships produced from the restricted trait sources are either weaker or not significant when  
249 biotope is excluded and models tend to include fewer components. There are two notable instances  
250 where there is a more significant correlation when biotope is excluded: both Thomas (2010) and  
251 Newland et al. (2015) include a component related to long-term occurrence change ( $p < 0.01$ ).  
252 Although this was more significant than when biotope was included the component involved  
253 (component 6) was minor, explaining 7.5% of the total variation (Newland et al., 2015) and 6% for  
254 Thomas (2010). For all trait sources the first component was also significantly related to the  
255 ‘colonfac’ scores ( $p < 0.001$  in all cases) of Dapporto and Dennis (2013).

#### 256 *Comparing trait types*

257 The models produced by the various permutations of the Dennis (2010) dataset generally mirrored  
258 those produced by the trait sources that used a more restricted set of traits. All of the trait subsets  
259 derived from Dennis (2010) produced a model that was significantly correlated ( $p < 0.001$ ) with all  
260 three measures of current occurrence (Table 4) from Fox et al. (2015). These models included either  
261 the first (for life-history alone and life-history and biotope traits) or the second component (for life-  
262 history and resource based traits and all traits) being significantly correlated with current abundance.  
263 Unlike the trait sources based on more restricted traits, most of the trait subsets of Dennis (2010)  
264 failed to produce a model that significantly correlated with long-term occurrence changes. The only  
265 subset to do so comprised life-history and biotope traits (Table 4). In this case the third and the fourth  
266 components were significantly correlated ( $p < 0.01$  to  $p < 0.05$ ) with long-term occurrence changes.  
267 All subsets of the traits from Dennis (2010) produced models that contained a component that was  
268 significantly correlated ( $p < 0.05$ ) with short term abundance changes. For the trait set containing only

269 life history traits this was the seventh component but for all other subsets this was the first component.  
270 None of the subsets of the trait data in Dennis (2010) produced models that were significantly  
271 correlated with long-term abundance change. With all traits included the first component separated  
272 species on the basis of voltinism (univoltine vs multivoltine) and overwintering stage (Table S4 &  
273 Figure 1A). With life-history and just biotope it becomes more challenging to see ecologically  
274 relevant relationships (see Table S4 & Figure 1B). With life-history and resource traits only, the first  
275 components separate species depending on whether they use arboreal structures (shrubs and trees)  
276 extensively during their life cycle vs species that primarily use grass and herbaceous structures (Table  
277 S4 and compare Figures 1A and 1C). The second component separated species of xeric grassland  
278 (typically Lycaenids) from generalist grassland species and those that are adapted to ruderal hostplants  
279 (typically Pieridae and *Aglais* species).

## 280 DISCUSSION

### 281 *Key results*

282 There is a significant disagreement in trait values between trait sources. The level of disagreement is  
283 similar to that reported for Canada which has a less studied butterfly fauna. The trait sources are more  
284 similar to each other than randomly generated trait sets and in general are highly co-correlated.  
285 Disagreement between trait sources is especially apparent for biotope descriptions. In general, most  
286 sources provide trait values that are adequate at explaining current occurrence but are not effective at  
287 explaining occurrence and abundance change over time. When comparing different trait types it is  
288 apparent that models are generally improved by including either biotope or resource based traits in  
289 addition to those that explain life-history. We recommend using more than one trait source to capture  
290 the full range of trait variation and to include as many traits as possible, at least during any initial  
291 analysis.

### 292 *Congruence and variation within traits*

293 A large range in congruence values for specific traits occurs between data sources. These were highest  
294 for traits relating to wingspan, overwintering stage and voltinism and lowest for traits relating to  
295 habitat preference and the adult behaviours of mudpuddling and hilltopping. All data sets tended to  
296 agree on perching and patrolling mate-locating strategy when this was present. Despite high levels of  
297 discordance being present for some traits, the different sources were more similar to each other than to  
298 randomly generated trait sets (Table 3). This indicates that the trait discordance does not obscure the  
299 broad differences between species present in the UK fauna.

300 The low levels of agreement found for traits describing habitat type are primarily due to inconsistent  
301 or imprecise descriptions in some trait sources. Some species have well characterised vegetation type  
302 associations (e.g. *Erebia epiphron* for *Nardus* grassland) (Emmet & Heath, 1989; Newland et al.,  
303 2015), but species occurring in a wide range of biotopes (e.g. *Pieris* and *Aglais* species) may be  
304 described as simply 'widespread' (e.g. Emmet & Heath, 1989). In such cases the level of detail is not  
305 suitable for quantitative analysis and subjective wording can lead to divergent coding and poor  
306 congruence amongst sources.

307 Adult behavioural traits such as mudpuddling and hilltopping had low congruence values and  
308 contained large amounts of missing data. Behavioural trait data is only currently being aggregated  
309 (e.g. Dennis et al., 2014) with Dennis (2010) giving the most comprehensive set of behavioural  
310 information. Highly congruent data types - wingspan, voltinism and overwintering stage - are either  
311 traits that have been well-documented from the early 20<sup>th</sup> century (e.g. South, 1906; Frohawk 1934) or  
312 the data have been repeated from one or more sources, most likely from Emmet and Heath (1989).  
313 Whilst this has led to consistency it does not follow that they are accurate, especially if the traits are  
314 spatially and temporally variable.

