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Changes in Land Use of Pyrenean Mountain Pastures—Ski Runs and Livestock Management—Between 1972 and 2005 and the Effects on Subalpine Grasslands

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Abstract

In recent decades, the use of some subalpine mountain grasslands in the Central Spanish Pyrenees has changed. Ski resorts have been developed and cattle herd management has shifted from the traditional ''rotational-type'' system in which grazing cattle are overseen by a herder to a ''continuous-type'' system that does not involve a herder. In 2005, the locations of 30 floristic inventories performed in 1972 were revisited and inventories were repeated in two adjacent similar areas, although one had been used for the development of ski runs and the other had not. The objective was to assess the effects of those changes on plant diversity and other characteristics of the grasslands. In both areas, plant diversity was significantly higher in 2005 than it was in 1972. Both areas had been grazed by cattle to a similar extent; thus, the results suggest that diversity was affected primarily by the change in the livestock grazing system. Livestock grazing within the skiing area appears to have counterbalanced any reduction in plant diversity that would have occurred because of the construction and use of ski runs. In the skiing area, legume cover and pastoral value decreased, the Ellenberg Nitrogen Index reflected lower soil nutrients available to plants, and the cover of plant species that regenerate by seeds increased between 1972 and 2005; such changes did not occur in the non-skiing area. The abundance of ruderal species increased more in the skiing area than in the non-skiing area. Between 1981 and 2000, the amount of bare ground increased only in the skiing area.

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Introduction

In addition to being a basic resource for extensively managed livestock, mountain grasslands have other benefits to society including the conservation of biodiversity, landscape preservation, animal welfare, and the quality of human foods (Ferrer et al., 2001). The subalpine mountain grasslands of the Central Spanish Pyrenees are semi-natural grasslands that were created and are maintained by humans, and whose persistence depends on grazing. In general, those grasslands have been used as extensive summer pastures for domestic livestock since antiquity (Vandvick and Birks, 2002) and, in the Central Spanish Pyrenees, for at least 5000 yr (Baldellou, 1989). Thus, pastoral activities are a historical aspect of the landscape and have influenced the natural and cultural history of the area (Montserrat and Fillat, 1990; Pärtel et al., 1999). Although extensive grazing in mountain areas has declined significantly (García-Ruíz and Lasanta, 1990; Gutiérrez and Peco, 2003), it persists in some areas of the Spanish Pyrenees, typically alongside other economic activities (e.g., winter and summer tourism), and has been influenced by changes in traditional livestock management.

Semi-natural grasslands are among the most species-rich and the most threatened ecosystems because of changes in land use associated with socio-economic and political changes in Europe (Cousins et al., 2003), where concern about the conservation of semi-natural grasslands has increased because of substantial reductions in these ecosystems (Ostermann, 1998). Many of those grasslands are of importance for conservation under the Habitat Directive of the European Commission (European Union, 1992; Barrantes et al., 2009). In North America, remnant native grasslands are among the most endangered landscapes (Sampson and Knopf, 1994).

Since the early 1970s, human pressure on mountain ecosystems has increased in several regions of the world because of the development of ski resorts, which compete for land with traditional agricultural activities (Isselin-Nondedeu et al., 2006), particularly in the mountains of industrialized countries (Titus and Tsuyuzaki, 1998), where the demands for recreational activities by urban populations have increased. In Europe, most ski runs are built on subalpine and alpine mountain grasslands.

In and around ski slopes, environmental deterioration is common (Pignatti 1993; Tsuyuzaki, 1994; Urbanska, 1994; Titus and Tsuyuzaki, 1998), including damage to vegetation, the development of bare areas, soil erosion, and landscape fragmentation (Bayfield, 1980; Watson, 1985; Tsuyuzaki, 1994, 2002; Isselin-Nondedeu et al., 2006). The development of skiing areas involves the use of heavy machinery for the construction of runs, topographic adjustment, the grooming of the snow cover to improve the skiing experience (Rixen et al., 2003; Gros et al., 2004; Delgado et al., 2007), and the production of machine-made snow, which has become more important in recent years (Rixen et al., 2003; Wipf et al., 2005). In addition, the disturbances associated with ski runs include the construction and maintenance of access roads and other infrastructures. Some skiing areas are used for tourism in summer

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(Needham et al., 2004), which can have significant negative effects such as increasing the amount of bare ground and altering plant diversity, floristic composition, and the nutritional state of the soil.

In mountain ecosystems that have extreme climates, the bare soil created in the process of building and maintaining ski runs is susceptible to erosion (Ries, 1996; Rixen et al., 2003; Gros et al., 2004). Those patches become desiccated and overheated, which leads to further erosion in the summer (Watson, 1985). Harsh high-mountain conditions and the mechanical damage caused to plants by the construction and maintenance of ski runs greatly retards primary succession and the recovery of the vegetation cover (Rixen et al., 2003; Wipf et al., 2005; Roux-Fouillet et al., 2011); consequently, extensive areas can remain bare in these environments (Tsuyuzaki, 1994; Urbanska, 1997; Rixen et al., 2008b; Lorite et al., 2010).

Ski runs can have negative effects on plant diversity and species richness (Forbes, 1992; Goñi and Guzmán, 2001; Wipf et al., 2005) and lead to changes in floristic composition (Puntieri, 1991; Fahey and Wardle, 1998; Tsuyuzaki, 2002; Titus and Tsuyuzaki, 1998; Ruth-Balaganskaya and Myllynen-Malinen, 2000; Rixen et al., 2003; Wipf et al., 2005; Roux-Fouillet et al., 2011). The factors that cause changes in the vegetation are complex and diverse (Rixen et al., 2008b); for instance, snowpack compaction changes the biotic, physical, and chemical properties of the soil (Gros et al., 2004), such as lower soil temperatures (Rixen et al., 2003; Wipf et al., 2005; Delgado et al., 2007; Rixen et al., 2008a; Zeidler et al., 2008), changes in soil microbial life (Gros et al., 2004), a reduction in soil microporosity, and changes in nitrogen fixation (Delgado et al., 2007). The composition of plant communities can change because snowmelt is delayed on ski runs, which shortens the growing season (Wipf et al., 2005; Rixen et al., 2008a; Zeidler et al., 2008). The use of machine-made snow can exacerbate phenological delays and change the plant community because of the additional water and ions (Rixen et al., 2003; Wipf et al., 2005; Roux-Fouillet et al., 2011). On the other hand, the disturbances caused by ski run construction and use can increase the presence of ruderal species (Puntieri, 1991; Delarze, 1994; Clarke and Martin, 1999; Goñi and Guzmán, 2001; Barni et al., 2007; Guleryuz et al., 2008). Changes in the floristic composition of grasslands caused by ski-run construction and use can reduce the pastoral value of the grasslands (Goñi and Guzmán, 2001).

