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3 1 **Complex influence of climate on the distribution and body size of an Alpine species.**

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6 3 Running Head: Climatic influences on *S. ursulae*

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10 5 **Abstract**

11 6 1. Alpine species with a limited distribution can act as sentinels of climate change, but first we have to  
12 7 identify their climate-sensitive traits. Here, we adopted a multi-level approach to define the influence of  
13 8 climate on the geographical distribution and body size of a steno-endemic Alpine grasshopper, the  
14 9 *Stenobothrus ursulae* Nadig, 1986.

15 10 2. We built a species distribution model (SDM) with the following climatic predictors: precipitation  
16 11 seasonality, precipitation of the wettest month, mean temperature of the driest quarter and isothermality.  
17 12 The model provides a satisfactory representation of the species geographical range, but it also identifies  
18 13 areas suitable in terms of climate in which the species was not found. Therefore, we suggest that  
19 14 climatic and geographic barriers combined with a poor dispersal ability might have limited its distribution.

20 15 3. We measured 309 individuals collected across the whole geographical range. Our results show that  
21 16 increasing elevation was linked both to a decline in *S. ursulae* body length (converse Bergmann's rule)  
22 17 and to a decline in sexual size dimorphism (converse Rensch's rule). We demonstrate also that the  
23 18 same climatic predictors that describe the species distribution affect its morphological variation.

24 19 4. Our results suggest that climate affects this species distribution and body size with opposite effects:  
25 20 suitable climatic conditions are found at high elevations, and the fitness-related trait (i.e. body size)  
26 21 declines with elevations. In the future, distribution and/or morphology of the species might change in  
27 22 order to successfully cope with the changing climate, but its very limited dispersal ability constitutes an  
28 23 issue of concern.

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31 25 Keywords: Bergmann's rule, bioclimatic envelope, body length, Gomphocerinae, Orthoptera, Rensch's rule,  
32 26 species distribution models, *Stenobothrus ursulae*, steno-endemic species, Western Alps.

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## 32 Introduction

33 Mountains host a large number of endemic species of plants and animals (Myers *et al.*, 2000; Nagy &  
34 Grabherr, 2009; Schmitt, 2009). These species are linked and often restricted to the many micro-climatic  
35 habitats created by the combination of elevation, exposure, slope and other geological or hydrological factors  
36 (Hewitt, 2000; Essl *et al.*, 2009). This specialization can lead to an increased vulnerability to climate change  
37 (Williams *et al.*, 2008). High-elevation species and habitats are expected to be among the most severely  
38 impacted by climate change (Beniston *et al.*, 1997; Theurillat & Guisan, 2001; Nogue-Bravo *et al.*, 2007;  
39 Dirnböck *et al.*, 2011). Upward shifts of alpine plants and treeline species (Grabherr *et al.*, 1994; Gindl, 1999;  
40 Paulsen *et al.*, 2000; Motta & Nola, 2001; Pauli *et al.*, 2001) have occurred and the composition of alpine  
41 communities has consequently changed (Keller *et al.*, 2000). Elevational range shifts may lead to structural  
42 changes in the composition of a particular habitat, or even its loss, therefore increasing fragmentation  
43 (Peñuelas & Boada, 2003; Gonzalez & Neilson, 2010). Climate change is, in effect, one of the major driving  
44 factors for species extinction process. Before reaching extinction, a species may develop adaptations to  
45 altered climatic conditions, through important modifications both at the species level, including shifts in  
46 geographical ranges either latitudinal or elevational and at the individual level, including changes in  
47 morphology (e.g. body size) (Root *et al.*, 2003; Bellard *et al.*, 2012).

48 Climate is the primary factor determining animal species distribution (Helmuth *et al.*, 2005). The range of  
49 climatic conditions to which the species is adapted define its climatic niche, an essential component of the  
50 fundamental niche (Hutchinson, 1957; Pearson & Dawson, 2003). Bioclimate envelope modelling approach  
51 identifies abiotic limitations on species distribution, defining its suitable climatic habitats. The realized niche  
52 can then be described considering observed species distribution, which is influenced also by biotic  
53 limitations, e.g. competition (Pearson & Dawson, 2003). A deep understanding on climatic niche is crucial to  
54 assess the vulnerability under a rapidly changing climate. Many species ranges have moved poleward or to  
55 higher elevations in the last century as an adaptation to climate change (Parmesan *et al.*, 1999; Thomas &  
56 Lennon, 1999; Parmesan & Yohe, 2003; Root *et al.*, 2003; Hickling *et al.*, 2005). Steno-endemic species, i.e.  
57 local endemism characterized by very limited distribution, are expected to be especially vulnerable and may  
58 be threatened by extinction (Schlumprecht *et al.*, 2010). Conservation biologists agree that efforts have to be  
59 concentrated on hotspots of biodiversity and endemic species. To identify the appropriate conservation  
60 strategies, a crucial step is to acquire detailed knowledge of the geographic distribution and basic biology of  
61 endemic species and, in the context of climate change, assess their sensitivity to climate (Sunday, 2002).

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3 62 Body size is a pivotal aspect of an organism's biology and ecology, it is often related to climate and can  
4 63 show broad scale patterns of variation (Whitman, 2008; Winterhalter & Mousseau, 2008; Sheridan &  
5 64 Bickford, 2011). Part of this relationship has been explained by some ecological rules, i.e. Bergmann's,  
6 65 Rensch's and their converse (Bergmann, 1847; Rensch, 1950). Bergmann's rule was proposed for  
7 66 endothermic animals and states that organisms show increased body size or mass in colder climates  
8 67 (Bergmann, 1847). Afterward, it was extended to the temperature variations along latitudinal and elevation  
9 68 gradient (e.g. Laiolo *et al.*, 2013). Body size is hypothesised to increase in colder climates because in  
10 69 endotherms heat generation capacity increases with body volume. Moreover, larger bodied organisms better  
11 70 retain body heat in cooler environments, thanks to a relatively lower surface area. The application of the  
12 71 Bergmann's rule on ectothermic animals, however, is still not certain, and multiple mechanisms behind the  
13 72 trend probably occurs (Shelomi, 2012; Vinarski, 2014). Ectotherms rely on environmental heat to  
14 73 thermoregulate. Therefore, in colder climate small bodied organisms are favoured because they are able to  
15 74 absorb heat faster. On the opposite, hot environments favour large bodied organisms because they perform  
16 75 better to avoid overheat. Another mechanism is commonly observed in ectotherms at higher  
17 76 latitudes/elevations. Here, the short growing season implies faster developmental rates, and therefore  
18 77 smaller adult individuals. For said reasons, the converse Bergmann's rule is often observed in ectotherms,  
19 78 especially those with a comparatively longer instar development time. In addition, the Bergmann's rule may  
20 79 relate to sexual size dimorphism (i.e. the inequality of body sizes between the two sexes; hereafter SSD)  
21 80 connecting it to another ecogeographic rule: Rensch's rule. It states that degree of SSD increases with body  
22 81 size in species with larger males, and decreases with body size in those with larger females (converse  
23 82 Rensch's rule assumes the opposite; Rensch, 1950; Abouheif & Fairbairn, 1997; Blanckenhorn *et al.*, 2006).  
24 83 In insects, hypoallometry of females versus males has been related to life-history trade-offs and to sexual  
25 84 selection. Males are commonly smaller than females in arthropods, and fecundity selection favouring large  
26 85 female size is often strong (Blanckenhorn *et al.*, 2007). Then we predict that SSD should increase with  
27 86 elevation in arthropods. However, there is still a scarcity of information about SSD intraspecific variation  
28 87 along elevation gradients.

