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Abstract

Climate projections predict major changes in alpine environments by the end of the 21st century. To avoid climate-induced maladaptation and extinction, many animal populations will either need to move to more suitable habitats or adapt *in situ* to novel conditions. Since populations of a species exhibit genetic variation related to local adaptation, it is important to incorporate this variation into predictive models to help assess the ability of the species to survive climate change. Here, we evaluate how the adaptive genetic variation of a mountain ungulate – the Northern chamois (*Rupicapra rupicapra*) – could be impacted by future global warming. Based on genotype-environment association analyses of 429 chamois using a ddRAD sequencing approach, we identified genetic variation associated with climatic gradients across the European Alps. We then delineated adaptive genetic units and projected the optimal distribution of these adaptive groups in the future. Our results suggest the presence of local adaptation to climate in Northern chamois with similar genetic adaptive responses in geographically distant but climatically similar populations. Furthermore, our results predict that future climatic changes will modify the Northern chamois adaptive landscape considerably, with various degrees of maladaptation risk.

INTRODUCTION

Climate models predict accelerated climate change in the coming years (Hock *et al.*, 2019; Pörtner *et al.*, 2019; Arneth *et al.*, 2019), and the negative effects of this change on biodiversity have already been reported for many ecosystems (Pecl *et al.*, 2017; IPCC, 2019). Rapid climate change can significantly alter the distribution of suitable habitats, prompting populations and species to move to more suitable areas or to tolerate new environmental conditions (Bellard *et al.*, 2012). These two responses are non-exclusive and potentially complementary. In the long term, species may also undergo genetic adaptation to novel environments *in situ*, which may prevent their decline and extinction (Parmesan, 2006; Hoffmann and Sgrò, 2011). Therefore, the response of a species to climate change will strongly depend on its dispersal ability, its degree of plasticity to adapt to the new climatic conditions and/or its capacity to evolve to track the new requirements of their local environments (Visser, 2008; Hoffmann and Sgrò, 2011).

Local adaptation is common in both plants and animals (e.g., Leimu and Fischer, 2008; Hereford, 2009). It occurs when populations of the same species are exposed to different environmental conditions, which results in the selection of locally adaptive traits in each population that maximize individual fitness (Rehfeldt *et al.*, 2002). This implies that local populations will perform better than foreigners in their native environment and, *vice versa*, will show reduced aptitude when placed in a foreign environment (Blanquart *et al.*, 2013). In the context of climate change, evolvability is likely to be facilitated when 'standing genetic variation' (SGV) at various adaptive traits is already present in the populations or available from adjacent populations through dispersal and gene flow (Savolainen *et al.*, 2013). Hence, SGV is one of the essential biodiversity variables (see Hoban *et al.*, 2022) and could become a key element of the adaptive response of populations to environmental change (Orr and Betancourt, 2000; Hermisson and Pennings, 2005). Therefore, identification of SGV in natural populations and its association with climate gradients are critical to informing science-based management strategies. In this regard, incorporating intraspecific genetic variation into

predictive models that estimate the capacity of species to cope with future climate change is becoming increasingly popular (Waldvogel *et al.*, 2020; Capblancq, Fitzpatrick, *et al.*, 2020; Hoffmann *et al.*, 2021; and see Lancaster *et al.*, 2022 for a special issue).

Until very recently, the potential impact of climate change on species' distributions has principally been predicted at the species level using species distribution models (Guisan and Thuiller, 2005). These models assume that the species is homogeneous across the landscape and neglect the adaptive variation underlying local adaptation of populations (Alberto *et al.*, 2013). In fact, the impact of climate change on populations may vary depending on the spatial distribution of adaptive alleles and the potential for them to spread in neighboring populations (Rehfeldt *et al.*, 2002; Razgour *et al.*, 2019; Chen *et al.*, 2021). Therefore, more recent studies have used knowledge of adaptive genetic variation to refine classic species distribution models and provide new insights into species conservation and management, for example by identifying populations at risk of local maladaptation (when a genotype does not produce an optimal phenotype in the local environment; Capblancq, Fitzpatrick, *et al.*, 2020). Firstly, these studies have used various genotype-environment association (GEA) methods to identify genetic variation that correlates with environmental parameters, then modeled the genetic ~ environment relationship to predict the changes in genetic composition that would be required for the population to track local climate change (Capblancq, Fitzpatrick, *et al.*, 2020) - the so-called 'genetic offset' (Fitzpatrick and Keller, 2015). However, contrary to species distribution models, genetic offset does not give information on spatial distribution shifts or reshuffling of adaptive variation across the changing climatic landscape. Therefore, the application of this metric for management or conservation remained mostly theoretical so far. In conservation, identifying adaptive units, corresponding to groups of individuals sharing similar adaptive genetic composition, is a promising approach in a global change context (Barbosa *et al.*, 2018; Hohenlohe *et al.*, 2021). Predicting how these units would be affected by future variation in climate thus appears critical for integrating that major threat into assessments of species vulnerability (Razgour *et al.*, 2019).

Here, we propose to bridge this gap using a landscape genomics approach that combines genotype-environment association methods with predictive models of adaptive potential, to determine the adaptive part of genetic variation, to identify the environmental factors that shape adaptive variation and to explore the capacity of a mountain ungulate, the Northern chamois (*Rupicapra rupicapra*), to adapt to climate change. Furthermore, by comparing the adaptive genetic composition of the Northern chamois under current and future conditions, our approach makes it possible to estimate a potential genetic offset (sensu Fitzpatrick and Keller, 2015), that populations would have to solve to avoid local extinction. Mountain biodiversity, from species and populations to their underlying gene pool, is particularly sensitive to ongoing climate change (Parmesan, 2006). In the European Alps, changes have already been observed for abiotic parameters such as temperature, snow cover, glacier extent or avalanche risk (Gobiet *et al.*, 2014), with consequences for alpine animal species including direct biological effects, loss of suitable habitats, and/or upslope shifts (Pauli *et al.*, 1996; Engler *et al.*, 2011). Animal populations inhabiting mountain habitats are particularly vulnerable to climate change because, even if suitable climates are still available at higher altitudes, these habitats are predicted to be restricted to ever smaller areas in the future (La Sorte and Jetz, 2010; White *et al.*, 2018). Therefore, species adapted to cold and extreme environment may be forced to move and/or adapt to new local conditions (Chen *et al.*, 2011). At the species scale, the Northern chamois occupies a large diversity of habitat types, from low-elevation forested areas to high-altitude Alpine meadows, or where the terrain is steep and rocky (Reiner *et al.*, 2021; Corlatti *et al.*, 2022). Chamois distribution currently covers a wide geographic gradient from the Mediterranean to the Black Sea and spans altitudes mainly ranging from 500 m to over 3,000 m a.s.l. (Corlatti *et al.*, 2011, 2022; Anderwald *et al.*, 2021). Nevertheless, the species is considered morphologically and physiologically adapted to cold environments (Ascenzi et al. 1993).

