

# *General declines in Mediterranean butterflies over the last two decades are modulated by species traits*

Article

Accepted Version

Creative Commons: Attribution-Noncommercial-No Derivative Works 4.0

Melero, Y., Stefanescu, C. and Pino, J. (2016) General declines in Mediterranean butterflies over the last two decades are modulated by species traits. *Biological Conservation*, 201. pp. 336-342. ISSN 0006-3207 doi: <https://doi.org/10.1016/j.biocon.2016.07.029> Available at <http://centaur.reading.ac.uk/83101/>

It is advisable to refer to the publisher's version if you intend to cite from the work. See [Guidance on citing](#).

To link to this article DOI: <http://dx.doi.org/10.1016/j.biocon.2016.07.029>

Publisher: Elsevier

All outputs in CentAUR are protected by Intellectual Property Rights law, including copyright law. Copyright and IPR is retained by the creators or other copyright holders. Terms and conditions for use of this material are defined in the [End User Agreement](#).

[www.reading.ac.uk/centaur](http://www.reading.ac.uk/centaur)

## **CentAUR**

Central Archive at the University of Reading

Reading's research outputs online

1 **General declines in Mediterranean butterflies over the last two decades are**  
2 **modulated by species traits**

3

4 Yolanda Melero<sup>a\*</sup>, Constantí Stefanescu<sup>a,b</sup>, Joan Pino<sup>a</sup>

5 <sup>a</sup>Centre de Recerca Ecològica i Aplicacions Forestals (CREAF), Universitat  
6 Autònoma de Barcelona, Bellaterra, Barcelona, Spain

7 <sup>b</sup>Butterfly Monitoring Scheme, Museu de Ciències Naturals de Granollers, Granollers  
8 (Barcelona), Spain

9

10 \*Corresponding author. Tel.: +34 935814677. E-mail addresses:

11 y.melero@creaf.uab.cat (Y. Melero), c.stefanescu@creaf.uab.cat (C. Stefanescu),

12 j.pino@creaf.uab.cat (J. Pino)

13

14 **Abstract**

15

16 Species' responses to environmental changes are highly idiosyncratic and context-  
17 dependent. Although intrinsic traits (i.e. those that define species niches) may play a  
18 key role, little empirical evidence exists regarding their relationship to demographic  
19 responses. We used data for 66 butterfly species representing five ecological and two  
20 life-history traits to study the effect these factors have on population growth rates and  
21 variations in populations. Using a novel methodological approach, we provide here  
22 improved estimates of population change. Our results reveal declines in 70% and  
23 increases in 23% of the studied species, clear evidence of more serious population  
24 declines in Catalan butterflies than those that have previously been reported. Declines  
25 were associated with species' degree of habitat specialisation and the number of

26 generations. For all species, fluctuations were greater within than between years and,  
27 on average, the latter was 1.5 times greater. Our results indicated that habitat  
28 specialists and multivoltine species are more likely to suffer severe annual  
29 fluctuations in population abundance; and that multivoltine species and extreme larval  
30 specialists had the most marked fluctuations within seasons. We also found higher  
31 resilience to environmental changes in generalist species, which is concordant with  
32 biotic homogenisation in disturbed communities. However, amongst the declining  
33 species there were also many generalists, which indicates a potential general  
34 reduction in this group that goes beyond faunal homogenisation. Given butterflies are  
35 biodiversity indicators, these patterns are a possible reflection of an overall  
36 impoverishment in biodiversity.

37

38 **Keywords**

39 Population trends, specialization, voltinism, species traits, butterflies, Bayesian  
40 hierarchical modeling

41

42 **1. Introduction**

43

44 Understanding the pressures affecting species population dynamics is a central issue  
45 in ecology and management, especially when the aim is to safeguard biodiversity  
46 (Sutherland et al. 2013). Pressures provoked by global change have accelerated the  
47 decline of many species (Vitousek 1997, Chapin et al. 2000, Vitousek et al. 2008),  
48 with some facing or undergoing extinction (Butchart et al. 2010, Pimm et al. 2014). In  
49 particular, climate change and habitat transformation (i.e. habitat loss and  
50 fragmentation) are among the main pressures exerted by global change that species  
51 are having to confront (Thomas et al. 2004a, Visconti et al. 2015).

52 Several studies have suggested that certain intrinsic ecological (i.e. those that define  
53 species ecological niches) and life-history traits predispose a species to respond  
54 distinctly to specific environmental pressures (Krauss et al. 2010, Murray et al. 2011,  
55 González-Suárez and Revilla 2013). For instance, species with better dispersal ability  
56 can shift their ranges faster than those with less capacity to disperse. This is an  
57 advantage in areas in which climate change is provoking asynchronies between the  
58 species niche and the environment (e.g. Croxall et al. 2002, Butchart et al. 2010, Chen  
59 et al. 2011). Species whose traits enable them to cope well with current pressures are  
60 expected to persist while the others might face declines and, eventually, local  
61 extinction. It is therefore not surprising that an increasing number of studies have  
62 evaluated the relationship between species traits and their responses to environmental  
63 pressures.

64 Previous studies have quantified these responses as changes in species richness and  
65 distributions for a wide range of taxa (e.g. Thuiller et al. 2008, Stefanescu et al.  
66 2011a, Eskildsen et al. 2015), or have evaluated extinction probabilities or

67 vulnerability (e.g. González-Suárez and Revilla 2013; Fernández-Chacón et al. 2014).  
68 However, few empirical studies have actually addressed demographic trends  
69 (Dapporto and Dennis 2013, Curtis et al. 2015), in part because of the difficulty in  
70 gathering high-quality data at relevant spatial and temporal scales. The recent upsurge  
71 in citizen-science projects has provided a useful way of obtaining the data needed for  
72 this kind of analysis (Schmeller et al. 2009, Devictor et al. 2010).

73 In this paper we examine the relationship between ecological and life-history traits,  
74 and demographic trends in a set of butterfly species. To do so, we used empirical  
75 count data gathered by a volunteer-based project, the Catalan Butterfly Monitoring  
76 Scheme, over 20 years in the Mediterranean region of north-eastern Spain. Butterflies  
77 are good indicators of biodiversity (Thomas 2005) and respond quickly to climate  
78 change and habitat transformation (Stefanescu et al. 2003, Thomas et al. 2004b,  
79 Krauss et al. 2010), thereby minimising – in comparison, for example, to plants and  
80 birds – the demographic time lag inherent in extinction debts (Krauss et al. 2010,  
81 Devictor et al. 2012, but see Sang et al. 2010). Therefore, butterfly demographic  
82 patterns in relation to species intrinsic traits can contribute to a better understanding  
83 of how a wide range of organisms (e.g. insects and other short-lived organisms)  
84 respond under such pressures.

