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A spatially explicit definition of conservation priorities according to population resistance and resilience, species importance and level of threat in a changing climate

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Abstract

Aim: Human-induced climate change requires conservation strategies incorporating its potential effects on species and communities. Key components of population persistence can be attributed to resistance (the capacity to remain unaffected) or resilience (capacity to absorb and recover) to climate change. In situ climatic refugia can act as resistant distribution units, and ex situ climatic refugia and the corridors to reach them may enhance resilience. We develop a novel approach selecting conservation priorities, resistant units and resilient areas according to structural connectivity and future distribution, to identify strategies that maximize the chances of species persistence in a changing climate.

Location: Italian Alps.

Methods: Conservation priorities were defined across species according to the regional conservation status and the level of threat from climate change, and across sites according to their suitability for target species and their related potential for population persistence (in situ climatic refugia, i.e., resistant units) or redistribution (ex situ climatic refugia and main corridors according to current and future connectivity, i.e., resilient units).

Results: Models suggested a marked loss of suitable area for all species by 2050 (ranging from ~50% for pygmy owl and water pipit, to 84% for snowfinch in the worst scenario), and a general loss of connectivity, which was particularly marked for pygmy owl and snowfinch. The approach applied to Alpine birds of different habitats led to a spatially explicit definition of conservation priorities.

Main conclusions: The spatial definition of conservation priorities according to species (regional importance and level of threat), resistance and resilience refines the definition of management/conservation priorities (including protected area definition), complementing the existing approaches to address climate change-induced threats in planning conservation and ecological networks.

KEYWORDS
Alps, birds, distribution, ecological connectivity, global warming, spatial planning

1 | INTRODUCTION

Human-induced climate change is one of the main threats to species and ecosystems (IPCC, 2013). Several species have shifted their distribution as a consequence (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011), especially towards upper elevations and/or higher latitudes (Walther et al., 2002). Models that relate species distributions and climate to predict the future geographical range of species in response to forecast climate change (Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012) have shown that species living at high altitudes are expected to be particularly threatened (Brambilla, Pedrini, Rolando, & Chamberlain, 2016; Chamberlain, Negro, Caprio, & Rolando, 2013; Dirnböck, Essl, & Rabitsch, 2011; Sekercioglu, Schneider, Fay, & Loarie, 2008; Viterbi et al., 2013). This situation requires conservation strategies that incorporate the potential effects of climate change on species and communities; hence, conservation planning that takes into account climate change impacts is a priority (Groves et al., 2012; Hannah et al., 2007). A key point is clearly whether the losses determined by climate change could be compensated by the species' colonization of the so-called new climate space (Pearson, Dawson, Berry, & Harrison, 2002), which will be conditioned by both species and landscape characteristics (Vos et al., 2008). Only species with good dispersal abilities and relying on widespread habitats are expected to react to climate change by expanding their range (Warren et al., 2001), and habitat availability and fragmentation may affect the species' response to climate warming (Hill, Hughes, Dytham, & Searle, 2006; Hill, Thomas, & Huntley, 1999; Opdam & Wascher, 2004). In this context, the maintenance of ecological connectivity has a crucial role for biodiversity conservation (Hannah, 2011) and for species persistence (Alagador, Cerdeira, & Araújo, 2016), and thus, it is particularly important to integrate connectivity and ecological network concepts in studies considering the potential effects of climate change (Mazaris et al., 2013; Verboom et al., 2010; Vos et al., 2008).

A common objective of strategies of adaptation to climate change is resilience (Morecroft, Crick, Duffield, & Macgregor, 2012), defined as "the ability of a social or ecological system to absorb disturbances while retaining the same basic structure and ways of functioning, the capacity for self-organization, and the capacity to adapt to stress and change" (IPCC, 2007). In ecology, resilient systems are those able to absorb disturbance and recover from its effects, by reorganizing so as to retain essentially the same characteristics (Walker, Holling, Carpenter, & Kinzig, 2004), and resilient populations are those able to recover when favourable conditions are re-established (Harrison, 1979). Resistant systems are those that can remain essentially unchanged despite disturbance (Grimm & Wissel, 1997), a definition which implies rather limited responses promoting the stability of an ecological system when facing a severe disturbance (e.g., Sternberg et al., 2015). Ideally, we can also apply the concepts of resistance and resilience to populations in relation to their regional distribution and use them for conservation planning, aiming to maximize their persistence in an era of climate change.

Identifying the sites that are and will remain suitable in future for a given species (resistant distribution units) would allow the most

important areas for the conservation of a species to be identified. In those areas, the species populations could remain largely unchanged in spite of the influence of climate change, at least from a distributional point of view (Ficetola et al., 2016).

Modelling potential connections among suitable habitat patches in current and future climatic conditions is of pivotal importance for identifying key corridors and connections which will promote the resilience of species to climate change (Hannah, 2011). Favouring colonization, dispersal and exchange of individuals across populations would promote the potential for species (and communities) to re-establish themselves under future conditions, especially by tracking suitable climates (Vos et al., 2008). Sites potentially suitable in future and connected with those currently occupied could be considered as resilient distribution units.

