



# Same landscape, different connectivity: contrasting patterns of gene flow in two sympatric ungulates in a mountain area

Roberta Lecis<sup>1</sup> · Roberta Chirichella<sup>2,5</sup> · Olivia Dondina<sup>3</sup> · Valerio Orioli<sup>3</sup> · Silvia Azzu<sup>1</sup> · Antonio Canu<sup>1</sup> · Elisa Torretta<sup>4</sup> · Luciano Bani<sup>3</sup> · Marco Apollonio<sup>1,5</sup> · Massimo Scandura<sup>1,5</sup>

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## Abstract

Comparative landscape genetics studies provide insights on the impact of landscape elements on gene flow patterns of different species inhabiting the same geographic area. We investigated the population genetic structure of two sympatric ungulates, roe deer *Capreolus capreolus* and Northern chamois *Rupicapra rupicapra*, in a mountain area of the central Italian Alps (Trentino, northern Italy). A total of 122 chamois and 72 roe deer samples were genotyped by two species-specific panels of 11 polymorphic microsatellite loci and analyzed by aspatial and spatially explicit analyses. While the roe deer population resulted unstructured, a clear population structure was detected in chamois, with two main groups, one inhabiting the eastern and the other spread in the western part of the study area. Landscape genetics analysis confirmed these scenarios and revealed a different effect of landscape on gene flow. An IBD (Isolation-By-Distance) model best explained genetic variation in roe deer, while IBR (Isolation-By-Resistance) was found as the process underlying genetic variation patterns in chamois, suggesting arable lands, coniferous forests, watercourses, and main roads as potential barriers. Species distribution and landscape use might explain these results: roe deer mostly occupy valley floors relatively connected to each other, and their spatial behavior may promote gene flow across areas. On the other hand, chamois prefer higher elevations and their movements may be hindered by valleys, rivers, and road networks. This study highlights the different impacts of natural and anthropic landscape elements on gene flow in two sympatric species, resulting from their different ecological requirements.

**Keywords** Alps · Gene flow · Landscape genetics · Northern chamois · Population structure · Roe deer

## Introduction

Landscape genetic analyses integrate ecology, spatial statistics, and population genetics to develop and assess predictions about the effect of landscape features on animal movements and gene flow, and to identify environmental elements

potentially acting as barriers and generating genetic discontinuities (Manel et al. 2003; Storfer et al. 2007). Landscape genetic studies could be particularly helpful to inform the management and conservation of different species/populations, including wild ungulate species, in a wide variety of situations (Segelbacher et al. 2010; Shafer et al. 2012; Portanier et al. 2018; Lecis et al. 2022). Besides a rich literature of landscape genetic studies focused on single taxa (e.g., Storfer et al. 2010; Keller et al. 2014; Richardson et al. 2016), comparative studies on distinct species inhabiting the same environment and/or geographic area have become more common (Olsen et al. 2011; Kierepka et al. 2016; Burkhart et al. 2017; Emel et al. 2019), providing interesting insights on different species' interactions with landscape that can lead to contrasting patterns of genetic connectivity.

Landscape might similarly influence the spatial distribution of genetic diversity in closely related and geographically overlapping species (Olsen et al. 2011). However, it is not predictable how connectivity relates to site-specific

✉ Roberta Lecis  
rlecis@uniss.it

<sup>1</sup> Department of Veterinary Medicine, University of Sassari, Via Vienna 2, 07100 Sassari, Italy

<sup>2</sup> Department of Humanities and Social Sciences, University of Sassari, Via Roma, 07100 Sassari, Italy

<sup>3</sup> Department of Earth and Environmental Sciences, University of Milano Bicocca, Piazza Ateneo Nuovo, 20126 Milan, Italy

<sup>4</sup> Department of Earth and Environmental Sciences, University of Pavia, Via Ferrata 1, 27100 Pavia, Italy

<sup>5</sup> National Biodiversity Future Center (NBFC), Palermo, Italy

conditions, and similar organisms may respond in a different way to the same landscape. For instance, three species of *Ambystomatid* salamanders showed different genetic structures in response to habitat fragmentation in USA (Whiteley et al. 2014), a motorway in Belgium was found to represent barrier to gene flow for red deer *Cervus elaphus* but not for wild boar *Sus scrofa* (Frantz et al. 2012), and different species–landscape interactions were described when analyzing two syntopic frog species in China (Garcia et al. 2017) and two closely related but ecologically distinct newt species in Poland (Antunes et al. 2022). Landscape effects on gene flow can thus sometimes differ strongly even among related sympatric species.

The Northern chamois (*Rupicapra rupicapra*, Linnaeus 1758) is an alpine ungulate inhabiting Europe and the Near East, with a typical range from 300 to 2500 m above sea level (a.s.l.) (Corlatti et al. 2022). In the past century, the species has been generally affected over most of its range by overhunting and consequent decline, although it now appears recovered and is widespread in the Alps (Buzan et al. 2013, Corlatti et al. 2022). Populations tend to be separated by low valleys, especially when these are impacted by human activities; however, they do not always represent barriers to chamois movements (Loison et al. 1999; Safner et al. 2019). Landscape genetic studies have been recently conducted on this species: Soglia et al. (2010) found three main clusters and genetic differences among chamois sampled over the Italian Alps, while Buzan et al. (2013) identified four geographically associated clusters in Slovenia and detected genetic isolation in some small populations. More recently, Leugger et al. (2022) described two main clades in the Alpine chamois population corresponding to south-western and eastern Alps, and limited connectivity in combination with large rivers or valleys acting as barriers to dispersal.

The European roe deer (*Capreolus capreolus*, Linnaeus 1758) is the most widespread ungulate species in Europe, inhabiting various ecosystems from the Mediterranean to Scandinavia, in a range between sea level and 2000 m a.s.l. (Lorenzini et al. 2022). At the beginning of the last century, the species was almost extinct in different European regions, but has subsequently recovered almost everywhere (Apollonio et al. 2010). Among the landscape genetics studies recently conducted on this species, Zannè et al. (2006) combined spatial and microsatellite analysis with animal morphology to define management units within the roe deer population in north-eastern Italy identifying two main regions, while Coulon et al. (2006) found that a combination of several landscape features with low permeability such as highways and rivers led to roe deer population differentiation in south-western France. Breyné et al. (2014) detected distance and infrastructure effects on Belgian roe deer populations, and Hepenstrick et al. (2012) identified

fenced freeways as the main obstacles to gene flow in roe deer in Switzerland.