29 88 We investigated the influence of climate on geographic distribution and body size in a steno-endemic  
30 89 species of the Italian Graian Alps, *Stenobothrus ursulae* Nadig, 1986. *S. ursulae* is a small size, annual and  
31 90 brachypterous grasshopper (Insecta: Orthoptera: Gomphocerinae), living between 1300 and 2556 m a.s.l.  
32 91 (Massa *et al.*, 2012; Sindaco *et al.*, 2012) and assessed as Vulnerable in the IUCN Red List, although there  
33 92 is no research published on the threats to this rare species so far (Zuna-Kratky *et al.*, 2016). Some

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3 93 populations are found in protected areas: Gran Paradiso National Park, Mont Avic Natural Park and five  
4 94 Natura 2000 Special Areas of Conservation (SACs). *S. ursulae* has been described on the basis of a good  
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6 95 series of specimens collected near Santa Elisabetta (Piedmont), between 1300 and 1500 m a.s.l. (Nadig,  
7  
8 96 1986). Another taxon, strictly related to this species, has been described as *S. nadigi* La Greca, 1987 on the  
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10 97 basis of a small series of specimens collected near Lake Chamolè (Aosta Valley) at 2300 m a.s.l. Later,  
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12 98 Nadig (1991) considered *S. nadigi* a synonym of *S. ursulae*, and this conclusion has been supported, with  
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14 99 new materials, by Massa (2010). The wide morphological variability presented by the species at different  
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16 100 elevations had misled taxonomists in the past, but the factors influencing it still remained unclear. *S. ursulae*  
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18 101 is known to show wide size variations both within and between sexes (total body length males: 10.5-17.3  
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20 102 mm, total body length females: 13.7-23.5 mm, pronotum length males: 2.4-3.3 mm, pronotum length  
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22 103 females: 2.9-4.2 mm, tegmina length males: 4.8-8.4 mm, tegmina length females: 4.5-8.0 mm, hind femurs  
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24 104 length males: 7.2-9.6 mm, hind femurs length females: 8.1-12.3 mm). Since this species inhabits just a small  
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26 105 portion of the available alpine and subalpine grasslands in the Western Alps, its distribution is likely to be  
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28 106 determined by factors other than habitat availability.

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30 107 In order to understand the effect of climate change on a species, it is important first to study how climate  
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32 108 influences the species characteristics. In this paper, we adopted a multi-level approach to define the possible  
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34 109 influence of climate on the geographical distribution and the body length of an alpine species. We  
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36 110 hypothesized that *S. ursulae* can act as sentinel of climate change, and we aimed to identify its climate-  
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38 111 sensitive traits. We focused on climate influences on body length, an individual trait that determines  
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40 112 individual fitness and dispersal, and on species geographic distribution, which may also be influenced by  
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42 113 these intrinsic factors. Clear evidence to link both species (range) and individual (phenotype) patterns to the  
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44 114 climate in high elevation-only species are still lacking. However, climate may affect multiple traits with  
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46 115 different magnitude and/or direction, e.g. a weak individual-level but a strong species-level effect or vice  
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48 116 versa. A multi-level approach on a single study system is then desirable to assess the role of the climate on  
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50 117 mountain species. In particular, insects inhabiting high elevations areas face relatively brief periods of  
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52 118 favourable climate conditions due to the strong seasonality of the environment. Thus, we focused on  
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54 119 isothermality, temperature and precipitation seasonality, and we tested if a species- and/or individual-level  
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56 120 effect in our study system does exist. Moreover, abiotic factors typically show variations along elevation  
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58 121 gradients. Temperature decreases at a rate of approximately 0.5 °C per 100 m of ascent, although this  
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60 122 general trend is strongly affected by local topography and meteorology. Temperature is also tightly  
123 associated with seasonality, and both have remarkable consequences on ectotherms, influencing their

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3 124 phenology, growth, reproduction and fitness-related traits such as body size (Laiolo & Obeso, 2017). Along  
4 125 elevation gradients, also atmospheric pressure and oxygen partial pressures decrease roughly linearly with  
5 126 elevation, influencing animal respiration processes. Unlike temperature and atmospheric pressure,  
6 127 precipitation shows non-linear relationships with elevation. It exhibits large spatial heterogeneity, with  
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8 128 different local and regional patterns. The whole range of annual precipitation values is represented in the  
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10 129 sector of the Graian Alps where *S. ursulae* occurs: particularly dry conditions are found in the Aosta Valley,  
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12 130 shadowed against directions with prevailing moisture bearing winds, while particularly large annual mean  
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14 131 values are observed along the rim of the Alps, towards the Po Plain (Isotta *et al.*, 2014).

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17 132 The aims of our study were to evaluate if climate affects *S. ursulae* distribution and body size and, if yes,  
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19 133 whether similar or opposite effects are found.

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## 22 135 **Materials and methods**

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### 25 26 137 **Study area, surveys and distribution data**

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28 138 The presence of *S. ursulae* is known in two regions of Italy, and in particular in the southern part of the Aosta  
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30 139 Valley and in the adjacent north-western part of Piedmont, and its geographical range is restricted to the  
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32 140 eastern Graian Alps. The known elevation range of the species is 1300-2300 m a.s.l. (Massa *et al.*, 2012)  
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34 141 and outside of that range, it was found in one single locality at 2556 m (Sindaco *et al.*, 2012). For the present  
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36 142 study, 23 elevation transects were walked in 2013 through 2017, from 1200 up to 3438 m a.s.l., to collect  
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38 143 presence data all across the distribution area of *S. ursulae*. Therefore, our study area is restricted to a few  
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40 144 side valleys of the Aosta Valley and to the type locality (near St. Elisabetta) in Piedmont. Each transect  
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42 145 covered from 6 to 21 km of distance and from 630 up to 1630 m of elevation. Considering the 23 transects  
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44 146 as a whole, we covered 250 km of distance and 21570 m of elevation. All the main categories of grassland  
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46 147 habitats were surveyed, with a uniform coverage of different exposure, elevation and different valleys. The  
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48 148 surveying was continuous along the transects, through direct observations, acoustic surveys and sweep  
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50 149 netting. We identified the specimens following Massa *et al.* (2012), and we excluded the nymphs due to the  
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52 150 risk of misidentification with other gomphocerine grasshoppers. Each presence site was georeferenced with  
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54 151 a precision <10 m and the geographical coordinates were reported in UTM WGS84 reference system.  
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56 152 Moreover, additional surveys have been carried out outside the known species distribution range; the area  
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58 153 covered by these samplings is shown with grey dots in Figure 1. For the distribution analysis, the final  
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60 154 database included the standardized data of the direct field surveys combined with a critical screening of the

