## Ecological determinants of butterfly vulnerability across the European continent
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| Abstract: | In drawing up Red Lists, extinction risks of butterflies and other insects are currently assessed by information on status and trends in distribution and abundance. Incorporating information on species traits may increase our ability to predict species responses under environmental change and, hence, their vulnerability. We derived ecologically relevant biological and climatic trait dimensions, and used these to explain the variation in vulnerability indicators for 397 European butterfly species, out of 482 species present in Europe. For all but one vulnerability indicator, climatic traits predicted more variation than biological traits. The biological trait component reflecting mobility, development rate and overwintering stage, proved the major biological determinant of species vulnerability. We propose that this trait component offers a preferable alternative to the frequently used, but ecologically misleading generalist-specialist continuum. Size was a phylogenetically based trait component, and not relevant to explain species vulnerability. Our analysis contributes to develop e trait-based approach to prioritize vulnerable species for conservation at European level. Further regional scale analyses are recommended as a next step to improve the biological basis for species vulnerability. |

1 **Ecological determinants of butterfly vulnerability across the European continent**

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6

7 **Abstract:**

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9 status and trends in distribution and abundance. Incorporating information on species traits may increase our ability

10 to predict species responses under environmental change and, hence, their vulnerability. We derived ecologically

11 relevant biological and climatic trait dimensions, and used these to explain the variation in vulnerability indicators

12 for 397 European butterfly species, out of 482 species present in Europe. For all but one vulnerability indicator,

13 climatic traits predicted more variation than biological traits. The biological trait component reflecting mobility,

14 development rate and overwintering stage, proved the major biological determinant of species vulnerability. We

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19 biological basis for species vulnerability.

20

21 *Keywords: Life-history traits, Vulnerability, Conservation, Red Lists, Butterflies*

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26    **Introduction**

27    The worldwide decline of biodiversity leads to losses of a broad array of ecosystem services, such as pollination in

28    agricultural landscapes and recreational and cultural benefits (Nelson et al. 2009, Cardinale et al. 2012, Garibaldi et

29    al. 2013). The European strategy and the Convention on Biological Diversity (CBD) aim to halt biodiversity loss by

30    2010-2020 (Balmford et al. 2005, European Commission 2011). Accomplishing this objective requires both

31    continuous assessments of biodiversity status and ecological understanding of species vulnerability in relation to

32    their environmental drivers. The threat status is currently assessed by the IUCN Red List methodology with

33    increasingly reliable data from national to continental scales (IUCN 2005, Rodrigues et al. 2006, Keith et al. 2013).

34    Data on insects are still limited however, despite signals that insects are particularly sensitive to environmental

35    change (Thomas et al. 2004, Settele et al. 2008, Rasmont et al. 2015). Butterflies form the exception; their biology is

36    comparatively well studied over a wide range of species and their conservation status is primarily based on

37    population trends and distribution changes derived from decades of systematic monitoring (Van Swaay et al. 2008,

38    2010, 2011). At present, 37 butterfly species are listed as threatened on the Red List in Europe (9%), but national

39    trends in abundance indicate alarming declines in many species; e.g., 48% in the Netherlands since 1992 and 76% in

40    UK since 1976 (Fox et al. 2015, Van Swaay et al. 2016). Moreover, predictive scenarios of increased economic

41    development and climate change suggest that as much as 78% of European butterfly species may lose >50% of the

42    climatic niche area by 2080 (Settele et al. 2008). However, the ecological understanding of species vulnerability in

43    relation to environmental change remains far from adequate. The growing recognition that the persistence of

44    butterfly populations strongly depends on species' intrinsic life-history characteristics to cope with environmental

45    change, provides the opportunity to derive an mechanistic understanding of the observed population and

46    distribution trends (e.g., Roy et al. 2001, Matilla et al. 2008, Diamond et al. 2011, Newbold et al. 2012, Nieto-Sánchez

47    et al. 2015, De Palma et al. 2015, Eskildsen et al. 2015).

48    Morpho-physio-phenological and behavioural traits impact fitness via their effects on growth, reproduction

49    and survival (Violle et al. 2007). A set of life-history traits within a species is therefore most likely to be the outcome

50    of long-term environmental selection of fitness and performance qualities for a population to persist (limited by the

51    available phylogenetic space of individual species). Consequently, environmental gradients are often indicative for

2

52    the composition of life-history traits (Carnicer et al. 2013, Leingärtner et al. 2014). Trait-continua in many taxa range

53    from specialized to more generalist species and/or from slow to fast life-styles, and are often the result of growth vs.

54    survival trade-offs that impact performance (Blackburn 1991, Wright et al. 2004, DeVictor et al. 2007, Bielby et al.

55    2007, Sæther et al. 2011, Janz and Nylin 2008). Previous studies suggest that environmental changes are likely to

56    filter out Lepidoptera species that display a narrow niche breadth (food and habitat), slow development and

57    sedentary behaviour (e.g., Matilla et al. 2006, 2011, Warren et al. 2001, Bartanova et al. 2014, WallisDeVries 2014).

58    Conversely, butterfly species equipped with a set of adaptive traits, including high dispersal capacity, multiple

59    generations per year and broad trophic as well as thermal niches, have the potential to expand their range and initiate

60    adaptive radiations (e.g., Börschig et al. 2013, Ohlemüller et al. 2008).

61        The transboundary nature of butterfly distributions, environmental change and butterfly conservation

62    efforts across the European continent, justifies up-scaling of trait-based studies. Here, we establish the relationships

63    between trait components and species vulnerability indicators (RL status, endemicity, range size, habitat

64    specialization, natural vs. anthropogenic habitat). We tested if, on a continental scale, (i) species can be ordered

65    along ecologically relevant life-history traits (e.g., specialized to more generalist species, slow to fast life-styles, low

66    to high mobility, narrow to broad climatic requirements), and (ii) that these main will explain a major part of the

67    variation in butterfly vulnerability.

68

69    **Methodology**

70    *Species traits*

71    For 397 European butterfly species, we incorporated five traits associated to species' climatic preferences (i.e.,

72    climate optima and breadth of organisms) and six traits associated to species' biology (i.e., morphological,

73    physiological, phenological and behavioural adaptations innate to an organism) (**Table 1, Suppl. Mat. Table 1**).

74    Climatic traits were adopted from Schweiger et al. (2014) and included species specific niche optima and breadth of

75    temperature, precipitation and soil water moisture content of the distribution area. For temperature and

76   precipitation, we selected the annual mean and sum respectively, as well as their mean annual range, in order to

77   capture main climatic variation along gradients of latitude, elevation and continentality (Schweiger et al. 2014).

