

Conservation biogeography of high-altitude longhorn beetles under climate change

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Abstract

1. High-altitude insects are expected to be strongly affected by climate change because of their limited range. Phytophagous species will be subject to further threats because of their dependence on host plants.
2. We investigated the impact of climate change on the distribution of Italian high-altitude longhorn beetles (Cerambycidae) using a maximum entropy approach based on bioclimatic variables. We used 510 presence records for 15 species distributed throughout the Italian Alps and Apennines. Then, we combined climate-based predictions with vegetation data to predict the future changes in the extent of suitable areas.
3. All species but two will move uphill to track suitable climates and will face a range contraction (with an average loss of 44%) under both climatic change scenarios considered. Suitable vegetation covers, on average, only 56% of the estimated current species ranges, which means that the future distribution will be even more limited. Given the importance of Italian mountains as hubs of diversity in the Mediterranean hotspot, these results are particularly alarming.
4. Conservation actions that can mitigate the effects of climate change on high-altitude cerambycids should be focused on contrasting habitat loss and degradation through land preservation and the adoption of appropriate forest management practices.

KEYWORDS

Alps, Apennines, Cerambycidae, Coleoptera, ecological niche modelling, habitat suitability, Italy

INTRODUCTION

Human-induced climate change is one of the most dramatic threats to biodiversity (Brodie et al., 2012; Cowie, 2012; Hodkinson et al., 2011; Wagner et al., 2021), possibly surpassing the role of habitat destruction as first cause of extinctions (Bellard et al., 2012). Insects are predicted to be significantly affected by climate change, with a 1%–2% decline in abundance per year because of various causes, including climate change as one of the principal stressors (Wagner et al., 2021). In principle, insects might respond to climate change through adaptation. However, their capacity to adapt to climate change will depend on the speed of climate change itself,

species' life-history characteristics, genetic architecture of key traits and the speed at which a species can change these key traits in response to climate change (Kellermann & van Heerwaarden, 2019), which makes unlikely that most species will adapt to the change in progress. This will harm especially the species living near their physiological limits, like high-altitude insects, since this circumstance reduces plastic responses (Dahlhoff et al., 2019; Hoffmann & Sgro, 2011; Yadav et al., 2021).

Species might track climate change and avoid extinction by changing their distribution. In fact, the fossil record of Quaternary insects shows no high extinction rates in response to climatic oscillations probably because of their ability to track the geographic shifts of

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tolerable climates (Coope, 1994). Yet, insect species might be unable to change their ranges as fast as needed to cope with the velocity of the current climate change and, at high altitudes, their ability to track a suitable climate might be further limited by geographical constraints.

Altitudinal range shifts are a common response of montane species to chase climate change (Crozier & Dwyer, 2006; Scalercio et al., 2006; Wilson et al., 2007), but high-altitude species living on mountain peaks cannot further shift their range upward (Dirnböck et al., 2011; Shah et al., 2020), which makes them extremely vulnerable to climate change (Halsch et al., 2021; Haslett, 1997).

Even when this would be possible, uphill retreats of species with past larger and more continuous distributions at lower elevations will lead to smaller and fragmented distributions (Hodkinson, 2005). Adaptation and survival of such populations isolated on mountain tops will be strongly reduced by genetic drift caused by genetic isolation and founder-effect or bottleneck episodes during range shifts (Arenas et al., 2011). The impact of such changes on insect biodiversity is expected to be particularly momentous, since mountains, in virtue of their isolation, history and environmental heterogeneity, are home to many endemic species (Fattorini et al., 2019).

The Mediterranean basin is recognised as one of the 36 global hotspots of biodiversity (Myers et al., 2000; Fattorini, 2021), and, at the same time, one of the most significantly altered (Pascual et al., 2011). The Italian peninsula, placed in the centre of the Mediterranean hotspot, has one of the richest faunas in Europe, with endemic species mainly concentrated in the two main mountain systems, the Alps and the Apennines (Dapporto, 2010; Menchetti et al., 2021; Ruffo & Stoch, 2005; Urbani et al., 2017).

Here, we investigate the impact of climate change on Alpine and Apennine high-altitude cerambycids (Coleoptera Cerambycidae). Cerambycids are one of the largest groups of beetles, including 36,000 known species worldwide (Wang, 2017). The Italian fauna includes some 300 species (Sama & Rapuzzi, 2011), which account for about one-third of the whole European fauna (Sama & Löbl, 2010).

Cerambycids, commonly known as longhorn beetles, are one of the most popular groups of insects among both amateur and professional entomologists (Vitali & Schmitt, 2017), so that their distribution in Italy, both past and present, is particularly well known (Sama, 1988, 2005). Since cerambycids are also frequently spotted by nature photographers and amateur naturalists (Malmusi et al., 2017; Sama & Rapuzzi, 2011), the recent diffusion of online forums or citizen-science platforms has further refined our knowledge of their distribution in Italy. This large amount of detailed distributional data makes the Italian cerambycids ideal organisms to predict the impact of future climate change on species distribution through habitat suitability models (HSMs) (Elith & Leathwick, 2009; Guisan et al., 2017; Zuur et al., 2009).

HSMs have been used to predict the effects of climate change among the Coleoptera (e.g. Barredo et al., 2015; Bosso et al., 2013; Brunetti et al., 2019; Buse et al., 2013; Iannella et al., 2019; Urbani et al., 2017), Orthoptera (e.g. Anselmo, 2019; Urbani et al., 2017), and Lepidoptera (e.g. Batalden et al., 2014; Sistri et al., 2021). The basic idea of climate-related HSMs is that of inferring the climatic niche of a

species from climatic predictors occurring in its range; then, based on this relationship, future values of climatic variables can be used to predict possible future changes in species' available areas (Bellard et al., 2012; Thuiller et al., 2011).

For phytophagous insects, climate-based HSM can identify places climatically suitable for a given species, but real occurrence is limited by the presence of the host plant(s). At the same time, the presence of the host plant does not imply the presence of the insect species, because insects and plants may have non-overlapping ranges due to ecological or historical reasons. Therefore, both climatic suitability and host plant presence should be considered to obtain more reliable models of current and future suitable areas.

Since all cerambycids are phytophagous, with larvae developing in dead or living plants, with different degrees of trophic specialisation (Sama, 2002; Švacha & Danilevsky, 1987), their distribution is also conditioned by that of the host plants, and insect-plant relationships can be used to refine climatic HSM predictions.

In this study, we use HSMs techniques to assess the future conservation status for Italian high-altitude cerambycids under climate change by predicting the extent of future suitable areas. In particular, we test whether cerambycids will show one or more of the following responses: (1) altitudinal range shifts, (2) local extinction, and (3) reduction of the suitable areas.

MATERIALS AND METHODS

Data collection and study area

Based on the elevational ranges reported for the Italian cerambycids (Sama, 2002, 2005), we selected 25 cerambycid species distributed mainly above 1000 m a.s.l. We chose this elevational threshold as roughly corresponding to the lower limit of the alpine belt environment in the study area (see Fattorini, 2013, 2014; Fattorini et al., 2020; Körner & Ohsawa, 2005; Marta et al., 2013). The study area covered the Italian peninsula and Sicily island (Biondi et al., 2013). Sardinia and Corsica were not considered because none of the selected species is present in these islands.

Occurrence data were obtained from literature, collection specimens, entomological forums and citizen-science platforms. Overall, 282 point records were obtained from the literature search. The main source was Sama (2005), from which 198 records were obtained, supplemented by further 84 records from Dioli et al. (1995), Grottolo and Pedersoli (2015), Hellrigl (2010) and Malmusi et al. (2017). Additional unpublished records were obtained from Pierpaolo Rapuzzi's personal database (42 records) and other private collections (94 records, see Acknowledgements). We also scrutinised data present in the two largest Italian entomological forums: Forum Entomologi Italiani (www.entomologiitaliani.net: last accessed 28th April 2019: 28 point records) and Forum Natura Mediterraneo (www.naturamediterraneo.com/ forum: last accessed 28th April 2019, 7 records). Finally, we retrieved data from Global Biodiversity Information Facility (GBIF, 2019a, 2019b, 2019c, 2019d, 2019e, 2019f, 2019g, 2019h, 2019i, 2019j, 2019k,

2019; www.gbif.org; last accessed 19th June 2019; 73 records) and in the citizen-science platform iNaturalist (www.inaturalist.org; last accessed 12th May 2019; the data from iNaturalist were all already present in GBIF database, but each observation has been validated on the website of iNaturalist). All data were critically filtered: ambiguous or incomplete data (e.g. uncertain identification, lack of locality names, etc.) were excluded. We considered only data after the year 1960, for consistence with WorldClim data, which refer to the period 1960–1990 (www.worldclim.org, v1.4).

