

Alpine landscape and canopy cover from 1973 to 2011: are roe and red deer population dynamics linked?

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Abstract

Context. Land-use change may represent a major driver for wildlife population trends in most ecosystems all over the world. In addition to land abandonment and forest management transformation in remote areas of developed countries, such as the European mountains, the intensification of human activities has, by and large, affected the settlement opportunities for wildlife species.

Aims. What changes occurred in the structure and extent of land use between 1973 and 2011 in the Central Eastern Alps, Italy? Are the abundance indices of roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*) driven by these landscape transformations? Is there any relationship between the increase in red deer and the decrease in roe deer abundance?

Methods. The study was conducted in a 1335-km² area (Central Eastern Alps, Italy). Through GIS photo interpretation techniques and patch analysis tools, we determined land-use changes between 1973 and 2011. Correlations between environmental modifications and climatic conditions, as well as between roe and red deer abundance indices (i.e. catch per unit effort (CPUE) and hunting bag data, respectively) were investigated for the 1973–2011 period by implementing linear mixed models.

Key results. The metrics thus calculated revealed a homogenisation of the woodland area and a general landscape simplification. By examining the effects of the climatic factors supposedly affecting population growth rate, roe and red deer trends seemed to be driven also by land-use evolution. Indeed, in the 1973–2011 period a negative trend in the availability of open areas below the tree line (−4.6%) and of agricultural zones (−1.9%) seemed to disfavour roe deer, while a fast increase in woodlands (+7.8%), scrublands (+3.3%) and canopy cover (+7.9%) was reported to be concomitant to red deer range expansion and density increase. Moreover, red deer growth rate impacted on roe deer population dynamics.

Conclusions and implications. Given the ongoing land-use changes, their effect on roe and red deer population trends and the competition issue between them, these results may help managers to apply an effective adaptive-management planning technique for target locations to keep the ecosystem balanced.

Additional keywords: alpine landscape, canopy cover, *Capreolus capreolus*, *Cervus elaphus*, climate characteristics, catch per unit effort (CPUE), foraging areas, population dynamics.

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Introduction

Land-use change represents a major threat to biodiversity in most ecosystems all over the world (Chemini and Rizzoli 2003; Araújo *et al.* 2008; Pellissier *et al.* 2013), with important consequences for their functions (Niedrist *et al.* 2009).

In the last few decades, the mechanisation of agriculture and set-aside policies of the European Union have led farmers to desert mountainous, marginal and less productive areas (Gellrich *et al.* 2007; Stoate *et al.* 2009; Lambin and Meyfroidt 2011; Melendez-Pastor *et al.* 2014). This socioeconomical process has determined a marked increase in forest cover in the eastern Italian Alps and, more generally, in the European mountains (Gehrig-Fasel *et al.* 2007; Tasser *et al.* 2007; Pellissier *et al.* 2013). The maintenance of open

land in such areas relies mostly on human intervention (Wu 2006) and is often funded by agricultural and conservation subsidies.

The environmental consequences of land-use change can be either beneficial (cf. Bowen *et al.* 2007; and Falcucci *et al.* 2008) or detrimental to biodiversity (cf. Pellissier *et al.* 2013; on the negative impact of the loss of open land). Through the modelling of potential future land-use changes by means of explorative scenarios, researchers, land managers and policy and decision makers can examine which processes are expected to occur in a given system under a set of defined, conceivable conditions (Price *et al.* 2015). However, such scenarios should take into account the impact of land-use change on ecosystem dynamics. In this framework, the analysis of adequate time-series datasets

may help evaluate the effect of landscape modification on target species.

Individual species may either decline or increase as a result of the interaction between exogenous and endogenous threats, including landscape modifications (Fischer and Lindenmayer 2007). Indeed, land-use changes were found to affect the distribution and abundance of some herbivore species in the recent past (see Acevedo *et al.* 2005; Gordon 2009). Accordingly, several authors advocated an integrated habitat–fauna management, one which focuses on the interactions between ungulates and vegetation (Weisberg and Bugmann 2003). The combination of time-series datasets and a thorough knowledge of land-use changes and trends over the long period (Danell *et al.* 2006; Owen-Smith 2010; Imperio *et al.* 2012) should help to gain a better understanding of such interaction dynamics.

Red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*) are among the most common European ungulates and the most important game species, together with wild boar (*Sus scrofa*; Apollonio *et al.* 2010). Nonetheless, they are also species of major conservation concern for a variety of reasons. Human interference – selective hunting regimes, translocations (Apollonio *et al.* 2014) and habitat fragmentation in particular – accounted for many management and conservation issues for local and regional populations (Linnell and Zachos 2011).

