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Title: Different effects of alpine woody plant expansion on domestic and wild ungulates

Running head: "Effects of woody plant expansion on ungulates"

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Abstract

Changes in land-use and climate affect the distribution and diversity of plant and animal species at different spatiotemporal scales. The extent to which species-specific phenotypic plasticity and biotic interactions mediate organismal adaptation to changing environments, however, remains poorly understood. Woody plant expansion is threatening the extent of alpine grasslands worldwide, and evaluating and predicting its effects on herbivores is of crucial importance. Here, we explore the impact of shrubification on the feeding efficiency of Pyrenean chamois (*Rupicapra p. pyrenaica*), as well as on the three most abundant coexisting domestic ungulate species: cattle, sheep and horses. We use observational diet composition from May to October and model different scenarios of vegetation availability where shrubland and woodland proliferate at the expense of grassland. We then predicted if the four ungulate species could efficiently utilise their food landscapes with their current dietary specificities measuring their niche breath in each scenario. We observed that the wild counterpart, due to a higher trophic plasticity, is less disturbed by shrubification compared to livestock, which rely primarily on herbaceous plants and will be affected 3.6 times more. Our results suggest that mixed feeders, such as chamois, could benefit from fallow landscapes, and that mountain farmers are at a growing economic risk worldwide due to changing land-use practices and climate conditions.

Introduction

Environmental and climatic changes are affecting biological and ecological systems across the globe at alarming rates (Steffen *et al.*, 2005). These trends influence fauna and flora in many ways, from habitat degradation to distributional range shifts, as well as phenological mismatch (Parmesan & Yohe, 2003; Root *et al.*, 2003; Pereira *et al.*, 2010). In fact, global land-use and climatic changes, through their influence on different aspects of the biology and ecology of species, have caused numerous extinctions (Vitousek *et al.*, 1997), with models predicting an intensification of these trends over the next century (Loarie *et al.*, 2009). Specialist species are predicted to decline at a faster rate due to their limited adaptive potential within their narrow environmental tolerances (Thuiller *et al.,* 2005; Morrison *et al.*, 2018). Understanding the species-specific potential and limitation to cope with global change is thus a central aspect of timely conservation studies (Nussey *et al.*, 2005; Charmantier *et al.*, 2008).

In this context, evaluating and predicting the impact of global change on wild herbivores has become a conservation priority globally, since their protection and management has been deemed crucial for the long-term conservation of ecosystems (e.g., Büntgen *et al.*, 2014). Indeed, herbivores fulfil key roles in the terrestrial trophic cascades and the maintenance of ecosystem health by affecting nutrient cycles and maintaining the diversity and stability of predators and primary producers (Bardgett & Wardle, 2010). They are also considered “environmental engineers” due to their fundamental role in the structure, composition, and functioning of ecosystems (Schmitz, 2008). Numerous questions regarding the effects of global change must be answered including whether or not herbivores will be able to maintain their role in a particular ecosystem subject to change.

European mountains are a paradigmatic representation of a changing ecosystem, host of a wide variety of wild and domestic herbivores. As in other mountain ranges around the world, they have undergone a biological shift since the mid-20th century due to profound agricultural land-use and climatic changes (Sanz-Elorza *et al.*, 2003; Mottet *et al.*, 2006; Steinbauer *et al.*, 2018). The dramatic decline in rural populations and agropastoral activities have led to a general decline in livestock densities (Didier, 2001; Gartzia *et al.*, 2016). Temperatures have simultaneously increased (IPCC, 2007), which have affected these ecosystems, albeit to a lesser degree, for example by stimulating shrub development or by upward shifting the tree line

(Peñuelas *et al.*, 2007; Ameztegui *et al.*, 2016). Consequently, plant succession at varying rates leads to woody plant expansion (Prévosto *et al.*, 2011; Mod & Luoto, 2016), resulting in a shift in dominance from herbaceous to woody plants in one of the richest habitats in the world: alpine grasslands (Wilson *et al.*, 2012). However, this so-called shrubification (Martin *et al.*, 2017) generally decreases the diversity of plant species (Tasser & Tappeiner, 2002; Koch *et al.*, 2015), the productivity of the environment (Lett & Knapp, 2003) and the diversity and total abundance of mammals (Stanton *et al.*, 2018). Community composition and ecological interactions between species, including herbivore-plant interactions, are being importantly restructured (Lurgi *et al.*, 2012). These trends will likely continue as models predict a continuous increase in temperature (López-Moreno *et al.*, 2008) and a decrease in rural agropastoral activities (Verburg *et al.*, 2010; Mann, 2013).

The Pyrenees, in southwest Europe, have experienced a major expansion and densification of shrubland and forested areas over the last century. For this reason, they constitute an ideal study case of the effects of land-use and climate change on natural communities. Not only have tree line ecotones increased on average by 35m (Ameztegui *et al.*, 2016), with forest cover in some areas expanding by at least two-thirds (Poyatos *et al.*, 2003; Lasanta-Martínez *et al.*, 2005), but they have also experienced an increase in recent summer temperatures occurring at an unprecedented rate (Büntgen *et al.*, 2008, 2017). These locally detected changes are consistent with a larger-scale trend across most (or even all) of the European mountain systems (Fig. 1).