After data collection, checking and filtering, overall, 526 georeferenced point records belonging to 16 species were used for HSM analyses (Figure S1 and Data S1), which in turn provided reliable results for the following 15 species (510 records): *Acanthocinus xanthoneurus* (Mulsant & Rey, 1852), *Acmaeops pratensis* (Laicharting, 1784), *Acmaeops septentrionis* (C.G.Thomson, 1866), *Brachyta interrogationis* (Linnaeus, 1758), *Evodinus clathratus* (Fabricius, 1792), *Judolia sexmaculata* (Linnaeus, 1758), *Lepturobosca virens* (Linnaeus, 1758), *Oxymirus cursor* (Linnaeus, 1758), *Pachyta lamed lamed* (Linnaeus, 1758), *Pidonia lurida* (Fabricius, 1792), *Pogonocherus eugeniae eugeniae* Ganglbauer, 1891, *Pogonocherus ovatus* (Goeze, 1777), *Saperda similis* Laicharting, 1784, *Tetropium fuscum* (Fabricius, 1787), *Tetropium gabrieli* Weise, 1905. The excluded species is *Callidium coriaceum* Paykull, 1800 (16 records). All these species to the exclusion of *B. interrogationis* are saproxylic and their conservation status was recently assessed (Carpaneto et al., 2015) as ‘near threatened’ in all cases but for *A. pratensis* and *O. cursor*, which are evaluated as ‘least concern’.

When not directly provided by collector(s), geographical coordinates were obtained from Google Earth Pro 7.3.2.5776 (64-bit) as those of the place names reported on the specimen labels or in the original publications. Coordinates were recorded in WGS84 format. For each species, a distribution map was built using QGIS 2.18.4 (QGIS Development Team, 2019).

Model building

Current and future species suitable areas were modelled using MaxEnt software (ver. 3.4.1), which is based on a maximum entropy approach coupled with machine learning techniques (Phillips, 2017; Phillips et al., 2006). When properly calibrated, MaxEnt outperforms other presence-only HSM algorithms in predictive accuracy (Merow et al., 2013), especially with small, sparse and irregularly sampled data (Urbani et al., 2015). This is particularly important for studies dealing with rare and endangered species, which are supposed to be present in few localities. The key feature of the programme is to process presence-only data, which avoids absence data that are usually difficult to obtain and can produce misleading results, since they can indicate either a true absence or a low detectability (Elith & Leathwick, 2009; Iannella et al., 2019).

MaxEnt has been widely used to predict the impact of climate change on the distribution of plants (e.g. Dobrowski et al., 2011; Rogora et al., 2018), amphibians (e.g. Iannella et al., 2017; Milanovich

et al., 2010), birds (e.g. Velásquez-Tibatá et al., 2013), mammals (e.g. Levinsky et al., 2013; Morueta-Holme et al., 2010) and several insect groups among the Coleoptera (Barredo et al., 2015; Bosso et al., 2013; Buse et al., 2013; Urbani et al., 2017), Orthoptera (Anselmo, 2019; Urbani et al., 2017), and Lepidoptera (Filz & Schmitt, 2015; Hernández-Baz et al., 2016; Kumar et al., 2015; Lemoine, 2015; Todisco et al., 2012; Tóth et al., 2013).

To calibrate the model for current climatic conditions, we obtained an initial set of 19 climatic variables from the WorldClim – Global Climate database (Hijmans et al., 2005; <http://www.worldclim.org>, ver. 1.4) at 30 arc-sec resolution ($\sim 1 \times 1$ km UTM cell, temperature values are expressed in $^{\circ}\text{C} \times 10$ and the precipitation in mm):

TABLE 1 Values of area under the curve (AUC) and percentages of contribution of the three most important variables (VAR 1, VAR 2 and VAR 3) resulting from MaxEnt models fitted for high-altitude cerambycids in Italy

Species	AUC	VAR 1	VAR 2	VAR 3
<i>Acmaeops pratensis</i>	0.789	BIO15	BIO9	BIO18
		32.20	14.90	11.70
<i>Acmaeops septentrionis</i>	0.788	BIO15	BIO18	BIO1
		89.50	6.30	2.60
<i>Brachyta interrogationis</i>	0.851	BIO10	BIO18	BIO19
		39.40	18.40	15.10
<i>Judolia sexmaculata</i>	0.834	BIO15	BIO18	BIO19
		47.50	21.20	20.40
<i>Lepturobosca virens</i>	0.783	BIO1	BIO15	BIO9
		10.20	60.10	18.00
<i>Pachyta lamed lamed</i>	0.913	BIO19	BIO15	BIO9
		55.60	42.70	1.10
<i>Pidonia lurida</i>	0.787	BIO19	BIO15	BIO18
		50.30	22.60	9.40
<i>Tetropium fuscum</i>	0.835	BIO19	BIO15	BIO9
		59.60	21.40	11.50
<i>Evodinus clathratus</i>	0.925	BIO5	BIO3	BIO19
		37.20	25.40	20.20
<i>Oxymirus cursor</i>	0.923	BIO19	BIO10	BIO5
		44.00	13.90	13.80
<i>Pogonocherus ovatus</i>	0.851	BIO3	BIO16	BIO1
		69.60	15.50	10.00
<i>Saperda similis</i>	0.851	BIO19	BIO4	BIO1
		64.10	17.80	14.90
<i>Tetropium gabrieli</i>	0.788	BIO1	BIO2	BIO19
		23.30	15.60	30.90
<i>Acanthocinus xanthoneurus</i>	0.917	BIO8	BIO19	BIO2
		57.10	19.70	10.90
<i>Pogonocherus eugeniae eugeniae</i>	0.958	BIO2	BIO7	BIO18
		33.60	4.80	56.20

Note: Codes of climatic variables are explained in the text.

TABLE 2 Changes in future extent of suitable areas for high-altitude cerambycids in Italy under two climatic scenarios (RCP 4.5 and RCP 8.5)

Species	Current presence (km ² × 1000)	Loss (4.5 scenario) (%)	Gain (4.5 scenario) (%)	Future presence (4.5 scenario) (km ² × 1000)	Loss (8.5 scenario) (%)	Gain (8.5 scenario) (%)	Future presence (8.5 scenario) (km ² × 1000)
<i>A. pratensis</i>	50.48	42.18	1.64	30.01	68.86	0.55	15.81
<i>A. septentrionis</i>	99.34	29.67	2.94	72.78	47.08	1.72	53.98
<i>B. interrogationis</i>	46.46	73.06	0.03	12.53	96.09	0.01	0.89
<i>J. sexmaculata</i>	47.49	65.75	0.15	16.33	80.91	0.13	9.01
<i>L. virens</i>	54.01	45.89	2.25	30.44	67.40	8.34	28.80
<i>P. lamed</i>	21.97	27.14	5.23	17.16	19.66	10.04	19.79
<i>P. lurida</i>	82.57	43.89	0.54	48.23	80.23	0.04	14.19
<i>T. fuscum</i>	54.32	28.94	11.9	45.06	65.04	10.70	24.48
<i>E. clathratus</i>	40.98	33.20	25.23	37.71	39.02	42.05	42.21
<i>O. cursor</i>	39.43	51.51	3.95	20.68	78.98	2.88	9.45
<i>P. ovatus</i>	79.60	18.67	25.05	84.68	20.88	18.12	77.15
<i>S. similis</i>	117.64	12.52	1.56	104.75	30.24	2.26	84.25
<i>T. gabrieli</i>	93.87	39.98	5.91	61.89	58.37	0.20	15.91
<i>A. xanthoneurus</i>	16.20	73.75	0.00	4.25	92.85	0.01	1.36
<i>P. eugeniae</i>	17.48	62.60	0.89	6.69	90.92	0.01	1.95