In addition to the expansion of ski runs in the Central Spanish Pyrenees, cattle herd management has changed from a traditional ''rotational-type'' system in which the animals are led by a herder to a ''continuous-type'' system without a herder. Driven by socio-economic factors, the change has occurred in other mountain systems where, traditionally, a herder managed a single herd that belonged to the village (Gibon et al., 2004).

Livestock grazing is an important disturbance that often alters plant diversity through trampling, dunging, defoliation, and the dispersing of plant species (Crawley 1983; Milchunas et al., 1988; Vandvick and Birks, 2002; Pykälä, 2004). The type of livestock, stocking rate, and the type of grazing system (rotational or continuous) can influence the effects of grazing on plant diversity, primarily through their influence on selective grazing (Loiseau et al., 1998; Bullock et al., 2001; Pavlů et al., 2003).

Many studies have examined either the effects of ski-run construction and use or the effects of livestock grazing on vegetation, but few have been conducted in areas where both of these activities occur. Areas where the two activities occur together illustrate the multi-functionality of the grasslands (Isselin-Nondedeu et al., 2006). Some studies have suggested that livestock (particularly cattle) can counterbalance the damage caused by the construction and use of ski runs (Goñi and Guzmán, 2001; Isselin-Nondedeu and Bedecarrats, 2007), prevent reductions in plant diversity (Goñi and Guzmán, 2001), and aid in the restoration of eroded areas through trampling and exozoochoria (Isselin-Nondedeu et al., 2006).

To gain insight into the extent and causes of the changes in the vegetation in various ecosystems, some researchers have conducted ''revisitation'' studies (e.g., Debussche et al., 1996; Kahmen et al., 2002; Prach, 2008; Stevanovic et al., 2008; Peter et al., 2009; for a review, see McGovern et al., 2011), which have demonstrated that this approach can be useful in assessing the effects of a changing environment on natural and semi-natural ecosystems over long periods (McGovern et al., 2011). In 2005, we revisited 30 floristic inventories that had been conducted in the Central Spanish Pyrenees in 1972 (Ferrer, 1981). The objective was to assess the effects of the development and use of ski runs and changes in the livestock grazing system on the floristic composition, plant diversity, and other aspects of subalpine mountain pastures.

Methods

STUDY AREA

The study area was located in subalpine mountain pastures grazed by cattle in summer in the Tena Valley, municipality of Panticosa, Central Axial Spanish Pyrenees (Aragon, northeastern Spain) (Fig. 1). In the study area, the climate is mountain oceanic and elevation ranges between 1500 and 2295 m a.s.l. (Ferrer, 1981; García-Ruíz and Lasanta, 1990). At 1660 m a.s.l. (Panticosa Balneario Station), the mean annual precipitation is 1581 mm, including an average of 52 d of snowfall per year ($n = 82$ yr), and about a third of the precipitation falls as snow. The mean annual air temperature is 6.8 °C ($n = 54$ yr) (http://www.chebro.es). Above 1600 m a.s.l., usually, most of the ground is covered by snow from November through April.

The geology consists of Paleozoic deposits that were folded by the Hercynian and Alpine orogenies, and the predominant lithology includes slate and limestone (Ferrer, 1981). The soils are classified as Leptosols and Cambisols (dystric, haplic, or eutric) according to the FAO-Classification system (IUSS Working Group WRB, 2006), and as Entisols, Inceptisols, and Mollisols according to the Soil Taxonomy (Soil Survey Staff, 2006).

Those biophysical characteristics, together with glacial and postglacial activity and other forms of erosion, define several geomorphological units and traditional land uses (Ferrer, 1981; Montserrat and Fillat, 1990; García-Ruíz and Lasanta, 1990): specifically, at 1200–1500 m a.s.l., villages, farms, meadows, and crops on alluvial plains in the valley bottoms or on gentle slopes or terraced fields; at 1500–1600 m a.s.l., forests on steep slopes; and, at 1600–2200 m a.s.l., summer pastures above the timberline within wide glacial basins. At lower elevations within that range, cattle graze on undulating and smooth slopes that have high vegetation