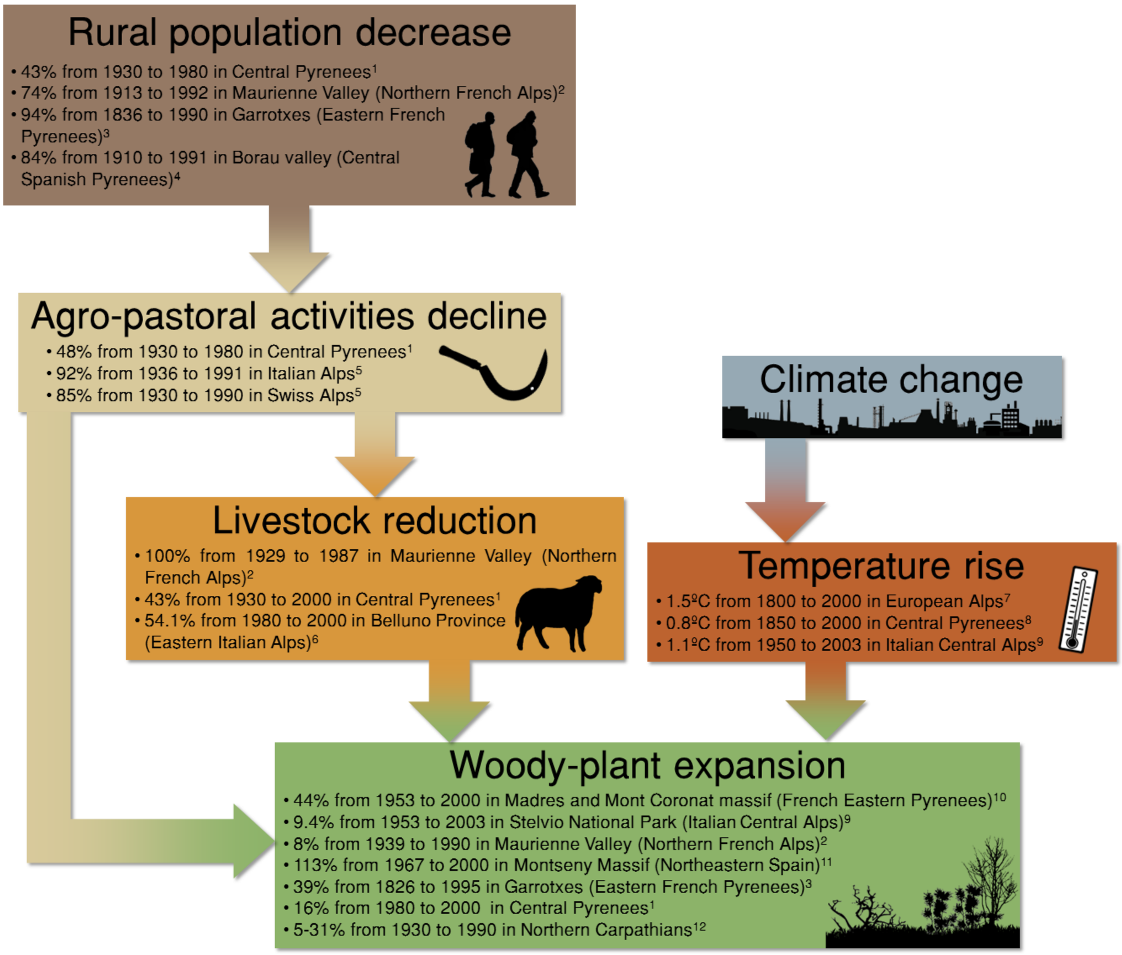

Figure 1. Schematic representation of the primary causes of woody plant expansion in European alpine ecosystems. The decrease in mountain rural populations causes a decline in agropastoral activities and therefore a reduction in livestock densities. At the same time, temperatures increase due to climate change. The combination of these factors leads to the expansion of woody plants in alpine grasslands (1. Gartzia *et al.*, 2016; 2. Didier, 2001; 3. Metailié & Paegelow, 2005; 4. Lasanta-Martínez *et al.*, 2005; 5. Collantes, 2006; 6. Sturaro *et al.*, 2005; 7. Büntgen *et al.*, 2006; 8. Büntgen *et al.* 2017; 9. Cannone *et al.*, 2007; 10. Roura-Pascual *et al.*, 2005; 11. Bartolomé *et al.*, 2005; 12. Kozak *et al.*, 2007)

Through evolution, and in some cases further domestication, large herbivores present in the Pyrenean grasslands display a wide range of body sizes, digestive systems and feeding behaviours adapted to specific diets. They are consequently expected to respond differently to habitat change (Somero, 2010) and are thus good models for the study of species-specific effects of woody plant expansion.