The two species are widespread over the Italian Alps. Chamois are represented by populations with varying densities, and in Trento province (covering around 6,200 km<sup>2</sup>), a total of 29,810 heads were estimated in 2020 (Provincia Autonoma di Trento Dipartimento Risorse Forestali—official data 2020). Roe deer inhabit most of central and northern Italy, after recovering due to natural dispersal and re-introductions (Apollonio et al. 2010; Lecis et al. 2023). In Trento province, a total of 35185 individuals were estimated in 2020 (Provincia Autonoma di Trento Dipartimento Risorse Forestali—official data 2020). These two ungulates have different ecology, land use, and altitude preferences, with chamois ranging at higher altitudes, forest, steep and rocky terrains, and roe deer usually inhabiting a wider range of habitats including woods and pastures. Italian Alps, and specifically the study area, are characterized by natural and artificial elements which can restrict species movements, such as topography, roads, valley urbanization, and fences used in agricultural practices.

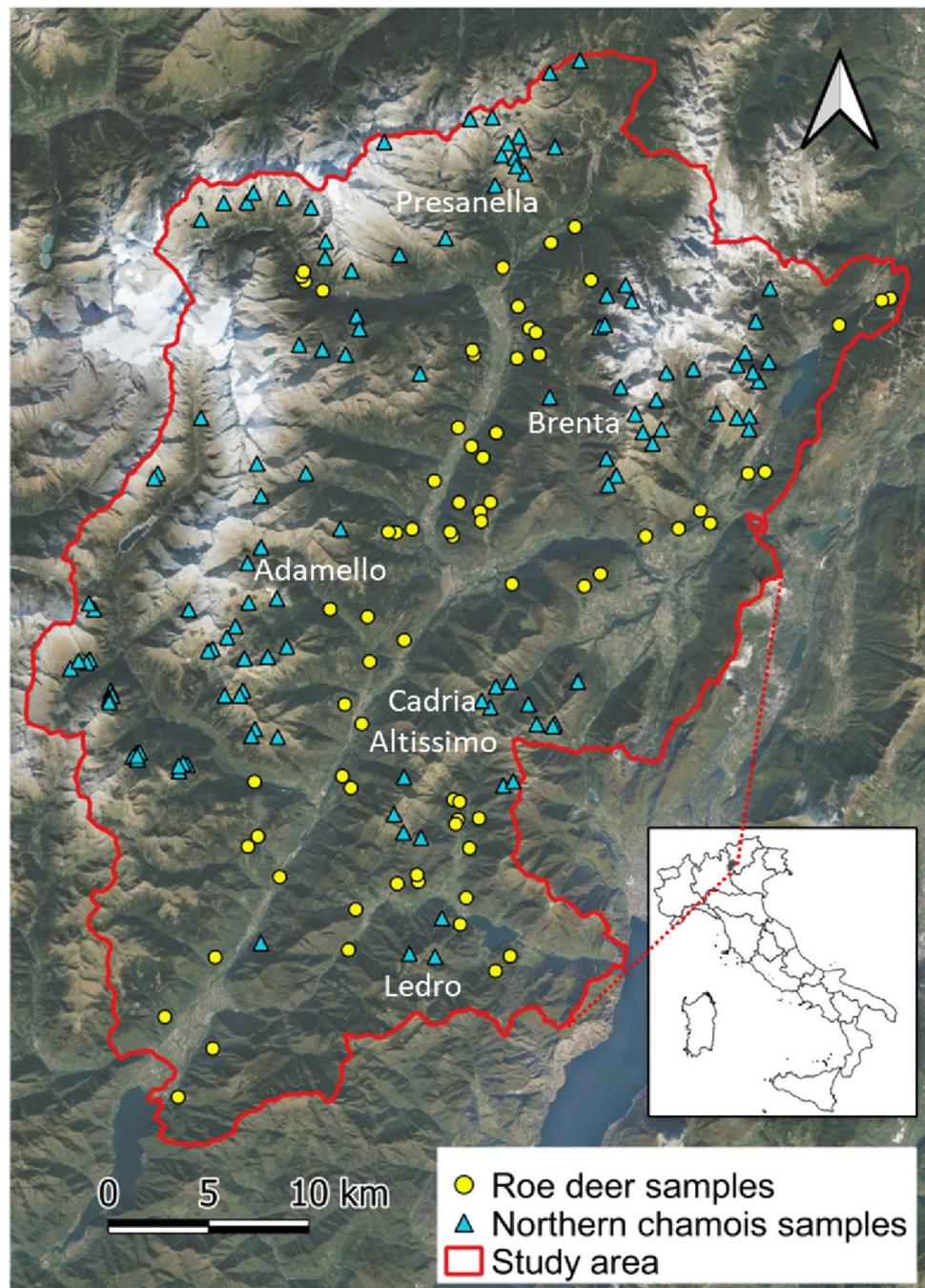
Herein, we apply a comparative landscape genetic approach to two sympatric populations of Northern chamois and roe deer in an Alpine area, with the following objectives: (i) to estimate levels of genetic diversity and test for past bottlenecks in both populations, (ii) to assess the population genetic structure of the two species in the area, and (iii) to investigate spatial patterns and identify the effect of barriers or landscape connectivity on gene flow in both species.