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3 155 data derived from the literature (Nadig, 1986, 1991; Massa, 2010; Massa *et al.*, 2012; Sindaco *et al.*, 2012),  
4 156 and from the Italian fauna data base (Fontana *et al.*, 2005). In particular, the only record of the species in  
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6 157 Valle di Susa, first mentioned in Fontana *et al.* (2005) and subsequently cited in Massa *et al.* (2012), derived  
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8 158 from a wrongly reported information present in La Greca (1986). Moreover, the finding of this species in  
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10 159 Slovenia reported by Schraut (1999) is due to a misidentification with *Chorthippus alticola* Ramme, 1921 (S.  
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12 160 Gomboc, comm. pers.). Localities of each observation were added and validated in ESRI's ArcGIS Desktop  
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14 161 ArcMap 10.2.2 software (Esri, 2014) to construct a distribution map, using a UTM WGS84 reference system.  
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### 17 163 **Environmental variables**

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19 164 Twenty-two environmental variables were initially chosen as potential predictors of habitat distribution.  
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21 165 Environmental variables included 19 bioclimatic factors (BIO1–BIO19) and 3 topographic factors: elevation  
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23 166 (ALT), aspect (ASPECT) and slope (SLOPE). The bioclimatic variables were obtained from WorldClim -  
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25 167 Global Climate Data (version 1.4 available at <http://www.worldclim.org>) developed by Hijmans *et al.* (2005)  
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27 168 and were derived from monthly weather station measurements of temperature and rainfall. Our modelling  
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29 169 area covers two different Italian regions and part of France and Switzerland (Figure 1). Those provided from  
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31 170 WorldClim are the more precise and homogeneous data available for the whole area. The reliability of  
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33 171 WorldClim data is not problematic, as we confirmed in a comparison with locally measured meteorological  
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35 172 data in the Aosta Valley region. These data have been used in some other SDM studies for insects with  
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37 173 restricted alpine distribution (Urbani *et al.*, 2015; Biella *et al.*, 2017) and for plants (Casazza *et al.*, 2013).  
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39 174 WorldClim bioclim variables are biologically meaningful, and capture annual ranges, seasonality, and limiting  
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41 175 factors useful for niche modelling (such as monthly and quarterly temperature and precipitation extremes).  
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43 176 Elevation data (ALT) were obtained from Digital Elevation Model, while the individuals capture points'  
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45 177 elevations were provided by GPS as UTM coordinates and were used in the models involving the body length. Elevation  
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47 178 data were used to generate the variables SLOPE, that is the incline or steepness of the surface, and  
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49 179 ASPECT, that is the compass direction that a topographic slope faces (both variables were derived from the  
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51 180 layer ALT and are expressed in degrees) using the "surface tool" in ArcGIS Spatial Analyst (Esri, 2014). All  
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53 181 digital information was obtained or created at a spatial resolution of 30 arc second (~1 km). A mask was  
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55 182 created in order to reduce the extent of all the environmental variable layers to the size of the study area.  
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57 183 Since the WorldClim variables were derived from a common set of temperature and precipitation data, they  
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59 184 could exhibit multicollinearity (Hijmans *et al.*, 2005). Before model fitting, it was proceeded with the detection  
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185 of the effect of collinearity by evaluating the variance inflation factors (VIFs) for the variable set. In order to



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3 186 understand the collinearity inside of the study area, only the values inside of the mask were considered. The  
4 187 variable with the highest VIF was sequentially omitted using a threshold value of 3.0 (Zuur *et al.*, 2009). Only  
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6 188 the variables that showed minimal levels of collinearity were retained, also taking into account their  
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8 189 relevance for our research aims during the variables selection (ASPECT, BIO 3, BIO9, BIO13 and BIO 15),  
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10 190 obtaining the set of uncorrelated variables used in the modelling (Table 1). Finally, the final variable set  
11 191 (masked to fit the extent of the study area) was entered into Maxent as an ASCII raster grid.

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### 14 193 **Maxent modelling procedure**

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17 194 Maximum Entropy Species Distribution Modelling (Maxent; Phillips *et al.*, 2006; Phillips & Dudík, 2008)  
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19 195 version 3.3.3k (<https://www.cs.princeton.edu/~schapire/maxent/>) was adopted to model the environmental  
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21 196 suitability of *S. ursulae*. Maxent is a software package that estimates the distribution of a species using a  
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23 197 presence-only dataset by finding the probability distribution of maximum entropy (Phillips *et al.*, 2006). We  
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25 198 used an analysis methodology based on presence-only data because it is almost impossible to determine  
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27 199 the absence of a species (MacKenzie, 2005). In particular, the detectability of *S. ursulae* is dependent on the  
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29 200 annual abundance and it has been observed to differ considerably from year to year (DB, personal observ.).  
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31 201 Maxent was chosen among several techniques in predicting species distribution from presence-only data,  
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33 202 because in recent comparisons, it was found to be one of the most effective and it had also a particularly  
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35 203 good performance when analysing data sets with a small number of records (Elith *et al.*, 2006; Hernández *et*  
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37 204 *al.*, 2006). Moreover, the reliability of Maxent results had been confirmed by its good prediction on new  
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39 205 presence localities for poorly known species (Pearson *et al.*, 2007).

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41 206 We defined the modelling area as a rectangle of 14.700 Km<sup>2</sup> comprising the whole study area, the  
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43 207 surrounding main mountain massifs ecologically comparable to the study area and also some adjacent  
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45 208 unsuitable surface that we supposed to be potential ecological barriers, such as the Po Plain. To generate a  
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47 209 potential prediction map, the input has to consist of a set of presence data and their georeferenced locations  
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49 210 and in a set of environmental variables (Phillips *et al.*, 2006; Elith *et al.*, 2011, Phillips, 2017). The software  
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51 211 can also calculate the relative importance of the different environmental features used as input. The  
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53 212 selection of the functions for the predictor variables (feature type) was carried out automatically (auto  
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55 213 features), so the program selects the appropriate function depending on the number of available data  
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57 214 (Phillips, 2017). The parameter settings were set to the default values, following advice of Elith *et al.* (2011),  
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59 215 i.e. 500 as maximum iterations, 0.00001 as convergence threshold, 10,000 as maximum number of  
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216 background points, 1 as the regularization multiplier and “crossvalidate” as replicated run type (Phillips &

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3 217 Dudík, 2008). The models obtained were calibrated using 75% of the available records for each species as  
4 218 training data (calibration data), and the remaining 25% were used as test data to validate the model  
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6 219 internally. The logistic value output was selected because it gives an estimate ranging from 0 (unsuitable) to  
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8 220 1 (suitable) of habitat suitability, and it is therefore the easiest to conceptualize (see Phillips & Dudík, 2008  
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10 221 and <http://www.cs.princeton.edu/~schapire/maxent/tutorial/tutorial.doc> for further details). Logistic output  
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12 222 estimates probability of presence assuming that the sampling design is such that typical presence localities  
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14 223 have probability of presence of about 0.5. The Area Under the Curve (AUC) value and a P value less than  
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16 224 0.05 for at least one binomial test were used to evaluate the goodness of fit of the models (Pawar *et al.*,  
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18 225 2007), and both can be obtained from the program. AUC provides a single measure of overall accuracy that  
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20 226 is not dependent upon a particular threshold and is therefore used as an index to evaluate models (Fielding  
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22 227 & Bell, 1997). The value of the AUC ranges between 0 and 1. Values from 0.5 to 0.7 indicate a performance  
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24 228 no better than random; from 0.7 to 0.8 an acceptable performance; from 0.8 to 0.9 a good performance; and  
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26 229 above 0.9 a highly accurate or excellent performance (Manel *et al.*, 2001). The models were generated in  
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28 230 ascii format, and exported directly in ArcGIS 10.2.2 (Esri, 2014). A potential distribution map with a habitat  
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30 231 suitability classification ranging from 0 (unsuitable) to 1 (suitable) was obtained as output of the model. The  
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32 232 map was imported in ArcGIS and reclassified using the 0.5 threshold value.