315 Unlike Fitzsimmons (2013) we chose to not weight some characteristics, making no *a priori* decisions  
316 about the relative importance of particular traits or the reliability of the information. Despite this, our  
317 conclusions are similar; the lowest congruence occurs in those traits that need direct field observation  
318 (e.g. adult behavioural characteristics). It is surprising that data from Britain and Canada share this

319 trend, given the long history of butterfly ecology literature in the British Isles, the limited size of its  
320 fauna (c.56 species cf. 263 for Canada) and publication of the first guide to Canadian butterflies being  
321 relatively recent (Layberry, Hall & Lafontaine, 1998).

322 Disagreement between trait sources suggests that variation in trait values within species is not  
323 adequately described by any of the sources (e.g. voltinism may be more geographically variable than  
324 previously assumed). Although the expectation is that trait variation between species will increase  
325 with the number of species, our analysis produced similar Kappa values to Fitzsimmons (2013),  
326 which used a much larger number of species. Our results support those of Fitzsimmons (2013), who  
327 suggested that measures of inter-source concordance should be included in analyses and reliance on  
328 single sources should be avoided. Further work into the variability *within* traits, both temporally and  
329 spatially, will help determine how much is caused by real error rather than an underestimate of  
330 underlying variation.

### 331 *The relationships between different traits*

332 For each data source the first principal component separated species that were found across many  
333 habitats (habitat generalists) from those found in few (habitat specialists). The relationship between  
334 this first principal component and the ‘colonfac’ measure (Dapporto & Dennis, 2013) indicates that  
335 this component represents some aspect of the specialist-generalist continuum. The first or third  
336 components derived from each trait source are primarily related to the degree of hostplant specialism.  
337 Hostplant specificity has long been regarded as an important indicator of overall 'generalism'  
338 (Wiklund, 1981; Carnicer, Stefanescu, Vila, Dincă, Font & Peñuelas, 2013; Eskildsen, Carvalhiero,  
339 Kissling, Biesmeijer, Schweiger & Høye, 2015), and relates to distribution status (Dennis et al., 2004,  
340 2005; Carnicer et al., 2013), although there are widespread ubiquitous species that use single host-  
341 plant species (e.g. *Aglais urticae* and *A. io*). Also for some species, hostplant specificity varies within  
342 geographic range (e.g. *Callophrys rubi* (Dennis, 1992)). The second extracted component is generally  
343 related to voltinism, also proposed as another important explanatory trait (Carnicer et al., 2013;  
344 Dapporto & Dennis, 2013; Dennis, Hardy & Dapporto, 2015) as it can be used as a measure of

345 mobility, being a proxy for flight period duration. However, it is not commonly included as part of the  
346 specialism/generalism continuum (Bartonova, Benes & Konvicka, 2014).

347 *Selecting ‘good’ traits - moving away from biotopes and towards resources*

348 In comparing the models produced using different trait types it is apparent that adding either biotope  
349 or resource traits (either separately or in combination) helps to simplify the models produced but does  
350 not increase their explanatory power; fewer components are returned in the best models as the number  
351 of traits included is increased. For example, when only life-history traits are included, there are seven  
352 components that each explain more than 5% of total variation; this is reduced to five components  
353 when all the traits are included. Our results closely match those of Shreeve et al. (2001) who used an  
354 earlier version of Dennis’ (2010) database employed in this study. Like Shreeve et al. (2001) we  
355 found that when we included the full dataset the first component primarily separated species into a  
356 continuum from species associated with arboreal structures, typical of forest and shrubland biotopes  
357 to species that occupied what would be typically described as grassland biotopes. This relationship  
358 was recoverable without including biotope as an original variable, which shows that ecologically  
359 relevant information can be revealed without the risk of circular reasoning that biotope traits  
360 inevitably introduce into any trait-based analysis. The overall results indicate that if information  
361 about complex traits is collected, the explained variation becomes greater and potentially of more  
362 value for practical conservation. One common criticism of trait-based studies is that their conclusions  
363 are often ambiguous and difficult to translate into practical conservation policy (Cardillo & Meijaard,  
364 2012). Our results indicate that it is possible to link species responses to environmental change using  
365 detailed traits and for these traits to produce components that explain ecologically meaningful  
366 groupings. Resource-based traits as used here and by Shreeve et al. (2001), can be used to determine  
367 how groups of species are likely to respond to management practices, whereas imprecise descriptors  
368 such as ‘woodland’ do not indicate which components of that biotope are important. Thus biotope  
369 occupancy, often used as a trait to explain changes of butterfly abundance and distribution, is only of  
370 marginal use in explaining changes of status. It primarily explains this status change as a function of

371 the status of the biotope without identifying interactions of species with resource distributions and  
372 abundance. The responses of species within any biotope to management, landscape and climate  
373 changes will therefore be unique as the occurrence and quality of individual species' resource sets will  
374 respond individually to changing conditions.

#### 375 *Comparisons with previous work*

376 Recent works, (e.g. Pöyry et al., 2008; Diamond, Frame, Martin & Buckley, 2011; ESKILDSEN et al.,  
377 2015) generally use a narrower range of traits than either our study or the studies of Dennis and  
378 colleagues. Whilst simple relationships between traits can be extracted from limited trait sets there is a  
379 risk of oversimplification, especially if traits are treated as being invariant. We have found that trait  
380 information varies considerably between sources, so it is unwise to select individual traits and treat  
381 them as fixed values especially over the long time scales that are necessary for effective conservation  
382 (e.g. ESKILDSEN et al., 2015).