A recent study determined that the reduction of body mass in Northern chamois, an important indicator of ungulate fitness (Gaillard *et al.*, 2000), was due to the direct effect of

climate warmings (Mason, Apollonio, *et al.*, 2014). The direct effect of rising temperatures could induce increases in the intensity of competition and decreases in time spent foraging (Mason, Apollonio, *et al.*, 2014), but indirect effects on fitness through effects on resource productivity or phenology have been documented on alpine herbivores, such as ibex, *Capra ibex* (Aublet *et al.*, 2009). Behavioral response to recent environmental changes has already been observed in chamois populations, where individuals select colder forest habitat to counteract the impacts of climate change (Reiner *et al.*, 2021). Therefore, behavioral adaptation, e.g., change in habitat selection, could buffer the effects of summer warmings for alpine ungulates. In a recent study, Leugger et al., (2022) investigated how climate variation during the last millennia shaped the current distribution of the Northern chamois in Europe and influenced the species contemporary neutral genetic variation across the Alps. Yet, the potential evolutionary responses of the species to environmental change, and in particular mechanisms of local adaptation to climatic conditions, remain unexplored. This is all the more relevant because previous studies have found indications of selection for alpine environments in ungulates, for example in Dall sheep (*Ovis dalli dalli*) on genes involved in immune and disease-regulating functions or respiratory health (Roffler *et al.*, 2016).

In this study, we aim to: (i) investigate whether climatic variables drive genetic differentiation of chamois populations along the European Alps and Dinaric Mountains; (ii) uncover genetic variation strongly associated with large climatic gradients, signaling local adaptation; (iii) use these signals of climate adaptation to delineate adaptive units; and (iv) model the maladaptation risk of adaptive units in a context of climate change. To achieve these objectives, we first used two different GEA approaches applied to a single-nucleotide polymorphism (SNP) data set obtained from double-digest restriction-site associated DNA sequencing (ddRADseq), to investigate the association between genetic variation and environmental gradient(s) across the Northern chamois distribution range. Second, using the set of putatively adaptive markers, we delineated four adaptive units along the Alps and Dinaric Mountains, distinguishing individuals genetically adapted to Mediterranean conditions

from those adapted to more alpine environments. Finally, projecting the geographical distribution of adaptive units into the future, we predicted that the adaptive landscape of the northern chamois will change considerably, with varying degrees of maladaptation risk for this mountain mammal in the coming decades.

MATERIAL AND METHODS

Genetic data

Samples of 465 Northern chamois (*Rupicapra rupicapra*) were obtained from the continuous range of the species in the European Alps and Dinaric Mountains (Figure 1), thanks to a network of collaborators (e.g., hunting administrations and associations, non-governmental organizations, national parks, biobanks; see Acknowledgements). The species' range extends beyond this geographical area, and isolated populations occupy territories at lower altitudes and on plains elsewhere e.g., in France, Germany, the Czech Republic and the Balkans (Corlatti *et al.*, 2022). We did not take these populations into account in this study, which focused on alpine areas characterized by a strong environmental gradient. A genetic dataset of 30,970 SNPs was generated for these individuals using a double-digest Restriction-site Associated DNA sequencing approach (ddRADSeq; Peterson *et al.*, 2012).

The procedure regarding ddRADSeq library construction, sequencing and data processing is detailed in Leugger et al., (2022), and provided in the Supplementary Materials. Briefly, we used STACKS v2.4 (Catchen *et al.*, 2011, 2013) to demultiplex data, build a *de novo* SNP catalog, and call genotypes. SNPs were filtered if they were genotyped for less than 85% of the samples, when the SNP error rate was greater than 2.5% based on the analysis of replicates (~12.5% of the samples, n=81; Figures S2-S7), when the minor allele frequency (MAF) was lower than 1% (i.e., fewer than 8 allelic copies; Lowry *et al.*, 2017a) and when sequencing read depth was lower than 10X or greater than 25X (equals to mean + 4 * sqrt(mean), see Supplementary Materials). The final dataset only included samples that were

genotyped for > 75% of all SNPs. From the initial sample set, we removed the isolated populations of Slovakia and Switzerland (Ticino), because they showed extreme genetic discontinuity with the rest of the sampling (see Roques, 2021; Leugger *et al.*, 2022), potentially biasing the detection of selection in the genome (Foll and Gaggiotti, 2008). The final data used for subsequent analyses included 429 samples and 20,904 SNPs (only one SNP was randomly selected from each RAD-fragment, Figure S8). Missing data were imputed with the median genotype.

Overall genetic differentiation among individuals

We inferred genetic units based on overall genetic differentiation, i.e., using all 20,904 SNPs (e.g., Barbosa *et al.*, 2018; Hohenlohe *et al.*, 2021) using a principal component analysis (PCA) implemented in the *adegenet* R-package (Jombart, 2008), using all 20,904 SNPs. Individual scores along the first two axes of this PCA (PC1 and PC2; Figure S9) were then used as a proxy of genetic structure to condition the search for selection in the genome (see variance partitioning section). We also investigated overall population structure using a discriminant analysis of principal components (DAPC; Jombart *et al.*, 2010) implemented in the package *adegenet*. Without prior information, we used the function *find.cluster* to determine the optimal number of clusters; more precisely, we ran successive K-means clustering with an increasing number of clusters ranging from K=2 to K=6 (based on previous inspection of values of BIC versus number of clusters). We then performed a stratified cross-validation analysis to identify the optimal number of principal components (PCs) to retain in the DAPC analysis. This cross-validation procedure was carried out using the function *xvalDapc*, with 100 replicates for each number of PCA axes retained and using 90% of the data for training and the remaining 10% for validation. Because several runs conducted with the same number of clusters K showed different results, we performed 10 independent runs for each K and selected the run with the highest assignment success mean after cross-validation.

Environmental variables selection

To explore the environmental factors that influence chamois genetic variation, we considered the 19 bioclimatic variables available from Worldclim 2 database (Fick and Hijmans, 2017). The set of variables are frequently used in similar studies (e.g., Thuiller *et al.*, 2014; Bay *et al.*, 2018; Rochat *et al.*, 2021) and are already known to influence chamois distribution (Thuiller *et al.*, 2018). We extracted the value of the bioclimatic variables within a 1500 m buffer radius around each sampling location (i.e., in area of ~ 5 km² in agreement with home range size and dispersal patterns observed in chamois; Loison et al., (1999a), Loison et al., (2008), Nesti et al., (2010), Seigle-Ferrand *et al.*, (2022), based on raster with a spatial resolution of 30 seconds (~1 km at the equator; Fick and Hijmans, 2017). To avoid collinearity among variables, we included only uncorrelated variables (based on a principal component analysis) and favored seasonal variables, because these better reflect climatic variation among sampling locations in comparison with variables measured on shorter (i.e., monthly) or longer (i.e., annual) time periods. In this way, 12 out of 19 bioclimatic variables were selected (Figure S12). Next, we wanted to select only variables that were significantly correlated with genetic variation for subsequent analyses. To identify these, we used a forward selection procedure based on Redundancy Analysis (RDA; Blanchet *et al.*, 2008) during which the standardized variables that explained most of the model variance were added sequentially to a null model, until the addition of any remaining variable did not increase the global model R^2 (Capblancq and Forester, 2021). This procedure was performed using the function *ordiR2step* from the R-package *vegan* (Oksanen *et al.*, 2019). Finally, we retained the 12 variables during the forward selection because they all explained a significant and independent component of genetic variation (Table S3).