## Materials and methods

### Study area and sample collection

The study site is represented by the western part of Trento province, in the east-central Italian Alps. The area includes the Adamello-Presanella and Brenta massifs in the north and Mt. Cadria-Altissimo and Ledro Alps in the south (Fig. 1). The northern part of the study site is occupied by the Adamello Brenta Natural Park. Climate is transitional between semi-continental and alpine, average temperatures range between −5 and −10 °C in January and 20–25 °C in July (Chirichella et al. 2020). Elevation ranges from 65 to 3550 m a.s.l. (Presanella Massif). The study site, covering 1366 km<sup>2</sup>, is represented by a typical montane habitat, with more than 60% of the area above 1000 m a.s.l., and covered by forests (51% of the entire study area, among which 45% coniferous forests, 42% mixed forests, and 13% broad-leaved forests), shrubs (10%), meadows (8%), and rocky outcrops (21%). Two main rivers cross the area: Chiese and Sarca, and the region is characterized by a rich diversity of flora and fauna. Apart from Northern chamois and roe deer, red deer (*Cervus elaphus*) are abundant but seldom use the areas above the tree line (2000 m a.s.l.). European

**Fig. 1** Study area in Trentino (Italy) and sampling sites (72 roe deer—yellow circles—and 122 chamois—blue triangles)



mouflon (*Ovis gmelini musimon*) and Alpine ibex (*Capra ibex*), which potentially use chamois habitat, are limited to few locations, having been introduced and reintroduced in the recent past only. Potential terrestrial predators include a stable population of brown bears (*Ursus arctos*), a small number of lynx (*Lynx lynx*), and occasionally wolves (*Canis lupus*; Groff et al. 2023). The golden eagle (*Aquila chrysaetos*; Pedrini et al. 2005) might rarely predate upon juveniles and is present in the area (Adamello Brenta Nature Park 2011). Rendena valley divides the study area in a NE-SW

direction, separating western (Adamello, Presanella) from eastern massifs (Brenta, Cadria-Altissimo, Ledro). An orographic barrier might be represented by Canyon Limarò, between Cadria-Altissimo massif and Brenta Dolomites. Roads and linear infrastructures, urban settings along the valleys, fences used in agricultural practice, and human-exploited land are among the main potential landscape barriers found in this area (see Fig. S1).

The study site includes seven Northern chamois management areas (Adamello, Destra Chiese, Presanella, Brenta,

Cadria-Altissimo, Misone-Casale, and Ledro) and four roe deer management districts (Chiese, Ledro, Rendena, Giudicarie), as well as a total of 90 hunting reserves. For the purpose of this study, a total of 122 chamois samples were collected between 2010 and 2015, while 72 roe deer samples were gathered during the 2011 hunting season (Fig. 1). Sampling was designed to be as representative as possible of local population distribution for both species. All samples consisted of ear tissue stored in absolute ethanol and at  $-20^{\circ}\text{C}$  until the analysis.

### Microsatellite amplification and genotyping

DNA extraction was performed using GenElute Mammalian Genomic DNA Miniprep Kit (Sigma), following the manufacturer's instructions. Roe deer samples were analyzed with a panel of 11 polymorphic autosomal microsatellites (Roe01, Roe06, Roe08, Roe09, NV16, NV21, NV24, RT1, ILSTS011, FCB304, BMC1009, Fickel and Reinsch 2000), amplified in three multiplex PCRs (multiplex 1A: Roe01, Roe08, Roe09; multiplex 2A: RT1, BMC1009; multiplex 1B: Roe06, ILSTS011), and the remaining loci in four simplex PCRs (NV16, NV21, NV24, FCB304) (Biosa et al. 2015; Lecis et al. 2023). Chamois samples were also genotyped at 11 microsatellite loci (ILSTS05, ILSTS011, BMC1009, FCB304, SRCRSP05, SRCRSP08, SRCRSP09, ETH10, ETH225, INRA05, INRA11, Arevalo et al. 2009). Three multiplex reactions were developed to amplify 9 loci (multiplex 1: ILSTS05, INRA05, SRCRSP08, SRCRSP09; multiplex 2: FCB304, SRCRSP05; multiplex 3: INRA11, ETH10, ETH225), and the remaining 2 loci (ILSTS011, BMC1009) were amplified independently. PCR conditions are reported in Supplementary Material (Tables S1 and S2).

PCR products were analyzed by BMR Genomics (Padova, Italy) using capillary electrophoresis on an ABI PRISM 3130xl Avant automatic sequencer (Applied Biosystems). Allele size was determined by analyzing electropherograms in Peak Scanner 1.0 software (Applied Biosystems).

### Genetic diversity and population structure

Micro-Checker 2.2.3 (Van Oosterhout et al. 2004) was used to detect evidence of null alleles, stuttering, or large allele dropout. Microsatellite genotypes were then analyzed in GenAlex v.6.5 (Peakall and Smouse 2012) to calculate observed heterozygosity ( $H_o$ ), expected heterozygosity ( $H_e$ ), mean number of alleles per locus ( $k$ ), inbreeding coefficient ( $F_{is}$ , 1000 permutations), and to calculate  $F_{st}$  indexes in both populations. We used SPAGeDi (Hardy and Vekemans 2002) to compute pairwise relatedness (Rousset's  $a_r$ ) in both species. Genepop v. 4 (Raymond and Rousset 1995) was implemented to assess deviations from Hardy-Weinberg equilibrium (HWE) and from linkage equilibrium (LE), using

10,000 dememorizations, 50 batches, and 10,000 iterations per batch in both tests. Sequential Bonferroni corrections for multiple comparisons were used to find significance levels. Evidence of recent effective population size reductions was investigated using the program Bottleneck V.1.2.02 (Piry et al. 1999), to test whether local *C. capreolus* and *R. rupicapra* populations showed an excess of heterozygosity, as expected after a recent bottleneck. The test was performed under a two-phase mutation model (TPM with 95% SMM, step mutation model), assessing significance by the Wilcoxon sign-rank test.

Population genetic structure was analyzed by Bayesian clustering and assignment tests implemented in Structure 2.3.4 (Pritchard et al. 2000; Falush et al. 2003) for both species, in order to identify the most likely number of genetic clusters within both datasets. Our results were based on simulations from 1 to 10 inferred populations ( $K=1-10$ ), and the following settings were applied for both species: admixture ancestry model, no population information, correlated allele frequencies, 200,000 burn-in, and 200,000 subsequent iterations of data collection. Results were summarized and the best  $K$  value was calculated using the  $\Delta K$  approach developed by Evanno et al. (2005) in Structure Harvester (Earl and VonHoldt 2012) to identify the best clustering solution. We employed Pophelper (Francis 2017) to edit Structure results and produce the final plots. GenAlex was used to assess genetic differentiation across samples by principal coordinate analysis (PCoA) and to examine micro-geographic patterns of genetic structure by spatial genetic autocorrelation analysis. The latter was based on matrices of pairwise inter-individual genetic distances and pairwise topographic distances estimated by the program. Up to five different distance classes of relatively even sample size were selected, and 95% confidence interval was estimated by 999 permutations.