85 To gather species demographic patterns we estimated (i) their population growth rate,  
86 i.e. the direction of the population trend (positive, stable or negative) and its strength,  
87 and (ii) the population variation, i.e. the dispersion of temporal changes in population  
88 numbers due to intrinsic (density-dependence processes) and external (cyclic or  
89 stochastic) factors.

90 We hypothesised that habitat specialisation will decrease population growth rate but  
91 increase population variability (hypothesis 1), an idea that is based on previous

92 studies suggesting the existence of a relationship between this trait and population  
93 trends in butterflies (e.g. Stefanescu et al. 2011a; see Dapporto and Dennis 2013 for a  
94 comprehensive discussion). Nevertheless, other traits besides habitat specialisation  
95 could also influence demographic trends as the species respond to global change. For  
96 instance, dispersal ability in fragmented landscapes is directly related to colonisation  
97 and the persistence of butterfly populations (Fernández-Chacón et al. 2014).  
98 Therefore, we predicted that better dispersal ability will increase growth rate and  
99 reduce population variability (hypothesis 2). Furthermore, during a period of climate  
100 warming, we would expect thermophilous species to have more positive population  
101 trends and less population variability than those adapted to colder climates (as seen in  
102 birds; e.g. Stephens et al. 2016) (hypothesis 3). In addition, traits influencing  
103 butterflies' responses to increasing temperatures may also be important for explaining  
104 population trends (e.g. Diamond et al. 2011). A series of studies have suggested that  
105 an increase in the number of generations per reproductive season (i.e. the production  
106 of extra generations) occurs under climate warming, although its effect on populations  
107 remains unclear (e.g. Altermatt 2010, Van Dyck et al. 2015). Intuitively, a positive  
108 effect is expected since a larger proportion of adults will develop and reproduce  
109 during the season and so we hypothesised that there will be a higher growth rate in  
110 multivoltine than in univoltine species (hypothesis 4). Finally, we also predicted more  
111 positive trends and less variation in species overwintering in mature (pupa and adult)  
112 than in immature stages (egg and larva; hypothesis 5) given previous findings that  
113 suggest that species overwintering in the egg stage or as unfed neonate larva are  
114 currently undergoing the most serious declines (Breed et al. 2012).

115

## 116 **2. Material and Methods**

117

118 *2.1. Study area and data collection*

119

120 The study area was the Mediterranean region of Catalonia, Menorca (north-east  
121 Spain) and Andorra. This area is a biodiversity hotspot in which butterfly species are  
122 threatened by climate warming (e.g. increasing aridity; Stefanescu et al. 2011a) and  
123 habitat transformation (e.g. the abandonment of traditional land use and increasing  
124 urbanisation; Herrando et al. 2015).

125 Data were obtained from monitoring surveys carried out in 1994–2014 as part of the  
126 Catalan Butterfly Monitoring Scheme (CBMS; see: [www.cbms.org](http://www.cbms.org)) and the Andorran  
127 Butterfly Monitoring Scheme (BMSAnd; see [www.iea.ad/bmsand](http://www.iea.ad/bmsand)). Both schemes  
128 consist of a network of sites in which visual counts of adult butterflies along transects  
129 are undertaken by volunteers every week between March and September (i.e. the  
130 whole flight period of most species). Transects are fixed routes of about 2 km in  
131 length and 5 m in width, which are divided into shorter sections corresponding to  
132 homogeneous habitat types (average section length: 186 m, median: 162 m, range:  
133 20–871 m). The transects used in our study (n = 116) are located at 0–1650 m a.s.l.  
134 and cover a comprehensive range of environmental conditions (Fig. A.1). Although  
135 the number of surveyed transects varied between years, an important fraction  
136 remained stable throughout the whole recording period (for further details, visit  
137 [www.catalanbms.org](http://www.catalanbms.org)). Nevertheless, our modeling approach allowed us to assess  
138 species abundance at sites in years in which surveys were not performed via updating  
139 with the Markov Chain Monte Carlo (see next section).

140

141 *2.2. Species selection and modeling approach*



142

143 A total 183 species were sampled, of which we selected 82 species representative of a  
144 diverse range of ecological and life-history traits (Table A.1) and regularly recorded  
145 across all years and sites.

146

147 To test our hypotheses, we applied an open-population binomial mixture Bayesian  
148 hierarchical model (Kéry et al. 2009). This model estimates abundance over time  
149 using count data from open populations corrected by the imperfect detection inherent  
150 to observational error (see full model description in Appendix B and R code in  
151 Appendix C). In previous studies (e.g. Stefanescu et al. 2011b; Herrando et al. 2015),  
152 population trends were calculated via the widely used TRIM software (Pannekoek and  
153 Strien 2005). Nevertheless, this methodological approach does not take into account  
154 the detection probability that observational counts are subject to or its variation over  
155 time. This could mask real abundances and temporal trends in populations and their  
156 drivers (Kéry 2004, Kéry and Plattner 2007, Kéry et al. 2009).

157 For each species, abundance was set as time and section specific, and its estimation  
158 was extended to include the relationship with the population growth rate ( $r_{sp}$ ) and the  
159 seven major habitat types in the area (meadows, forests, arable crops, woody crops,  
160 gardens, ruderal vegetation, and non-suitable habitat). Habitat types were not  
161 significantly correlated and were expressed as a percentage of habitat per section  
162 (Table A.2). The detection probability – with which species abundance was corrected  
163 – was set as time-specific.

164

165 The time step was set as intervals of two weeks to account for seasonality in both the  
166 abundance and the detection probability, and to include a closure period for the

167 repeated counts used to analyse detectability. Two-week intervals have been  
168 postulated as an acceptable closure period for butterfly species richness (Kéry and  
169 Plattner 2007). Although slight changes in butterfly abundance may occur at this  
170 resolution level, we consider that they are small enough to ensure that our model  
171 remains valid.

172

### 173 *2.3. Temporal population variability of species abundance*

174

175 Population variability was assessed using the coefficient of variation (i.e. the  
176 dispersion around the mean), a relative measure of variation that is independent of the  
177 population size and so can be used to compare species. We used two temporal  
178 windows: seasonal (i.e. within years;  $CV_W$ ) to include the seasonality (excluding the  
179 seasonality related to non-surveyed months: October-February), and inter-annual  
180 variation (i.e. between years;  $CV_B$ ). Seasonal variation was defined as the ratio of the  
181 standard deviation to the mean of the time series of abundance within each year,  
182 which gave a total of 20 values per species (one for each of the 20 years recorded). To  
183 obtain the inter-annual variation without including the seasonal variation in the  
184 calculation, we calculated the standard deviation and mean abundance per year and  
185 defined  $CV_B$  as their ratio, which generated a single value for each species.