- BIO1 = annual mean temperature
- BIO2 = mean diurnal range (mean of monthly [max temp – min temp])
- BIO3 = isothermality (BIO2/BIO7) (×100)
- BIO4 = temperature seasonality (standard deviation ×100)
- BIO5 = Max temperature of warmest month
- BIO6 = Min temperature of coldest month
- BIO7 = temperature annual range (BIO5–BIO6)
- BIO8 = mean temperature of wettest quarter
- BIO9 = mean temperature of driest quarter
- BIO10 = mean temperature of warmest quarter
- BIO11 = mean temperature of coldest quarter
- BIO12 = annual precipitation
- BIO13 = precipitation of wettest month
- BIO14 = precipitation of driest month
- BIO15 = precipitation seasonality (coefficient of variation)
- BIO16 = precipitation of wettest quarter
- BIO17 = precipitation of driest quarter
- BIO18 = precipitation of warmest quarter
- BIO19 = precipitation of coldest quarter

To avoid multicollinearity-related biases, four correlation matrices were built for each set of climatic predictors cut on four main areas (Alpine, Apennine, Alpine-Apennine and Apennine-Sicily districts, chosen on the basis of the area accessible by the species; Barve et al., 2011), using the ‘Band Collection Statistics’ tool in ArcMap 10.0 (ESRI, 2010). When for a pair of variables the absolute value of Pearson’s correlation exceeded 0.85 (Elith et al., 2006), we discarded the one of the two variables that, based on the current knowledge about species’ ecology, was considered to be possibly less important

(Brandt et al., 2017; Iannella et al., 2019). Thus, we retained BIO1, BIO7, BIO8, BIO9, BIO10, BIO18, BIO19 for the Alpine district; BIO2, BIO3, BIO4, BIO7, BIO8, BIO9, BIO12, BIO13, BIO14, BIO15, BIO18, BIO19 for the Apennine district; BIO1, BIO3, BIO4, BIO5, BIO10, BIO12, BIO19 for the Apennine and the Alpine district; and BIO2, BIO3, BIO4, BIO7, BIO8, BIO9, BIO12, BIO13, BIO15, BIO18, for the Apennine and Sicily district.

To assess models’ discrimination performance, the receiver operating characteristic (ROC) values were considered by means of the corresponding area under the curve (AUC, calculated as sensitivity vs. [1 – specificity]). As an additional indication of model fitting, we also considered the omission rate curve.

MaxEnt parameter settings used in our analyses were as follows: convergence threshold = 0.00001, replicates = 5, replicate run type = cross-validate, regularisation multiplier = 1, maximum number of iterations = 500; other parameters were retained with their default values (see Merow et al., 2013; Morales et al., 2017). We chose the jackknife test option to see the contribution of each variable; the background was created using 10,000 random points. A tenth-percentile training threshold (Freeman & Moisen, 2008) was used to binarize predictions (Elith et al., 2011; Lahoz-Monfort et al., 2014). This threshold omits all areas with a habitat suitability lower than the suitability values for the lowest 10% of records, thus assuming that the 10% of records in the least suitable habitat are not occurring in regions that are representative of the species overall habitat. This threshold is more cautious than a threshold based on the lowest predicted suitability, which may be strongly affected by outliers represented by inconsistencies in georeference or identification of species (e.g. Escalante et al., 2013).

For calculating range projection under expected climatic change, we used the aforementioned climatic variables with the values

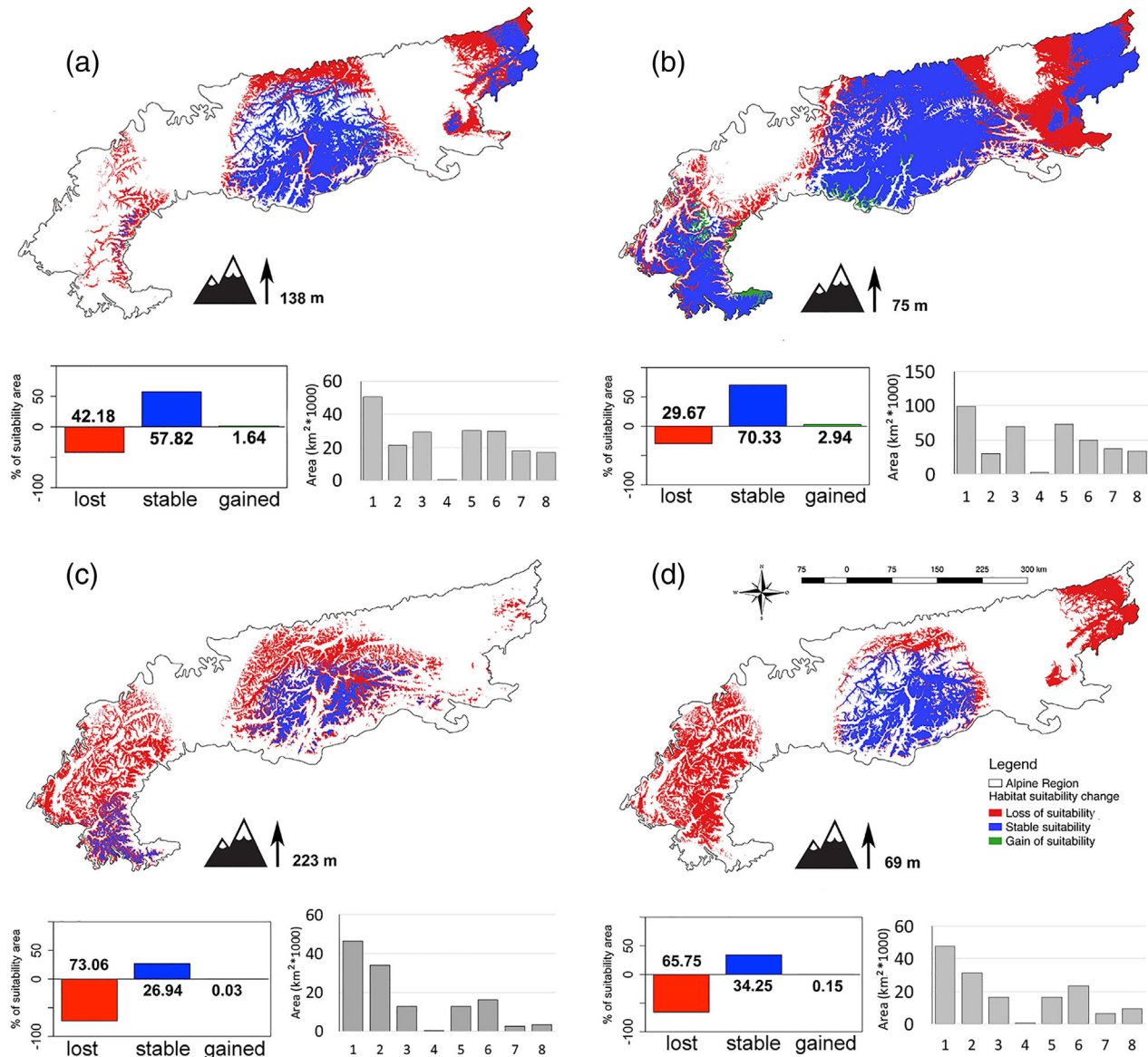


FIGURE 1 Range shifts predicted for *Acmaeops pratensis* (a), *A. septentrionis* (b) *Brachyta interrogationis* (c) and *Judolia sexmaculata* (d). Range shifts predicted with RCP 4.5 (2100): loss of suitable area (red), stable suitable area (blue), stable unsuitable area (white), gain of suitable area (green). Lower left insets: lost, stable and gained area expressed in percentage of the current suitable area. Lower right insets: areas predicted expressed in square kilometres \times 1000: occupied with current climate (1), losing suitability (2), remaining suitable (3), gaining suitability (4), occupied with future climate (5), occupied with current climate and with suitable land cover (6), occupied with future climate and suitable land cover (Corine 1) (7), occupied within suitable land cover (Corine 2) (8). Central insets with the arrow indicate the vertical shifts (in metres) of species ranges

predicted for the next future (year 2100). The International Panel on Climate Change (IPCC) developed various potential scenarios (indicated as RCP 2.6, 4.5, 6.5 and 8.5) on the basis of the expected concentrations of gases and aerosols in the future, with a predominant role of CO_2 concentration. To account for uncertainty of the models, we performed our analyses with the climatic values predicted under the RCP 4.5 and 8.5 scenarios. The 4.5 scenario is currently considered the most optimistic among the realistic ones, whereas the 8.5 scenario is the less optimistic one (Sanford et al., 2014). Among the models available in Worldclim, we chose the CNRM-CM5 climate

model (Voldoire et al., 2013), since it is particularly appropriate for the study area (Urbani et al., 2017).

