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2 Climate conditions and resource availability drive return elevational migrations in a single-brooded  
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24 advice.

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26 **Abstract** Seasonal elevational migrations have important implications for life-history evolution, and  
27 ecological responses to environmental change. However, evidence is still scarce for their existence and  
28 potential causes for most species, particularly invertebrates. We tested the extent to which seasonal  
29 abundance patterns in central Spain for overwintering (breeding) and summer (non-breeding)  
30 individuals of the butterfly *Gonepteryx rhamni* were consistent with three hypotheses explaining  
31 elevational migration: resource limitation (host plant and flower availability), physiological constraints  
32 of weather (maximum temperatures) and habitat limitation (forest cover for overwintering). For  
33 overwintering adults, abundance was positively associated with host plant density during two intensive  
34 survey seasons (2007-2008), and the elevational distribution was relatively stable over a seven-year  
35 period (2006-2012). The elevational distribution of summer adults was highly variable, apparently  
36 related both to temperature and habitat type. Sites occupied by adults in summer were on average 3°C  
37 cooler than their breeding sites, and abundance showed negative associations with summer  
38 temperature, and positive associations with forest cover and host plant density in 2007 and 2008. The  
39 results suggest that the extent of uphill migration in summer could be driven by different factors  
40 depending on the year, mostly consistent with physiological constraint and habitat limitation  
41 hypotheses. In contrast, the patterns for overwintering adults suggest that downhill migration can be  
42 explained by resource availability. Climate change could generate bottlenecks in the populations of  
43 elevational migrant species by constraining the area of specific seasonal habitat networks, or reducing  
44 the proximity of environments used at different times of year.

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46 **Keywords** Climate change · elevational distribution · *Gonepteryx rhamni* · Lepidoptera · seasonal  
47 movements

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## 49 **Introduction**

50 Animal migration involves costs and benefits: potential costs include energetic expenses, increased  
51 predation risk and reproductive costs, whereas potential benefits include increased survival and  
52 reproduction due to exploitation of new resources and avoidance of adverse environmental conditions  
53 (Rankin and Burchsted 1992). Migration is expected to evolve only under circumstances in which  
54 remaining in natal habitat would be detrimental relative to migrating to a different site (Southwood  
55 1977; Rankin and Burchsted 1992). Migration has been classified in different ways depending on the  
56 organism, and spatial or temporal attributes (Dingle and Drake 2007). Typical migrations involve  
57 seasonal displacements over hundreds of km between high-latitude summer habitats and low-latitude  
58 spring habitats (e.g. Chapman et al. 2012). Depending on the life cycle duration, organisms may breed  
59 multiple times within a season producing several generations as populations migrate polewards during  
60 spring and summer, and equatorwards during autumn, or alternatively the same individuals may  
61 perform the complete round trip (Ramenofsky and Wingfield 2007).

62 Organisms also show shorter-distance seasonal movements over elevational gradients called  
63 elevational migrations. Elevational migrations have been reported from nearly all continents and from  
64 several vertebrate and insect taxa, but most evidence is based on birds (McGuire and Boyle 2013).  
65 Nevertheless, potential hypotheses explaining bird elevational migration are applicable to other taxa,  
66 since they involve resource availability (e.g. Boyle 2010), physiological constraints of weather (e.g.  
67 Boyle et al. 2010), predation risk (e.g. Boyle 2008), habitat limitation, and competition for mates  
68 (McGuire and Boyle 2013).

69 Elevational migration has been documented through different methods with different  
70 discriminatory power (McGuire and Boyle 2013). Ideally, telemetry of animals will provide spatially  
71 and temporally detailed movement information at an individual level (e.g. Norbu et al. 2013). This  
72 approach is feasible for some vertebrates, but in the case of many insects, the combination of small  
73 sizes, short life cycle, large populations and relatively high flying speed make it difficult to follow  
74 individuals (Osborne et al. 2002; but see Urquhart and Urquhart 1978; Wikelski et al. 2006).

75 Alternatively, elevational migration can be documented through abundance or distribution surveys at  
76 multiple elevations and periods (McGuire and Boyle 2013). Then, correlative distribution models can  
77 be applied to assess the importance of different variables in determining elevational shifts between  
78 periods. This approach has been successfully applied to several species and provided important clues  
79 in relation to the drivers of elevational migrations (e.g. Brambilla et al. 2012; Marini et al. 2013).

80 The importance of seasonal migration to the life-cycles of some Lepidoptera is well established  
81 (e.g. Williams 1930). The monarch butterfly *Danaus plexippus* exemplifies the typical insect engaged  
82 in mass latitudinal migrations over long distances (e.g. Urquhart and Urquhart 1978), and latitudinal  
83 migrations of other Lepidoptera at Temperate latitudes have been well documented (e.g. Mikkola  
84 2003; Stefanescu et al. 2007, 2013; Brattström et al. 2010; Chapman et al. 2012). Elevational  
85 migrations have been reported for several Lepidoptera species (e.g. Larsen 1976, 1982; Shapiro 1973,  
86 1974a, b, 1975, 1980, Stefanescu 2001), but in most cases, no explicit assessment of potential  
87 hypotheses explaining the phenomenon has been made. One exception is a study on the butterfly  
88 *Vanessa atalanta*, in which the resource availability hypothesis was supported (Stefanescu 2001).

89 In this paper, we test the resource availability, physiological constraints of weather, and habitat  
90 limitation hypotheses as potential explanations for uphill and downhill movements of the brimstone  
91 butterfly *Gonepteryx rhamni* (L.), in a mountain area in Spain. This species is particularly appropriate  
92 to study elevational migrations because it has a relatively high mobility (Gutiérrez and Thomas 2000),  
93 and regional movements between hibernating and breeding areas have been hypothesised to occur  
94 along elevational gradients (Larsen 1976, 1982; García-Barros et al. 2013). *G. rhamni* is a single-  
95 brooded species which develops from egg to adult in spring and has a non-reproductive period in  
96 summer until hibernation, after which the mating season occurs the following spring (Wiklund et al.  
97 1996). In our study, we first determine the extent of the migration by examining abundance patterns  
98 over elevation for overwintering (breeding) and summer (non-breeding) individuals. Then, we model  
99 separately the abundance of overwintering and summer individuals based on environmental resources  
100 and conditions to assess the relevance of the three proposed hypotheses. We expected stronger support  
101 for the resource availability hypothesis (based on host plant abundance) for overwintering individuals,

102 because of the requirement for breeding sites. In contrast, the distribution of summer (non-breeding)  
103 individuals could have been driven by physiological constraints (temperature), habitat limitation (e.g.  
104 overwintering sites) and/or resource availability (e.g. flower abundance).

## 105 **Materials and methods**

### 106 **Study system**

107 *Gonepteryx rhamni* (L.) is a widespread species in Europe, whose larvae feed on shrubs from the  
108 family Rhamnaceae. It has one adult generation per year (emerging in June-August), and hibernates as  
109 an adult (resuming activity in late winter) (Tolman and Lewington 1997). In Spain, *G. rhamni* is a  
110 relatively common species, but in the southern half of the country the populations are more frequent in  
111 mountains (García-Barros et al. 2004). There are no detailed records of overwintering habitats for *G.*  
112 *rhamni* in the study area, but wooded areas have been suggested elsewhere in Europe (Pollard and  
113 Hall 1980).

114 The Sierra de Guadarrama (central Spain) is an approximately 100 x 30 km mountain range located  
115 at 40°45' N 4°00' W. The mountain range is bordered by plains with elevations of c. 700 m (to the  
116 north) and c. 500 m (to the south) and reaches a maximum elevation of 2428 m (Fig. 1). The main  
117 regional host plants reported for *G. rhamni* are *Frangula alnus* Mill. and *Rhamnus cathartica* L.  
118 (based on oviposition and larval records, D. Gutiérrez and R.J. Wilson, unpublished data), although at  
119 least two other species from the family Rhamnaceae occur in the study area (*R. lycioides* L. and *R.*  
120 *alaternus* L.).