186

### 187 *2.4. Species ecological and life-history traits*

188

189 For each species, we used a total of seven intrinsic traits divided into five ecological  
190 (i-v) and two life-history (vi-vii) traits: (i) adult habitat specialisation measured using  
191 the Species Specialisation Index (SSI), quantified as the coefficient of the variations

192 in the average density in the available habitat, as defined by Julliard et al. (2006); (ii)  
193 larval trophic specialisation, ranging from 1 (extreme specialists) to 3 (extreme  
194 generalists), following Stefanescu et al. (2011a) and Fernández-Chacón et al. (2014);  
195 (iii) the degree of preference for forests versus open areas, as evaluated by Herrando  
196 et al. (2015); (iv) average forewing length (measured in mm), which has been shown  
197 to act as a satisfactory proxy for dispersal ability in butterflies (Kuussaari et al. 2014;  
198 but see Sekar 2012); for this measurement, data were extracted from García-Barros et  
199 al. (2013) with sexes pooled given their close correlation (Fig. A.2); (v) the Species  
200 Temperature Index (STI), as defined in Schweiger et al. (2014); (vi) voltinism,  
201 categorised as uni-, bi- or multivoltine ( $\geq 3$  generations/year), according to Stefanescu  
202 et al. (2011a) and Fernández-Chacón et al. (2014); and (vii) overwintering stage,  
203 either immature (i.e. egg or larva) or mature (i.e. pupa or adult), with a third category  
204 for migratory species (i.e. not overwintering in the region), as per García-Barros et al.  
205 (2013).

206

## 207 *2.5. Statistical analyses*

208

209 The effects of the seven species traits on the growth rate estimates were tested using  
210 linear regressions (i.e. the growth rate fitted to a Gaussian distribution).

211 Both seasonal and inter-annual population variability were analysed in terms of the  
212 described traits using a Generalised Linear Mixed Model (GLMM) and a Generalised  
213 Linear Model (GLM), respectively. These two models were fitted to a Gamma  
214 distribution given that the coefficients of variation were positive, continuous, skewed  
215 and of increasing variance; species identity was set as a random effect.

216 For each analysis, a global model was first defined containing all the above  
217 mentioned covariates and potential interactions. Model selection was carried out by  
218 discarding terms sequentially. In the case of the linear regression analysis model,  
219 selection was based on the adjusted r-squared to take into account the number of  
220 observations and of model parameters. Model selection for the generalised models  
221 was based on AICc selecting those models differing from  $\Delta AICc < 2$ . Model  
222 averaging and estimates weighting for the most likely models were obtained via R  
223 package MuMIn (Bartoń 2014). Analyses were performed in R using package lme4  
224 (Bates et al. 2014).

225

226 Temporal changes in the detection probability were tested in relation to species  
227 voltinism. We used a Generalised Additive Mixed Model (GAMM), with two-week  
228 intervals throughout the year (1–15) set as the non-linear term and species as a  
229 random effect, to account for the inherent specific variability. The detection  
230 probability was fitted to a Gamma distribution with an inverse link. Analyses were  
231 performed in R using package gamm4 (Wood 2014).

232

### 233 **3. Results**

234

235 Sixteen of the 82 regularly recorded species failed to converge in our modeling  
236 approach (Table A.3). The remaining 66 species were all present in more than 10  
237 transects, which conferred inferential strength on the analysis (e.g. Oliver et al. 2010).  
238 Annual population growth rates ranged between -0.11 and 0.04 ( $r_{\text{average}} = -0.02$ ); 15  
239 species (22.7%) had a significantly positive rate, five (7.6%) were stable and 46  
240 (69.7%) had a negative rate. Significance was based on the exclusion of zero values in

241 the Bayesian Credible Interval values at 95% (Appendix D). When testing for  
242 significance using a conventional Poisson regression, only one species (*Euphydryas*  
243 *aurinia*) was considered as stable ( $r = 0.00035$ ,  $z = 0.92$ ,  $p = 0.36$ ; Appendix D).

244

### 245 *3.1. Population growth rate and species traits*

246

247 The best models for the estimated population growth rates included habitat  
248 specialisation, the degree of preference for forests versus open areas, wing length and  
249 voltinism (Table A.4).

250 Population growth rates decreased with the increase in habitat specialisation, thereby  
251 indicating lower population growth rate in habitat specialists ( $p = 0.021$ , Table 1a,  
252 Fig. 1b). Nevertheless, several generalist species did also show declines (e.g. 71% of  
253 those species with  $SSI < 1.5$ , for range, median and average values of 0.62–2.18, 1.23  
254 and 1.24, respectively). Multivoltine species had a steeper negative rate than both uni-  
255 and bivoltine species (Table 1a, Fig. 1b). Results also suggested steeper negative rates  
256 in forest species; however, this effect was not significant. The effect of wing length –  
257 similarly not significant – was nearly negligible despite being included in the best  
258 models (Table 1a).

259

### 260 *3.2. Temporal variation of abundance and species traits*

261

262 Seasonal variation was greater than inter-annual variation in species abundance  
263 (range = 0.004–1.54 and 0.05–0.72, respectively), although the mean value of the  
264 inter-annual variation was 1.5 times higher (average = 0.14 and 0.22 for seasonal and  
265 inter-annual variation, respectively; Fig. A.3).

266 Although 38% of the seasonal variation was species-specific, voltinism was the main  
267 factor involved, as variation increased from uni- to multivoltine species (all  $p$   
268  $<0.0001$ ; Table 1b, Fig. 2a). Seasonal variation was lesser in larval trophic generalists  
269 (i.e. larval specialisation 3,  $p = 0.006$ ) and species overwintering in an immature stage  
270 ( $p = 0.003$ ; Table 1b, Fig. A4). Habitat specialisation and the degree of preference for  
271 forests versus open areas were also included in the best models but without any  
272 significant relationship (Tables 1b and A.5a).

273 Voltinism and habitat specialisation were the main factors defining inter-annual  
274 variation, both leading to increased values ( $p < 0.04$ ; Table 1c, Fig. 2b). The degree of  
275 preference for forests versus open areas was included in the best models (Table A.5b),  
276 increasing the inter-annual variation non-significantly (Table 1c). No other traits were  
277 included in the best models (Table A.5).

