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Trait-modulated decline of carabid beetle occurrence along elevation gradients across the European Alps

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3 1 **Trait-modulated decline of carabid beetle occurrence along elevation**
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5 2 **gradients across the European Alps**
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10 **Running title:** Trait-elevation interactions in carabids
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1
2
3 31 **Abstract**
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5 32 **Aim:** To assess how species traits modulate the responses of carabids to elevation gradients, and
6
7 33 how consistent these relationships are across different Alpine regions.

8 34 **Location:** Italian Alps.

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10 35 **Taxon:** Coleoptera, Carabidae (ground beetles)

11 36 **Methods:** Carabid communities were sampled using pitfall traps along elevation gradients (697-2840
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13 37 m) in 433 study sites comprising a range of habitat types. The probability of carabid occurrence was
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15 38 modelled in relation to elevation, region and their interactions with two key traits, body size and
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17 39 wing development, using a mixed-modelling framework.

18 40 **Results:** Carabid occurrence declined with increasing elevation, although this relationship was
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20 41 modulated by both body size and wing development. Smaller species were less likely to occur than
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22 42 larger bodied species at lower elevations, but the probability of occurrence of smaller species did
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24 43 not vary greatly across the gradient, whereas for larger species, there was a steep decline in
25
26 44 occurrence from low to high elevation. Occurrence of brachypterous species (reduced wings) was
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28 45 greater at lower elevations, but declined steeply as elevation increased, whereas dimorphic and
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30 46 macropterous species (fully winged) declined along the gradient, but less steeply. However, these
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32 47 patterns also varied regionally, indicating that trait-elevation interactions are not geographically
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34 48 consistent. Habitat could not explain the differences between regions.

35 49 **Main conclusions:** Species traits are important in explaining the distribution of carabids along
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37 50 elevation gradients in mountains, and they may help to identify the species that are the most
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39 51 vulnerable, and the most resilient, to future environmental change. Increased probability of
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41 52 occurrence of smaller, winged species at higher elevations suggests that these species are likely to
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43 53 be particularly threatened in the future. However, the difference in responses to elevation between
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45 54 regions has important implications for modelling species distributions, as it suggests low model
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47 55 transferability, i.e. a trait-based model derived from one region cannot necessarily be used to
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49 56 project relative elevational shifts in a wider area.

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58 **KEYWORDS**

59 Alpine, carabids, elevation gradient, species traits, body size, wing development.
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1 | INTRODUCTION

The study of species traits can provide key insights into mechanisms that drive species distributions, as these traits can modulate species responses to the environment (Pollock et al., 2012). Species' sensitivity to environmental change is in part related to intrinsic factors, so particular traits shown by different species may to some extent dictate their responses (Moretti et al., 2017; Nolte et al., 2019), and ultimately the consequences for the population as a whole. Indeed, there are studies that have demonstrated that particular traits are associated with population declines and local extinction risk (e.g. Kotze & O'Hara 2003; Driscoll & Weir 2005; Nolte et al., 2019). As such, traits can be useful indicators of responses to environmental disturbance (Vanderwalle et al., 2010; Kotze et al., 2011).

Carabid beetles (Coleoptera: Carabidae), also known as ground beetles, are good candidate ecological indicators as they are sensitive to habitat heterogeneity and land-use, they are sufficiently abundant and relatively easy to study (Vanbergen et al., 2005; Gobbi & Fontaneto 2008; Vanderwalle et al., 2010; Gobbi et al., 2015). In carabids, two species traits have been studied in particular, body size and wing development. Body size is well known to vary in relation to environmental gradients in a range of organisms (Blackburn et al., 1999), including carabids (Gutiérrez & Mendez, 1997; Homburg et al., 2013) as it is related to food availability in the environment and to the length of larval development (Blake et al., 1994; Lövei & Magura, 2006). Wing development varies in carabids from species with fully developed hind wings (macropterous) to flightless species with undeveloped hindwings (brachypterous). There are also some species ('dimorphic') which have both macropterous and brachypterous individuals. Wing development is thus a trait which is linked to dispersal ability and hence may be important in terms of how species may respond (i.e. move) to a particular environmental change (Brandmayr 1983; Kotze et al., 2011).

Studying variations in species traits across elevation gradients provides a useful means to assess potential environmental change impacts in mountains in the absence of long-term monitoring data, as this approach provides a space-for-time substitution when considering conditions along the gradient (Hodkinson, 2005). A greater proportion of brachypterous species tend to be found in carabid communities at increasingly higher elevations at both large (Homburg et al., 2013) and small (Maveety & Browne, 2014) scales. However, the relationship between body size and elevation is less clear. In some cases, body size increases with elevation (Cvetkovska-Gjiogjievaska et al., 2017), while others have found weak (Pizzolotto et al., 2016), variable (Maveety & Browne, 2014) or no (Homburg et al., 2013) association. However, body size has been shown to be associated with habitat type (Gobbi & Fontaneto, 2008; Pizzolotto et al., 2016), and environmental productivity and stability (Homburg et al., 2013; Nolte et al., 2019). It therefore seems that a number of factors may

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3 94 affect trait responses to the environment, and it thus follows that such relationships may vary
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5 95 regionally. If species-environment relationships are to be used to draw inferences on species'
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7 96 vulnerability to environmental change, then it is important to understand the extent to which such
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9 97 relationships are consistent over different spatial contexts (e.g. Whittingham et al., 2007), which
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11 98 includes the role of species traits in driving species distributions along ecological gradients.

12 99 In this study, we consider the role that two key traits, body size and dispersal ability
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14 100 (represented by hind wing development), play in determining the elevational distribution of carabids
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16 101 in three different regions of the European Alps. Mountains in general, and the European Alps in
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18 102 particular, face a number of pressures including climate change, increasing human disturbance and
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20 103 changes in livestock management, all of which may have potentially profound effects on high
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22 104 elevation biodiversity (e.g. Dirnböck et al., 2011; Payne et al., 2017), and they also harbour a number
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24 105 of endemic and endangered species (e.g. Negro et al., 2008; Rabbitsh et al., 2016). As a result of both
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26 106 climate and land use changes, carabid beetles have tended to shift towards summits over the past
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28 107 decades (Pizzolotto et al., 2014), and changes in vegetation have resulted in a reduced area of open
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30 108 habitats, with subsequent negative effects for high elevation species (Pizzolotto et al., 2016).
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32 109 Therefore, an understanding of how traits modulate species responses to elevation gradients may
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34 110 help to identify which species (i.e. with particular traits) may be negatively impacted by, and which
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36 111 species will be resilient to, future environmental change, if we consider our environmental gradient
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38 112 as a climate gradient and a space-for time substitution (Blois et al., 2013). Specifically, we assess how
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40 113 species traits modulate the responses of carabids to elevation and habitat gradients, and
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42 114 importantly, how consistent these relationships are across three main Alpine regions (Western,
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44 115 Central-Eastern and Eastern Alps).

45 116 46 117 47 118 **2 | MATERIALS AND METHODS**

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49 120 A database of carabid species presence from a range of different sampling locations in the Italian
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51 121 Alps was compiled from several different studies (a list of sampling locations, years of sampling, and
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53 122 the number of traps set per location is given in Appendix S1). There was a total of 433 sampling
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55 123 sites. There were three main regions of study, corresponding to the three main groups participating
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57 124 in the study (Fig. 1): the Western Alps (n = 264 sites, henceforth W-Alps) in Piedmont and Val
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59 125 d'Aosta in the northwest of Italy; the Central-Eastern Alps in the regions of Trentino-Alto Adige (the
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126 western part) and Lombardy, (n = 125 sites, henceforth CE-Alps); and the Eastern Alps in Trentino-
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128 Alto Adige (the eastern part) and the Veneto Dolomites (n = 44 sites, henceforth E-Alps).

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3 128 Furthermore, sites were grouped into study areas which referred to the geographic location of a
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5 129 cluster of sites, often a single valley and from the same study (e.g. a group of sites distributed along
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7 130 an elevation gradient that were sampled under the same project). All studies adopted the same
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9 131 general pitfall trapping method: plastic vessels, c. 10 m apart, measuring about 8 cm mouth
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11 132 diameter, and 10 cm in depth, containing c. 20 ml of an attracting and preserving mixture of white
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13 133 wine vinegar and sodium chloride, and covered with some rocks (which allowed access to beetles,
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15 134 but which prevented the trap filling with rain, and discouraged interference from larger animals;
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17 135 Brandmayr et al., 2005). Modifications for non-lethal traps were made in areas with species of
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19 136 conservation concern (Negro et al., 2013). The number of traps and the number of days for which
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21 137 traps were active ('exposure days') varied between sites (respectively a range of 2 to 15 traps per
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23 138 site, which were active from 14 to 150 days). This variation in effort was taken into consideration in
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25 139 the analysis (see below).

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27 140 The database consisted of the presence or absence of each species recorded per site, the
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29 141 total number of traps used and the total number of exposure days. In addition, broadscale habitat
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31 142 data from the Corine land cover classification was derived for each site, based on the central grid
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33 143 coordinate of each site, which comprised the following land cover classes, estimated as percentage
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35 144 cover within a 100m radius of the central grid coordinate: coniferous forest, mixed forest,
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37 145 broadleaved forest, grass, shrubs, rock, sparse vegetation, crops, water, snow/glaciers and urban
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39 146 (henceforth referred to as habitat types). Elevation was also extracted from a Digital Terrain Model.

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41 147 For each species, mean body length (mm) and hind wing development was obtained from
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43 148 Brandmayr et al., (2005), Homburg et al., (2014), Gobbi et al., (2015), Gobbi et al., (2017), Pizzolotto
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45 149 et al., (2016), Hůrka (1996) and direct observations under a stereomicroscope. Body size was centred
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47 150 and scaled prior to statistical analyses. Wing development was defined into three groups: (i)
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49 151 brachypterous – flightless species with reduced (wing shorter than the elytron) or absent hind wings,
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51 152 expected to be poor dispersers; (ii) macropterous – flying species with fully developed hind wings
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53 153 (unfolded wing longer than the elytron); (iii) dimorphic – species which can show both
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55 154 brachypterous and macropterous individuals.

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58 156 **1.1 | Statistical analyses**

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60 157 The goal of the analyses was to determine the extent to which two specific traits, body size and hind
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62 158 wing development, modulated the probability of carabid presence along the elevation gradient, the
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64 159 extent to which the traits effect varied regionally, and the role of habitat in driving both trait-
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66 160 elevation and trait-region interactions by adopting a mixed modelling approach (following Carboni et
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68 161 al., 2018).