78   Biological traits included average male/female forewing length and egg-volume. Wing size may play a role

79   in dispersal capacity and survival ability, while egg size can act as a phylogenetic corrective for wing-size, given the

80   allometric slopes between wing-size and egg-size for many butterfly subtaxa (García-Barros 2002). Larval diet breadth

81   is an important limiting factor in butterfly vulnerability, in terms of range size, dispersal capacity and landscape use

82   (e.g., García-Barros & Romo Benito 2010). Species phenology is associated to colonization ability, ranging from

83   restricted climatic environments to wide distributions across a variety of climatic environments. Phenological traits

84   included voltinism (i.e., the average number of generations per year), and overwintering stage (i.e., indicating how

85   early species can reproduce in the season). Vagrancy reflects dispersal capacity and landscape use, and was based

86   on a slightly adapted version of the classification by Dennis et al. (2004), complemented by expert knowledge for a

87   total of 220 species. We used a linear regression model with voltinism, wingspan and range size to explain vagrancy

88   with available data, and made predictions for the remaining 177 species ($R^2$ = 0.505, $df_{1,219}$, SE = 1.128), using the

89   following equation:

90   Vagrancy = -0.472 + 0.482*(Voltinism) + 0.44*(Wingspan) + 0.001(Range Size)

91

*Species vulnerability*

93   Vulnerability indicators included the *Red List status*, *Endemicity*, *Range size*, species *Affinity for natural habitats* and

94   *Habitat specificity* (**Table 1**). The *Red List status* and *Endemicity* and *Range size* were adopted from Van Swaay et al.

95   (2010); in further analyses *Red List status* and *Endemicity* were treated as binary values (Red List status: 1 if 'Near

96   Threatened' or higher threat category, *Endemicity*: 1 for European endemics), because of small sample size of

97   individual categories. Butterfly *Affinity for natural habitats* was derived from Van Swaay et al. (2006) as recorded

98   occurrence in CORINE biotopes (Moss & Wyatt 1994). Species were categorized species into users of (1) natural

99   landscapes and (2) agricultural land and artificial landscapes (see details in **Suppl. Mat. Table 2**). *Habitat specificity*

100   was assessed on the basis of the above-mentioned habitat use data by Van Swaay et al. (2006), using the species

101  specialization index (SSI) (Julliard et al. 2006); the SSI takes into account variation in density among occupied habitats,

102  assuming equal densities in occupied habitat and null densities in others. Values for wing size, egg size, range size

103  and SSI were $\log_{10}$-transformed prior to analysis.

104

105  *Statistical analysis*

106  We applied principal component analysis (PCA) to assess the scores of individual species along the main orthogonal

107  axes of adaptive species traits. We separated biological and climatic traits in order to assess their relative

108  contributions. We repeated PCA trait-based analyses at the level of butterfly families, to assess family-related

109  differences. We chose not to apply further post-correction for phylogeny. Multiple linear least square regressions

110  were used to identify the relative contribution of the species specific PC values (predictive variables) to vulnerability

111  indices (response variables). Analyses were executed in JMP software (Sall et al. 2005).

112      The trend data underlying the European Red List still rely to a substantial degree on expert opinion due to a

113  lack of systematic monitoring data. Therefore, we checked if the obtained results of the multiple regression of

114  vulnerability indicators against trait components at a European scale were consistent with two more quantitatively

115  based vulnerability indicators at the national scale in the Netherlands: Red List category (on a scale from 1-6; Bos et

116  al. 2006) and abundance trend slopes for the period 1992-2015 from the Dutch Butterfly Monitoring Scheme (Van

117  Swaay et al. 2016)

118

119  **Results**

120  *Trait components on Principal Component Axes*

121  For biological traits, three components explained 78% of trait variation between species (**Table 2**). The first axis was

122  strongly positively correlated to *Vagrancy*, *Voltinism* and *Overwintering stage*. The second axis was correlated to *Size*

123  (wing and egg), whilst the third and least important axis was highly correlated to the degree of larval *Food plant*

124  *specialization*.

125     For the climatic traits, we found two equally important axes, explaining 88% of variation (**Table 2**). The first

126     rotated axis was best represented by a negative relationship between *Temperature range* on the one hand, and on

127     the other hand, *Precipitation range* and *Species temperature index*. The $2^{nd}$ axis was also correlated to the *Species*

128     *temperature index* and in addition to water availability through *Annual precipitation* and *Soil moisture content*. Thus,

129     *Species temperature index* played contributed to both axes.

130     The correlation between biological and climatic trait components was significant in four out of six cases

131     P<0.01 for r>0.13), but its magnitude was low. The strongest correlation, r=-0.33 between PC-B1 and PC-C2, suggests

132     an association of species from cool, moist climates with biological traits reflecting sedentary behaviour, producing a

133     single generation per year and overwintering in early developmental stages; such trait combinations are typically

134     found in artic-alpine species.

135     The PC values did vary significantly between butterfly families, but failed to produce significant family

136     contrasts with the exception of one biological trait component (**Table 3**). Only the size–determined trait component

137     PC-B2 showed substantial phylogenetic differences between families, with smallest values for Lycaenidae and largest

138     in Papilionidae.

139

*Relationship between traits and vulnerability indicators*

141     All five vulnerability indicators were strongly correlated or associated with each other (P<0.0001; generally positively,

142     with the evident exception for *Range size* which showed negative correlations and associations); only *Endemicity* and

143     *Habitat specificity* (SSI) were not significantly correlated with Red List status. The species-specific scores for biological

144     and climatic trait components (**Suppl. Mat. Table 1**), were used to explain the variation in five vulnerability indicators.

145     All five indicators were significantly related to a combination of several biological and climatic trait components. In

146     general, relative contributions from climatic traits were more important to explain species vulnerability than

147     biological traits, with the exception of the vulnerability indicator *Affinity for natural habitats*.

148     The explained variation in vulnerability indicators was highest for species *Range size* (**Table 4**). The

149     phylogenetically determined component PC-B2 (wing and egg size) was the only one not significantly correlated with

6

150    any of the vulnerability indicators. The contribution of trait components to the proportion of explained variation was

151    mostly higher for climatic variables than for biological traits, except for the affinity of species for natural habitats,

152    which was mainly determined by biological traits (**Fig. 1**). For the latter, the developmental traits were dominant,

153    whilst *Food specialism* was least important for *Affinity for natural habitats*.

154        *RL status* was least explained by the trait components, but the predicted occurrence of species on the *Red List*

155    still was adequately explained (83.4% correctly classified; kappa 0.16±0.06 P=0.0002). Species were more likely to be

156    on the Red List in cool and moist climates with high annual ranges in temperature and precipitation. All vulnerability

157    indicators, with the exception of the *Red List status*, were higher for species with strong host plant specialization. In

158    contrast, vulnerability was lower for vagrant species, for species with large *Range size* as well as for multivoltine

159    species overwintering at advanced developmental stages.

160        The response of vulnerability indicators to PC-C1 (annual temperature and precipitation range) was variable; it

161    was positive for *RL status,* negative for species' *Endemicity* and *Affinity for natural habitats* and curvilinear for the

162    other two vulnerability indicators. The results for *Range size* and *Habitat specificity* indicate that higher species

163    vulnerability occurs at either low or high values of species specific *Temperature* and *Precipitation ranges*. PC-C2

164    (moisture) also pointed to higher vulnerability at climatic extremes (dry / wet climates) for *Red List status*, *Range size*

165    and *Habitat specificity,* whereas *Endemicity* was typically higher in wetter climates.