278

### 279 *3.3. Temporal changes in detection probability*

280

281 The detection probability increased linearly over the years (Estimate =  $-0.006$ ) for all  
282 uni-, bi- and multivoltine species. Although there were no differences between these  
283 species ( $p_{\text{interactions}} > 0.11$ ), the detection probability was constantly lower for  
284 univoltine species ( $Q1 = 0.01$ ; Estimate =  $1.12$ ,  $p < 0.001$ ; Fig. 1a).

285

## 286 **4. Discussion**

287

288 This study reveals negative trends in 70% of the studied species, indicating a severe  
289 decline among Mediterranean butterflies. Population trends are partly predicted by the

290 ecological and life-history traits of the species. In particular habitat specialisation and  
291 voltinism have the highest influence, whilst other traits have a marginal or null effect.

292

#### 293 *4.1. Population trends and species traits*

294

295 Population growth rates decreased with increasing habitat specialisation. This finding  
296 agrees with the steeper declines detected in populations of butterfly specialists  
297 (compared to habitat generalists) in the same region (Stefanescu et al. 2011b; Carnicer  
298 et al. 2013) and in other European countries (van Swaay et al. 2006, Eskildsen et al.  
299 2015, Curtis et al. 2015). Habitat generalists have a wider range of available resources  
300 that can fulfil their needs, which give them an advantage in environments that are  
301 being transformed. Under a context of global change, this may in turn lead to a biotic  
302 homogenisation of natural communities, i.e. the substitution of many specialists by a  
303 few generalist species, a process that is one of the main drivers of declines in  
304 biodiversity worldwide (McKinney and Lockwood, 1999). This effect has been noted  
305 to occur in the butterfly fauna in several European countries (e.g. Ekroos et al. 2010,  
306 Ockinger et al. 2010).

307 Despite the negative relationship between habitat specialisation and population rates,  
308 many generalist species were also found to be in decline. This situation is comparable  
309 to some extent to other areas affected by severe anthropic pressure (Leon-Cortes et al.  
310 1999, 2000, Van Dyck et al. 2009). Further investigation is needed to evaluate  
311 whether or not these general negative trends can be explained by the interaction of  
312 environmental pressures such as climate change and habitat transformation, and by  
313 ecological traits. For example, Stefanescu et al. (2011a) suggested that habitat  
314 generalist species are most affected by the increase of aridity and landscape

315 intensification in lowlands, while specialists are more affected by land abandonment  
316 and climate warming in mountain areas.

317 In contrast to our intuitive expectation, uni- and bivoltine species registered similar  
318 trends, while multivoltine species had significantly steeper declines. For example, in  
319 Germany multivoltine species dominate butterfly communities when land use  
320 intensification is severe (Börschig et al. 2013). However, multivoltine species may be  
321 the most negatively affected by climate change in the Mediterranean when their last  
322 summer generations have to confront the most rigorous conditions and extreme  
323 drought events. To a degree, this situation is comparable with the recent decline of the  
324 generalist multivoltine butterfly *Lasiommata megera* in central Europe, where the  
325 addition of an extra generation represents a developmental trap resulting in high larval  
326 mortality (Van Dyck et al. 2015). Likewise, multivoltinism could expose a species to  
327 detrimental events several times in the same season and thus lead to a severe decline,  
328 a scenario that could become more relevant given longer and more frequent extreme  
329 climatic events, as predicted by Giorgi and Lionello (2008) for the Mediterranean  
330 region.

331 Strikingly, the degree of preference for forests versus open areas was not significant  
332 for either population growth rate or variation, which may indicate that we failed to  
333 capture this effect properly for the set of studied species. In a recent study this  
334 preference was found to be advantageous both for butterflies and birds, as woodland  
335 species had more positive population trends (Herrando et al. 2015). Nevertheless, in  
336 this study trends were evaluated in a subset of transects covered by natural vegetation  
337 affected by land abandonment ( $n = 74$ ) rather than in all available transects, as was  
338 the case in our study ( $n = 116$ ). The addition of other types of habitat transformations



339 such as increasing urbanisation probably diluted the positive trend of forests in natural  
340 areas at a regional scale.

341 Wing length, which we considered as a proxy for dispersal, had nearly no effect in our  
342 models. However, some authors have questioned its relationship with dispersal ability  
343 (see Sekar 2012). In addition, the fact that the Species Temperature Index did not  
344 predict population trends may initially be surprising given the prediction of general  
345 declines in cold-adapted species and the opposite trends in warm-adapted species in  
346 the current context of climate warming (e.g. Devictor et al. 2012). However, our  
347 results confirm some previous analyses at site level that show that population trends  
348 are in fact independent of the thermal niche of the species (Stefanescu et al. 2011b).  
349 Indeed, our findings suggest that interactions with other climatic and non-climatic  
350 factors may be more important for explaining population trends (Oliver et al. 2015,  
351 Settele and Wiemers 2015).

352

#### 353 *4.2. Temporal population variation and species traits*

354

355 Although seasonal variation was greater than inter-annual variation, average values  
356 showed the opposite pattern. Both measures were positively affected by voltinism,  
357 that is, population variation at differing time scales was higher in multivoltine species,  
358 which suggests that there was a higher risk of strong fluctuations.

359 To a lesser degree, seasonal variation was affected by extreme larval trophic  
360 generalism and the overwintering stage. The lower variability in larval trophic  
361 generalism supports the hypothesis of specialisation traits relating to higher sensitivity  
362 to environmental changes. Likewise, fewer seasonal variations were found in species  
363 overwintering in immature stages (egg or pupa), which could indicate a major

364 buffering capacity in immature stages against extreme climatic events, a result that  
365 contrasts with the findings of Breed et al. (2012). Indeed, species overwintering in  
366 mature stages will emerge earlier in the spring, thereby exposing themselves to  
367 extreme climatic events at the beginning of the season that could provoke fluctuations  
368 in populations.

369 In addition to voltinism, inter-annual variation was also affected by habitat  
370 specialisation, with habitat specialists showing consistently greater variation than  
371 habitat generalists. This interesting finding – that we interpret to be a reflection of the  
372 greater sensitivity of habitat specialists to environmental perturbations – highlights  
373 how difficult it is for these species to adapt to the ongoing environmental  
374 transformations (in both climate and landscape) in the region. This agrees with the  
375 differences in the relative impact of environmental perturbations on specialist and  
376 generalist species richness (Stefanescu et al. 2011a).

377

#### 378 *4.3. Modeling approach: open-population Binomial Hierarchical Bayesian*

379

380 The percentage of declining species obtained with our approach was almost two times  
381 higher than previously obtained with TRIM for the region (Fig. A.5; Stefanescu et al.  
382 2011b; Carnicer et al. 2013).