Several approaches have been proposed that link current and future distribution and potential connectivity to develop conservation planning considering the effects of climate change. Such studies are generally based on species-specific assessments, consider connectivity mostly in terms of dispersal distance (e.g., Mazaris et al., 2013) or rely on climate alone as a predictor of species distribution and connectivity (e.g., Alagador et al., 2016). Here, we use fine-scaled (see Seo, Thorne, Hannah, & Thuiller, 2009) species distribution models in conjunction with spatially explicit connectivity mapping (e.g., Phillips, Williams, Midgley, & Archer, 2008), considering the effect of both climate traits and habitat features (Virkkala, Heikkinen, Fronzek, Kujala, & Leikola, 2013). Our approach thus integrates distribution and connectivity models to identify spatial conservation priorities (considering both population resistance and resilience) among species potentially affected by climate change. We considered a set of species occupying different habitats to assign conservation and management priority to each spatial unit, and evaluated species distribution and connectivity among populations on the basis of both climate and land cover. To the best of our knowledge, this is the first time that future climate-induced variations in distribution and structural connectivity (based on landscape characteristics) have been considered together for conservation of a set of species dwelling in different habitats and hence requiring potentially different management options. To define conservation priorities among taxa in the face of climate change, we attributed a priority level to each target species, considering both the regional responsibility for the conservation of a given species, and the level of threat to which the species is subject due to climate change. We also assigned a priority value to areas according to their suitability for the target species and their related potential role for population persistence or connectivity.

We used Alpine bird species as biological models to illustrate our approach (see also Figure 1). We predicted the impact of climate change on the potential distribution and ecological connectivity for Alpine species inhabiting different habitats. Identifying areas where species can occur in current and future conditions can be used to define key sites to maximize resistance, whereas mapping (and conserving) key areas for connectivity among populations (both in current and in future conditions) is needed for the preservation of areas and habitats that will facilitate movement across sites, thus promoting resilience to climate change.

FIGURE 1 Flow chart summarizing our approach to the definition of spatial priorities for species conservation under a changing climate. [Colour figure can be viewed at wileyonlinelibrary.com]
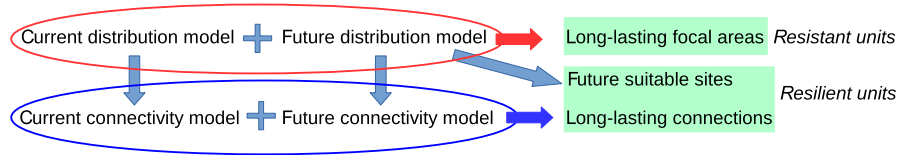
Conservation planning that incorporates effects induced by climate change (e.g., Williams et al., 2005) is particularly relevant in mountain regions such as the Alps (Brambilla et al., 2016; Walzer et al., 2013). The higher recent and projected increase in global temperature (Böhm et al., 2001), the impact of human activities (Chamberlain, Pedrini, Brambilla, Rolando, & Girardello, 2016) on species and ecosystems and the synergic interaction of human impacts and climate change (Mantyka-Pringle, Martin, & Rhodes, 2012) are posing severe threats to biodiversity in this and other mountain areas, and developing the most effective conservation strategies coherent with regional priorities is therefore an urgent task for the Alpine region.

2 | METHODS

2.1 | Study area and fieldwork

The study area encompassed a large portion of the Alps (c. 44,000 km^2), located in northern Italy (Figure 2). Within this area, bird occurrence data were collected between 2000 and 2015 (Supporting Information), mostly by means of point count surveys of 10-min duration (1,196 points throughout the area, distributed across the three main sectors, i.e., Piemonte and Valle d'Aosta, Lombardia, Trento Province, broadly in proportion to their relative extent) performed during the breeding season (Bibby, Burgess, Hill, & Mustoe, 2000). Owl data were collected using nocturnal and crepuscular playback techniques (broadcast male song) during the breeding season

(Brambilla, Bergero, Bassi, & Falco, 2015). Full details of these datasets are given in the relevant references (Chamberlain et al., 2013; Chamberlain, Brambilla, Caprio, Pedrini, & Rolando, 2016; Brambilla et al., 2015; Brambilla et al., 2016) and in Appendix S1. The majority of survey points were carried out in locations selected so as to be broadly representative of at least one (e.g., Brambilla et al., 2015) or both (e.g., Brambilla & Pedrini, 2016; Chamberlain, Brambilla et al., 2016) montane and Alpine and vegetation belts (sensu Körner, 2003), and there was no focus on, for example, protected areas or habitats subject to specific environmental pressures (e.g., skiing activities, urbanization, changes in livestock management). Further points were carried out in all parts of the study area at lower elevations, both in forest and in open habitats. In summary, considering diurnal surveys, in the western (and largest) part of the study area (Piemonte and Valle d'Aosta), 570 points were carried out, within the framework of different projects, sampling all main habitats along a wide altitudinal range (c. 100–2,900 m asl); in Lombardy (the central part of the study area), 248 point counts were surveyed within four different projects/areas (c. 220–2,800 m asl); in the Trento Province (the eastern part of the study area), 207 point counts were surveyed along altitudinal transects (c. 1,350–2,750 m asl) representative of the main mountain systems of the province, whereas 142 points were made in six areas at lower elevations (c. 350–1,400 m asl, Assandri, Bogliani, Pedrini, & Brambilla, 2016); a further 29 points were surveyed between c. 1000 and 1900 m asl within another project. The dataset so obtained was then integrated with further occurrence records collected by means
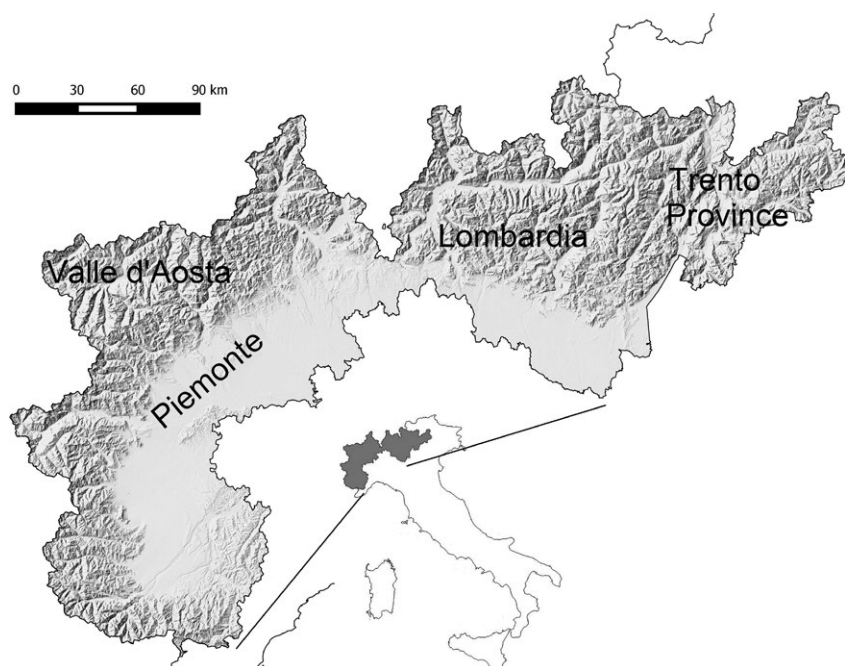