166

167    *Application to trends in the Netherlands*

168    The Red List status of 73 species native to the Netherlands was explained significantly by the European traits

169    ($R^2$=0.377) with 80% of the explained variation accounted for by the negative relation with the biological traits in PC-

170    B1 (F=27.23, P<0.0001). The climatic component PC-C1 was the only other factor contributing significantly (F=5.34,

171    P=0.024).

172        Abundance trend slopes of 40 species from the Dutch Butterfly Monitoring Scheme over the period 1992-

173    2015 were explained to a lesser extent by the five trait components ($R^2$=0.260), with only PC-B1 contributing

174    significantly (F=7.19, P=0.011).

7

175

**Discussion**

*Climatic dimensions of butterfly vulnerability*

178 We detected ecologically meaningful trait dimensions, and used these to predict variation in vulnerability indicators

179 for 397 European butterfly species, equivalent to 82% of the 482 species currently recognized for Europe. The

180 dimensions found reflect climatic conditions, mobility, development rate and larval food specialization. Size was a

181 major, phylogenetically based trait component, but was least relevant to explain species vulnerability. Climatic traits

182 predicted more variation in vulnerability indicators, except for species *Affinity for natural habitats*, which was mostly

183 influenced by biological traits. The low degree of variation at family-level in the trait components affecting species

184 vulnerability, suggested that phylogeny is a minor factor in determining the vulnerability of butterfly species.

185 We found that species restricted to the extremes of climatic gradients across the European continent are

186 particularly vulnerable. In support of this result, the climatic rarity syndrome hypotheses (Willis and Whittaker 2000,

187 amended by Ohlemüller et al. 2008), postulate that centres of high species rarity coincide with unusual climate

188 conditions, that differ greatly from the surrounding areas. Various centres of high species rarity are higher and colder

189 and harbour numerous isolated relics that presumably resulted from climatic warming since the last ice-age. The

190 organisms in these vulnerable areas will be affected disproportionally by environmental change.

191 For butterflies, areas of special conservation concern can be found in the Alps, Pyrenees and the Carpathians

192 that face increasing temperatures, shorter snow seasons, longer growing seasons (Ceppi et al. 2012, Brocard et al.

193 2013, Lindner et al. 2008, Gilbert & Vincent 2013, Beniston 2012). Consequently, species shift to higher elevations

194 (Badeck et al. 2001, Wilson et al. 2005, Lenoir et al. 2010, Karolewski et al. 2007, Vanhanen et al. 2007), or northward

195 in the case of boreal regions (EEA 2009). In addition, climatic variability may strongly impact insect development,

196 predictability of food availability and phenological synchronicity between interdependent taxa (Walther et al. 2005,

197 Vasseur et al. 2014). For the Alps, wetter winter/spring conditions in combination with drier summers are expected

198 (Nemec et al. 2013, EEA 2009). Prolonged droughts are of particular concern for the Mediterranean, Central Europe

199 and the Black Sea region, potentially leading to decreased growth rates, reduced fecundity and survival in insects

200 (Cannon 1998, Ayres and Lombardero, 2000, Bale et al. 2002, Parmesan 2006, Rouault et al. 2006). These

201 aforementioned areas concur largely with three priority areas for conservation conveyed by traditional biogeography

202 (Glacial Mediterranean refugia, Glacial refugia in the eastern Palearctic and arctic and/or alpine refugia to the North

203 and/or into the high mountain systems), although more potentially important areas have been distinguished since

204 (e.g., Schmitt and Varga 2012).

205

206 *Biological dimensions of butterfly vulnerability*

207 We found that the "biological trait complex" of voltinism, overwintering stage & mobility explains a large share of

208 variation in species vulnerability. In explaining, well-established population trends and Red List status of butterfly

209 species in the Netherlands, this even proved the major contributing trait component. To a lesser extent, the degree

210 of larval food specialization also constitutes a significant factor determining species vulnerability. These results are

211 in agreement with the regional-scale analysis for North-western Europe (WalisDeVries 2014; see **Suppl. Mat. Table**

212 **3** for correlations between trait components from that study with the present one), indicating that slow-growing

213 sedentary species are most at risk for the European continent. Similarly, Matilla et al. (2006, 2008, 2011)

214 demonstrated that diet and habitat specificity, overwintering in larval and pupal stages and short flight period and

215 body size predispose Lepidoptera in Finland to distribution decline. Other studies highlighted the role of hostplant

216 growth form and life strategies in relation to butterfly development, voltinism and larval specificity (Dennis et al.

217 2004, Cizek et al. 2006, 2012, Bartanova et al. 2014). We propose that the abovementioned "biological trait complex"

218 offers a suitable substitute to the widely used, but misleading specialist-generalist continuum (e.g. Dapporto &

219 Dennis 2013). We find the term misleading because the inferred specialization does not have a biological basis, but

220 is rather determined by the modern context of anthropogenic influence instead of the ecological conditions under

221 which species evolved (see WallisDeVries 2014). Indeed, we showed that species affinity with natural habitats was

222 mainly determined by this trait component.

223 The low but significant correlation between climate and biological traits in this study, may reflect the

224 influence of climatic gradients on the coincidence of plant-host relationships and butterfly phenology. In agreement,

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225 butterflies from the Iberian Peninsula and the Alps, exhibit a trait continuum with altitude, ranging from multivoltine

226 trophic generalists with high dispersal capacity and broad climatic niches, to univoltine, trophic specialist species with

227 restricted dispersal and narrow climatic niches (Carnicer et al. 2013, Leingärtner et al. 2014).

228

229 *Challenges and opportunities in conservation*

230 Trait-based approaches to species vulnerability pose certain limitations. Shifts in response to climate warming vary

231 greatly among species, suggesting that range shifts depends on multiple species traits and external drivers of change

232 (e.g. Chen et al. 2011), while potentially important traits may not be included for all species, due to gaps in knowledge

233 of species ecology. Detailed trait information, such as was available for species from Northwestern Europe

234 (WallisDeVries 2014), remains to be collected for many other European species. We did initially consider a number

235 of additional traits (host plant growth form, aestivation, altitudinal limits, as well as other climatic variables, such as

236 standard deviation of temperature and precipitation), but we decided to exclude them from the analysis due to

237 methodological issues of trait variation and correlations between climatic variability and range size. Also we chose

238 not to do detailed phylogenetic corrections, since taxonomic data are still incomplete (e.g., taxonomical changes for

239 cryptic species). Moreover, there is considerable debate about the added value phylogenetic correction in trait-based

240 studies, and in fact, numerous studies showed that correlative patterns among life-history traits remain largely

241 undistorted even after a correction for phylogeny (Matilla et al. 2006, 2008, 2011, Päivinen et al. 2005, Wilson et al.

242 2004, Pavoine et al. 2012, Bartanova et al. 2014, Leingärtner et al. 2014). However, increasingly detailed trait data

243 might also reveal regional differences for traits of the same species. Traits are, after all, primarily the result of

244 environmental adaptation and filtering. Also evolutionary plasticity of traits likely varies between species and

245 between populations of the same species. Depending on the genetic variation and environmental pressure, traits

246 continue to change. A final point of attention, is that endemicity was typically higher in wetter climates, but as Europe

247 constitutes the northwestern Edge of the Palaearctic region, as good as all species preferring dry or steppic conditions

248 are not endemic (most of them also occur in Asia or Africa), making endemicity a biased variable.