#### 383 *Trait selection for conservation*

384 Although limited trait sets were reasonably good at explaining some recent changes of abundance and  
385 occurrence, the reliance on biotope or vegetation association descriptors in trait-based analyses has an  
386 inherent risk despite these traits increasing the overall explanatory power of the analyses. Recent  
387 increases in global temperatures are relatively modest in comparison to future projections (IPCC,  
388 2014). Vegetation associations are expected to change in response, with potentially more fundamental  
389 changes in microhabitat structure and microclimate. It is unlikely that current vegetation associations  
390 are analogous to those from the early Holocene or earlier (Dennis & Shreeve, 1988) and equally no  
391 assumption should be made about future associations (Vera, 2000). Previous studies have shown that  
392 if the right traits are chosen, biotope traits are not necessary to predict meaningful relationships with  
393 environmental change (WallisDeVries, 2014). Additionally, biotope occupancy-based traits are likely  
394 to have decreasing predictive power over long time scales and trait-based analyses should focus on  
395 traits that govern specific vegetation and physical structure usage and describe resource use, rather



396 than relying on the interaction of these resource requirements with current vegetation structures, i.e.  
397 current biotope associations.

398 In conclusion, we recommend that wherever possible, trait-based analyses should be focused  
399 explicitly on a resource-based view of traits, especially when aiming to investigate complex inter-  
400 species and species-environment relationships. Trait over-splitting should be avoided, and a rigorous  
401 analysis of inter-trait correlations should be performed prior to any analyses. Conservation actions and  
402 biogeographic appraisals should rely on finely audited resource usage traits that are ideally spatially  
403 and temporally explicit. For many European taxa, this level of trait information is not collated but  
404 much exist in the literature. A promising amount of data has been gathered for UK Lepidoptera using  
405 UKBMS transects (Curtis et al., 2015), with which the role of traits in species distributions and  
406 abundances can be tested. In recent years, other European countries have started similar projects and  
407 we argue that for butterflies the construction of a Europe-wide trait-database should be a priority for  
408 future research. Our analyses are based on the UK butterflies which may have more restricted niche  
409 dimensions and trait states in comparison to their potential trait states in mainland Europe. A  
410 European trait-database has the potential to address the issue of the effects of trait plasticity on species  
411 responses to environmental changes. Outside of Europe and North America detailed trait information  
412 may not currently exist, although we believe that information on the Lepidoptera may not be as sparse  
413 as for other groups.

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#### 418 AUTHORS' CONTRIBUTIONS

419 The concept was designed by JMW, TGS and RAW and refined by RLHD and LD. All authors  
420 refined the analyses and contributed equally to the drafting and revisions of the article.

421 DATA ACCESSIBILITY

422 Data deposited in the Dryad Digital Repository: <http://doi.org/10.5061/dryad.017vp2q>, (Middleton  
423 Welling et al. 2018)

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624

625 SUPPORTING INFORMATION

626

627 Additional supporting information may be found in the online version of this article.

628 Table S1. Eigenvalues and explained variance of PCAs using species x trait values from six trait  
629 sources A) with and B) without biotope information

630 Table S2 Beta coefficients of PCA loadings from six trait sources, A) with and B) without biotope  
631 information

632 Table S3 Summary of the results of the best generalised linear models relating principal components  
633 to changes of abundance and distribution from six data sources.

634 Table S4 The major traits contributing to the PCA ordination of UK butterflies, using different  
635 combinations of life-history, resource-use and biotope occupancy, from data in Dennis (2010).

636

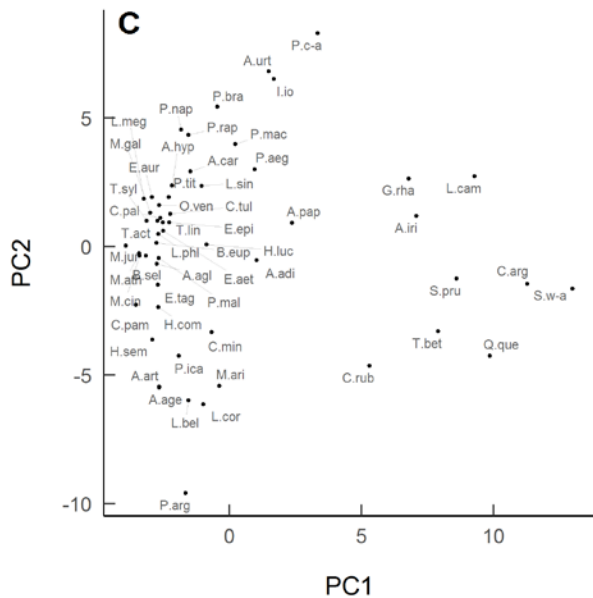
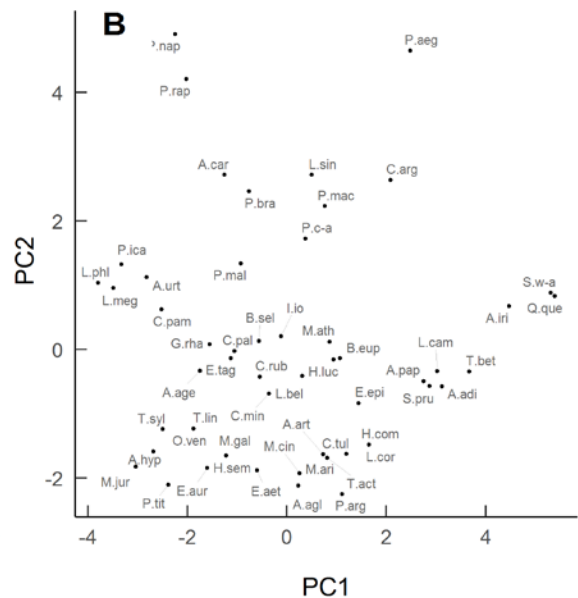
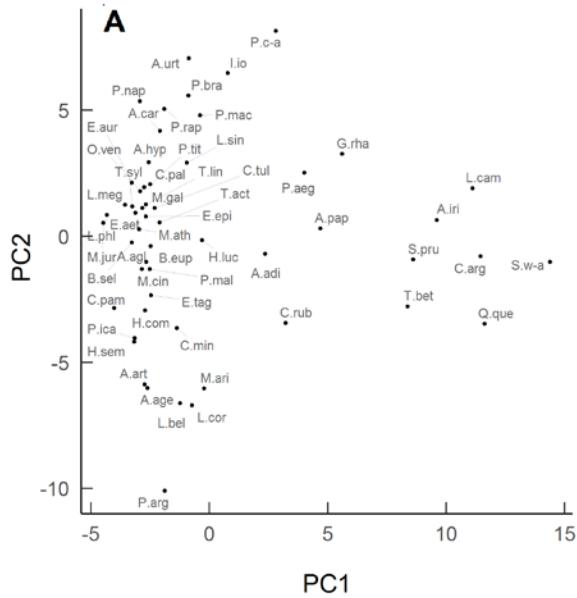
637 Figure Legend