FIGURE 2 Study area and mountain relief. The inset shows its location within Italy

of other surveys (e.g., ptarmigan- or grouse-specific counts) and occasional observations of target species.

2.2 | Selecting model species

We chose species representative of the main types of landscapes at medium-high elevation in the Alps: (1) subalpine coniferous forest, (2) high-altitude open habitats (i.e., alpine grassland and rocky habitats), and (3) transitional belt habitats, which connect the former two. Model species were chosen from those which show a distribution potentially affected by climatic variables (northerly distributed species that in the Alps are close to their lower latitudinal range limits, and/or are high-altitude specialists strictly tied to mountain habitats). For (subalpine) forest habitats, we chose pygmy owl (*Glaucidium passerinum*) and boreal owl (*Aegolius funereus*), two nocturnal raptors known to be affected by climate, for which the Alps represent a relict portion of their former range in a colder past (Brambilla et al., 2015). For open habitats, we selected rock ptarmigan (*Lagopus muta*), water pipit (*Anthus spinoletta*) and white-winged snowfinch (henceforth snowfinch; *Montifringilla nivalis*), all species likely to be impacted by climate change (Brambilla et al., 2016; Brambilla, Cortesi et al., 2017; Chamberlain et al., 2013; Pernollet, Korner-Nievergelt, & Jenni, 2015; Revermann, Schmid, Zbinden, Spaar, & Schröder, 2012) and occupying high-elevation habitats. For transitional habitats (around the tree line, where forest and grassland intergrade), black grouse (*Tetrao tetrix*) was chosen according to its preference for edge habitats and cold climates (Braunisch, Patthey, & Arlettaz, 2016; Loneux & Lindsey, 2003; Ludwig et al., 2006; Spidsø, Hjeljord, & Dokk, 1997). All those species are largely resident species, with the exception of water pipit, which is mostly a short-range migrant, commonly wintering in lowland sites within the study area. Sample sizes are reported in Table 1.

2.3 | Modelling species distributions

We used MAXENT (release 3.3.3k; Phillips, Anderson, & Schapire, 2006) to model species distributions (Braunisch et al., 2013), which is routinely adopted for distribution modelling with data collected under different field protocols (Elith et al., 2011; Engler, Rödder, Stiels, & Förschler, 2014). We used bird occurrence data with a spatial resolution ≤100 m for Passeriformes and <1 km for other species to build models at a relatively fine spatial scale (1 km). As environmental variables, we considered land cover, topographical and bioclimatic factors.

All variables were calculated for 1 km × 1 km cells, within which we measured the total cover of 11 land cover types derived from CORINE Land Cover (CLC2006; EEA, 2007): arable land, pastures, broadleaved forest, coniferous forest, mixed forest, natural grassland, transitional woodland–shrub, bare rocks, sparsely vegetated areas, lakes, built-up areas (urban and productive areas, large infrastructures; several different categories summed together; Supporting Information). Average slope for each cell was derived from a 20-m resolution Digital Terrain Model, but was considered for non-Passeriformes only (see Supporting Information). For the same 1 km × 1 km cells, we calculated six climate variables (downloaded from WorldClim v.1.4; Hijmans, Cameron, Parra, Jones, & Jarvis, 2005; http://www.worldclim.org; resolution: 30 arc-seconds) that we a priori believed could be important determinants of species distributions: annual average temperature (BIO 1), maximum temperature of the warmest month (BIO5), mean temperature of warmest quarter (BIO10), annual precipitation (BIO12), precipitation of the warmest quarter (BIO18) and precipitation of the coldest quarter (BIO19). However, variance inflation factors (VIFs) calculated for these variables showed a high degree of collinearity and, in particular, a strong correlation with annual temperature. Given the degree of collinearity, and that average annual temperature has a major importance in dictating the distribution of our model species in the Alps (Brambilla et al., 2015; Brambilla et al., 2016) and is likely to be particularly important for our largely resident species, it was decided to use annual temperature as the only climatic variable in the model. Annual temperature therefore acted as a surrogate for general climatic conditions in order to reduce the risk of overfitting the effects of climate change on species distribution.