The aim of this study is to explore the potential impact of the expansion of woody plant coverage on four herbivore species in the eastern Spanish Pyrenees - the wild Pyrenean chamois (*Rupicapra p. pyrenaica*), as well as seasonal domestic cattle, sheep and horses - that inhabit the same alpine habitats. Traditional farming is based on livestock freely living and grazing on alpine grasslands during the summer to reduce the economic costs involved in livestock maintenance. Once the yield of these human-created grasslands decay, livestock is then moved to the hay meadows in the lower parts of the valleys until the following spring (Montserrat & Fillat, 1990). The Pyrenean chamois is a medium-sized wild caprinae well adapted to mountain environments. They are considered mixed feeders, which consume a wide variety of resources depending on the habitat and season, following the annual cycle of primary productivity (Espunyes *et al.*, 2019). Together, these four species represent a contrasting collection of energetic requirements (large- vs medium-sized herbivores), feeding behaviours (grazers vs mixed feeders), digestive physiologies (rumen vs hindgut fermenters), and origins (livestock vs wildlife).

We devised various scenarios of shrubification based on the current vegetation cover, where shrubland and woodland proliferate at the expense of grassland following models of projected woody plant expansion. We then use these shrubification scenarios and the diet composition of the ensemble of herbivores to predict how phenotypic plasticity and biotic interactions mediate the effects of shrubification. Given the diverse dietary requirements of our four species, we hypothesise that changes in land cover would affect each species differently, with grazers being more severely and rapidly affected than mixed feeders.

Methods

Study area

The study was carried out in the Freser-Setcases National Game Reserve (FSNGR), in the eastern part of the Spanish Pyrenees (42°22′N, 2°09′E). This area of 410 ha is known as Costabona and ranges from 1500 to 2400 m.a.s.l. It belongs to the sub-humid subalpine and alpine bioclimatic belts of the southern slopes of the Pyrenees, with a noticeable Mediterranean climatic influence (Vigo, 2008). Mean annual temperature for 2009-2012 was 5.7 ºC (daily min=-18.2, max=26.6), and mean yearly accumulated rainfall for the same period was 1042.4 mm (yearly min=762.6, max=1282.8). These data were obtained from the Nuria meteorological station at 1971 m a.s.l. in the core of the FSNGR (Servei Meteorològic de Catalunya).

The vegetation cover of our study area was assessed in June 2011 following the line-intercept method proposed by Cummings and Smith (2000). The cover of all plant species present was recorded along six randomly selected transects of 10×0.1 m at different altitudes.

Collection and analysis of faeces

Fresh faecal samples from each of the four ungulates considered in this study (namely Pyrenean chamois, cattle, horses and sheep) were collected monthly from June to October 2011 and 2012 (except in September 2012 when sampling was not possible due to adverse meteorological conditions), coinciding with the presence of the four species in the area. Once every month, two observers walked a transect of about 5 km, covering the entire altitudinal range and main vegetation communities of the study area. Fresh faecal samples from at least five individuals per species were collected and pooled together before being transported to the laboratory and frozen at -20 ºC after every session. A total of nine pooled samples was obtained per species. This sampling procedure was used to obtain a general overview of the variability of feeding in the field during the three periods of plant phenology in our study area (namely: green-up, plateau greenness and senescence periods; Villamuelas et al., 2016).

A faecal cuticle microhistological analysis was used to determine dietary composition, adapted from a protocol described by Stewart (1967). The samples were thawed, washed and ground to separate the epidermal fragments. Ten grams of sample were then placed in a test tube containing 5 ml of 65% concentrated nitric acid, boiled in a water bath for 1 min, and diluted with 200 ml of water. This suspension was passed through 1.00- and 0.25-mm filters. The 0.25-1.00 mm fraction was spread on glass microscope slides in 50% glycerol, and cover-slips were fixed with DPX microhistological varnish. Two slides were prepared from each sample. The slides were microscopically examined by the same operator at magnifications of 100× and 400×, and 200 fragments of plant epidermis were identified per sample. An epidermis collection of the 55 main plant species in the study area were collected and used for fragment identification. Plant cuticles were identified to the species or genus level depending on the difficulty of the task.

Simulation of woody plant expansion

Patterns of expansion of woody plants into grasslands have been studied worldwide (Olsson *et al.*, 2000; Bartolomé *et al.*, 2005; Falcucci *et al.*, 2007; Eldridge *et al.*, 2011). This plant succession can proceed at different speeds and with different numbers of stages depending on land-use patterns, initial state, altitude, or topography (Tasser & Tappeiner, 2002; Vacquié *et al.*, 2016). This process can nevertheless be synthesised in a first successional stage when herbaceous species are replaced by shrubs, followed by a second successional stage when shrubs are replaced by trees (Gellrich *et al.*, 2007; Tasser *et al.*, 2007; Wallentin *et al.*, 2008;

Améztegui *et al.*, 2010). Succession can be fast; descriptive and predictive studies have demonstrated that woody plant cover can increase by 0.5-5% per year (Barger *et al.*, 2011; Komac *et al.*, 2013).

To simulate the effects of woody plant expansion, we devised eight hypothetical scenarios where shrubland and woodland proliferate at the expense of grassland without any agricultural practices or forestry management. Based on the original vegetation availability in the study area, we designed shrubification scenarios where woody plants increased and graminoids and forbs decreased proportionally. The initial state of the system (i.e. original scenario) comprised a relative abundance of woody species of 21.4% (19.6% shrubs and 1.8% trees). Total relative abundance of woody plants was then increased by intervals of 10% per scenario until reaching 100% of woody plant cover (except the first scenario which increased by 8.6% to achieve 30% woody plant cover). This procedure yielded nine scenarios of woody plant cover (the original scenario plus eight hypothetical): 21.4%, 30%, 40%, 50%, 60%, 70%, 80%, 90% and 100%, respectively. The increase in woody plant cover was distributed proportionally across the plant species included in this category according to their relative abundance. For example, if woody plant cover increased by 20% and the plant *Juniperus communis* represents 50% of the total woody plant cover then a 10% increase of that plant was simulated. Conversely, the cover of forbs and graminoids was decreased by the same fraction of woody plant increase. This decrease was also distributed proportionally between the species of these categories (see Supplementary Table S1).