### 121 **Elevational abundance of *G. rhamni***

122 To study the elevational patterns of *G. rhamni* abundance, butterflies (including *G. rhamni*, if present)  
123 were counted in 2007 and 2008 on standardised 500 m long by 5 m wide transects at 40 sites ranging  
124 558-2251 m in elevation. A subsample of 24 of those 40 sites were also visited following identical  
125 methodology in 2006 and 2009-2012 to examine the temporal variability of elevational patterns.

126 Transects were walked during suitable conditions for butterfly activity (sunshine and no more than

127 light wind, between 10:00 h and 17:00 h European Summer Time; Pollard and Yates, 1993), every two  
128 weeks from April to October in 2006, and from March to October since 2007. Due to snow cover and  
129 unsuitable weather, transect walking started later than March or April in some years at sites above  
130 1700-1800 m.

131 During counts, we explicitly distinguished overwintering from summer *G. rhamni* adults based on  
132 wing condition. In the Sierra de Guadarrama, overwintering adults fly from early March (some  
133 occasional records in February in warm winters) to June, whereas summer adults fly from June to  
134 October. Because overwintering adults are increasingly worn over the season, they are easily  
135 distinguished from recently emerged summer adults (in excellent condition) over the potential overlap  
136 in flight period of both generations in June. Sexes were recorded separately in the field but were  
137 pooled together for analyses, because of no obvious sex-related patterns and a much smaller sample  
138 size for females. For each site and year, overwintering and summer adult abundances were calculated  
139 as the sum of all counts of overwintering and summer individuals over the season. During transect  
140 walking and additional visits to sites, information on reproductive (oviposition) and feeding  
141 (nectaring) behaviour was also recorded.

## 142 **Environmental variables**

143 Universal Transverse Mercator (UTM) coordinates were recorded c. every 100 m along transects using  
144 a handheld Garmin GPS unit, and were used to plot transects in a geographic information system  
145 (ArcGIS) (ESRI 2001). The average elevation of 100 m cells intercepted by transects was determined  
146 using a digital elevation model (Farr et al. 2007).

147 To examine potential determinants of the elevational distribution of overwintering and summer  
148 adults, we collected environmental variables from the field (spring and summer temperatures, host  
149 plant density, summer flower abundance) and from digital layers (forest cover). The biological  
150 significance of each variable is detailed in Table 1.

151 For the period 2006-2012, hourly air temperature was recorded by HOBO H8 Pro HR/Temp and  
152 U23 HR/Temp loggers in semi-shaded conditions at each of the 40 sampling sites (one logger per

153 site). Twenty data loggers were started in spring 2004 (20 of the 40 sampling sites) and twenty in  
154 spring 2006. Mechanical failure or damage to some data loggers due to snow, animals or human  
155 interference, generated gaps of variable duration in the data set. Therefore daily average, maximum  
156 and minimum temperature time series had to be interpolated for some loggers to subsequently estimate  
157 spring and summer temperatures (Electronic supplementary material, ESM, Appendix S1).

158 Interpolated daily maximum temperature data were used to calculate both monthly mean maximum  
159 temperatures and subsequently spring (March-May) and summer (June-August) mean maximum  
160 temperatures. Seasonal temperatures were based on maximum instead of mean daily temperatures  
161 because they more likely represent the conditions experienced by a daylight flying insect like *G.*  
162 *rhamni* (e.g. Wiklund et al. 1996). Spring and summer mean maximum temperatures were highly  
163 correlated, respectively, with spring and summer mean temperatures both in 2007 and 2008 (all four  
164 Spearman's rank correlation coefficients  $r_s$  ranged 0.92-0.97).

165 The abundance of host plants was estimated at each of the 40 transect sites in 2006, with some  
166 additional records in 2008. The route of the 500 m transect was followed in August–September 2006  
167 and the number of plants of *F. alnus*, *R. cathartica* and *R. lycioides* (*R. alaternus* was absent from  
168 sampling sites) that occurred in the 5 m wide butterfly transect was recorded, to give a density of each  
169 species per 0.25 ha (500 × 5 m). If none of the plant species were present in the 5 m wide transect,  
170 then the transect was repeated with increasing widths of 10 m, 20 m, and up to a maximum of 50 m  
171 width (i.e. 25 m on either side of the recorder). In this case, host plant density per 0.25 ha was  
172 estimated based on the increased transect width. Host plant species were considered present at a site if  
173 they were found in transects of  $\leq 50$  m wide (Merrill et al. 2008). To test for temporal variability in  
174 host plant density, the number of plants that occurred in the 5 m wide transect was counted again in  
175 2009.

176 Summer flower abundance was estimated during the summer adult flight peak in 2007 and 2008 by  
177 taking twenty 0.25 m<sup>2</sup> quadrats (50 x 50 cm) at 25 m intervals along each transect. We set quadrats in  
178 late July 2007 and late July-early August in 2008, and flower abundance was estimated by counting  
179 the number of 2.5 x 2.5 cm sub-quadrats (100 per quadrat) containing more than 4 cm<sup>2</sup> surface of

180 flowers. Data from elsewhere in Spain show that *G. rhamni* is not a specialist flower visitor  
181 (Stefanescu and Traveset 2009), and therefore we considered that all flowering species could be  
182 potential nectar sources.

183 Forest cover was estimated from regional land-cover maps obtained in vector format at 1:50,000  
184 scale (Ministerio de Medio Ambiente, 2000, 2002a, b, 2003), which showed good agreement for all  
185 transects with our own field observations of general vegetation type (Gutiérrez Illán et al. 2010).  
186 Vector data from the land-cover maps (minimum cartographic unit 2.25 ha) were used to determine  
187 the proportional contribution of total forest cover to each 100-m grid cell. Forest cover for each site  
188 was estimated as the mean for 100 m grid cells intercepted by each transect.

### 189 **Elevational abundance models**

190 To analyse *G. rhamni* abundance, we applied **Generalised Linear Models (GLMs)** with a quasi-  
191 likelihood estimation of regression coefficients using a log-link and setting the variance equal to mean  
192 (quasi-Poisson regression, McCullagh and Nelder 1989). The information-theoretic approach  
193 (Burnham and Anderson 2002) was used to model *G. rhamni* abundance. First, elevational trends in  
194 abundance for overwintering and summer individuals in 2007 and 2008 were analysed, and second,  
195 more complex models including environmental variables were tested to explain the observed trends in  
196 abundance over the elevational gradient. For analysing elevational trends in abundance, linear and  
197 quadratic models including elevation only were fitted. The more complex models for potential  
198 explanatory factors included three candidate variables (spring mean maximum temperatures, host plant  
199 density, forest cover) for overwintering individuals and four variables (summer mean maximum  
200 temperatures, host plant density, flower abundance, forest cover) for summer individuals (Table 1).  
201 Pair-wise correlations between the independent variables had absolute values lower than 0.7  
202 (commonly applied threshold for testing for collinearity, Dormann et al. 2013). Linear and quadratic  
203 terms for the environmental condition variables and only linear terms for the strictly resource variables  
204 were included (Table 1). Confidence sets were based on the Akaike Information Criterion for small  
205 sample size (QAIC<sub>c</sub>; Burnham and Anderson 2002; ESM, Appendix S2).



206 Following model selection, model-averaging was used to obtain model coefficients based on the  
207 confidence sets (Burnham and Anderson 2002). This approach incorporates model selection  
208 uncertainty whilst weighting the influence of each model by the strength of its supporting evidence.  
209 Model-averaged coefficients were calculated by weighting using Akaike weights, and averaging  
210 coefficients over all models in the confidence sets. Averaging over all models means that in those  
211 cases in which a given variable was not included in a particular model, its coefficient value was set to  
212 zero. Relative variable importance (parameter lying in the range 0-1, which provides evidence about  
213 the relevance of each variable relative to the others) was calculated as the sum of Akaike weights  
214 across all models in the confidence set that contain that variable. Model selection and averaging were  
215 performed using 'MuMIn' package (R Development Core Team 2012; Bartoń 2012).