Range changes

The binary maps generated by processing MaxEnt outputs were handled with QGIS 2.18.4 (QGIS Development Team, 2019). Each raster was vectorised and the total extent of suitable area of each species was calculated. Then, by overlapping current and future suitable areas,

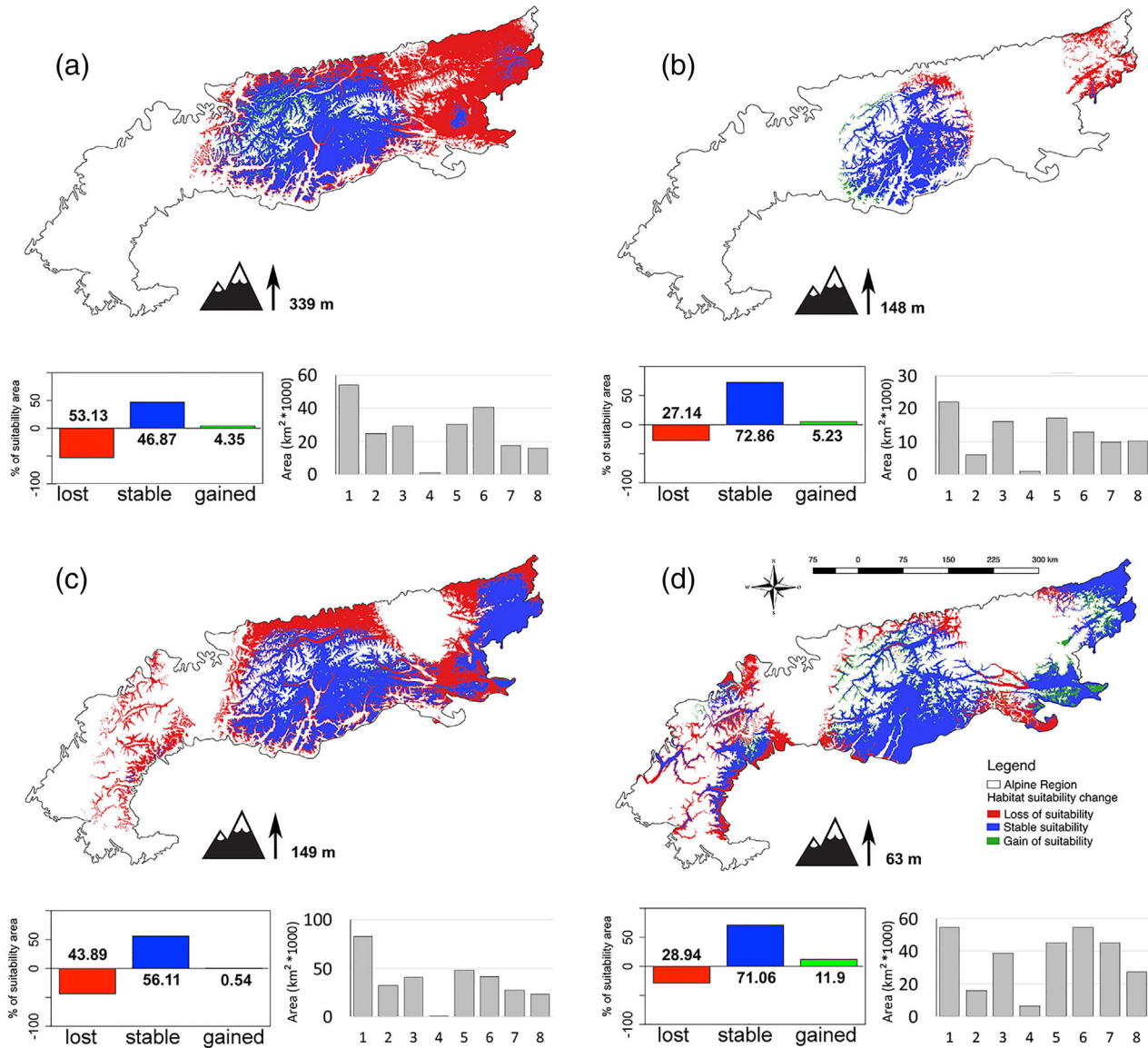


FIGURE 2 Range shifts predicted for *Lepturobosca virens* (a), *Pachyta lamed lamed* (b), *Pidonia lurida* (c) and *Tetropium fuscum* (d). Range shifts predicted with RCP 4.5 (2100): loss of suitable area (red), stable suitable area (blue), stable unsuitable area (white), gain of suitable area (green). Lower left insets: lost, stable and gained area expressed in percentage of the current suitable area. Lower right insets: areas predicted expressed in square kilometres \times 1000: occupied with current climate (1), losing suitability (2), remaining suitable (3), gaining suitability (4), occupied with future climate (5), occupied with current climate and with suitable land cover (6), occupied with future climate and suitable land cover (Corine 1) (7), occupied within suitable land cover (Corine 2) (8). Central insets with the arrow indicate the vertical shifts (in metres) of species ranges

a suitability status change index (SSCI) was calculated for each cell as the intersection between present and future distributions (Ceccarelli & Rabinovich, 2015). SSCI index can assume the following values: -1 (loss of suitability), 1 (stable suitability) and 2 (gain of suitability).

Relationships between species distributions and habitats

Since vegetation plays a critical role in determining cerambycid species distributions, we intersected potential current climate-based

distributions with the distribution of suitable vegetation. To obtain the current extent and distribution of forests, we referred to the Corine Land Cover (CLC) data, as they offer a high spatial resolution, with a minimum mapping unit of 25 ha (Copernicus Land Monitoring Service – <https://land.copernicus.eu/pan-european/corine-land-cover>). In particular, we mapped the land surface occupied by the CLC classes 311, 312, and 313, which correspond to the various forms of forest vegetation occurring in the study area. For *Brachyta interrogationis* (which is a prairie species), we used as suitable land that occupied by prairies and high-altitude pastures (CLC 242, 321, 323). Then, we intersected suitable vegetation with MaxEnt predictions for the present to calculate the fraction of the land cover suitable area