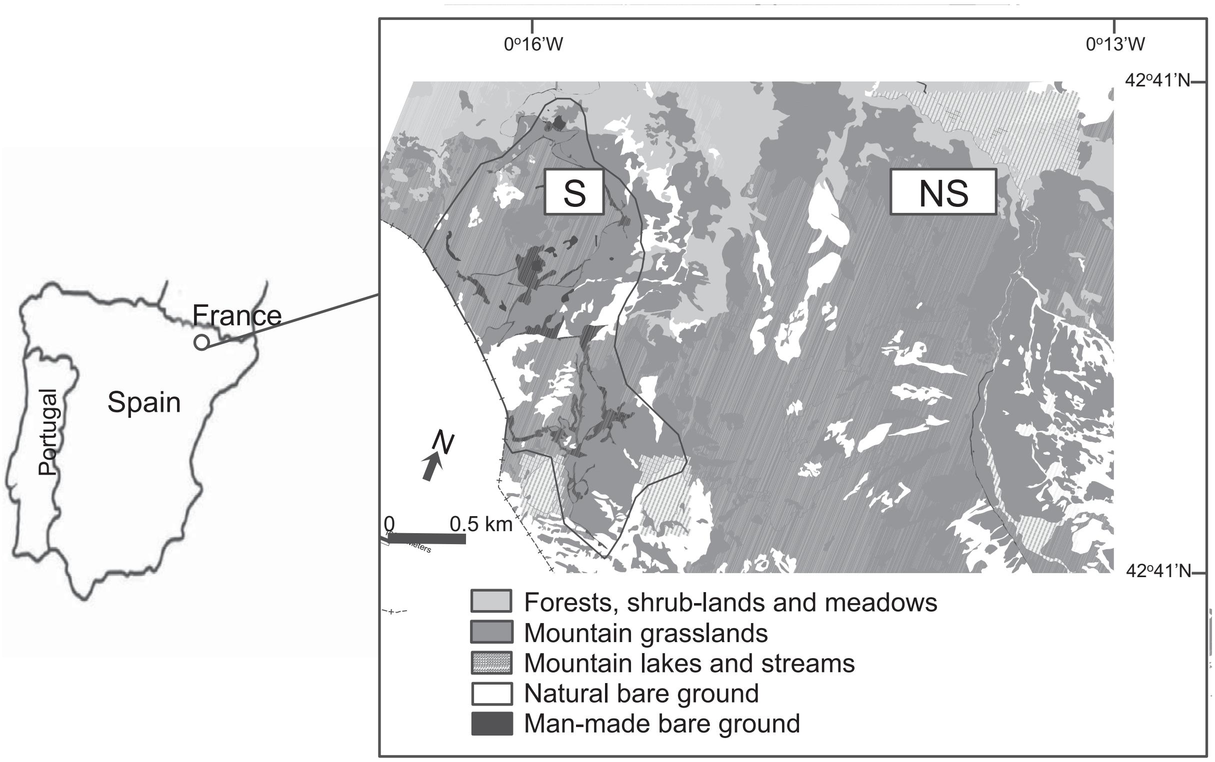

FIGURE 1. Skiing (S) and non-skiing (NS) areas within the study area in Tena Valley, Central Spanish Pyrenees, based on aerial photographs taken in (a) 1981 and (b) 2000. The western boundary of the map is the western limit of Panticosa municipality.

cover; at high elevations, sheep graze on steep slopes that have limited vegetation cover.

Two climax belts of the Eurosiberian region occur in the study area (Rivas Martínez, 1987): a montane belt of the *Echinosparto horrido–Pineto sylvestris sigmetum* series (up to 1600 m a.s.l.) and a subalpine belt of *Rhododendro-Pineto uncinatae sigmetum* (1600–2200 m a.s.l.). Many centuries ago, the subalpine climax forest was removed through clear-cutting, burning, and livestock grazing, which increased the amount of herbaceous pasture (Ferrer, 1981; Montserrat and Fillat, 1990; García-Ruíz and Lasanta, 1990).

CHANGES IN LAND USE AFTER 1970

Since antiquity, and until a few decades ago, the land within the study area was used for livestock husbandry based on a traditional pastoral system. Between 1970 and at least until 2005, substantial changes in land use occurred that involved the construction and use of ski runs and changes in livestock grazing management. Within the study area were two areas that had similar biophysical characteristics and livestock management, but one was undisturbed (''non-skiing area'') and the other was used for the construction of ski runs (''skiing area'') (Fig. 1).

Ski-Runs Construction and Use

In the early 1970s, a few ski runs were established within the study area near 1500 m a.s.l.; since 1980, they were progressively expanded to encompass the entire study area up to 2200 m a.s.l. Grading machines were used to construct the ski runs. The ski runs were not seeded or subjected to any other form of grassland restoration. Since 1992, the ski resorts have produced machine-made snow using pure water (no additives are used) from two lakes to the southeast (Fig. 1). Ski resorts in the area comprise 34 km of ski runs, 15 km of ski lifts, and have the capacity for 13,355 skiers per hour (Lasanta et al., 2007). Since 1970, roads and tracks have been constructed in the skiing area, which receives hundreds of visitors in summer.

Livestock Grazing Management

In the region, beef cattle graze the subalpine pastures in summer and, at other times of the year, are fed conserved grass from the natural meadows and forage crops from the valley bottom. In winter, some of the cattle can take part in a short transhumance to pre-Pyrenean Mediterranean pastures. About 70% (970 ha) of the study area is cattle pasture, which is used in a communal management system.

Before 1988, the cattle herd was led by a herder who managed the animals using a ''rotational grazing system'' that followed a circuit during the summer. For socio-economic reasons common to other Pyrenean valleys, since 1988, cattle have been managed using a ''continuous grazing system'' in which the livestock graze freely in small groups or alone in the absence of a herder. The rotational grazing system alternates periods of grazing and rest among three or more paddocks within a grazing management unit. In that system, the herd is regularly and systematically moved to a fresh pasture so as to maximize the quality and quantity of pasture growth. In the continuous grazing system, animals have unrestricted and uninterrupted access on a unit of land while they are there (Allen et al., 2011). Livestock census data (Fig. 2) were from

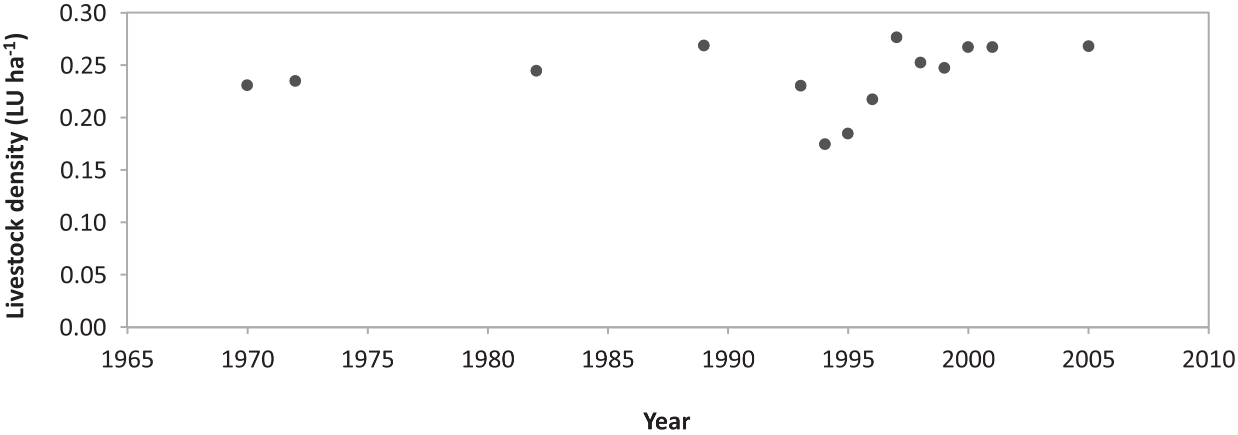

FIGURE 2. Livestock density (livestock units per hectare, LU ha^{-1}) in Panticosa Municipality, Central Spanish Pyrenees, between 1970 and 2005.