216 Spatial autocorrelation can influence the reliability of ecological analyses, and potentially generates  
217 models containing a relatively larger number of predictors in information theoretic approaches (e.g.  
218 Diniz-Filho et al. 2008). To test for spatial autocorrelation, all-directional correlograms (Legendre and  
219 Legendre 1998) were generated for abundance data of overwintering and summer adults in 2007 and  
220 2008 by plotting values of Geary's  $c$  coefficient (recommended for variables departing from  
221 normality) against Euclidean distances between sites. Geary's  $c$  calculation and testing for significance  
222 were performed using 4999 Monte Carlo permutations in Excel add-in Rookcase (Sawada 1999). No  
223 correlogram was globally significant, suggesting that spatial autocorrelation in *G. rhamni* abundance  
224 data was negligible.

225 After identifying the model confidence sets for *G. rhamni* abundance, hierarchical partitioning  
226 (HP) was used to assess independent and joint effects of each parameter in single models with all  
227 parameters (Chevan and Sutherland 1991; Mac Nally 1996). Poisson regression and log-likelihood as  
228 the goodness-of-fit measure were used for HP calculations, and statistical significance of the  
229 independent contributions was tested by a randomization routine (1000 permutations) based on Z-  
230 scores (Mac Nally 2002). HP was conducted using the 'hier.part' package (Mac Nally and Walsh  
231 2004). One of the limitations of HP as currently implemented in the 'hier.part package' is that it  
232 depends on monotonic relationships between the response and predictor variables. However, all

233 relationships of abundances of overwintering and summer adults against environmental variables were  
234 monotonic (see below) and hence this was not a major problem.

### 235 **Temporal variability in elevational patterns**

236 To examine variability in elevational abundance patterns over time, we used *G. rhamni* abundance  
237 data collected at 24 sites over a 7-year period (2006-2012). Mean elevation was calculated separately  
238 for overwintering and summer individuals each year by averaging the elevations of all sites where *G.*  
239 *rhamni* was present, weighted by abundance at each site. To test the potential dependency over time of  
240 elevational abundance patterns on climate conditions, mean elevations of overwintering and summer  
241 adults were compared with spring and summer mean maximum temperatures, respectively, using  
242 Spearman's rank correlation coefficients ( $r_s$ ). To examine the importance of temperature, host plant  
243 density and forest cover on *G. rhamni* abundance in different years, quasi-Poisson regressions were  
244 performed based on the 24-site data set and using the same approach as for the 40-site data set.

245 To examine the extent to which *G. rhamni* adults maintain the temperatures experienced from  
246 spring to summer, weighted mean temperature was calculated separately for overwintering (March-  
247 May temperatures) and summer (June-August temperatures) individuals using the same approach as  
248 for weighted mean elevation. Finally, to determine the extent to which the breeding sites have greater  
249 temperatures in summer than those experienced by adult butterflies, mean temperatures were  
250 calculated at sites where larval host plants were present.

### 251 **Results**

252 A total of 212 overwintering and 116 summer *G. rhamni* individuals were counted in 2007, and 238  
253 overwintering and 96 summer individuals in 2008. The phenology of overwintering adults was similar  
254 in 2007 and 2008, whereas that of summer adults was delayed in 2008 relative to 2007 (Fig. 2). Eight  
255 females were recorded ovipositing on *F. alnus* and *R. cathartica* at transect sites; the earliest  
256 oviposition record was on 1 April 2011 and the latest on 12 June 2008. A total of 70 nectaring records  
257 were collected over 2007-2012 from 16 plant genera from 13 different families, supporting the idea  
258 that *G. rhamni* adults are not specialist flower visitors (Stefanescu and Traveset 2009). Mean

259 maximum and minimum temperatures peaked in July or August depending on site (ESM, Fig. S1).

260 The warmest mean maximum temperature was in July at the lowest site (c. 38°C) and in August at the  
261 highest site (c. 20°C).

## 262 **Elevational patterns**

263 In 2007, overwintering adults were recorded at 23 sites (739-1635 m elevation range) and summer  
264 adults at 25 sites (1020-2251 m); in 2008, overwintering adults were recorded at 23 sites (844-1925 m)  
265 and summer adults at 21 sites (1056-1976 m). Maximum local abundances were 39 overwintering (at  
266 1270 m) and 22 summer (at 1499 m) individuals in 2007, and 54 overwintering (at 960 m) and 14  
267 summer (at 1270 and 1327 m) individuals in 2008 (Fig. 3).

268 There were quadratic relationships between abundance and elevation for overwintering and  
269 summer individuals in both study years (Table 2, Fig. 3). Models including only the linear term for  
270 elevation had a QAIC<sub>c</sub> difference of more than 6 from the quadratic (best) model (indicating that they  
271 were not well supported; Burnham and Anderson 2002; Richards 2008), in all four cases. Modelled  
272 maximum abundance for overwintering individuals peaked at 1214 m in 2007 and 1152 m in 2008,  
273 and for summer individuals at 1604 m in 2007 and 1387 m in 2008. Abundances of overwintering and  
274 summer adults were not significantly correlated in 2007 ( $r_s = 0.23$ ,  $P = 0.158$ ,  $N = 40$ ), but they were  
275 in 2008 ( $r_s = 0.46$ ,  $P = 0.003$ ,  $N = 40$ ). No significant correlation was found between summer adult  
276 abundance in 2007 and overwintering adult abundance in 2008 (the same generation at different times)  
277 ( $r_s = 0.14$ ,  $P = 0.377$ ,  $N = 40$ ).

278 A total of 16 transect sites included potential larval host plants in 2006, with the three host plants  
279 (*F. alnus*, *R. cathartica* and *R. lycioides*) present, respectively, at nine, nine and one of the transect  
280 sites. The distribution of *R. lycioides* was restricted to the lowest site (558 m) of the study area  
281 (additional field searches showed that *R. cathartica* also occurs below 600 m), but all host plants were  
282 absent from the highest elevations (maximum elevation: 1504 m for *F. alnus*). Additional field  
283 searches at 90 sites included in a related study (Gutiérrez Illán et al. 2010) did not encounter any of the  
284 host plants above 1504 m. Hence, there was a c. 750 m elevational gap (1504-2251 m) without host

285 plants in the study area (Fig. 3). Mean elevation was 1208 m for all sites containing host plants. There  
286 was a highly significant positive correlation between host plant density (based on 5 m wide transect  
287 data) in 2006 and 2009 ( $r_s = 0.96$ ,  $P < 0.001$ ,  $N = 40$ ), suggesting that this variable was relatively  
288 constant in time.

289 Spring and summer mean maximum temperatures were highly negatively correlated with elevation  
290 in both study years. Summer flower abundance had no apparent elevational pattern in any year, and  
291 forest cover declined significantly with increased elevation (ESM, Fig. S2).

292 Weighted mean elevation within each season (at four-week intervals) was relatively stable for  
293 overwintering adults in 2007 and 2008 (Fig. 4; see ESM, Fig. S3 for results for males and females  
294 separately). However, for summer adults, weighted mean elevation increased over the season in 2007,  
295 and increased till August to subsequently decrease in September in 2008.

## 296 **Abundance models**

297 For the abundance of overwintering adults, model confidence sets consisted of two models both in  
298 2007 and 2008 (Table 3). The final averaged models included positive relationships with host plant  
299 density and forest cover (in 2007), and with host plant density and spring mean maximum temperature  
300 (in 2008). Relative variable importance was 1 for host plant density in both years, indicating it was the  
301 most important variable explaining overwintering adult abundance. Spring mean maximum  
302 temperature was also well supported in 2008 (variable importance  $\geq 0.9$ ).