Variance partitioning

To disentangle the relative contribution of environment, geographic distance, and evolutionary history in explaining genetic variation across chamois populations, we used partial redundancy

analysis (pRDA). Partitioning variance using pRDAs allows an estimation of the proportion of genetic variation explained by a particular group of variables (e.g., climate) while considering the effect of other variables (e.g., geography and/or overall population structure). If some of them are spatially correlated on a large scale, pRDAs can help disentangling their relative contribution to genetic variation. We followed Capblancq and Forester (2021) and considered 3 different sets of independent variables potentially influencing the distribution of genetic variation: 1) geography: derived from individual spatial coordinates (longitude and latitude); 2) evolutionary history: expressed as proxies of overall population structure (i.e., PC1 and PC2 from the PCA conducted above), and 3) environment: represented by the 12 bioclimatic variables retained during the forward variable selection (Table S3). We ran four models with individual genotypes as dependent variables (using the complete genetic dataset), one model for each set of variables (e.g., a pure climate model using the 12 bioclimatic variables as explanatory variables and either longitude, latitude, PC1 or PC2 as conditioning variables) and the full model using all variables. To estimate the independent contribution of each set of variables and their confounded effect with the other sets, we compared the sum of variance explained by each pRDA model. The procedure was conducted using the function *rda* of the R-package *vegan* and default parameters (Oksanen et al., 2019) and we used anova for significance testing (i.e., 999 permutations)

Genotype-environment association

To identify genetic variants that covary with environmental predictors (i.e., putatively linked to local adaptation), we used two genotype-environment association (GEA) approaches commonly used in the recent literature: a univariate method – or latent factor mixed models (LFMM; Frichot *et al.*, 2013), and a multivariate method – or redundancy analysis (RDA; Forester *et al.*, 2018; Capblancq *et al.*, 2018). Both approaches use linear regressions to identify loci associated with environmental variation, with individual genotypes as response variables and environmental data as explanatory variables, while also considering the past evolutionary history of the populations. LFMM, executed using the *lfmm_ridge* and *lfmm_test* functions from the R-package *lfmm* (Caye *et al.*, 2019), estimates the correlation between

environmental and genetic variation considering one environmental variable at a time. Population structure is modeled during the procedure using latent factors and we used *K*=4 latent factors, as suggested by the results of the genetic PCA (Figure S13). RDA, performed using the function *rda* of the R-package *vegan* (Oksanen et al., 2019), detects adaptive variation by considering multiple environmental predictors together and identifies the environmental gradients that are the most correlated with adaptive variation. We used PC1 and PC2 from the genetic PCA conducted above to condition the RDA model and account for overall population genetic structure. We then used the first five RDA axes (based on the screeplot shown in Figure S14) to compute Mahalanobis distances and identify outliers. For both methods, we estimated corrected *p-values* for multiple non-independent tests *(i.e.,* later termed *q-value*) using the *qvalue* function implemented in the *qvalue* R-package (Dabney and Storey, 2011). Outliers were then detected using a q-value threshold of 0.05, which corresponds to a false discovery rate (FDR) of 5% (Steane *et al.*, 2014; Forester *et al.*, 2018; González-Serna *et al.*, 2020). Finally, we retained the outliers identified with both LFMM and RDA for subsequent analysis.

Adaptive unit delineation

To explore the distribution of adaptive genetic variation across chamois natural range, we first used RDA to identify groups of individuals sharing a similar adaptive genetic composition (*i.e.*, sharing similar alleles) by considering only loci that were detected as putatively under selection for climate (i.e., outliers). We then used an "adaptively enriched" RDA space (*sensu* Steane *et al.*, 2014) created using these adaptive loci and the 12 environmental variables to predict the turnover of adaptive genetic composition across the species climate landscape. To do so, we followed the formula from Steane *et al.* (2014):

$$Adaptive\ index\ = \sum_{i=1}^{n} a_i b_i$$

where *a* is the value of the standardized bioclimatic variable at the focal location, *b* is the RDA score of the bioclimatic variable for the concerned axis, and *i* corresponds to the different

bioclimatic variables used in the RDA model. Adaptive indices were estimated for the two first RDA axes (based on the screeplot shown in Figure S17) and for each raster cell of the geographic range of the species. We considered here the IUCN geographic range of the species (Anderwald *et al.*, 2021) at a 30-seconds spatial resolution (Figure 1). Subsequently, the indices were not weighted by their contribution to its associated RDA axis model (i.e., eigenvalues) because each index represents a potential genetic adaptation linked to the environment and we decided to avoid favoring one adaptation over another. These indexes were then used to group the cells through a clustering procedure using the function *clara* of the R-package *cluster* (Kaufman and Rousseeuw, 1990), this function is an extension to k-medoids (PAM) methods to deal with data containing a large number of objects. To select the appropriate number of clusters to be produced, the Elbow method was computed using the function *fviz_nbclust* from the R-package *factoextra* (Kassambara and Mundt, 2020). These units were mapped to illustrate the species' adaptive landscape (for an example, see Capblancq, Morin, *et al.*, 2020).

Future predictions and genetic offset

The adaptive genetic units identified above were used to investigate the potential mismatch between their current distribution and that forecasted in the coming decades under predicted climatic conditions. We considered the MIROC-ES2L global climate models (GCM) and two shared socio-economic pathways (SSP), *i.e.,* SSP2-4.5 and SSP5-8.5), available for Worldclim 2 bioclim variables (Fick and Hijmans, 2017). The moderate SSP2-4.5 scenario corresponds to a "middle of the road" world where trends broadly follow their historical patterns, and the extreme SSP5-8.5 scenario corresponds to a world of rapid and unconstrained growth in economic output and energy use (Riahi *et al.*, 2017).

We projected the adaptive genetic indices estimated from the adaptively enriched RDA (see above) for the 2021-2100 time-period. To allow comparison between current and future environments, the values of future bioclimatic variables were standardized using the same standardization parameters (i.e., mean and standard deviation) previously used for the current

bioclimatic variables (see Breed *et al.*, 2019 for a similar approach). Each value was also weighted by the percentage of variance explained by each RDA axis. Based on RDA1 and RDA2 adaptive genetic indexes, each pixel of the bioclimatic raster was assigned to a cluster from the adaptive units defined in the present time. If future RDA scores were outside of the current RDA score range, the adaptive unit was assigned to a new group called 'Outsider'. In other words, the environmental conditions predicted for these locations were not experienced by Northern chamois within its current range, so we decided not to infer an optimal genetic composition for these climate conditions, because they were outside our model training space. Finally, we estimated the evolution of the spatial distribution of each of the chamois adaptive units in the Alps depending on different climatic scenarios, measuring changes in surface area and elevation for each adaptive unit over time.

In parallel to exploring spatial changes for each adaptive unit, we identified the regions that would be the most severely affected by a change in climatic conditions through the estimation of genetic offset (Fitzpatrick and Keller, 2015; Bay *et al.*, 2018; Capblancq, Fitzpatrick, *et al.*, 2020). Genetic offset, also known as genetic vulnerability, is defined here as a distance between the current and future optimal genetic compositions depending on the change between current and future climatic conditions. Therefore, genetic offset is a predictive measure of how much the distribution of locally adapted alleles will be perturbed by the shift between current and future environmental conditions (Fitzpatrick and Keller, 2015). We estimated a rate of adaptive score change for each climatic cell included in the current range of chamois in the Alps. To do this, we calculated the Euclidean distance between each cell's RDA score in the present and in the future. Only the first two axes (RDA1 and RDA2) of the adaptively enriched RDA were used for this estimation.