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3 162 First, the extent to which body size and the frequency of different wing development types
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5 163 was compared between regions using, respectively, ANOVA and χ^2 -tests. The two traits were then
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7 164 modelled separately using Generalized Linear Mixed Models (GLMMs). The presence of a carabid
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9 165 species at a given site was modelled in relation to elevation, two-way interactions between elevation
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11 166 and region, and elevation and trait, and the interaction between all three variables. Following
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13 167 Carboni et al. (2018), the trait was not modelled as a main effect, but only as an interactive effect, as
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15 168 we were interested in the modulating effect it had on the relationship between elevation and
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17 169 carabid presence. We ran GLMMs using the glmer function of the lme4 package in R. Species
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19 170 identity was included as a random effect as per Carboni et al. (2018). In addition, study area was
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21 171 specified as a further random effect to account for non-independence of sampling sites from the
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23 172 same location and study (Dormann et al., 2007; Gobbi & Brambilla, 2016). Other variables (body size
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25 173 or wing development, elevation, region and land cover variables) were specified as fixed effects. A
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27 174 binomial error distribution was specified. Model outputs estimate the probability of occurrence of
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29 175 the 'average' species across the whole community in relation to fixed effects. Potential residual
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31 176 spatial autocorrelation was examined by plotting variograms (Zuur et al., 2009). Significance of fixed
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33 177 effects was approximated by using the Anova function in the car package (Fox & Weisberg, 2011).
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35 178 Including all 195 species resulted in convergence problems for many models, hence rare species ($n =$
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37 179 28) that occurred only once in the whole sample were omitted. The final database consisted of 167
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39 180 species from 433 sites, making a total of 72311 observations.

35 181 Using the above model structure, a series of exploratory analyses were first undertaken to
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37 182 assess effects of sampling effort, and to consider potential biases or model fitting problems by
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39 183 including certain habitats. Effort in terms of both the number of traps and the exposure days varied
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41 184 between sampling locations. In order to assess the potential effect of effort on probability of
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43 185 carabid presence, an initial analysis was carried out using the total number of exposure days x the
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45 186 number of traps per sampling site as a measure of effort. This variable was log-transformed, centred
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47 187 and standardized before analysis. A GLMM was then run, modelling species presence in relation to
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49 188 linear and quadratic effects of effort, specifying species as a random factor (as above). There was a
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51 189 highly significant effect of both linear ($\chi^2 = 36.22, p > 0.0001$) and quadratic effort terms ($\chi^2 = 9.94, p$
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53 190 > 0.001), showing the probability of occurrence increased at an accelerating rate with an increase in
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55 191 effort (Appendix S2). Linear and quadratic effort terms were included in all subsequent models to
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57 192 account for this effect.

55 193 To address the main objectives, data were first analysed across the whole data set,
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57 194 considering the interaction between trait and elevation. Second, the extent to which the trait-
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59 195 elevation interaction was modulated by region was also considered by adding region, and the three-
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3 196 way interaction between region, trait and elevation was tested. Where there were significant region
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5 197 interactions, analyses were run separately according to the three regions. Third, the effect of habitat
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7 198 variation was considered by substituting elevation with habitat in the above models. A large number
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9 199 of habitat variables were recorded, and there was a strong degree of inter-correlation between
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11 200 them due to the marked changes in habitat along the elevation gradient considered (e.g. from forest
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13 201 to shrub-forest mosaics to alpine pasture as elevation increases). The habitat data were therefore
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15 202 analysed using Principal Components Analysis (PCA) in order to try and identify meaningful
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17 203 environmental gradients which were then used in subsequent models.

16 204 Model performance was assessed by comparing Akaike's Information Criterion (AIC) for
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18 205 models with different fixed effects. Models with lower AIC values are considered to be better
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20 206 performing, and when a difference in AIC between models (ΔAIC) is less than 2, models are
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22 207 considered of equivalent performance (Burnham & Anderson, 2002).

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25 209 **3 | RESULTS**

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28 211 Of the total 195 species recorded, 44% (85 species) were brachypterous, 15% dimorphic (29 species)
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30 212 and 41% macropterous (81 species). Most species were medium sized (5.4-10.75mm, 42%, 81
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32 213 species), while extra large species were the least frequent (22-35mm, 8%, 16 species). Large species
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34 214 (11-21.5mm, 32%, 62 species) were more frequent than small species (2.7-5.25mm, 18%, 36
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36 215 species). A total of 19% of species were classed as steno-endemic or endemic, i.e. with very
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38 216 restricted geographical range, e.g. *Carabus olympiae*, *Duvalius breiti*, *Trechus dolomitanus*, while
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40 217 most species (44%) showed wide or very wide distributions, e.g. *Amara eurynota*, *Calathus fuscipes*,
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42 218 *Pseudophonus rufipes*.

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44 220 **3.1 | Habitat description**

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46 221 For most of the 11 habitat types considered, there were either cover values close to 100% or close to
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48 222 0%, reflecting the fact that most sample sites were either in forest or alpine grasslands and other
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50 223 open habitats above the treeline, with few sites in ecotone habitats. There were also some habitats
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52 224 which were rare, occurring on $\leq 5\%$ of sites across the sample (crops, water, snow/glaciers, and
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54 225 urban). These were not considered further. For the seven other habitats (coniferous forest, mixed
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56 226 forest, broadleaved forest, grass, shrubs, rock, sparse vegetation), cover was converted to
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58 227 presence/absence per site. Differences between regions were then analysed for each of these latter
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60 228 habitat types using a GLM specifying binomial errors. There were a number of significant differences
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230 229 between regions (Table 1). Notably, sampling sites in the W-Alps were more likely to have broad-

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3 230 leaved and mixed forest and less likely to have sparse vegetation, those in the E-Alps were more
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5 231 likely to have grass, and those in CE-Alps were more likely to have rock. The mean elevation differed
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7 232 between regions ($\chi^2 = 18.13$, $P > 0.001$), where sampling sites in CE-Alps and E-Alps were on average
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9 233 higher than in the W-Alps (mean \pm sd, W-Alps = 1766 ± 33 m, $n = 264$; C-Alps = 1990 ± 48 m, $n = 125$;
10 234 E-Alps = 1965 ± 57 m, $n = 44$), although E-Alps had a notably smaller elevation range than W-Alps or
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12 235 CE-Alps (respectively 1540m, 2075m and 2126m).

13 236 The seven more widespread habitat variables were analysed using PCA. The first two PCA
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15 237 axes accounted for 37% of variation in the data. The first axis represented a gradient from closed
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17 238 (coniferous forest) to open (grassland and rock) habitats, whereas the second axis was a gradient
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19 239 from broadleaved and mixed forest to coniferous forest and grassland, and was therefore
20 240 representative of the elevation gradient (Appendix S2). Indeed, Axis 2 was positively correlated with
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22 241 elevation ($r = 0.45$), whereas Axis 1 was less strongly and negatively correlated with elevation ($r = -$
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24 242 0.32). Lower axes were harder to interpret and were not considered further.

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26 244 **3.2 | Trait and elevation**

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29 245 Overall, the probability of carabid occurrence decreased with increasing elevation. This is reflective
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31 246 of the general decrease in species richness with elevation (Poisson regression with study area as a
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33 247 random effect, slope \pm se = -0.558 ± 0.059 , $p < 0.0001$). There was a significant negative effect of
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35 248 elevation on the probability of carabid occurrence which was modulated by body size (Fig. 2), as
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37 249 shown by the significant interaction between elevation and body size ($\chi^2 = 102.70$, $p > 0.0001$; note
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39 250 full model details are given in Appendix S3). This means that the probability of occurrence increased
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41 251 with smaller body sizes at higher elevations, whereas species with larger body sizes were much more
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43 252 likely to occur at lower elevations, and this probability declined rapidly at higher elevations. There
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45 253 was also a significant interactive effect of elevation and wing development on the probability of
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47 254 carabid occurrence ($\chi^2 = 44.21$, $p < 0.001$). In this case, the probability of occurrence of
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49 255 brachypterous species (low dispersal) was highest at lower elevations, but decreased markedly as
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51 256 elevation increased, whereas for the other two categories, the rate of decrease was much less (Fig.
52
53 257 3). The body size model was a better fit than the wing development model (Δ AIC = 63.6), suggesting
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55 258 body size has a greater modulating effect than wing development. There was a suggestion of
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57 259 residual spatial autocorrelation in that there was some trend evident in the residuals (Appendix S4).

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59 260 Note that estimates of probability of occurrence in the figures are for an average species.
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261 Given that the overall occurrence rate (i.e. the number of presences as a proportion of the total
262 number of site \times species combinations) was 0.042, these probabilities are small. Nevertheless, the
263 patterns were generally consistent when considering only more widespread species. For example,

264 the models testing for interactions between trait and elevation were generally similar, especially
265 body size, to those above when considering only the 49 species which occurred in at least 20 sites
266 (Appendix S5).

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268 **3.3 | Region effects**

269 The next stage was then to assess whether the above models were influenced by region (full model
270 details are given in Appendix S3). There was no evidence of an overall difference in body size
271 between regions (ANOVA comparing body sizes of all species present in each region: $F_{2,182} = 0.31$, $p =$
272 0.73). In the mixed effects model, there was a significant three-way interaction between body size,
273 elevation and region ($\chi^2 = 34.79$, $p > 0.0001$). This model was better performing than the elevation-
274 only model in terms of AIC ($\Delta\text{AIC} = 38.0$), suggesting important additional variation is explained by
275 region. Therefore, the interactions were considered separately by region. Patterns in W-Alps and E-
276 Alps were similar to each other, and to the overall model (Fig. 4), although probability levels were
277 somewhat lower in the latter region. The interaction between body size and elevation was
278 significant in both regions (W-Alps $\chi^2 = 144.11$, $p > 0.0001$; E-Alps $\chi^2 = 13.85$, $p > 0.001$). CE-Alps,
279 however, showed a rather different pattern (Fig. 4B) and there was no significant interaction
280 between body size and elevation ($\chi^2 = 0.80$, $p = 0.37$). Instead, there was a rather uniform decrease
281 in probability of occurrence with increasing elevation across different body sizes – in other words
282 the probability of occurrence of carabids of small or large body size was equal for any given
283 elevation. For all three regions, there was less evidence of spatial autocorrelation in the data
284 according to variograms (Appendix S4) compared to the model without region (i.e. Fig. 2).

285 There was no evidence that the frequency of the different wing development classes was
286 associated with any particular region ($\chi_4^2 = 7.41$, $p = 0.13$). In common with body size, there was a
287 significant three-way interaction between wing development, elevation and region ($\chi^2 = 195.45$, $p >$
288 0.0001) in the model, which was much better performing than the elevation-only model ($\Delta\text{AIC} =$
289 329.6). When analysed separately by region, there was a highly significant interaction between wing
290 development and elevation in W-Alps ($\chi^2 = 173.21$, $p > 0.0001$) and CE-Alps ($\chi^2 = 19.88$, $p > 0.0001$),
291 but not in E-Alps ($\chi^2 = 4.13$, $p = 0.13$). The probability of occurrence of brachypterous species
292 decreased with elevation in W-Alps, whereas there was an increase in macropterous and dimorphic
293 species (Fig. 5A). However, in CE-Alps, there were declines in the probability of occurrence of all
294 three groups with elevation (Fig. 5B).