638

639 Figure 1 PCA plots produced from data in Dennis (2010) comparing different trait sets A) with life-  
640 history , biotope and resource traits, B) with life-history and biotope and C) with life-history and  
641 resource traits.

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T.syl – *Thymelicus sylvestris*; T.Lin – *Thymelicus lineola*; T.act – *Thymelicus acteon*; H.com – *Hesperia comma*; O.syl – *Ochlodes sylvanus*; C.pal – *Carterocephalus palaemon*; P.mal – *Pyrgus malvae*; E.tag – *Erynnis tages*; G.rha – *Gonepteryx rhamni*; P.bra – *Pieris brassicae*; P.rap – *Pieris rapae*; P.nap – *Pieris napi*; A. car – *Anthocharis cardamines*; L. sin – *Leptidea sinapis* – P.mac – *Papilio machaon*; C.rub – *Callophrys rubi*; T.bet – *Thecla betulae*; S.pru – *Satyrrium pruni*; S.w-a – *Satyrrium w-album*; N.que – *Neozephyrus quercus*; C.arg – *Celastrina argiolus*; C.min – *Cupido minimus*; A.age – *Aricia agestis*; A.art – *Aricia artaxerxes*; P.arg – *Plebeius argus*; P.ica – *Polyommatus icarus*; P.bel – *Polyommatus bellargus*; P.cor – *Polyommatus coridon*; M.ari – *Maculinea arion*; L.phl – *Lycaena phlaeas*; H.luc – *Hamearis lucina*; M.ath – *Melitaea cinxia*; B.sel – *Boloria selene*; B.eup – *Boloria euphrosyne*; A.adi – *Argynnis adippe*; A.agl – *Argynnis aglaja*; A.pap – *Argynnis paphia*; L.cam – *Ladoga camilla*; A.iri – *Apatura iris*; A.urt – *Aglais urticae*; I.io – *Inachis io*; P.c-a – *Polygona c-album*; M.gal – *Melanargia galathea*; P.aeg – *Pararge aegeria*; L.meg – *Lasiommata megera*; H.sem – *Hipparchia semele*; P.tit – *Pyronia tithonus*; M.jur – *Maniola jurtina*; A.hyp – *Aphantopus hyperatus*; E.epi – *Erebia epiphron*; E.aet – *Erebia aethiops*; C.pam – *Coenonympha pamphilus*; C.tul – *Coenonympha tullia*

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Table 1. Traits used in analysis of congruence between UK butterfly trait source data and in the ordination of species.

Trait type <sup>1</sup>	Data type	Source availability <sup>2</sup>	Number of species compared	Possible trait states
Myrmecophily	Categorical	All	16	0/1
Biotope use (Nine variables)	Categorical	All	55	0/1 for each biotope
Hilltopping	Categorical	All	25	0/1
Mate choice strategy	Categorical	All	25	1/2/3
Mudpuddling	Categorical	All	33	0/1
Overwintering stage	Categorical	All	53	1/2/3/4
Patrolling	Categorical	All	25	0/1
Perching	Categorical	All	25	0/1
Hostplant number	Continuous	All	55	Continuous
Wingspan (average)	Continuous	1,4,5	55	Continuous
Wingspan (max)	Continuous	1,4,5	55	Continuous
Wingspan (min)	Continuous	1,4,5	55	Continuous
Flight period start month	Ordinal	1-5	53	1-12
Flight period end month	Ordinal	1-5	53	1-12
Max. no. of generations	Ordinal	All	55	1-3
Min. no. of generations	Ordinal	All	55	0.5-3
Number of biotopes occupied	Ordinal	All	55	1-8
Hostplant specificity	Ordinal	All	55	1-5