RESULTS

Global genetic variation

We conducted a discriminant analysis of principal components (DAPC) to characterize global genetic variation in Northern chamois (Figure 3B). At the highest hierarchical level (i.e., K=2), we observed genetic differentiation among individuals from the western and eastern Alps, with a transition located approximately along the France-Switzerland border (see "2 clusters" panel; Figure S10). From K=2 to K=6, there were additional genetic groups identified in the western Alps (i.e., from south-eastern France to eastern Switzerland), splitting the eastern Alps in two groups along a longitudinal gradient (Figure S10 with 6 clusters). Using the BIC criterion, we concluded that the most likely number of independent genetic clusters in the study area was four (see adaptive landscape section for details): two clusters in the western Alps, and two in the east. The genetic clusters are structured geographically, with the two most distant clusters on the first axis of the DAPC plot also the most distant across the Alps (i.e., clusters 3 and 4 in Figure 3B).

Variance partitioning

The full RDA model that included climatic variation, geography and genetic structure variables explained 12% of the total genetic variability (Table 1). The significant results from the four pRDAs showed that 37.4% of this explainable genetic variance was linked to climatic variation ($p < 0.001$), 6.2% was associated with geographic variation (geographic coordinates; $p < 0.001$), 11.0% was associated with overall genetic structure ($p < 0.001$), and 45.4% was not specifically attributable to any of these groups of variables. The high proportion of variance that was not attributable to specific predictors (i.e., confounded) suggested substantial covariation between environmental gradients, latitude and/or longitude and overall genetic variation across the species range. That result support the use of covariables to correct the GEA scans for the potential confounding effect of demographic history.

Genotype-environment association

The LFMM genome scan, using K=5 latent factors, retained 536 loci as outliers among the 20,904 SNPs tested (Figure S15). Those outliers were only associated with 7 of the 12

selected variables: Bio3, Bio4, Bio9, Bio15, Bio16, Bio17 and Bio18. Most of the outliers are associated with Bio9 (n = 214 outliers) and Bio18 (n = 354 outliers), which correspond to the mean temperature of the driest quarter and the precipitation of the warmest quarter, respectively (Figure S15). The RDA-based genome scan procedure retained 2205 loci as outliers (Figure S16). The intersection of the two outlier sets, i.e., the outliers that overlapped according the two approaches yielded 275 unique outlier loci. These 275 loci (out of 20,904 SNPs, i.e., 1.3% of all SNPs) were considered as markers of genomic regions putatively associated with environmental adaptation in Northern chamois.

Adaptive landscape

The adaptively enriched RDA was conducted using the 275 outlier SNPs (Figures S18 and S20). Most of the adaptive genetic variance was explained by the first two RDA axes (i.e., 46.6% and 24.38%, respectively; Figures 2A and S17). RDA1 was correlated with temperature seasonality (Bio4) and mean temperature of the warmest quarter (Bio10; Figure 2A). RDA2 was correlated with most of the environmental variables used in the analysis but principally with mean temperature of driest quarter (i.e., Bio9), and precipitation of the warmest quarter (i.e., Bio18; Figure 2A). We present allele and genotype frequency changes for the most significant association between outlier SNPs and climate variables in supplementary materials (Figures S18 to S21).

We extrapolated adaptive genetic turnover across the Alps and Dinaric Mtns by estimating RDA1 and RDA2 scores for the entire range of chamois in the study area (Figure 2). The RDA1 index seemed to represent an altitudinal gradient (Figure 2B). The RDA2 index mainly followed a latitudinal gradient with higher values in the south-east, south-west and western front of the Alps, and lower values in the central and north-eastern Alps (Figure 2C). We then used those two indices to delineate different adaptive units across the species distribution range (from two to six clusters, Figure S19). According to the clustering procedure, the most parsimonious number of clusters was four (Figure S20). South-eastern France and Croatia were always included in the same adaptive unit as a small

part in the Alps representing the Ticino region (cluster 1; Figure 3A). Similarly, Slovenia and the center

of Switzerland were grouped together (cluster 2; Figure 3A), grouping areas located between the

southern-western Alps (cluster 1; Figure 3A) and the northern Alps (clusters 2, 3 and 4; Figure 3A).

This latter area was also characterized by higher mean temperatures and mean precipitation of the

wettest quarter, low mean temperatures of the driest quarter and high mean precipitation of the

warmest quarter. The difference between clusters 2, 3 and 4 was mostly linked to altitudinal gradient

and temperature seasonality. Moreover, clusters 2 and 3 differed according to the mean precipitation

of the warmest and wettest quarters (i.e., Bio18 and Bio16, respectively; Table S3).

Global versus adaptive genetic unit delineation

We observed a clear distinction between global and adaptive genetic units (Figure 3): the

spatial distribution systematically differed between global and adaptive genetic clustering,

regardless of the number of clusters (Figures S10 and S22). Adaptive genetic units clustered

individuals associated with the same environmental conditions even if these were

geographically distant from one another, such as south-eastern France and Croatia (Figure

3A, Cluster 1), whereas global genetic units clearly group individuals from the same

geographic area (Figure 3B). Therefore, the most likely number of genetic units was four for

adaptive genetic variation (Figure S23), that we compare with the four global genetic units

obtained with all markers using DAPC. Even if the pRDAs highlighted an effect of geography

and past demographic history on chamois genetic variation, we were able to delineate multiple

genetic units associated with specific environmental conditions along the European Alps and

Dinaric Mountains.

Future predictions and genetic offset

The spatial projection of the four adaptive genetic units differed substantially depending on

the time-period and the SSP scenarios considered. Overall, and as expected, changes were

more substantial for the SSP5-8.5 than for the SSP2-4.5 scenario. For both scenarios, we

predicted an increase in mean habitat elevation for all four adaptive units by the end of the

century (Figure 4). The maximum difference between current and future elevations was 503 m, predicted for cluster 3 using SSP5-8.5, while the minimum difference was 124 m, predicted for cluster 1 for the SSP2-4.5 scenario (Table 2). We predicted an overall decrease in suitable habitat, especially for clusters 3 and 4 (Figure 4 and Table 2). Conversely, cluster 2 will expand its distribution, up to 94% according to the SSP5-8.5 extreme scenario (Figure 4 and Table 2). Approximately 30% of the study area will no longer be suitable according to our model based on SSP5-8.5 (Figure 5 and Table 2). These future unsuitable areas represent climatic conditions that are either not currently experienced by the chamois we sampled and thus may represent climatic combinations that are not suitable for the Northern chamois of the study area, or for which we lack information about the species adaptive potential.

Estimates of genetic offset calculated using the differences between current and future climates in species ranges, identified areas where important genetic changes (i.e., changes in allele frequency) would need to occur for populations to track climate change. Overall, Switzerland and Slovenia were the regions with the highest required adaptive change (Figure 6). Changes were widespread throughout the study area, but more pronounced in the Mediterranean region.