During the late nineteenth and early twentieth centuries, roe deer faced a serious decline in Europe, both in numbers and distribution, especially due to hunting (Apollonio *et al.* 2010). During the last decades, while red deer showed a steady increase in the Italian Alps, roe deer, despite a general moderate increase, showed a reduction in the region of Trentino-Alto Adige (Central Eastern Alps). Such decrease is likely due to a combination of factors, such as high hunting pressure, environmental changes and competition with other ungulates (Carnevali *et al.* 2009; Raganella Pelliccioni *et al.* 2013). In fact, when resources are limited, competition tends to be higher among sympatric species: evidence of this was reported in large herbivores with overlapping habitats and nutritional niches (e.g. see Bartos *et al.* (2002) for white tailed deer *Odocoileus virginianus*, fallow deer *Dama dama*, red deer and roe deer; Focardi *et al.* (2006) for roe deer and fallow deer; Hemami *et al.* (2004) for roe deer and muntjac *Muntiacus reevesi*; Marshal *et al.* (2008) for feral ass *Equus asinus* and mountain sheep *Ovis canadensis*). Similarly, Richard *et al.* (2010) found evidence of competition between roe and red deer. Within this framework, a better understanding of the interactions between land-use changes and roe and red deer population trends over broad time scales is necessary to improve our knowledge of wider ecosystem dynamics and, consequently, to make better decisions for the management of ungulate species (e.g. formulation and/or adjustment of shooting plans, removal of limiting factors, environmental improvement policies), as well as for the wildlife of that ecosystem.

The aim of this study is to describe the changes that occurred in the structure and extent of land use between 1973 and 2011 in Central Eastern Alps (Italy) and to determine their potential effects on roe and red deer population trends. By controlling the effects of climatic factors and management regimes supposedly affecting population dynamics, we assessed whether land-use change affected the abundance of roe and red deer. Moreover,

given the remarkable increase in both population density and distribution of red deer (Milner *et al.* 2006; Apollonio *et al.* 2010) and the reported evidence of a competition with roe deer (e.g. Richard *et al.* 2010), we investigated whether the competition between these two species also occurs in this area.

Materials and methods

Study area

The study area (1335 km²) covered the Adamello Brenta Nature Park (Province of Trento, Central Eastern Alps, Northern Italy, 46°10'N, 10°45'E) and the surrounding area within a 5-km radius. Elevations range from 65 m above sea level (a.s.l.) on the southern border of Lake Garda to 3558 m a.s.l. in the Presanella Massif. According to the latest version of CORINE Land Cover dataset (CLC) (Commission of the European Communities 2012), 41.1% of this area was forested (up to the tree line at ~2000 m), 17.6% was covered by scrub and/or herbaceous vegetation associations and 29.9% consisted of bare ground with little or no vegetation. Agricultural zones covered 9.7% of the study site, with only 1.3% covered by urban settlements and the remaining 0.4% by inland waters. In addition to red and roe deer, large herbivores included Alpine chamois (*Rupicapra rupicapra*), mouflon (*Ovis orientalis musimon*) and Alpine ibex (*Capra ibex*). A small and yet stable population of brown bear (*Ursus arctos*), a few lynxes (*Lynx lynx*) and an occasional wolf (*Canis lupus*) were the potential terrestrial predators of deer species (Groff *et al.* 2016). However, predation events in the study area were very rare (pers. comm., Adamello Brenta Nature Park, Province of Trento, Italy).

Data collection and landscape analysis

Land-use changes were assessed by creating a layer of 100 random points with the extension Hawth's Analysis Tools for ArcGIS 9.3 (Beyer 2004; ESRI 2008; Fig. 1). We selected eight land-use classes: (1) agricultural zone; (2) inland bodies and/or courses; (3) meadows; (4) open areas below the tree line; (5) scree slope; (6) scrubland; (7) urban area; and (8) woodland. Then, we associated each point with the corresponding land-use class obtained by inspection of orthophotomaps taken in six different years (1973, 1994, 2000, 2006, 2008 and 2011; pixel = 1 m). We followed CORINE Land Cover I level categories (Commission of the European Communities 2012) and considered physical and physiognomic entities at a higher level of detail for 'forests and seminatural areas' (CLC class = 3), also balancing a proper visual interpretation of orthophotomaps and the biological and ecological basic needs of both roe and red deer species.

Moreover, we inferred land-use data for 10 sample sites (total 90 km²; i.e. 7% of the entire study area), which were representative of all the aspect-classes and all the degrees of human presence reported in it; see Fig. 1 for the geographical position of the sample sites.

Each sample site consisted of three rectangles of 3 × 1 km, extending from valley floors to high-altitude areas. Through the analysis of the orthophotomaps (photo-interpretation techniques – 1:2000 m digital scale) for the 6 years of timeframe, we determined land-use allocation of each sample site.