249     In spite of the limitations, this study clearly shows a weak response of the Red List status in relation to

250 species traits, which begs the question if the Red List status should be more strongly rooted in a biological basis. An

251 important candidate for improving underlying biological arguments, could be the trait complex of voltinism,

10

252 overwintering stage & mobility. Here, we propose a tentative list of 56 candidate Red List species with below-median

253 values for PC-B1 and for range size (**Suppl. Mat. Table 4;** a further 18 species meeting these criteria are already on

254 the Red List). Similar attempts to predict extinction risk using multiple ecological traits, Kotiaho et al. (2005) for

255 instance, revealed that threatened butterflies are characterized by narrow niche breadth, restricted resource

256 distribution, poor dispersal ability, and short flight period. Based on this study, they were able identify seven

257 vulnerable species for which the conservation status should be reconsidered in Finland.

258 Complementary regional analyses, for which specific biological trait information is more complete and climatic

259 variation is less pronounced are still necessary to deepen our mechanistic understanding of species vulnerability. For

260 the present study, the variation in climatic conditions across broad spatial scales is large, e.g., variation in

261 continentality / oceanity with longitude or daily as well as seasonal variation in temperature and precipitation

262 regimes with latitude and altitude (Settele et al. 2013, Schweiger et al. 2014). Again here, it seems advisable to

263 distinguish regions on ecologically relevant grounds. Thermoclimatic conditions relevant to butterflies may, for

264 instance, be incorporated as variables to select geographical areas for further disentanglement of biological traits in

265 spatially explicit studies.

266 In conclusion, this analysis provides a basis to identify ecologically relevant species groups and prioritizes

267 vulnerable species for conservation at European level. Although trait information is still limited at the European scale,

268 our study indicates its potential to assess species vulnerability. Species vulnerability indicators were significantly

269 determined by species specific traits, primarily climate requirements. Furthermore, the biological trait complex

270 reflecting mobility, development rate and overwintering stage proved another consistent determinant of species

271 vulnerability that may be used to replace the anthropogenically determined specialist-generalist continuum. Further

272 systematic regional scale analyses are recommended as a next step to improve the biological basis for species

273 vulnerability.

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275 **References**

11

276 Ayres MP, Lombardero MJ (2000) Assessing the consequences of global change for forest disturbance from

277 herbivores and pathogens. Sci Tot Environ 262:263–286

278 Badeck FW, Lischke H, Bugmann H, Hickler T, Höniger K, Lasch P, Lexer MJ, Mouillot F, Schaber J, Smith B (2001)

279 Tree species composition in European pristine forests: Comparison of stand data to model predictions.

280 Clim Chang 51:307–347

281 Bale JS, Masters GJ, Hodkinson ID, Awmack C, Bezemer TM, Brown VK, Butterfield J, Buse A, Coulson JC, Farrar J,

282 Good JEG, Harrington R, Hartley S, Jones HT, Lindroth RL, Press MC, Symrnioudis I, Watt AD, Whittaker JB

283 (2002) Herbivory in global climate change research: direct effects of rising temperature on insect

284 herbivores. Glob Change Biol 8:1–16

285 Balmford A, Bennun L, Brink BT, Cooper D, Cote IM, Crane P et al (2005) The convention on biological diversity's

286 2010 target. Science 307:212–213

287 Bartanova A, Benes J & Konvicka M (2014) Generalist-specialist continuum and life history traits of Central

288 European butterflies (Lepidoptera) – are we missing a part of the picture? Eur J Entomol 111:543-553

289 Beniston M (2012) Is snow in the Alps receding or disappearing? WIRES Clim Chang 3:349–358

290 Bielby J, Mace GM, Bininda-Emonds OP, Cardillo M, Gittleman JL, Jones KE, Orme CDL,Purvis A (2007) The fast–slow

291 continuum in mammalian life-history: an empirical reevaluation. Amer Nat 169:748–757

292 Blackburn TM (1991) Evidence for a fast slow continuum of life-history traits among parasitoid hymenoptera. Funct

293 Ecol 5:65–74

294 Börschig C, Klein AM, von Wehrden H, Krauss J (2013) Traits of butterfly communities change from specialist to

295 generalist characteristics with increasing land-use intensity. Basic Appl Ecol 14:547–554

296 Bos FG, Bosveld MA, Groenendijk DG, Van Swaay CAM, Wynhoff I. & De Vlinderstichting (2006). De Dagvlinders van

297 Nederland: Verspreiding en Bescherming. Leiden: Nederlandse Fauna 7. Nationaal Natuurhistorisch

298 Museum Naturalis (in Dutch), KNNV Uitgeverij and EIS-NL

299 Brocard E, Philipona R, Jeannet P, Begert M, Romanens G, Levrat G, Scherrer SC (2013) Upper air temperature

300 trends above Switzerland 1959–2011. J. Geophys Res Atmos 118: 4303–4317

301 Cannon RJC (1998) The implications of predicted climate change in the UK, with emphasis on non-indigenous

302 species. Glob Change Biol 4:785–796

303 Cardinale BJ, Duffy JE, Gonzalez A, Hooper DU, Perrings C, Venail P, Narwani A, Mace GM, Tilman D, Wardle

304 DA, Kinzig AP, Daily GC, Loreau M, Grace JB,Larigauderie A, Srivastava DS, Naeem S. (2012) Biodiversity loss

305 and its impact on humanity. Nature 486:59–67

306 Carnicer J, Stefanescu C, Vila R, Dinca V, Font X, Peñuelas J (2013) A unified framework for diversity gradients: the

