



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

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

3

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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) and the Andorran
127 Butterfly Monitoring Scheme (BMSAnd; see 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). 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 (≥ 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

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430

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442

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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><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*

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