To further minimize the risk of overfitting species–habitat or species–climate relationships, we fitted all distribution models by means of linear and quadratic terms only. The continuous output of MAXENT models was transformed into a presence/absence value, selecting the most appropriate threshold for each single species by comparing the output of the reclassification with the current distribution of the species in Italy (Nardelli et al., 2015). To produce as general and robust models as possible, we applied a masked geographically structured evaluation of models for most species (Radosavljevic & Anderson, 2014). We partitioned the study area into four different longitudinal belts (Brambilla et al., 2016), and built models using records and 10,000

TABLE 1 Basic statistics of distribution models for the target species. *N*: sample size (number of presence points comprising 1,196 points surveyed and additional records); AUC: area under the curve. Training values refer to data used to build the models and to their performances, testing values to data used to test the models (and to their relative performance on the independent dataset used for validation). For owl species, AUC and standard errors were calculated using cross-validation, due to the relatively small sample sizes

	Rock ptarmigan *Lagopus muta*	Water pipit *Anthus spinoletta*	Snowfinch *Montifringilla nivalis*	Black grouse *Tetrao tetrix*	Pygmy owl *Glaucidium passerinum*	Boreal owl *Aegolius funereus*
N training	132	179	26	257	42	49
N testing	53	577	71	66	5	6
AUC training	0.95	0.96	0.97	0.95	0.94 ± 0.00	0.91 ± 0.01
AUC testing	0.94	0.96	0.97	0.95	0.91 ± 0.08	0.89 ± 0.04

background points from two belts. We then evaluated models using the occurrence records from the other two belts as test data. Values of the area under the curve (AUC) of the receiver-operator plot were very similar between training and test data for all species, thus suggesting model stability (Table 1). Given the reduced sample size, we preferred not to divide the sample into training and test sets for the owl species. Instead, we carried out a 10-fold cross-replication of models, and calculated test and training AUC over the different subsets produced for each replicate. As for the other models, the close values between testing and training subsets suggested model stability (Table 1).

Although we used mean temperature as the sole predictor of distribution, due to the high level of collinearity among the climatic variables, this is an infrequent practice in species distribution modelling. Furthermore, there is a risk of overestimating the effect of climate change on a given species when its whole range is not considered (Barbet-Massin, Thuiller, & Jiguet, 2010). Therefore, we tested whether mean temperature produced good distribution models at a broader scale. We followed a previously adopted approach (Brambilla, 2015; Brambilla et al., 2016), where we assessed the reliability of the modelled climatic niche (specifically, thermal niche) for a species by modelling distribution as a function of annual temperature across a large part of Europe, and validating it with the known species range at larger national and European scales derived from independent data sources (BirdLife International, 2015; Nardelli et al., 2015; Brambilla et al., 2016; see Supporting Information). We obtained a reliable prediction of species distribution in relation to temperature for all species (Supporting Information), thus confirming that the use of a single measure representing thermal niche (i.e., annual temperature) provides a good general surrogate of climatic niche that can be used to predict species distributions.

We re-projected distribution models over future conditions, by varying mean annual temperature according to two different scenarios characterized by increasing values of representative concentration pathways (RCPs; Moss et al., 2010; van Vuuren et al., 2011; Diffenbaugh & Field, 2013). Following previous work (Brambilla et al., 2015; McQuillan & Rice, 2015), we chose the two RCP values of +4.5 and +8.5 W/m^2, respectively, representing a rather optimistic and pessimistic future (Meinshausen, 2011). The two scenarios correspond to an average increase of +1.4 and 2.0°C in global temperature by c. 2050 (IPCC, 2013), respectively. We obtained the annual temperature values for 2050, according to the Hadley Global Environment Model 2 (HadGEM2-ES), at the finest available resolution (30 arc-seconds). In developing the method, we treated land cover as constant over the time period considered (up to 2050; see Supporting Information). Our approach is therefore fairly conservative in that potential habitat losses that may occur as a result of climate change (especially of open habitats; Chamberlain et al., 2013) are not incorporated (but see Discussion).

2.4 | Modelling connectivity

For each species, we modelled connectivity as a function of habitat suitability and of the spatial arrangement of habitat patches with different levels of suitability. We used our target species as exemplars for particular macrohabitat types in order to evaluate (structural) landscape connectivity, and thus to have wider relevance for other species inhabiting the same habitats. We modelled structural connectivity for the selected species using CIRCUITSCAPE (ver. 4.0.5; http://www.circuitscape.org; Araújo & Townsend Peterson, 2008; McRae, Shah, & Mohapatra, 2013). CIRCUITSCAPE adopts an approach that combines circuit and graph theories and fits connections following a random walk and evaluates the contributions of multiple dispersal pathways (Araújo & Townsend Peterson, 2008; see Supporting Information for details). This approach needs a map of conductance (or its opposite, resistance) of the study landscape, and a set of focal areas, which are habitat patches where the current is injected or is tied to ground, representing source areas or areas where individuals may settle after dispersing (Araújo & Townsend Peterson, 2008). The procedure considers all focal areas and uses the conductance/resistance map to estimate the current flow among patches, and sums up all the obtained current maps to produce a final map, representing the total current in each cell of the landscape (Araújo & Townsend Peterson, 2008). This final value can be taken as the probability of a random walker passing through an individual cell (Doyle & Snell, 2000), and is thus used to weight the importance of individual cells and of pathways in connectivity models (Araújo & Townsend Peterson, 2008). It therefore provides a suitable measure of the structural landscape connectivity we aimed to evaluate. As conductance maps, we used the continuous value of environmental suitability calculated by the output of MAXENT models (Rödder, Nekum, Cord, & Engler, 2016).

Focal areas are suitable habitat patches from which animals can start or finish a dispersal event. In our approach, they are equivalent to "key patches" (Verboom, Foppen, Chardon, Opdam, & Luttikhuizen, 2001), which are relatively large areas with a preeminent role in habitat networks. We defined focal areas as continuous blocks (considering patches as contiguous according to a rook connection scheme) of potentially suitable habitats with a minimum extent of 500 ha (large enough to permit regular occurrence and breeding for all the model species). Patches smaller than this extent were excluded from focal areas, but they still contributed to connectivity estimation within models.

CIRCUITSCAPE was run under the pairwise mode, which iterates across all pairs of focal areas, using the four-neighbour-connection scheme (Engler, Balkenhol, Filz, Habel, & Rödder, 2014).