Landscape-use efficiency

The breadth of a resource niche can be used as a proxy for species performance (Rotenberry & Wiens, 1980) or to quantify the extent to which organisms are able to exploit their environment (Krebs, 1999). We used the measure of niche breadth proposed by Smith (1982) as a proxy for the efficiency in the use of resources by the herbivores (i.e. landscape-use efficiency, LUE).

LUE for each herbivore in each shrubification scenario was calculated as:

$$LUE = \sum \left(\sqrt{P_j \times A_j} \right)$$

where P_j is the proportion of plant j in the diet of the herbivore, and A_j is the proportion of plant j available in the study area. This index ranges from nearly zero, for the narrowest possible niche when a species is specialised in eating the rarest resources, to one, for the broadest possible niche when a species uses resources in proportion to their availability. This index is thus low when a species inefficiently uses the resources of its habitat and is high when a species uses them efficiently (i.e. proportionally to the availability).

Statistical analysis

After describing the diets of our studied species by basic statistics, we performed a non-parametric multivariate analysis of similarity (ANOSIM; Clarke, 1993) to check for differences in diets between herbivores. The ANOSIM statistic *R* is based on the difference of mean ranks between groups and within groups and a high value of *R* in this analysis indicates a high dissimilarity between groups. A nonmetric multidimensional scaling (NMDS) plot based on Bray–Curtis dissimilarity indices was created to visually identify the patterns in dietary similarities between species. Stress, a measure of goodness of fit should be <0.2 in order to have a good representation with no prospect of misinterpretation (Clarke & Warwick, 2001). Our NMDS stress was 0.0985 so our representation was considered to be sufficiently well-described in two dimensions. The ANOSIM and the NMDS plot were performed using the R vegan package (version 2.4-5, Oksanen *et al.*, 2017).

We then evaluated the impact of woody plant expansion (i.e. woody plant abundance in the scenarios) on the LUE of each species by a linear model (LM). LUE of each species was the response variable in our LM whereas the interaction between animal species and degree of woody plant expansion were our fixed explanatory factors. Interspecific differences of LUE values were analysed with a pairwise Mann-Whitney U test using the FSA package (version 0.8.17, Ogle, 2017).

Normality of residuals and homogeneity of variance assumptions were checked previous to the performance of any analysis. All statistical analyses were performed using R version 3.4.3 (R Core Team, 2018).

Results

Initial state of the system and herbivore diets

We recorded 65 plant species in our study area. Graminoids represented half of the vegetation cover (51.6%), where *Festuca* spp. was clearly dominant (32.3%), followed by *Carex cariophyllea* (12.4%). Forbs covered almost one-third of the area and were dominated by *Trifolium alpinum* (7.5%), followed by *Trifolium repens* (1.5%) and *Hippocrepis comosa* (1.4%). The other plants were woody species (shrubs and trees, 21.2%), where dwarf shrubs (*Calluna vulgaris* and *Juniperus communis*) and legumes *Cytisus* spp. were the most common (See Table S1).

The ANOSIM indicated that the differences in dietary composition were higher between Pyrenean chamois and the livestock than amongst the livestock species (Table 1). Among the livestock diets, horse diet differed the most from the rest, while cattle and sheep showed more similar dietary compositions. The NMDS plot supported these interspecific dietary differences (Fig. 2).

	Cattle	Horses	Sheep
Chamois	R=0.506 p= 0.002	R=0.692 p=0.001	R=0.569 p=0.001
Sheep	R=0.246 p=0.013	R=0.427 p=0.001	
Horses	R=0.386 p=0.002		

Table 1. Differences in dietary composition between alpine ungulates in the Pyrenees. Summary of the pairwise ANOSIM of the differences in dietary composition between Pyrenean chamois, cattle, horses, and sheep from June to October 2011 and 2012 in the eastern Spanish Pyrenees. A high value of R in this analysis indicates a high dissimilarity between groups.

