



Climatic changes and the fate of mountain herbivores

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Abstract

Mountains are strongly seasonal habitats, which require special adaptations in wildlife species living on them. Population dynamics of mountain ungulates are largely determined by the availability of rich food resources to sustain lactation and weaning during summer. Increases of temperature affect plant phenology and nutritional quality. Cold-adapted plants occurring at lower elevations will shift to higher ones, if available. We predicted what could happen to populations of mountain ungulates based on how climate change could alter the distribution pattern and quality of high-elevation vegetation, using the “clover community-Apennine chamois *Rupicapra pyrenaica ornata*” system. From 1970 to 2014, increasing spring temperatures (2 °C) in our study area led to an earlier (25 days) onset of green-up in Alpine grasslands between 1700 and 2000 m, but not higher up. For 1970–2070, we have projected trends of juvenile winter survival of chamois, by simulating trajectories of spring temperatures and occurrence of clover, through models depicting four different scenarios. All scenarios have suggested a decline of Apennine chamois in its historical core range, during the next 50 years, from about 28% to near-extinction at about 95%. The negative consequences of climate changes presently occurring at lower elevations will shift to higher ones in the future. Their effects will vary with the species-specific ecological and behavioural flexibility of mountain ungulates, as well as with availability of climate refugia. However, global shifts in distributional ranges and local decreases or extinctions should be expected, calling for farsighted measures of adaptive management of mountain-dwelling herbivores.

Keywords Climate change · Extinction risk · Mountain herbivores · Population modelling · *Rupicapra* · Temperature increase

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1 Introduction

Climate changes are not a new event; for example, over 50 climate changes occurred during the Pleistocene and the Holocene (Lourens 2004; Wanner et al. 2015), with most of them lasting a minimum of several hundred years (Crawford 2014). Many species of plants and animals survived either by adapting to the new local conditions or by moving to refuge areas (climate refugia: Dobrowski 2011; Gavin et al. 2014; Morelli et al. 2016, for reviews), where they could tolerate the local environmental conditions and from which they later recolonised their earlier range, when climate conditions turned again suitable (Hewitt 1996; Lorenzini and Lovari 2006; Crawford 2014; Li et al. 2016). Organisms which neither adapted nor moved to refugia went extinct. Species living in extreme conditions, e.g. in Polar regions and deserts, may find it particularly difficult to quickly change their adaptations developed over millions of years or to find suitable refuge areas (Parmesan 2006, for a review). In addition, changes in distribution of other species with wider ecological tolerance may further contribute to the decline of highly specialised species through competition (Hersteinsson and Macdonald 1992; Lovari et al. 2013; Stenseth et al. 2015; Ferretti et al. 2018).

Species adapted to high-elevation habitats are also particularly sensitive to climatic changes, in some cases leading to local extinctions (Nogués-Bravo et al. 2007; Parmesan 2006). Cold-adapted plant associations on mountains have shifted to higher elevations because of warmer conditions (Lenoir et al. 2008; Gottfried et al. 2012; Pauli et al. 2012; Telwala et al. 2013). Presumably, herbivores feeding on them will also tend to follow the vegetation shift, although evidence is still scanty (Büntgen et al. 2017). In the warm months, access to high-quality forage is crucial for reproductive success of mountain ungulates, as juvenile growth, which then affects winter survival, is strongly dependent on summer food availability and quality (Festa-Bianchet 1988; Festa-Bianchet and Jorgenson 1998; Coté and Festa-Bianchet 2001; Scornavacca et al. 2016). Mountain ungulates are not a taxonomic group, although the large majority of them (75%; $n = 41$ species; Table S1, Supplementary Material 1) belongs to the subfamily Caprinae (Bovidae) and nearly all of them (92%) inhabit the Holarctic bioregion (Shackleton 1997). They show adaptations to climb and use rocky or rugged ground for escape terrain, differently from other ungulates which may also occur at high elevations (Schröder 1985). Mountain ungulates present special conservation problems: 70% ($n = 41$ species; Table S1, Supplementary Material 1) are in the Near-Threatened or in the Threatened IUCN risk categories and could be further imperilled by the ongoing climate change. Refuge areas are more likely to be available on mountains with a greater elevational gradient (Şekercioğlu et al. 2012), which should provide a wider opportunity for vegetation shifts and herbivore movements compared to mountains with a limited elevational range. Physiographic factors shaping topoclimatic effects also determine the occurrence of microrefugia, particularly on mountains (Dobrowski 2011). Although availability of refuge areas varies with mountain topography (Elsen and Tingley 2015), about 50% of mountain groups in the Holarctic bioregion—where the large majority of mountain ungulates dwells—shows a decrease of refuge areas with increasing elevation (Elsen and Tingley 2015). Therefore, especially in this bioregion, cold-adapted vegetation on mountains with a limited elevational range (< 2000 m) is expected to show earlier the effects of the temperature increase because of snowmelt, in respect to vegetation of mountains with higher elevations (cf. Martin et al. 1994; Beniston 1997; Beniston et al. 2018; Rogora et al. 2018), thus allowing predictions on the evolution of Alpine ecosystems with time.

Climate change patterns may vary between geographical regions in terms of snow and rain (Parmesan and Matthews 2006), with a global increase of temperatures (Hegerl et al. 2018), sometimes even having locally contrasting effects on population dynamics of mountain ungulates (Loison et al. 1999), thus making it difficult to predict a general pattern. In spite of local variations, it has been suggested that warmer weather during the vegetative season may have particularly negative effects on body mass (Rughetti and Festa-Bianchet 2012; Mason et al. 2014a), fecundity of females (Corlatti et al. 2018) and offspring survival (Douhard et al. 2018; Ferretti et al. 2018), affecting population dynamics of mountain herbivores.