Changes in the percentage of land-use classes (obtained by comparing data derived from sample sites and random points),

spatial analysis of patches and modelling of associated attributes were calculated by means of Patch Analyst for ArcGis 9.3 (ESRI 2008; Rempel *et al.* 2012). We extracted 14 metrics describing patch density, size, edge, shape, diversity and interspersation at landscape (see Table 1 for the complete list of metrics used and for those chosen following the advice and criteria discussed by Gergel and Turner (2002)) and class level (see Table S1 in Supplementary Material). Differences in metrics' means between

the beginning and end of our study period (1973 vs 2011) in the 10 sample sites were tested with a paired *t*-test. Moreover, by using ImageJ software 1.6.0 (Schneider *et al.* 2012), we assessed the canopy cover (i.e. the percentage of land occupied by the orthogonal projection of the tree crown) in 30 squares of 300 m, randomly selected within the woodland class in 1973. In this analysis, each pixel was classified as tree or no tree both with the Thresholding method and by using the Colour Segmentation plugin (Algorithm:

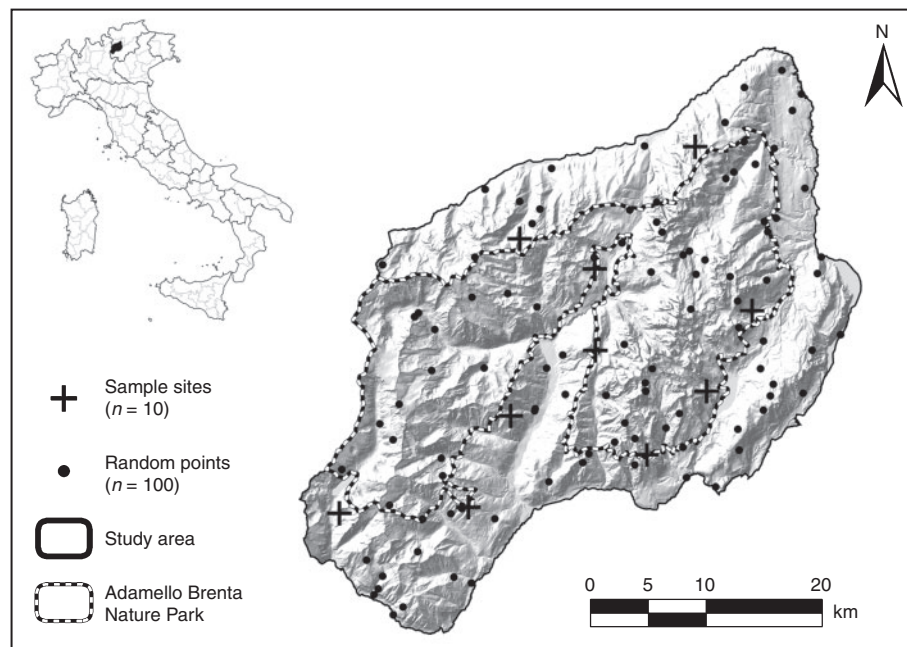


Fig. 1. Digital elevation model of the 1335-km² study area and its location in the Province of Trento (Central Eastern Alps, Italy). Black circles and black crosses represent 100 random points and 10 sample sites used in landscape analysis between 1973 and 2011.

Table 1. Landscape modification (landscape level; length in m and areas in m²) in 10 sample sites (total 90 km²) for 3 years (1973, 1994 and 2011)

See McGarigal and Marks (1994, 1995) for metric definitions

Code	Name	1973	1994	2011
Patch density and size metrics				
Number of Patch ^A	NumP	1118	836	747
Mean Patch Size ($\times 10^3$)	MPS	81	108	120
Median Patch Size	MedPS	5151	4942	6226
Patch Size Coefficient of Variance	PSCoV	399	377	359
Patch Size Standard Deviation ($\times 10^3$)	PSSD	321	405	432
Edge metrics				
Total Edge ($\times 10^3$)	TE	1328	992	946
Mean Patch Edge ^A	MPE	1188	1186	1266
Shape metrics				
Mean Shape Index ^A	MSI	1.60	1.50	1.50
Area Weighted Mean Shape Index	AWMSI	2.92	2.43	2.35
Mean Perimeter–Area Ratio	MPAR	0.09	0.11	0.08
Mean Patch Fractal Dimension	MPFD	1.39	1.38	1.37
Area Weighted Mean Patch Fractal Dimension	AWMPFD	1.34	1.31	1.30
Diversity and interspersion metrics				
Shannon's Diversity Index ^A	SDI	1.32	1.22	1.21
Shannon's Evenness Index	SEI	0.68	0.63	0.62

^AMetrics associated to deer indices. Metrics were chosen following the advice and criteria discussed by Gergel and Turner (2002).