Ocaña (1978), the Directorio Ganadero del Gobierno de Aragón (http://www.aragon.es), and the Zona Veterinaria de Jaca (unpublished data), and farmers in the area provided information on the management of livestock.

VEGETATION SURVEYS

To improve the understanding of the ecology of the subalpine vegetation in the Tena Valley, in 1972, 30 phytosociological inventories were recorded in the summer cattle pastures (Ferrer, 1981) based on the Braun-Blanquet species abundance-dominance scale (six coefficients from + to 5) (Braun-Blanquet, 1965). Plot size was based on the criterion of minimum size relevé (Braun-Blanquet, 1965). The inclination, elevation, and slope orientation of each plot were recorded, each plot was photographed, and its location was plotted on a topographic map (scale 1:25,000). Slope ranged between 0° and 30°, elevation ranged between 1610 m and 2074 m a.s.l., and the main slope orientations were northeast and southeast. In all of the inventories, the vegetation cover was 100%.

In 2005, the locations of the 30 phytosociological inventories recorded in 1972 were revisited. The fieldworker who recorded the inventories in 1972 conducted the inventories in 2005 using the maps, photographs, and descriptions (inclination, elevation, aspect of the slope) from 1972 to identify the locations of the original inventories. If the location of the original plot was uncertain, the inventory was not repeated in 2005. One-third of the original inventories were not repeated in 2005 because the precise location of the plot was uncertain ($n = 3$ inventories) or the vegetation had been replaced by infrastructures (e.g., pathways, pipelines; $n = 7$ inventories). The inventories that were repeated in 2005 were either in the skiing area ($n = 11$ inventories) or in an undisturbed non-skiing area ($n = 9$ inventories). The two areas had similar topographies, lithologies, and soils. In the skiing area, elevation ranged between 1610 and 2045 m a.s.l., slope ranged between 0° and 24°, and soil pH ranged between 5.2 and 6.7. In the non-skiing area, elevation ranged between 1767 and 2074 m a.s.l., slope ranged between 5° and 30°, and soil pH ranged between 4.8 and 6.7. Slope orientation was similar in the two areas. Species abundance was assessed using the same method in 1972 and 2005. Most of the plant communities were *Bromion erecti* Koch 1926 and *Nardion strictae* Br.-Bl. 1926 phytosociological alliances. Species nomenclature followed Tutin et al. (1972). To estimate the amount of bare ground in aerial photographs of the study area taken in 1981 and 2000, we used ArcGIS software.

DATA ANALYSIS

To assess the temporal changes in diversity indices, plant species attributes, and the pastoral value of the grassland communities, we compared (i) the data from 2005 and 1972, i.e. for ''time effects,'' both in the skiing area and in the non-skiing area, and (ii) skiing and non-skiing areas in 1972 and in 2005. The raw cover-abundance data were transformed into values of percentage cover for subsequent analyses based on Braun-Blanquet coefficients: + = 0.1%, 1 = 5%, 2 = 17.5%, 3 = 37.5%, 4 = 62.5, and 5 = 87.5% (Van der Maarel, 1979).

The diversity of the grassland community was quantified based on the inventory data using the Shannon Information Index, H′ (Shannon and Weaver, 1949). The evenness of the plant community was measured using the Pielou Index (Pielou, 1975). Local plant species richness was the number of species recorded in each inventory for each area. Regional plant species richness was calculated for each area as the total number of species in the plots. Beta diversity (Magurran, 2003) was calculated as the ratio between total species richness and the average species richness in three groups of three randomly selected inventories for each area. Sampling effort influences plant species richness; therefore, an even number of inventories (9 per area, 36 in total) was used to calculate plant species richness, diversity, and evenness, although the results based on the analysis of all 40 of the samples were qualitatively similar to those of the restricted data set. To assess the extent of the replacement of some species by others over time, we used Sorensen's Similarity Index, which was computed between randomly paired transects for each combination of two treatments using EstimateS software (Colwell, 2006).

Grassland species were categorized based on four biological classifications that were likely to identify functional groups that differ in their responses to the changes that can result from the development of ski runs and changes in livestock management. Plant species were classified as follows: (1) as either grasses, legumes, or forbs, which are basic life forms of herbaceous species, have different life strategies, and differ in their nutritional value for livestock; (2) based on the Ellenberg Nitrogen Index (Ellenberg, 1979), which is an indicator of a plant's realized niche (Hill et al., 1999) based on the species' preferred soil nutrient level (McGovern et al., 2011). Species are assigned to one of nine categories (1 = species affiliated with poor nutrient conditions, 9 = species affiliated with rich nutrient conditions); (3) based on regenerative strategy (Grime, 1979) and classified as either by ''vegetative expansion by rhizomes'' or by ''seeds''. Non-vegetative regenerative strategies are better adapted to disturbance than are vegetative strategies (Grime, 2001). In addition, the regeneration phase is critical in response to environmental changes (Hobbs, 1997); and (4) as either ruderal or non-ruderal species, because ruderal species can be associated with skiing areas (e.g., Bayfield, 1980; Guleryuz et al., 2008). Percent cover and the relative number of species (%) of each group were calculated for the two years and two areas. The Grime and Ellenberg plant attributes were based on the database of Hill et al. (2004). To identify ruderal species, we used Ferrer (1981), Villar et al. (1997–2001), Aeschimann et al. (2004), and IPE-DGA (2005). In our study, plant species were ''ruderal'' if all of those sources classified the species as such. Six plant species met that criterion: *Cirsium eriophorum*, *Carduus carlinifolius*, *Veronica serpyllifolia*, *Silene vulgaris*, *Chenopodium bonus-henricus*, and *Polygonum aviculare* (in order of abundance).

For each inventory, an index of ''pastoral value'' was calculated based on the Daget-Poissonet Method (Daget and Poissonet, 1972), which has been used extensively in mountain pastures and can be used to identify potential or optimal livestock stocking rates (Loiseau et al., 1998).