The chamois *Rupicapra* spp. (Bovidae: Caprinae) is an abundant ungulate found in the main mountain groups of Europe and the Near East (c. 500,000 adult individuals; iucnredlist.org, accessed on 24.06.2020). It shows a number of physical, behavioural and ecological adaptations to life on mountains (Corlatti et al. [in press](#)). The Apennine chamois *R. pyrenaica ornata* lives on the Apennines, a mountain chain crossing the Italian Peninsula longitudinally. In the Apennines, most mountain tops range between 1500 and 2000 m a.s.l., with the highest summit (Corno Grande, 2912 m) in the Gran Sasso Massif, Central Apennines. Up to the Holocene, chamois occurred all over the Apennine range and neighbour areas, but at the end of the ice age, they retreated to some mountain tops of the Central and Southern Apennines (Masini and Lovari 1988). Ferrari et al. (1988) showed that, while male Apennine chamois are more catholic in diet, females and juveniles concentrate their summer food habits on several plant communities, especially the glacial relict grassland with clover *Trifolium thalii* which supplies a particularly protein-rich and fibre-poor diet. This forb is rare and extra-zonal in the Northern and Central Apennines, whereas it is common in the Alpine vegetation belt of the Alps (Pignatti 1982). It grows on slightly acidic soils, in shallow dolines with long-lasting snow cover (Ferrari et al. 1988; Ferrari and Rossi 1995), thus being particularly sensitive to temperature increases, e.g. because of climatic variations, and can be used as a proxy to assess temperature-driven vegetation changes.

As population dynamics of mountain ungulates is strongly dependent on food resources, one could expect that a dramatic change in availability and quality of vegetation, e.g. driven by an increase of temperature, has negative effects on the survival of mountain ungulates (e.g. Douhard et al. 2018; Ferretti et al. 2018, see also above). The system formed by the plant community with *T. thalii* and the Apennine chamois can be used as a case study of what could happen to populations of mountain ungulates when climatic changes alter the distribution pattern and quality of cold-adapted vegetation (Lenoir et al. 2008; Gottfried et al. 2012; Pauli et al. 2012; Telwala et al. 2013). Our work aims to predict the population dynamics of mountain ungulates when local key-food resources are altered because of an increase of temperature.

2 Materials and methods

2.1 Study area and population

Our study was conducted in the Abruzzo, Lazio and Molise National Park (ALMNP), in the Central Apennines (Italy; latitude: 42°00'37" to 41°35'25" N, longitude: 13°29'17" to 14°02'33" E; size: 507.86 km²; Fig. 1a). Elevation ranges between 500 and 2249 m a.s.l. (highest peak: Mt. Meta), with most of the area lying between 1100 and 1900 m (Primi et al. 2016).

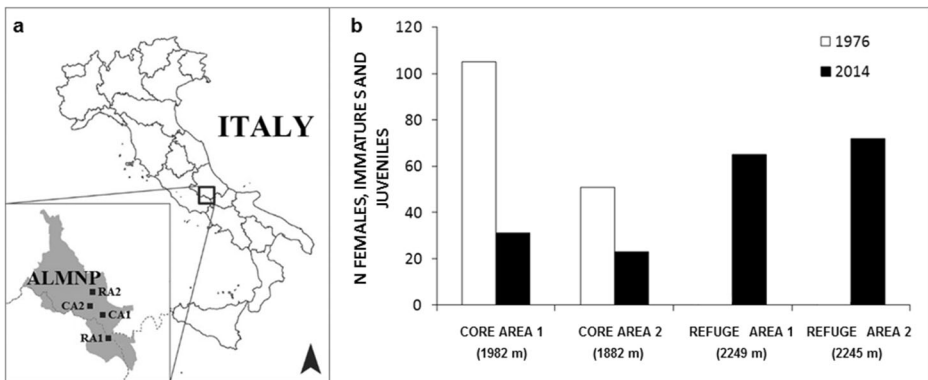


Fig. 1 **a** Location of the Abruzzo, Lazio and Molise National Park (ALMNP) and **b** changes in minimum numbers of female, immature and offspring chamois, recorded in 1976 (Perco et al. 1976) and 2014 (Latini and Asprea 2014), in historical core areas (CAs) and in recently colonised ones, i.e. refuge areas (RAs)

There is no dry season, and snow cover lasts from mid-November until mid/late spring, depending on the elevation. The vegetation changes according to elevational belt (Primi et al. 2016). Natural timberline occurs at less than 1900 m (Ravazzi and Aceti 2004). Below the tree line, vegetation includes forests dominated by beech *Fagus sylvatica* and secondary grasslands. The subalpine belt occurs above the tree line (> 1700 m) and includes natural/semi-natural grasslands (hereafter, “Alpine grasslands”, *c.* 10% of land cover) and screes with sparse vegetation; snow cover lasts until early June. Most of the Alpine grasslands (*c.* 92%) lie between 1700 and 2000 m, while only a smaller proportion (*c.* 8%) lies above 2000 m (see Sect. 2.3, below).

The ALMNP includes the historical range of the Apennine chamois, which survived only in two sites of this area (Lovari 1977). Since the early 1990s, it has been translocated for conservation purposes to other protected areas of the Central Apennines, with a current total population of less than 2500 individuals (Corlatti et al. *in press*). Even in ALMNP, Apennine chamois went nearly extinct during World War II, because of increased poaching (Lovari 1985). Its numbers slowly recovered and, between 1970 and 1990, oscillated at *c.* 300 individuals, which have nearly doubled after the Park boundaries were extended to include the Mainarde chain (1990-present; Lovari 1985; Duprè et al. 2001; Mari and Lovari 2006; Asprea 2016). During the last few decades, numbers of chamois have decreased in historical core areas of ALMNP (*c.* 70% decrease in core area 1: upper Val Di Rose/Mt. Boccanera; *c.* 50% decrease in core area 2: Mt. Amaro; Fig. 1b; cf. Perco et al. 1976 with Latini and Asprea 2014), because of heavy winter mortality of juveniles, related to a lower availability of appropriate food resources (Lovari et al. 2014; Ferretti et al. 2015; Corazza et al. 2016; Scornavacca et al. 2016; Ferretti et al. 2018). Conversely, an increase in the population of chamois was recorded in two new areas both above 2000 m a.s.l. (refuge area 1: Mt. Meta; refuge area 2: Mt. Marsicano; Fig. 1b; Latini and Asprea 2014), where a maximum of only five or six males were present in 1975s–1980s, with no mixed group of females, yearlings and juveniles (S.L., unpublished; Perco et al. 1976).