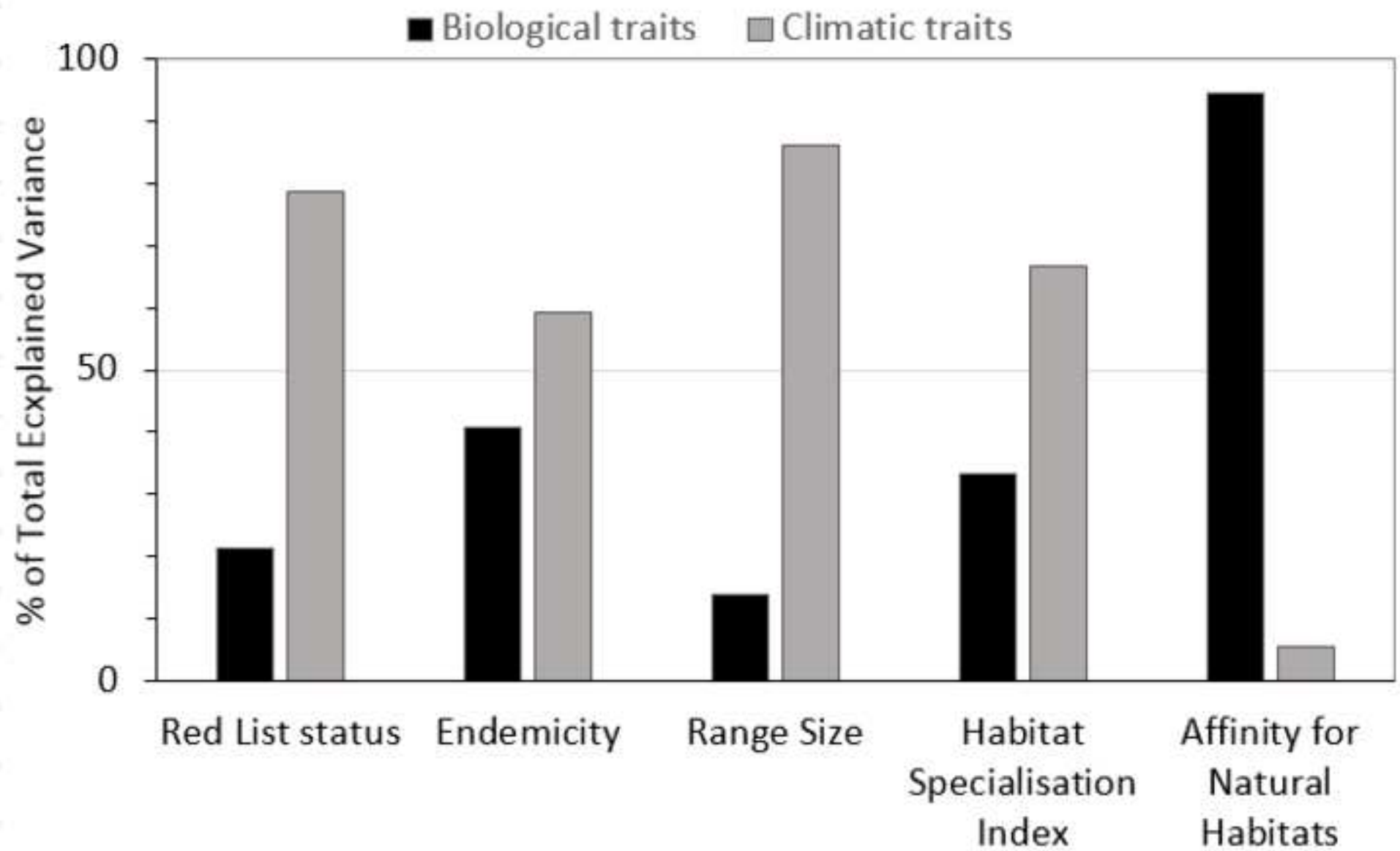307 adaptive trait continuum. Glob Ecol Biogeogr 22:6–18

12

308 Ceppi P, Scherrer SC, Fischer AM, Appenzeller C (2012) Revisiting Swiss temperature trends 1959–2008. Int J Climat
309     32:203–213

310 Cizek L, Fric Z, Konvicka M (2006) Host plant defences and voltinism in European butterflies. Ecol Entomol 31:337–
311     344

312 Chen I-C, Hill JK, Ohlemüller R, Roy DB, Thomas CD (2011) Rapid range shifts of species associated with
313     high levels of climate warming. Science 333:1024–1026

314 Dapporto L, Dennis RLH (2013) The generalist–specialist continuum: Testing predictions for distribution and trends
315     in British butterflies. Biol Conserv 157:229–236

316 De Palma A, Kuhlmann M, Roberts SP, Potts SG, Börger L, Hudson LN, Lysenko I, Newbold T, Purvis A (2015)
317     Ecological traits affect the sensitivity of bees to land-use pressures in European agricultural landscapes. J
318     Appl Ecol 52:1567-1577

319 Dennis RLH, Hodgson JG, Grenyer R, Shreeve TG, Roy DB (2004) Host plants and butterfly biology. Do host-plant
320     strategies drive butterfly status? Ecol Entomol 29:12–26

321 Devictor V, Julliard R, Jiguet F (2008) Distribution of specialist and generalist species along spatial gradients of
322     habitat disturbance and fragmentation. Oikos 117(4):507–514

323 Diamond S, Frame A, Martin R, Buckley L (2011) Species' traits predict phenological responses to climate change in
324     butterflies. Ecology 92:1005–1012

325 EEA (2009) Regional climate change and adaptation. The Alps facing the challenge of changing water resources.
326     Copenhagen, Denmark, 143 p. http://www.riob.org/IMG/pdf/EEA_Report_8-2009_Alps.pdf. Accessed 20
327     May 2016

328 Eskildsen A, Carvalheiro LG, Kissling WD, Biesmeijer JC, Schweiger O, Høye TT (2015) Ecological specialization
329     matters: longterm trends in butterfly species richness and assemblage composition depend on multiple
330     functional traits. Divers Distrib 21:792–802

331 European Commission (2011) Our life insurance, our natural capital: an EU biodiversity strategy to 2020. COM
332     (2011) 244. Brussels.

333 Fox R, Brereton TM, Asher J, August TA, Botham MS, Bourn NAD, Cruickshanks KL, Bulman CR, Ellis S, Harrower CA,
334     Middlebrook I, Noble DG, Powney GD, Randle Z, Warren MS, Roy DB (2015). The State of the UK's
335     Butterflies 2015. Butterfly Conservation and the Centre for Ecology & Hydrology, Wareham, Dorset.

336 Garcia-Barros E (2002) Taxonomic patterns in the egg to body size allometry of butterflies and skippers
337     (Papilionoidea & Hesperiidae). Nota lepidopterologica 25:161–176

338 Garcia-Barros E, Romo Benito H (2010) The relationship between geographic range size and life history traits: is
339     biogeographic history uncovered? A test using the Iberian butterflies. Ecography 33:392–401

340  Garibaldi LA, Steffan-Dewenter I, Winfree R, Aizen MA, Bommarco R, et al. (2013) Wild pollinators enhance fruit set
341      of crops regardless of honey bee abundance. Science 339:1608–1611

342  Gilbert A, Vincent C (2013) Atmospheric temperature changes over the 20th century at very high elevations in the
343      European Alps from englacial temperatures. Geophys Res Lett 40:2102–2108

344  IUCN (2005) Guidelines for Using the IUCN Red List Categories and Criteria, IUCN-SSC
345      http://www.iucn.org/webfiles/doc/ SSC/RedList/RedListGuidelines.pdf. Accessed December 2015

346  Janz N, Nylin S (2008) The oscillation hypothesis of host plant range and speciation. Specialization, speciation, and
347      radiation: the evolutionary biology of herbivorous insects (ed. by K.J. Tilmon), University of California
348      Press, Berkeley, CA, pp. 203–215

349  Julliard R, Clavel J, Devictor V, Jiguet F, Couvet D (2006) Spatial segregation of specialists and generalists in bird
350      communities. Ecol lett 9:1237–44

351  Karolewski P, Grzebyta J, Oleksyn J, Giertych MJ (2007) Effects of temperature on larval survival rate and duration
352      of development of *Lymantria monacha* (L.) on needles of *Pinus silvestris* (L.) and of L. dispar (L.) on leaves
353      of *Quercus robur* (L.). Pol J Ecol 55:595–600

354  Keith DA, Rodríguez JP , Brooks TM, Burgman MA, Barrow EG, Bland L, Comer PJ, Franklin J, Link J, McCarthy
355      MA, Miller RM, Murray NJ, Nel J, Nicholson E, Oliveira-Miranda MA, Regan TJ, Rodríguez-Clark KM, Rouget,
356      M, Spalding MD ( 2015) The IUCN red list of ecosystems: motivations, challenges, and applications. Cons
357      letters 8: 214-226