### Landscape genetics analyses

A landscape genetics approach was used to test the effect of Isolation-By-Distance (IBD) and Isolation-By-Resistance (IBR) on the genetic variation patterns of the roe deer and chamois populations in the study area. We parametrized landscape resistance by simultaneously optimizing multiple categorical and continuous surfaces through the genetic algorithm implemented in the R package ResistanceGA (Peterman 2018). Based on species ecology, we tested the effect of two categorical (land cover and main roads) and three continuous (elevation, slope, and snow cover) surfaces on chamois and roe deer gene flow. The land cover surface (500×500-m pixel resolution) was obtained by overlapping the Trentino digital forest map ([http://www.territorio.provincia.tn.it/portal/server.pt/community/portale\\_geocartografico\\_trentino/254/portale\\_geocartografico\\_trentino/18994](http://www.territorio.provincia.tn.it/portal/server.pt/community/portale_geocartografico_trentino/254/portale_geocartografico_trentino/18994)) over the Corine Land Cover

2018 (<https://land.copernicus.eu/pan-european/corine-land-cover/clc2018>). The original land cover classes at the 4th CLC level were reclassified into ten categories: urban areas, arable lands, mixed broadleaved forests, beech forests, coniferous forests, meadows and pastures, transitional vegetation, rocky areas, glaciers, water bodies. The road surface was obtained from OpenStreetMap (OpenStreetMap contributors 2023) rasterized at a 500×500-m resolution map where cells crossed by roads had a value equal to 1 while all other cells had a value equal to 0. Elevation and slope surfaces were derived from the Digital Elevation Model of Trentino ([http://www.territorio.provincia.tn.it/portal/server.pt/community/portale\\_geocartografico\\_trentino/254/](http://www.territorio.provincia.tn.it/portal/server.pt/community/portale_geocartografico_trentino/254/) portale\_geocartografico\_trentino/18994) resampled at a 500×500-m pixel resolution. Finally, the snow cover surface was obtained by averaging the maximum snow cover over the period 2000–2015 (Hall and Riggs 2021). The optimization process proceeds by calculating pairwise ecological distances from alternative single or composite resistance surfaces and by regressing genetic against ecological distances and fitting linear mixed-effects models with a maximum likelihood population effects parameterization (MLPEs) (Peterman 2018). Optimization is repeated until the best model is found, according to parametrization of the genetic algorithm and a chosen goodness-of-fit measure. We used the pairwise Rousset's  $a_r$  genetic distance (Rousset 2000) calculated for all pairs of individuals as dependent variable, and the ecological distance calculated using Circuitscape 5.0 implemented in Julia (Hall et al. 2021; McRae et al. 2008, 2016) as fixed effect. For categorical surfaces, the optimization process iteratively develops alternative resistance surfaces by assigning a new set of resistance values to each class. For continuous variables, alternative resistance surfaces are obtained by transforming original values through alternative functions, described by a shape and a magnitude parameter. For this study, we tested four alternative functions: monomolecular, reverse monomolecular, inverse monomolecular, inverse-reverse monomolecular (Peterman 2018). For both categorical and continuous surfaces, we set a maximum resistance value equal to 100. We compared all possible combinations of surfaces, including single and multiple, which are composed by summing up alternative single surfaces.

Models were ranked according to AICc and those with a  $\Delta AICc < 2$  were considered as equally valid. A pseudo bootstrap procedure ( $N = 100$ ) was applied to assess the contribution of each surface and to evaluate model performance by reducing type I error rates (Winiarski et al. 2020). Pairwise genetic and ecological distance matrices generated from each optimized surface were subsampled (75% of the complete sample) without replacement, each time the MLPE model was refitted and the AICc values calculated (Peterman 2018). Surface contribution is defined as the frequency at which a model is the top-ranked. For each species, we ran the whole optimization procedure three times to confirm

convergence and parameter estimates (Peterman 2018). We used the optimized resistance surface to develop a current density map of the study area to represent the species' gene flow. Following the approach of Koen et al. (2014), we designed a 12-km-wide buffer around the study area, roughly 20% of its length and 30% of its width, and randomly selected 100 nodes around the buffer perimeter. Circuitscape was run on these 100 nodes, and then, the buffer was removed to obtain a current density map independent from the geographic location of the original samples. Analyses were performed using R v. 4.2.0 (R Core Team 2022) within the GALILEO 100 HPC System at CINECA ([www.hpc.cineca.it/](http://www.hpc.cineca.it/)).

## Results

A total of 72 roe deer samples and 122 chamois samples were successfully genotyped at 11 microsatellite loci respectively, with no evidence of genotyping error or null alleles identified by the preliminary inspection in Micro-Checker. Alleles ranged from 2 to 14 per locus in chamois and from 2 to 9 per locus in roe deer. In sampled chamois, the less polymorphic locus was ILSTS011 (2 alleles,  $He = 0.025$ ) and the most polymorphic loci were INRA11 and FCB304 (14 alleles,  $He = 0.755$  and 12 alleles,  $He = 0.809$ , respectively), while in roe deer, Roe01 resulted as the less variable locus (2 alleles,  $He = 0.488$ ), and RT1 and NV21 were the most polymorphic (9 alleles,  $He = 0.801$  and 8 alleles,  $He = 0.810$ , respectively). Tables 1 and 2 summarize genetic diversity statistics in chamois and roe deer populations.