In ALMNP, previous studies have shown that chamois account for a negligible proportion of the diet of the grey wolf *Canis lupus* (< 2%; Patalano and Lovari 1993; Ciucci et al. 2020) and the Apennine brown bear *Ursus arctos marsicanus* (0.05%; Ciucci et al. 2014), with the former relying especially on abundant populations of other ungulate species. Stable to growing

populations of red deer *Cervus elaphus* (Latini et al. 2015a), roe deer *Capreolus capreolus* (Latini et al. 2015a) and wild boar *Sus scrofa* (Fabbri et al. 1983; S.L., N.F., F.F., own observations) occur in ALMNP. The golden eagle may prey mainly on juvenile chamois, although chamois antipredator defence usually does not allow it (Scornavacca and Brunetti 2015).

2.2 Meteorological data

We obtained temperature data of the study area at the terrain level from the NCEP/NCAR reanalysis project (NOAA/OAR/ESRL PSD, Boulder, CO, USA; Kalnay et al. 1996) using the specific R package ‘RNCEP’ (Kemp et al. 2012). These data have been customarily used in climatological and ecological research (Kaskaoutis et al. 2014; Panuccio et al. 2016). They cover the variation of atmospheric variables from 1957 to present. These data have a spatial resolution of $2.5^\circ \times 2.5^\circ$ and a temporal resolution of 6 h (00:00, 06:00, 12:00, 18:00 h UTC) (Kemp et al. 2012). We used daily temperature data taken from 1970 to 2014 at 12:00 (solar time).

2.3 Vegetation productivity data

We analysed vegetation activity through the Enhanced Vegetation Index (EVI; Huete et al. 2002), a satellite-derived index that identifies the photosynthetically active signal of vegetation. This index is based on light absorption by chlorophyll in the red wavelength of the optical spectrum, while mesophyll scatters light in the near infrared. Because EVI is correlated positively with vegetation productivity (Running et al. 2004), this index may be used to assess the timing of phenological changes of vegetation in grasslands (Ballesteros et al. 2013; Villamuelas et al. 2016). Furthermore, the EVI has been shown to be a proxy reflecting the diet quality of our study species, in spring (Villamuelas et al. 2016). EVI is less sensitive than NDVI (Normalized Difference Vegetation Index) to the influence of atmospheric aerosol, which improves its sensitivity to vegetation signals (Huete et al. 2002).

We obtained EVI data from the MOD13Q1 product of the MODIS sensor (Moderate Resolution Imaging Spectroradiometer) from the TERRA satellite of NASA (Huete et al. 2002; Justice et al. 2002) accessible from the Earth Explorer website of the United States Geological Survey (USGS; <https://earthexplorer.usgs.gov>, accessed on 1 Aug 2016). We used 342 scenes of MODIS from 2000 to 2014, with a temporal time resolution of 16 days and a spatial resolution of 250 m.

Only data for Alpine grasslands were considered. First, we superimposed a grid with cells of 200×200 m to the study area and we classified as ‘grassland’ the cells containing at least 70% of grasslands based on the 4th level Corine Land Cover map of the study area. Further, we selected only the cells located at more than 1700 m of elevation, based on the digital elevation model with a spatial resolution of 25 m (Alpine grasslands; 5196 ha). Finally, we separated the Alpine grasslands in ‘lower elevation’ (1700–2000 m; 47.76 km²) and ‘higher elevation’ (>2000 m; 4.2 km²) ones, to assess potential differences in vegetation dynamics. EVI data are available only from 2000 onwards. For 1970–1999, we estimated EVI by modelling the relationships between the available EVI values (2000–2014) and meteorological data (see Supplementary Material 1). We determined three EVI metrics to explore vegetation phenology through the estimated (1970–1999) or obtained (2000–2014) EVI values: (i) the onset of green-up, (ii) the integrated EVI (iEVI) of April and (iii) the duration of the greenness

plateau (Fig. S1, Supplementary Material 1). The onset of green-up is the beginning of the growing season and was defined as the time when the maximum increase of EVI between two consecutive dates occurred (Pettorelli et al. 2005, 2007; Garel et al. 2011). We used the integrated EVI of April because it correlates with vegetation biomass (Pettorelli et al. 2005) and was calculated as the sum of positive EVI values of April (Pettorelli et al. 2005; Pettorelli et al. 2007; Hamel et al. 2009; Garel et al. 2011). We chose April because in this month, there was the maximum rate of increase in plant productivity during green-up, in our study area. The duration of the greenness plateau corresponds to the period of high photosynthetic activity (Pettorelli et al. 2005) and was calculated as the difference between the time when the EVI started to decrease and the time when the EVI plateau began.

2.4 Clover vegetation and chamois numbers

We used data from Rossi (1985), in 1980s, and Lovari et al. (2014), in 2010s, in the core area of chamois (upper Val di Rose and surroundings), to analyse the frequency of occurrence of clover *T. thalii*, as a proxy of cold-adapted vegetation particularly sensitive to temperature variations. Rossi (1985) and Lovari et al. (2014) estimated visually presence/absence of clover through vegetation surveys in circular plots, using the phytosociological method (Braun-Blanquet 1964). In the same area, we estimated the mortality of chamois juveniles over winter by the ratio between yearlings counted in year t and the number of juveniles counted in year $t-1$ (hereafter, yearling $_t$ /juvenile $_{t-1}$ ratio), through personal observations (1980s: S.L., unpublished; Rossi 1985; 2010s: Lovari et al. 2014; Ferretti et al. 2015; Scornavacca et al. 2016; Ferretti et al. 2018). For this purpose, we used the maximum number of individuals belonging to each age class observed daily in summer, each year (range: $c.$ 89–120 h of observation per year; Rossi 1985; S.L. unpublished; Lovari et al. 2014; Ferretti et al. 2015; Scornavacca et al. 2016; Ferretti et al. 2018). In each observation day, 2–3 trained observers searched actively for each herd, which should provide reliable information on age, structure and numbers of the local herds. In fact, groups of females, kids and yearlings of Apennine chamois use open habitats from mid-June to November (Lovari and Cosentino 1986) and show a marked site fidelity (data based on GPS/VHF radio-tracking: Latini et al. 2013). In addition, some yearlings appear to depart from the maternal group mainly from the autumn (Fattorini et al. 2019).