For all species, connectivity models were built for current and future (RCP +8.5) conditions. To identify areas potentially suitable for species-specific connectivity, we considered as suitable for species movement all the sites with a predicted electric current higher than the 10th percentile of the current values for species locations in the present scenario (Supporting Information; Engler, Rödder et al., 2014; Liu, Berry, Dawson, & Person, 2005; Peterson, Raxworthy, Nakamura, & Peterson, 2007).

The whole modelling approach is summarized in Fig. 3.

2.5 | Defining priorities for species conservation

To define conservation priorities among species, we considered both the relative importance (and hence the "responsibility") that the Alps
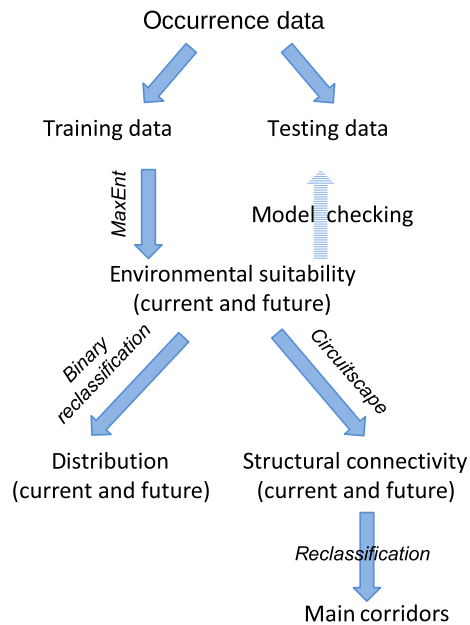
FIGURE 3 Graphical summary of the modelling approach adopted to estimate species distribution and connectivity across sites. [Colour figure can be viewed at wileyonlinelibrary.com]

have for the conservation of each species at a European scale, and the estimated decrease in potential modelled distribution. By incorporating the two concepts, we combined relative importance and level of threat into one single estimate of conservation priority. To estimate the relative importance of the Alpine region, we calculated the proportion of the European population that occurs in the Alps. This proportion was then multiplied by the estimated range contraction for each species. The resulting value was used as a conservation priority index for each species (Table 2). We also repeated this process at

the subspecies level, in order to assess whether conservation priority rankings changed when prioritizing at a finer taxonomic level (see Supporting Information).

2.6 | Ranking areas for conservation to maximize resistance and resilience

We identified two types of priorities for sites (i.e., cells in our approach) in order to carry out a spatially explicit definition of priority conservation targets which considered the need to maximize both resistance and resilience (Figure 1). Resistant distribution units are current focal areas for threatened species which will remain so in future. Such areas are putative in situ refugia ("areas where negatively impacted biota can persist as anthropogenic climate change progresses with the potential to expand if suitable regional climate conditions return," Keppel et al., 2012) and are crucial for population resistance in the face of climate change. They could also contribute to population resilience (Selwood, Thomson, Clarke, McGeoch, & Mac Nally, 2015).

Resilient distribution units include two functionally different kinds of sites: key areas for connectivity (i.e., areas suitable for movement both currently and in future) and sites that are currently unsuitable for threatened species, but will become so in future (ex situ refugia, Keppel et al., 2012). These types of priority sites are key areas for resilience to climate change, as their conservation would allow populations to move towards, or colonize, new suitable areas.

Some sites may be resistant or resilient distribution units for more than one species and may include different habitats and thus require different management and conservation strategies. The main nesting macrohabitat (subalpine forest, open habitat, transitional belt) was identified for each species. All species of each of these habitats were considered together. Given that we have analysed three species for high-elevation habitats, but only two for subalpine forests and one for

TABLE 2 Species (and subspecies) conservation priority in the study area according to percentage of the European population harboured by the Alps and to the predicted decline by 2050 in the worst climatic scenario

Taxon	Approximate % of European population in the Alps	Predicted % decline (2050, RCP +8.5 W/m^2)	Priority index	Priority rank
Species				
Rock ptarmigan *Lagopus muta*	13.02	58.56	7.63	3
Black grouse *Tetrao tetrix*	4.77	55.78	2.66	6
Pygmy owl *Glaucidium passerinum*	7.57	49.98	3.78	5
Boreal owl *Aegolius funereus*	8.06	66.74	5.38	4
Water pipit *Anthus spinoletta*	19.02	51.95	9.88	2
Snowfinch *Montrifringilla nivalis*	12.28	84.09	10.33	1
Subspecies				
Rock ptarmigan *Lagopus muta helvetica*	100	58.56	58.56	2
Black grouse *Tetrao tetrix tetrix*	4.79	55.78	2.67	6
Pygmy owl *Glaucidium p. passerinum*	7.57	49.98	3.78	5
Boreal owl *Aegolius f. funereus*	8.06	66.74	5.38	4
Water pipit *Anthus s. spinoletta*	19.02	51.95	9.88	3
Snowfinch *Montrifringilla n. nivalis*	73.67	84.09	61.95	1

transitional habitats, we considered only the first two (sub)species (in order of priority index) for the high-elevation habitats. We gave priority to resistant distribution units (long-lasting focal areas, which could also promote resilience; Mackey et al., 2012) rather than to resilient units (sites suitable in future and key sites for connectivity). Within the resilient distribution units, priority was given to key connectivity areas rather than to sites suitable in future. In the case of overlapping resistant units for different species, we selected focal areas according to the species hierarchy obtained by the priority index (as described above; see also Results). The same was carried out in the case of overlapping resilient units.