**Table 1** Genetic diversity statistics in chamois populations inhabiting the study area

Locus	Allele size	<i>N</i>	<i>He</i>	<i>Ho</i>	<i>Fis</i>
ILSTS05	153–173	8	0.785	0.744	0.0564
ILSTS011	263–267	2	0.025	0.025	−0.0086
BMC1009	279–323	10	0.602	0.474	0.2226*
FCB304	126–152	12	0.809	0.775	0.0459
SRCRSP05	155–175	8	0.788	0.702	0.1126
SRCRSP08	219–247	11	0.800	0.686	0.1464**
SRCRSP09	123–137	6	0.691	0.656	0.0548
ETH10	205–217	5	0.567	0.454	0.2042
ETH225	127–160	11	0.721	0.636	0.0982**
INRA05	137–163	8	0.747	0.622	0.1713
INRA11	203–231	14	0.755	0.675	0.1098
All loci		8.63	0.663	0.586	0.1163*

*N* number of alleles per locus, *He* expected heterozygosity, *Ho* observed heterozygosity, *Fis* inbreeding coefficient

A significant deviation from HWE is indicated by asterisks: \* $p < 0.005$ ; \*\* $p < 0.001$

**Table 2** Genetic diversity statistics in roe deer populations inhabiting the study area

Locus	Allele size	<i>N</i>	<i>He</i>	<i>Ho</i>	<i>Fis</i>
Roe01	130–132	2	0.488	0.792	−0.6169**
Roe06	85–107	7	0.624	0.528	0.1615*
Roe08	57–81	6	0.755	0.732	0.0368**
Roe09	173–177	3	0.453	0.542	−0.1882
NV16	154–176	7	0.750	0.710	0.0606
NV21	156–179	8	0.810	0.789	0.0467
NV24	127–145	7	0.833	0.667	0.2092
RT1	219–241	9	0.801	0.757	0.0618
ILSTS011	263–275	7	0.781	0.831	−0.0565
FCB304	166–190	7	0.796	0.736	0.0816
BMC1009	277–289	8	0.683	0.611	0.1116
All loci		6.45	0.707	0.699	0.0057

*N* number of alleles per locus, *He* expected heterozygosity, *Ho* observed heterozygosity, *Fis* inbreeding coefficient

A significant deviation from HWE is indicated by asterisks: \* $p < 0.005$ ; \*\* $p < 0.001$

Overall, genetic diversity was higher in roe deer ( $He = 0.707$ ,  $Ho = 0.699$ ) than in chamois ( $He = 0.663$ ,  $Ho = 0.586$ ).

Departure from Hardy-Weinberg equilibrium, due to heterozygote deficiency, was highly significant at two loci (SRCRSP08, ETH225) and significant at locus BMC1009 in the chamois population (see Table 1), while deviation resulted significant at three loci (Roe01, Roe06, Roe08) in roe deer. In the latter, there was evidence of heterozygote excess only at one locus (Roe01, Table 2). No evidence of non-random association of genotypes at different loci was detected by linkage equilibrium analysis (non-significant *p*-values for all locus pairs after sequential Bonferroni correction). The values of *Fis* over all loci resulted low and not significant in roe deer ( $Fis = 0.0057$ , ns) indicating low levels of local inbreeding, but high and significant in chamois ( $Fis = 0.1163$ ,  $p < 0.001$ ) showing local isolation of different nuclei. There was no evidence of bottleneck effects by analyzing data of chamois and roe deer, as both analyses showed a normal L-shaped distribution of allele frequencies

and no significant deviation from the expected levels of heterozygosity in Bottleneck (TPM model, Wilcoxon test not significant for both species: chamois  $p = 0.995$ ; roe deer  $p = 0.319$ ). Spatial correlation analysis performed on the roe deer population showed a significant positive correlation for the first distance class only ( $< 8$  km;  $p = 0.004$ ) and values not significantly different from zero at higher distances (see Supplementary Information, Fig. S2).

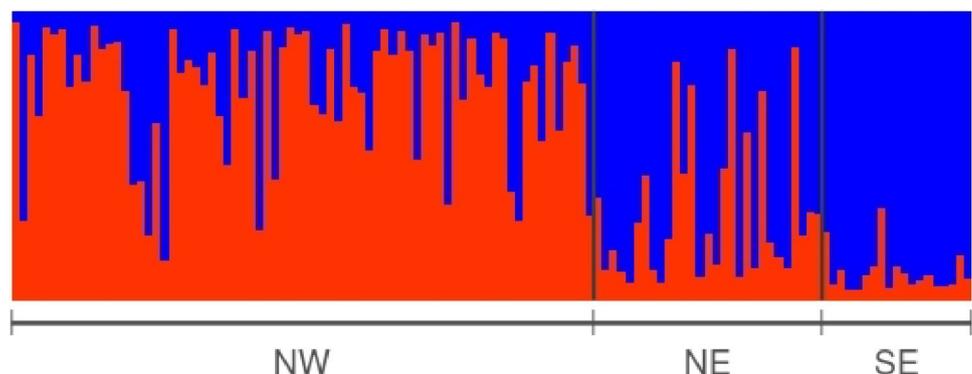
Bayesian analyses of population structure revealed sharply different results for chamois and roe deer populations in Trento province. When analyzing the chamois population dataset, the most likely partition was identified at  $K = 2$  (Fig. S3), with individuals' assignment to cluster I averaging  $q = 0.46$ , while  $q = 0.54$  to cluster II. After mapping the chamois specimens over the sampling area, the Northwest (NW, Adamello-Presanella) appeared predominantly inhabited by animals assigned to cluster I (mean  $q_{I} = 0.735$ ), while the Southeast (SE, Cadria-Altissimo-Ledro) was occupied by individuals mostly assigned to cluster II (mean  $q_{II} = 0.905$ ). Chamois sampled in the Northeast (NE, Brenta) region appeared intermediate between the two clusters (mean  $q_{II} = 0.680$ , Fig. 2). Instead, cluster analysis of roe deer genotypes did not evidence any structure, showing a slight likelihood decrease when increasing *K*, and therefore suggesting a panmictic population (Figs. S4 and 3).