2.5 Analysis of changes in temperature and vegetation productivity

We ran linear regressions on the time series of both the temperature and the EVI metrics (Zuur et al. 2007) to assess the temporal variation of climate and vegetation phenology in the Alpine grasslands of the ALMNP, between 1970 and 2014. We tested the significance of the regression slope by one-way ANOVA (Wang and Carter 1983). We checked normality and temporal autocorrelation of residuals with the Kolmogorov-Smirnov test (Legendre and Legendre 1998) and the autocorrelation function plot (Cowpertwait and Metcalfe 2009), respectively. All models showed normally distributed and temporally uncorrelated residuals (Table S8, Fig. S2 and Fig. S3, Supplementary Material 1).

2.6 Simulation of trajectories of spring temperatures

Of all seasons and variables we considered, only spring temperatures showed a statistically significant increase over the last decades (Table S9; Fig. S4, Supplementary Material 1). Thus,

we considered mean spring temperatures (x) from 1970 to 2014 to predict trajectories for the next 56 years, up to 2070. Since the early twentieth century, there have been linear/exponential increases of temperatures (Hegerl et al. 2018: 3); therefore, we have assumed no major variation of the trend of temperatures in the next few decades, up to 2070. From 2015 to 2070, 10,000 trajectories of mean spring temperatures were simulated according to the following linear model

$$x_{it} = \alpha + \beta t + \varepsilon_{it}, \quad i = 1, \dots, 10\,000, \quad t = 2015, \dots, 2070$$

where x_{it} denotes the mean spring temperature of the i -th trajectory for the year t and α and β were the OLS estimates obtained from mean spring temperatures for the period 1970–2014 (Table S10, Supplementary Material 1), while ε_{it} was the error term assumed to be a normal random variable with expected average 0 and variance σ^2 estimated by the residual variance of the OLS regression (Table S10, Supplementary Material 1). As OLS regression of mean spring temperatures during 1970–2014 did not show autocorrelated residuals (Durbin-Watson test; $p = 0.124$), we did not assume them in our simulations.

The temperature change we predicted up to 2070 is consistent with that projected in our study area through the ensemble of 44 CMIP5 scenarios based on 11 Global Circulation Models coupled with four Representative Concentration Pathways reflecting the possible range of future radiative forcing (see Supplementary Material 2).

2.7 Simulation of trajectories of proportion of plots containing clover

We ran our simulations according to four different scenarios relating proportion of plots containing clover (c) to mean spring temperatures, with $0 \leq c \leq 100$. We considered different types of relationships to reach widely reliable predictions, as temperature is the ultimate driver of quantity of growing clover *T. thalii* (Ferrari and Rossi 1995). The first scenario (A) assumed a linear relationship between proportion of plots with clover at year t and mean spring temperature at the same year, the second (B) and the third (C) scenarios assumed a power relationship with negative and positive exponent, respectively, whereas the fourth (D) assumed a sigmoidal relationship (Fig. S5, Supplementary Material 1). From any trajectory of both observed and simulated temperatures, the corresponding trajectory of proportions of plots containing clover vegetation for the period 1970–2070 was generated, depending on which scenario, by the following four models:

$$\begin{aligned}
 c_{it} &= \alpha + \beta x_{it} + \varepsilon_{it}, \quad i = 1, \dots, 10\,000, \quad t = 1970, \dots, 2070 && \text{scenario A} \\
 c_{it} &= \alpha + \beta x_{it}^{-\gamma} + \varepsilon_{it}, \quad i = 1, \dots, 10\,000, \quad t = 1970, \dots, 2070, \quad \gamma > 0 && \text{scenario B} \\
 c_{it} &= \alpha + \beta x_{it}^{\gamma} + \varepsilon_{it}, \quad i = 1, \dots, 10\,000, \quad t = 1970, \dots, 2070, \quad \gamma > 0 && \text{scenario C} \\
 c_{it} &= 100 - \frac{100}{1 - (\frac{x_{it}}{A_{it}})^a} + \varepsilon_{it}, \quad i = 1, \dots, 10\,000, \quad t = 1970, \dots, 2070 && \text{scenario D}
 \end{aligned}$$

where c_{it} denoted the proportion of plots containing clover in the i -th trajectory for the year t ; the parameters α , β , and γ were determined in such the way that regression curves passed through the observed values (Table S11, Supplementary Material 1); as customary when modelling rates, proportions or percentage, ε_{it} was an error term generated from a beta distribution (e.g. Johnson and Kotz 1970) in the range $-A_{it}, A_{it}$, with $A_{it} = \min \{c_{it}, 100 - c_{it}\}$ to have low error term variances at the bounds of the percentage values (i.e. 0 and 100) and have shape parameters $a = b = 4$.

For an alternative explanation of data in the range 0–100, we have also fitted these data through beta regression models (Ferrari and Cribari-Neto 2004), assuming the four

relationships (A, B, C, D) between the logit of c and the mean spring temperature (see Supplementary Material 3). However, beta regression strongly depended from the precision parameter and the trends were quite similar to those obtained under the assumption of a direct relationship between c and the mean spring temperature (see Supplementary Material 3). By contrast, as similar results were achieved even for $a = b = 20$, our results assuming a direct relationship were stable with respect to the shape parameters a and b .