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### 34 234 **Grasshopper measurements and statistical analysis**

35 235 Three hundred and nine individuals (152 males and 157 females) were collected in 49 sites during the  
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37 236 months of August and September 2014. The sites were distributed in the whole geographical range of the  
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39 237 species, from 1445 up to 2878 m a.s.l. We aimed to collect similar numbers of males and females. The  
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41 238 individuals were measured using the LAS Core Image Program (Leica Application Suite software, version  
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43 239 3.1; Leica Imaging Systems Ltd., Cambridge, UK) with the camera Leica EC3 by means of a stereo LEICA  
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45 240 M80 with a 0.75-6.0 zoom, fitted with an ocular Leica 10450023 10x/23. Specimens have been vouchered  
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47 241 and stored in alcohol in the first author's collection at the Regional Natural Science Museum, Aosta Valley.  
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49 242 Two different proxies for body size were measured: (i) total body length (from the head to the last abdominal  
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51 243 tergite, excluding supra-anal and subgenital plates), (ii) length of right hind femur (Duke & Crossley, 1975;  
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53 244 Butlin *et al.*, 1987; Willott & Hassall, 1998; Laiolo *et al.*, 2013). Data were  $\log_{10}$ -transformed, scaled and  
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55 245 centred prior to the analysis. Total body length had been used as a proxy of condition-dependent body size  
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57 246 (Laiolo *et al.*, 2013). The length of the hind femur had proven to be partly determined by sex-linked genes  
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59 247 (Reinhold, 1994) and was often used as a proxy for body size in general on Orthoptera (Mousseau, 1997;



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3 248 Bidau & Martí, 2007; Lehmann & Lehmann, 2008) and in particular for structural body size (Laiolo *et al.*,  
4 249 2013). We therefore decided to use both total body length and hind femur length as measures of body size,  
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6 250 because the two measurements are differently related to sex and may also subtend different biological  
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8 251 implications. To test Bergmann's rule, it was analysed whether total body length and hind femur length  
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10 252 varied between sexes and with elevation by means of generalized linear mixed models (GLMMs). To better  
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12 253 appreciate SSD variation with elevation, the interaction of elevation  $\times$  sex was tested. This allowed elevation  
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14 254 gradients to vary between sexes. In this analysis we used elevation data for each sampling point measured  
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16 255 in the field with the GPS. Latitude and longitude were entered also as covariates to control for the  
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18 256 nonindependence of data from close populations. The site was entered as a random factor to control for  
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20 257 pseudoreplication (Laiolo *et al.*, 2013). It was then tried to assess the effect of climatic variation on body size  
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22 258 in the two sexes with GLMMs with as before, site as random factor. For each analysis, a candidate set of  
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24 259 models was compared including all the possible models with the possible predictors (BIO3, BIO9, BIO13 and  
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26 260 BIO15, sex of the grasshopper and their two-way interactions, i.e. climatic variable  $\times$  sex), including the  
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28 261 intercept-only model. Models were ranked on the basis of their Akaike's Information Criterion corrected for  
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30 262 small sample size (AICc) values (Akaike, 1973; Buckland *et al.*, 1997), the difference in terms of AICc  
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32 263 between the top model and the other models ( $\Delta$ AICc), and the Akaike weights, which sums to one and  
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34 264 shows the relative support for each model in the set. The models with  $\Delta$ AICc  $\leq$  2.0 were then used for model  
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36 265 averaging (Burnham & Anderson, 2002), unless there were no models that performed better than the null. All  
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38 266 statistical analyses were performed with R 3.3.1 (R Core Team, 2017), using the packages *lme4* (Bates *et*  
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40 267 *al.*, 2015) and *lmerTest* (Kuznetsova *et al.*, 2016) for GLMMs, and the package *MuMin* (Bartoń, 2011).  
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42 268 Elevation, latitude and longitude were measured in m (a.s.l. or UTM).  
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## 45 270 **Results**

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### 47 272 **Survey and habitat suitability results**

48 273 The survey generated 149 presence points, of which 140 were previously unpublished (93.96 % of the total)  
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50 274 (Figure 1). The species range estimated from minimum convex polygon and based on currently available  
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52 275 presence data resulted extended 826.3 km<sup>2</sup>.  
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54 276 The simple probability test conducted from the Jackknife test confirmed that the prediction was significantly  
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56 277 better than at random (P = 0.038). AUC values of model sets calculated for the test (AUC = 0.959) and  
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58 278 training data (0.965), were all greater than 0.90 and indicate a high power of Maxent for predicting potential  
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279 habitat for the studied grasshopper species, suggesting satisfactory discrimination of suitable versus  
280 unsuitable areas. All these results justified the construction of the final habitat suitability model with all the  
281 available points. The AUC value for the final model with total records was 0.966. The predictors which have  
282 high percent contribution are BIO15, BIO13 and BIO3, and are supported by the permutation importance  
283 (Table 2). Moreover, the Jackknife test demonstrated that BIO15, BIO13 and BIO9 had the highest gain  
284 when used in isolation. The SDM map (Figure 2) shows large suitable area inside the minimum convex  
285 polygon. It also identifies areas suitable in terms of climate in which the species was not found, especially in  
286 the peaks at the border between Italy and Switzerland.

### 288 **Morphological analysis**

289 All size measurements were highly correlated for both sexes (all Pearson's  $R > 0.65$ ,  $P < 0.05$ ). Total body  
290 length varied between 13.66 and 22.56 mm (mean  $\pm$  SD:  $17.54 \pm 1.92$ ) for females and between 11.83 and  
291 17.31 mm (mean  $\pm$  SD:  $13.57 \pm 1.08$ ) for males. Regarding hind femur length, females varied between 8.12  
292 and 11.51 mm (mean  $\pm$  SD:  $9.49 \pm 0.77$ ) and males varied between 7.18 and 9.64 mm ( $8.13 \pm 0.57$ ). The  
293 species was sexually size dimorphic with females being larger than males (Wilcoxon-Mann-Whitney test for  
294 total body length:  $W = 22700$ ,  $P < 0.001$ ; for hind femur length:  $W = 21089$ ,  $P < 0.001$ ). When looking at body  
295 measurements in relation to elevation, the models with only linear and both linear and quadratic terms were  
296 tested. The model that included also the quadratic terms had a lower AICc in both cases (for total body  
297 length,  $\Delta AICc = 33.08$ ; for hind femur length,  $\Delta AICc = 11.17$ ). Both considering hind femur length or taking  
298 into account total body length, *S. ursulae* showed an elevation cline that significantly varied with sex: at  
299 higher elevations female measurements became proportionally shorter than in males (Table 3). As shown by  
300 the direction (sign) of the sex effect and by its interaction with elevation (Table 3), the species dimorphism  
301 decreased with elevation (see also Figure 3). Regarding climate, the models for both total body length and  
302 hind femur length with lower AICc values were the ones that included at least the interaction between sex  
303 and one of the two climatic variables (Table 4). The two sexes showed a different relationship with the two  
304 variables used as proxies for temperature and precipitations (Table 5). Body measurements appear to  
305 increase with increasing temperature and precipitation seasonality. Even if body size increases with  
306 seasonality for both sexes, it increases more strongly for females than for males. Because both temperature  
307 and precipitation seasonality are correlated with elevation, these results are in line with the expectation that  
308 the morphological variation observed along the elevation gradient is climate related.