383 Different estimates of abundance between models are to be expected whenever trends  
384 in detection probability occurred, as our model accounted for the error in the  
385 observational process while TRIM does not. In the later model type, abundances are  
386 likely to be underestimated when the detection probability is low. The increasing  
387 probability of detection over time in our data (Fig. 1A) means that population trends  
388 will be underestimated when the population trend is negative because there will be

389 fewer differences between the (under)estimates of abundances during the first years of  
390 surveys and the estimates during the latter years. However, they will be overestimated  
391 when the population trend is positive since there will be greater differences between  
392 the (under)estimates of abundances during the first years of surveys and the estimates  
393 during the latter years. In our case, the detection probability increased over time,  
394 probably due to the lower amount of experience of the volunteers at the start of the  
395 project. Thus, our estimations gained in accuracy by adding the detection probability.  
396 The benefit of accounting for the detection probability has been demonstrated by Dail  
397 and Madsen (2011) and Pellet et al. (2012).  
398 The differences in the results obtained using our approach and TRIM could also be  
399 explained by the different parameterisation of the time scale of the models (every two  
400 weeks versus annual) and the model structure (lineal versus non-lineal). Therefore,  
401 although we recommend the use of models that take into account the detection  
402 probability to reduce uncertainty caused by observational error, we are unable to  
403 endorse any particular approach until further comparisons between these two  
404 methodologies using equal parameterisations have been conducted.

405

## 406 **5. Conclusions**

407

408 Our results indicate a very serious general decline of the butterfly fauna in the western  
409 Mediterranean, affecting 70% of the studied species. Although this decline also  
410 covers many generalist species, overall the highest vulnerability in terms of  
411 population trends was found for specialist and multivoltine species. Taken together  
412 with previous work, our analysis suggests that global change – including land  
413 abandonment and intensification and climate change – is behind the observed

414 negative trends (Stefanescu et al. 2003, 2011a,b; Herrando et al. 2015). Moreover,  
415 changes in land cover and more extreme climatic events are expected to exacerbate  
416 these serious declines in the future. Furthermore, given that butterflies are also  
417 regarded as good indicators for other terrestrial insects (Thomas 2005; but see  
418 Musters et al. 2013), the observed patterns may also be indicative of global biological  
419 impoverishment. Under this scenario, local habitat management (i.e. conservation  
420 aimed at increasing habitat availability and connectivity) focused on the requirements  
421 of declining species might help mitigate these negative trends (Curtis et al. 2015) or  
422 even potentially revert population declines (e.g. Dapporto and Dennis 2013).  
423 Finally, this study also highlights the potential of models that take into account  
424 detection probability and provides empirical evidence for their robustness and  
425 usefulness with volunteer-based projects and monitoring programs. Therefore, we  
426 recommend their use if temporal or spatial variation in the observational error is  
427 suspected to occur.

428

## 429 **Acknowledgements**

430

431 We would like to thank all the volunteers who helped gather the data in the butterfly  
432 monitoring schemes, as well as Chris Sutherland for checking the R code for the  
433 Bayesian model and Arco van Strien for providing useful comments on the  
434 manuscript. Ferran Páramo provided technical assistance. The CBMS is funded by the  
435 Departament de Territori i Sostenibilitat de la Generalitat de Catalunya and the  
436 BMSAnd by the Andorran Research Institute. Funding was also provided by  
437 Barcelona Provincial Council as part of the SITxell project. YM was supported by a  
438 Beatriu de Pinos-B grant (2013 BP-B 00168) from AGAUR for postdoctoral

439 researchers. We are also grateful to the three anonymous reviewers for their help in  
440 improving the manuscript. A professional scientific proof-reader (Mike Lockwood)  
441 revised the manuscript.

442

## 443 **References**

444

- 445 Altermatt, F. 2010. Climatic warming increases voltinism in European butterflies and  
446 moths. *Proceedings of the Royal Society B* 277:1281–1287.
- 447 Bartoń, K. 2014. MuMIn: Multi-model inference. R package version 1.10.5.
- 448 Bates, D., M. Maechler, B. Bolker, and S. Walker. 2014. lme4: Linear mixed-effects  
449 models using Eigen and S4 version 1:1-7.
- 450 Börschig, C., A.-M. Klein, H. von Wehrden, and J. Krauss. 2013. Traits of butterfly  
451 communities change from specialist to generalist characteristics with increasing  
452 land-use intensity. *Basic and Applied Ecology* 14:547–554.
- 453 Breed, G. A., S. Stichter, and E. E. Crone. 2012. Climate-driven changes in  
454 northeastern US butterfly communities. *Nature Climate Change* 3:142–145.
- 455 Butchart, S. H. M., M. Walpole, B. Collen, A. van Strien, J. P. W. Scharlemann, R. E.  
456 A. Almond, J. E. M. Baillie, B. Bomhard, C. Brown, J. Bruno, K. E. Carpenter,  
457 G. M. Carr, J. Chanson, A. M. Chenery, J. Csirke, N. C. Davidson, F. Dentener,  
458 M. Foster, A. Galli, J. N. Galloway, P. Genovesi, R. D. Gregory, M. Hockings,  
459 V. Kapos, J.-F. Lamarque, F. Leverington, J. Loh, M. A. McGeoch, L. McRae,  
460 A. Minasyan, M. H. Morcillo, T. E. E. Oldfield, D. Pauly, S. Quader, C.  
461 Revenga, J. R. Sauer, B. Skolnik, D. Spear, D. Stanwell-Smith, S. N. Stuart, A.  
462 Symes, M. Tierney, T. D. Tyrrell, J.-C. Vié, and R. Watson. 2010. Global  
463 Biodiversity: Indicators of Recent Declines. *Science* 328:1164–1168.
- 464 Carnicer, J., C. Stefanescu, R. Vila, V. Dinca, X. Font, and Josep Peñuelas. 2013. A  
465 unified framework for diversity gradients: the adaptive trait continuum. *Global*  
466 *Ecology and Biogeography* 22:6–18.
- 467 Chapin, F. S. I., E. S. Zavaleta, V. T. Eviner, R. L. Naylor, P. M. Vitousek, H. L.  
468 Reynolds, D. U. Hooper, S. Lavorel, O. E. Sala, S. E. Hobbie, M. C. Mack, and  
469 S. Diaz. 2000. Consequences of changing biodiversity. *Nature* 405:234–242.
- 470 Chen, I.-C., J. K. Hill, R. Ohlemüller, D. B. Roy, and C. D. Thomas. 2011. Rapid  
471 range shifts of species associated with high levels of climate warming. *Science*  
472 333:1024–1026.
- 473 Croxall, J. P., P. N. Trathan, and E. J. Murphy. 2002. Environmental change and  
474 Antarctic seabird populations. *Science* 297:1510–1504.
- 475 Curtis, R. J., T. M. Brereton, R. L. H. Dennis, C. Carbone, and N. J. B. Isaac. 2015.  
476 Butterfly abundance is determined by food availability and is mediated by  
477 species traits. *Journal of Applied Ecology* 52:1676–1684.