2.8 Simulation of trajectories of chamois yearling_{*t*}/juvenile_{*t-1*} ratio

Ferretti et al. (2018) showed that juvenile winter survival of chamois can be negatively influenced by hot-dry weather conditions during spring-summer, through depletion of key-food resources. Our simulations assumed a correlation between juvenile chamois yearling_{*t*}/juvenile_{*t-1*} ratio (s) and proportion of plots containing clover, where $0 \leq s \leq 1$ (Table S12, Supplementary Material 1). For each scenario and for each trajectory of simulated proportions of plots containing clover, the corresponding trajectory of chamois yearling_{*t*}/juvenile_{*t-1*} ratio for the period 1970–2070 was generated according to the following linear model

$$s_{it} = \alpha + \beta c_{it} + \varepsilon_{it}, \quad i = 1, \dots, 10\,000, \quad t = 1970, \dots, 2070$$

where s_{it} denoted the yearling_{*t*}/juvenile_{*t-1*} ratio in the i -th trajectory for the year t , and α and β were the OLS estimates obtained from the observed proportions of plot containing clover and yearling_{*t*}/juvenile_{*t-1*} ratio in the period 1970–2014 (Table S12, Supplementary Material 1). As for the simulations of proportion of plots containing clover, ε_{it} was the error term assumed to be a beta random variable in the range $-A_{it}, A_{it}$, with $A_{it} = \min\{c_{it}, 1 - c_{it}\}$ to have low error term variances at the bounds of the yearling_{*t*}/juvenile_{*t-1*} ratio (i.e. 0 and 1) and have shape parameters $a = b = 4$.

3 Results

3.1 Changes in temperature and vegetation productivity

Between 1970 and 2014, temperatures increased in spring by $c. 2^\circ\text{C}$, but they did not increase in other seasons (Table S9; Fig. S4, Supplementary Material 1). An earlier ($c. 25$ days) onset of green-up in the Alpine grasslands has been found between 1700 and 2000 m ($\beta = -0.484 \pm 0.194$; $F_{1,44} = 6.217$, $p = 0.016$, $R^2 = 0.124$; Fig. 2a), but not higher up ($\beta = -0.124 \pm 0.106$; $F_{1,44} = 1.356$, $p = 0.251$, $R^2 = 0.124$; Fig. 2b). The maximum rate of growth in early spring increased through time, at both the lower and higher elevations ($\beta = 0.002 \pm 0.001$; $F_{1,44} = 8.272$, $p = 0.006$, $R^2 = 0.158$, Fig. 2c; $\beta = 0.001 \pm 0.0003$; $F_{1,44} = 5.109$, $p = 0.029$, $R^2 = 0.104$, Fig. 2d). Over the years, the duration of the greenness plateau did not change at the lower elevations ($\beta = -0.017 \pm 0.014$; $F_{1,44} = 1.520$, $p = 0.224$, $R^2 = 0.033$; Fig. 2e), but decreased at the higher ones ($\beta = -0.037 \pm 0.014$; $F_{1,44} = 6.888$, $p = 0.012$, $R^2 = 0.135$; Fig. 2f).

3.2 Changes in chamois population dynamics

Trends of yearling_{*t*}/juvenile_{*t-1*} ratio from 2015 until 2070 were obtained by simulating trajectories of mean spring temperatures (Fig. 3) and proportions of plots with clover (Fig. S6, Supplementary Material 1), through models depicting four different scenarios (see Methods