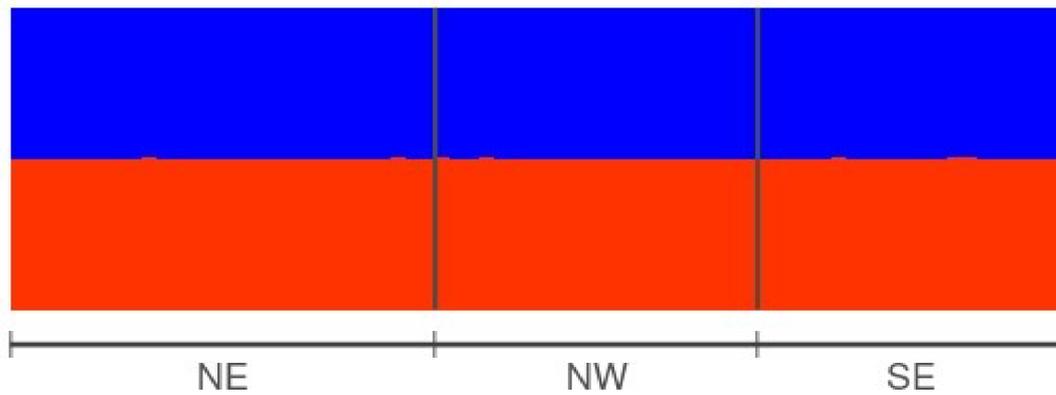
PCoA analyses confirmed these results, with some degree of differentiation and a partial overlap among chamois from different massifs (NW, NE, SE, Fig. 4), and complete overlap among roe deer from different areas (Fig. 5).

Landscape genetics analyses revealed a different effect of landscape composition and configuration on each species' gene flow.

As for the chamois, the AICc-based bootstrap model selection supported IBR as the process underlying the observed genetic variation patterns. Specifically, two optimized surfaces, a single surface (land cover) and a multiple surface (land cover + main roads), were associated to the first (land cover: avg.weight = 0.52,  $\Delta$ avg.AICc = 0, 71% top model) and second (land cover + main roads: avg.weight = 0.26,  $\Delta$ avg.AICc = 1.93, 24% top model) top

**Fig. 2** Bar plots illustrating the genetic structure of chamois in Trento province, inferred by Bayesian cluster analysis in Structure.  $K = 2$  was selected as the best clustering option and individual assignment proportion (*q*-value) to the two inferred clusters is represented by colors. Population codes: NW, North-West; NE, North-East; SE, South-East





**Fig. 3** Bar plots illustrating the absence of genetic structure in roe deer in Trento province, inferred by Bayesian cluster analysis in Structure ( $K=2$ ). Individual assignment proportion ( $q$ -value)

to the two inferred clusters is represented by colors. The best solution is represented by  $K=1$ . Population codes: NE, North-East; NW, North-West; SE, South-East

models, respectively. Since models were both valid ( $\Delta\text{avg. AICc} < 2$ ), we considered the resistance values generated in the resistance map built from the multiple surface (land cover + main roads) to account for all landscape features that had a non-negligible effect in driving chamois gene flow. In the optimized resistance map, the lowest resistance to the chamois movement was offered by rocky areas (i.e., optimal habitat type for the species) followed by urban areas, glaciers, beech forests, and transitional vegetation cover. Intermediate resistance values were associated with mixed broadleaved forests and meadows and pastures, while highest values were associated with arable lands, water bodies, and coniferous forests (Table 3). In cells crossed by roads, the resistance value of each land cover class increased by about 50 units, showing that these linear infrastructures appeared to act as barriers to chamois (Table 3). Conversely, when analyzing the roe deer population, the Euclidean distance model was the top-ranked by the AICc-based bootstrap model selection (avg.weight = 0.96,  $\Delta\text{avg. AICc} = 0$ , 100%

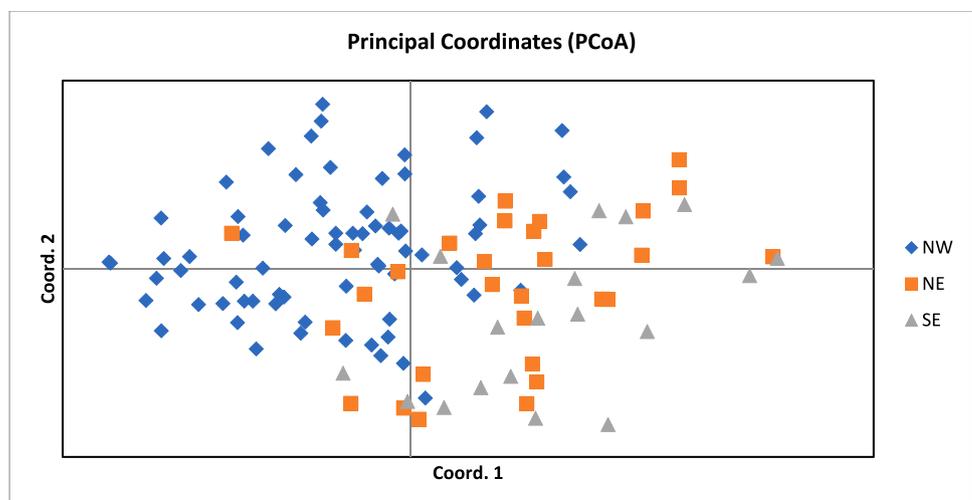
top model), showing that an IBD process drove the genetic variation patterns observed for this species.

A current density map was generated for chamois from the resistance surface optimized under the IBR hypothesis and is reported in Fig. 6, showing corridors for the species' gene flow obtained from the optimized multisurface "land cover + main roads."