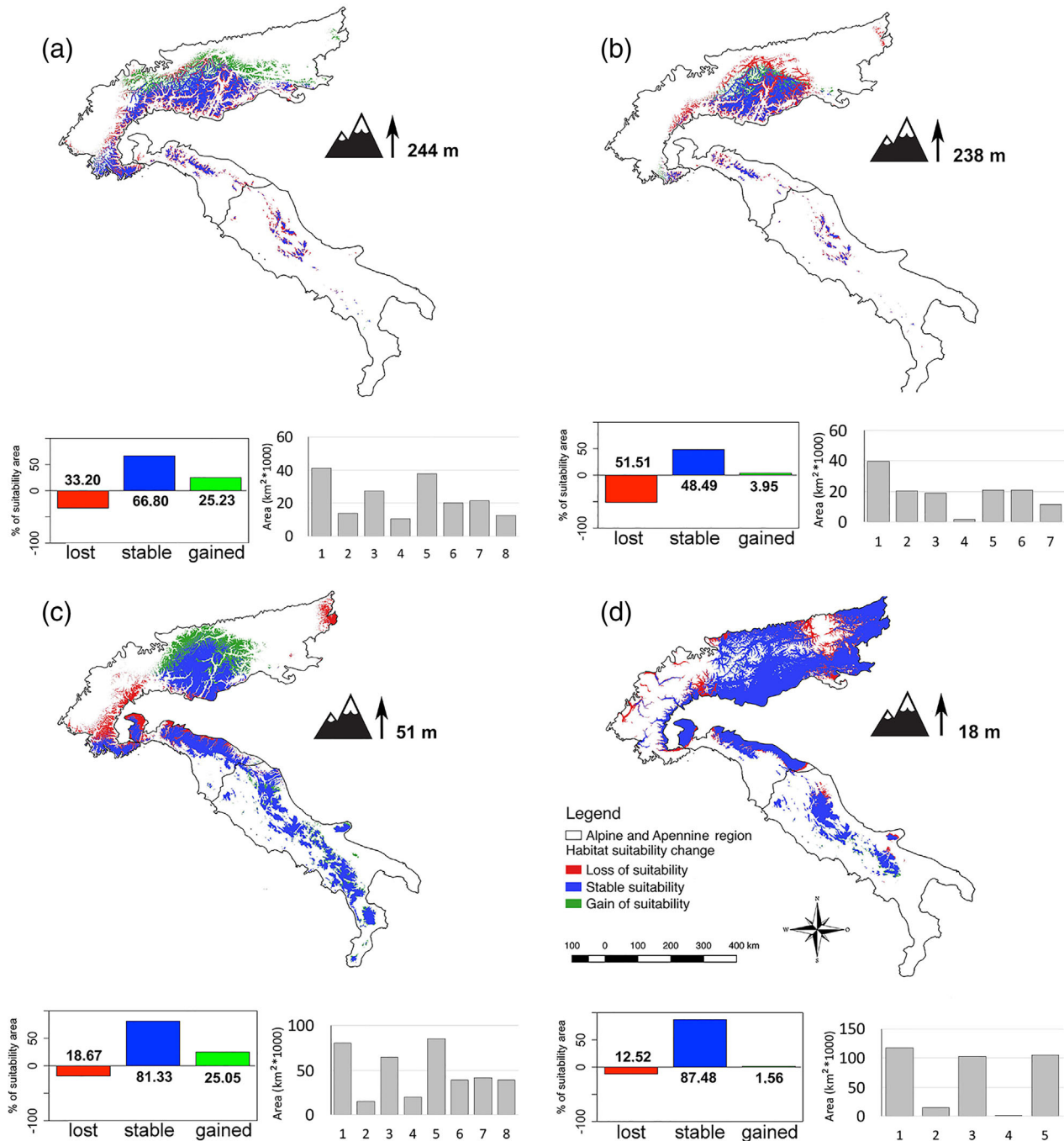


FIGURE 3 Range shifts predicted for *Evodinus clathratus* (a), *Oxymirus cursor* (b), *Pogonocherus ovatus* (c) and *Saperda similis* (d). Range shifts predicted with RCP 4.5 (2100): loss of suitable area (red), stable suitable area (blue), stable unsuitable area (white), gain of suitable area (green). Lower left insets: lost, stable and gained area expressed in percentage of the current suitable area. Lower right insets: areas predicted expressed in square kilometres \times 1000: Occupied with current climate (1), losing suitability (2), remaining suitable (3), gaining suitability (4), occupied with future climate (5), occupied with current climate and with suitable land cover (6), occupied with future climate and suitable land cover (Corine 1) (7), occupied within suitable land cover (Corine 2) (8). Central insets with the arrow indicate the vertical shifts (in meters) of species ranges

within the climatically suitable area. In the absence of scenarios of future CLC, we computed the extent of suitable areas in two different ways. The first one (Corine 1) assumes that despite possible changes in the position of suitable vegetation, the covered percentage area will remain stable, overall. Accordingly, we calculated the putative area occupied by suitable vegetation in the future by multiplying the future

range area predicted by the model by the fraction of suitable vegetation calculated for the current range. The second one (Corine 2) assumes that the vegetation will not shift upwards fast enough to support cerambycid communities, which often need old trees. In this case, we calculated the putative area occupied in the future by intersecting the suitable vegetation map available for the present with the

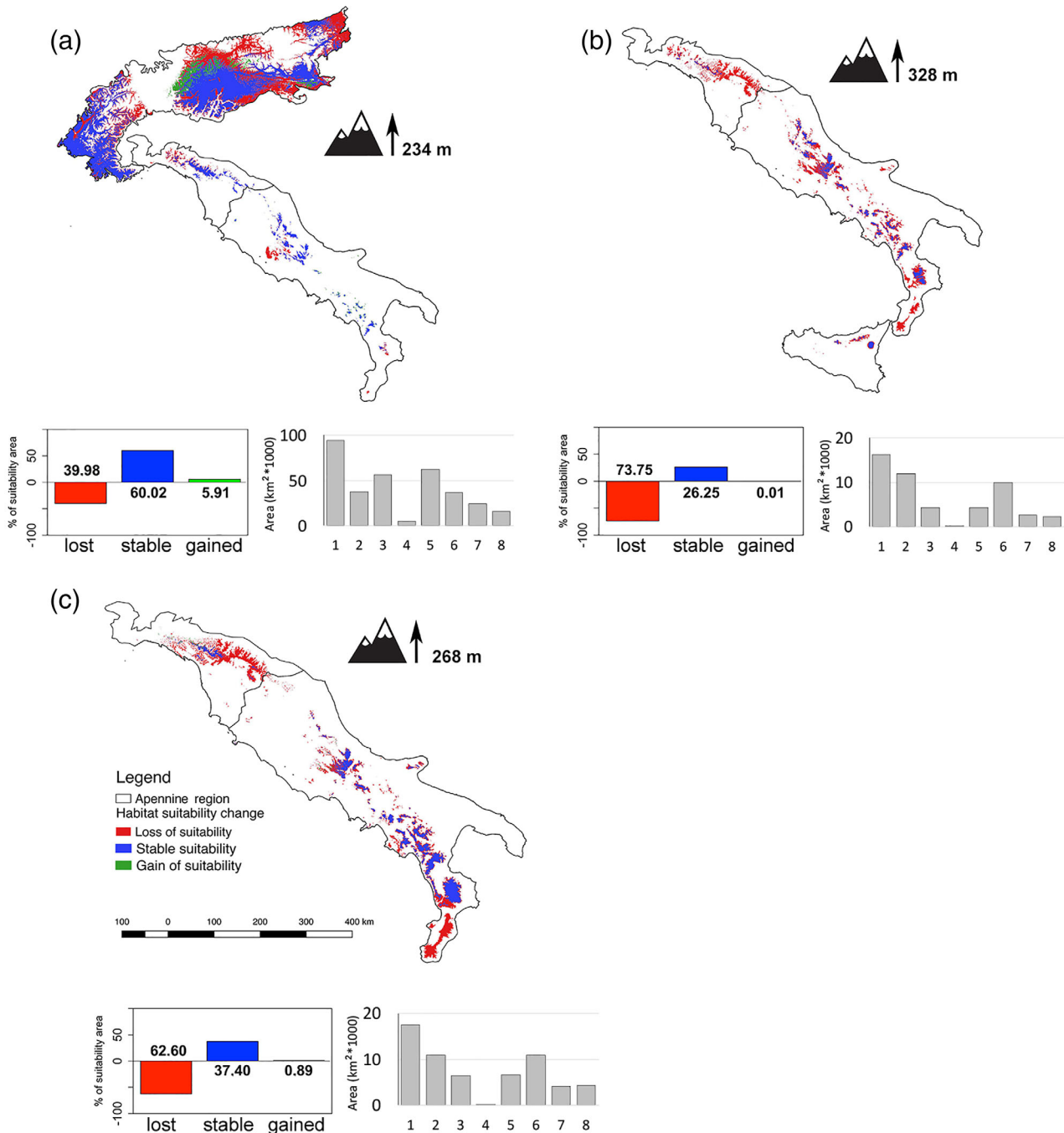


FIGURE 4 Range shifts predicted for *Tetropium gabrieli* (a), *Acanthocinus xanthoneurus* (b) *Pogonocherus eugeniae* (c). Range shifts predicted with RCP 4.5 (2100): loss of suitable area (red), stable suitable area (blue), stable unsuitable area (white), gain of suitable area (green). Lower left insets: lost, stable and gained area expressed in percentage of the current suitable area. Lower right insets: areas predicted expressed in square kilometres \times 1000: occupied with current climate (1), losing suitability (2), remaining suitable (3), gaining suitability (4), occupied with future climate (5), occupied with current climate and with suitable land cover (6), occupied with future climate and suitable land cover (Corine 1) (7), occupied within suitable land cover (Corine 2) (8). Central insets with the arrow indicate the vertical shifts (in meters) of species ranges