3 | RESULTS

3.1 | Current and future distribution of model species and ecological connectivity

All models performed equally or nearly so over the training and testing datasets, thus confirming a good level of model stability and validity over all the area (Table 1), which was supported by a critical comparison with the reported species occurrence (Appendix S2). Model details are reported in Table S1. All the model species were predicted to undergo range contractions (Table 2 and Figures 4–6, Appendix S3), with a progressive shrinkage towards upper elevations as a result of the temperature increase. Forecast range contraction was most pronounced for snowfinch, but the other species were also predicted to lose at least half of their current potential range under the pessimistic climatic scenario (RCP +8.5) considered here (Table 2).

Ecological connectivity across focal areas was predicted to decrease for all species and within all habitats (Appendix S4). Snowfinch and pygmy owl were predicted to be particularly

subjected to loss of connectivity, but significant reductions were found for all species.

3.2 | Priority for species conservation

Combining responsibility and predicted contraction led to the following prioritization hierarchy (according to the priority index for species): snowfinch, water pipit, rock ptarmigan, boreal owl, pygmy owl and black grouse. When considering the subspecies inhabiting the Alps, the order was almost the same, with only a change between rock ptarmigan (which ranked second) and water pipit (now third; Table 2). Therefore, open-habitat species had consistently the highest priority index, followed by subalpine forest species and finally by black grouse, our model species for transitional habitats. Considering the value of the endemic rock ptarmigan subspecies, we took the ranking at the subspecific value and thus considered snowfinch and rock ptarmigan as target species for open habitats.

3.3 | Prioritizing areas for conservation and management

Given the results of the priority index for species/subspecies, the ranking relative to habitat type was the following: open habitat, subalpine forest, transitional belt. This order was followed to select the priority group at sites where there was overlap for resistant or resilient units for species inhabiting different habitats. Therefore, the hierarchy adopted to select priorities was the following: long-lasting focal areas for open-habitat species, long-lasting focal areas for subalpine forest species, long-lasting focal areas for transitional belt species, key connectivity areas for open-habitat species, key connectivity areas for subalpine forest species, key connectivity areas for transitional belt species, future suitable sites for open-habitat species, future suitable
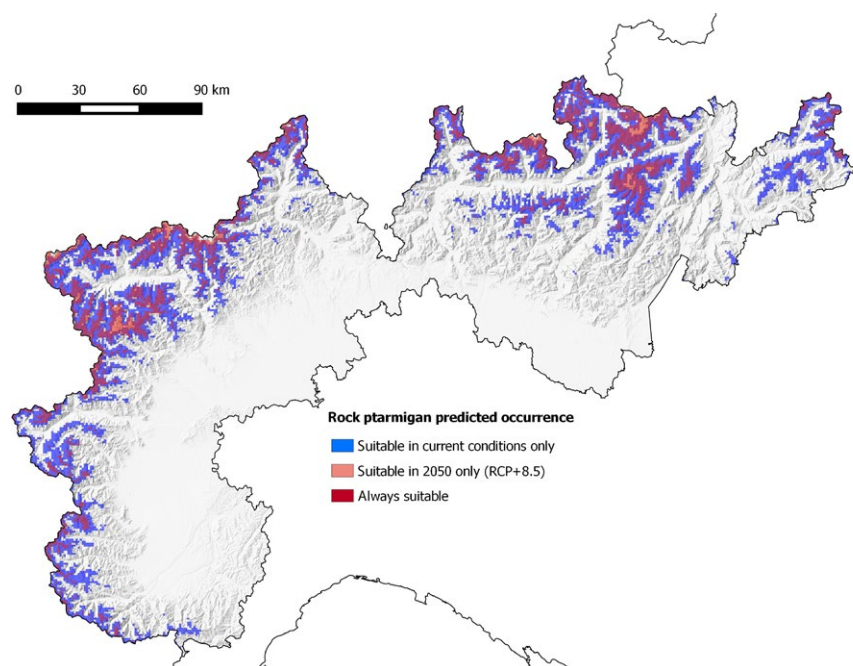

FIGURE 4 Current and future distribution for rock ptarmigan (*Lagopus muta helvetica*), an open-habitat species living at high elevation. [Colour figure can be viewed at wileyonlinelibrary.com]
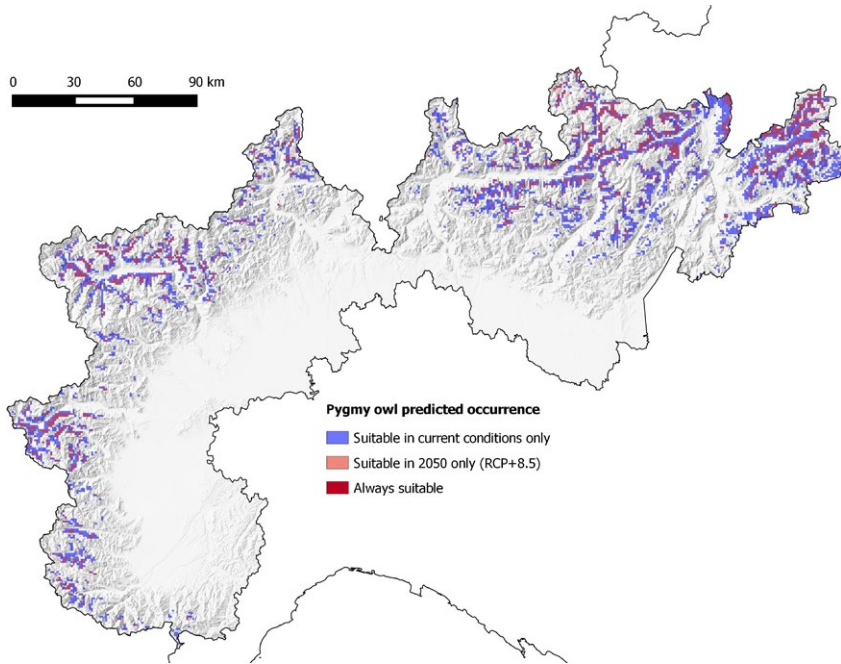
Rock ptarmigan predicted occurrence
- Suitable in current conditions only
- Suitable in 2050 only (RCP+8.5)
- Always suitable