- 478 Dail, D., and L. Madsen. 2011. Models for estimating abundance from repeated  
479 counts of an open metapopulation. *Biometrics* 67:577–87.
- 480 Dapporto, L., and R. L. H. Dennis. 2013. The generalist–specialist continuum:  
481 Testing predictions for distribution and trends in British butterflies. *Biological*  
482 *Conservation* 157:229–236.
- 483 Devictor, V., C. van Swaay, T. Brereton, L. Brotons, D. Chamberlain, J. Heliölä, S.  
484 Herrando, R. Julliard, M. Kuussaari, Å. Lindström, J. Reif, D. B. Roy, O.  
485 Schweiger, J. Settele, C. Stefanescu, A. Van Strien, C. Van Turnhout, Z.  
486 Vermouzek, M. WallisDeVries, I. Wynhoff, and F. Jiguet. 2012. Differences in  
487 the climatic debts of birds and butterflies at a continental scale. *Nature Climate*  
488 *Change* 2:121–124.
- 489 Devictor, V., R. J. Whittaker, and C. Beltrame. 2010. Beyond scarcity: citizen science  
490 programmes as useful tools for conservation biogeography. *Diversity and*  
491 *Distributions* 16:354–362.
- 492 Diamond, S. E., A. M. Frame, R. A. Martin, and L. B. Buckley. 2011. Species’ traits  
493 predict phenological responses to climate change in butterflies. *Ecology*  
494 92:1005–1012.
- 495 Ekroos, J., J. Heliölä, and M. Kuussaari. 2010. Homogenization of lepidopteran  
496 communities in intensively cultivated agricultural landscapes. *Journal of Applied*  
497 *Ecology* 47:459–467.
- 498 Eskildsen, A., L. G. Carvalheiro, W. D. Kissling, J. C. Biesmeijer, O. Schweiger, and  
499 T. T. Høye. 2015. Ecological specialization matters: long-term trends in butterfly  
500 species richness and assemblage composition depend on multiple functional  
501 traits. *Diversity and Distributions* 21:792–802.
- 502 Fernández-Chacón, A., C. Stefanescu, M. Genovart, J. D. Nichols, J. E. Hines, F.  
503 Páramo, M. Turco, and D. Oro. 2014. Determinants of extinction-colonization  
504 dynamics in Mediterranean butterflies: the role of landscape, climate and local  
505 habitat features. *Journal of Animal Ecology* 83:276–285.
- 506 García-Barros, E., M. L. Munguira, C. Stefanescu, and A. Vives Moreno. 2013.  
507 *Lepidoptera Papilionoidea. Fauna Ibérica. Museo Nacional de Ciencias*  
508 *Naturales. CSIC, Madrid.*
- 509 Giorgi, F., and P. Lionello. 2008. Climate change projections for the Mediterranean  
510 region. *Global and Planetary Change* 63:90–104.
- 511 González-Suárez, M., and E. Revilla. 2013. Variability in life-history and ecological  
512 traits is a buffer against extinction in mammals. *Ecology Letters* 16:242–251.
- 513 Herrando, S., L. Brotons, M. Anton, F. Páramo, D. Villero, N. Titeux, J. Quesada, and  
514 C. Stefanescu. 2015. Assessing impacts of land abandonment on Mediterranean  
515 biodiversity using indicators based on bird and butterfly monitoring data.  
516 *Environmental Conservation*:1–10.
- 517 Julliard, R., J. Clavel, V. Devictor, F. Jiguet, and D. Couvet. 2006. Spatial segregation  
518 of specialists and generalists in bird communities. *Ecology Letters* 9:1237–1244.
- 519 Kéry, M. 2004. Extinction Rate Estimates for Plant Populations in Revisitation  
520 Studies: Importance of Detectability. *Conservation Biology* 18:570–574.

- 521 Kéry, M., R. M. Dorazio, L. Soldaat, A. van Strien, A. Zuiderwijk, and J. A. Royle.  
522 2009. Trend estimation in populations with imperfect detection. *Journal of*  
523 *Applied Ecology* 46:1163–1172.
- 524 Kéry, M., and M. Plattner. 2007. Species richness estimation and determinants of  
525 species detectability in butterfly monitoring programmes. *Ecological*  
526 *Entomology* 32:53–61.
- 527 Krauss, J., R. Bommarco, M. Guardiola, R. K. Heikkinen, A. Helm, M. Kuussaari, R.  
528 Lindborg, E. Ockinger, M. Pärtel, J. Pino, J. Pöyry, K. M. Raatikainen, A. Sang,  
529 C. Stefanescu, T. Teder, M. Zobel, and I. Steffan-Dewenter. 2010. Habitat  
530 fragmentation causes immediate and time-delayed biodiversity loss at different  
531 trophic levels. *Ecology Letters* 13:597–605.
- 532 Kuussaari, M., M. Saarinen, E.-L. Korpela, J. Pöyry, and T. Hyvönen. 2014. Higher  
533 mobility of butterflies than moths connected to habitat suitability and body size  
534 in a release experiment. *Ecology and Evolution* 4:3800–3811.
- 535 Leon-Cortes, J. L., M. J. R. Cowley, and C. D. Thomas. 1999. Detecting decline in a  
536 formerly widespread species: how common is the common blue butterfly  
537 *Polyommatus icarus*? *Ecography* 22:643–650.
- 538 Leon-Cortes, J. L., M. J. R. Cowley, and C. D. Thomas. 2000. The distribution and  
539 decline of a widespread butterfly *Lycaena phlaeas* in a pastoral landscape.  
540 *Ecological Entomology* 25:285–294.
- 541 McKinney, M. L., and J. L. Lockwood. 1999. Biotic homogenization: a few winners  
542 replacing many losers in the next mass extinction. *Trends in Ecology &*  
543 *Evolution* 14:450–453.
- 544 Murray, K. A., D. Rosauer, H. McCallum, and L. F. Skerratt. 2011. Integrating  
545 species traits with extrinsic threats: closing the gap between predicting and  
546 preventing species declines. *Proceedings of the Royal Society B* 278:1515–23.
- 547 Musters, C. J. M., V. Kalkman, and A. van Strien. 2013. Predicting rarity and decline  
548 in animals, plants, and mushrooms based on species attributes and indicator  
549 groups. *Ecology and Evolution* 3:3401–3414.
- 550 Ockinger, E., O. Schweiger, T. O. Crist, D. M. Debinski, J. Krauss, M. Kuussaari, J.  
551 D. Petersen, J. Pöyry, J. Settele, K. S. Summerville, and R. Bommarco. 2010.  
552 Life-history traits predict species responses to habitat area and isolation: a cross-  
553 continental synthesis. *Ecology Letters* 13:969–979.
- 554 Oliver, T. H., H. H. Marshall, M. D. Morecroft, T. Brereton, C. Prudhomme, and C.  
555 Huntingford. 2015. Interacting effects of climate change and habitat  
556 fragmentation on drought-sensitive butterflies. *Nature Climate Change* 5:941–  
557 945.
- 558 Oliver, T., D. B. Roy, J. K. Hill, T. Brereton, and C. D. Thomas. 2010. Heterogeneous  
559 landscapes promote population stability. *Ecology Letters* 13:473–484.
- 560 Pannekoek, J., and A. Strien. 2005. TRIM 3. Trends and indices for monitoring data.  
561 CBS, Statistics Netherlands, Voorburg, Netherlands.
- 562 Pellet, J., J. T. Bried, D. Parietti, A. Gander, P. O. Heer, D. Cherix, and R. Arlettaz.  
563 2012. Monitoring butterfly abundance: beyond Pollard walks. *PloS ONE*