295 The W-Alps region covered a larger geographic range than the other two regions, including
296 three study areas from the Maritime Alps in the south-western area of the Alpine arc (Fig. 1).
297 Including the Maritime Alps as a separate region resulted in model convergence problems. Omitting

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3 298 these three study areas ($n = 17$ sites), however, had no marked effect on the outcomes of either the
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5 299 elevation model, nor the regional model, for either trait (Appendix S6).
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8 301 **3.4 | Habitat effects**

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10 302 Elevation was substituted by, separately, Axis 1 and Axis 2 (i.e. two separate models) in the body
11 303 size- elevation model for all regions (i.e. that in Fig. 1) in order to assess if habitat variations could
12 304 explain the effect of elevation (model details are given in Appendix 7). There was no significant
13 305 interaction between body size and Axis 1 ($\chi^2 = 0.031$, $p = 0.86$) or Axis 2 ($\chi^2 = 0.257$, $p = 0.61$).
14 306 Similarly, there was no evidence that the body size-elevation association varied according to region
15 307 (i.e. no significant PCA axis \times elevation \times region interaction) for either Axis 1 ($\chi^2 = 0.857$, $p = 0.65$) or
16 308 Axis 2 ($\chi^2 = 0.200$, $p = 0.91$). In common with body size, there was no evidence of an interactive
17 309 effect between habitat and wing development on the probability of carabid occurrence (Axis1*wing
18 310 development, $\chi^2 = 1.08$, $p = 0.58$; Axis2*wing development, $\chi^2 = 1.40$, $p = 0.50$), nor was there
19 311 evidence of a three-way interaction with region (Axis1 $\chi^2 = 10.77$, $p = 0.10$; Axis2 $\chi^2 = 2.68$, $p = 0.85$).
20 312 Model performance was always worse in habitat models ($\Delta AIC > 90$).
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34 315 **4 | DISCUSSION**

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36 317 There was a general decline in probability of carabid occurrence along the elevation gradient in all
37 318 models, reflecting the decrease in species richness at higher elevations. This result is in agreement
38 319 with carabid species richness patterns investigated in other mountain areas (e.g. Maveety et al.,
39 320 2011; Zou et al., 2014; Winkler et al., 2018). Our results highlighted that the studied species traits
40 321 (i.e. body size and wing morphology) take part in modulating the species richness elevational trend,
41 322 but that these relationships were in general not consistent across different Alpine regions.
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45

46 323 In general, smaller species were less likely to occur than larger bodied species at lower
47 324 elevations, but the probability of occurrence of smaller species did not vary greatly across the
48 325 gradient, whereas for larger species, there was a steep decline in occurrence from low to high
49 326 elevation. Body size is correlated with many aspects of carabid life history, i.e. reproductive rate,
50 327 dispersal, resource utilization, energetic balance and competition (Homburg et al., 2013; Nolte et al.,
51 328 2019). A change in body size of a population in a habitat may indicate environmental stress (Blake et
52 329 al., 1994; Garbalińska & Skłodowski, 2008). Smaller species can be found at all elevations: we found
53 330 that they are relatively more likely to live at high elevations compared to larger species, where they
54 331 show a shorter larval development that likely enables them to exploit the short snow-free season
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3 332 when reproduction is possible. This seems to follow the hypothesis of the negative effect of
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5 333 elevation on body size (Horne et al., 2017). In addition, most of the small species living at medium-
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7 334 low altitudes in riparian habitats or human-managed areas have completely developed wings, thus
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9 335 they are able to disperse better, and so they respond quickly to environmental stress/perturbation,
10 336 hence they are dominant in harsher, less predictable conditions (Brandmayr, 1983, 1991; Pizzolotto,
11 337 2009). The occurrence of larger species is positively linked to the successional stage of a habitat,
12 338 whereas it is negatively linked to environmental stress (Melis et al., 2010; Gobbi & Fontaneto, 2008).
13 339 At low elevations, larger carabids are dominant in woodlands, their occurrence declining with
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15 340 increasing elevation due to climatic and trophic, and thus ultimately physiological, constraints that
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17 341 positively select for small size species.

20 342 There was an analogous pattern in relation to wing development, where brachypterous
21 343 species occurrence was greater at lower elevations, but declined steeply as elevation increased,
22 344 whereas dimorphic and macropterous species declined along the gradient, but less steeply. It was
23 345 notable that dimorphic and macropterous species showed very similar trends in all models,
24 346 suggesting that species with variable wing development are similar ecologically to fully
25 347 macropterous species (as per Homburg et al., 2013). A greater prevalence of brachypterous species
26 348 along the elevation gradient has been reported for insects in general (Hodkinson, 2005), and
27 349 carabids in particular (Homburg et al., 2013; Maveety & Browne 2014), and has been explained by
28 350 reduced flight activity in harsh cold environments (Hodkinson, 2005) where wind is also likely a
29 351 limiting factor. Our results do not support this contention, showing instead a marked decrease in
30 352 brachypterous compared to macropterous or dimorphic species along the elevation gradient.
31 353 Rather, our results support the hypothesis of Brandmayr (1991) who tried to draw the evolutionary
32 354 pathway leading to wing reduction in carabid beetles. He assumed that the amount of
33 355 brachypterous species increases among two main axes interacting in an additive way: the dynamic
34 356 stability of a habitat (successional stages) and the hydric stability of the soil (water balance).
35 357 Brachypterous species likely have a lower gene flow with respect to macropterous species because
36 358 they have low dispersal abilities. Therefore, they are prone to local extinction due to strong
37 359 environmental perturbations, thus unlike macropterous species that are potentially able to shift on
38 360 all kind of habitats, brachypterous species are linked to low elevation natural and climax habitats
39 361 (i.e. stable successional stages such as mountain forests). The progressive and marked decline of
40 362 brachypterous species as elevation increases can thus be explained by increasing environmental and
41 363 micro-climatic pressure at high elevation: only few brachypterous species are adapted to live above
42 364 c. 2000 m, because these elevations are characterized by lower food availability, low annual mean
43 365 temperatures, and shorter breeding and growing seasons. Species able to fly are likely more able to
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3 366 maintain more connected subpopulations of a metapopulation in the patchy habitats located above
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5 367 the treeline.

6 368 Relationships between traits and elevation showed some notable regional variations,
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8 369 suggesting that the way traits modulate the occurrence-elevation relationship are not consistent
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10 370 geographically. Pizzolotto et al. (2016) found that in some mountain groups, species traits were
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12 371 weakly correlated with elevation, but were instead more directly driven by the habitat type. We
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14 372 might therefore expect that regional differences could be explained on the basis of habitat
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16 373 variations. However, there was no evidence that habitat was associated with carabid occurrence,
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18 374 nor that this was modulated by traits, both overall and at regional levels. Elevation provided a
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20 375 better model fit in each case, suggesting that elevation relationships are not driven by habitat
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22 376 variations. It should be noted, however, that the habitat data used were based on land cover types
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24 377 that were more related to general habitat structure than vegetation species composition, hence we
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26 378 can only draw conclusions about habitat measured at a fairly coarse resolution. It is possible that
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28 379 finer-scale micro-habitats, in particular plant species, topography or microclimate, and the degree of
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30 380 human disturbance, can all play important roles.

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32 381 Climate is likely to be a key driver in the overall relationship between occurrence, elevation
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34 382 and traits, as smaller and better dispersing (i.e. macropterous) species are better adapted to harsher
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36 383 conditions at high elevation (Brandmayr, 1991; Okuzaki et al., 2015). We have used elevation as a
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38 384 proxy for climatic conditions, as the elevation gradient is correlated with a range of environmental
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40 385 factors, most notably temperature, but also precipitation, atmospheric pressure, wind speed, and
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42 386 radiation input (Barry, 1992), all of which may influence carabid distributions along elevation
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44 387 gradients through physiological constraints triggered by the climatic conditions (Hodkinson, 2005).
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46 388 Variations between regions may therefore be due to a range of climatic influences in addition to
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48 389 temperature, and their effects may interact with each other and with other factors such as
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50 390 topography. Teasing apart the precise elements that dictate regional differences in carabid
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52 391 distributions therefore represents a challenge.

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54 392 Climate change is likely to threaten high elevation species in particular as they are pushed
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56 393 increasingly towards mountain summits, and eventually these species may have 'nowhere to go' as
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58 394 these summits become climatically unsuitable (e.g. Dirnböck et al., 2011; Pizzolotto et al., 2016).
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60 395 This study suggests that smaller, winged carabids are likely to be most vulnerable to such climate
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62 396 change impacts, and also that species with these characteristics would be good candidate indicators
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64 397 of environmental change in mountains (Brandmayr et al., 2013). However, it is also important to
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66 398 highlight that among the steno-endemic species, which are all low dispersal species and cover a wide
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68 399 body size range, from medium-large species (e.g. *Carabus* spp., *Oreonebria* spp.) to smaller-sized
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3 400 species (*Trechus* spp.), local extinctions have been already documented (Pizzolotto et al., 2014), thus
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5 401 they must also be considered very sensitive to environmental and climate change in mountains.

6 402 The difference in responses to elevation between regions has important implications for
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8 403 modelling species distributions, as it suggests low model transferability, i.e. a trait-based model
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10 404 derived from one region cannot necessarily be used to project relative elevational shifts in a wider
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12 405 area. In order to improve our understanding of regional differences in how traits modulate carabid
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14 406 distributions along elevation gradients, the contributions of individual climatic components, as well
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16 407 as the effects of finer-scale habitat features, need to be assessed.
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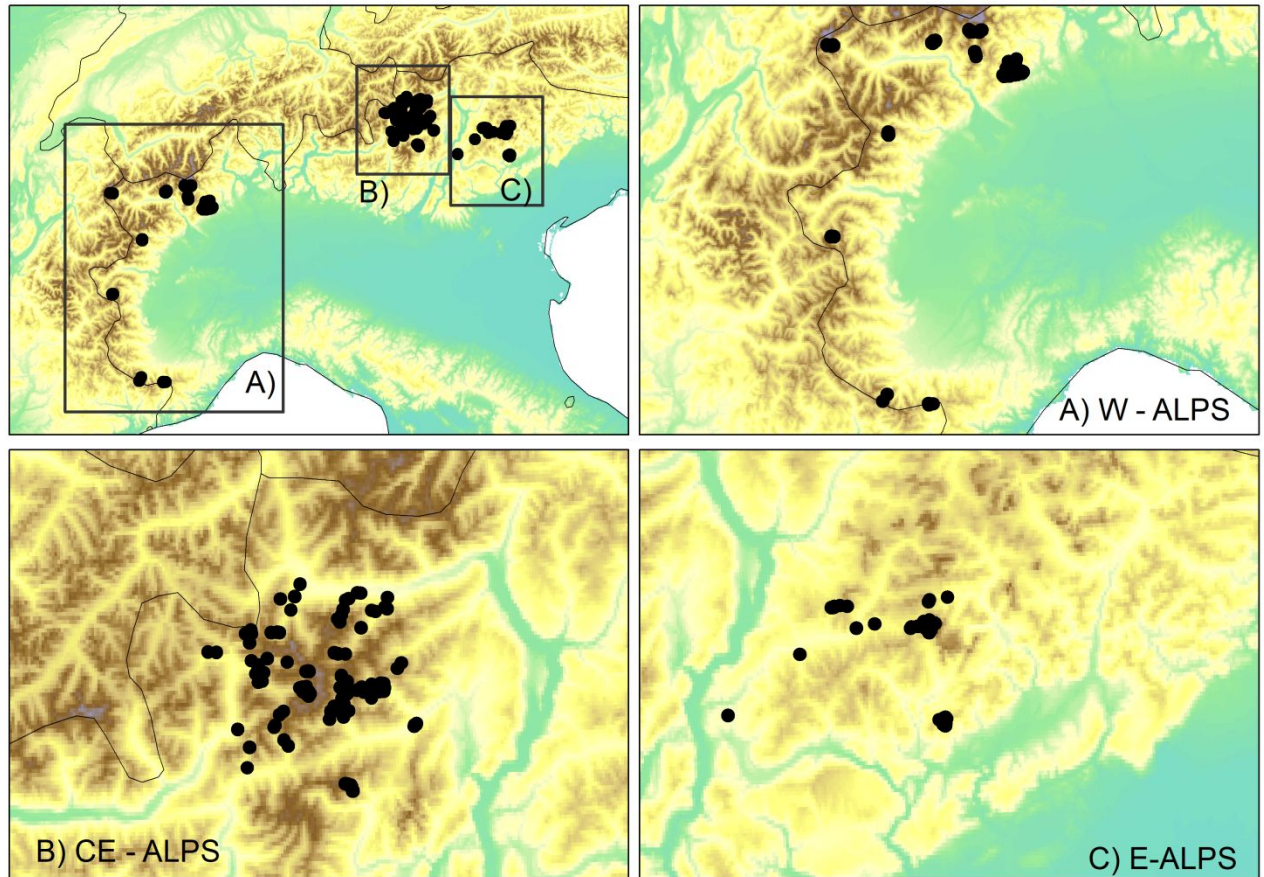
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TABLE 1. Parameter estimates \pm se for the probability of occurrence (on a logit scale) of habitats across carabid sampling sites in the Italian Alps. % freq, indicates the percentage of presences across the sample of 433 sites. W-Alps n = 264, CE-Alps n = 125, E-Alps n = 44.