648 1. Trait type: *Myrmecophily*: larval and/or pupal association with ants. *Hilltopping*: assembling at hilltops as part of mating  
649 strategy. *Mate searching strategy*: 1 - perching, 2 - patrolling and 3 - perching and patrolling. For PCA analysis only, mate  
650 location coded as two binary traits: *Perching* and *Patrolling*. *Mudpuddling*: adults feeding from puddles/ damp patches.  
651 *Overwintering stage*: 1 – egg, 2 – larva, 3 – pupa, 4 - adult (with multiple overwintering stages the earliest stage was scored).  
652 *Hostplant number*: maximum number of plant species used. *Wingspan*: wing length from base to tip (mm), coded as mean,  
653 maximum and minimum. *Flight period*: start and end month number. *Number of generations*: maximum and minimum  
654 number of generations per year. Partial generations were rounded up. *Number of biotopes occupied*: sum of biotopes  
655 occupied. *Hostplant specificity*: 1 - single hostplant, 2 - multiple hostplants within the same genus, 3 - multiple hostplants  
656 within the same family, 4 - multiple hostplants within the same order, 5 - multiple hostplants in multiple orders.

657 2. Trait source: 1 - Emmet and Heath (1989), 2 - Asher et al. (2001), 3 - Thomas (2010), 4 - Newland et al. (2015), 5 - Eeles  
658 (2016), 6 - Dennis (2010).

659

660 Table 2. Individual trait agreement values between six trait sources for UK butterflies. Ordinal and categorical  
 661 traits are compared with Fleiss's Kappa and continuous traits with a two-way intra-class correlation coefficient  
 662 (ICC). For trait definitions see Table 1.

<b>Categorical Traits</b>	<b>Kappa</b>	<b>Trait sources</b>
Overwintering	0.973	All
Perching	0.778	All
Patrolling	0.745	All
Mate choice strategy	0.678	All
Biotope G	0.654	All
Biotope E	0.637	All
Biotope B	0.524	All
Biotope I	0.501	All
Biotope D	0.443	All
Biotope C	0.428	All
Myrmecophily	0.422	All
Biotope F	0.394	All
Biotope J	0.288	All
Mudpuddling	0.273	All
Biotope H	0.207	All
Hilltopping	0.173	All
<b>Ordinal Traits</b>	<b>Kappa</b>	<b>Trait sources</b>
Generations (max)	0.812	All
Hostplant specificity	0.66	All
Flight Period (start)	0.512	1-5
Generations (min)	0.475	All
Flight period (end)	0.457	1-5
Biotope total	0.236	All
<b>Continuous traits</b>	<b>ICC</b>	<b>Trait sources</b>
Wingspan (av.)	0.998	1,4,5
Wingspan (max)	0.995	1,4,5
Wingspan (min)	0.993	1,4,5
Hostplant number	0.355	All

663

664 Trait source: 1 - Emmet and Heath (1989), 2 - Asher et al. (2001), 3 - Thomas (2010), 4 - Newland et al. (2015), 5 - Eeles  
 665 (2016), 6 - Dennis (2010).

666

Table 3. Pairwise Procrustes regression values between PCA ordinations of UK butterflies constructed on the basis of traits obtained from six data sources and the average ordination of 50 randomly assembled species x trait matrices (\* p < 0.05, \*\* p < 0.01, \*\*\* p < 0.001). Upper right, with biotope information included; lower left, without biotope information.

	<b>Emmet &amp; Heath (1989)</b>	<b>Asher et al. (2001)</b>	<b>Thomas (2010)</b>	<b>Newland et al. (2015)</b>	<b>Eeles (2016)</b>	<b>Dennis (2010)</b>	<b>Random</b>
<b>Emmet &amp; Heath (1989)</b>		0.657***	0.601***	0.676***	0.662***	0.641***	0.256
<b>Asher et al.(2001)</b>	0.581***		0.646***	0.673***	0.720***	0.692***	0.288
<b>Thomas (2010)</b>	0.666***	0.683***		0.692***	0.729***	0.665***	0.300
<b>Newland et al. (2015)</b>	0.558***	0.628***	0.667***		0.683***	0.642***	0.310
<b>Eeles (2016)</b>	0.685***	0.733***	0.764***	0.643***		0.688***	0.290
<b>Dennis (2010)</b>	0.638***	0.647***	0.673	0.628***	0.713***		0.286
<b>Random</b>	0.336	0.307	0.373	0.326	0.339	0.339	

Table 4. Summary of the results of the best generalised linear models from data in Dennis (2010) comparing how various trait types correlate with criteria of status change in Fox et al. (2015). Components shown are those that are significantly correlated with measures of status (\* p < 0.05, \*\* p < 0.01, \*\*\* p < 0.001).