303 For summer adults, the confidence sets consisted of three models both in 2007 and 2008. In 2007,  
304 the final model included positive relationships with host plant density and forest cover, and a negative  
305 relationship with summer mean maximum temperature. In 2008, the final model included those three  
306 variables plus a negative relationship with flower abundance. The most important variables explaining  
307 summer adult abundance were summer mean maximum temperature (variable importance 0.86-1) and  
308 forest cover (variable importance 0.81-1). Nevertheless, host plant density and flower abundance  
309 showed relatively high variable importance values in 2008 ( $> 0.8$ ).

310 In hierarchical partitioning, the independent effect of host plant density was the only statistically  
311 significant variable for overwintering adults in 2007 and 2008 (Fig. 5). The independent contributions  
312 were not significant for the two remaining variables in 2007 or for forest cover in 2008. For summer  
313 adults, summer mean maximum temperature had the only statistically significant independent  
314 contribution in 2007, but there were significant effects of host plant density and forest cover in 2008.

315 The negative joint contributions of summer mean maximum temperature, forest cover and flower  
316 abundance for summer adults (Fig. 5b, d) indicate that the joint action of other variables suppresses or  
317 masks the independent contribution of those particular predictors (Chevan and Sutherland 1991; Mac  
318 Nally 1996).

### 319 Temporal variability in elevational patterns

320 Weighted mean elevation was consistently higher and more variable for summer than for  
321 overwintering adults over the 7-year period (Fig. 6). Summer mean maximum temperatures were on  
322 average c. 12°C higher than spring mean maximum temperatures over the elevation gradient (Fig. 6).  
323 Spring and summer mean maximum temperatures tended to follow a similar pattern over the 7-year  
324 period, but the correlation was not significant ( $r_s = 0.68$ ,  $P = 0.094$ ,  $N = 7$ ). No correlation of  
325 overwintering or summer mean elevation of butterfly adults against the corresponding seasonal  
326 temperatures was significant ( $P > 0.5$ ). However, summer mean elevation was significantly positively  
327 correlated with summer mean maximum temperature if 2007 (the coldest summer) was excluded from  
328 analysis ( $r_s = 0.83$ ,  $P = 0.042$ ,  $N = 6$ ), suggesting that *G. rhamni* adults generally occurred at higher  
329 elevations in warmer summers (Fig. 6).

330 Models based on the 24 sites revealed that host plant density was the most important variable  
331 explaining overwintering adult abundance in all years, but spring mean maximum temperature was  
332 also included in all models with a positive effect (six years) or quadratic effect (one year) (ESM, Table  
333 S1). Summer mean maximum temperature was the most important variable associated with summer  
334 adult abundance with negative (three years) or quadratic (two years) effects. Host plant density was

335 positively associated with summer abundance in four years, three of which were relatively cold (ESM,  
336 Table S1, Fig. 6).

337 Weighted mean temperatures experienced by overwintering adults in spring ranged 15.4-18.9°C,  
338 and by summer adults 23.7-27.4°C. Mean temperatures at host plant sites in spring ranged 15.4-  
339 18.4°C, and in summer 26.5-30.4°C. Mean difference between weighted mean temperatures for  
340 butterflies and mean temperatures for host plants were +0.5°C in spring and -3°C in summer.

341 Correlations ( $r_s$ ) between overwintering and summer adult abundances within the same year ranged  
342 -0.01-0.58 ( $N = 24$  in all cases), with the only significant coefficient in 2008 ( $P = 0.003$ ; consistent  
343 with the analysis with a larger sample size above). Correlations between summer adult abundance in  
344 one year and overwintering adult abundance in the immediately following year ranged 0.04-0.48 ( $N =$   
345 24), and they were significant for summer adults 2008-overwintering adults 2009 ( $P = 0.026$ ) and  
346 summer adults 2011-overwintering adults 2012 ( $P = 0.017$ ), corresponding to years with relatively  
347 cold summers (Fig. 6).

## 348 Discussion

349 Our results show marked differences between the elevational abundance patterns for overwintering  
350 and summer *G. rhamni* adults. In both intensive study years (2007 and 2008), summer adults were on  
351 average at higher sites than overwintering adults, and this pattern was maintained over five additional  
352 years in which a smaller number of sites were sampled.

## 353 Migration as a mechanism to explain elevational abundance patterns

354 The differences in abundance patterns for overwintering and summer adults were consistent with  
355 seasonal elevational migration by *G. rhamni*. Our oviposition records, albeit relatively limited, were  
356 consistent with the univoltine life cycle reported for *G. rhamni* with spring breeding (García-Barros et  
357 al. 2013). As a result, the same individuals emerging in summer that migrate uphill must migrate back  
358 down to breed the next spring. The steadily higher weighted mean elevation of summer adults until  
359 late August suggested that uphill migration was a gradual phenomenon over summer (Fig. 4). The  
360 decreased weighted mean elevation of summer adults in September 2008 was consistent with downhill

361 migration in autumn, but this was not supported by 2007 data. Occasional observations of adult *G.*  
362 *rahamni* flying down in October and late winter suggest that downhill migration could occur in both  
363 periods, but this point would require further research.

364 One intriguing result (found also in the UK, Pollard and Yates 1993) is the fact that the abundance  
365 of overwintering individuals based on all sites was larger than that recorded in the previous summer  
366 (Table 2 and ESM, Table S1). This is clearly ecologically impossible (assuming that there is no  
367 significant immigration from outside the study area at some point in the season) because the number of  
368 individuals must decrease during hibernation. The exact reason for this is unknown, but it could be  
369 related to differences in behaviour in spring and summer, leading to differences in detectability  
370 (Pollard and Yates 1993). Reduced summer activity could also make difficult to quantify potential  
371 downhill movement in late summer.

372 Abundance models and hierarchical partitioning suggested that explanations for migration in one  
373 direction may not explain return movements in the opposite direction. We tested for effects of resource  
374 availability, physiological constraints of weather and habitat limitation (McGuire and Boyle 2013) and  
375 found that they were differentially supported for uphill and downhill migrations.

376 Several hypotheses could explain uphill migration of *G. rhamni*. In 2007, the strongest effect  
377 explaining summer adult abundance was summer mean maximum temperature (Table 3, Fig. 5), with  
378 *G. rhamni* more abundant at cooler sites during the summer period. This is in line with the  
379 physiological constraints of weather hypothesis, wherein climatic factors may pose direct challenges  
380 to survival (McGuire and Boyle 2013). Central Spain is characterised by a continental Mediterranean  
381 climate with extremely hot temperatures in summer exceeding 35°C at lower sites, but much cooler (c.  
382 20°C) higher up in the mountains (ESM, Figs S1 and S2). Extremely hot temperatures could affect  
383 survival and flight willingness in *G. rhamni*, but demonstrating this would require experimentation  
384 (e.g. Pruess 1967). In an experiment with caged individuals, Swedish *G. rhamni* showed higher flight  
385 willingness at 23-29°C than at 14-20°C, but temperatures above 29°C were not tested (Wiklund et al.  
386 1996). In 2008, the main variables explaining summer adult abundance were host plant density and  
387 forest cover. This year showed the smallest difference in elevation between overwintering and summer

388 adults, suggesting reduced elevational migration. The effect of forest cover was consistent with the  
389 habitat limitation hypothesis, which in the case of *G. rhamni* could be associated with availability of  
390 overwintering sites (Pollard and Hall 1980). Weighted mean elevations for summer adults were much  
391 more variable than those for overwintering adults (Fig. 6). This result, along with the different  
392 contributions of explanatory variables to abundance models based on 40 and 24-site data sets, suggests  
393 that uphill migrations could be driven by different factors depending on the particular year.  
394 Specifically, the physiological constraints of weather hypothesis would be expected to be more  
395 important in hotter summers. This fact was supported by the positive trend between weighted mean  
396 elevation for summer adults and summer mean maximum temperature (Fig. 6) (but we do not have  
397 any plausible explanation for the year 2007 outlier), and the negative or quadratic effects (based on 24  
398 sites) of summer mean maximum temperature in the warmest years (ESM, Table S1). Surprisingly, the  
399 resource availability hypothesis for adults was not supported at all, because summer flower abundance  
400 was only included in some models but with a negative effect (Table 3).