Hidden Markov Model) for the 6 years of investigation. We tested the variation in canopy cover between the beginning and end of our study period (1973 vs 2011) with a paired *t*-test. Given the trends of the data collected from the six maps and the absence of environmental perturbation in the whole study area, we assumed linear changes in landscape variables and canopy cover for each period considered in our analysis.

Management, distribution and population dynamics of roe and red deer

In the Province of Trento, roe and red deer are stalked from mid-September to the end of December. Hunting is controlled through licenses issued by local wildlife boards and hunting quotas are planned yearly on the basis of spring (end of March–April) spotlight counts. Hunting regimes of roe and red deer changed during the study period from hunting plans including only adult males to a gradual balancing of the sex and age classes culled (females and fawns started to appear in the shooting plans of the Province of Trento in 1977). The study area includes 85 municipalities (mean size = 15.7 km²), which form part of five hunting management units. Since roe deer was hunted under a quota regime with no individual assignment to hunters, and given the maximum effort typical of the beginning of each hunting season, we used the number of animals culled during the first 8 days (i.e. 8 days starting from the first Sunday in September) divided by the number of hunters licenced in the shooting plan of each municipality to account for the relative hunting efforts (i.e. catch per unit effort, CPUE) as an indirect measure of the abundance of this species (ROE-In). Roe deer population trend was evaluated by referring to the hunting records of the 1973–2011 period.

As for the red deer, we used the total number of animals culled during the whole hunting season as a proxy of the population trend, in that red deer culls were associated to individual hunters simply on the basis of their abundance. In fact, the hunting effort during the first days of the hunting season was not expected to be greater than at subsequent times and, as Corlatti *et al.* (2016) demonstrated in a neighbouring population (i.e. inside the Stelvio National Park, Italy), spring spotlight counts proved to be reliable indices of relative abundance (RED-In). Moreover, we checked for the absence of bias among red deer observed, harvest quotas and hunted animals by means of Pearson correlation (r_p). These indices were correlated with the landscape modifications, environmental characteristics and climatic data revealed by our analyses (see Table 2 for a complete list of the variables taken into consideration).

We analysed the variation of ROE-In and log(RED-In + 1) (i.e. the logarithmic transformation of red deer abundance index) by fitting a set of linear mixed effect models (LMM) with the maximum likelihood (ML) method (Zuur *et al.* 2009). The site (sampling unit) was fitted as a random factor to avoid pseudoreplication of data (Machlis *et al.* 1985). We used the Information–Theoretic (IT) approach based on the Akaike information criterion, corrected for small sample sizes (AICc; Burnham and Anderson 2002; Symonds and Mousalli 2011), to select the best fitting model. We looked at VIFs (variance inflation factors) of all selected models, dropping any models with VIFs greater than 3 (threshold suggested by Zuur *et al.* 2010).

Table 2. Independent variables and codes used in the starting of model selection for the present study

Variables from each class were selected according to roe and red deer habitat selection, climatic limiting factors for population dynamics, spatial ecology and hunting regimes

Code	Description
Agr	Agriculture zone allocation
Canopy	Canopy cover
Meadow	Meadows allocation
Open area	Open areas below the tree line allocation
Scrub	Scrubland allocation
Wood	Woodland allocation
Snow depth	Average of daily snow depth (cm) during December–March period
SprR	Average of total rainfall (mm) during April–June period
SprT	Average of daily mean temperature (°C) during April–June period
SumR	Average of total rainfall (mm) during July–September period
SumT	Average of daily mean temperature (°C) during July–September period
NumP	Number of patches
MPE	Mean patch edge (m)
MSI	Mean shape index
SDI	Shannon's Diversity Index
RED-In ^A	Red deer abundance
%M	Percentage of males in the hunting bag

^AIndependent variable considered only in model selection as roe deer limiting factor. See the Materials and methods section for an accurate description of this variable and an explanation of its use.

The final set of models obtained was then refitted by using the restricted maximum likelihood REML estimation and validated by checking the assumptions of normality, homoscedasticity and independence, by inspecting the standardised residual plots as described in Zuur *et al.* (2009). Akaike's weights w_i for each *i* model were computed. The effect of each variable (i.e. parameter estimation) included in a confidence set of models with $\sum_{i=1}^n w_i \geq 0.9$ was obtained via model averaging in an AICc framework (model.avg function in MuMin package for R; Burnham and Anderson 2002; Symonds and Mousalli 2011; Barton 2015). Following Magee (1990), to describe the way models fitted the data observed, we estimated R^2 as follows: $R^2 = 1 - \exp(-2/n(\log L_M - \log L_0))$, where *n* is the number of observations, log L_M is the standard log-likelihood of the model (which includes fixed and random effects) and log L_0 is the standard log-likelihood of the intercept-only model. Statistical analyses were performed by using R version 3.1 (R Development Core Team 2011).