STATISTICAL ANALYSIS

To assess the statistical significance of temporal changes in diversity indices, vegetation cover, the relative abundance of species, species attributes, and pastoral values of the grassland communities in the two areas, we used Wilcoxon's Paired-Sample Signed Rank Test (two-tailed). Sorensen's Similarity Index between paired samples was evaluated using a Student's *t*-test. Initial and final site conditions were tested using the Mann-Whitney U-test. Analyses were performed using the SPSS software (Version 15.0, SPSS, Inc., Chicago, Illinois, U.S.A.).

Results

Within the study area in the municipality of Panticosa (Central Spanish Pyrenees), livestock density did not change significantly between 1972 and 2005 (Fig. 2). With the exception of lower densities in 1994 and 1995, livestock densities ranged between 0.22 and 0.27 livestock units per hectare (LU ha^{-1}).

In 1981, only 1.5% (4.3 ha) of the skiing area (281.7 ha) was man-made (i.e., caused by the construction of ski runs) bare ground; however, in 2000, 10.8% (30.5 ha) of the area was man-made bare ground (Fig. 1). The amount of bare ground in the non-skiing area (0.5%, 6.5 ha) did not differ significantly between 1972 and 2005.

In both the skiing and non-skiing areas, plant species diversity was significantly higher in 2005 than it was in 1972 (Table 1) because evenness had increased in the skiing area, and evenness and richness had increased in the non-skiing area. Evenness increased in both areas because of increases in the number of species that had intermediate and low relative abundance and reductions in the abundance of species such as *Festuca rubra*, *Trifolium pratense*, and *T. repens* (in the skiing area) and *T. alpinum* and *Rhinanthus pumilus* in the non-skiing area (Table 3). In both areas, beta diversity did not differ significantly between 1972 and 2005. In both 1972 and 2005, species diversity, evenness, local richness, and beta diversity did not differ significantly ($P > 0.05$) between the two areas. Sorensen's Similarity Indices (Table 2) indicated that the changes in the plant communities between 1972 and 2005 were similar in the two areas.

Between 1972 and 2005, legume cover decreased and forbs increased significantly ($P < 0.01$) only in the skiing area (Table 4). Furthermore, only the relative number of legume species in the non-skiing area decreased significantly between 1972 and 2005. In the skiing area only, the Ellenberg Nitrogen Index changed significantly between 1972 and 2005, which suggests that the soil nutrient status of this area had changed. In 2005, the species composition of the plant community suggested a greater preference for poorer soils than it did in 1972, which indicated a possible reduction in the nutrient content of the soil. In both 1972 and 2005, the cover and relative abundance of grasses, legumes, and forbs, and the Ellenberg Nitrogen Index of the two areas did not differ significantly ($P > 0.05$), although in 2005 the relative number of grass species was significantly lower in the skiing area than it was in the non-skiing area (U value = 20.000, $P < 0.05$).

TABLE 1

Mean (SE) diversity (H′), evenness, local and regional richness, and beta-diversity of plant species in a skiing area and a non-skiing area in the Tena Valley, Central Spanish Pyrenees, based on plot sampling in 1972 and 2005. Statistical comparison between years based on Wilcoxon's Paired-Sample Test. For Diversity, Evenness, and Richness, $N = 36$; for beta-diversity, $N = 12$.

Index	Non-skiing area		Skiing area		*Z* value (1972 *vs*. 2005)	
	1972	2005	1972	2005	Non-skiing area	Skiing area
Diversity (H′)	1.64 (0.09)	2.35 (0.16)	1.53 (0.16)	2.28 (0.11)	−2.310*	−2.547*
Evenness	0.53 (0.04)	0.69 (0.03)	0.51 (0.04)	0.72 (0.02)	−2.310*	−2.666**
Local richness	25.44 (2.99)	31.33 (3.60)	21.00 (2.68)	24.33 (2.22)	−2.431*	−1.244
Regional richness	77	92	71	83	—	—
Beta-diversity	1.89 (0.10)	1.73 (0.09)	1.92 (0.10)	1.96 (0.05)	−1.604	−0.535

* $P < 0.05$; ** $P < 0.01$.

TABLE 2

Mean (SE) Sorensen's Similarity Index between paired transects for each combination of two dates in the non-skiing area ($N = 72$) and the skiing area ($N = 99$). Statistical comparison between areas based on Student's *t*-test.

	Sorensen's Similarity Index	t value	P
1972 *vs.* 2005 in the non-skiing area	0.397 (0.012)	0.444	0.658
1972 *vs.* 2005 in the skiing area	0.391 (0.009)		

TABLE 3

Composition of plant communities in a skiing area and a non-skiing area in the Tena Valley, Central Spanish Pyrenees, based on inventories in 1972 and 2005. Ruderal habitat based on Ferrer (1981), Villar et al. (1997–2001), Aeschimann et al. (2004), and IPE-DGA (2005); regenerative strategy and species soil nutrient level preference based on Hill et al. (2004). Only plant species with cover >1% are included.