Status	Trait combination			
	Life-history	Life-history and biotope	Life-history and resources	All
% change Occurrence (all)	5*,7*	3*,4**	none	none
% change Occurrence (recent)	None	none	none	none
% change Abundance (all)	None	none	none	none
% change Abundance (recent)	7**	1*,	1*	1**
UKBMS Sites occupied	1**	1***,2***,3*,6*	2**	2**
10km grid squares occupied	1***,5*	1***,2***,3**,4*,5**,6**,7**	2**,3**	2***,3*
1km grid squares occupied	1***	1***,2***,3**,4**,5*,6**	2***,3**	2***,3*



**Supplementary material: Optimising trait and source selection  
for explaining occurrence and abundance changes: a case study  
using British Butterflies**

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## Functional Ecology

Table S1. Eigenvalues and explained variance of PCA using species x trait values from six trait sources for UK butterflies A) with biotope type and breadth included and B) with biotope type and breadth excluded

Component	Emmet & Heath (1989)		Asher et al. (2001)		Thomas (2010)		Newland et al. (2015)		Eeles (2016)		Dennis (2010)	
	Eigen value	%variation explained	Eigen value	%variation explained	Eigen value	%variation explained	Eigen value	%variation explained	Eigen value	%variation explained	Eigen value	%variation explained
<b>A) with biotope</b>												
1	5.07	28.17	5.08	28.21	3.67	20.38	4.59	25.5	3.84	21.31	4.99	27.75
2	2.40	13.31	2.32	12.90	2.53	14.08	2.35	13.03	2.59	14.37	2.15	11.93
3	1.63	9.05	1.80	9.97	2.30	12.77	2.10	11.67	1.83	10.15	1.87	10.37
4	1.43	7.95	1.54	8.53	1.88	10.44	1.66	9.23	1.47	8.19	1.47	8.18
5	1.31	7.27	1.20	6.67	1.30	7.25	1.27	7.06	1.30	7.24	1.28	7.08
6	1.19	6.60	1.01	6.05	1.03	5.73	1.204	6.69	1.24	6.89	1.06	5.90
7	1.07	5.98							1.02	5.64		
<b>B) without biotope</b>												
1	2.15	26.86	2.39	29.82	2.32	29.05	2.57	32.10	2.41	30.06	2.21	27.66
2	1.37	17.10	1.60	20.00	1.58	19.71	1.33	16.62	1.37	17.09	1.51	18.86
3	1.10	13.76	1.27	15.90	1.14	14.21	1.22	15.30	1.22	15.27	1.26	15.78
4	1.03	12.92	1.00	12.53					1.01	12.68		

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## Functional Ecology

Table S2. Beta coefficients of PCA loadings from six trait sources 1-Emmet and Heath (1989), 2- Asher et al. (2001), 3 - Thomas (2010), 4 -Newland et al. (2015), 5 -Eeles (2016), 6 - Dennis (2010) regressed against measures of occurrence and changes of occurrence and abundance (from Fox et al.,2015) with biotope information included (A) and without biotope information (B).

### A With biotope information included

	Emmet and Heath (1989)						
	PC1	PC2	PC3	PC4	PC5	PC6	PC7
% change occurrence (1976-2014)	-0.221	-0.048	-0.099	-0.010	0.200	-0.058	0.099
% change occurrence (2005-14))	0.100	-0.071	-0.156	0.127	0.076	0.055	0.263
% change abundance (1976-2014)	0.268	0.104	0.149	0.041	0.057	0.208	0.123
% change abundance (2005-14)	-0.330*	0.280*	0.080	0.119	-0.156	0.034	0.026
UKBMS Sites	-0.588***	0.067	-0.032	0.093	0.146	-0.171	-0.166
10km grid squares	-0.676***	0.009	-0.073	0.069	0.183	-0.174	-0.094
1km grid squares	-0.680***	0.069	-0.017	0.045	0.238	-0.164	-0.059

	Asher (2001)					
	PC1	PC2	PC3	PC4	PC5	PC6
% change occurrence (1976-2014)	-0.186	-0.265	0.003	0.098	-0.234	-0.133
% change occurrence (2005-14))	0.120	-0.099	-0.052	0.024	0.056	0.047
% change abundance (1976-2014)	0.279*	-0.151	0.323*	-0.050	-0.029	-0.070
% change abundance (2005-14)	-0.250	0.047	0.140	-0.190	0.278	0.332*
UKBMS Sites	-0.611***	-0.055	-0.090	-0.003	-0.043	0.015
10km grid squares	-0.709***	-0.176	-0.085	0.066	-0.106	0.044
1km grid squares	-0.720***	-0.269	-0.002	0.046	-0.012	0.097

## Functional Ecology

Table S2A continued

	Thomas (2010)					
	PC1	PC2	PC3	PC4	PC5	PC6
% change occurrence (1976-2014)	0.163	-0.242	0.191	-0.059	-0.037	-0.028
% change occurrence (2005-14))	-0.091	-0.071	-0.111	-0.204	0.221	0.142
% change abundance (1976-2014)	0.326*	0.167	-0.382	-0.005	0.040	0.063
% change abundance (2005-14)	0.295*	0.271*	-0.167	-0.040	-0.70	-0.236
UKBMS Sites	0.464***	-0.128	0.201	-0.073	-0.012	-0.226
10km grid squares	0.578***	-0.102	0.316*	-0.098	-0.091	-0.281
1km grid squares	0.505***	-0.031	0.408**	0.668	-0.134	-0.202
	Newland et al. (2015)					
	PC1	PC2	PC3	PC4	PC5	PC6
% change occurrence (1976-2014)	-0.177	0.264	0.151	-0.113	-0.038	-0.093
% change occurrence (2005-14))	0.097	0.003	-0.017	-0.174	-0.174	0.025
% change abundance (1976-2014)	0.298*	0.001	-0.151	0.132	-0.065	-0.069
% change abundance (2005-14)	-0.323*	-0.023	-0.249	0.060	-0.224	-0.248
UKBMS Sites	-0.633***	0.144	-0.056	0.006	-0.034	-0.195
10km grid squares	-0.729***	0.282*	0.100	-0.119	0.040	-0.212
1km grid squares	-0.716***	0.353**	-0.018	-0.071	0.055	-0.143