564 7:e41396.

565 Pimm, S. L., C. N. Jenkins, R. Abell, T. M. Brooks, J. L. Gittleman, L. N. Joppa, P.  
566 H. Raven, C. M. Roberts, and J. O. Sexton. 2014. The biodiversity of species and  
567 their rates of extinction, distribution, and protection. *Science* 344:1246752.

568 Sang, A., T. Teder, A. Helm, and M. Pärtel. 2010. Indirect evidence for an extinction  
569 debt of grassland butterflies half century after habitat loss. *Biological*  
570 *Conservation* 143:1405–1413.

571 Schmeller, D. S., P.-Y. Henry, R. Julliard, B. Gruber, J. Clobert, F. Dziock, S.  
572 Lengyel, P. Nowicki, E. DériI, E. Budrys, T. Kull, K. Tali, B. Bauch, J. Settele,  
573 C. Van Swaay, A. Kobler, V. Babij, E. Papastergiadou, and K. Henle. 2009.  
574 Advantages of Volunteer-Based Biodiversity Monitoring in Europe.  
575 *Conservation Biology* 23:307–316.

576 Schweiger, O., A. Harpke, M. Wiemers, and J. Settele. 2014. CLIMBER: Climatic  
577 niche characteristics of the butterflies in Europe. *ZooKeys* 367:65–84.

578 Sekar, S. 2012. A meta-analysis of the traits affecting dispersal ability in butterflies:  
579 can wingspan be used as a proxy? *Journal of Animal Ecology* 81:174–84.

580 Settele, J., and M. Wiemers. 2015. Biodiversity: Interacting global change drivers.  
581 *Nature Climate Change* 5:913–914.

582 Stefanescu, C., J. Carnicer, and J. Peñuelas. 2011a. Determinants of species richness  
583 in generalist and specialist Mediterranean butterflies: the negative synergistic  
584 forces of climate and habitat change. *Ecography* 34:353–363.

585 Stefanescu, C., J. Penuelas, and I. Filella. 2003. Effects of climatic change on the  
586 phenology of butterflies in the northwest Mediterranean Basin. *Global Change*  
587 *Biology* 9:1494–1506.

588 Stefanescu, C., I. Torre, J. Jubany, and F. Páramo. 2011b. Recent trends in butterfly  
589 populations from north-east Spain and Andorra in the light of habitat and climate  
590 change - Springer. *Journal of Insect Conservation* 15:83–93.

591 Stephens, P. A., L. R. Mason, R. E. Green, R. D. Gregory, J. R. Sauer, J. Alison, A.  
592 Aunins, L. Brotons, S. H. M. Butchart, T. Campedelli, T. Chodkiewicz, P.  
593 Chylarecki, O. Crowe, J. Elts, V. Escandell, R. P. B. Foppen, H. Heldbjerg, S.  
594 Herrando, M. Husby, F. Jiguet, A. Lehikoinen, A. Lindstrom, D. G. Noble, J.-Y.  
595 Paquet, J. Reif, T. Sattler, T. Szep, N. Teufelbauer, S. Trautmann, A. J. van  
596 Strien, C. A. M. van Turnhout, P. Vorisek, and S. G. Willis. 2016. Consistent  
597 response of bird populations to climate change on two continents. *Science*  
598 352:84–87.

599 Sutherland, W. J., R. P. Freckleton, H. C. J. Godfray, S. R. Beissinger, T. Benton, D.  
600 D. Cameron, Y. Carmel, D. A. Coomes, T. Coulson, M. C. Emmerson, R. S.  
601 Hails, G. C. Hays, D. J. Hodgson, M. J. Hutchings, D. Johnson, J. P. G. Jones,  
602 M. J. Keeling, H. Kokko, W. E. Kunin, X. Lambin, O. T. Lewis, Y. Malhi, N.  
603 Mieszekowska, E. J. Milner-Gulland, K. Norris, A. B. Phillimore, D. W. Purves,  
604 J. M. Reid, D. C. Reuman, K. Thompson, J. M. J. Travis, L. A. Turnbull, D. A.  
605 Wardle, and T. Wiegand. 2013. Identification of 100 fundamental ecological  
606 questions. *Journal of Ecology* 101:58–67.