401 The hypotheses explaining uphill migration by *G. rhamni* strongly contrast with those supported  
402 for other butterfly species. For instance, uphill migration by *V. atalanta* has been suggested as a  
403 strategy to track larval resources through space and time (resource availability hypothesis) (Stefanescu  
404 2001). Although based on less detailed information, the same hypothesis has also been invoked to  
405 explain uphill migration by other species (e.g. Shapiro 1974a, 1975, 1980).

406 Resource availability for early stages apparently drives return downhill migration (either in  
407 autumn, or following hibernation) by *G. rhamni* individuals before spring breeding. Host plant density  
408 was the most important variable explaining overwintering adult abundance in 2007 and 2008 and in  
409 2006-2012 based on the reduced 24-site data set (Table 3, Fig. 5, ESM, Table S1). In addition,  
410 weighted mean elevation for overwintering adults was relatively constant over the 7-year study period  
411 and close to the mean elevation for host plants, regardless of climatic conditions (Fig. 6). Given the  
412 relative host plant specialism of *G. rhamni*, looking for larval host plants is probably one of the  
413 strongest evolutionary pressures favouring downhill migration in this species. Failure to do so will  
414 result in the highest fitness cost of no breeding at all.



415 One further hypothesis to explain elevational migration not considered in our study is predation  
416 risk, which states that migration has evolved in response to elevational differences in predation  
417 pressure (e.g. Boyle 2008). In the case of butterflies, this hypothesis has been discussed in terms of  
418 larval parasitism (e.g. Stefanescu et al. 2012). However, this is not applicable to *G. rhamni* because  
419 adults do not reproduce in summer. Evaluation of the predation risk hypothesis would require the  
420 difficult task of collecting information about adult predators.

421 Hilltopping (a mating strategy of some insect species in which males occupy prominent  
422 topographic features due to female scarcity) has been suggested as a component of uphill migration by  
423 some Hymenoptera (Hunt et al. 1999). However, *G. rhamni* is a spring-breeding species with  
424 patrolling behaviour, so hilltopping cannot explain the observed distribution of migrant adults in  
425 summer.

426 A final possibility is that differential survival might contribute to the elevational shifts shown in  
427 this study. Greater adult abundance at higher sites in summer relative to spring could arise from  
428 increasing survival of *G. rhamni* juvenile stages or adults with increasing elevation. However, three  
429 findings do not support this possibility as the main explanation: (1) substantial numbers of adults were  
430 recorded at elevations above the elevation range of larval host plants; (2) large numbers of individuals  
431 were recorded at lower elevations in spring following hibernation; (3) no significant correlation was  
432 found between overwintering and summer abundance within the same year for all years but one  
433 (2008); if *in situ* survival made a substantial contribution to the abundance of summer adults, some  
434 degree of correlation between overwintering and summer abundance would be expected (e.g. Pollard  
435 and Greated-Davies 1998).

436 One particularity of *G. rhamni* is that individuals make a return migration to the area from which  
437 they bred. This is the most common type of migration in birds and mammals, but has rarely been  
438 documented in insects (Holland et al. 2006; but see Samraoui et al. 1998). The best-known case of  
439 return latitudinal migration (associated with overwintering areas) is that performed by the best-studied  
440 migratory insect, the monarch butterfly (*Danaus plexippus*), but successive broods are involved while  
441 progressing northwards (Flockhart et al. 2013). Possible return elevational migrations have been

442 reported for some butterfly species in other areas with hot and dry summers, including *G. rhamni*  
443 (Larsen 1982). In this case, individuals were thought to breed at high elevations in summer and then to  
444 migrate downhill in autumn to overwinter (Larsen 1976). This opens questions regarding the extent to  
445 which variability in regional climates, resource distributions and seasonality may drive divergent  
446 elevational migration patterns within the same species, and the extent to which they may be subject to  
447 change in a changing climate. Our results suggest phenotypic plasticity in the extent and timing of  
448 return elevational migration by *G. rhamni*, probably linked to the fact that it is a univoltine species  
449 with long-lived adults. In this sense, the study of possible migration patterns in other species with  
450 similar life cycles could shed light on the life-history and evolution of elevational migration in insects.

451 The results presented here have some implications in the context of climate change. It was found  
452 that *G. rhamni* summer adults occurred at sites which were on average 3°C cooler than breeding (host  
453 plant) sites; that summer abundance was sometimes negatively associated with summer mean  
454 maximum temperatures; and that higher sites may have been occupied in warmer summers.  
455 Furthermore, numbers of post-overwintering adults per site were only significantly correlated with  
456 numbers of pre-hibernating adults after two relatively cool summers (2008 and 2011). Assuming that  
457 temperature is an important determinant of summer elevational distribution, this evidence suggests  
458 that a warming climate could eventually generate a bottleneck in *G. rhamni* populations in the Sierra  
459 de Guadarrama through the constraint of its summer habitat network. This is in line with the idea that  
460 climate change could affect elevational migrants (Inouye et al. 2000), but through a completely  
461 different mechanism to phenological synchrony with resources.

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- 470

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- 612

613 **Table 1** List of environmental variables included in the present study, classified by their biological  
 614 significance. Spring and summer mean maximum temperatures, and summer flower abundance were  
 615 recorded separately in 2007 and 2008. Host plant density was square-root transformed for analyses to  
 616 avoid influential effects of individual sites (Zuur et al. 2007)

Environmental variable (units)		Code	Mean (min-max)
Conditions: adult thermoregulation and larval development			
Spring mean maximum temperature (°C)	2007	Sprtmax	13.26 (5.67-20.54)
	2008		13.24 (5.49-21.44)
Summer mean maximum temperature(°C)	2007	Sumtmax	24.52 (16.74-34.45)
	2008		24.91 (17.54-35.90)
Resources: larval host plants and adult nectar sources			
Host plant density (number of plants 0.25 ha <sup>-1</sup> )		Hostpl	2.43 (0-29)
Summer flower abundance (percent cover)	2007	Flowab	3.08 (0-11.25)
	2008		1.64 (0-5.50)
Conditions and resources: conditions and sites for adult overwintering			
Forest cover (proportion cover)		Forest	0.63 (0-1)

617

618 **Table 2** GLMs (quasi-Poisson error and log-link) for the abundance of overwintering and summer *G.*  
 619 *rahamni* adults in 2007 and 2008 with elevation (km). The total number of individuals (Ind) and  
 620 coefficients (SE) for elevation and elevation<sup>2</sup> are shown. In the four cases, the quadratic models  
 621 showed QAIC<sub>c</sub> values which were lower by more than 6 units from those for the linear models (not  
 622 shown).  $N = 40$  sites in all cases

Model	Ind	Elevation	Elevation <sup>2</sup>	Intercept
Overwintering adults 2007	212	33.52 (8.89)	-13.81 (3.67)	-17.63 (5.32)
Summer adults 2007	116	13.54 (5.28)	-4.22 (1.73)	-9.14 (3.95)
Overwintering adults 2008	238	21.10 (9.57)	-9.16 (4.05)	-9.50 (5.54)
Summer adults 2008	96	26.35 (7.26)	-9.50 (2.62)	-16.52 (5.00)

623

624

625 **Table 3** Confidence set GLMs (quasi-Poisson error and log-link) for the abundance of overwintering  
 626 and summer *G. rhamni* adults in (a) 2007 and (b) 2008 ( $N = 40$  sites in all cases). The table indicates  
 627 the variables included in the model and the direction of their coefficients (+/-; codes in Table 1);  
 628 number of parameters (K, including one extra parameter for over-dispersion factor in QAIC<sub>c</sub>); Akaike  
 629 Information Criterion for small sample size corrected for over-dispersed count-data (QAIC<sub>c</sub>);  
 630 difference in QAIC<sub>c</sub> between current and best model ( $\Delta$ QAIC<sub>c</sub>). Relative importance (Imp), model-  
 631 averaged coefficients (Coef) and unconditional standard errors (SE) for each variable are also shown.  
 632 Dispersion parameter is for the full model  
 633 a) Overwintering adults 2007