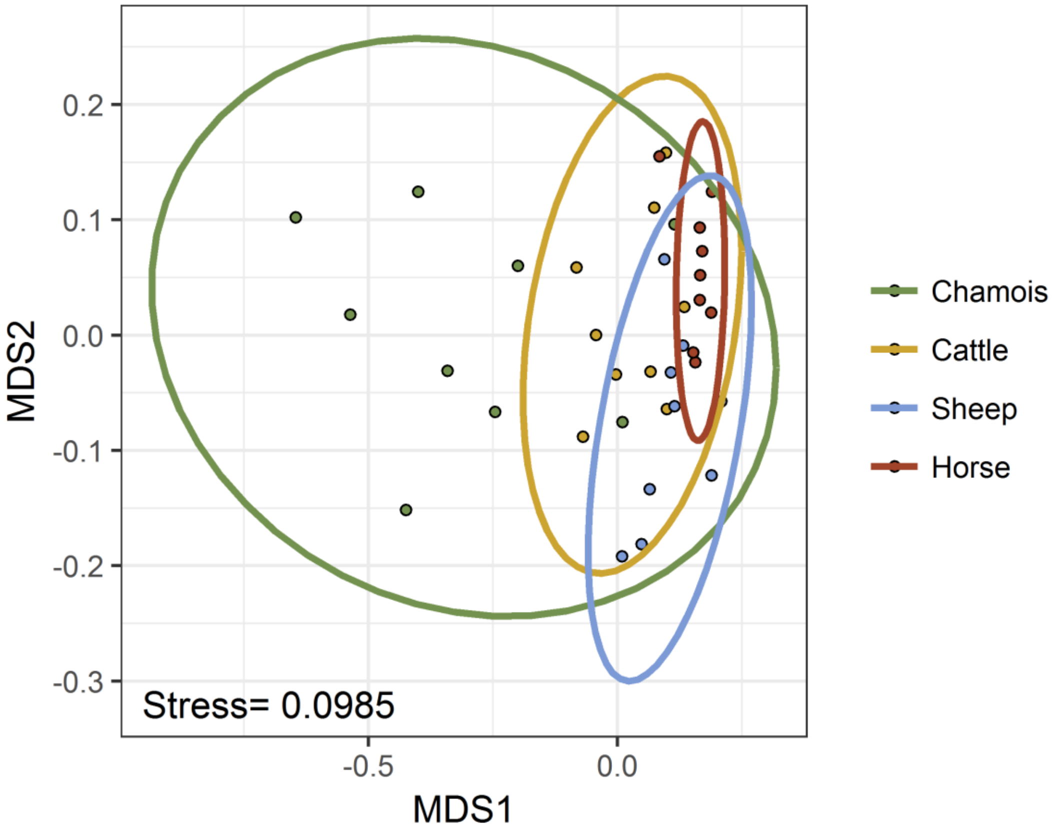

Figure 2 Diet dissimilarity among alpine ungulates in the Pyrenees. Nonmetric multidimensional scaling (NMDS) plot representing dietary dissimilarity for seasonal livestock (cattle, horses, and sheep) and Pyrenean chamois from June to October 2011 and 2012 in eastern Spanish Pyrenees. When stress, a measure of goodness of fit, is <0.2, NMDS reproduces an adequate depiction of the groups.

Analysis of diet composition for livestock during summer and autumn showed a larger overall content of graminoid and forb fragments compared to woody plants. Horses were the most extreme livestock species with the highest consumption of graminoids (63.7%) and the lowest consumption of woody plants (5.9%; see Table 2). On the contrary, Pyrenean chamois faeces had the highest content of woody plant fragments (48.6%) and the lowest content of graminoids (25.8%) and forbs (25.3%). Cattle and sheep had similar diets (*R*=0.246, see table

1), but cattle showed a higher content of graminoids (cattle: 49.8%; sheep: 45.9%) and woody plants (cattle: 16.2%; sheep: 12.4%) and a lower content of forbs (Cattle: 34.1%; sheep: 41.6%).

	Chamois	**Cattle**	**Horses**	**Sheep**
Woody plants				
Calluna vulgaris	24.6 (0.0-6.0)	10.9 (1.0-22.5)	2.2 (0.0-12.0)	2.1 (0.0-29.5)
Cytisus spp.	17.3 (3.5-51.5)	0.1 (0.0-0.5)	0.0 (0.0-0.0)	0.3 (0.0-6.0)
Other woody plants	7.1 (0.0-17.5)	5.2 (2.0-8)	3.7 (0.5-9.5)	10.1 (3.0-17.0)
Total	**48.6**	**16.2**	**5.9**	**12.4**
Graminoids				
Festuca spp.	22.0 (8.5-50.0)	40.4 (26.5-52.0)	52.4 (43.0-63.5)	40.4 (27.5-52.0)
Avenula pratensis	1.8 (0.0-6.5)	3.2 (0.0-6.5)	1.8 (0.0-6.0)	2.1 (0.0-4.5)
Other graminoids	2.1 (0.0-6.5)	6.2 (3.0-11.5)	9.5 (5.0-13.0)	3.4 (2.0-7.0)
Total	**25.8**	**49.8**	**63.7**	**45.9**
Forbs				
Anthyllis vulneraria	1.3 (0.0-5.0)	2.2 (0.0-7.0)	1.5 (0.0-4.5)	4.1 (2.0-6.5)
Plantago monosperma	3.6 (0.0-9.0)	3.5 (2.0-5.0)	3.9 (2.0-8.0)	5.2 (3.0-10.0)
Potentilla spp.	2.5 (0.0-6.0)	3.9 (2.0-6.0)	2.2 (0.5-4.5)	4.7 (1.5-8.0)
Trifolium spp.	11.2 (2.0-17.5)	13.4 (5.5-21.0)	13.8 (7.0-20.0)	14.2 (6.0-21.5)
Other forbs	6.7 (2.5-10.5)	10.9 (4.0-17.0)	9.1 (5.0-19.0)	13.5 (8.5-20.0)
Total	**25.3**	**34.1**	**30.4**	**41.6**

Table 2. Dietary composition of Pyrenean chamois and seasonal cattle, horses, and sheep in the Pyrenees. Data from June to October 2011 and 2012 in the Freser-Setcases National Game Reserve (eastern Spanish Pyrenees). Values represent mean percentages of fragment frequency (min-max).