DISCUSSION

Evidence of association between genetic and environmental variation

Exploring the effects of environment, geography, and evolutionary history on Northern chamois genetic variation, we found that climatic factors played a significant role in driving population genetic differentiation. We identified putative signatures of selection linked to climate variation in the species genome, suggesting the presence of local adaptation across the global distribution of the species. According to our results, this adaptation seems to be mainly driven by temperature and precipitation during the summer months (i.e., mean temperature of the driest quarter and the precipitation of the warmest quarter). The Northern chamois exhibits physical, behavioral, and ecological adaptations to mountain life (Corlatti *et al.*, 2022) and is known to be particularly sensitive to heat during the spring-summer period, with important effects reported on life-history traits, directly or indirectly linked to fitness related traits (Rughetti and Festa-Bianchet, 2012; Mason, Apollonio, *et al.*, 2014). Summer temperatures are known to influence the physiology and behavior of many ungulates, from northern regions (van Beest and Milner, 2013) to the Mediterranean (Marchand *et al.*, 2015) and at high elevations (Semenzato *et al.*, 2021). Therefore, variability in chamois sensitivity to thermal stressors during summer may be due to genetic adaptation to the local environment. Similarly, signatures of local adaptation to cold environments have also been reported in the mountain goat *Oreamnos americanus* (Martchenko *et al.*, 2020). Analyzing the relationship between genetics and environment across the European Alps, we also detected a strong collinearity between environmental gradients, geographic distances and variables reflecting the recent evolutionary history of the species. The variance partitioning analysis identified that 46.6% of the explainable genetic variation was confounded among these three factors (Table 1) and it was not possible to totally differentiate their relative influence. It confirms the difficulty of entirely untangling the impact of the environment from the influence of past demographic processes and/or isolation by distance when exploring the drivers of intraspecific genetic variation (Frichot *et al.*, 2015; Capblancq and Forester, 2021).

We mapped the outlier loci found under putative selection for the environment against the well-annotated goat reference genome (*Capra hircus*, ID ARS1; BioSample: SAMN03863711) in the Ensembl project (https://www.ensembl.org/). We found that some of the outliers fell in the vicinity of genes involved in skin properties such as CDH2 which was also involved in local adaptation to climate in domestic goats (Alimperti and Stelios, 2015; Rochat and Joost, 2019). However, we must also acknowledge that our genotyping method – ddRAD sequencing – produced a reduced representation of the Northern chamois' large genome, which is probably ~2.5 Gbp long, similarly to close relatives (Martchenko *et al.*, 2020). Considering this genome size, the 20,9048,829 genotyped SNPs are, on average, 280,000 bp apart from each other. Such a low density of markers is not optimal to identify all the genes responsible for local adaptation (Lowry *et al.*, 2017b) but likely some of them, as described above. Genome-wide diversity, estimated using a genotyping-by-sequencing approach, was also found a good indicator for adaptive variation and for predicting evolutionary responses, and better than the population history reflected by the inbreeding level (Ørsted *et al.*, 2019). Overall, we believe our data were good enough to differentiate multiple SNPs putatively constrained (or linked to genomic regions putatively constrained) by selection for climate variations and then strongly differing from the neutral genetic pattern.

Identifying adaptive genetic units

Once the putative adaptive genetic component was identified, we were able to project the underlying genetic variation across the species range to characterize patterns of intraspecific adaptive divergence across the climate landscape (Steane *et al.*, 2014; Fitzpatrick and Keller, 2015). This type of approach is increasingly used to visualize spatial gradients of genetic turnover (i.e., changes in adaptive allele frequency) associated with local adaptation to climate (Bay *et al.*, 2018; Ruegg *et al.*, 2018). In Northern chamois, this turnover was mainly driven by variation in high temperature and low precipitation (i.e., high mean temperature of the driest quarter and low precipitation of the warmest quarter). The adaptive gradient differentiates southern from northern parts of the Alps, irrespective of longitude. We also found adaptive

variation to be related to a gradient of precipitation during the wettest quarter and temperature seasonality. Rochat and Joost (2019) already found adaptive alleles associated with precipitation of the warmest quarter in domestic goats (*Capra hircus*) from several breeds in Morocco and Europe, for genes related to properties of the cornea and skin, possibly conferring adaptations to drought conditions such as high UV-radiation.

When looking for coherent groups along these adaptive gradients we were able to delineate four adaptive genetic units that greatly differed from inferred global genetic populations. Most prominently, two populations, one from south-eastern France and the other from Croatia were grouped into the same adaptive unit while being 700 km apart from each other and assigned to two well-differentiated global genetic clusters, suggesting different evolutionary histories. These two populations most likely clustered together because they experienced a similar climate and were probably subject to similar selective pressures. Further analyses would help to determine whether this clustering is an example of parallel evolution or more likely result from past evolutionary history of adaptation and shared ancestral polymorphism among regions. Finally, additional investigations, probably with denser genomic data from an annotated reference genome would be required to determine if the same genes are involved in local adaptation in Northern chamois and to confirm the influence of bioclimatic variables on genetic divergence in mountain ungulates.

Future of the Northern chamois in the Alps

Major environmental changes are predicted by the end of the century, especially changes in temperature and precipitation (Hoegh-Guldberg *et al.*, 2018), with dramatic consequences on mountain ecosystems (Gobiet *et al.*, 2014; Hoegh-Guldberg *et al.*, 2018). Previous studies on alpine ungulates (e.g., the mountain goat; White *et al.*, 2018) and more specifically on chamois (Thuiller *et al.*, 2018; Lovari *et al.*, 2020) predicted an important contraction of the future distribution ranges. Using a species distribution model approach, Mason *et al.* (2014) predicted an elevational shift of 15 to 30 meters up-slope by the year 2100 for chamois in the Gran Paradiso National Park, in Italy. However, using an integrative approach, Thuiller *et al.*

(2018) found that the inclusion of biotic interactions in species distribution models (*i.e.,* plant resources) produced more optimistic predictions than models based on climate only. Using the relationship between intraspecific genetic variation and climate, we went a step further than previous models and predicted a shrinking of the range for all but one adaptive unit, together with an elevation shift towards higher altitudes. By the end of the 21st century, the mean elevation inhabited by all four adaptive units of chamois is predicted to rise, on average, by 200 m. This altitudinal shift is also predicted to lead to the disappearance of the adaptive unit already living at high elevation.

By including intraspecific genetic variation in future projections, we were able to evaluate the impact of climate change on local adaptation equilibrium in Northern chamois. Overall, the integration of adaptive variation into predictive models may improve our estimation of species dynamics under scenarios of environmental changes (Waldvogel *et al.*, 2020). Interestingly, in Northern chamois, it is not the Mediterranean region that is predicted to experience the strongest disruption of the adaptive equilibrium (i.e., genetic offset), but the central part of the species range, in Switzerland and Slovenia. Potentially because population in these areas currently have intermediate allele frequencies but will have to specialized toward the warmer end of the adaptive gradient in the future. The genetic offset metric is very complementary to the projection of shift in distribution of adaptive genetic units. Indeed, change in the distribution of adaptive units showed their future optimal location based on current genetic adaptation, while genetic offset highlighted the location where extreme adaptive genetic changes would be required to track the change in climate. In that sense, even where genetic offset is low, the future climate can be beyond the adaptive range of the current units (e.g., south-eastern France or Croatia). On the other hand, a high estimate of genetic offset for a particular unit could result in its replacement by another genetic group when such a group is already present nearby (i.e., central Switzerland).