Results

A preliminary analysis carried out by associating each of the 100 random points located within the study area with their land-use class showed a remarkable increase in forest (from 35% to 51% of the points classified) and shrub cover (from 5% to 12%), and a dramatic decrease in open areas (from 20% to 1%) over the 1973–2011 period. The increase in urban areas (from 1% to 2%) was counterbalanced by the decrease in agricultural zones

(from 5% to 4%), meadows (from 17% to 14%) and scree slopes (from 17% to 16%).

Analysis of the data from the 10 sample sites revealed an increase of 7.8% for woodland and 3.3% for scrubland, whereas 4.6% of open areas and 4.5% of meadows disappeared during the almost 40 years examined (see Fig. 2 and Table 3 for more details).

On landscape level, a decrease was recorded in Number of Patches ($\alpha < 0.05$) (from 1118 to 747; $t_{(df=9)} = 2.77$, $P = 0.02$), Total Edge (from 1328 to 946 km; $t_{(df=9)} = 4.52$, $P < 0.01$), Mean Shape Index (from 1.59 to 1.49; $t_{(df=9)} = 3.17$, $P = 0.01$), and Mean Patch Fractal Dimension (from 1.60 to 1.50; $t_{(df=9)} = 5.46$, $P < 0.01$). Moreover, Shannon's Diversity Index (from 1.32 to 1.21; $t_{(df=9)} = 12.04$, $P < 0.01$) and Shannon's Evenness Index (from 0.68 to 0.62; $t_{(df=9)} = 11.77$, $P < 0.01$) revealed a decrease in landscape diversity as well as in the heterogeneity of habitat distribution (see Table 1). A complete description of the modifications detected on class level was reported in the Supplementary Materials (Table S1).

The percentage of tree-covered area, evaluated in 30 squares of 300 m side randomly selected within the woodland class in 1973,

was 49.9% in 1973 and 57.8% in 2011 (i.e. we found a reduction in the distance between tree crowns and an increase in tree density). The difference recorded between the beginning and the end of our study period (1974 versus 2011) was significant ($t_{(df=29)} = 5.56$, $P < 0.01$).

No bias among red deer observed, harvest quotas and hunted animals was detected with Pearson correlation (red deer observed versus harvest quotas: $r_P = 0.994$; harvest quotas versus red deer culled: $r_P = 0.993$) over the study period. Thus, the red deer population trend, expressed by the number of red deer culled within each hunting reserve, was positive inside the whole study area (total red deer culled: 2 in 1973, 404 in 1994, and 606 in 2011, Fig. 3). The number of hunting management units increased from 2 in 1973 to 42 in 1994 and 66 in 2011, for a total of 86 units and an average of $20.35 \pm 2.66 \text{ km}^2$. In contrast, the roe deer population decreased (Fig. 3).

The final set of LME models predicting ROE-In and log (RED-In + 1) is reported in Table 4. The LME models selected (roe deer: $\text{AICc} = 4323.81$, $R^2 = 0.59$; red deer: $\text{AICc} = 639.12$, $R^2 = 0.41$) had a 50% and 36% probability (for roe and red deer, respectively) of being the most precise models. We thus

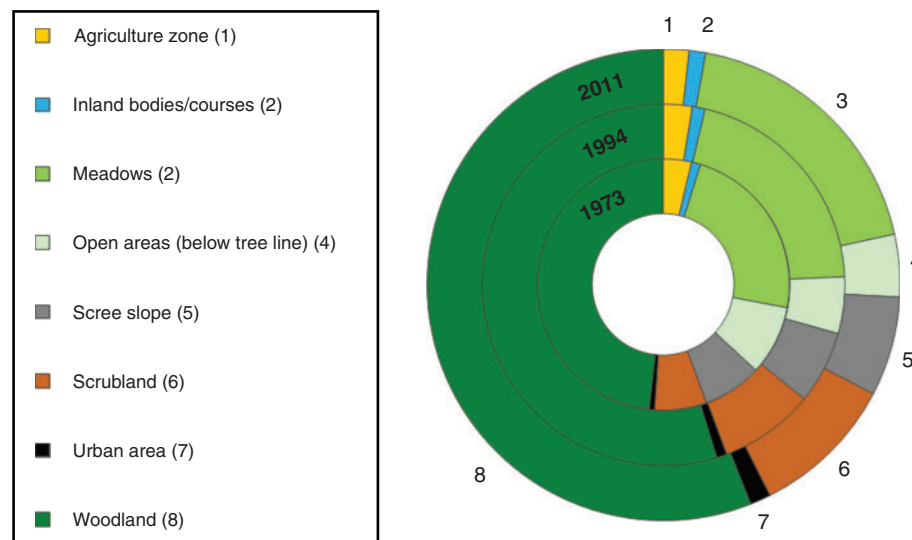


Fig. 2. Percentage of land-use classes recorded in the 10 sample sites through the analysis of orthophotomaps (photo-interpretation techniques – 1 : 2000 m digital scale) for 3 years (1973, 1994 and 2011).