Simulation of woody plant expansion and LUE

Changes in LUE through the hypothetical scenarios of woody plant expansion suggested that horses would be most affected by the disappearance of grasslands in the Pyrenees. Pyrenean chamois, on the other hand, could even benefit during the early stages of expansion (Fig. 3).

Current LUE is lower for chamois (median=0.72, min=0.57, max=0.75) than livestock (cattle: median=0.76, min=0.70, max=0.79; horses: median=0.74, min= 0.71, max=0.79; sheep: median=0.73, min=0.69, max=0.77; significantly different only between cattle and chamois, w=73, p=0.0028). Our LM revealed that 76.8% of the observed LUE variability was explained by the interaction between woody plant expansion and ungulate species ($F_{3,316}$ = 149.2, p<0.001).

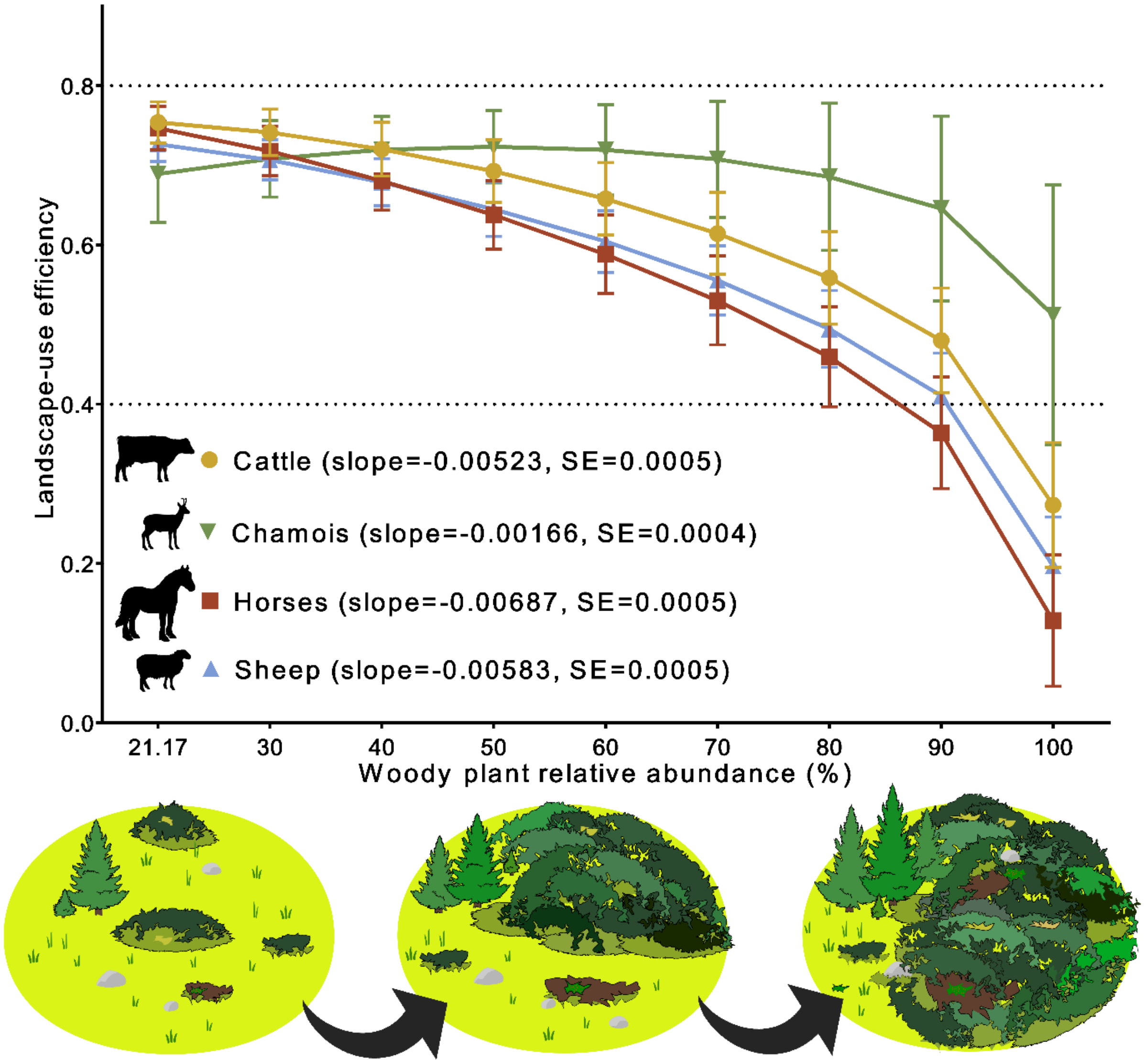

Figure 3. Evolution of the landscape-use efficiencies (LUE) of Pyrenean chamois and seasonal livestock along different scenarios of woody plant expansion. Slopes of the linear regression are also reported for each species.