Habitat	% freq.	W-Alps	CE-Alps	E-Alps	χ^2	<i>p</i>
Coniferous forest	34	-0.693 \pm 0.131	-0.419 \pm 0.182	-1.068 \pm 0.349	3.21	0.20
Broad-leaved forest	16	-1.119 \pm 0.143	-4.127 \pm 0.713	-3.738 \pm 1.011	51.80	<0.001
Mixed forest	12	-1.530 \pm 0.161	-2.99 \pm 0.418	-3.738 \pm 1.012	20.74	<0.001
Grass	34	-0.626 \pm 0.129	-1.036 \pm 0.203	0.140 \pm 0.306	10.50	0.005
Shrubs	9	-2.741 \pm 0.258	-1.858 \pm 0.261	-2.277 \pm 0.525	5.74	0.057
Rock	16	-1.946 \pm 0.186	-1.112 \pm 0.207	-1.819 \pm 0.440	8.85	0.012
Unvegetated	6	-4.466 \pm 0.581	-2.162 \pm 0.292	-1.194 \pm 0.361	33.52	<0.001

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FIGURE 1. Study area in the Italian Alps, showing the 433 study sites (black dots) and the three regions considered.

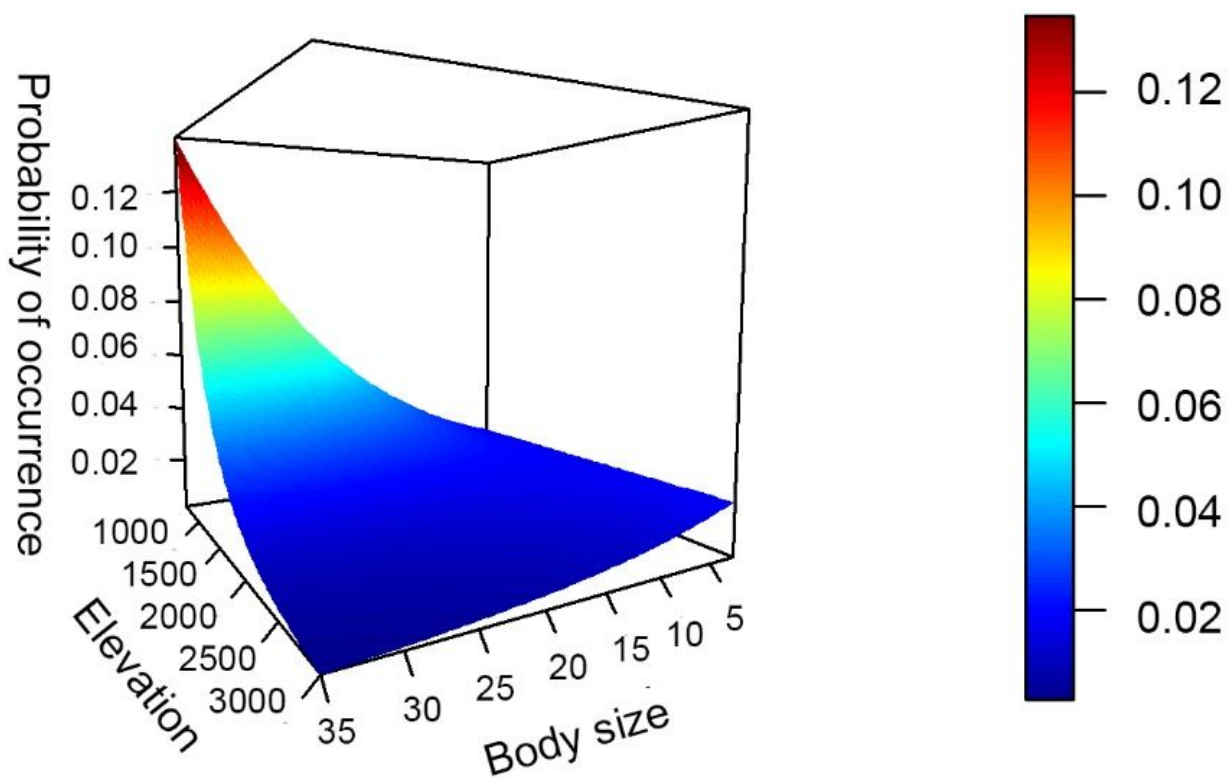


FIGURE 2. Probability of carabid presence in relation to elevation and body size combining data from all regions.

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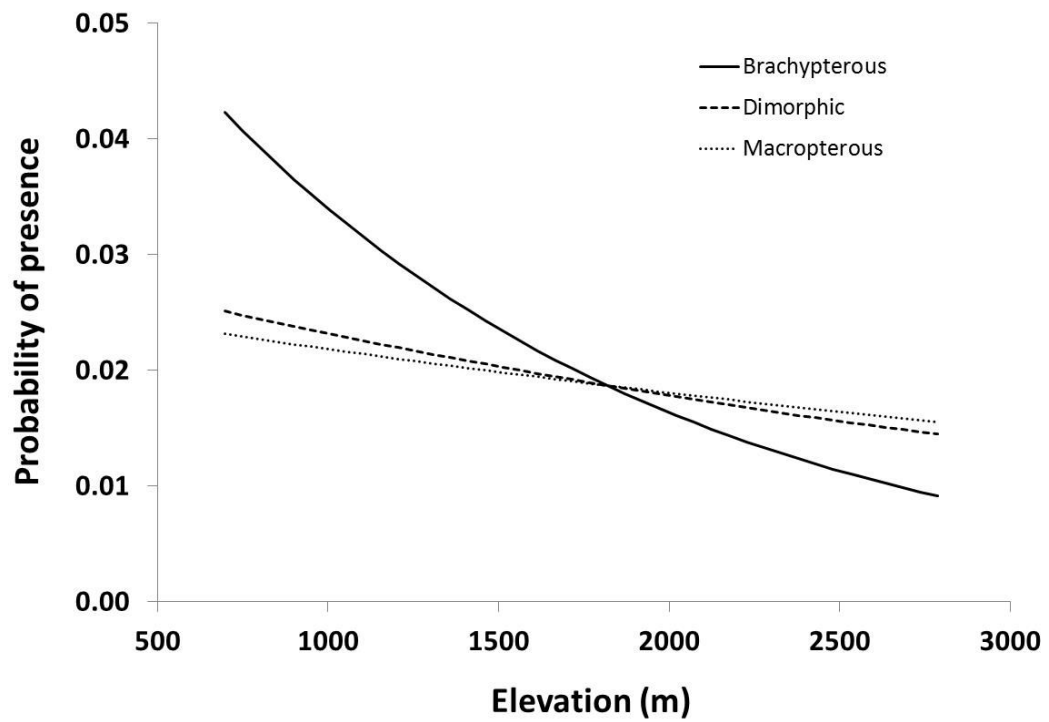
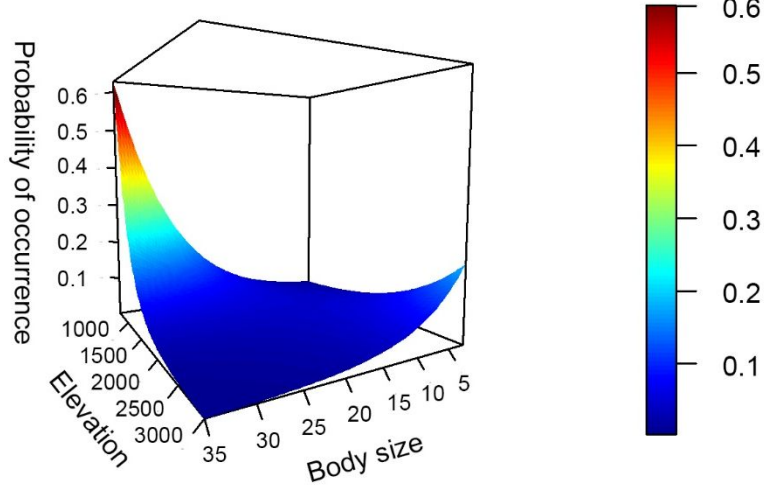


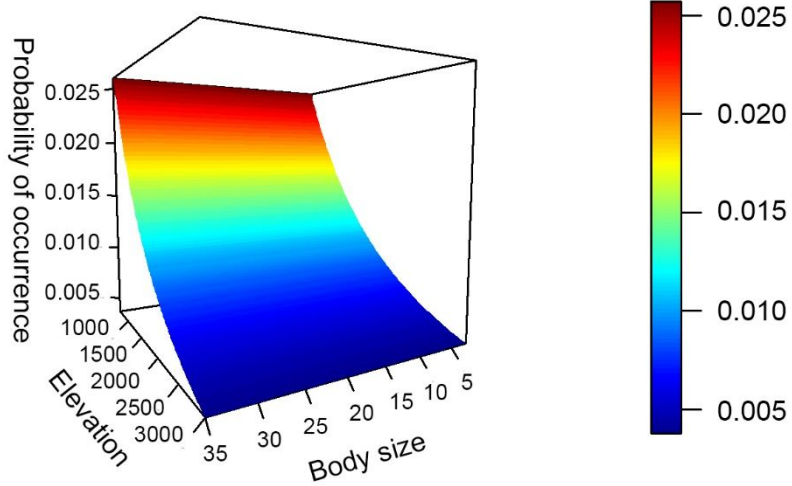
FIGURE 3. Probability of carabid presence in relation to elevation and wing development combining data from all regions.