Our results also suggest that the Northern chamois is currently genetically adapted to environments that are predicted to be no longer available in the future (by 2100), especially at higher elevation (> 1000 m; see Figure 5). Conversely, at lower elevation (< 800 m), our model

predicted a change in environmental conditions that would push the climate conditions beyond the adaptive space currently occupied by the species, potentially making these areas climatically unsuitable for Northern chamois in a near future. It is important to note here that this result does not necessarily mean that the Northern chamois will go extinct at low elevation, but we are currently unable to infer genome-environment association for climatic conditions that the samples we considered in this study does not currently experience. Depending on the predicted scenario, these unsuitable climatic areas represent up to approximately 50% of the chamois current distribution range across the Alps (*e.g*, for the SSP5-8.5 scenario). The lower elevation areas, especially Mediterranean areas such as south-eastern France and Croatia, would be the most impacted and populations would require strong genetic change (*i.e.*, change in allele frequency) to cope with future climatic conditions. Because our projections are relatively short term (i.e., 60 to 80 years), and considering the comparatively long generation time of Northern chamois (i.e., ~6 years; Loison *et al.*, 1999b), beneficial mutations may not arise for evolutionary rescue (Bell, 2013) and spread fast enough to enable the populations to adapt to the changing climates (Barrett and Schluter, 2008), although adaptation may still be possible in such a short period of time, if sufficient standing genetic variation (SGV) is already present in the populations (Epstein *et al.*, 2016; Lai *et al.*, 2019; Bitter *et al.*, 2019). Interestingly, Roques (2021) has shown that the areas that were predicted to experience the most marked changes here (i.e., south-eastern France) are also those with the highest global genetic diversity, giving some raw material for selection to filter and shape new patterns of adaptive variation.

Although our models can explore the current climatic niche of the species using observable adaptive variability and predict its potential future disruption, we cannot predict to what extent the species will react to these changes. In particular, the dispersal capacities of chamois could help them track suitable climates over long distances and behavioral changes could locally mitigate the impact of global warming. Our predictions also suffer from potential shortcomings. Firstly, we did not assess the strength of the relationship between adaptive genetic variability and environment, and its quantitative effects on Northern chamois fitness.

Validating the negative correlation between genetic offset and fitness is critical to do in the future if one wants to use such framework to inform conservation. That would require acquiring more data on fitness related traits and potentially set up common garden experiments (Browne *et al.*, 2019; Fitzpatrick *et al.*, 2021), which is not easily done with wild large mammals. Secondly, the current spatial distribution of Northern chamois across the Alps is also influenced by past and current human activities, such as hunting, farming, tourism, and habitat fragmentation, which may have pushed the species towards higher elevations during the last millennia, as well as other components of the environment including topography and edaphic factors, and not only climate. This could have artificially reduced the extent of the species' realized climatic niche that we can measure and led to missing a section of the adaptive gradient with our models. For example, the species occupied low to mid-altitude mountain areas of Western Europe, e.g., in the Jura Mountain, the Vosges Mountain, the Massif Central (Corlatti *et al.*, 2022), and, the species appears to be continuously expanding its range into the lowlands and forested habitats, e.g., in France (Deinet *et al.*, 2013) and also in Poland/Slovakia (Ciach and Pęksa, 2019), suggesting that the species can quickly adapt to warmer habitats by moving into forests. Thirdly, the Northern chamois has already evolved behavioral strategies to cope with climate fluctuations and resource availability, such as seasonal vertical migration to avoid heat stress (Papaioannou *et al.*, 2015). In this study, we did not consider the ability of the species to react to environmental change via plastic responses, which could possibly mitigate our evolutionary predictions, especially at low elevations (Chirichella *et al.*, 2021). Indeed, recent investigations suggest that the future of chamois will not only depend on how the species adapts to changing climatic conditions, but also on the plasticity of the species (e.g., Reiner *et al.*, 2021), in relation to a range of factors, e.g., climate change (Lovari *et al.*, 2020), resource availability (Thuiller *et al.*, 2018), competition (Corlatti *et al.*, 2019) or even disease outbreaks (Rossi *et al.*, 2019).

Conservation and management implications

Identifying adaptive units can be directly applied to the planning and execution of conservation and management programs (e.g., Flanagan *et al.*, 2018; Hoban *et al.*, 2020). For example, if translocations are used to restore or reinforce populations, considering source populations belonging to the same adaptive unit would help prevent the introduction of maladapted individuals and the deleterious effect of outbreeding depression (Aitken and Whitlock, 2013). In that sense, landscape genomics is a promising framework for translating knowledge of global and adaptive genetic diversity into guidelines for conservation policy and management strategies (Hohenlohe *et al.*, 2021). However, it is quite difficult in practical situations to use continuous proxies of adaptation such as the ones presented in Figure 3. Often, it is more efficient to delineate discrete units of management, based on neutral genetic variation in the field of conservation (Funk *et al.*, 2012) or seed or breeding zones in forestry (O'Neill and Aitken, 2004). Here we propose what we believe is the first use of RDA to delineate such types of units and a framework to identify adaptive genetic groups within a species. Although, Fernandez-Fournier *et al.*, (2021) recently questioned the need to "identify adaptive genetic variation when prioritizing populations for conservation" considering standing genetic variation can be used as a proxy for the adaptive genetic variation, Funk *et al.*, (2012) and others (Hohenlohe *et al.*, 2021) stressed the necessity to use both global and adaptive markers to make optimal management decisions (e.g., see Barbosa *et al.*, 2018 for an empirical application). We believe that information on species' evolutionary potential offers important new insights that can help refining conservation strategies and management policies (Borrell *et al.*, 2020; Hohenlohe *et al.*, 2021). It is worth noting, however that, in practice, in a rapidly changing and uncertain environment, we cannot totally rule out the importance of considering genome-wide genetic variation as an indicator of evolutionary potential in management strategies (Flanagan *et al.*, 2018; Fernandez-Fournier *et al.*, 2021; Hoban *et al.*, 2022), because the foundations of adaptive variation are complex and not fully understood, it is currently impossible to make a definitive dichotomy between adaptive and neutral variation (Harrisson *et al.*, 2014).

One management action that is gaining interest recently is the translocation of pre-adapted individuals to either genetically reinforce populations that will suffer from climate change - assisted gene flow - or colonize a previously unoccupied habitat that became suitable since the climate started to change - assisted colonization (Aitken and Whitlock, 2013; Aitken and Bemmels, 2016; Browne *et al.*, 2019; Segelbacher *et al.*, 2022). As far as we know, such actions have not yet been implemented in nature, but they could facilitate the establishment of adaptive alleles and help species with long generation times or low dispersal capacities to adapt to future climatic conditions. (Rellstab *et al.*, 2016; Capblancq, Fitzpatrick, *et al.*, 2020; Seaborn *et al.*, 2021). It should be noted that other studies have warned of the risks and limitations of assisted migration in conservation management (Park and Talbot, 2012; Montwé *et al.*, 2018). Translocation and reintroduction programs are already common management strategies for chamois throughout its range (Soorae, 2010; Apollonio *et al.*, 2014), without any consideration of their genetic composition, and even more their adaptive genetic background. The results of the present study can help refine the selection of individual genotypes for management programs and maximize future reintroduction success.

CONCLUSIONS

Using a combination of landscape genomic approaches, our study sheds light on the association between genetic and climate variation in a mountain ungulate, the Northern chamois, across the European Alps and the Dinaric Mts. We developed an approach that makes use of RDA to identify adaptive groups from genetic and climatic data and allow us to spatially investigate the potential response of the species to future climate changes. Our projections highlight that genetic change could be required in Northern chamois populations to be able to track climate change, especially if they cannot easily disperse, although the species may also take advantage of its behavioral plasticity to adapt to such changes. Current adaptive units are predicted to undergo a major shift in distribution, both spatially (a decrease

in area and a change in location) and altitudinally, and some populations will need to adapt to new climate conditions. Considering our results, accounting for intraspecific adaptive genetic variation in management strategies appears important for future conservation efforts (Aitken and Whitlock, 2013; Hoffmann *et al.*, 2021), and our approach could be a pertinent tool for such purpose.