Table 3. Land-use allocation (km^2 and percentage) in 10 sample sites (total 90 km^2) over 3 years (1973, 1994 and 2011)

The last column shows the percentage of variation in land use over the 40-year period

Land-use classes	1973 km^2 (%)	1994 km^2 (%)	2011 km^2 (%)	Δ % (2011–1973)
Agriculture zone	3.28 (3.64)	2.29 (2.55)	1.56 (1.73)	–1.91
Inland bodies/courses	1.05 (1.17)	1.02 (1.14)	1.02 (1.13)	–0.04
Meadows	20.86 (23.18)	18.55 (20.61)	16.82 (18.68)	–4.50
Open areas (below tree line)	8.02 (8.91)	4.55 (5.05)	3.85 (4.28)	–4.63
Scree slope	6.79 (7.54)	5.88 (6.53)	6.14 (6.82)	–0.72
Scrubland	5.97 (6.63)	7.63 (8.48)	8.94 (9.93)	3.30
Urban area	0.63 (0.70)	0.81 (0.90)	1.27 (1.42)	0.72
Woodland	43.41 (48.23)	49.27 (54.74)	50.40 (56.01)	7.78

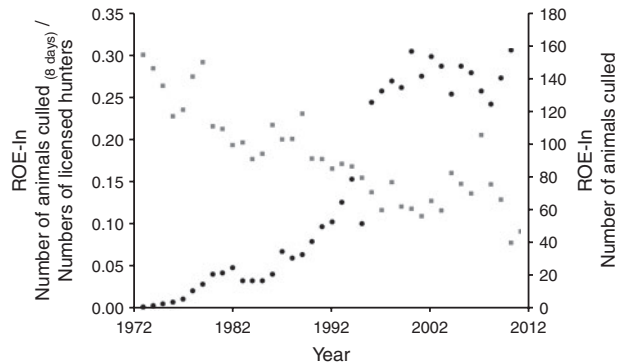


Fig. 3. Roe (in grey) and red deer (in black) population trends represented respectively by the ratio of roe deer culled in the first 8 days of the hunting season divided by the number of hunters licenced in the shooting plan and the total number of red deer culled during the hunting seasons in the municipalities considered from 1973 to 2011 (ROE-In and RED-In, respectively).

Table 4. Selection of Linear Mixed Effect Models predicting the variability of ROE-In and $\log(\text{RED-In}+1)$ in the Central Eastern Alps, Italy (1973–2011)

AICc, Akaike information criterion value corrected for small sample size; ΔAICc , difference in the AICc value between a given model and the most parsimonious model (i.e. lowest AICc); w_i , Akaike weight. Models with $\Delta\text{AICc} < 10$ were displayed. Parameters were calculated for a confidence set of models with a cumulative Akaike weight equal to 0.90 via model averaging and are reported in Table 5. See Table 3 for description of independent variables

Model structure and description	AICc	ΔAICc	w_i
Dependent variable: ROE-In			
Agric + Open area + Red-In	4323.81	0.00	0.50
Agric + Open area	4325.32	1.51	0.23
Agric + Open area + Scrub + Red-In	4326.15	2.34	0.15
Agric + Open area + Scrub	4327.01	3.20	0.10
Agric + Open area + Scrub + SumR + Red-In	4331.53	7.72	0.01
Agric + Open area + Scrub + SumT + Red-In	4332.59	8.78	0.01
Dependent variable: $\log(\text{RED-In}+1)$			
Canopy + Wood + Snow depth	639.12	0.00	0.36
Canopy + Wood + Snow depth + SumT	639.84	0.72	0.25
Canopy + Scrub + Wood + Snow depth	640.03	0.91	0.23
Canopy + Wood + Snow depth + SumT + SprT	641.11	1.99	0.13
Canopy + Scrub + Wood + Snow depth + SumT + SprR	643.76	4.64	0.03

considered a confidence set of models with a cumulative Akaike weight equal to 0.90. Parameter estimation was obtained via model averaging (Table 5). Residual plots are reported in Fig. S1.

The reduction of open areas below the tree line negatively affected roe deer abundance. Our analyses also showed the importance of agricultural zone for this species: the decrease in rural areas contributed to predict ROE-In reduction. At the same time, roe deer dynamics were negatively affected by scrubland increase. As far as the environmental effects on population dynamics are concerned, the fast increase in red deer distribution and abundance also had a negative effect on ROE-In. No climate-related effects were detected (Table 5).