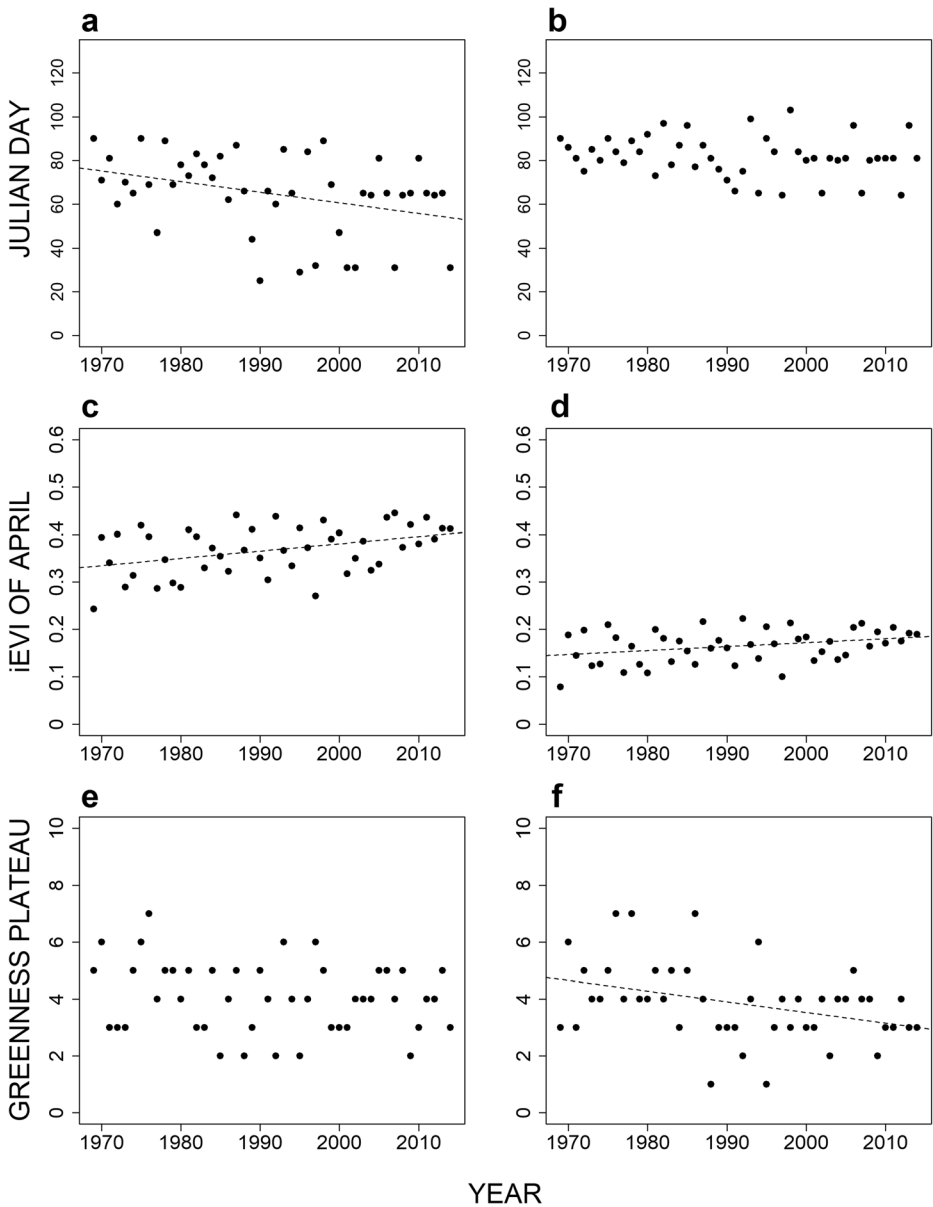


Fig. 2 Changes in onset of green-up (as Julian days) through 1970–2014, in 1700–2000 m (a) and > 2000 m (b) Alpine grasslands. Changes in maximum rate of growth in early spring (iEVI of April) through 1970–2014, in 1700–2000 m (c) and > 2000 m (d) Alpine grasslands. Changes in duration of the greenness plateau (no. of days) through 1970–2014, in 1700–2000 m (e) and > 2000 m (f) Alpine grasslands. When, significant, a regression line has been added

and Fig. S5, Supplementary Material 1). In all scenarios, the yearling_t/juvenile_{t-1} ratio of chamois showed a decreasing trend over the years, from a median of *c.* 85% to 99% (Fig. 4a–d). Furthermore, the observed ratios (Fig. 4a–d, dots) fall within the variability intervals of simulated values for all the scenarios, which validates the predicted yearling_t/juvenile_{t-1} ratios.

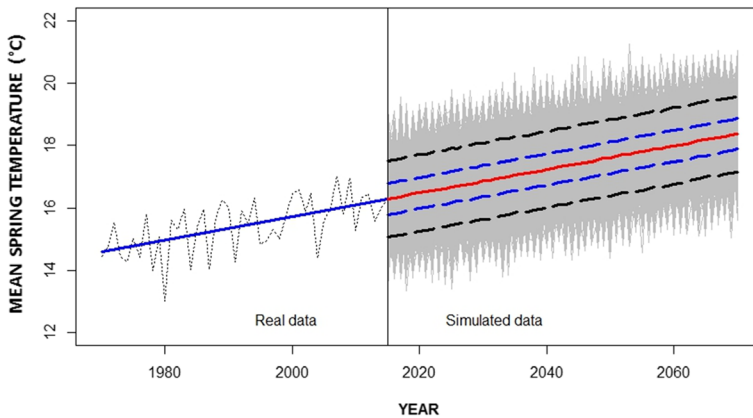


Fig. 3 1970–2014: observed mean spring temperatures (dotted line), with trend estimated by OLS regression (blue line). 2015–2070: simulated trajectories of mean spring temperature (grey area), with red line denoting the median of simulated temperature, at each year (blue dashed lines: 75th and 5th percentiles; black dashed lines: 25th and 95th percentiles)

For each scenario, the percentage of simulated trajectories reaching a $\text{yearling}_t/\text{juvenile}_{t-1}$ ratio equal to 0 are shown in Fig. 4e (see also Table S13, Supplementary Material 1, for raw values). All scenarios predicted a decreasing trend in $\text{yearling}_t/\text{juvenile}_{t-1}$ ratios, with an optimistic decrease of *c.* 28% (scenario B, assuming a power relationship with negative exponent occurring between temperature and proportion of plots containing clover) to a pessimistic one of *c.* 95% (scenario C, a power relationship with positive exponent) (Fig. 4e).

4 Discussion

Over the last five decades, in the Central Apennines, an increase of temperature (2 °C) has anticipated the onset of green-up in montane grasslands (*c.* 1700–2000 m) by nearly 1 month, but not at higher elevations (*c.* 2000–2200 m). Ungulates living on low mountain ranges, such as the Apennines, may be the first to experience the effects of the ongoing climatic changes on vegetation, because of the absence of upper elevations as potential refuge areas. Conversely, ungulates inhabiting higher mountains have the opportunity to shift their elevational range following the changing distribution of key-plant associations (Lenoir et al. 2008; Gottfried et al. 2012; Pauli et al. 2012; Telwala et al. 2013). Yet, in the Quaternary, few climate changes have lasted less than 200–300 years, with temperature oscillations between *c.* 1.5 and *c.* 20 °C (Lourens 2004; Crawford 2014; Wanner et al. 2015), and there is no reason to expect that the ongoing one should be an exception. Even if its origin were solely human, the effects of the present load of greenhouse gases in the atmosphere would last at least 100 more years (Steffen et al. 2018). As to mountain ungulates, far greater effects than those which are detected presently will occur, also on high mountain ranges, especially in case of a further increase of temperature. For example, habitat losses due to climatic changes have been predicted for Nilgiri tahr *Nilgiritragus hylocrius*, Western Ghats, India (Sony et al. 2018), for Marco Polo argali *Ovis ammon polii*, in Tajikistan (Salas et al. 2018), and for other ungulate species in the Tibetan plateau (Schaller 2012; Luo et al. 2015; Jiang et al. 2020).