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Author contributions

GY and LP coordinated the project. GY and TC designed the study and supervised AH. EB, LC, BC, HCH, and NS contributed to the sample collection. TB and GY performed the bioinformatic analysis. AH analyzed the data with TC and GY. AH, TC, and GY interpreted the results with contribution from TB, CP, and LD. AH, TC and GY wrote the manuscript with comments and editing of all authors. The final version of the manuscript has been read and approved by all authors.

Competing Interests. The authors declare that they have any competing financial interests in relation to the work described.

Data Archiving. Raw reads are available under the NCBI bioproject "PRJNA813419" (Accession number for BioSamples: SAMN26501511 - SAMN26502071 and SRA: SRR18252263-SRR18252823).

Additional information. Supplementary information are available on Heredity's website

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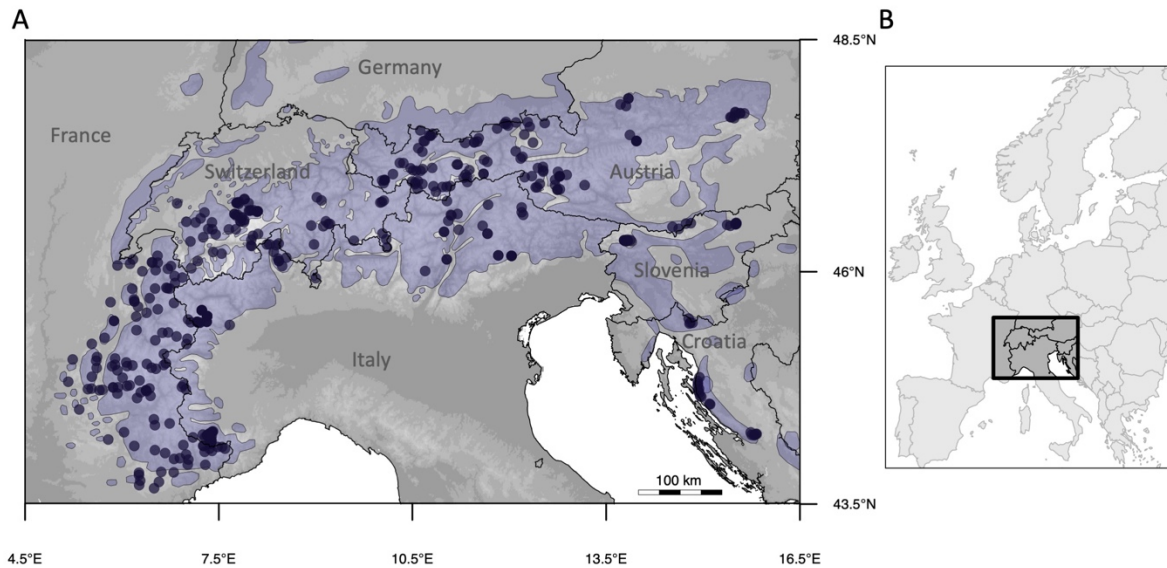
Figures

Figure 1. (A) Northern chamois sampling (n=429) in the Northern chamois distribution range along the Alps and Dinaric Mts. The bluish contours on the map show the contemporary distribution range of Northern chamois (Anderwald et al., 2021). (B) Location of study area in Central Europe. Black lines on the maps correspond to the country borders. The m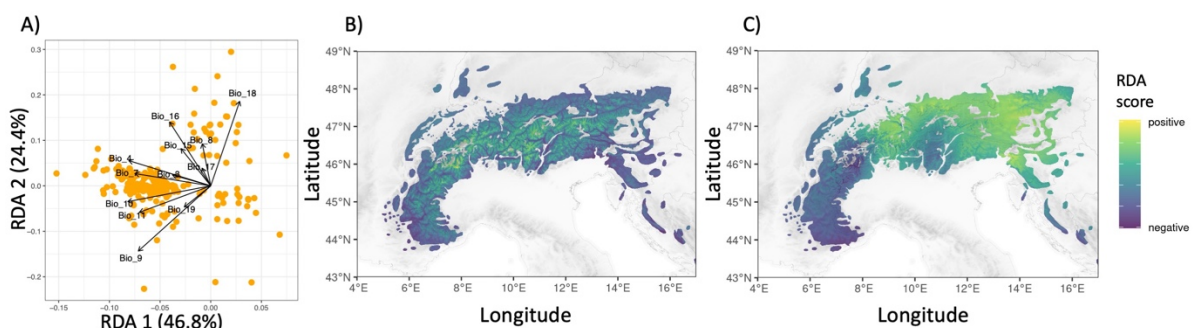aps are projected in the world geodetic system 1984 (WGS 84) Black lines on the maps correspond to the country borders. The maps are projected in the world geodetic system 1984 (WGS 84).

Figure 2. (A) Projection of bioclimatic variables (in black) and outlier SNP markers (in orange) into the adaptively enriched genetic RDA space and (B, C) spatial extrapolation of RDA1 and RDA2 gradients, respectively, in the Northern chamois distribution range along the Alps and Dinaric Mts for the current climatic conditions. See Table S3 for a description of the bioclimatic variables.
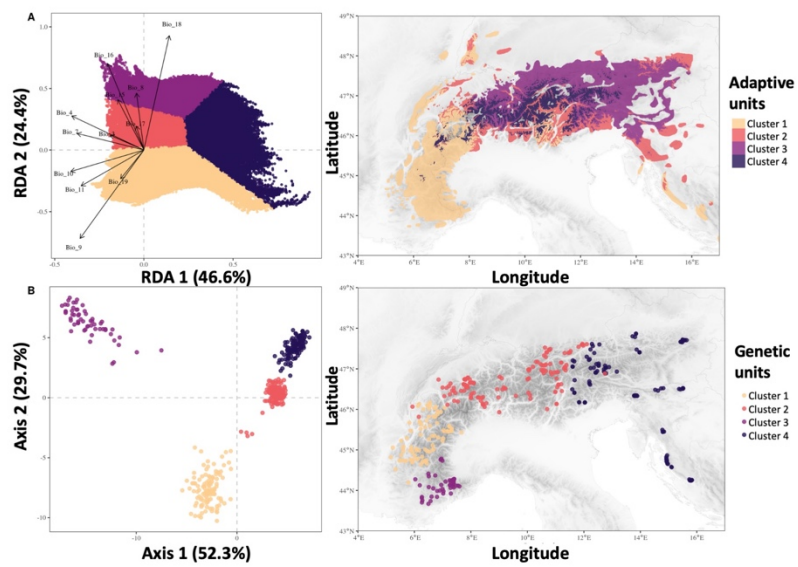
Figure 3. (A) the four adaptive units delineated in the adaptively enriched RDA genetic

space (left) and spatially mapped (right) across the species distribution range, and (B) the