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A. W-Alps



B. CE-Alps



C. E-Alps

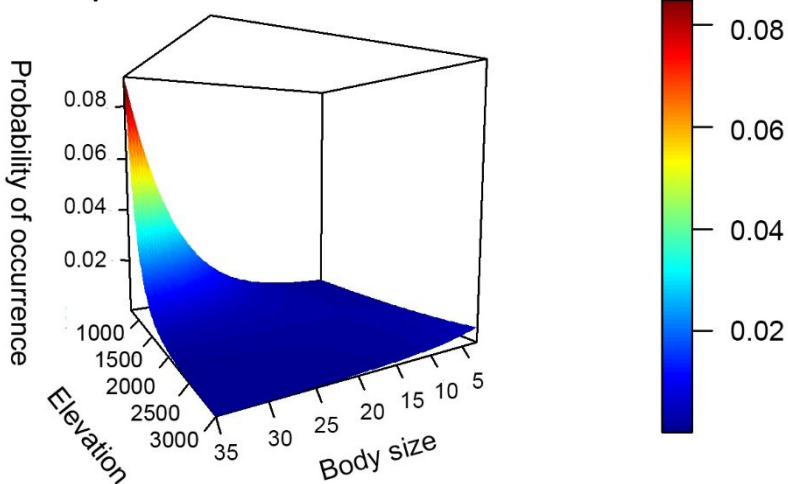


FIGURE 4. Probability of carabid presence in relation to elevation and body size in different Alpine regions.

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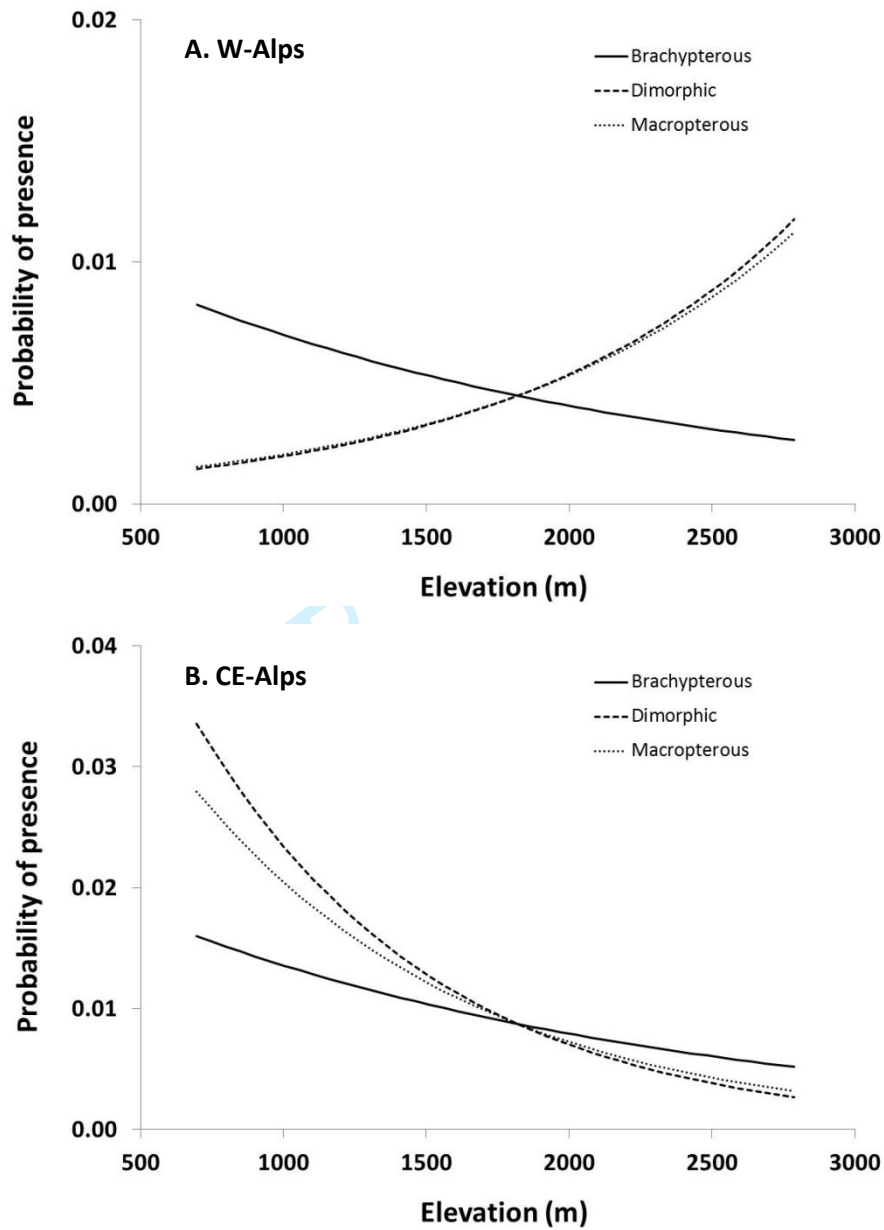


FIGURE 5. Probability of carabid presence in relation to elevation and wing development in different Alpine regions where there was a significant elevation×region×trait interaction. Note that there was no significant region interaction in E-Alps.

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For Peer Review

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Biosketch

Dan Chamberlain works on impacts of environmental change on animal biodiversity, and has a special interest in the ecology of high elevation species, and how they are likely to be affected by climate change. He is an Associate Professor in Animal Ecology at the University of Turin.

Author contributions: AR conceived the concept of the paper; DC analysed the data; all other authors collected the data and helped compile the database; DC and MB led the writing with contributions from all authors.

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Appendix 1. Site details.**Table S1.** Locations of study areas, years sampling undertaken and references if relevant. Coordinates (EPSG 32632) are given for the approximate central sampling site.

Region	Study area	Geographic coordinates (easting; northing)	No. sites	No. traps/site	Year	Reference
CE-Alps	Val D'Amola	632064; 5117932	15	3	2011-12	Gobbi et al. 2017
W-Alps	Argentera	335649; 4975695	5	3-8	2010	Unpubl.
W-Alps	Bettaforca	405849; 5079719	24	4	2010	Negro et al. 2013a
W-Alps	Monte Bianco Miage	336054; 072292	6	6	2006	Gobbi et al. 2011
CE-Alps	Braulio	608061; 5152841	4	5	2013-14	Unpubl.
E-Alps	Passo Rolle, Pale di S. Martino	693850; 5135550	29	3-6	2008-9	Brandmayr & Zetto Brandmayr 1988; Pizzolotto et al. 2014; Unpubl.
CE-Alps	Val Cedec Pasquale	621721; 5145647	5	6	2007	Gobbi et al. 2010
E-Alps	Vette di Feltre	719800; 5108200	14	3-6	1983-4	Brandmayr & Pizzolotto 1987
CE-Alps	Valle dei Forni	620990; 5141563	13	6	2004-05	Gobbi et al. 2007
W-Alps	Gabiet	411470; 5079782	24	4	2007	Negro et al. 2010; 2013a
CE-Alps	Val Grande	607084; 5124529	6	5	2013-14	Unpubl.
W-Alps	Gressoney	409104; 5066965	25	3	2006	Negro et al. 2009
W-Alps	Gressoney La Trinità	406669; 5079314	4	2-7	2010	Unpubl.
C-Alps	Laas	630223; 5162607	8	5	2014-15	Unpubl.
W-Alps	Val Grande, Lanzo	364285; 5027361	3	5-8	2010	Unpubl.
W-Alps	Limone Piemonte	385060; 4890223	8	12	2011	Unpubl.
W-Alps	Lourusa	363909; 4895302	4	12	2008	Unpubl.
CE-Alps	Val Martello	635104; 5155380	9	5	2014-15	Unpubl.
C-Alps	Val di Peio	628040; 5135496	21	3-15	2008-14	Gobbi et al. 2013; 2015; Unpubl.
E-Alps	Altopiano di Pine	669654; 5110691	1	15	2009	Unpubl.
C-Alps	Val di Rabbi	641274; 5140947	17	5-15	2008-14	Gobbi et al. 2013; 2015; Unpubl.
W-Alps	Monte Rosa	417142; 5091161	3	6	2014	Tampucci et al. 2017
CE-Alps	Sobretta Gavia	612125; 5140636	6	5	2013-14	Unpubl.
CE-Alps	Val di Sole	646227; 5133203	4	3	2013-14	Gobbi et al. 2013; 2015; Unpubl.
CE-Alps	Stilfs	610871; 5155656	7	5	2014-15	Unpubl.
W-Alps	Torgnon	388579; 5075027	48	3	2006	Negro et al. 2009
CE-Alps	Val d'Ultimo	645380; 5151327	2	5	2014-15	Unpubl.
CE-Alps	Val di Dentro	598626; 5150057	3	5	2013-14	Unpubl.
W-Alps	Valletta	361744; 4891722	5	12	2008	Unpubl.
W-Alps	Val Sessera	612207; 5148526	105	5	2010	Negro et al. 2013b
CE-Alps	Val Zebrù	612197; 5148496	5	5	2013-14	Unpubl.

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Appendix S2. Preliminary analyses and Principal Components Analysis of habitat

The potential effect of sampling effort on probability of carabid presence were assessed by defining exposure days x the number of traps per sampling site as a measure of effort. This variable was log-transformed, centred and standardized before analysis. A GLMM was then run, modelling species presence in relation to linear and quadratic effects of effort, specifying species as a random factor. There was a highly significant effect of both linear ($\chi^2 = 36.22$, $p > 0.0001$) and quadratic effort terms ($\chi^2 = 9.94$, $p > 0.001$), showing the probability of occurrence increased at an accelerating rate with an increase in effort (Fig. S1). Linear and quadratic effort terms were included in all subsequent models to account for this effect. There were 58 sites on ski pistes, all from W-Alps. A preliminary model (including effort, as above) found no evidence of a difference between the probability of carabid occurrence on ski pistes compared to other habitats within this region ($\chi^2 = 0.142$, $p = 0.71$), so these were included in subsequent analyses.

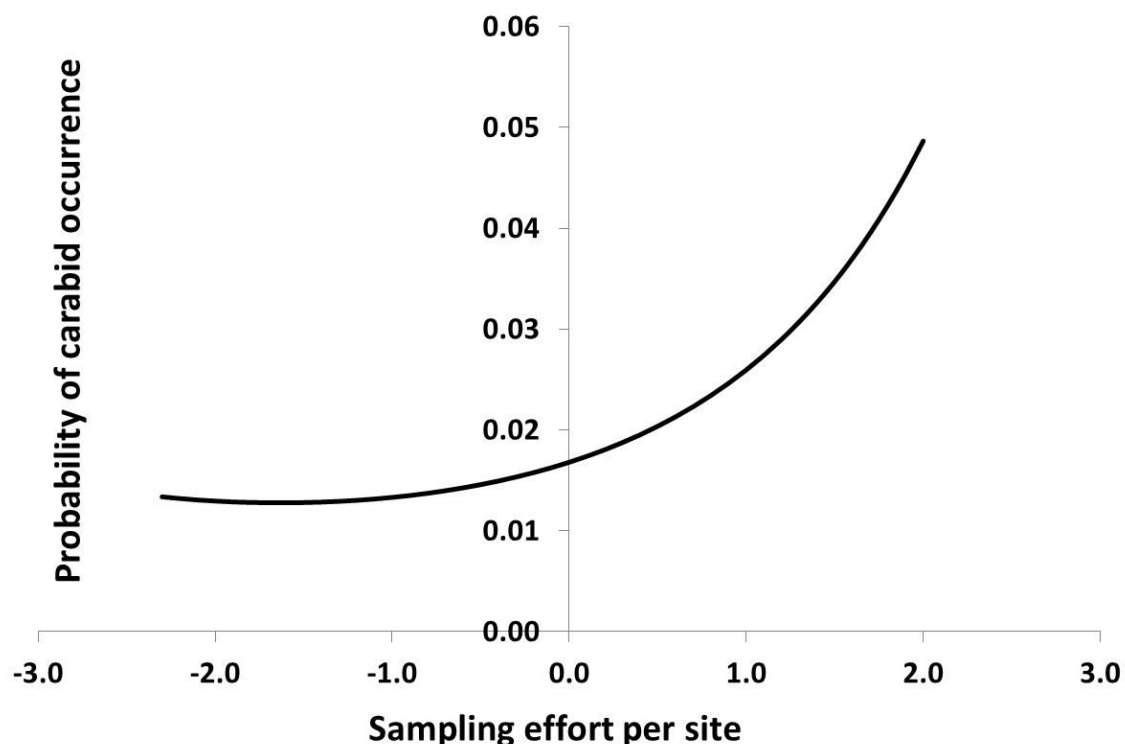


FIGURE S1. Fitted model of the effect of sampling effort per site (the product of the number of traps and the total exposure days, log-transformed, scaled and centred) on the probability of carabid presence combining data from all regions.