358  Kotiaho JS, Kaitala V, Komonen A, Päivinen J (2005) Predicting the risk of extinction from shared ecological
359      characteristics. PNAS 8:1963–1967

360  Leingärtner A, Krauss J, Steffan-Dewenter I (2014) Species richness and trait composition of butterfly assemblages
361      change along an altitudinal gradient. Oecologia 175:613–623

362  Lenoir J, Gégout JC, Guisan A, Vittoz P, Wohlgemuth T, Zimmermann NE, Dullinger S, Pauli H, Willner W, Grytnes JA,
363      Virtanen R, Svenning JC (2010) Cross-scale analysis of the region effect on vascular plant species diversity
364      in southern and northern European mountain ranges. PLoS ONE 5:1–13

365  Lindner M, Garcia-Gonzalo J, Kolström M, Green T, Reguera R, Maroschek M, Seidl R, Lexer MJ, Netherer S, Schopf
366      A, Kremer A, Delzon S, Barbati A, Marchetti M, Corona P (2008) Impacts of climate change on European
367      forests and options for adaptation. Report to the European Commission Directorate General for
368      Agriculture and Rural Development 173 p.
369      http://ec.europa.eu/agriculture/analysis/external/euro_forests/full_report_en.pdf. Accessed 22 May 2016

370  Mattila M, Kotiaho JS, Kaitala V, Komonen A (2008) The use of ecological traits in extinction risk assessments: A
371      case study on geometrid moths. Biol Conserv 141:2322–2328

372 Mattila N, Kaitala V, Komonen A, Kotiaho JS,Paivinen J (2006) Ecological determinants of distribution decline and

373         risk of extinction in moths. Conserv Biol 20:1161–1168

374 Mattila N, Kaitala V, Komonen A, Paivinen J, Kotiaho JS (2011) Ecological correlates of distribution change and range

375         shift in butterflies. Insect Conserv Diver 4:239–246

376 Moss D, Wyatt BK (1994) The CORINE biotopes project: a database for conservation of nature and wildlife in the

377         European community. Appl Geogr 14(4):327–349

378 Nelson E, Mendoza G, Regetz J, Polasky S, Tallis J, Cameron DR, Chan KMA, Daily GC, Goldstein J, Kareiva

379         PM, Londsdorf E, Naidoo R, Ricketts TH, Shaw MR (2009) Modeling multiple ecosystem services,

380         biodiversity conservation, commodity production, and tradeoffs at landscape scales. Front Ecol Environ

381         7:4–11

382 Nemec J, Grube C, Chimani B, Auer I (2013) Trends in extreme temperature indices in Austria based on a new

383         homogenised dataset. Int J Climatol 33:1538–1550

384 Newbold T, Butchart SHM, Sekercioglu CHS, Purves DW, Scharlemann JPW (2012) Mapping functional Traits:

385         comparing abundance and presence-absence estimates at large spatial scales. PLoS ONE 7(8):e44019

386 Nieto-Sánchez S, Gutiérrez D, Wilson RJ (2015) Long-term change and spatial variation in butterfly communities

387         over an elevational gradient: driven by climate, buffered by habitat. Divers Distrib 21:950–961

388 Ohlemüller R, Anderson BJ, Araujo MB, Butchart SHM, Kudrna O, Ridgely RS, Thomas C (2008). The coincidence of

389         climatic and species rarity: high risk to small-range species from climate change. Biol Lett 4:568–572

390 Päivinen J, Grapputo A, Kaitala V, Komonen A, Kotiaho JS, Saarinen K, Wahlberg N (2005) Negative density

391         distribution relationship in butterflies. BMC Biology 3:5

392 Parmesan C (2006) Ecological and evolutionary responses to recent climate change. Annu Rev Ecol Evol S 37:637–

393         669

394 Pavoine S, Baguette M, Stevens VM, Leibold MA, Turlure C, Bonsall MB (2014) Life history traits, but not phylogeny,

395         drive compositional patterns in a butterfly metacommunity. Ecology 95:3304–3313

396 Rasmont P, Franzén M, Lecocq T, Harpke A, Roberts S, Biesmeijer J, Castro L, Cederberg B, Dvorak L, Fitzpatrick Ú,

397         Gonseth Y, Haubruge E, Mahé G, Manino A, Michez D, Neumayer J, Ødegaard F, Paukkunen J, Pawlikowski

398         T, Potts S, Reemer M, Settele J, Straka J, Schweiger O (2015) Climatic Risk and Distribution Atlas of

399         European Bumblebees. BioRisk 10:1–236

400 Rodrigues ASL, Pilgrim JD, Lamoreux JF, Hoffman M, Brooks TM (2006) The value of the IUCN Red List for

401         conservation. Trends Ecol Evol 21:71–7

402 Rouault G, Candau JN, Lieutier F, Nageleisen LM, Martin JC, Warzée N (2006) Effects of drought and heat on forest

403         insect populations in relation to the 2003 drought in Western Europe. Annals of Forest Science 63:613–624

404 Roy DB, Rothery P, Moss D, Pollard E, Thomas JA (2001) Butterfly numbers and weather: predicting historical trends
405      in abundance and the future effects of climate change. J Anim Ecol 70:201–217

406 Sæther BE, Grøtan V, Engen S, Noble DG, Freckleton RP (2011) Rarity, life history and scaling of the dynamics in
407      time and space of British birds. J Anim Ecol 80:215–224

408 Sall J, Creighton L, Lehman A (2005) JMP Start Statistics: a guide to statistics and data analysis using JMP and JMP IN
409      software. Brooks/Cole-Thomson Learning, Belmont.

410 Schmitt T, Varga Z (2012) Extra-Mediterranean refugia: The rule and not the exception? Front Zool 9:22

411 Schweiger O, Harpke A, Wiemers M, Settele J (2014) CLIMBER: Climatic niche characteristics of the butterflies in
412      Europe. ZooKeys 367:65–84

413 Settele J, Kudrna O, Harpke A, Kühn I, Van Swaay C et al (2008) Climatic Risk Atlas of European Butterflies. Moscow:
414      Pensoft

415 Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC, Erasmus BFN, de Siqueira MF,
416      Grainger A, Hannah L, Hughes L, Huntley B, van Jaarsveld AS, Midgley GF, Miles L, OrtegaHuerta MA,
417      Peterson AT, Phillips OL, Williams SE (2004) Extinction risk from climate change. Nature 427:145–148

418 Van Swaay C, Cuttelod A, Collins S, Maes D, López Munguira M, Šašić M, Settele J, Verovnik R, Verstrael T, Warren
419      M, Wiemers M, Wynhof I (2010) European Red List of Butterflies.
420      http://ec.europa.eu/environment/nature/conservation/species/redlist/downloads/European_butterflies.p
421      df. Accessed December 2015

422 Van Swaay C, Maes D, Collins S, Munguira ML, Sasic M, Settele J, Verovnik R, Warren M, Wiemers M, Wynhoff I,
423      Cuttelod A (2011) Applying IUCN criteria to invertebrates: how red is the Red List of European butterflies?
424      Biol Conserv 144:470–478

425 Van Swaay C, Piotr N, Settele J, van Strien J (2008) Butterfly monitoring in Europe: methods, applications and
426      perspectives Biodivers Conserv 17:3455–3469