Rank	Hostpl	Forest	Intercept	K	QAIC <sub>c</sub>	$\Delta$ QAIC <sub>c</sub>	QAIC <sub>cw</sub>
1	+	+	+	4	56.84	0.00	0.71
2	+		+	3	58.63	1.78	0.29
Imp	1	0.71					
Coef	0.49	0.88	0.27				
SE	0.09	0.66	0.63				

634 Dispersion parameter = 6.05

635 Summer adults 2007

Rank	Sumtmax	Hostpl	Forest	Intercept	K	QAIC <sub>c</sub>	$\Delta$ QAIC <sub>c</sub>	QAIC <sub>cw</sub>
1	-		+	+	4	58.44	0.00	0.81
2	-	+		+	4	62.53	4.09	0.10
3	-			+	3	62.80	4.36	0.09
Imp	1	0.10	0.81					
Coef	-0.18	0.02	1.24	4.35				
SE	0.08	0.15	0.67	1.55				

636 Dispersion parameter = 4.49

637

## 638 b) Overwintering adults 2008

Rank	Sprtmax	Hostpl	Intercept	K	QAIC <sub>c</sub>	ΔQAIC <sub>c</sub>	QAIC <sub>cw</sub>
1	+	+	-	4	59.72	0.00	0.94
2		+	+	3	65.09	5.37	0.06
Imp	0.94	1					
Coef	0.15	0.62	-1.41				
SE	0.06	0.08	1.12				

639 Dispersion parameter = 5.61

## 640 Summer adults 2008

Rank	Sumtmax	Hostpl	Flowab	Forest	Intercept	K	QAIC <sub>c</sub>	ΔQAIC <sub>c</sub>	QAIC <sub>cw</sub>
1	-	+	-	+	+	6	79.28	0.00	0.74
2		+	-	+	-	5	82.61	3.33	0.14
3	-	+		+	+	5	83.02	3.74	0.11
Imp	0.86	1	0.89	1					
Coef	-0.09	0.46	-0.28	1.94	1.36				
SE	0.05	0.10	0.14	0.65	1.40				

641 Dispersion parameter = 2.19

642

643 **Figure legends**

644 **Fig. 1** Site distribution for *G. rhamni* in 2006-2012. Squares show 2006-2012 sites ( $N = 24$ ) and  
 645 circles additional 2007-2008 sites ( $N = 16$ ) for modelling abundance. Filled symbols are sites where *G.*  
 646 *rhamni* was observed in 2007-2008, open symbols where absent. Elevation bands are shown as 0.25  
 647 km increments from  $< 0.75$  km (pale grey) to  $> 2$  km (black). The inset map shows the geographical  
 648 context of the study area in Spain. Georeferencing units are in UTM (30T; ED50)

649

650 **Fig. 2** Phenology of *G. rhamni* overwintering (dashed lines) and summer (solid lines) adults  
 651 throughout the seasons 2007 (thick lines) and 2008 (thin lines). Phenology data are shown as the sum  
 652 of all individuals counted at all transects during a given transect fortnight. Dates were calculated as the  
 653 mean date for all transect counts in a given fortnight

654

655 **Fig. 3** Abundance of *G. rhamni* and density of its host plants with elevation. (a) *G. rhamni* in 2007 and  
 656 (b) *G. rhamni* in 2008 for overwintering (empty circles, dashed line) and summer (black circles, solid  
 657 line) adults; (c) host plants (sum of plants of *F. alnus*, *R. cathartica* and *R. lycioides*). Lines plotted  
 658 based on equations in Table 2. The vertical dashed thin line indicates the maximum elevation at which  
 659 host plants were recorded

660

661 **Fig. 4** Weighted mean elevation of *G. rhamni* overwintering (dashed lines) and summer (solid lines)  
 662 adults within season in 2007 (thick lines) and 2008 (thin lines). The horizontal thin lines indicate the  
 663 mean (solid) and maximum (dashed) elevation at which host plants were recorded. **Figures next to**  
 664 **symbols are sample sizes.**

665

666 **Fig. 5** The independent (black) and joint contribution (white) (given as the percentage of the total  
 667 variance explained by the model) of the environmental variables estimated from hierarchical  
 668 partitioning for *G. rhamni* abundance of (a) overwintering adults in 2007, (b) summer adults in 2007,

669 (c) overwintering adults in 2008, and (d) summer adults in 2008. \* indicates significant ( $P < 0.05$ )  
670 independent contributions from randomisation tests. Variable codes as in Table 1.  $N = 40$  sites in all  
671 cases. Note the different y-axis scales

672

673 **Fig. 6** Relationship between *G. rhamni* mean elevation and mean temperature over the period 2006-  
674 2012 for (a) overwintering (empty circles) and (b) summer (black circles) adults. Figures next to  
675 symbols are years. Horizontal thin lines as in Fig. 4