Table S2. Loadings for the first two axes of a Principal Components Analysis on the cover of different habitat types in 433 sites in the Italian Alps. Numbers in brackets are the percentage variation in the data explained by each axis. Black cells indicate loadings close to zero on each axis.

Habitat	Axis 1 (20%)	Axis 2 (17%)
Coniferous forest	0.767	0.357
Mixed forest		-0.470
Broad-leaved forest	-0.109	-0.501
Grass	-0.616	0.581
Shrubs		-0.125
Rocks	-0.133	-0.196
Unvegetated		

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Appendix S3. Details of models analysing carabid species presence in relation to traits, elevation and region.

Table S3. Model results derived from GLMMs which specified species and study area as random effects. Wing indicates wing development (d = dimorphic, m = macropterous). For factorial variables, CE-Alps (for Region) and brachypterous species (Wing development) were set as reference levels.

(a) Body size and elevation (n = 72311 observations, 31 study areas, 167 species, AIC = 21111.1)

Explanatory variable	Estimate \pm se	z	P
Intercept	-3.978 \pm 0.125	-31.824	<0.001
Effort	0.257 \pm 0.055	4.621	<0.001
Effort ²	0.079 \pm 0.032	2.441	0.013
Elevation	-0.228 \pm 0.036	-6.255	<0.001
Elevation \times Size	-0.193 \pm 0.019	-10.140	<0.001

(b) Wing development and elevation (n = 72311 observations, 31 study areas, 167 species, AIC = 21174.7)

Explanatory variable	Estimate \pm se	z	P
Intercept	-3.967 \pm 0.125	-31.684	<0.001
Effort	0.252 \pm 0.055	4.552	<0.001
Effort ²	0.078 \pm 0.032	2.466	0.014
Elevation	-0.380 \pm 0.040	-9.517	<0.001
Elevation \times Wing(d)	0.242 \pm 0.052	4.654	<0.001
Elevation \times Wing(m)	0.280 \pm 0.048	5.863	<0.001

(c) Body size, elevation and region (n = 72311 observations, 31 study areas, 167 species, AIC = 21073.1)

Explanatory variable	Estimate \pm se	z	P
Intercept	-3.974 \pm 0.126	-31.519	<0.001
Effort	0.257 \pm 0.056	4.567	<0.001
Effort ²	0.079 \pm 0.032	2.463	0.014
Elevation	-0.237 \pm 0.037	-6.490	<0.001
Elevation \times Size	-0.033 \pm 0.032	-1.041	0.296
Size \times Region(E-Alps)	0.018 \pm 0.060	0.295	0.768
Size \times Region(W-Alps)	0.074 \pm 0.041	1.793	0.073
Elevation \times Size \times Region(E-Alps)	-0.194 \pm 0.074	-2.639	0.008
Elevation \times Size \times Region(W-Alps)	-0.241 \pm 0.041	-5.852	<0.001

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60**(d) Body size and elevation, W-Alps (n = 44088 observations, 13 study areas, 167 species, AIC = 9843.9)**

Explanatory variable	Estimate \pm se	z	P
Intercept	-5.430 \pm 0.259	-20.981	<0.001
Effort	0.422 \pm 0.143	2.945	0.003
Effort ²	0.152 \pm 0.105	1.452	0.146
Elevation	0.115 \pm 0.085	1.351	0.177
Elevation \times Size	-0.376 \pm 0.031	-12.005	<0.001

(e) Body size and elevation, CE-Alps (n = 20875 observations, 15 study areas, 167 species, AIC = 6272.0)

Explanatory variable	Estimate \pm se	z	P
Intercept	-4.750 \pm 0.215	-22.062	<0.001
Effort	0.242 \pm 0.139	1.744	0.081
Effort ²	0.132 \pm 0.069	1.906	0.057
Elevation	-0.448 \pm 0.042	-10.567	<0.001
Elevation \times Size	-0.028 \pm 0.032	-0.895	0.370

(f) Body size and elevation, E-Alps (n = 7348 observations, 3 study areas, 167 species, AIC = 2310.3)

Explanatory variable	Estimate \pm se	z	P
Intercept	-6.289 \pm 0.842	-7.461	<0.001
Effort	-0.162 \pm 0.141	-1.153	0.259
Effort ²	0.052 \pm 0.115	0.453	0.642
Elevation	-0.046 \pm 0.098	-0.469	0.657
Elevation \times Size	-0.292 \pm 0.079	-3.722	<0.001

(g) Wing development, elevation and region (n = 72311 observations, 31 study areas, 167 species, AIC = 20845.1)

Explanatory variable	Estimate ± se	z	P
Intercept	-3.814 ± 0.129	-29.658	<0.001
Effort	0.207 ± 0.050	4.173	<0.001
Effort ²	0.086 ± 0.029	2.982	0.003
Elevation	-0.238 ± 0.057	-4.195	<0.001
Elevation×Wings(d)	-0.440 ± 0.084	-5.256	<0.001
Elevation×Wings(m)	-0.308 ± 0.077	-4.005	<0.001
Wingsb×Region(E-Alps)	0.561 ± 0.201	2.787	<0.001
Wingsd×Region(E-Alps)	0.169 ± 0.227	0.743	0.458
Wingsm×Region(E-Alps)	-0.834 ± 0.266	-3.134	0.002
Wingsb×Region(WAlps)	-0.147 ± 0.133	-1.109	0.268
Wingsd×Region(WAlps)	-1.135 ± 0.156	-7.290	<0.001
Wingsm×Region(WAlps)	-0.535 ± 0.144	-3.714	0.238
Elevation×Wings(b)×Region(E-Alps)	0.137 ± 0.116	1.181	<0.001
Elevation×Wings(d)×Region(E-Alps)	0.672 ± 0.182	3.692	<0.001
Elevation×Wings(m)×Region(E-Alps)	1.169 ± 0.300	3.900	<0.001
Elevation×Wings(b)×Region(WAlps)	-0.056 ± 0.094	-0.598	0.550
Elevation×Wings(d)×Region(WAlps)	1.108 ± 0.125	8.891	<0.001
Elevation×Wings(m)×Region(WAlps)	0.958 ± 0.111	8.651	<0.001

(h) Wing development and elevation, W-Alps (n = 44088 observations, 13 study areas, 167 species, AIC = 9830.5)

Explanatory variable	Estimate ± se	z	P
Intercept	-5.427 ± 0.257	-21.105	<0.001
Effort	0.422 ± 0.142	2.982	0.003
Effort ²	0.155 ± 0.103	1.505	0.132
Elevation	-0.278 ± 0.087	-3.215	0.001
Elevation×Wing(d)	0.791 ± 0.082	9.844	<0.001
Elevation×Wing(m)	0.766 ± 0.067	11.427	<0.001

(i) Wing development and elevation, CE-Alps (n = 20875 observations, 15 study areas, 167 species, AIC = 6254.7)

Explanatory variable	Estimate ± se	z	P
Intercept	-4.766 ± 0.214	-22.213	<0.001
Effort	0.275 ± 0.141	1.947	0.052
Effort ²	0.119 ± 0.070	1.698	0.090
Elevation	-0.276 ± 0.058	-4.731	<0.001
Elevation×Wing(d)	-0.358 ± 0.088	-4.085	<0.001
Elevation×Wing(m)	-0.270 ± 0.084	-3.223	<0.001

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(j) Wing development and elevation, E-Alps (n = 7348 observations, 3 study areas, 167 species, AIC = 2322.0)

Explanatory variable	Estimate \pm se	z	P
Intercept	-6.242 \pm 0.908	-7.079	<0.001
Effort	-0.161 \pm 0.140	-1.150	0.250
Effort ²	0.053 \pm 0.115	0.463	0.643
Elevation	-0.186 \pm 0.115	-1.622	0.105
Elevation \times Wing(d)	0.112 \pm 0.203	0.549	0.583
Elevation \times Wing(m)	0.589 \pm 0.291	2.027	0.043

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3 **Appendix S4. Variograms based on residuals from elevation×body size and elevation×body size×region**
4 **models.** Note variograms were very similar when considering residuals from wing development models.
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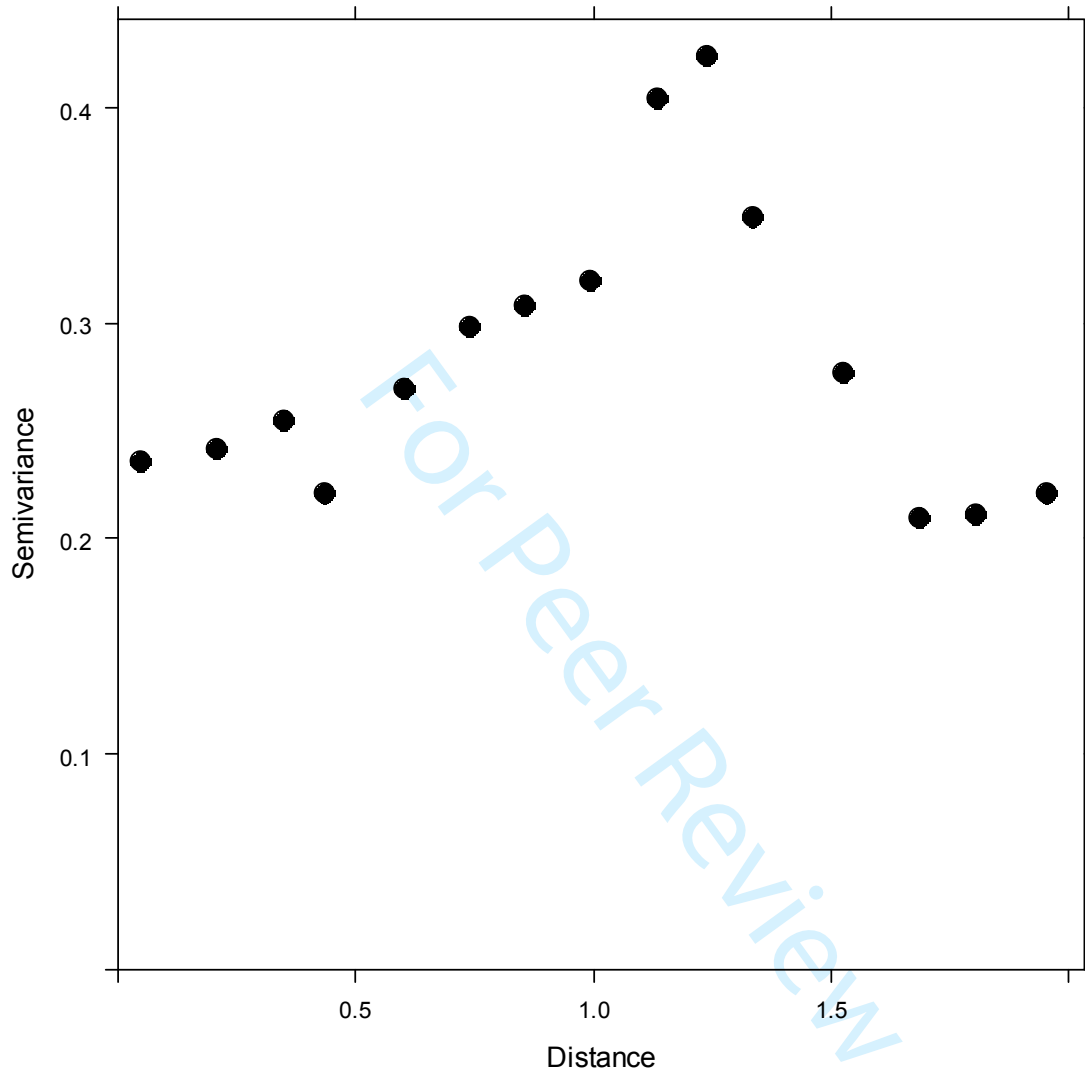


Fig. S2. Variogram of model residuals from Fig. 2.