future range predicted by the model. Both approaches should be considered quite optimistic since we can expect that the fraction of suitable land will be reduced because of processes of habitat loss and degradation independent of climatic change (e.g. inappropriate forest management). *Saperda similis* was excluded from these analyses because of its strict association with debilitated *Salix caprea* trees, which can be

found in a wide range of habitats (open grasslands, rocky habitats and forest borders) that cannot be unambiguously assigned to any CLC unit. To investigate the role of existing natural reserves in protecting high-altitude cerambycids under climate change, we intersected species potential future distributions with the current distribution of protected areas using the World Protected Areas shapefile (UNEP-WCMC and

IUCN, 2016). To maintain a conservative approach, these analyses were applied only to the 4.5 scenario.

Elevation shifts in species ranges

Since uphill shift in elevational range is one of the most commonly observed patterns of species response to climate change (Shah et al., 2020; Wilson et al., 2007), maps of current and future distributions were interpolated with shapefiles of elevation, and differences between current and future average, minimum and maximum elevations were tested using paired Student's *t*-tests (one-tailed, with the null hypothesis being no shift, and the alternative hypothesis being an uphill shift).

RESULTS

Influence of climatic variables and model evaluation

The models showed good discrimination performance for 15 out of 16 species, with AUC > 0.750 (mean AUC \pm SE = 0.853 \pm 0.016); the only species with a poor fit, *Callidium coriaceum*, was excluded from further analyses (Table 1). The most influential variables were BIO19 (precipitation of the coldest quarter, for 10 species), followed by BIO15 (precipitation seasonality, 8 species) and BIO1 (annual mean temperature), BIO9 (mean temperature of driest quarter), and BIO18 (precipitation of warmest quarter) (5 species) (Table 1, Figure S2). All

species whose distribution is restricted to the Alps were influenced by precipitation, namely BIO15, with exception of *Brachyta interrogationis*. The Apennine species were mainly influenced by temperature, in particular BIO2 (mean diurnal range), BIO8 (mean temperature of wettest quarter), BIO7 (temperature annual range), and by winter precipitation (BIO19). The species occurring in both the Alps and the Apennines were influenced by both temperature and precipitation. High probability values were predicted for BIO8 in the interval -5 °C to 5 °C, steeply declining to zero at 10 °C. All the 10 species influenced by BIO19 (Table 1) occur in the Alps or in both the Alps and the Apennines; generally, low BIO19 values corresponded to higher probabilities of occurrence.

Predicted modifications of species' ranges based on climatic data

Among the 15 species with good model performance, 14 showed a possible decline in the extent of their suitable areas under future climate conditions (Table 2; Figures 1–4) in both the 4.5 and the 8.5 scenarios. *P. ovatus* was the only species that showed an increase in the 4.5 scenario and *Evodinus clathratus* an increase in the 8.5 scenario (Table 2). Most species showed a greater decline with the 8.5 scenario compared to the 4.5 scenario, except *E. clathratus* and *Pachyta lamed lamed*, which showed an increase (Table 2).

The expected loss of suitable area in some species was very large (e.g. 73% for *B. interrogationis*), with minimal future gains under both

TABLE 3 Current and projected values of species mean elevation for high-altitude cerambycids in Italy under two climatic scenarios (RCP 4.5 and RCP 8.5)

Species	Current elevation (m) Mean (min–max)	Future elevation with 4.5 scenario (m) Mean (min–max)	Future elevation with 8.5 scenario (m) Mean (min–max)	Elevation difference with 4.5 scenario (m)	Elevation difference with 8.5 scenario (m)
<i>A. pratensis</i>	1294 (151–3098)	1432 (151–3098)	1642 (237–3098)	138	348
<i>A. septentrionis</i>	1453 (82–3660)	1528 (64–3660)	1504 (143–1847)	75	51
<i>B. interrogationis</i>	1836 (316–3522)	2059 (817–3522)	2292 (1251–3001)	223	456
<i>J. sexmaculata</i>	1532 (187–3581)	1601 (240–2987)	1565 (265–2915)	69	33
<i>L. virens</i>	1345 (187–3127)	1684 (226–3522)	1899 (280–3586)	339	554
<i>P. lamed lamed</i>	1366 (187–2987)	1514 (187–2987)	1469 (206–2987)	148	103
<i>P. lurida</i>	1308 (151–3522)	1457 (187–3522)	1662 (265–2987)	149	353
<i>T. fuscum</i>	1100 (62–3581)	1164 (62–3005)	1461 (143–2987)	63	360
<i>E. clathratus</i>	1598 (143–3522)	1842 (417–3591)	1909 (366–3630)	244	311
<i>O. cursor</i>	1558 (223–3522)	1796 (366–3522)	1912 (303–3357)	238	354
<i>P. ovatus</i>	1250 (6–3773)	1300 (9–3773)	1332 (15–3634)	51	82
<i>S. similis</i>	1074 (13–3098)	1092 (32–3098)	1161 (43–3522)	18	87
<i>T. gabrieli</i>	1375 (40–3586)	1609 (240–3586)	1730 (289–3522)	234	355
<i>A. xanthoneurus</i>	1117 (137–3244)	1444 (140–3244)	1679 (728–3244)	328	563
<i>P. eugeniae eugeniae</i>	976 (35–2662)	1245 (140–2662)	1344 (640–2662)	268	368
Mean \pm standard error for average values	1345.5 \pm 59.1	1517.8 \pm 67.7	1637.4 \pm 73.9		
Mean \pm standard error for minimum values	128.0 \pm 22.6	218.5 \pm 51.9	344.9 \pm 81.3		
Mean \pm standard error for maximum values	3365.7 \pm 80.0	3318.6 \pm 84.1	3131.9 \pm 121.0		

TABLE 4 Suitable areas covered by forests and protected areas for high-altitude cerambycids in Italy and areas covered by protected areas

	Current Corine (%)	Current Corine (km ² × 1000)	Future Corine (1) (km ² × 1000)	Future Corine (2) (km ² × 1000)	Protected areas (km ² × 1000)	Protected areas (%)
<i>A. pratensis</i>	59.28	29.92	17.79	17.03	16.04	31.77
<i>A. septentrionis</i>	50.63	50.29	36.85	34.33	36.37	36.61
<i>B. interrogationis</i>	23.64	10.99	2.96	2.56	19.16	41.24
<i>J. sexmaculata</i>	49.56	23.54	11.02	9.41	16.81	35.41
<i>L. virens</i>	57.28	40.63	22.90	15.96	22.41	31.60
<i>P. lamed</i>	58.42	12.84	10.02	10.28	6.73	30.63
<i>P. lurida</i>	57.36	41.74	24.38	23.14	23.11	31.76
<i>T. fuscum</i>	99.88	54.25	45.00	27.41	13.39	24.65
<i>E. clathratus</i>	49.34	20.22	19.48	12.66	30.45	74.31
<i>O. cursor</i>	52.68	20.77	11.61	8.15	15.99	40.54
<i>P. ovatus</i>	48.40	38.53	40.98	39.08	30.48	38.30
<i>S. similis</i>	NA	NA	NA	NA	33.97	28.88
<i>T. gabrieli</i>	39.16	36.76	24.24	16.23	26.73	28.47
<i>A. xanthoneurus</i>	61.50	9.96	2.62	2.42	8.30	59.16
<i>P. eugeniae</i>	62.59	10.94	4.19	4.29	9.39	53.73

Note: Values occupied by suitable vegetation according to Corine classification of land cover were calculated assuming either that vegetation will track climate change (1) or not (2).

the 4.5 and 8.5 scenarios (Table 2). Under the 4.5 scenario, six species showed a range decline greater than 50% and four a decline greater than 30%, with an average loss of 44% and an average gain of 6% (Table 2). Under the 8.5 scenario, declines were larger; 10 species showed a decline greater than 50% and two species a decline greater than 30%, with an average loss of 62% and, again, an average gain of 6% (Table 2).