310 **Discussion**

311

312 This research increased the data on this previously poorly investigated species. The elevation range limits  
313 were expanded from 1300-2556 (Massa *et al.*, 2012; Sindaco *et al.*, 2012) to 1300-3000 m a.s.l. Several  
314 populations were found in alpine meadows above 2600 m, in mountain areas previously not surveyed by  
315 entomologists. Thanks to the additional surveys, we found *S. ursulae* on M. Bellagarda (Lanzo Valleys),  
316 expanding 12 km south-west its known range margins. All the other surveys outside the previously known  
317 distribution had negative outcomes. Moreover, some historical presence data have not been confirmed:  
318 Nivolet in Valsavarenche and Lauson in Cogne Valley. Future surveys are recommended to collect the  
319 necessary data for determining the species occurrence at the western margins of the species distribution.  
320 Here, in the last decades a species range contraction may have occurred. Therefore, *S. ursulae* was found  
321 to have a remarkably small range size and to be among the few endemic Orthoptera of the western Alps  
322 (*Anonconotus baracunensis* Nadig, 1987; *A. ghilianii* Camerano, 1878; *A. ligustinus* Galvagni, 2002; *A.*  
323 *mercantouri* Galvagni & Fontana, 2003; *A. occidentalis* Carron & Wermeille, 2002; *A. pusillus* Carron &  
324 Sardet, 2002; *Dolichopoda chopardi* Baccetti, 1966; *Epipodisma pedemontana* Brunner von Wattenwyl,  
325 1882; *Podisma amedegnatoae* Fontana & Pozzebon, 2007; *P. eitschbergeri* Harz, 1973; *Arcyptera alzonai*  
326 Capra, 1938; *Chorthippus cialancensis* Nadig, 1986; *C. sampeyrensis* Nadig, 1986). Our study was the first  
327 attempt to investigate if climate may explain the distribution of an Alpine endemic grasshopper. The potential  
328 distribution obtained as output of the Maxent model well predicted the known distribution range, which is  
329 continuous and surrounded by unsuitable areas. The importance of climate is supported by the unsuitable  
330 area north-west of the species distribution, predicted by the model using climatic predictors only. This area  
331 was thoroughly searched, but the species was never found. Here, rocky grasslands apparently suitable to  
332 this species are largely available and there is habitat continuity with the area where the species is present.  
333 Thus, the only variation in precipitation and temperature variables may constitute a climatic barrier. However,  
334 the species is also expected elsewhere using climatic niche modelling. Therefore, a few notes regarding the  
335 model have to be made. Both habitat and climatic barriers may prevent this flightless species to colonize the  
336 potentially ecologically suitable area predicted by the model north-east of its distribution range. Here, a 10-15  
337 km wide ecological barrier (low elevation, woodland and high anthropogenic pressure) divides the two  
338 ranges. In mountains, speciation processes, related to the many micro-climatic habitats, are promoted by a  
339 low dispersal ability often linked to wing reduction and flightlessness (McCulloch *et al.*, 2009; Ikeda *et al.*,  
340 2012; Mitterboeck & Adamowicz, 2013). The brachypterous nature of the species represents a serious

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3 341 limitation to range expansion or shift. Low vagility may prevent steno-endemic species to readily colonize  
4 342 suitable areas when its availability changes, e.g. after the species disappearance from a peak because of  
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6 343 climate change. Moreover, the suitable areas where the species is absent may related to the relatively recent  
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8 344 origin of Gomphocerinae species, which are still expanding their range after the last glacial period, and to the  
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10 345 isolation of alpine brachypterous species, which is related to the retreat of the ice at the end of the last  
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12 346 glaciation (Bella *et al.*, 1991; Bailey *et al.*, 2004). The species range may not be in equilibrium with the  
13  
14 347 environment because it had not enough time to colonize all the climatic suitable areas potentially available.  
15  
16 348 Another steno-endemic species presents very similar distribution limits, the *Anonconotus pusillus* (Carron *et*  
17  
18 349 *al.*, 2002), despite the fact that are two phylogenetically distant Orthoptera species. On the other hand, along  
19  
20 350 the Alps (in Piedmont) the model predicted more potential areas with good suitability for the species.  
21  
22 351 Therefore, *S. ursulae* may be found further south than currently known and future specific surveys in this  
23  
24 352 undersampled area are recommended to test if the Maxent model's southern distribution limit is related to  
25  
26 353 dispersal limitations or to inadequate sampling.  
27  
28 354 While considering an endemic species, considerable consequences can arise from the modification of its  
29  
30 355 fundamental traits due to altered climatic conditions (Bellard *et al.*, 2012). The model highlighted the  
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32 356 importance of climate influences on distribution of this endemic grasshopper. As a matter of fact, the model  
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34 357 fitted the distribution data well despite a layer with vegetation data was not used. Moreover, this species was  
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36 358 found in rocky grasslands above 1300 m a.s.l., widely available in the Alps. This could be explained by the  
37  
38 359 fact that grasshoppers are generalist herbivores, and therefore, lack a specific relationship with the  
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40 360 vegetation composition (Bernays & Minkenberg, 1997). The model results highlighted the importance of  
41  
42 361 seasonality, e.g. precipitation seasonality had a negative effect on its distribution. The species accordingly  
43  
44 362 preferred more stability in terms of precipitations. Moreover, *S. ursulae* preferred narrow range of values for  
45  
46 363 climatic variables based on temperature. In this sense, it may be considered a climate specialist. At high  
47  
48 364 elevations in the Alps, as occurs at high latitude, it has been demonstrated that several grasshopper species  
49  
50 365 are high-temperature specialists, although strong variations exist in their temperature sensitivity (Willott &  
51  
52 366 Hassall, 1998). Moreover, the efficiency of thermoregulatory behaviour, combined with a plastic life history,  
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54 367 can compensate for a physiology poorly adapted to cool temperatures (Willott & Hassall, 1998).  
55  
56 368 Climatic variables were shown to correlate with the pronounced body length variability that characterise the  
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58 369 species. The role of the elevation has been tested too with the aim of assessing the validity of the two  
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60 370 ecogeographical rules for this species. Conversely to Bergmann's original rule, *S. ursulae* showed a decline  
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62 371 in body length with increasing elevation. Reverse of Bergmann's rule has been frequently found among