## Functional Ecology

Table S2A continued

	Eeles (2016)						
	PC1	PC2	PC3	PC4	PC5	PC6	PC7
% change occurrence (1976-2014)	0.221	-0.048	-0.099	0.010	0.200	-0.057	0.099
% change occurrence (2005-14))	0.102	-0.043	0.029	0.085	-0.167	-0.167	0.233
% change abundance (1976-2014)	0.252	0.024	0.080	0.119	-0.156	0.227	0.192
% change abundance (2005-14)	-0.330*	-0.280*	-0.906	1.745	-0.075	0.034	0.026
UKBMS Sites	-0.656***	0.174	0.020	0.092	-0.007	-0.131	-0.186
10km grid squares	-0.772***	0.240	0.020	0.056	0.022	-0.233	-0.523
1km grid squares	-0.725***	0.269*	0.196	0.140	-0.018	-0.156	0.007

	Dennis (2010)					
	PC1	PC2	PC3	PC4	PC5	PC6
% change occurrence (1976-2014)	-0.294*	-0.250	-0.067	0.044	0.031	-0.088
% change occurrence (2005-14))	0.109	-0.080	0.001	-0.010	0.030	0.117
% change abundance (1976-2014)	0.196	-0.157	0.030	0.144	0.122	0.091
% change abundance (2005-14)	-0.071	0.186	0.076	-0.252	0.213	0.102
UKBMS Sites	-0.532***	0.006	0.008	-0.057	0.042	0.142
10km grid squares	-0.655***	-0.063	0.049	-0.088	-0.013	0.047
1km grid squares	-0.643***	-0.119	0.078	0.1102	0.137	-0.039

## Functional Ecology

Table S2 continued

### B) without biotope

	Emmet and Heath (1989)			
	PC1	PC2	PC3	PC4
% change occurrence (1976-2014)	0.271*	-0.055	0.208	-0.061
% change occurrence (2005-14))	-0.069	-0.193	0.204	-0.139
% change abundance (1976-2014)	-0.210	-0.148	-0.065	-0.015
% change abundance (2005-14)	0.046	-0.218	-0.067	-0.177
UKBMS Sites	0.442***	-0.064	-0.022	0.159
10km grid squares	0.541***	-0.085	0.074	0.114
1km grid squares	0.553***	-0.098	0.087	0.170
	Asher et al. (2001)			
	PC1	PC2	PC3	PC4
% change occurrence (1976-2014)	-0.294*	-0.250	-0.067	0.045
% change occurrence (2005-14))	0.109	-0.080	0.001	-0.010
% change abundance (1976-2014)	0.196	-0.157	-0.030	0.144
% change abundance (2005-14)	-0.071	0.187	0.076	-0.252
UKBMS Sites	-0.532***	0.006	0.008	-0.057
10km grid squares	-0.655***	-0.063	0.049	-0.088
1km grid squares	-0.643***	-0.119	0.078	-0.110

Table S2B continued

Thomas (2010)			
	PC1	PC2	PC3
% change occurrence (1976-2014)	-0.291	0.025	0.036
% change occurrence (2005-14)	0.093	0.299*	-0.057
% change abundance (1976-2014)	0.252	0.017	-0.009
% change abundance (2005-14)	0.020	0.050	-0.97
UKBMS Sites	-0.406**	0.010	-0.170
10km grid squares	-0.522***	-0.031	-0.158
1km grid squares	-0.489***	-0.078	-0.173
Newland et al. (2015)			
	PC1	PC2	PC3
% change occurrence (1976-2014)	-0.124	0.184	-0.007
% change occurrence (2005-14)	0.094	0.229	0.123
% change abundance (1976-2014)	0.240	0.007	-0.104
% change abundance (2005-14)	-0.077	0.193	-0.081
UKBMS Sites	-0.393**	0.124	-0.082
10km grid squares	-0.464***	0.193	0.055
1km grid squares	-0.431**	0.255	0.044

## Functional Ecology

Table S2B continued

	Eeles (2016)			
	PC1	PC2	PC3	PC4
% change occurrence (1976-2014)	-0.337*	0.056	-0.061	0.109
% change occurrence (2005-14))	0.107	0.114	-0.167	0.213
% change abundance (1976-2014)	0.165	-0.043	0.037	-0.016
% change abundance (2005-14)	-0.074	0.077	-0.018	-0.262
UKBMS Sites	-0.539***	-0.010	-0.065	-0.110
10km grid squares	-0.659***	0.022	-0.001	-0.095
1km grid squares	-0.640***	0.078	-0.034	-0.144

	Dennis (2010)		
	PC1	PC2	PC3
% change occurrence (1976-2014)	0.232	0.261	0.192
% change occurrence (2005-14))	-0.181	0.126	0.031
% change abundance (1976-2014)	-0.054	-0.277*	0.016
% change abundance (2005-14)	0.102	0.081	-0.175
UKBMS Sites	0.450***	0.259	-0.017
10km grid squares	0.497***	0.370	0.026
1km grid squares	0.512***	0.342	-0.012