427 Van Swaay CAM, Termaat T, Kok J, Huskens K, Poot M (2016) Vlinders en libellen geteld. Jaarverslag 2015 (in
428      Dutch). Report VS2016.001, De Vlinderstichting, Wageningen

429 Van Swaay C, Warren M, Loïs G (2006) Biotope use and trends of European butterflies. J Insect Conserv 10:189–209

430 Vanhanen H, Veteli TO, Pailvinen S, Kellomaki S, Niemala P (2007) Climate change and range shifts in two insect
431      defoliators: gypsy moth and nun moth – a model study. Silva Fennica 41:621–638

432 Vasseur DA, DeLong JP, Gilbert B, Greig HS, Harley CDG, McCann KS, Savage V, Tunney TD, O'Connor MI (2014)
433      Increased temperature variation poses a greater risk to species than climate warming. Proc R Soc B
434      281:20132612

435 Violle C, Navas ML, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E (2007) Let the concept of trait be functional!
436        Oikos 116:882–892

437 WallisDeVries MF 2014. Linking species assemblages to environmental change: Moving beyond the specialist-
438        generalist dichotomy. Basic Appl Ecol 15:279–287

439 Walther GR, Beißner S, Burga C (2005) Trends in the upward shift of alpine plants. J Veg Sci 16:541–548

440 Warren MS, Hill JK, Thomas JA, Asher J, Fox R, Huntley B, Roy DB, Telfer MG, Jeffcoate S, Harding P, Jeffcoate G,
441        Willis SG, Greatorex-Davies JN, Moss D, Thomas CD (2001) Rapid responses of British butterflies to
442        opposing forces of climate and habitat change. Nature 414:65–69

443 Willis KJ, Whittaker RJ (2000) Paleoecology—the refugial debate. Science 287:1406–1407

444 Wilson RJ, Gutiérrez D, Gutiérrez J, Martínez D, Agudo R, Monserrat VJ (2005) Changes to the elevational limits and
445        extent of species ranges associated with climate change. Ecol Lett 8:1138–1146

446 Wilson RJ, Thomas CD, Fox R, Roy DB, Kunin WE (2004) Spatial patterns in species distributions reveal biodiversity
447        change. Nature 432:393–396

448 Wright IJ, Reich PB, Westoby M et al (2004) The worldwide leaf economics spectrum. Nature 428:821–827

Figure 1 TIF file

| | Variables | Data scale | Values |
|---|---|---|---|
| **Biological traits** | Vagrancy | Ordinal | (1) rare record ex habitat, (2) occasional colonization events over <10 km, (3) urban areas and gardens, (4) occasional colonization events over >10 km, (5) rapid range expansions over >100 km in 10 years, (6) short-distance overseas dispersal - at sea records - island populations, (7) incidental long-distance (mass) movements, (8) regular reversed long distance migrations |
| | Voltinism | Ordinal | (1) 0.5, (2) 1, (3) 1–2, 4) 2, (5) 2–3, (6) 3–4 (generations per year) |
| | Overwintering | Ordinal | (1) egg), (2) first instar larva, (3) half-grown, (4) last instar, (5) pupa, (6) adult, (7) no hibernation |
| | Wing size | Continuous | mm (average male / female) |
| | Egg volume | Continuous | mm³ |
| | Specialization | Ordinal | (1) polyphagous (multiple species, >1 plant family), (2) polyphagous (multiple species, 1 plant family), (3) oligophagous, (4) monophagous |
| **Climatic traits** | Temperature index | Continuous | °C (monthly average across species range) |
| | Precipitation sum | Continuous | mm (annual sum across species range) |
| | Temperature range | Continuous | °C (maximum – minimum monthly average across species range) |
| | Temperature range | Continuous | mm (maximum – minimum monthly average across species range) |
| | Soil water content | Continuous | Units 0 to 1, water availability in the upper horizon (0.5 m) |
| **Vulnerability** | Red List status | Binary | (0-1); 0) least concern, 1) near threatened, vulnerable  endangered or critically endangered |
| | Range size | Continuous | Occupancy in number of 50 km² grid cells |
| | Endemicity | Binary | (1) European endemics, (0) species also occurring outside Europe |
| | Habitat use | Binary | (0) natural, (1) anthropogenic |
| | Habitat specificity | Continuous | SSI index* |

**Table 1**. Species traits and indicators for species vulnerability used in this study. *See text.

| Rotated PCs | Biological traits | | | Climate traits | |
|---|---|---|---|---|---|
| | PC-B1 | PC-B2 | PC-B3 | PC-C1 | PC-C2 |
| Variance | 1.99 | 1.68 | 1.01 | 2.20 | 2.19 |
| % Explained | 33.2 | 28.0 | 16.8 | 44.1 | 43.7 |
| Vagrancy | **+0.83** | -0.26 | -0.10 | | |
| Voltinism | **+0.84** | +0.19 | +0.02 | | |
| Overwintering stage | **+0.71** | +0.04 | -0.05 | | |
| Wingspan | +0.18 | **-0.91** | +0.01 | | |
| Egg Volume | -0.21 | **-0.86** | -0.07 | | |
| Foodplant specialisation | -0.08 | 0.04 | **+0.99** | | |
| Range Annual Temperature | | | | **+0.92** | -0.05 |
| Range Annual Precipitation | | | | **-0.85** | +0.05 |
| Species Temperature Index | | | | **-0.74** | **-0.65** |
| Soil Water Content | | | | +0.16 | **+0.96** |
| Annual Precipitation | | | | -0.25 | **+0.91** |
| PC-C1 | -0.15 | +0.01 | -0.15 | | |
| PC-C2 | -0.33 | -0.09 | -0.13 | | |

**Table 2.** Principal components of trait associations for 384 European butterfly species with correlation coefficients of trait variables with the rotated principal component axes. The strongest correlations for each variable have been marked in bold. Correlation coefficients between biological and climatic trait components are listed below. (PC: Principal Component of combined traits, B for biological and C for Climatic traits).

| | N species | Biological traits | | | Climate traits | |
|---|---|---|---|---|---|---|
| Family | | PC-B1 | PC-B2 | PC-B3 | PC-C1 | PC-C2 |
| Hesperiidae | 43 | $-0.23^b$ | $+0.53^b$ | $-0.09^{ab}$ | $-0.12^a$ | $-0.10^{ab}$ |
| Lycaenidae | 104 | $+0.02^b$ | $+1.10^a$ | $+0.27^a$ | $-0.03^a$ | $-0.25^b$ |
| Nymphalidae | 193 | $-0.20^b$ | $-0.63^d$ | $-0.12^b$ | $+0.03^a$ | $+0.22^a$ |
| Pieridae | 43 | $0.96^a$ | $+0.04^c$ | $-0.09^{ab}$ | $+0.16^a$ | $-0.24^{ab}$ |
| Other | 14 | $+0.34^{ab}$ | $-1.22^e$ | $+0.19^{ab}$ | $-0.39^a$ | $-0.11^{ab}$ |
| | | $F_{4,392}=14.4^{****}$ | $F_{4,70.6}=142.3^{****}$ | $F_{4,70.6} = 2.9^*$ | $F_{4,392} = 1.0^{ns}$ | $F_{4,70.9}=4.7^{**}$ |