Figure 1

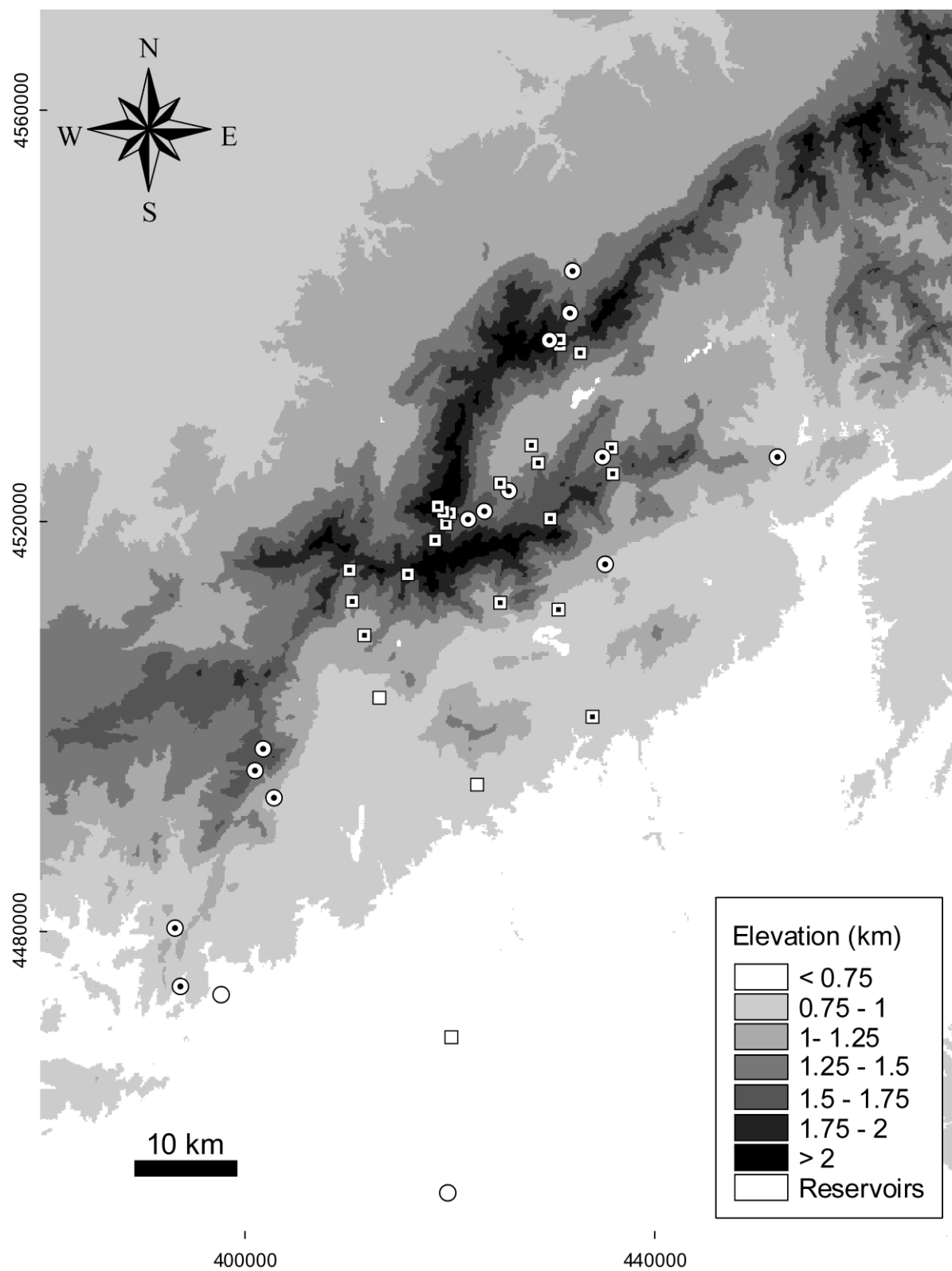




Figure 2

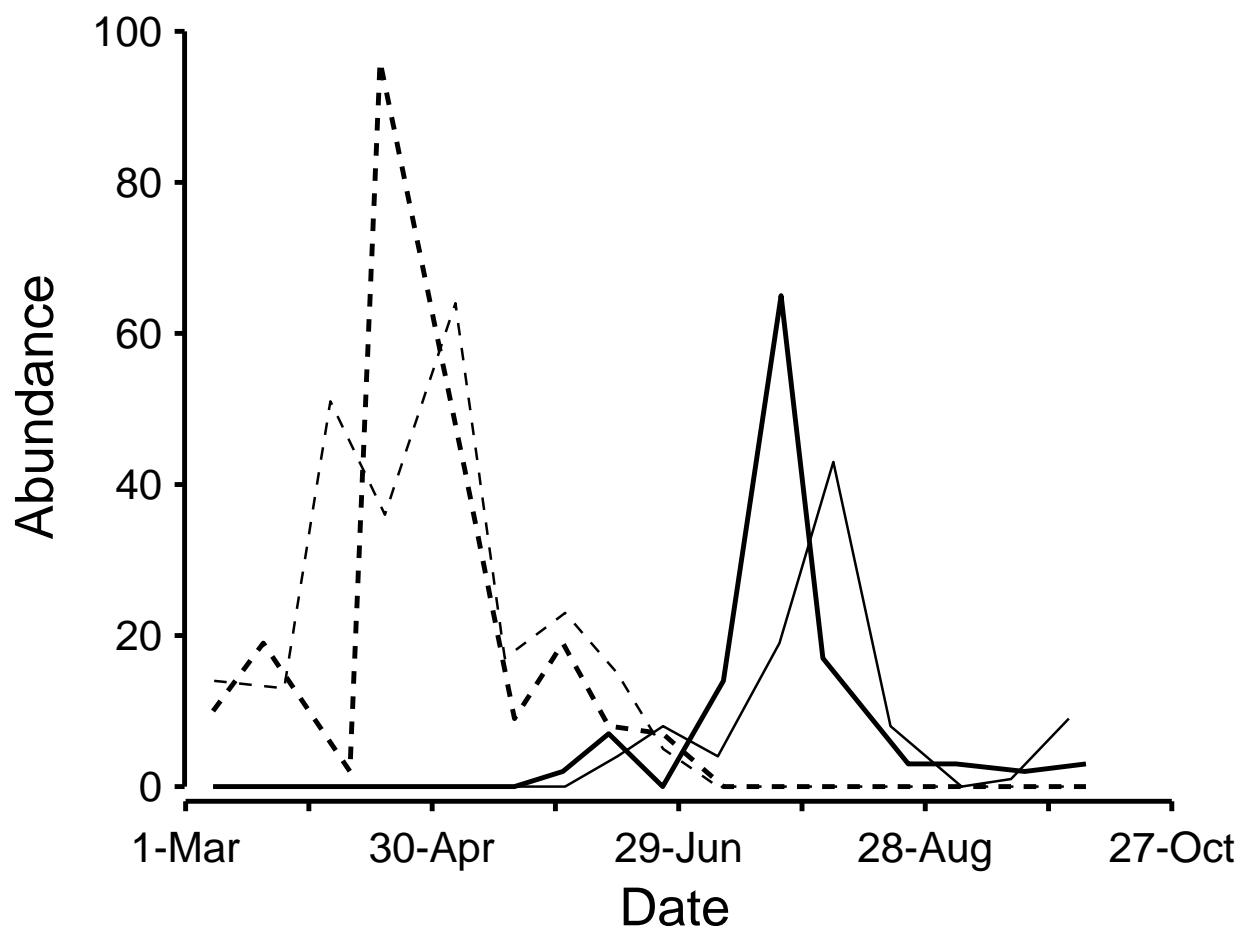


Figure 3