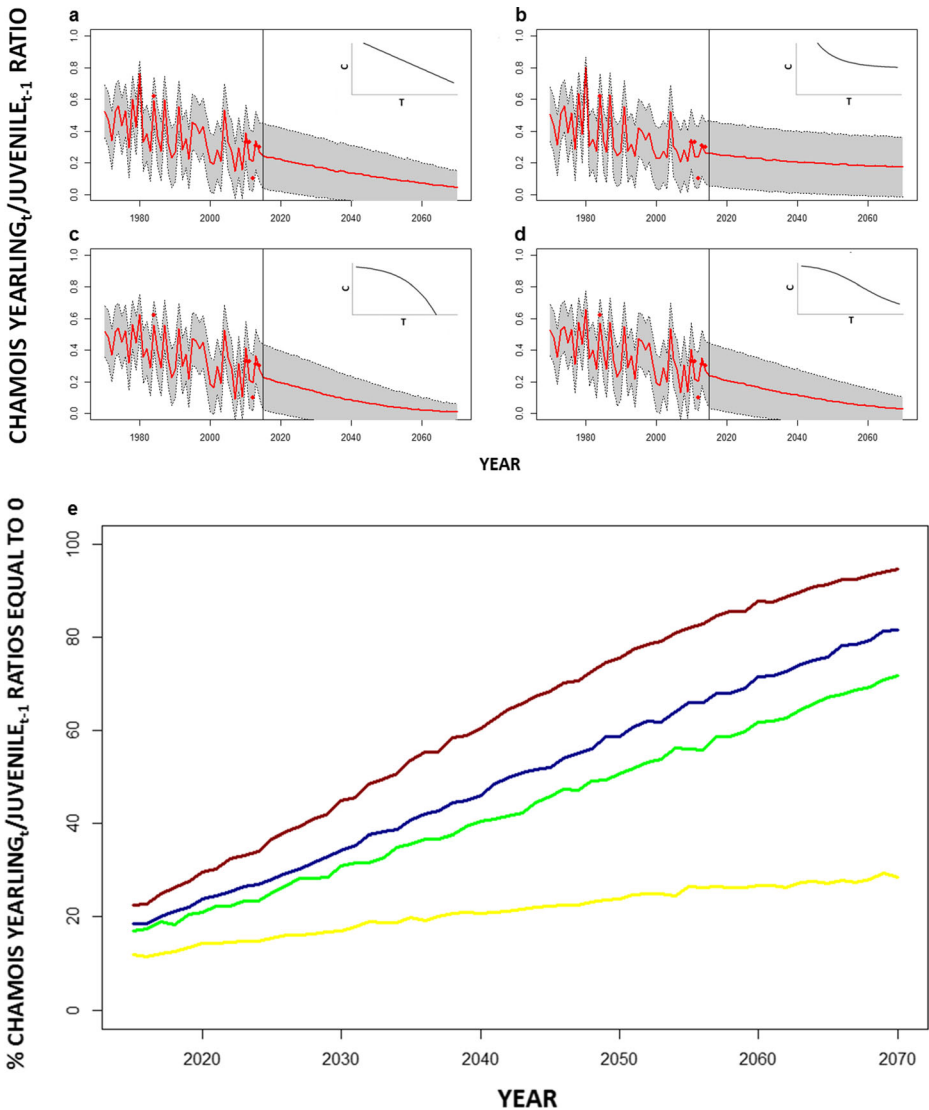


Fig. 4 **a–d** Simulated trajectories of yearling/juvenile_{t-1} ratio of chamois (red line: average; grey area: standard deviation) obtained by trajectories of proportion of plots containing clover, through models depicting four scenarios (**a** linear; **b** positive power; **c** negative power; **d** sigmoidal; cf. Methods). Insets: assumed relationships between spring temperature and proportion of plots containing clover which underlie each scenario; T: mean spring temperature (°C), C: percentage of plots containing clover. **e** Percentages of simulated trajectories of chamois yearling/juvenile_{t-1} ratio equal to 0 (i.e. juvenile winter mortality) in four different scenarios (A: green line; B: yellow line; C: red line; D: blue line), up to 2070

A mountain ungulate may survive the new conditions either by adapting through behavioural plasticity or by shifting its range to higher elevations. When neither compensatory mechanisms occur, the effect of increasing temperature could be detrimental. Behavioural adaptations have been suggested for the Alpine chamois *R. rupicapra rupicapra*, which increased both bite and step rates when foraging in less productive patches and at higher

temperatures (Puorger et al. 2018). Conversely, the ibex *Capra ibex* shifts its foraging areas upslope to fulfil thermoregulatory requirements with increasing temperature, although with ensuing nutritional deficits (Mason et al. 2017). Likewise, Büntgen et al. (2017) reported that, in the last 22 years, Alpine chamois and especially ibex have increased the elevation of their ranges considerably, in the Central Alps (see also Brivio et al. 2019, for ibex). In the absence of compensatory processes, effects could be negative. Mason et al. (2014b) suggested that Alpine chamois will reduce the time spent foraging with the projected increase of temperatures in the next decades. Accordingly, a sharp decline in body mass of juvenile Alpine chamois has been recorded in the last 30 years, in an Alpine area—although a local increase of density could have been involved (Mason et al. 2014a). Mountain ungulates inhabiting low mountains, e.g. the Apennines (this paper) and the Nilgiri Ghats (Sony et al. 2018), and/or sub-arid massifs e.g. Al Hajar Mountains (Ross et al. 2019) and North-African massifs (DGF and UICN 2017), will be unable to shift their range upslope. Furthermore, even when mountain-dwelling ungulates can shift their ranges to higher elevations, the conical shape of mountains usually implies a lower availability of potentially suitable areas with increasing elevation (White et al. 2018; Brivio et al. 2019), although this pattern may vary with mountain topography (Elsen and Tingley 2015). Comparable effects of climatic changes, i.e. elevational range shift and/or habitat loss, have been also predicted for other mountain herbivores (American pika *Ochotona princeps*: Schwalm et al. 2016, Johnston et al. 2019; Royle’s pika *Ochotona roylei*: Bhattacharyya et al. 2018; Alpine marmot *Marmota marmota*: Rézouki et al. 2016; mountain hare *Lepus timidus*: Rehnus et al. 2018) and, in turn, for cold-adapted predators (Arctic fox *Vulpes lagopus*: Tannerfeldt et al. 2002; snow leopard *Panthera uncia*: Aryal et al. 2016; Li et al. 2016). In fact, global effects of climatic changes have been suggested from invertebrates to endotherms (Harrington et al. 1999; Root et al. 2003).