**Table 3.** Mean values of biological and climatictrait components for different butterfly families. Species of families Papilionidae (N=13) and Riodinidae (N=1), were grouped in "Other". Different Letters a-e indicate significant differences between families (Tukey HSD); F-values from ANOVA with lower d.f. values after accounting for inhomogeneity of variances (significance: * P<0.05, ** P<0.01, **** P<0.0001). (PC: Principal Component of combined traits, B for biological and C for Climatic traits).

| | | Biological traits | | | Climate traits | | | | $R^2$ |
|---|---|---|---|---|---|---|---|---|---|
| Variable | Regression type | PC-B1 | PC-B2 | PC-B3 | PC-C1 | PC-C12 | PC-C2 | PC-C22 | |
| Red List status | Logistic | $4.8^{-}$ | $2.8^{ns}$ | $0.1^{ns}$ | $12.3^{+++}$ | | $5.0^{-}$ | $11.0^{+++}$ | 0.105 |
| Edemicity | Logistic | $19.4^{----}$ | $1.5^{ns}$ | $14.1^{+++}$ | $35.8^{----}$ | | $15.3^{++++}$ | | 0.272 |
| Range Size | Least Squares | $68.6^{++++}$ | $0.3^{ns}$ | $27.4^{----}$ | $128.4^{++++}$ | $172.8^{----}$ | $127.2^{++++}$ | $175.9^{----}$ | 0.638 |
| Habitat specificity | Least Squares | $96.1^{----}$ | $0.9^{ns}$ | $6.0^{+}$ | $62.8^{----}$ | $51.4^{++++}$ | $23.9^{----}$ | $69.0^{++++}$ | 0.487 |
| Affinity for Natural Habitats | Logistic | $63.0^{----}$ | $0.0^{ns}$ | $6.7^{++}$ | $4.0^{-}$ | | $0.0^{ns}$ | | 0.364 |

**Table 4.** Results of the multiple regression between species-specific vulnerability indicators and Principal Component of combined traits, B for biological and C for Climatic traits (significance: * P<0.05, ** P<0.01, **** P<0.0001).
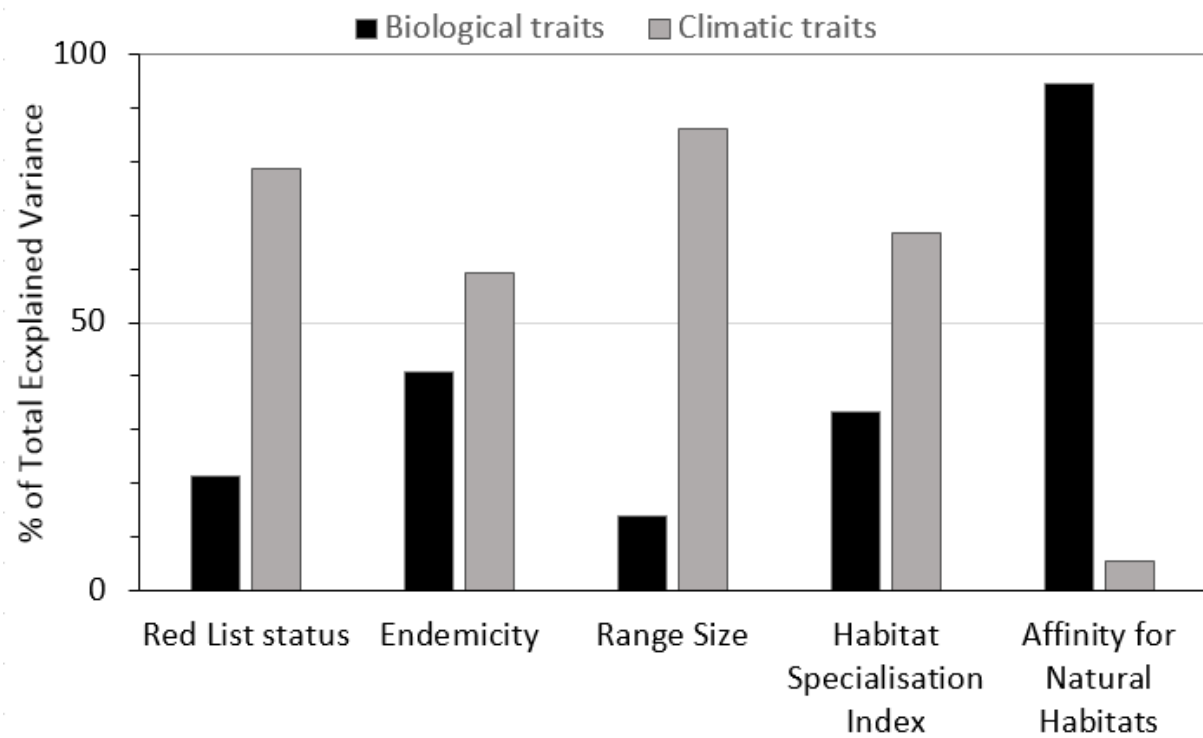
**Figure 1.** Relative contribution (out of 100%) of biological traits (black bars) and climate traits (grey bars) in explaining variation in vulnerability indicators for European butterfly species.

**Supplementary material in separate Exel file attached.**

**Suppl. Mat. Table 1**: Species list of European butterflies used in this study, with *Red List categories* (LC least concern, NT near threatened, VU vulnerable, EN endangered, CR critically endangered, NA not assessed), *Endemicity* and *Range size* from van Swaay et al. (2010), Species specialization index (SSI) based on Julliard et al. (2006), *Affinity for natural habitat* as recorded occurrence in CORINE biotopes (Moss & Wyatt 1994), and correlation scores with PCA axes (B for biological variables and C for climatic variables).

**Suppl. Mat. Table 2:** Classification of Corine habitat types as natural, anthropogenic or indistinct (i.e. if habitat types may be natural, but often are significantly modified by anthropogenic influence). Species classification after relative proportion of habitat mentions in Van Swaay et al. (2006). Classification criteria were: (i) exceedance of the median value of the percentage of habitat mentions in either natural or anthropogenic habitats, (ii) the difference in percentage of habitat mentions in natural habitats minus the percentage in anthropogenic habitats being 50% or greater, (iii) the percentage of habitat mentions in indistinct habitats: if this was >50%, then species were only assigned as 'anthropogenic' if the percentage in anthropogenic habitats exceeded 10%, (iv) for 8 species exclusively listed in indistinct habitats, we assigned an intermediate value of 0.5.

**Suppl. Mat. Table 3:** Correlations between the species scores of five main trait component from this study and values from the four main trait components for 145 nortwest-European butterfly species from WallisDeVries (2014) (significance: * P<0.05, ** P<0.01, **** P<0.0001).

**Suppl. Mat. Table 4:** A tentative list of 56 candidate Red List species (present status LC or NA) with below-median values for PC-B1 and for range size (in number of occupied 50x50 km grid cells); a further 18 species that satisfy the criteria already are included on the Red List (status NT, EN or CR). Red List categories: LC least concern, NT near threatened, VU vulnerable, EN endangered, CR critically endangered, NA not assessed).

Supplementary Material (Video Files)

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Suppl tables_EcolDetermButterflies.xlsx