With the 4.5 scenario, patterns of distribution changes indicated that most Alpine species will be affected by a range contraction especially along the peripheral mountains (e.g. the Prealps) and in mountains near the sea, whereas loss in the central Alps will be less marked (Figures 1 and 2). For these species, overall loss of suitable area ranged about 30%–73% (see insets in Figures 1 and 2). *Judolia sexmaculata* (Figure 1d) showed a loss of suitable areas in the western and eastern Alps and a local extinction in the western and eastern Alps, possibly surviving only in the central Alps, with an overall loss of 66% of suitable area. *Lepturobosca virens* (Figure 2a) and *Pachyta lamed lamed* (Figure 2b) are predicted to lose almost all their suitable areas in the eastern Alps, with an overall loss of about 53% and 27%, respectively. As for the species occurring in the both the Alps and the Apennines (Figures 3 and 4a), range contractions will particularly affect the Northern Apennine sector, with overall loss ranging between 13% and 52% (see insets in Figures 3 and 4). Three species living both in the Alps and in the Apennines would experience gains of suitable areas in the Alps but virtually no gain in the Apennines: *Evodinus clathratus* (Figure 3a, with an overall gain of 25%), *Oxymirus cursor* (Figure 3b, with an overall gain of 4%) and *Tetropium gabrieli* (Figure 4a, with an overall gain of 6%). For these species, suitability loss was 33%, 52%, and 40%, respectively.

For the two species endemic to the Apennines (*Acanthocinus xanthoneurus* and *Pogonocherus eugeniae* Figure 4b,c), we observed two areas with almost complete loss of suitability: the Tosco-Romagnolo Apennine in Northern Italy and the Aspromonte Massif in Southern Italy, with an overall loss of 74% (the highest value among the investigated species) and 63%, respectively (see insets in Figure 4b,c). *A. xanthoneurus* (Sicily) will experience a strong contraction of suitable areas along the Madonie and Nebrodi Massifs, whereas on Mount Etna suitability will be lost only at lower elevations.

All species showed an expected upward shift in their altitudinal distribution (Figures 1–4, Table 3). Overall, species mean elevations were predicted to increase significantly under both the 4.5 scenario ($t = 6.451$, $p < 0.0001$) and the 8.5 scenario ($t = 6.370$, $p < 0.0001$), with an average increase of 172.3 ± 26.7 m a.s.l. (4.5 scenario) and 291.9 ± 45.8 m a.s.l. (8.5 scenario). Average increase under the 8.5 scenario was significantly higher than that predicted under the 4.5 scenario ($t = 4.234$, $p < 0.001$). Also, we detected significant increases in the minimum elevations under both scenarios ($t = 2.475$, $p = 0.013$ for the 4.5 scenario, and $t = 3.070$, $p = 0.004$ for the 8.5 scenario). No significant differences were found for the maximum elevations ($t = -0.756$, $p = 0.769$ for the 4.5 scenario, and $t = -1.638$, $p = 0.062$ for the 8.5 scenario). The 8.5 scenario predicted, on average, higher minimum elevations than the 4.5 scenario ($t = 2.397$, $p = 0.016$) but not for maximum elevations ($t = -1.433$, $p = 0.913$).

The overlap between climate-based models and suitable vegetation showed a lack of suitable habitats in a large fraction of the species' climatically suitable area (see Table 4 and values of categories 6–8 in insets of Figures 1–4). On average, only 56% of the area

climatically suitable is occupied by suitable vegetation. Even assuming that the fraction of suitable land cover will remain stable, a future negative trend is observed in the extent of predicted distributions for all species (Table 4). On average, only 39% of the future climatically suitable areas will be included in current protected land (Table 4).

DISCUSSION

Several studies using HSMs have shown the importance of climatic factors in constraining species ranges of cerambycids (e.g. Aguilar et al., 2016; Bosso et al., 2018; Kadej et al., 2017; Lachat et al., 2013; Peterson & Scachetti-Pereira, 2004; Rukavina et al., 2018; Silva et al., 2016). We found that the distribution of high-altitude cerambycids on Italian mountains is strongly constrained by climatic variables. In particular, Alpine species are mainly limited by very high values of winter precipitation, which corresponds to a high abundance and long persistence of snow cover (Harris et al., 2019). The only exception is *Brachyta interrogationis*, that is the only non-forest species, living in open grasslands. A possible explanation is that the influence of snowfall and precipitation is less important for herbaceous vegetation and for the larva of this species, which feeds in rhizomes of *Geranium sylvaticum* (Sama, 2002). In contrast, Apennine species, which live in a drier and warmer climate, are mainly limited by the temperature in the wettest quarter, a parameter that also influences the presence of snowfall in Mediterranean regions, where winter is the wettest season (Mooney et al., 2001). Therefore, future climate changes affecting snow cover persistence will have important consequences on their distribution.

In response to increasing temperature, species may track more favourable climates by moving latitudinally (polewards) and upwards (towards higher elevations). As the vertical temperature gradient is more rapid than the latitudinal one, species can compensate for warming more easily moving upwards than northwards, and uphill movements in response to climate change are now well documented for a variety of taxa (e.g., Cerrato et al., 2019; Chen et al., 2011; Doak & Morris, 2010; Harsch et al., 2009; Merckx et al., 2013; Moritz et al., 2008). However, elevational shifts cannot be used by all species to track climate change; for example, species that are already on mountain tops have no place to go. Moreover, because of the roughly conical shape of mountains and the isolation of mountain tops, upslope range shifts, even when possible, will transform previously large and continuous ranges into smaller and fragmented distributions (Fattorini et al., 2020).

In the case of strong selection, sufficient genetic variation and heritability of the relevant traits, some species might undergo rapid evolutionary changes generating evolutionary rescue (Catallo et al., 2019). However, even in the hypothesis of high heritability for the traits associated with climate adaptation, given the long generation time (2–3 years for most cerambycid species, Švacha & Danilevsky, 1987, 1988) and the scarce connectivity that many species show in the model, such a rescue seems unlikely. In addition, a recent meta-analysis (Diamond, 2017) of experimental values of

heritability of heat-tolerance in insects (which is probably a relevant character for climate change adaptation) reported modest values of heritability, with higher values in species living in areas with broader temperature variations.

In the Alps and Apennines, many high-altitude species occur in mountain tops and therefore cannot shift upwards; thus, the risk of local extinctions is high. This expectation is largely confirmed by our findings. All analysed species are predicted to shift towards higher altitudes and hence to reduce their ranges. Most species would increase their average elevation under both scenarios used in this study, with shifts ranging from about 20 to about 340 m under the less pessimistic scenario (under the less optimistic scenario, expected increases ranged between about 80 and 560 m). The highest shifts (>300 m) under the less pessimistic scenario are expected for *Leptura virens* (an Alpine species) and *Acanthocinus xanthoneurus* (an Apennine species), but most of the species (about 70%) would move for more than 100 m. Interestingly, we detected shifts also for the minimum elevations but not for the maximum elevations. This may be explained by the progressive reduction of suitable area at increasing elevations, which constraints potential uphill movements.