Plant species	Family	Life-form	Ruderal	Regenerative strategy	Soil nutrient level preference	Abundance (% of total cover)			
						Non-skiing area		Skiing area	
						1972	2005	1972	2005
Trifolium alpinum	*Leguminosae*	HEMICR		rhizome	medium	14.62	8.61	6.24	1.72
Festuca eskia	*Poaceae*	HEMICR		rhizome	poor	11.98	14.57		
Festuca rubra	*Poaceae*	HEMICR		rhizome	medium	10.82	15.96	26.10	22.77
Rhinanthus pumilus	*Scrophulariaceae*	THEROPH		seed	poor	9.24	1.80		
Agrostis capillaris	*Poaceae*	HEMICR		rhizome	medium	5.95	2.75	1.74	2.36
Plantago alpina	*Plantaginaceae*	HEMICR		rhizome	poor	5.78	1.64	4.27	4.21
Nardus stricta	*Poaceae*	HEMICR		rhizome	poor	5.50	3.41	9.44	10.36
Meum athamanticum	*Apiaceae*	HEMICR		rhizome	poor	4.74	4.98		
Poa alpina	*Poaceae*	HEMICR		rhizome	poor	4.55	1.60	7.11	1.38
Leontodon hispidus	*Asteraceae*	HEMICR		rhizome	poor	3.85	1.70		
Trifolium montanum	*Leguminosae*	HEMICR		rhizome	medium	3.30	1.91	4.90	2.43
Phleum pratense	*Poaceae*	HEMICR		seed	rich	2.84			
Plantago media	*Plantaginaceae*	HEMICR		rhizome	poor	2.14		6.01	3.98
Euphorbia cyparissias	*Euphorbiaceae*	HEMICR		root	poor	1.85	1.32		
Galium verum	*Rubiaceae*	HEMICR		rhizome	poor	1.69	4.91		5.84
Merendera montana	*Liliaceae*	GEOPH		bulb	medium	1.67	1.63		
Geranium sylvaticum	*Geraniaceae*	HEMICR		seed	medium	1.32	1.15		
Trifolium repens	*Leguminosae*	HEMICR		rhizome	rich	1.20		8.56	3.32
Phleum alpinum	*Poaceae*	HEMICR		rhizome	medium	1.18		1.61	
Thymus pulegioides	*Labiatae*	CHAMAEPH		nodule	poor				1.82
Trifolium pratense	*Leguminosae*	HEMICR		rhizome	medium		6.20	8.99	4.61
Potentilla erecta	*Rosaceae*	HEMICR		rhizome	poor				1.62
Luzula nutans	*Cyperaceae*	HEMICR		rhizome	medium		2.69		
Campanula scheuchzeri	*Campanulaceae*	HEMICR		rhizome	medium		1.34		
Achillea millefolium	*Asteraceae*	HEMICR		rhizome	medium		1.57		2.72
Lotus alpinus	*Leguminosae*	HEMICR		seed	poor				3.21
Anthyllis vulneraria	*Leguminosae*	HEMICR		rhizome	rich			1.48	
Pilosella officinarum	*Asteraceae*	HEMICR		stolon	poor		1.56		
Senecio doronicum	*Asteraceae*	HEMICR		seed	rich		1.04		
Carduus carlinifolius	*Asteraceae*	HEMICR	yes	seed	medium				1.05
Eryngium bourgati	*Apiaceae*	HEMICR		seed	poor			1.38	3.31
Carex caryophyllea	*Cyperaceae*	HEMICR		seed	poor				3.54
Centaurea debeauxii	*Asteraceae*	HEMICR		seed	poor			1.44	2.23
Pimpinela saxifraga	*Apiaceae*	HEMICR		seed	poor				1.11
Arrhenatherum elatius	*Poaceae*	HEMICR		rhizome	rich		1.08		
Trifolium thalii	*Leguminosae*	HEMICR		rhizome	medium			2.57	
Cirsium eriophorum	*Asteraceae*	HEMICR	yes	seed	medium				3.01
Scabiosa columbaria	*Dipsacaceae*	HEMICR		seed	poor				1.05

HEMICR = hemicryptophyte; THEROPH = therophyte; GEOPH = geophyte; CHAMAEPH = chamaephyte.

TABLE 4

Mean (SE) cover (%) and relative abundance (%) of grasses, legumes, and forbs, and mean (SE) Ellenberg Nitrogen Index (N-Index) (Hill et al., 2004) in a skiing area and a non-skiing area in the Tena Valley, Central Spanish Pyrenees, based on inventories in 1972 and 2005. $N = 40$. Statistical comparisons between years based on Wilcoxon's Paired-Sample Test.

	Non-skiing area		Skiing area		*Z* value (1972 vs. 2005)	
	1972	2005	1972	2005	Non-skiing area	Skiing area
Cover (%)						
Grasses	43.23 (5.34)	42.68 (5.38)	46.50 (7.09)	39.16 (4.57)	−0.059	−1.334
Legumes	19.80 (4.50)	18.94 (2.17)	33.99 (5.87)	16.65 (3.16)	−0.059	−2.667**
Forbs	36.98 (8.00)	38.38 (6.81)	19.51 (4.17)	44.19 (4.77)	−0.059	−2.756**
Relative species number (%)						
Grasses	18.73 (1.88)	21.91 (1.69)	21.48 (2.90)	18.10 (1.80)	−1.718	−0.533
Legumes	15.62 (1.95)	12.35 (1.89)	14.75 (1.30)	15.60 (1.41)	−2.073*	−0.089
Forbs	65.65 (1.92)	65.74 (2.30)	63.77 (2.24)	66.30 (2.01)	−0.178	−0.800
N-Index	3.61 (0.19)	3.70 (0.16)	4.10 (0.12)	3.59 (0.13)	−0.652	−2.934**

* $P < 0.05$; ** $P < 0.01$.

Between 1972 and 2005, the coverage of plant species that regenerate through rhizomes decreased, and species that regenerate through seeds increased significantly in the skiing area only (Table 5). In both 1972 and 2005, the cover/relative abundances of rhizomes and seed-regenerated species did not differ significantly between the two areas ($P > 0.05$).

The coverage of ruderal species increased significantly between 1972 and 2005 in the non-skiing area ($P = 0.025$) and, especially, in the skiing area ($P = 0.007$) (Table 6)—primarily, because of an increase in *Cirsium eriophorum* (see Table 3). Similar results were found in terms of the relative number of ruderal species. In 1972, the cover by and number of ruderal species did not differ significantly between the two areas ($P > 0.05$); however, in 2005, the number of ruderal species was significantly higher in the skiing area than it was in the non-skiing area (U value = 20.000; $P = 0.025$). Between 1972 and 2005, the pastoral value in the skiing area decreased significantly, but it remained the same in the non-skiing area. In 1972, the pastoral value was higher in the skiing area than it was in the non-skiing area (U value = 23.000; $P = 0.044$); however, in 2005, the pastoral values of the two areas did not differ significantly ($P > 0.05$).

Discussion

Between 1981 and 2000, in the study area in the Tena Valley, Spain, the proportion of the area that was bare ground increased from 1.5% to 10.8% in the skiing area, but did not increase in the non-skiing area. Ski runs construction and use can have severe negative effects on the natural vegetation cover. In a study on ski slopes in Australia in a ~30-yr period, the proportion of the area that was bare ground increased from 10% to 20% relative to control sites (Clarke and Martin, 1999). In Switzerland, the grading of ski slopes reduced vegetation cover from 87% to 47% (Roux-Fouillet et al., 2011) and, in a previous study, Wipf et al. (2005) found that the proportion of the ground that was not covered by vegetation was 16.1% on ski runs and 7.0% off-pistes. In Japan, bare ground covered about half of the area on ski runs that had a mean slope angle of 24° (Tsuyuzaki, 1994). In Canada, the ski sites that were

TABLE 5

Mean (SE) cover (%) and relative abundance (%) of plant species that use either rhizomes or seeds as regenerative strategy in a skiing area and a non-skiing area in the Tena Valley, Central Spanish Pyrenees, based on inventories in 1972 and 2005. $N = 40$. Statistical comparisons between years based on Wilcoxon's Paired-Sample Test.