Table 5. Parameter estimates (β), standard errors (s.e.), 95% Confidence Intervals (CI), degree of freedom (df) and P -values (P) for the best set of models ($\sum_{i=1}^n w_i \geq 0.9$) explaining the variability of ROE-In and RED-In in the Central Eastern Alps, Italy (1973–2011)

See Table 3 for description of independent variables

Parameter	β	s.e.	CI		df	<i>P</i>
			Lower	Upper		
Dependent variable: ROE-In						
Intercept	−64.59	19.72	−103.25	−25.93	376	<0.01
Agric	3.55	0.16	3.24	3.86	376	<0.01
Scrub	−0.24	0.03	−0.30	−0.19	376	<0.01
Open area	3.61	0.12	3.38	3.84	376	<0.01
Red-In	−1.08	0.16	−1.40	−0.76	376	<0.01
Dependent variable: log(RED-In + 1)						
Intercept	16.46	1.03	14.44	18.48	373	<0.01
Scrub	0.09	0.02	0.05	0.13	373	0.04
Canopy	1.13	0.04	1.05	1.21	373	<0.01
Wood	1.21	0.03	1.15	1.27	373	<0.01
Snow depth	−1.09	0.08	−1.25	−0.93	373	<0.01
SprR	0.34	0.04	0.26	0.42	373	0.06
SprT	−0.21	0.02	−0.25	−0.17	373	0.07
SumT	−1.02	0.07	−1.16	−0.88	373	<0.01

Unlike roe deer dynamics, red deer abundance was affected by climate conditions. Spring rainfall had a positive effect on red deer increase, while high temperature in spring and summer and winter harshness had a negative impact. As for the land-use changes reported during the study period, forest modifications were found to be crucial: the increase in scrubland, woodland and canopy cover favoured the red deer population dynamics (Table 5).

Discussion

The land-cover dynamics we observed on a local scale in our study area are consistent with the large-scale dynamics detected in Europe, particularly in mountainous zones, where the decreasing significance of agriculture has led to an increasing land abandonment (Stoate *et al.* 2009; Lambin and Meyfroidt 2011; Melendez-Pastor *et al.* 2014). The land-use changes observed in the present study include the loss of open-land habitats, which usually became forested habitats, thus possibly leading to significant consequences for biodiversity and species composition (Queiroz *et al.* 2014; Price *et al.* 2015).

Falcucci *et al.* (2007) analysed the changes in land-use and land-cover patterns over the period 1960–2000 on a national scale, subdividing the Italian peninsula into six macro-regions. The study showed an increase in forests since the 1960s, especially in mountainous and hilly areas (mainly on the Alps and Apennines), and a decrease in pastures.

As for landscape metrics and land-use evaluation, our study revealed an increase in woodland and scrubland and, by contrast, a marked decrease in meadows and in open areas below the tree line. Moreover, both wood-range and canopy cover were reported to increase between 1973 and 2011, thus showing increasingly less distance between tree crowns and increasingly higher tree density (e.g. Poyatos *et al.* 2003; Gehrig-Fasel *et al.* 2007).

Land-use and/or land-cover changes, and the associated habitat loss, are usually regarded as most important factors causing changes in animal exploitation rates within a given

ecosystem (Brooks *et al.* 2002; Serrouya *et al.* 2011). Indeed, herbivores' habitat selection is determined by the abundance and quality of forage (Bowyer *et al.* 1998), as well as by level of cover (Mysterud and Østbye 1999; Dussault *et al.* 2005; Borkowski and Ukalska 2008). While foraging in open and productive habitats, individuals must trade off risks (i.e. higher probability to be preyed) with benefits (i.e. better foraging sites; Lima and Dill 1990; Johnson *et al.* 1995; Massé and Côté 2009). Indeed, several studies reported that ungulates select feeding sites located at the edge of open and forested habitats that provide protective cover (Tufto *et al.* 1996; Mysterud and Østbye 1999).

Our study assessed the correlations between environmental modifications and climatic conditions over the period 1973–2011 and investigated roe and red deer population abundance indices. As Stephens *et al.* (2015) reported, proxies for population abundance are widely used, though often criticised. Nonetheless, the use of these indices is still widespread for several reasons: first, if compared with absolute estimates of abundance, it offers a low-cost approach; second, in some cases, absolute estimates of density are unnecessary luxuries; third, evidence suggests that indices can provide a reasonable proxy for abundance. In our case study, long-term monitoring of red deer (i.e. spring spotlight counts) was found to have a strong relationship with the abundance population index chosen. In the case of roe deer, in fact, the use of CPUE index was effective in providing a reasonable proxy for abundance (Schmidt *et al.* 2005; Imperio *et al.* 2010; Boyce *et al.* 2012). By analysing these indices, we can argue that the negative trend of roe deer and the increase in red deer distribution range and density between 1973 and 2011 seemed to be driven, among other factors, by the land-use and/or land-cover evolution. Indeed, the decline of open areas below the tree line and of agricultural zones and the increase in scrublands were all related to the reduction in roe deer quantity. On the contrary, the development of woodlands and scrublands and the increase in canopy cover favoured the red deer expansion range and density. This is consistent with the trend reported for these species nationwide (Carnevali *et al.* 2009; Apollonio *et al.* 2010): roe deer were initially favoured by the abandonment of agriculture in hills and mountains, and strongly increased in number thanks to the creation of wide ecotone areas. However, as this process took place and woodland replaced scrubland, red deer prevailed as they better adapted to the new habitat.