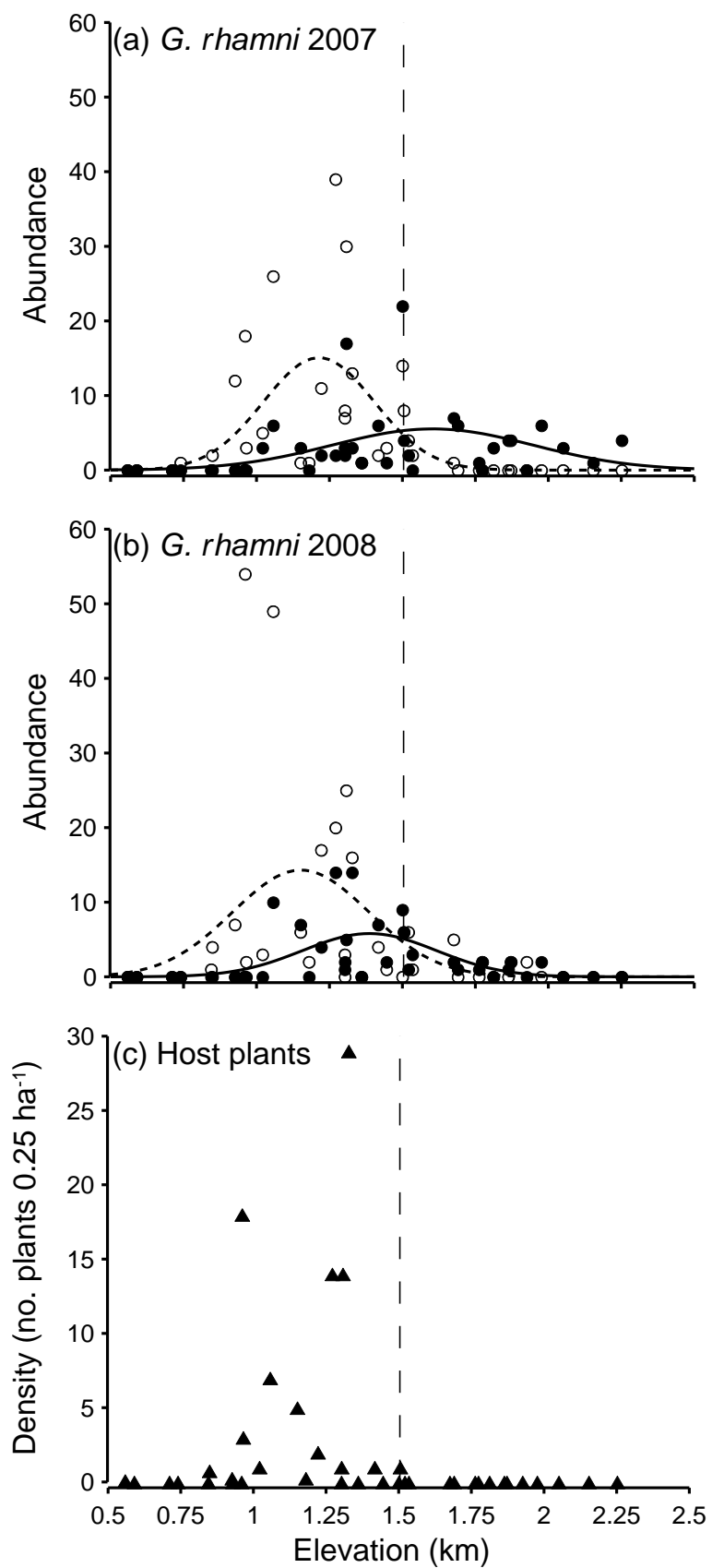


Figure 4

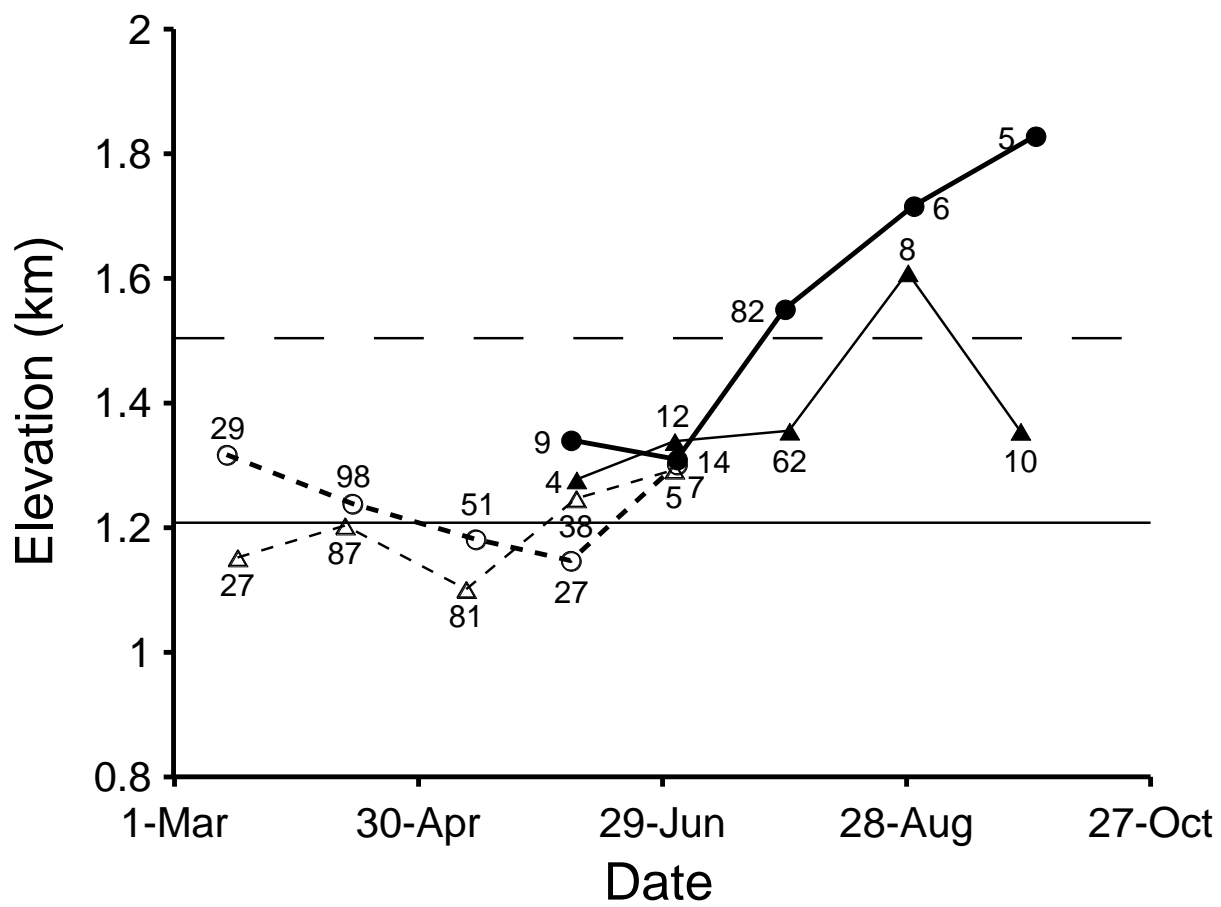


Figure 5

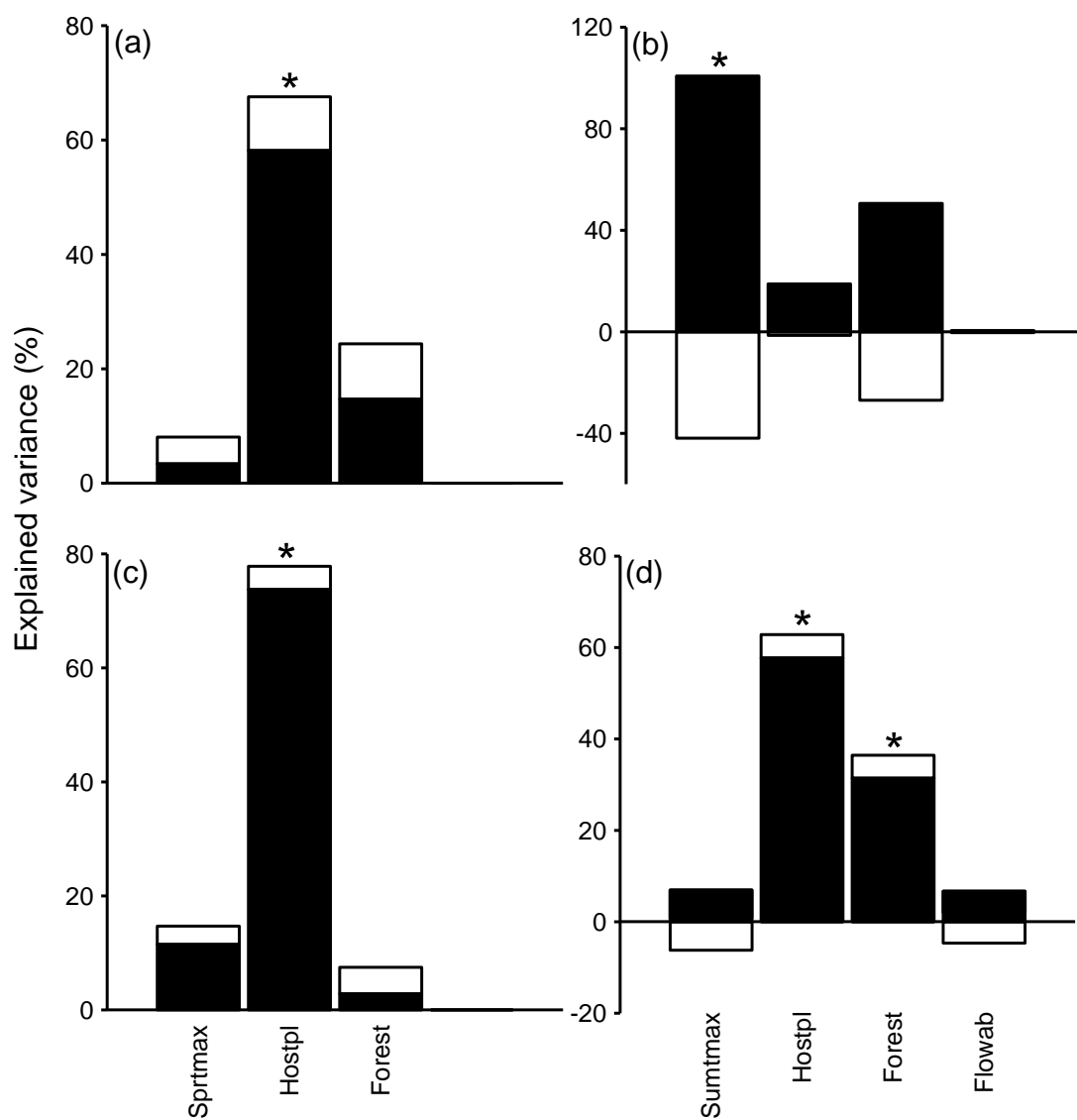


Figure 6