607 Thomas, C. D., A. Cameron, R. E. Green, M. Bakkenes, L. J. Beaumont, Y. C.



- 608 Collingham, B. F. N. Erasmus, M. F. de Siqueira, A. Grainger, L. Hannah, L.  
609 Hughes, B. Huntley, A. S. van Jaarsveld, G. F. Midgley, L. Miles, M. A. Ortega-  
610 Huerta, A. Townsend Peterson, O. L. Phillips, and S. E. Williams. 2004a.  
611 Extinction risk from climate change. *Nature* 427:145–148.
- 612 Thomas, J. A. 2005. Monitoring change in the abundance and distribution of insects  
613 using butterflies and other indicator groups. *Philosophical transactions of the*  
614 *Royal Society of London. Series B, Biological sciences* 360:339–57.
- 615 Thomas, J. A., M. G. Telfer, D. B. Roy, C. D. Preston, J. J. D. Greenwood, J. Asher,  
616 R. Fox, R. T. Clarke, and J. H. Lawton. 2004b. Comparative losses of British  
617 butterflies, birds, and plants and the global extinction crisis. *Science* 303:1879–  
618 81.
- 619 Thuiller, W., C. Albert, M. B. Araújo, P. M. Berry, M. Cabeza, A. Guisan, T. Hickler,  
620 G. F. Midgley, J. Paterson, F. M. Schurr, M. T. Sykes, and N. E. Zimmermann.  
621 2008. Predicting global change impacts on plant species' distributions: Future  
622 challenges. *Perspectives in Plant Ecology, Evolution and Systematics* 9:137–152.
- 623 Van Dyck, H., D. Bonte, R. Puls, K. Gotthard, and D. Maes. 2015. The lost  
624 generation hypothesis: could climate change drive ectotherms into a  
625 developmental trap? *Oikos* 124:54–61.
- 626 Van Dyck, H., A. J. Van Strien, D. Maes, and C. A. M. Van Swaay. 2009. Declines in  
627 Common, Widespread Butterflies in a Landscape under Intense Human Use.  
628 *Conservation Biology* 23:957–965.
- 629 Van Swaay, C., M. Warren, and G. Lois. 2006. Biotope Use and Trends of European  
630 Butterflies. *Journal of Insect Conservation* 10:189–209.
- 631 Visconti, P., M. Bakkenes, D. Baisero, T. Brooks, S. H. M. Butchart, L. Joppa, R.  
632 Alkemade, M. Di Marco, L. Santini, M. Hoffmann, L. Maiorano, R. L. Pressey,  
633 A. Arponen, L. Boitani, A. E. Reside, D. P. van Vuuren, and C. Rondinini. 2015.  
634 Projecting Global Biodiversity Indicators under Future Development Scenarios.  
635 *Conservation Letters* 9:5–13.
- 636 Vitousek, P. M. 1997. Human Domination of Earth's Ecosystems. *Science* 277:494–  
637 499.
- 638 Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 2008. Human  
639 Domination of Earth's Ecosystems. Pages 3–13 *Urban Ecology: An International*  
640 *Perspective on the Interaction Between Humans and Nature*. Springer.
- 641 Wood, F. S. 2014. gamm4: Generalized additive mixed models using mgcv and  
642 lme4. R package version 0.2-3.

643 **Fig 1.** Observed (dots) and model derived predictions (lines) for (a) the detection  
644 probability in relation to years; (b) population growth rates ( $r$ ) in relation to the  
645 Species Specialisation Index (SSI) for univoltine (black), bivoltine (yellow) and  
646 multivoltine species (blue). In both figures,  $n_{\text{univoltine}} = 30$ ,  $n_{\text{bivoltine}} = 11$  and  $n_{\text{multivoltine}}$   
647  $= 25$ . Parameters were estimated using weighted estimates of the best models.  
648 Continuous lines relate to the estimated fit that sets all the other covariates as constant  
649 at their median value; dashed lines denote the 95% confidence intervals.  
650

651 **Fig 2.** (a) Violin plots for the seasonal coefficient of variation in the abundance of the  
652 butterfly species ( $CV_W$ ) in relation to their voltinism, grey shapes show the density  
653 distribution of the y-axis covariate, grey circles stand for the median, black bars for  
654 the quartiles Q1 and Q3; (b) observed data (dots) and model-derived predictions  
655 (lines) for the inter-annual variation ( $CV_B$ ) in relation to the Species Specialisation  
656 Index (SSI) for univoltine (black squares), bivoltine (yellow circles) and multivoltine  
657 species (blue triangles). In both figures,  $n_{\text{univoltine}} = 30$ ,  $n_{\text{bivoltine}} = 11$  and  $n_{\text{multivoltine}} =$   
658  $25$ . Parameters were estimated using weighted estimates of the best models.  
659 Continuous lines relate to the transformed estimated fit setting all the other covariates  
660 as constant at their median value; dashed lines denote the 95% confidence intervals.  
661

662 **Table 1.** Weighted parameter estimates of the effect sizes and the associated standard  
663 errors of the species traits retained in the best models for (a) population growth rates,  
664 (b) the seasonal ( $CV_W$ ) and (c) inter-annual ( $CV_B$ ) coefficients of variation in the  
665 abundance of the butterfly species. Models for CV were fitted to a Gamma  
666 distribution with an inverse link (i.e. estimates are produced with an inverted sign);  
667 estimates are expressed within this distribution. Significant p values are marked in  
668 italics.

669

Parameter	Estimate	Std. Error	t or z value	p value ( $H_0 = \text{Estimate} = 0$ )
(a)				
Intercept: vol-univoltine	8e-4	9e-4	0.837	0.403
vol-bivoltine	1e-4	6e-4	0.170	0.865
vol-multivoltine	-0.001	4e-4	2.163	<i>0.031</i>
SSI	-0.001	6e-4	2.304	<i>0.021</i>
of-e	-0.007	0.012	0.558	0.577
wl	4e-4	1e-5	0.274	0.784
(b)				
(Intercept): ls-1, ow- immature, vol-univoltine	6.003	0.457	13.127	<i>&lt;2e-16</i>
vol-bivoltine	-1.585	0.399	-3.970	<i>7e-5</i>
vol-multivoltine	-1.769	0.325	-5.444	<i>1e-7</i>
SSI	-0.200	0.388	0.515	0.607
ls-2	0.554	0.325	1.702	0.088
ls-3	1.099	0.403	2.724	<i>0.006</i>

of-e	12.025	8.475	1.419	0.156
ow-mature	-0.957	0.326	2.934	0.003
ow-migratory	0.113	0.683	0.165	0.869
<i>random effect</i>	Variance	Std.Dev.	Residual	Std.Dev.
Species	0.380	0.617	0.436	0.660
(c)				
Intercept: vol-univoltine	8.686	1.169	7.285	$<2e-16$
vol-bivoltine	-1.764	0.842	2.057	0.039
vol-multivoltine	-2.423	0.715	3.325	$8e-4$
SSI	-2.231	0.722	3.031	0.002
of-e	-16.843	17.755	0.939	0.348

670

671 *SSI: Species Specialisation Index; ls: larval trophic specialisation; of-e: open-forest*

672 *estimate; wl: wing length; STI: Species Temperature Index; vol: voltinism; ow:*

673 *overwintering stage*

674

675

676

677

678