Climate change will determine different responses in populations of mountain ungulates in relation to their specific ecological requirements. Nevertheless, one should expect not only range shifts—where possible—but also local decreases and extinctions. Our findings suggest that increasing spring temperatures will reduce the availability of snowbed vegetation (cf. Liberati et al. 2019), including the best food resources for Apennine chamois, in turn leading to negative demographic consequences. Juvenile mortality is one of the main factors influencing the demographic pattern of animal populations (Gaillard et al. 2000, for ungulates). Our most optimistic scenario has predicted that the yearling/juvenile₋₁ ratios equal to 0 (i.e. juvenile winter mortality) will increase to *c.* 28% by 2070, while the most pessimistic one has predicted a local near-extinction (*c.* 95% losses). The Apennine chamois does not seem to show compensatory adaptations (but see Puorger et al. 2018, for the Alpine chamois): its foraging efficiency has apparently decreased in “poor” areas (Ferretti et al. 2015) and with increasing temperature or decreasing rainfall (Ferretti et al. 2018). In turn, the negative consequences of warmer weather should be very important for mountain-dwelling ungulates living at relatively low elevations, as the Apennine chamois. Interspecific interactions can modify the impact of climate changes: ecologically flexible species may not be affected so much as specialised ones, with the former outcompeting the latter (fish: Van Zuiden et al. 2016; birds: Wittwer et al. 2015; mammals: Tannerfeldt et al. 2002). The use of grassland by red deer is an important factor accelerating the depletion of resources for chamois (Central Alps: Anderwald et al. 2015; Corlatti et al. 2019; Central Apennines: Lovari et al. 2014; Ferretti et al. 2015). The spread of unpalatable pioneer tall grass (for the Central Apennines: Malatesta et al. 2019) and the concurrent reduction of foraging areas (for our study area: Lovari et al. 2014; Corazza et al. 2016) may also play a role, helping the recolonisation of Alpine grasslands by woodland

(Gehrig-Fasel et al. 2007; Espunyes et al. 2019). A warming temperature may also influence the life cycle of parasites, leading to a faster development rate, a longer period when a transmission is possible and increasing transmission rate (e.g. Kutz et al. 2005, 2009), further affecting individuals weakened by food depletion (Craig et al. 2008; Hughes et al. 2009). As to female Apennine chamois, pasture depletion has been associated with a reduction of feeding efficiency and diet quality (Ferretti et al. 2015), to an increase of intra-group feeding interference and endogenous response to stress (Fattorini et al. 2018), as well as to a reduced intensity/frequency of suckling provided to juveniles (Scornavacca et al. 2016). Mountain ungulates must give birth at the beginning of the green-up period, as the mother's milk and the food resources on which the offspring will be weaned are more nutritious (e.g. Pettorelli et al. 2007). Our data show that, in an area of the Central Apennines, there has been a significant increase of spring temperatures, an anticipation by *c.* 25 days in the onset of green-up, with no increase in the duration of the “greenness” plateau. Conversely, the timing of the chamois rut and births have not changed over the last few decades (1979–2014; Lovari 1984; Lovari and Locati 1991; S.L., personal observations), suggesting a decrease in temporal availability of nutritious pasture for chamois offspring and their mothers. A poor pasture will influence milk quality/quantity as well as the availability of rich food resources for weaning juveniles, in turn reducing their body growth and increasing their winter mortality (e.g. Festa-Bianchet 1988; Coté and Festa-Bianchet 2001; Douhard et al. 2018), which is a crucial determinant of changes in population size of ungulates (Gaillard et al. 1998, 2000).

Not surprisingly, chamois numbers have been increasing in areas where they were recently reintroduced, as there they are still in the colonizing phase (*sensu* Caughley 1970), following release in suitable habitat (Mari and Lovari 2006). In most of the translocation areas, the occurrence of higher elevations (> 2000 m) could be an important factor promoting the future viability of chamois populations. For example, in Majella National Park, at higher elevations (2400–2790 m a.s.l.) than in our study area, *T. thalii* nutritious patches have been increasing in response to the milder temperatures of the last few decades (e.g. + *c.* 300% abundance in grasslands, in 1972–2014; Evangelista et al. 2016), confirming our hypothesis of an upward shift of vegetation where higher elevations are available. In spite of their recent increase on mountains above 2000 m, Apennine chamois have decreased by *c.* 20% in their original range from ALMNP (Latini et al. 2015b). The increase of numbers in translocated populations should not be taken as a sign of long-lasting recovery as—all other factors remaining equal—the negative effects of climate changes, presently impinging on chamois populations at lower elevations, should be expected to shift to the higher ones, in the future. Furthermore, red deer have been reintroduced to all areas of translocation of Apennine chamois and one should expect an increase in competition between deer and chamois. If we consider that few Quaternary climate changes have been shorter than 200–300 years and that the present one started less than 100 years ago (Crawford 2014), with a sharp increase in the last 50 years, effects at population level can be expected to be long-lasting and profound.

Global conclusions on absolute extinctions may not be drawn, as the effects of climate changes will vary with the ecological and behavioural flexibility of different species of mountain ungulates, geographical heterogeneity in mountain topography, topoclimatic effects shaping the availability of microrefugia, as well as with the arrival of ecologically competing species. However, shifts in distribution ranges and local decreases up to extinctions should be expected (Wiens 2016, for a review). This will require farsighted measures of adaptive management (e.g. avoiding the introduction of alien species and the human alteration of suitable habitats, as well as contrasting the arrival of potentially competing species; Ferretti and Lovari 2014) to help the conservation of mountain species of herbivores at risk.

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Compliance with ethical standards

Conflicts of interest The authors declare that they have no conflict of interest.

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