The LUE of all the herbivores studied decreased to some degree from the initial to the final scenario, (Fig. 3). However, this decrease was sharper in livestock species. In fact, the LUE of chamois remained practically stable until woody plant cover reached 90%. It even increased slightly in scenarios of initial shrubification and then began to decrease moderately from the fourth hypothetical scenario (60% woody plant abundance) onwards, acquiring at the same time the highest values relative to the other species. Livestock, however, lost their foraging resilience at very early degrees of shrubification (Fig. 3). The LUE of cattle (β = -0.005, SE = 0.0005, $p < 0.001$), sheep (β = -0.004, SE = 0.0005, $p < 0.001$) and horses (β = -0.005, SE = 0.0005, $p < 0.001$), steadily decreased from the first scenario of shrubification. The LUE of sheep and horses were significantly smaller than chamois from the third hypothetical scenario onwards (50% woody plant cover; w= 74, p<0.005 and w==75, p<0.005, respectively) and cattle differed from the fourth scenario onwards (60% woody plant cover; w=14, p<0.05).

The lowest LUE values were detected in our final scenario of shrubification, where woody plants occupied the entire area, notably decreasing livestock LUE (cattle: median=0.29, min=0.14, max=0.41; sheep: median=0.17, min=0.06, max=0.29; horses: median=0.09, min=0.14, max=0.29). LUE was significantly higher for chamois (median=0.56, min=0.21, max=0.70) than cattle (w=13, p=0.014), sheep (w=76, p<0.0001), and horses (w=79, p<0.001) due to its moderate decrease in niche breadth along the scenarios. Livestock LUEs differed significantly only between cattle and horses (w=71, p=0.006).

Discussion

Our results suggest that woody plant expansion in an unmanaged environment will affect herbivores in alpine grasslands during summer and autumn but that the magnitudes and direction of these effects will vary between species. Animals with a preference for herbaceous plants will have difficulties to follow the same diet and they will need to acclimatise to a higher consumption of woody plants in order to remain in these areas. At the same time, competition for the most consumed plants, such as *Festuca* spp. or *Trifolium* spp., would lead to overgrazing, one of the main causes of rangeland degradation worldwide (Du Toit *et al.*, 2010; Hilker *et al.*, 2014).

Changes in woody plant cover importantly restructure the wild herbivore assemblage as grazer densities decrease when woody cover increases (Smit & Prins, 2015). The increasing woody plant expansion in alpine environments will render grazers less efficient users of their landscape, as our predictions suggested, therefore decreasing their density in response to food availability. Livestock are highly dependent on the availability of montane grasslands, and the number of livestock grazers will have to decrease to prevent a reduction in productivity. In fact, increases in woody plant cover are already having repercussions on livestock production and reproduction (Anadon *et al.*, 2014). The need to maintain sustainable levels of production will force farmers to move livestock to more suitable areas. Habitat diversity will consequently decline even faster in alpine areas, because plant species richness is maintained by grazing in these human-created herbaceous communities (Bakker, 1998; Boulanger *et al.*, 2018).

Horses feed mostly on graminoids and, to a lesser extent, on forbs and thus would be more quickly and broadly affected by woody plant expansion. This strong dependence on herbaceous plants has been widely described in feral and free-ranging horses (Olsen & Hansen, 1977; Salter & Hudson, 1979; Patrick, 1992; Celaya *et al.*, 2011). The consumption of grasses

(50% of total consumption) can be lower in some extreme environments, such as the Chihuahuan Desert (Hansen, 1976), but animal growth is usually restricted when high-quality pastures are not readily available (Dawson *et al.*, 1945; Andreyev, 1971; Celaya *et al.*, 2011). The production of horse meat in the Pyrenees, as in other parts of Europe, is exclusively free-range. Animals make use of grasslands at different altitudes according to the season and, as a consequence, depend highly on montane pastures to subsist (Martin-Rosset & Trillaud-Geyl, 2015). Woody plant expansion is therefore a real threat to horse meat production.

Our results support those of several studies that found that free-ranging cattle generally consume higher proportions of forbs and woody plants than horses (Krysl *et al.*, 1984; Menard *et al.*, 2002; Celaya *et al.*, 2011; Scasta *et al.*, 2016). Woody plant expansion would thus affect cattle less than horses. Diets can be more variable and contain more woody species in free-ranging cattle than horses, although diets of cattle can also be high in graminoids and forbs (Aldezabal *et al.*, 2002; Scasta *et al.*, 2016). The high content of plant secondary metabolites in shrubs, such as tannins, can affect intake, digestion, and metabolism in herbivores and can be toxic if consumed in large amounts (Hanley *et al.*, 1992; Burrit & Provenza, 2000). Cattle can consume a relatively high proportion of woody plants in specific habitats and conditions, but this rusticity and adaptability are only observed in some local breeds (Guevara, 1996; Bartolomé *et al.*, 2011). However, local breeds have been gradually abandoned in recent decades for the benefit of highly productive commercial breeds (Taberlet *et al.*, 2008) and consequently, many locally adapted breeds have already become extinct (Scherf, 2000). At the same time, the use of these breeds is impaired by important inbreeding situations and small effective population sizes (Taberlet *et al.*, 2008), highlighting future challenges of livestock farming in areas were local adaptations will be needed.