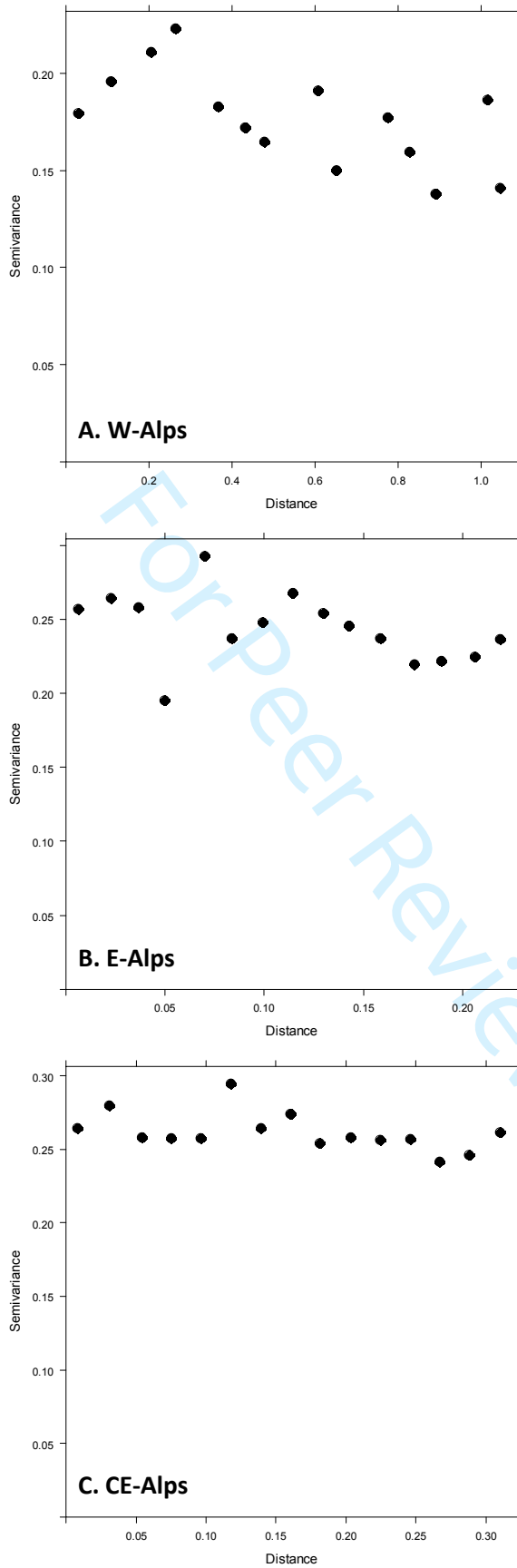


Fig. S3. Variogram of model residuals from Fig. 3.

Appendix S5. Details of models analysing carabid species presence in relation to traits and elevation considering only relatively common species (at least 20 occurrences in the data set).

Table S4. Results derived from GLMMs which specified species and study area as random effects. Wing indicates wing development (d = dimorphic, m = macropterous). For factorial variables, CE-Alps (for Region) and brachypterous species (Wing development) were set as reference levels.

(a) Body size (n = 21217 observations, 31 study areas, 49 species, AIC = 13469.5)

Explanatory variable	Estimate \pm se	z	P
Intercept	-2.525 \pm 0.138	-18.309	<0.001
Effort	0.223 \pm 0.069	3.240	0.0012
Effort ²	0.074 \pm 0.039	1.893	0.0584
Elevation	-0.246 \pm 0.043	-5.667	<0.001
Elevation \times Size	-0.205 \pm 0.024	-8.557	<0.001

(b) Wing development (n = 21217 observations, 31 study areas, 49 species, AIC = 13456.7)

Explanatory variable	Estimate \pm se	z	P
Intercept	-2.523 \pm 0.137	-18.411	<0.001
Effort	0.224 \pm 0.069	3.256	0.001
Effort ²	0.075 \pm 0.039	1.899	0.058
Elevation	-0.407 \pm 0.047	-8.666	<0.001
Elevation \times Wing(d)	0.513 \pm 0.060	8.611	<0.001
Elevation \times Wing(m)	0.368 \pm 0.062	5.937	<0.001

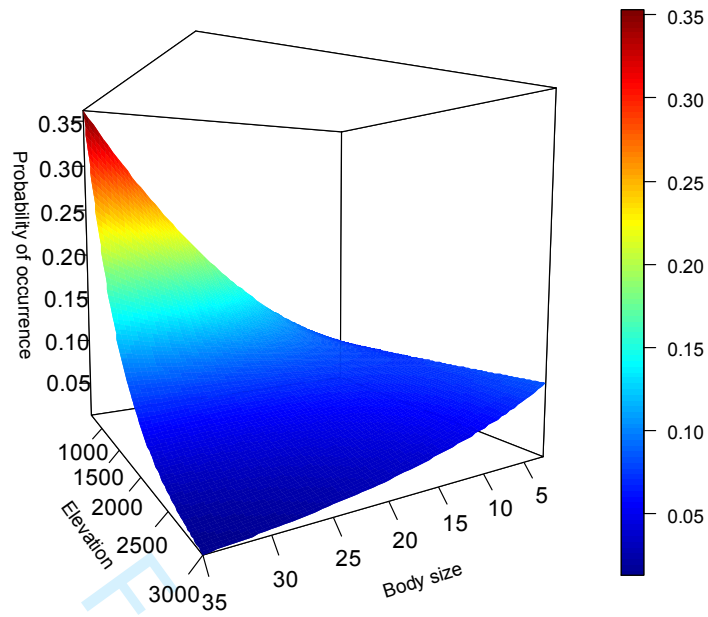


Fig. S4. Probability of carabid presence in relation to elevation and body size, considering only species with at least 20 occurrences in the whole sample.

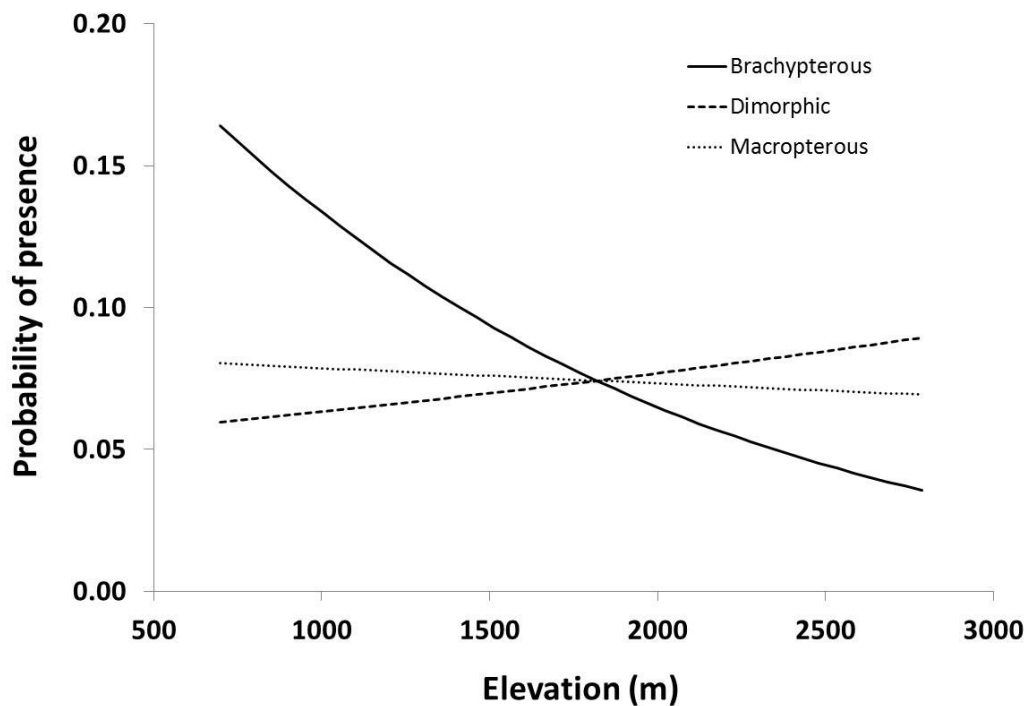


Fig. S5. Probability of carabid presence in relation to elevation and wing development, considering only species with at least 20 occurrences in the whole sample.

Appendix S6. Details of models analysing carabid species presence in relation to traits, elevation and region omitting sites (n = 17) from the Maritime Alps (part of the W-Alps region).

Table S5. Results derived from GLMMs which specified species and study area as random effects. Wing indicates wing development (d = dimorphic, m = macropterous). For factorial variables, CE-Alps (for Region) and brachypterous species (Wing development) were set as reference levels.