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3 372 ectotherms and probably represents the norm for the Orthoptera (Dean, 1982; Scott & Dingle, 1990; Orr,  
4 373 1996; Mousseau, 1997; Telfer & Hassall, 1999; Blanckenhorn & Demont, 2004; Berner & Blanckenhorn,  
5 374 2006; Bidau & Martí, 2007; Whitman, 2008; Winterhalter & Mousseau, 2008; Ciplak *et al.*, 2008; Laiolo *et al.*,  
6 375 2013; Eweleit & Reinhold, 2014; Levy & Nufio, 2015). The explanation of this climate-driven size cline may  
7  
8 376 rely in local adaptations and/or phenotypic plasticity (Laiolo & Obeso, 2017). The consequences of harsh  
9  
10 377 climates at higher elevations (i.e. significant resource limitations and time constraints) may result in earlier  
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12 378 egg hatching and/or rapid development (Dingle *et al.*, 1990; Hodkinson, 2005b; Berner & Blanckenhorn,  
13 379 2006). The length of growing season and the resource availability might have limited the body length *S.*  
14  
15 380 *ursulae* can achieve, larger body size requires longer development time (Berner *et al.*, 2004; Chown &  
16  
17 381 Gaston, 2010). Moreover, a shorter development time (i.e. instar duration and frequency of moulting) is  
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19 382 favoured by natural selection because early maturation increases reproductive success and could therefore  
20  
21 383 be an adaptation strategy to adverse conditions at higher elevations (Roff, 1983, 1992; Stearns & Koella,  
22 384 1986; Dingle *et al.*, 1990; Stearns, 1992; Hodkinson, 2005a). Current data do not allow us to confirm or  
23  
24 385 dismiss local adaptation, but there is evidence of genetic influences or gene-environment covariations in  
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26 386 grasshoppers (Berner *et al.*, 2004; Roff *et al.*, 2005; Berner & Blanckenhorn, 2006; Laiolo & Obeso, 2015).  
27  
28 387 Our results showed that in *S. ursulae* SSD increased as conditions improved and body length increased,  
29  
30 388 which was consistent with a converse Rensch's rule. At the intra-population level, the size of the larger sex  
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32 389 disproportionally increased and it was more variable than the smaller sex size. In the studied species, SSD  
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34 390 was strongly female biased, as in the vast majority of orthopteroid insects (Bidau *et al.*, 2015), and the  
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36 391 relationship between the degree of SSD and elevation suggest that at high elevations, where climate was  
37  
38 392 harsher, females body size adjusted more plastically. The females respond more strongly to harsher  
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40 393 conditions, and at higher elevations we can assume that males perform better attaining their optimal body  
41  
42 394 size (Teder & Tammaru, 2005; Blanckenhorn *et al.*, 2007). Orthoptera SSD variations were found to follow  
43  
44 395 either the Rensch's rule, its converse, as in *S. ursulae*, or even to have no pattern at all (Bidau & Martí,  
45  
46 396 2008; Hochkirch & Gröning, 2008; Lehmann & Lehmann, 2008; Laiolo *et al.*, 2013; Eweleit & Reinhold,  
47  
48 397 2014). The validity of Rensch's rule had given contrasting results in the majority of insect groups (Abouheif &  
49  
50 398 Fairbairn, 1997; Blanckenhorn *et al.*, 2007; Bidau *et al.*, 2015). Moreover, few studies examined intraspecific  
51  
52 399 SSD variation, while the vast majority have focused on the interspecific level trends. The observed patterns  
53  
54 400 of variation in SSD may be due to the female higher plasticity, because it occurred over small spatial scales  
55  
56 401 and body size is a condition dependent trait. However, this between sex variation may be also due to an  
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58 402 adaptation, or result on selection on developmental time. At lower elevations, females may also add an  
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3 403 additional instar to larval development increasing adult body size (Esperk et al., 2007). Therefore, female  
4 404 plasticity and/or natural selection during development may lead to better adjustments of body size to the  
5  
6 405 prevailing local conditions. These mechanisms have been detected also in other grasshoppers occupying  
7  
8 406 mid-high elevations (Laiolo *et al.*, 2013).

9  
10 407 Our main findings suggest that climatic variables are a good predictor for this species distribution, and also  
11  
12 408 the strong variation in body size consistently correlates with these variables. Indeed, climate is a strong  
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14 409 selection agent at high elevations, and climate change entails complex and contrasting responses in life  
15  
16 410 cycle modifications, such as phenological shifts (Buckley *et al.*, 2015). These shifts may lead to mismatches  
17  
18 411 between resource requirements and availability (Both *et al.*, 2009). On the other hand, the morphological  
19  
20 412 variation shown by this species may result in an increased body length as a response to climate warming.  
21  
22 413 Larger body size is associated with a fitness advantage, i.e. increased insect's fecundity (Honěk, 1993;  
23  
24 414 Telfer & Hassall, 1999), longevity (Hodin, 2009) and starvation resistance (Slansky & Scriber, 1985).  
25  
26 415 However, extreme changes may disrupt the plastic response, and since reaction norm shapes are likely to  
27  
28 416 be genetically constrained, body size cannot increase indefinitely under sustained environmental change  
29  
30 417 (Chevin *et al.*, 2010). Climate warming may also imply a heavy reduction of habitat availability, because  
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32 418 reforestation at lower elevations and advancing treeline will not correspond to a proportional increase in  
33  
34 419 habitat availability at higher elevations (Cannone *et al.*, 2007; Chamberlain *et al.*, 2013). Thus, more studies  
35  
36 420 are needed to assess the impact of climate change on Alpine steno-endemic species of conservation value.

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## 38 422 **Conclusion**

39 423 The very limited distribution range of *S. ursulae* is probably due to low dispersal ability and to habitat and  
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41 424 climatic barriers. The species also presents a good degree of morphological variation at least partly related  
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43 425 to climate. Our results suggest that climate affects both the geographic distribution and the body size  
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45 426 variations, but with opposite effects: suitable climatic conditions for this grasshopper are found at high  
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47 427 elevations, and the fitness-related trait (i.e. body size) declines with elevations. In the future, this species  
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49 428 may modify its distribution and/or its morphology to successfully respond to climate change. Overall, the  
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51 429 dispersal ability of steno-endemic mountaintop insects is very limited, because they are very often flightless  
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53 430 (Roff, 1994; Ikeda *et al.*, 2012; Mitterboeck & Adamowicz, 2013; McCulloch *et al.*, 2017). The limited  
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55 431 dispersal ability of this and others flightless endemic insects certainly constitutes an issue in responding to  
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57 432 climate change. More research is needed about where in a species range individuals are most likely to  
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59 433 survive, migrate or adapt to rapid environmental change (Willis & Birks, 2006). Our results should encourage



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3 434 conservationists to focus long-term monitoring of Alpine grasshoppers, detecting in time distributional  
4 435 contractions due to climate change.

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716 **Tables**717 **Table 1**

718 Bioclimatic and topographic variables used in the modelling.

Variable	Description	Source
ASPECT	compass direction that a topographic slope faces	ArcGIS from ALT
BIO3	isothermality (i.e. the mean diurnal range divided by the annual temperature range)	WorldClim
BIO9	mean temperature of the driest quarter	WorldClim
BIO13	precipitation of the wettest month	WorldClim
BIO15	precipitation seasonality (i.e. the standard deviation of the monthly precipitation estimates expressed as a percentage of the annual mean)	WorldClim

719

720 **Table 2**

721 Estimates of the percent contribution and the permutation importance of the selected environmental  
722 variables in Maxent model.