FIGURE 5 Current and future distribution for pygmy owl (*Glaucidium passerinum*), a nocturnal raptor occupying coniferous forests. [Colour figure can be viewed at wileyonlinelibrary.com]
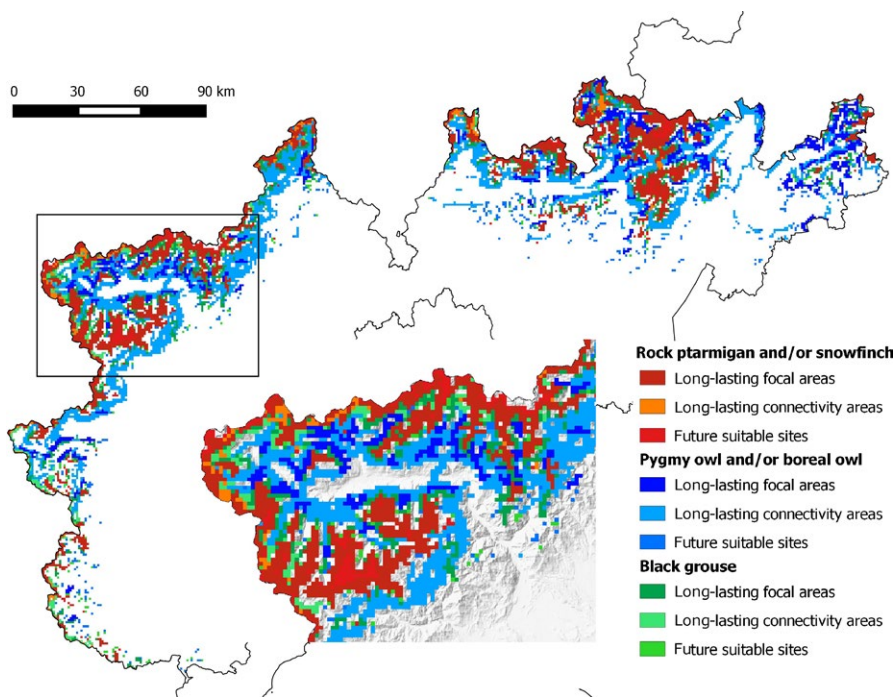

FIGURE 6 Spatial priorities for conservation and management according to the current and future suitability of sites as focal areas or corridors and according to the species hierarchy (see text). The inset shows a detailed view of Valle d'Aosta region, to show the spatial relationship among the three different types of management/conservation priorities (high-elevation open habitats, forests, transitional belt). [Colour figure can be viewed at wileyonlinelibrary.com]

sites for subalpine forest species and future suitable sites for transitional belt species.

This procedure for the selection of priority areas led to the map shown in Figure 6: in large parts of the "true" Alps, priority areas were rather continuous for all the three main habitats, and mirror the typical altitudinal stratification forest–transitional belt–open habitats. However, in most prealpine areas (the southern portions of the Lombardy and Trento mountains) and in the south-western Alps, the dramatic reduction in distribution and connectivity forecast for most species led to a fragmented and discontinuous distribution of priority areas.

4 | DISCUSSION

4.1 | Resistance, resilience and distribution: implications for conservation planning in the face of climate change

Species survival in a warming climate depends on several factors, such as physiological and phenological adaptation, dispersal ability, behavioural traits, interspecific interactions, habitat stability (Bellard et al., 2012), and on the availability of in situ and ex situ refugia (Keppel

et al., 2012). All or nearly all of those key components of population persistence can be attributed to resistance or resilience to climate change. In this study, we considered populations to be potentially resistant to climate change when they occupied suitable habitats, likely to remain suitable in a warmer future (in situ climatic refugia-resistant distribution units; see also Ficetola et al., 2016). In our approach, resilience to climate change was considered in terms of potential range shifts to track suitable conditions (e.g., to reach ex situ climatic refugia), at a spatial scale where the dispersal ability of all the bird species we considered should enable such shifts (resilient distribution units).

Integrating these two issues allowed a more informed and thorough identification of sites of strategic importance for species conservation (see also Alagador et al., 2016). Resistance-only approaches ignore the potential effect of increasing isolation, and the associated risk of identifying areas too small and isolated to allow long-term persistence (Verboom et al., 2001), while resilience-only strategies may miss the overwhelmingly important resistant refugia (Ficetola et al., 2016; Keppel et al., 2012). We believe that an integrated strategy may maximize the chance of species persistence and should therefore be encouraged for conservation planning.

Modelling connectivity has been accomplished by considering dispersal distance in relation to distribution changes (e.g., Mazaris et al. (2013), using network flows (e.g., Alagador et al., 2016; Phillips et al., 2008) or according to graph-theoretical approaches (e.g., Kang, Minor, Lee, & Park, 2016). Our approach could provide a significant improvement in our ability to develop sound conservation policies, thanks to the continuous evaluation of structural connectivity in current and future scenarios, based on both climate conditions and habitat cover, calculated according to a circuit theory approach. For the owl and passerine species we considered, a limited decrease in landscape connectivity could be a minor issue (Spina & Volponi, 2008), thanks to good dispersal abilities. On the other hand, black grouse is a low- and female-biased dispersal species, for which connectivity could be a key issue, especially in marginal or contracting populations (Warren & Baines, 2002). Contrasting evidence has been reported for rock ptarmigan, suggesting isolation in the Pyrenean populations (Bech, Boissier, Drovetski, & Novoa, 2009), but not in the Alps (Collini, 2011). More importantly, our model species may be used as "umbrella" species for the respective Alpine communities which include those with similar ecological (climate, main habitat) requirements, but with much more restricted dispersal capabilities (e.g., small terrestrial vertebrates and arthropods, and plants). The use of structural landscape connectivity metrics was indeed selected to offer the broadest possible evaluation of connectivity for living organisms, as such a connectivity estimate is less dependent on species-specific dispersal distance or abilities.