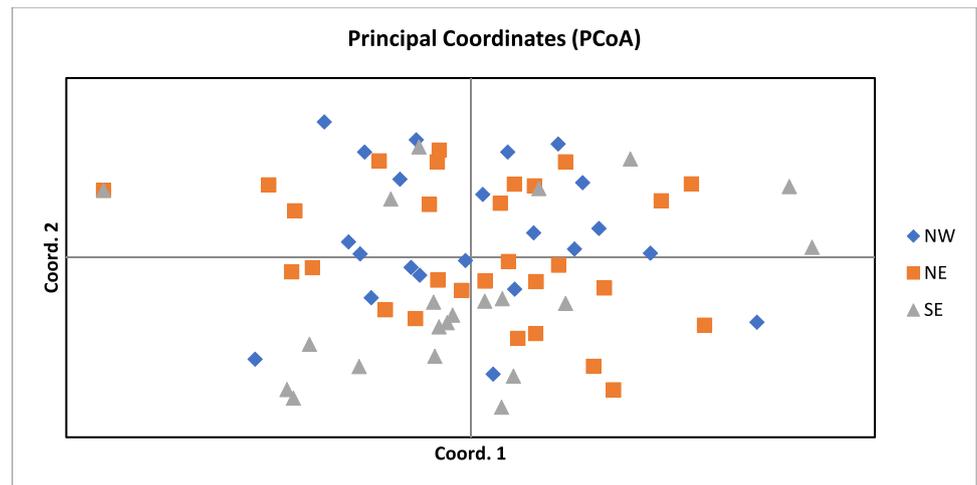
### Discussion

Genetic and landscape genetics results obtained in this study, based on roe deer and Alpine chamois sampled over the Trento province in Northern Italy, allow us to infer several aspects of their population structure and their relationships with the same landscape elements and potential barriers. Both ungulate populations apparently retain a good amount of genetic variability, with some differences. Observed heterozygosity values in chamois appeared lower than expected,

**Fig. 4** PCoA plot of chamois from the three areas of Adamello-Presanella (NW), Brenta (NE), and Cadria-Altissimo-Ledro (SE) in Trento province, Italy



**Fig. 5** PCoA plot of roe deer from the three areas of Adamello-Presanella (NW), Brenta (NE), and Cadria-Altissimo-Ledro (SE) in Trento province, Italy



while in roe deer, expected and observed heterozygosity values almost coincided (Tables 1 and 2). These results are consistent with those obtained in previous studies on Northern chamois (Crestanello et al. 2009; Soglia et al. 2010) and on roe deer inhabiting other European areas (Coulon et al. 2006; Biosa et al. 2015; Vasiljevic et al. 2022). No bottleneck effect was detected in the two populations analyzed, consistently with the described genetic variation. Chamois in Trento province were however characterized by a high inbreeding coefficient ( $F_{is}$ , see Table 1), especially when compared to the value observed in roe deer (Table 2), although a large  $F_{is}$  variation among loci was detected in both species.

In order to maintain such levels of genetic variation, preserving gene flow within these two native wild populations would be essential. Bayesian cluster analysis performed using Structure highlighted a different scenario when applied to the two ungulate populations analyzed. We did not

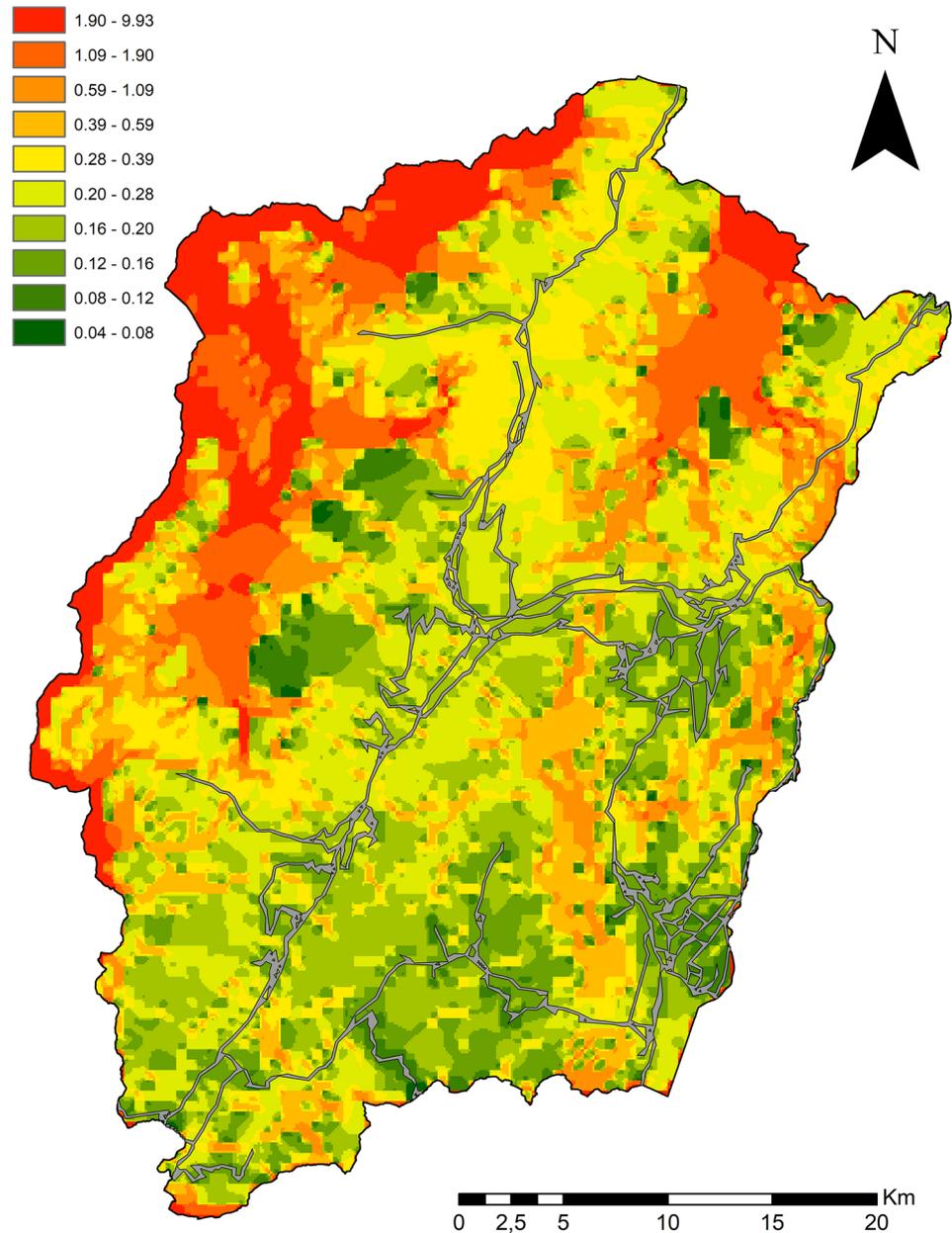
find any significant population structure in sampled roe deer inhabiting the study area, apparently connected by gene flow (Fig. 3). Instead, a clear population structure was detected in chamois, with two main clusters: one predominant in individuals sampled in the North-West (NW) of the study area (Adamello, Presanella) and the other found in animals inhabiting Mt Cadria in the South-East (SE) and prevalent in chamois sampled in the North-East (NE), corresponding to the Brenta massif (Fig. 2).