Variable	Contribution (%)	Permutation importance	Response
BIO15	64.7	51.8	-
BIO13	13.5	13.1	-
BIO3	11.7	29.0	Quadratic
BIO9	8.9	6.0	Quadratic
ASPECT	1.3	0.1	Quadratic

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724 **Table 3**

725 Results of generalized linear mixed models testing for the effect of elevation on body size in *Stenobothrus*  
 726 *ursulae* while considering for sexual dimorphism. Body size was expressed in terms of length of the total  
 727 body and the hind femur. The site was entered as a random factor and latitude and longitude as covariates  
 728 to control for the spatial autocorrelation of data.  
 729

	<b>b</b>	<b>SE</b>	<b>t</b>	<b>P</b>
<u>Total body length</u>				
(Intercept)	17.580	0.097	180.99	< 0.001
Elevation	-15.549	2.224	-6.99	< 0.001
Elevation <sup>2</sup>	7.207	1.666	4.33	< 0.001
Sex	-4.066	0.127	-31.90	< 0.001
Elevation X Sex	10.973	2.215	4.96	< 0.001
Elevation <sup>2</sup> X Sex	-4.187	2.218	-1.89	0.060
Longitude	-0.814	0.161	-5.06	<b>0.008</b>
Latitude	-0.357	0.144	-2.48	0.058
<u>Hind femur length</u>				
(Intercept)	9.567	0.087	109.65	< 0.001
Elevation	-3.958	0.806	-4.91	< 0.001
Elevation <sup>2</sup>	0.834	0.561	1.49	0.138
Sex	-1.404	0.040	-34.95	< 0.001
Elevation X Sex	3.214	0.707	4.55	< 0.001
Elevation <sup>2</sup> X Sex	-0.456	0.715	-0.64	0.524
Longitude	-0.653	0.125	-5.23	< 0.001
Latitude	-0.312	0.101	-3.08	<b>0.010</b>

730

731 **Table 4**

732 List of the GLMMs with  $\Delta AICc \leq 2$  used for testing for the effect of climate on body size in *Stenobothrus*  
 733 *ursulae* while considering for sexual dimorphism. Models were ranked according to AICc values. Body size  
 734 was expressed in terms of length of the total body and the hind femur. Predictive variables were sex of the  
 735 grasshopper, climatic variables (BIO3, BIO9, BIO13 and BIO15) and all the interactions climatic variable  $\times$   
 736 sex. Site was entered as a random factor.  
 737

Model	df	logLik	AICc	$\Delta AICc$	weight
<u>Total body length</u>					
Sex + BIO3 + BIO15 + Sex X BIO15	7	-119.75	253.88	0	0.175
Sex + BIO3 + BIO13 + Sex X BIO13	7	-119.84	254.05	0.171	0.161
Sex + BIO13 + Sex X BIO13	6	-121.15	254.58	0.703	0.123
Sex + BIO15 + Sex X BIO15	6	-121.5	255.28	1.404	0.087
Sex + BIO3 + BIO13 + BIO15 + Sex X BIO15	8	-119.42	255.33	1.45	0.085
Sex + BIO3 + BIO9 + BIO13 + Sex X BIO13	8	-119.45	255.39	1.508	0.082
Sex + BIO13 + BIO15 + Sex X BIO15	7	-120.56	255.49	1.609	0.078
Sex + BIO3 + BIO13 + BIO15 + Sex X BIO13 + Sex X	9	-118.5	255.62	1.737	0.074
BIO15					
Sex + BIO13 + BIO15 + Sex X BIO13 + Sex X BIO15	8	-119.63	255.75	1.874	0.069
Sex + BIO9 + BIO13 + Sex X BIO13	7	-120.72	255.83	1.946	0.066
<u>Hind femur length</u>					
Sex + BIO15 + Sex X BIO15	6	-462.38	937.03	0	0.24
Sex + BIO9 + BIO13 + BIO15 + Sex X BIO15	8	-460.43	937.34	0.308	0.206
Sex + BIO13 + BIO15 + Sex X BIO15	7	-461.49	937.35	0.316	0.205
Sex + BIO9 + BIO15 + Sex X BIO15	7	-461.69	937.77	0.733	0.167
Sex + BIO9 + BIO13 + BIO15 + Sex X BIO9 + Sex X BIO15	9	-460.15	938.92	1.889	0.093
Sex + BIO13 + BIO15 + Sex X BIO13 + Sex X BIO15	8	-461.27	939.03	1.996	0.089

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743 **Table 5**

744 Parameter estimates, standard error (SE) and relative variable importance for variables included in the  
 745  $\Delta AICc \leq 2$ . GLMMs set testing for the effect of climate on body size in *Stenobothrus ursulae* while  
 746 considering for sexual dimorphism. Body size was expressed in terms of length of the total body and the hind  
 747 femur. Predictive variables were sex of the grasshopper, climatic variables (BIO3, BIO9, BIO13 and BIO15)  
 748 and all the interactions climatic variable  $\times$  sex. Sector identity was entered as a random factor.

Variable	Total body length			Hind femur length		
	Estimate	SE	Importance	Estimate	SE	Importance
Intercept	15.542	0.182		8.838	0.194	
Sex (male vs. female)	-4.051	0.128	1.000	-1.394	0.041	1.000
BIO3				0.051	0.059	0.577
BIO9	-0.192	0.279	0.466	-0.039	0.134	0.149
BIO13	-0.224	0.269	0.593	-0.086	0.104	0.738
BIO15	1.293	0.24	1.000	0.022	0.074	0.567
Sex X BIO9	-0.024	0.13	0.093			
Sex X BIO13	0.024	0.148	0.089	0.178	0.179	0.575
Sex X BIO15	-1.407	0.296	1.000	-0.185	0.184	0.567

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4 752 **Figure captions**

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8 754 **Figure 1**

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10 755 Presence points of *Stenobothrus ursulae* (red dots) with minimum convex polygon (range: 826.3 km<sup>2</sup>). All the  
11 756 surveyed points where the species was not found are also shown on this map (grey dots).