4.2 | Prioritization of species and areas

Predicted distributions and connectivity among suitable areas for all Alpine bird species are both predicted to decrease as a consequence of rising temperatures. Our results thus confirmed the findings of previous work on distributional changes from largely overlapping areas of the Alps (Chamberlain et al., 2013; Brambilla et al., 2015; Brambilla

et al., 2016) and further highlighted a negative effect on landscape connectivity.

Our approach combined the relative importance of Alpine populations and climate change-induced threats, and allowed us to rank species in terms of priority for development of conservation strategies in the Alps. Using species or subspecies resulted in only minor changes, but in other geographical contexts, changing the reference taxonomic level could result in substantial re-ordering of ranks.

The prioritization of areas for conservation and management was based on both the species hierarchy and the attribution of a higher-priority level to resistant distribution units than to resilient ones. Resistant units are more important because they offer suitable conditions to the target species irrespective of climate change, their identification is less subject to the uncertainties in future climatic scenarios (such sites would be suitable under current conditions as well as under the worst possible scenario), and they could also promote resilience.

4.3 | Modelling issues

All models appeared fairly robust, in line with the consistent species–habitat relationships found for bird species in the Italian Alps (Chamberlain, Brambilla et al., 2016). Moreover, the output they provided matched fairly well the current distribution for all species except the owls, although the apparent overestimation predicted in parts of their range was most likely due to the lack of dedicated surveys in those sites (Beraudo, Caula, & Pettavino, 2012; Nardelli et al., 2015), rather than problems with the modelling approach (Supporting Information). The underlying species–environment relationships and the resulting predicted distribution seemed therefore highly reliable, even if we did not consider other potentially meaningful climatic variables in addition to annual temperature. It is important to note that annual temperature had been repeatedly reported to be by far the most important climatic driver of avian species' occurrence in the Alps (see, e.g., Brambilla et al., 2016; Chamberlain et al., 2013).

Although we used the same spatial scale to build all models, our target species have fairly different spatial requirements. For the non-Passeriformes, the landscape grain we adopted for distribution models was roughly equivalent to their territory or home-range size (Brambilla et al., 2015), whereas for the smaller species, the 1 km × 1 km cells are clearly larger than the extent actually used by a breeding pair of those species (and which should ideally be taken as the grain size for modelling, e.g., Brambilla et al., 2016). Despite this limitation, good results (in terms of the models' statistical performance and consistency with the reported distribution) were also obtained for the two passerine species we considered, suggesting that this grain is still adequate to evaluate the effect of land cover and temperature on species occurrence at this scale. Nevertheless, the increasing availability of fine-scale data on land cover and other environmental predictors of species occurrence would allow deeper insights into species–habitat relationships and consequently into species distribution modelling.

We did not consider land use/land cover changes. Although we considered a rather limited timeframe, such changes are possible,

and even likely around the tree line (Harsch et al., 2009), and in sites where land abandonment is driving encroachment over open habitats. The approach adopted here is therefore conservative in estimating potential decreases in species distributions and in connectivity for most of the model species considered. This is because habitat losses caused by upward shifts in vegetation zones, and in particular the tree line, are likely to reduce more open habitats. The lack of consideration of habitat changes in our approach means that predictions could be even more dramatic than suggested by our models (Brambilla et al., 2016). Further developments of our method could incorporate scenarios of future habitat change (see, e.g., Ficetola et al., 2010; Wisz et al., 2008), although modelling such changes is a considerable challenge.

Connectivity models are based on the continuous environmental suitability calculated by MAXENT models. However, the identification of the main connectivity areas was based on the application of specific threshold values. We chose the 10th percentile of the current values of connectivity for species locations as the threshold to identify strong priorities for connectivity; when translating such areas into landscape planning, an expert-based enlargement or buffering around the main connectivity areas should be considered.

5 | CONCLUSIONS

Incorporating species prioritization and future variation in structural connectivity, our work provides a novel framework for the definition of conservation priorities potentially relevant for management under a changing climate. Knowing what guild of species (high-elevation, forest, transitional habitat) should be considered as a priority in a given site is key information for conservation planning, enabling management strategies to focus on certain habitat(s) and habitat traits. Considering both sites that will maintain suitable climate in future for the species they already harbour (in situ refugia), and sites crucial for connecting habitat patches, the potential resistance and resilience of species populations to climate change can be maximized through appropriate conservation planning.

This kind of approach may be replicated over different areas, sets of species/habitats and scenarios of environmental changes, including different climate predictions, land cover change or human exploitation (Brambilla et al., 2016; Chamberlain et al., 2013).

AUTHOR CONTRIBUTIONS

M.B. conceived the idea and developed the main parts along with D.C., D.S., C.C., G.B., P.P., R.F. and A.R.; all authors contributed to data collection; M.B. led the analyses helped by D.C., D.S. and E.C.; G.A., E.B., R.B., M.B., D.S. and P.P. critically assessed models' outcomes; M.B., D.C. and D.S. led the writing; all authors contributed to the final version of the manuscript.

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BIOSKETCH

Our research group conducts studies on animal ecology and conservation in the Alps, with a particular focus on the effects of environmental change and human-related impacts on alpine species and habitats.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.