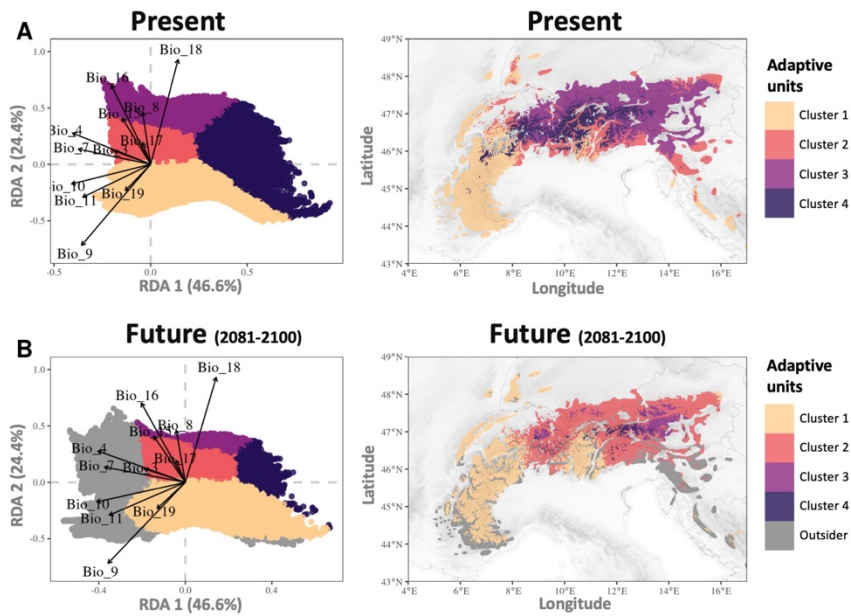four evolutionary significant units defined by the DAPC (left) and spatially mapped (right),

Figure 4. Representation of the four adaptive genetic units across the current distribution range of Northern chamois along the Alps and Dinaric Mts. (A) in the present and (B, C) in the future (2081-2100) for the SSP5-8.5 scenario. The left panels show the projection into the adaptively enriched RDA space (and the right panels show the same on a map of the Alps and Dinaric Mts. In gray, the new group called "Outsider" depends on a bioclimatic gradient which does not currently exist meaning it is outside the current adaptive range observed for Northern chamois.
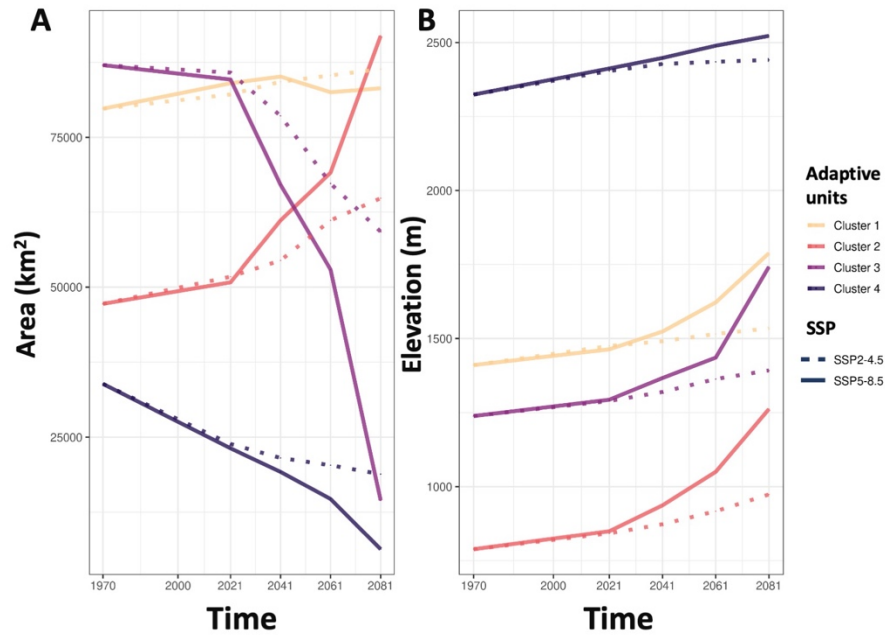
Figure 5. (A) Surface area change and (B) mean elevation shift of the four adaptive genetic clusters over time from 1970 to 2100 according the two scenarios SSP2-4.5 and SSP5-8.5.
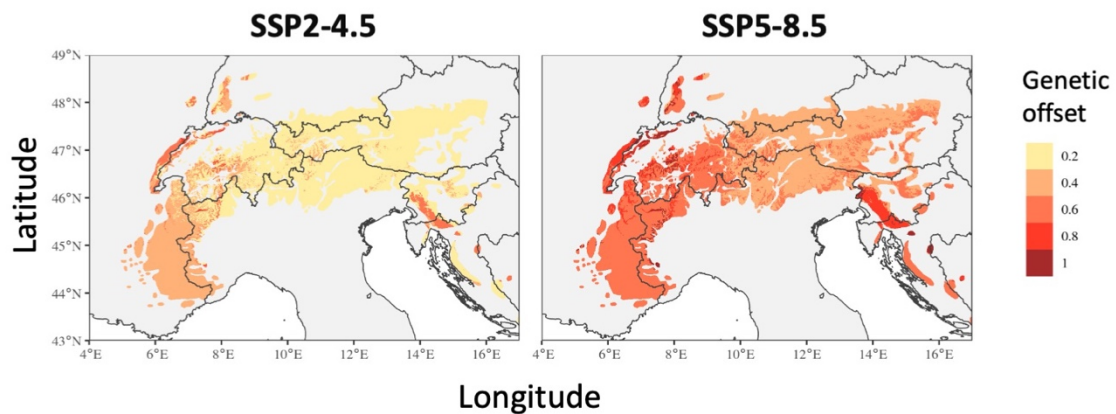

Figure 6. Representation of genetic offset between current and future climatic conditions for the two scenarios SSP2-4.5 and SSP5-8.5 for Northern chamois along the Alps and Dinaric Mtns.

1   **Table 1.** Decomposition of the influence of climate (i.e., *clim*.), geography (i.e., *geo*.) and

2   global population genetic structure (i.e., *anc.*) on genetic variation using partial redundancy

3   analyses. For each model, we calculated its statistical significance, the percentage of

4   explained genetic variance compared to the variance explained by the full model and

5   compared to the total variance present in the data set.

Partial RDA models	Inertia	R^2	P(>F)	Proportion of explainable variance	Proportion of total variance
Full model : F ~ clim. + anc. + geo.	208.01	0.118	0.001***	1.00	0.118
Pure climate : F ~ clim. | (anc. + geo.)	77.84	0.044	0.001***	0.374	0.044
Pure geography : F ~ geo. | (anc. + clim.)	12.84	0.007	0.001***	0.062	0.007
Pure ancestry : F ~ anc. | (geo. + clim.)	22.90	0.013	0.001***	0.110	0.013
Confounded climate/geography/ancestry	94.43			0.454	0.054
Total unexplained	1553.18				0.882
Total inertia	1761.19				1.000

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7

8   **Table 2.** Changes in the area and elevation for each adaptive genetic unit from 1970-2000 to

9   2081-2100. The group called "Outsider" corresponds to individuals predicted to occupy

10   bioclimatic gradient which does not currently exist, meaning it is outside the current adaptive

11   range observed for Northern chamois in the study area.

12

SSP	Cluster	Area change range rate (%)	Elevation difference (m)
	Cluster 1	8.28	124.1
	Cluster 2	37.27	185.18
SSP2-4.5	Cluster 3	-31.94	154
	Cluster 4	-44.39	116.95
	Outsider	326.65	184.63
	Cluster 1	4.28	377.46
	Cluster 2	94.67	473.27
SSP5-8.5	Cluster 3	-83.38	503.45
	Cluster 4	-81.39	198.09
	Outsider	880.33	302.82

13