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15 758 **Figure 2**

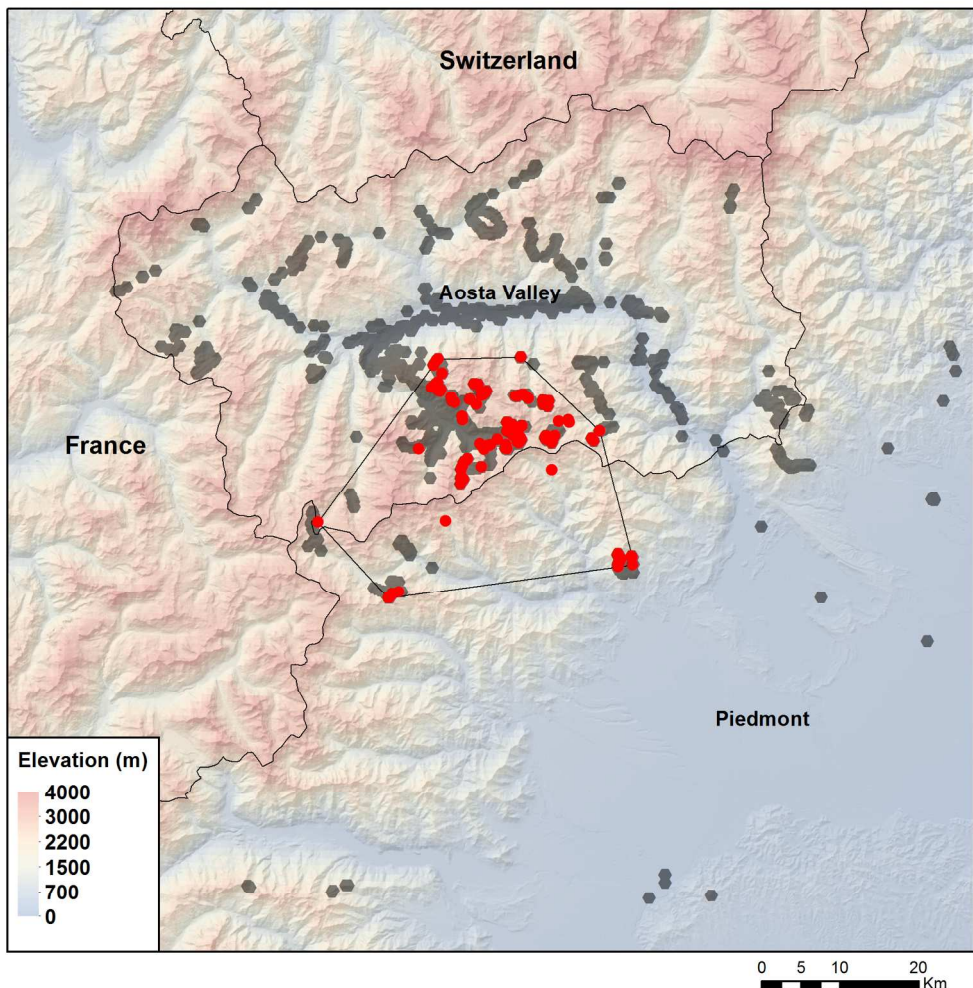
16  
17 759 The potential distribution map of *Stenobothrus ursulae* with minimum convex polygon classified using the 0.5  
18 760 threshold (grey). The margins of this figure fit precisely with the modelling area rectangle.

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20 761

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22 762 **Figure 3**

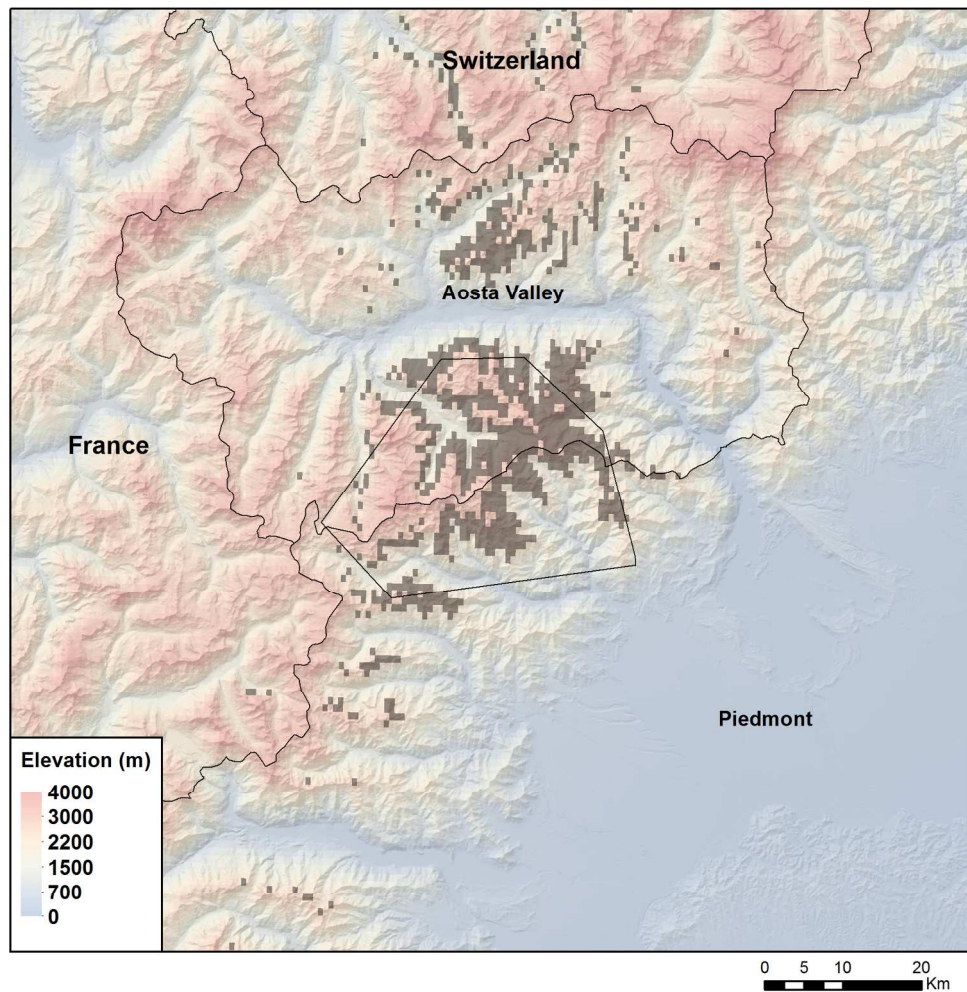
23  
24 763 Elevation clines for total body length and hind femur length (mm) of females (light grey) and males (dark  
25 764 grey) of *Stenobothrus ursulae*.

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**Figure 1** Presence points of *Stenobothrus ursulae* (red dots) with minimum convex polygon (range: 826.3 km<sup>2</sup>). All the surveyed points where the species was not found are also shown on this map (grey dots).

170x170mm (300 x 300 DPI)

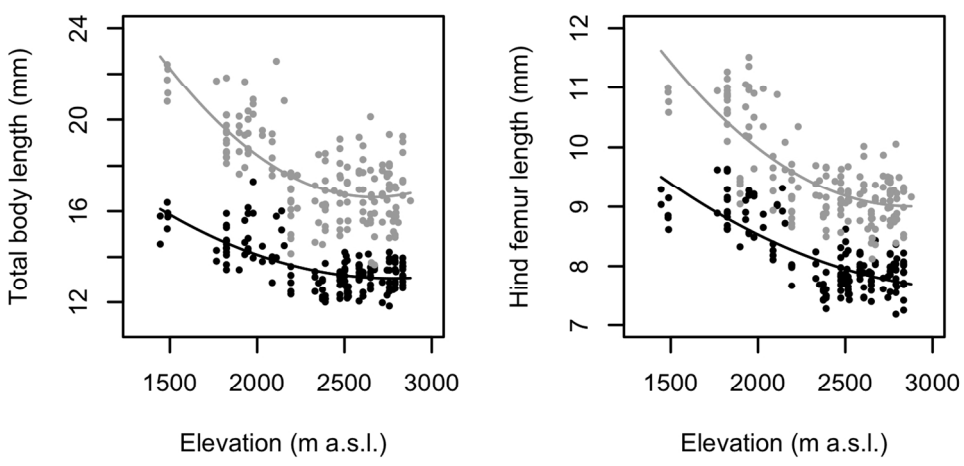


**Figure 2** † The potential distribution map of *Stenobothrus ursulae* with minimum convex polygon classified using the 0.5 threshold (grey). The margins of this figure fit precisely with the modelling area rectangle.

170x170mm (300 x 300 DPI)



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**Figure 3**  
Elevation clines for total body length and hind femur length (mm) of females (light grey) and males (dark grey) of *Stenobothrus ursulae*.

564x282mm (72 x 72 DPI)

view Only