Medium-sized herbivores, such as sheep, tend to have a proportionally higher maintenance cost per body weight unit (Kleiber, 1961). They therefore need to forage on plants higher in nutritional value compared to larger herbivores, such as cattle or horses. Sheep can select preferred components in fine-scale mixtures due to their smaller size, which determines gape size, and can therefore feed on the more nutritional parts of plants (Gordon & Illius, 1988). Studies on the composition of diets have reported higher contents of forbs and woody plants by sheep than by large herbivores (La Morgia & Bassano, 2009; Karmiris & Nastis, 2010). Still, the consumption of graminoids and forbs by sheep and cattle in our study was similar, probably due to the high availability of these resources in our study area, generating a strong overlap in the use of resources.

The societal demand for livestock products is increasing the development of research programmes focusing on animal behaviour and genetics for developing animals able to use shrubs more efficiently (Estell *et al*., 2012). The productivity of these breeds, however, is currently relatively low (Verrier *et al.*, 2005), and animals in mountainous areas have adaptations and functional traits of interest for the montane farming system but a lower production of muscle or milk than commercial breeds (Verrier *et al.*, 2005). The use of shrub-dominated areas for meat or milk production does not presently meet animal requirements (Casasús *et al.*, 2005). These practices appear unsustainable due to the necessity of management intervention (e.g. thinning and spraying) and intensive supplementary feeding (Gutman *et al.*, 2000; Brosh *et al.*, 2006). As a consequence, livestock farming in areas suffering from woody plant expansion will be at high economic risk due to the impossibility of maintaining sustained economic incomes.

Livestock farming in mountainous areas is important to local economies and cultural heritages and is often essential for the livelihood of rural populations worldwide (Mann, 2013). In fact, 32% of Kenyans inhabiting mountains mainly depend on livestock farming to subsist and in Nepalese mountains, where 59% of the population lives below the poverty line, livestock contribute to 21.2% of total household incomes (Abington, 1992; Golicha et al., 2012). Besides a direct nutritional income through meat or milk, livestock also play a vital role in supporting farming systems providing wool, manure, working traction, transportation, cash income and risk diversification (Sherman, 2005). In rural areas where subsistence agriculture is prevalent, the loss of pasture land would have a dramatic socio-economic impact, regardless of the causes of the local shrubification.

We found that Pyrenean chamois during summer and autumn would be favoured by a moderate to high expansion of woody plants due to their ability to balance their feeding behaviour between grazing and browsing. In fact, chamois can have extremely diverse dietary preferences depending on the habitat and season (Herrero *et al.*, 1996; La Morgia & Bassano, 2009) and can even be exclusively dependent on woody species (Yockney & Hickling, 2000). This high phenotypical plasticity is due to their capacity to alternate between ruminal and hindgut fermentation depending on forage quantity and quality (Hofmann, 1989). Because chamois evolved during thousands of years in unmanaged environments (Masini & Lovari, 1988) it is not surprising that the reversion to unmanaged conditions could favour them. The chamois diet in our study area differed from the diets of all the livestock species and showed an evenly distributed consumption of herbaceous and woody plants, despite a lower availability of the latter. This behaviour will allow the chamois to have a higher theoretical LUE than the other herbivores in scenarios of future woody plant expansion. Furthermore, mixed feeders may even be able to slow shrub expansion (Olofsson *et al.*, 2009; Schulze *et al.*, 2018), highlighting the importance of the conservation of these herbivores to maintain open habitats. Our results suggest that the LUE of chamois would be impaired in scenarios of extreme shrubification, despite their adaptation to a high consumption of woody plants. However, the phenotypic capacity of chamois could allow them to consume more woody plants than observed in our study area but further studies would be necessary to assess the effect of these dietary adaptations on the performance of this species. At the same time, this study focussed on summer and autumn diets of chamois because there are key for the reproduction and survival of the species (Garel *et al.*, 2011; Scornavacca *et al.*, 2016). Food availability during winter may also determine chamois survival, but there is no information on that process. Hence, further investigations will be required to determine the impact of shrubification on the survival of chamois during winter.

Our data also suggest that extensive land management and human intervention (e.g. manual shrub clearance), will be necessary for maintaining semi-natural grasslands and free-range farming systems. Keeping in mind that half of the European network of Natura 2000 sites are associated with farming, agricultural land abandonment may have important impacts on landscape and biodiversity in Europe (MacDonald et al., 2000). Moreover, in a kind of vicious circle, the capital investment needed and the time and effort of the demanding work to reverse woody plant expansion on agricultural land is leading to an intensification of the abandonment of farmland and rural areas, accelerating shrubification (MacDonald et al., 2000). Being a driver of woody plant expansion, temperature increase in mountainous environments will also impair biodiversity and efforts to limit global warming will be capital for the future of these environments (Steffen *et al.*, 2018).

Finally, the consequences of our results are not only representative of a Pyrenean scenario or a European montane ecosystem. Considering that shrubification is a global issue affecting other habitats and ecosystems worldwide, from the African savannah to the arctic tundra (Tape *et al.*, 2006; Naito & Cairns, 2011), lessons learned from this paradigmatic case example can be extrapolated to a global scale.

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