Our results also showed a different trade-off between forage abundance and quality and protective cover used by roe and red deer. The presence of a forest cover is important for both roe and red deer in hunted populations (Borkowski and Ukalska 2008), though the forest's characteristics seem to have a greater importance for red deer population dynamics (Brazaitis *et al.* 2014). On the contrary, because of its small body size and income breeder strategy, roe deer is strongly dependent on high quality trophic resources (Duncan *et al.* 1998) and, as a consequence, on the availability of open areas below the tree line.

Roe deer has been extensively studied in the last few decades. Long-term monitoring of marked populations provided detailed information as to survival population dynamics and density-dependent effects (Gaillard *et al.* 1993, 1997, 1998, 2003; Hewison and Gaillard 1996; Focardi *et al.* 2002; Kjellander *et al.* 2004; Pettorelli *et al.* 2005). Besides, complex

behavioural adaptations were reported for this species throughout its range and Andersen *et al.* (1998) recorded a considerable life-history variation (e.g. Mysterud 1999; Rossi *et al.* 2003; Saïd *et al.* 2009; Scheibe *et al.* 2009). The role of land-use changes in roe deer population trends is particularly important in ecosystems that are gradually being re-inhabited by large carnivores and increasingly occupied by such a competitor as red deer, as is currently the case of the Alps. In fact, during the last four decades, roe deer has had to cope with a remarkable increase in both population density and distribution of red deer (Milner *et al.* 2006; Apollonio *et al.* 2010), and evidence of a competition has been reported. For instance, Latham *et al.* (1997) found a negative correlation between the densities of these two species in Scottish forest, while Richard *et al.* (2010) demonstrated that roe deer performance was negatively affected by the increase in red deer density by using a long-term monitoring of sympatric populations in France. After checking for possible confounding effects (i.e. date of shooting, climatic conditions, roe deer density), the latter study showed that red deer density in a given year had a markedly negative influence on the body mass of roe deer fawns born in the same year and in the following one. Thus, roe deer dynamics were modelled by a combination of factors including land-use change due to land abandonment and forest management transformation, and the increase in red deer abundance. Contrary to our expectations, the change from hunting plans including only adult males to more appropriate hunting regimes (i.e. with a gradual balancing of the sex and age classes culled) had no influence on roe deer dynamics. This result may be due to the delayed effect of the implementation of such strategy.

Red deer increased exponentially over the study period, with a slowdown in the final years. This paradigm is typical in the ecology and management of large herbivores that, following a phase of expansion to a new range as well as after both reintroductions and releases, usually increase at a high rate (e.g. McCullough 1997; Forsyth and Caley 2006).

While land-use evolution towards woodland positively affects red deer population trends (Brazaitis *et al.* 2014), high temperature can negatively affect this species' dynamics in summer as well as in spring, as both seasons can be related to changes in plant phenology. Plant phenology has a strong impact on plant quality, because young plants generally have a high nutritional value with low levels of secondary plant chemicals (Demment and Van Soest 1985; Van Soest 1984). Specifically, the start of vegetation growth, which is assumed to be strongly determined by snow depth and spring conditions (Langvatn *et al.* 1996; Post and Stenseth 1999), is regarded as a key period for herbivores. Indeed, in spring, animals have to recover from the winter harshness and face the most demanding period in terms of energy (i.e. lactation) (Clutton-Brock *et al.* 1982; Illius and O'Connor 2000), and any mismatch between biological cycles and green-up time prove detrimental to the ungulate population (Pettorelli *et al.* 2007; Plard *et al.* 2014). In addition, snow depth should be considered a key factor in red deer population dynamics, not only in determining vegetation growth, but also as a direct cause of death (Jędrzejewski *et al.* 1992; Loison *et al.* 1999).

In conclusion, on the one hand, the ongoing land-cover dynamics (particularly in mountainous zones) seem to favour

red deer distribution range and abundance. On the other hand, they have a direct (i.e. decrease in preferred habitat) and indirect (i.e. red deer increase) negative effect on roe deer population dynamics. Accordingly, an improved knowledge of ecosystem dynamics may allow for an effective adaptive management for target and/or identified locations to keep the ecosystem balanced.

Conflicts of interest

The authors declare no conflicts of interest.

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