P < 0.05, \*\* P < 0.01, \*\*\* P < 0.001

## Functional Ecology

Table S3: Summary of the results of the best linear models relating trait sources to criteria of status change in Fox et al. (2015)., A) with and B) without biotope information included. Models were initially produced using all the significant principle components and then simplified using AIC. Retained components are numbered and those that are significantly correlated with measures of status are indicated (\* p < 0.05 , \*\* p < 0.01, \*\*\* p < 0.001). Trait sources- 1-Emmet and Heath (1989), 2- Asher et al. (2001), 3 - Thomas (2010), 4 -Newland et al. (2015), 5 -Eeles (2016), 6 - Dennis (2010)

A) with biotope included	Trait source					
	1	2	3	4	5	6
% change Occur (all)	1,5	1,2*,5	2,3,	1,2*,8	1*,2*,4,5,6,7,8*	1*,2
% change Occurrence (recent)	7	none	4,5	7	7	none
% change Abundance (all)	1*,6	1*,3*	1*	1*,7*	1,6,7	1
% change Abundance (recent)	1,2**,3*,4,5*,6,7	1*,4,5*,6**	1*,2*,3,6	1*,3,5,6*,8	1**,2*,7*	4,5
UKBMS Sites	1***,6,7,	1***	1***,3,6	1***,2,6,7*	1***,2,7	1***
10km grid squares	1***,5,6,	1***,2	1***,3**,6**	1***,2**,4,6*	1***,2**,6**,8	1***
1km grid squares	1***,5*,6,	1***,2,5*,6	1***,3***,6	1***,2***,6	1***,2**,3*,4,6	1***

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Table S3 continued

B) with biotope included	Trait source					
	1	2	3	4	5	6
% change Occurrence (all)	1*,3	1*,2	1*,6**	2,6**	1*	1,2*,3,4*
% change Occur (recent)	2,3,6	none	2*	2,4	4	none
% change Abundance (all)	1	1	1	1	none	2*
% change Abundance (recent)	2,4,6,7**	2,4	4***	2,5*	4,5	5
UKBMS Sites	1***,7	1***	1**,3,6	1**,6*	1***	1***,2*,6*
10km grid squares	1***,7*	1***	1***,3,4*,6	1***,6*	1***	1***,2***,6***
1km grid squares	1***,3,7**	1***	1***,3,4**,6**	1***,6**	1***	1***,2**,5*,6*



## Functional Ecology

Table S4. The first five factors contributing to the first three components of PCA analyses of data from 6 trait sources A) with biotope information and B) without information

Trait sources: 1 -Emmet and Heath (1989), 2- Asher et al. (2001), 3 - Thomas (2010), 4 -Newland et al. (2015), 5 -Eeles (2016), 6 - Dennis (2010).

Trait	Trait source						Trait source						Trait source					
	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6
<b>A) with biotope</b>																		
	<b>PC1</b>						<b>PC2</b>						<b>PC3</b>					
Biotone total	-0.419	-0.414	0.473	-0.429	-0.457	-0.427												
Biotope .B				-0.300		-0.310	0.377											
Biotope C				-0.258		-0.312	0.545		0.477	0.347	-0.332					-0.355	0.348	
Biotope D							0.545		0.486	0.347						-0.355	0.335	
Biotope E								0.300					0.361		-0.373			0.489
Biotope F			0.309		-0.302						-0.296		-0.260	-0.504				
Biotope G									-0.234	0.339		-0.386	-0.616	-0.526				
Biotope H	-0.317	-0.315							0.361	-0.362	-0.285							
Biotope I	-0.346	-0.298			-0.268	-0.305									0.305			-0.292
Biotope J	-0.352	-0.273	0.321				0.309		-0.430								-0.404	
Overwintering			0.268	-0.296	-0.304										0.312		0.377	-0.290
Hostplant specialism			0.288	-0.284			-0.262		-0.252		0.353					0.297		
Hostplant number						-0.286	-0.283		-0.280		0.342		0.343				-0.332	
Generations (max)	-0.307	-0.317			-0.310		-0.302								0.478	0.334		-0.347
Generations (min)											0.376	0.2422			0.357	0.401		
Perch								-0.387				-0.476						
Patrol								-0.364				0.459		0.269				
Mudpuddling													-0.312	0.251				-0.520
<b>B) without biotope</b>																		
Overwintering	0.376	-0.391	-0.362	-0.386	-0.370	0.366	-0.401	-0.051		0.269		0.242	0.258					
Hostplant.Specialism	0.370	-0.465	-0.472	-0.473	-0.464	0.449				0.331	-0.413		0.346	-0.484	0.462	-0.162		0.490
Hostplant number	0.411	-0.446	-0.400	-0.405	-0.414	0.445	0.307	-0.129		0.419	-0.448			-0.479	0.577	-0.211		0.475
Generations (max)	0.538	-0.489	-0.454	-0.456	-0.496	0.401			-0.216	-0.479		0.356		0.477	-0.456		0.244	-0.419
Generations (min)	0.477	-0.429	-0.466	-0.425	-0.467				-0.182	-0.547	0.378		-0.319	0.532	-0.432		0.272	-0.459
Perch							0.487	-0.648	0.583		0.441	0.607	0.394			0.473	-0.458	0.322
Patrol						0.405	0.645	-0.529	-0.622			-0.435				-0.685	0.742	
Mudpuddling								0.523	0.438		0.339	0.497	0.710	-0.141		-0.429	0.199	

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