	Non-skiing area		Skiing area		*Z* value (1972 vs. 2005)	
	1972	2005	1972	2005	Non-skiing area	Skiing area
Cover (%)						
Rhizomes	79.86 (8.12)	83.51 (3.30)	90.30 (3.10)	75.97 (3.30)	−0.533	−2.845**
Seeds	15.71 (7.06)	11.26 (3.09)	7.84 (3.00)	20.49 (3.31)	−0.770	−2.756**
Relative species number (%)						
Rhizomes	60.80 (2.47)	59.25 (2.86)	62.94 (3.27)	57.66 (3.99)	−0.652	−1.067
Seeds	31.64 (2.94)	32.98 (3.23)	28.98 (3.88)	33.40 (3.36)	−0.533	−0.889

** $P < 0.01$.

TABLE 6

Mean (SE) cover (%) and relative abundance (%) of ruderal plants and pastoral value in a skiing area and a non-skiing area in the Tena Valley, Central Spanish Pyrenees, based on inventories in 1972 and 2005. $N = 40$. Statistical comparisons between years based on Wilcoxon's Paired-Sample Test.

	Non-skiing area		Skiing area		Z value (1972 vs. 2005)	
	1972	2005	1972	2005	Non-skiing area	Skiing area
Ruderal cover (%)	0.04 (0.01)	0.07 (0.02)	0.03 (0.01)	4.24 (1.81)	−2.240*	−2.701**
Ruderal relative species number (%)	2.43 (0.91)	4.19 (0.95)	1.54 (0.65)	4.31 (0.87)	−2.103*	−2.293**
Pastoral value	28.74 (4.19)	27.78 (3.06)	41.81 (3.54)	28.08 (2.88)	−0.415	−2.934**

* $P < 0.05$; ** $P < 0.01$.

subjected to considerable trampling and other disturbances by visitors exhibited the most bare soil (Thompson and Hutchinson, 1986). However, in Spain, an increase in bare ground cover (from 1% to 17%) on ski runs over 30 yr was reduced in a livestock-grazed area (Goñi and Guzmán, 2001).

The grading of ski slopes and the mechanical impact of skiers and snow-grooming vehicles are likely responsible for the largest proportion of bare ground (Roux-Fouillet et al., 2011). The construction of ski runs affects the soil by altering the properties of the substrate (Gros et al., 2004), which results in soils that are unfavorable for the establishment and growth of plants and, consequently, a reduction in vegetation cover (Barni et al., 2007). The compacted soils under ski runs can hinder plant growth and reduce infiltration rates and water-storage capacity, which fosters soil erosion (Roux-Fouillet et al., 2011). The absence of plant cover can induce a positive feedback, which increases erosion rates (Pohl et al., 2009). Ski runs that have high proportions of bare ground are particularly prone to increases in surface runoff and further erosion during heavy rains (Wipf et al., 2005). Plant cover is probably the most important mechanism for preventing erosion in alpine habitats (Rixen et al., 2008b). An increase in bare ground cover, as recorded in our study, can lead to habitat fragmentation (Goñi and Guzmán, 2001), which is a serious threat to plant communities (Tilman et al., 1994) because of habitat loss, isolation, and habitat degradation (Ewers and Didham, 2006).

Despite the construction and use of ski runs in one part of our study area, plant diversity (H′) increased between 1972 and 2005 in both the skiing and non-skiing areas. This increase can be explained by a change in livestock grazing management, which used a rotational system until 1988, but a continuous system thereafter. In the non-skiing area, plant species diversity and species richness increased between 1972 and 2005. In Iowa, U.S.A., Barker et al. (2002) found higher diversity and species richness in pastures where a continuous, rather than a rotational grazing system, was used. In addition, the species richness of patches varied more under continuous stocking than it did under rotational stocking. In the Czech Republic, Pavlů et al. (2003) found similar results in the last year of a 5-yr experiment. In the Flooding Pampa, Argentina, Jacobo et al. (2006) found that a continuous grazing system increased species richness over the long term. In Iowa, U.S.A., Guretzky et al. (2005) found that forb diversity was greater under a continuous stocking system on backslopes, and was positively correlated with species richness.

In a rotational system, in which cattle forage in a herd, the proximity of other animals limits the opportunity for an individual to forage selectively among plant species (Augustine and McNaughton, 1998) because of social relationships of dominance-subordination hierarchy within herds (Dumont et al., 2001). In a continuous system, livestock assort themselves based on their social affinities, and exploit different patches, individually or in small groups, which reduces the aggression between individuals (Hodgson et al., 1994). Thus, selective grazing is minimized in a rotational system and enhanced in a continuous system, and selective grazing by cattle can contribute to an increase in species richness (Barker et al., 2002), i.e., continuous grazing can promote an increase in diversity through stronger selection on the species that the cattle eat (Guretzky et al., 2005).

In the skiing area, species richness was similar in 1972 and 2005, and, within that period, H′ diversity increased, which was unlike the negative effects that skiing activities had on plant species richness or diversity reported elsewhere. In Canada, Forbes (1992) found that the presence of ski vehicles consistently reduced species richness. In Switzerland, Wipf et al. (2005) found that ski runs had negative effects on species richness. In our study, it is likely that the presence of livestock coupled with the change in livestock management forestalled any reduction in plant species richness that might have occurred because of the development of ski runs. In the Central Spanish Pyrenees, Goñi and Guzmán (2001) found that plant diversity was higher in ski runs that supported livestock grazing than it was in non-grazed ski runs and, in France, Isselin-Nondedeu and Bedecarrats (2007) observed that livestock counterbalanced the damage caused by ski runs through the disturbances they caused by grazing such as the microdepressions created by trampling and exozoochoria, which played a positive role in maintaining diversity. Nevertheless, to avoid detrimental effects on seedlings (particularly, immediately after seeding) and the possibly that erosion will be enhanced, caution must be exercised in restoration processes that are aided by cattle (Isselin-Nondedeu and Bedecarrats, 2007). Herbivores should be excluded in the early years after the restoration of the vegetation on ski runs above the tree line because the damage caused by grazing might severely hinder the establishment of transplanted plants (Fattorini, 2001).