Reduction in suitable area varied among species and according to the adopted scenario. Average loss was higher under the most pessimistic scenario (62%), but even the less pessimistic showed a substantial reduction (44%). This loss in climatically suitable area is only slightly contrasted by gains of new suitable areas (with an average value of 6% for both scenarios). The highest values of suitability loss were observed for the Alpine species *B. interrogationis* and the Apennine species *A. xanthoneurus*, which are expected to lose more than 70% of their suitable area. The impact of climate change on these species will be likely even worse because of the reduced extent of the area occupied by suitable vegetation within the climatically suitable area.

Although our study was restricted to a single group of beetles, we expect that other groups of high-altitude insects would show the same patterns. As Alpine and Apennine high-altitude faunas are rich of endemics (Menchetti et al., 2021; Urbani et al., 2017), the impact of climate change on the Mediterranean biodiversity hotspot appears particularly alarming.

Climatic suitability is a necessary, but not sufficient condition for the presence of phytophagous beetles, because of their dependence on the co-occurrence of their host plant(s). Some insights from leaf beetles (Chrysomelidae) suggest that host plants are a potentially important predictor of species ranges, although less than climate (Cerasoli et al., 2019) and these two factors together (climate suitability and habitat availability) proved to be the most effective to predict the northwards shifts in response to climate change (Platts et al., 2019). Thus, whereas the predicted loss of suitable area is realistic and probably underestimated, the gain is more uncertain, because in the gained areas the host plants might not be present.

To take into account the dependence of cerambycid species on their host plants, we used the extent of suitable vegetation based on CLC maps to refine our climate-based predictions. We found that roughly half (56%) of the climatically suitable area also presents a vegetation which likely includes the host plants. As there is no available

projection of the future distribution of CLC, to calculate species future areas of presence we optimistically assumed that this percentage will remain stable. Even if the most common response of vegetation to climate change is shifting upwards to find cooler temperatures, there is no guarantee that this will happen. Firstly, several studies did not find a significant upward shift of forest vegetation over the last decades (Scherrer et al., 2020). Secondly, even when an upslope movement can occur, this might be more limited by tree demography (as host tree may have a long-life cycle that does not allow a rapid colonisation), and competition with other species (more plastic and with shorter life cycles), than by dispersal possibilities (Scherrer et al., 2020). Currently, observed shift rates in most plant species seem to be insufficient to keep up with climate change (Chen et al., 2011; Corlett & Westcott, 2013; Loarie et al., 2009). Actually, on the Alps, there is evidence of ongoing upward shifts in plant elevational ranges, which is interpreted as a result of both climate change and decreasing grazing pressure (Frei et al., 2010; Leonelli et al., 2011; Vitasse et al., 2021; Wieser et al., 2019). However, woody plants show, on average, a positive shift in optimum elevation of about 33 m per decade, which appears too slow to track isotherm shifts induced by climate warming (Vitasse et al., 2021).

Also, there is evidence that some plants could shift downwards instead of upwards in more humid habitats to track water availability which is a limiting factor (Crimmins et al., 2011; Lenoir et al., 2010). This can also explain our findings that for some cerambycids the upslope movement will be less pronounced with the 8.5 than with the 4.5 scenario, probably because of nonlinear relationships with climate or because of an important role of other factors, such as water availability.

Although there is indication that some terrestrial insects might have an upward shift of their leading edge within the range of the pace of climate warming, or higher (Vitasse et al., 2021), responses are species specific and are not necessarily valid for the cerambycids as a whole. Even assuming that both plants and beetles will move upwards with a sufficient velocity, this does not mean that beetles will be really able to use the newly formed forests. The development of appropriate new habitats uphill needs long time periods, especially for species adapted to mature forests with abundance of dead wood, such as xylophagous cerambycids. In fact, the simple presence of the host plants is not a sufficient condition for most of the investigated species, which require old forests with abundance of dead wood (Sama, 2002; Švacha & Danilevsky, 1987, 1988), a resource that is clearly lacking in a recently grown forest. This highlights the importance of having pristine or properly managed forests for the conservation of cerambycids. Small gains of climatic suitability can be also virtually null, if the climatically gained areas do not have the host plants or if the habitats are not properly managed. This becomes even more evident considering that, on average, only 39% of the predicted suitable species ranges will be included in protected areas, which could guarantee the protection of habitats and a careful management of forest resources.

It is important to stress that, in addition to climate change, many other forms of anthropogenic pressures affect mountain areas

(Fattorini et al., 2020), with possible detrimental effects on cerambycids and their host plants. For example, like other xylophagous insects, cerambycids are threatened by deforestation, invasion of exotic plants, wildfire, inappropriate forest management, pollution, and so on (Cálix et al., 2018). Thus, in addition to range contraction and population fragmentation due to climate change, high-altitude cerambycids might suffer from various forms of habitat loss and degradation. For these reasons, it is important a more widespread adoption of appropriate forest management practices. For example, traditional silviculture in Italy considers negatively the presence of dead trunks and wood (Carpaneto et al., 2015). As a result, in many managed forests, the undergrowth is systematically 'cleaned' from dead wood, even in protected areas, which has serious negative effects on cerambycids and other xylophagous beetles.

This study was restricted to the Italian territory, although many species have much wider distributions. This means that they might be more variable in habitat requirements than estimated from our data. However, species with disjunct or fragmented distributions tend to develop local adaptations when the dispersal capabilities of the species do not overcome the distance (Savolainen et al., 2013; Storz, 2005). Therefore, including data from the entire species ranges might result in the opposite problem of overestimating niche sizes, and hence species plasticity of local populations. In fact, data on butterflies indicate that several Alpine and Apennine populations represent distinct lineages and that the Alps and the Apennines are to be considered different functional refugia during climatic cycles (Menchetti et al., 2021). On this basis, it might be suggested that not differentiating Alpine and Apennine populations might lead to an overestimation of true species plasticity. We have decided to collectively use all Italian data as a compromise between the need of avoiding the risk of mixing populations with potentially too different adaptations (entire ranges) and that of excessively underestimating niche size (separate analyses for the Alpine and the Apennine populations). Finally, we have overlooked the possibility that species might change habitat requirements under global change. For example, species might be less demanding in substrate conditions (such as the diameter of dead wood, its state of degradation, or the range of suitable tree species). However, these adaptations would require important changes in morphological, physiological and developmental characteristics that are unlikely to evolve in short time.

CONCLUSIONS

Our results indicate that, even under an optimistic scenario, climate change will produce strong contractions in high-altitude cerambycids in Italian mountains. In response to increasing temperature, mountain species may track more favourable climates by moving upwards. However, while tracking favourable climatic conditions by uphill movements, mountain cerambycids will experience a substantial reduction of their climatically suitable areas. Moreover, since not all the climatically suitable area of a given species is occupied by its host plants, the true suitable area will be even more reduced. Given the

importance of Italian mountains as hubs of diversity in the Mediterranean hotspot, these results are particularly alarming for the conservation of montane biotas. Conservation actions able to mitigate the effects of climate change on high-altitude cerambycids should be focused on contrasting habitat loss and degradation through land preservation and the adoption of appropriate forest management practices.

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CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

AUTHORS CONTRIBUTION

Riccardo Poloni, Mattia Iannella, Giuseppe Fusco, and Simone Fattorini conceived and planned the study, Riccardo Poloni collected the data, Riccardo Poloni, Mattia Iannella, and Simone Fattorini analysed the data, Simone Fattorini and Riccardo Poloni took the lead in writing the manuscript, Mattia Iannella and Giuseppe Fusco supported the writing. All authors contributed to manuscript editing and approved the final manuscript.

DATA AVAILABILITY STATEMENT

Data available in article supplementary material.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

Data S1 Distributional records used in the study.

Figure S1 Map of the study area and GPS coordinates of species records. Terrain background from Stamen: maps.stamen.com/terrain-background/

Figure S2 Marginal response curves obtained for the three most contributing climatic variables resulting from models' calibration of 15 high-altitude cerambycids in Italy. Blue bands represent standard deviations; abbreviations of climatic variables are reported in the main text.

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