(a) Body size and elevation (n = 69472 observations, 28 study areas, 167 species, AIC = 19857.6)

Explanatory variable	Estimate \pm se	z	P
Intercept	-4.066 \pm 0.137	-29.746	<0.001
Effort	0.263 \pm 0.058	4.513	<0.001
Effort ²	0.082 \pm 0.033	2.520	0.012
Elevation	-0.227 \pm 0.037	-6.163	<0.001
Elevation \times Size	-0.196 \pm 0.019	-10.224	<0.001

(b) Wing development and elevation (n = 69472 observations, 28 study areas, 167 species, AIC = 19922.4)

Explanatory variable	Estimate \pm se	z	P
Intercept	-4.054 \pm 0.137	-29.689	<0.001
Effort	0.259 \pm 0.058	4.438	<0.001
Effort ²	0.081 \pm 0.033	2.500	0.012
Elevation	-0.379 \pm 0.040	-9.377	<0.001
Elevation \times Wing(d)	0.245 \pm 0.052	4.738	<0.001
Elevation \times Wing(m)	0.289 \pm 0.048	5.911	<0.001

(c) Body size, elevation and region (n = 69472 observations, 28 study areas, 167 species, AIC = 19821.9)

Explanatory variable	Estimate \pm se	z	P
Intercept	-4.063 \pm 0.138	-29.496	<0.001
Effort	0.263 \pm 0.059	4.461	<0.001
Effort ²	0.083 \pm 0.033	2.502	0.012
Elevation	-0.236 \pm 0.037	-6.361	<0.001
Elevation \times Size	-0.034 \pm 0.032	-1.077	0.281
Size \times Region(E-Alps)	0.013 \pm 0.060	0.225	0.822
Size \times Region(W-Alps)	0.035 \pm 0.043	0.804	0.421
Elevation \times Size \times Region(E-Alps)	-0.195 \pm 0.074	-2.647	0.008
Elevation \times Size \times Region(W-Alps)	-0.253 \pm 0.042	-6.094	<0.001

(d) Body size and elevation, W-Alps (n = 41249 observations, 10 study areas, 167 species, AIC = 8456.7)

Explanatory variable	Estimate ± se	z	P
Intercept	-5.932 ± 0.334	-17.757	<0.001
Effort	0.399 ± 0.418	0.956	0.339
Effort ²	0.110 ± 0.246	0.448	0.654
Elevation	0.146 ± 0.094	1.557	0.120
Elevation×Size	-0.407 ± 0.033	-12.177	<0.001

(e) Wing development, elevation and region (n = 69472 observations, 28 study areas, 167 species, AIC = 19592.4)

Explanatory variable	Estimate ± se	z	P
Intercept	-3.883 ± 0.138	-28.072	<0.001
Effort	0.171 ± 0.055	3.094	0.002
Effort ²	0.092 ± 0.030	3.115	0.002
Elevation	-0.249 ± 0.057	-4.341	<0.001
Elevation×Wings(d)	-0.434 ± 0.084	-5.186	<0.001
Elevation×Wings(m)	-0.310 ± 0.077	-4.011	<0.001
Wingsb×Region(E-Alps)	0.549 ± 0.214	2.569	0.010
Wingsd×Region(E-Alps)	0.151 ± 0.238	0.636	0.525
Wingsm×Region(E-Alps)	-0.848 ± 0.276	-3.074	0.002
Wingsb×Region(WAlps)	-0.269 ± 0.159	-1.687	0.092
Wingsd×Region(WAlps)	-1.267 ± 0.180	-7.054	<0.001
Wingsm×Region(WAlps)	-0.725 ± 0.170	-4.264	<0.001
Elevation×Wings(b)×Region(E-Alps)	0.135 ± 0.117	1.154	0.249
Elevation×Wings(d)×Region(E-Alps)	0.665 ± 0.182	3.646	<0.001
Elevation×Wings(m)×Region(E-Alps)	1.174 ± 0.302	3.888	<0.001
Elevation×Wings(b)×Region(WAlps)	-0.001 ± 0.097	-0.013	0.990
Elevation×Wings(d)×Region(WAlps)	1.159 ± 0.127	9.128	<0.001
Elevation×Wings(m)×Region(WAlps)	1.033 ± 0.114	9.023	<0.001

(f) Wing development and elevation, W-Alps (n = 41249 observations, 10 study areas, 167 species, AIC = 8544.0)

Explanatory variable	Estimate ± se	z	P
Intercept	-5.913 ± 0.331	-17.881	<0.001
Effort	0.934 ± 0.411	0.959	0.338
Effort ²	0.111 ± 0.242	0.461	0.645
Elevation	-0.246 ± 0.095	-2.579	0.010
Elevation×Wing(d)	0.805 ± 0.084	9.572	<0.001
Elevation×Wing(m)	0.795 ± 0.071	11.234	<0.001

Appendix S7 Details of models analysing carabid species presence in relation to traits, habitat and region.

Table S6. Results derived from GLMMs which specified species and study area as random effects. Wing indicates wing development (d = dimorphic, m = macropterous). For factorial variables, CE-Alps (for Region) and brachypterous species (Wing development) were set as reference levels. Habitat was defined according to two PCA axes (Axis1 and Axis2, defined in Table 2).

(a) Body size and Axis1 (n = 72311 observations, 31 study areas, 167 species, AIC = 21266.5)

Explanatory variable	Estimate \pm se	z	P
Intercept	-4.069 \pm 0.132	-30.930	<0.001
Effort	0.341 \pm 0.057	6.028	<0.001
Effort ²	0.104 \pm 0.033	3.146	0.002
Axis1	-0.022 \pm 0.017	-1.321	0.186
Axis1 \times Size	0.003 \pm 0.015	0.175	0.861

(b) Body size and Axis2 (n = 72311 observations, 31 study areas, 167 species, AIC = 21268.0)

Explanatory variable	Estimate \pm se	z	P
Intercept	-4.096 \pm 0.132	-30.940	<0.001
Effort	0.340 \pm 0.057	6.017	<0.001
Effort ²	0.104 \pm 0.033	3.157	0.002
Axis2	-0.003 \pm 0.018	-0.188	0.851
Axis2 \times Size	0.008 \pm 0.016	0.507	0.612

(c) Wing development and Axis1 (n = 72311 observations, 31 study areas, 167 species, AIC = 21267.5)

Explanatory variable	Estimate \pm se	z	P
Intercept	-4.070 \pm 0.132	-30.936	<0.001
Effort	0.341 \pm 0.057	6.032	<0.001
Effort ²	0.104 \pm 0.033	3.144	0.002
Axis1	-0.022 \pm 0.022	-1.000	0.317
Axis1 \times Wing(d)	0.030 \pm 0.043	0.681	0.500
Axis1 \times Wing(m)	-0.023 \pm 0.040	-0.565	0.572

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60**(d) Wing development and Axis2 (n = 72311 observations, 31 study areas, 167 species, AIC = 21268.9)**

Explanatory variable	Estimate ± se	z	P
Intercept	-4.069 ± 0.132	-30.937	<0.001
Effort	0.340 ± 0.056	6.016	<0.001
Effort ²	0.104 ± 0.033	3.153	0.002
Axis2	0.016 ± 0.023	0.698	0.485
Axis2×Wing(d)	-0.045 ± 0.046	-0.970	0.332
Axis2×Wing(m)	-0.039 ± 0.042	-0.917	0.359

(e) Body size, Axis1 and region (n = 72311 observations, 31 study areas, 167 species, AIC = 21247.5)

Explanatory variable	Estimate ± se	z	P
Intercept	-4.070 ± 0.132	-30.934	<0.001
Effort	0.343 ± 0.057	6.020	<0.001
Effort ²	0.102 ± 0.033	3.075	0.002
Axis1	-0.023 ± 0.017	-1.355	0.175
Axis1×Size	0.008 ± 0.027	0.301	0.764
Size×Region(E-Alps)	-0.004 ± 0.059	-0.061	0.951
Size×Region(W-Alps)	0.181 ± 0.039	4.707	<0.001
Axis1×Size×Region(E-Alps)	-0.040 ± 0.050	-0.807	0.420
Axis1×Size×Region(W-Alps)	0.002 ± 0.033	0.062	0.950

(f) Body size, Axis2 and region (n = 72311 observations, 31 study areas, 167 species, AIC = 21249.6)

Explanatory variable	Estimate ± se	z	P
Intercept	-4.070 ± 0.132	-30.930	<0.001
Effort	0.343 ± 0.057	6.010	<0.001
Effort ²	0.102 ± 0.033	3.082	0.002
Axis2	-0.003 ± 0.018	-0.175	0.861
Axis2×Size	-0.001 ± 0.028	-0.049	0.961
Size×Region(E-Alps)	-0.005 ± 0.059	-0.081	0.935
Size×Region(W-Alps)	0.181 ± 0.039	4.703	<0.001
Axis2×Size×Region(E-Alps)	0.018 ± 0.055	0.334	0.738
Axis2×Size×Region(W-Alps)	0.014 ± 0.035	0.408	0.683

(g) Wing development, Axis1 and region (n = 69472 observations, 28 study areas, 167 species, AIC = 21116.3)

Explanatory variable	Estimate ± se	z	P
Intercept	-3.909 ± 0.145	-26.911	<0.001
Effort	0.304 ± 0.055	5.508	<0.001
Effort ²	0.119 ± 0.033	3.700	<0.001
Axis1	-0.001 ± 0.040	-0.010	0.992
Axis1×Wings(d)	0.058 ± 0.070	0.836	0.403
Axis1×Wings(m)	0.004 ± 0.065	0.061	0.951
Wingsb×Region(E-Alps)	0.516 ± 0.265	1.927	0.054
Wingsd×Region(E-Alps)	0.121 ± 0.283	0.427	0.670
Wingsm×Region(E-Alps)	-0.709 ± 0.295	-2.405	0.016
Wingsb×Region(WAlps)	0.006 ± 0.165	0.033	0.973
Wingsd×Region(WAlps)	-1.159 ± 0.184	-6.316	<0.001
Wingsm×Region(WAlps)	-0.583 ± 0.175	-3.337	<0.001
Axis1×Wings(b)×Region(E-Alps)	-0.132 ± 0.071	-1.865	0.062
Axis1×Wings(d)×Region(E-Alps)	-0.071 ± 0.111	-0.637	0.524
Axis1×Wings(m)×Region(E-Alps)	0.106 ± 0.126	0.835	0.404
Axis1×Wings(b)×Region(WAlps)	-0.004 ± 0.050	-0.080	0.936
Axis1×Wings(d)×Region(WAlps)	-0.114 ± 0.085	-1.347	0.178
Axis1×Wings(m)×Region(WAlps)	-0.118 ± 0.071	-1.654	0.098

(h) Wing development, Axis2 and region (n = 69472 observations, 28 study areas, 167 species, AIC = 21125.6)

Explanatory variable	Estimate ± se	z	P
Intercept	-3.911 ± 0.145	-26.954	<0.001
Effort	0.306 ± 0.055	5.546	<0.001
Effort ²	0.119 ± 0.032	3.698	<0.001
Axis2	0.014 ± 0.043	0.338	0.735
Axis2×Wings(d)	-0.047 ± 0.075	-0.617	0.537
Axis2×Wings(m)	-0.062 ± 0.069	-0.904	0.366
Wingsb×Region(E-Alps)	0.516 ± 0.264	1.953	0.051
Wingsd×Region(E-Alps)	0.117 ± 0.282	0.416	0.678
Wingsm×Region(E-Alps)	-0.696 ± 0.294	-2.369	0.018
Wingsb×Region(WAlps)	0.007 ± 0.164	0.042	0.966
Wingsd×Region(WAlps)	-1.164 ± 0.183	-6.356	<0.001
Wingsm×Region(WAlps)	-0.570 ± 0.174	-3.274	0.001
Axis2×Wings(b)×Region(E-Alps)	-0.004 ± 0.075	-0.054	0.957
Axis2×Wings(d)×Region(E-Alps)	0.127 ± 0.121	1.050	0.294
Axis2×Wings(m)×Region(E-Alps)	0.037 ± 0.140	0.264	0.792
Axis2×Wings(b)×Region(WAlps)	0.003 ± 0.052	0.060	0.952
Axis2×Wings(d)×Region(WAlps)	-0.051 ± 0.090	-0.574	0.566
Axis2×Wings(m)×Region(WAlps)	0.055 ± 0.074	0.735	0.463