On ski runs snow groomers compact the snow and alter the depth and density of the snowpack. A thinner, denser snow cover has greater thermal conductivity than an intact snow cover, which leads to a reduction in soil insulation, an increase in frost penetration into the soil, and colder soil temperatures (Fahey and Wardle, 1998; Rixen et al., 2003; Wipf et al., 2005; Delgado et al., 2007; Rixen et al., 2008a, 2008b; Zeidler et al., 2008). As a result, snowmelt is retarded on ski runs, which shortens the growing season and affects plant species composition, as many studies have shown (Fahey and Wardle, 1998; Wipf et al., 2005; Rixen et al., 2008b; Zeidler et al., 2008). Grasses and some forbs are better adapted to a shorter growing period (Kudo, 1991) than are legumes, which might have led to the poor performance of legumes and the reduction in legume cover in the skiing area of our study between 1972 and 2005. On the other hand, because roots are less deep in the presence of ice, in high-altitude ski runs in the Alps roots were shorter within than they were outside ski runs (Barni et al., 2007). Typically, legumes have deeper root systems than do grasses and forbs; therefore, the presence of ice might have more negative effects on the roots of legumes than on the roots of other types of plants, contributing to the decline in legumes in the skiing area of our study. In addition, soils can have reduced microporosity under ski runs (Fahey and Wardle, 1998; Delgado et al., 2007). This effect might have contributed also to the reduction in legumes in our study, because poor aeration can have adverse effects on the growth and N_2 fixation of pasture legumes (Menneer et al., 2004). Trampling by visitors in summer could have exacerbated those effects.

In the skiing area of our study, the supply of nutrients available to plants declined between 1972 and 2005, which might have been caused by a reduction in nitrogen fixation because of the reduction in legumes in the skiing area and changes in soil nutrient dynamics, which are strongly influenced by the soil temperature regime in winter. For instance, Guleryuz et al. (2011) found that the content of total nitrogen and other soil nutrients was reduced on ski slopes in proportion to the amount of disturbance, in a previous study Ruth-Balaganskaya and Myllynen-Malinen (2000) found that the soils under ski runs were nutrient poor, and Delarze (1994) observed that local conditions on seeded ski runs favored plants that were adapted to nutrient-poor soils.

The coverage by plant species that regenerate through seeds increased between 1972 and 2005 in the ski area, only, probably because a seed dispersal strategy was favored by disturbance. Non-vegetative regenerative strategies are adapted to disturbance because seeds are numerous, independent, and stress-tolerant, but vegetative expansion is most common in relatively undisturbed habitats (Grime, 2001). However, the colder temperatures under compacted ski runs might affect perennial herbs that have large underground storage organs because intracellular ice crystals cause cytolysis (Wanek, 1974), which might have contributed to the decrease in the cover of plants that regenerate by rhizomes.

In our study, the increase in the abundance of ruderal species in response to three decades of disturbance in the skiing area might have been influenced by the trampling and disturbance caused by snow groomers and walkers in winter and summer. Bayfield (1980) found that ruderal species were associated with road verges near ski lifts, and Clarke and Martin (1999) and Guleryuz et al. (2008) found them to be common on ski runs. Delarze (1994) recorded high proportions of ruderal species at ski sites below 2000 m a.s.l., and Grabherr (1985) indicated that alpine ruderal species were the first to re-colonize the disturbed areas on ski sites above 1400 m a.s.l. Thompson and Hutchinson (1986) reported extensive patches of diverse ruderal flora on ski sites that were exposed to considerable trampling and disturbance. Goñi and Guzmán (2001) found an increase in ruderal species around ski buildings. Puntieri (1991) observed an invasion by ruderal species in patches where the level of disturbance from skiing activities was high enough for these species to become established. In addition, Barni et al. (2007) noted that pioneer species that colonize debris and species that were associated with the disturbance of the soil by snow-grooming vehicles were the only native species on re-seeded ski runs.

In our study, the cover of ruderal species was negligible in 1972 and 2005 in the non-skiing area, although it increased slightly but significantly between 1972 and 2005, which might have been a result of the dispersal of the seeds of ruderal species by grazing animals (zoochory) because the non-skiing area was grazed by cattle later in the season than was the skiing area. In subalpine grasslands, livestock can be an important agent for the dispersal of many plant species and, thereby, increase the similarity in the species compositions among fragments; i.e., typically, grazing is a homogenizing process (Komac et al., 2011).

In our study, the increase in the abundance of spiny species such as *Cirsium eriophorum* and *Carduus carlinifolius* and other ruderal species, the increase in less palatable forbs, and the reduction in legumes that have high feed value contributed to the reduction in the pastoral value of the ski area between 1972 and 2005, which implies a reduction in the potential stocking rate of this area. Goñi and Guzmán (2001) found that the quality of pasture for livestock was lower in the area of ski runs. In our study, an increase in plant diversity between 1972 and 2005 did not translate into ‘‘useful’’ diversity in the ski area. As Dumont et al. (2001) stated, in animal production, ‘‘unuseful’’ diversity must be distinguished from ‘‘useful’’ diversity (recognizable species eaten by livestock).

Conclusions

In our study, approximately 20 yr (1981–2000) of skiing activities led to a significant increase in bare ground cover. Plant diversity increased between 1972 and 2005 both in the skiing and non-skiing areas, probably because of the shift from a rotational to a continuous grazing system. The absence of the negative effects of ski runs construction and use on plant diversity suggests that livestock counterbalanced those effects. In addition, the coverage of legumes in the skiing area declined between 1972 and 2005, which suggests shortened growing seasons related to possible changes in the insulation properties of the snow cover caused by snow groomers. Probably, a reduction in soil nitrogen content associated with the reduction in legume cover led to a species composition that reflected poorer soils in the skiing area. The coverage of plant species regenerated by seeds increased in the ski area, and ruderal species increased more in the ski area than they did in the non-skiing area, which suggests that ruderal species were favored by the disturbances associated with the construction and use of ski runs. The increase in the abundance of unpalatable ruderal species and reduction in legumes reduced the pastoral value for feeding livestock in the skiing area.

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