Landscape genetics analysis confirmed these scenarios and revealed a different effect of landscape on the two species' gene flow. In the case of chamois, IBR was identified as the process underlying the observed genetic variation patterns, and the selected model suggested the role of arable lands, coniferous forests, watercourses, and main roads as potential barriers for this species. Indeed, chamois prefer higher elevations and their movements may be hindered by landscape elements such as anthropized valleys, large rivers, and road networks. As already mentioned, this species inhabits most of the main mountain massifs in Europe, being adapted for life in rocky terrains, which represent escape grounds from predators, and cold climates (Corlatti et al. 2022). Chamois populations are found at elevations up to 2500 m a.s.l., in a range of habitats including alpine and subalpine meadows, pastures, forests, and clearings, but also on slopes, rocky areas, and shrublands (Corlatti et al. 2022). Lack of continuity in these habitats and overhunting (Baumann et al. 2005) highly fragmented chamois populations. Overall, the Northern chamois is a habitat specialist ungulate occupying "continental archipelagos" of fragmented high altitudes rocky habitats (Buzan et al. 2013). Our results suggest that connectivity among these "islands" might be limited, therefore playing a role in generating the observed genetic structure. However, the observed pattern refers to a limited geographic scale and might change when replicating the study over a broader area.

**Table 3** Resistance values associated to each land cover class (not crossed by roads or crossed by roads) in the optimized resistance map for chamois, obtained from the optimized multisurface land cover + main roads

Land cover class	Resistance value	
	Not crossed by roads	Crossed by roads
Rocky areas	1.00	50.28
Urban areas	1.09	50.37
Glaciers	3.48	-
Beech forests	4.96	54.24
Transitional vegetation	7.81	57.09
Mixed broadleaved forests	22.16	71.44
Meadows and pastures	32.81	82.10
Arable lands	41.32	90.60
Water bodies	43.38	92.67
Coniferous forests	50.50	99.78

**Fig. 6** Current density map obtained using Circuitscape, showing corridors for chamois gene flow obtained from the optimized multisurface “land cover + main roads.” The green-red color gradient indicates increasing current density values (threshold values of displayed classes are the quantiles of current density values distribution). Main roads are represented in grey



Landscape elements, local orography, and land use, as well as the different species' ecology, might thus explain our results. Rendena valley, that parts the study area in East-West direction, with western massifs (Adamello, Presanella) on one side and eastern massifs (Brenta, Cadria-Altissimo, Ledro) on the other side, is anthropized and crossed by Sarca river and SS239 road. The current density map (Fig. 6) shows that this valley represents a NE-SW barrier to gene flow, determining genetic isolation between chamois inhabiting the western and eastern massifs. Canyon Limarò, between Cadria-Altissimo massif and Brenta Dolomites, is also crossed by Sarca river, and apparently represents a semi-permeable barrier for the species movements, reducing

genetic connectivity between NE and SE of the study area. On the eastern side of the study area, a potential corridor is present between Cadria-Altissimo and Adamello, enabling North-South movements, due to higher valley elevation and less road network development. High connectivity levels can support North-South movements within the western part (Adamello, Presanella massifs) of the study area. Finally, Campo Carlo Magno (1700 m), an alpine pass in the north, might also represent a potential corridor for chamois.

Although gene flow might also be affected by other variables (such as demography, ethology, and genetic drift), the effect of orography on the connectivity between chamois populations was also highlighted in recent studies conducted

at the contact zone of two mountain ranges in Slovenia (Buzan et al. 2013) and across the Alps (Leugger et al. 2022).

As mentioned, no genetic structure was detectable in roe deer, and an IBD model was best explaining genetic variation in this species, which tends to occupy valley floors relatively connected to each other and is characterized by a spatial behavior promoting gene flow across areas, especially during the rut period (Debeffe et al. 2014). The observed pattern of genetic autocorrelation, indicating that individuals living within a range of 8 km are slightly more related than random pairs in the population, suggests that the apparent lack of structure and the IBD are generated by a majority of philopatric individuals and a minority of long-range dispersers in the population, as observed in this species (Debeffe et al. 2012). As reviewed by Lorenzini et al. (2022), roe deer is an ungulate species adapted to wooded habitat, particularly at edges with open areas providing good feeding resources for browsers. Roe deer also show behavioral plasticity, as habitat composition, availability, and distribution of resources might affect habitat selection. Main roads probably do not represent a significant barrier for roe deer, as demonstrated by the high number of road kills registered in Trento province (295 per year between 1993 and 2008, Mustoni et al. 2012), compared to a very low number (0.68 per year) registered for chamois in the same period. Previous studies on roe deer in Switzerland revealed the influence of transportation infrastructure on their genetic divergence, but no impact on genetic diversity (Kuehn et al. 2007) and no effect on gene flow of a highly frequented but unfenced railway track (Hepenstrick et al. 2012).

The different effects of landscape elements on the two ungulate species in this area were also suggested by a study promoted by Trento province, highlighting the diverse use of wildlife corridors by chamois and roe deer (Mustoni et al. 2012). Among 67 potential corridors for wild ungulates, only 7% were suitable for chamois, while 58% may be used by roe deer, providing a higher connectivity for this species' movements. Albeit our results' robustness would benefit from replication, they already highlight the different impacts of orography, land use, and anthropic infrastructures on gene flow in two sympatric species, as a result of their different ecological requirements. The observed population structure and restricted gene flow among chamois nuclei inhabiting the Trento province should be taken into account for future species management and conservation planning. Further research is recommended to improve landscape connectivity and assure the presence of potential corridors for wild ungulate species in the alpine region.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s10344-024-01796-1>.

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**Data availability** Datasets generated during the current study are available from the corresponding author on request.

## Declarations

**Ethical approval** No animals were killed specifically for the study. No living animals were sampled.

**Competing interests** MS is associate editor of the journal.

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