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**The impact of forest ski-pistes on diversity of ground-dwelling
arthropods and small mammals in the Alps**

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Running title

Ski-pistes, arthropods and small mammals diversity

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Abstract

Forest clearing for winter sport activities is the major force driving loss and fragmentation of the alpine forests. The establishment of ski-pistes involves impacts on every ecosystem component. To assess the extent of this threat we studied ground-dwelling arthropods (namely ground beetles and spiders) and small mammals (shrews and voles) at two ski resorts in north-western Italian Alps by pitfall trapping. Diversity parameters (mean abundance, species richness and Shannon index) of spiders and macropterous carabids increased from forest interior to open habitat (i.e. ski-piste or pasture), whereas parameters of brachypterous carabids significantly decreased from forest interior to open habitats. Diversity parameters of macropterous ground beetles were higher on pastures than on ski-pistes. Small mammals were virtually absent from ski-pistes. Observed frequencies in the three adjacent habitats were significantly different from expected ones for the bank vole *Myodes glareolus* and the pygmy shrew *Sorex minutus*.

Generalized linear models showed that abundance, species richness and diversity of spiders and macropterous carabids of ski-pistes were best modelled by combination of factors, including grass cover and width of the ski-piste. Indicator Species Analysis showed that species that significantly preferred ski-pistes were less than those preferring pastures, and species which were exclusive of ski-pistes were very few. To retain arthropod ground-dwelling fauna of open habitats environmentally friendly ways of

constructing pistes should be developed. After tree clearing, only the roughest ground surfaces should be levelled, in order to preserve as much natural vegetation as possible. Where necessary, ski-pistes should be restored through the recovery of local vegetation.

Keywords: alpine forests, diversity, ground beetles, ski-pistes, spiders, bank vole, pygmy shrew.

Introduction

From the beginning of the last century, the expansion of ski districts has severely disturbed the environment in the Alps. The establishment of ski-pistes, in particular, involves impacts on every ecosystem component along a broad altitudinal range that touches the montane and alpine belt (forest and treeless zone, respectively). During ski-piste construction pastures or forest tracts are abruptly clear-cut, bulldozers and power shovels are used for soil removal to provide suitable slopes for skiers (this is often referred as machine grading), and artificial seeding is carried out to control for soil erosion. These interventions affect soil properties (Delgado et al. 2007). Pistes which have been machine graded have lower vegetation cover, species diversity and abundance of early flowering species (Wipf et al. 2005). Vegetation is also damaged by skiing and ski-piste preparation by snow-grooming vehicles (Cernusca et al. 1999; Rixen et al. 2004b). Alpine soils of groomed pistes are also changed by an extensive heat loss (Rixen et al. 2004a). The use of artificial snow induces prolonged snowing which induces a delay in snowmelt and soil warming at the end of the season (Rixen et al. 2004b; Keller T et al. 2004) and may cause a delay in the vegetative re-sprouting (Rixen et al. 2003). The artificial snow can also add pollutants to soils and additives used to promote a rapid and long lasting freezing (Rixen et al. 2003). Furthermore, in summer, cutting of shrubs and machine-grading are carried to level rough or bumpy soil surfaces

(ground levelling), producing further damage to vegetation and soil (Bayfield 1996; Titus and Tsuyuzaki 1999; Barni et al. 2007).

Studies on animals were few. Birds of high elevation grasslands tend to avoid ski-pistes and, somehow, to avoid the nearby prairies too (Rolando et al. 2007). Below the tree line impacts of ski development were diverse. In the wooded superior montane belt, the expansion of ski districts caused clear damages to local black grouse populations (*Tetrao tetrix*) (Menoni and Magnani 1998; Zeitler and Glanzer 1998) which also suffer mortality induced from collision with cable wires (Observatoire des Galliformes de Montagne 2006). In areas interested by the practice of free-ride ski, the dejections of black grouses contained significant increased quantities of stress metabolites (Arlettaz et al. 2007); ski tourism also affected both habitat use and endocrine status in capercaillie *Tetrao urogallus* (Thiel et al. 2008). Bird communities living in forests crossed by ski-runs undergo a negative margin effect: the biodiversity is lower at the edge of the ski-runs than it is at the edge of pastures or inside the wooded patches (Laiolo and Rolando 2005). Apart from researches on birds, there is a substantial lack of studies on other animals and, therefore, to pinpoint the best conservation strategies, new researches on animal assemblages, especially those completely neglected so far (e.g. arthropods and small mammals), are strongly required.

Ground-dwelling arthropods are small, diverse, sensitive to environmental variability and may be therefore used as indication of habitat heterogeneity, ecosystem diversity and environmental stress (McGeoch 1998). Ground beetles (Coleoptera: Carabidae) and spiders (Araneae), in particular, have been widely recommended as bioindicators (Churchill 1997; Rainio and Niemelä 2003). The few researches which focused contemporaneously on both groups showed that both are negatively affected by anthropogenic activities (Alaruikka et al. 2002; Öberg and Ekbohm 2006; Pearce and Venier 2006). In the Alps, carabids and spiders have also been used to assess the chronosequence of a glacier foreland (Gobbi et al. 2006a).

Spiders and most ground beetles are predators which play a key role in regulating populations of soil invertebrates and serving as prey to salamanders, small mammals and birds (Clarke and Grant 1968; Hance 1990).

Carabids and spiders assemblages in the Alpine region are well known due to notable ecological studies conducted by several authors (Brandmayr et al. 2003a,b; Gobbi et al. 2006b, 2007; Frick et al. 2007; Muff et al. 2009).

Small mammals also play complex and diverse functional roles in ecosystems (Hayward and Phillipson 1979) and may be used as indicators of anthropogenic land use and forest structure (Fitzgibbon 1997; Ecke et al. 2002). A few previous studies investigated short-term effects of ski-runs on the dynamics of small mammal populations in a ski area located in Colorado, USA (Hadley and Wilson 2004a,b). Additional studies on impact of ski-runs are therefore needed to promote management strategies for maintaining populations of these forest-dwelling animals in the Alps.

The zone of transition between two different habitat types may be termed as ecotone and the sharp demarcation between them as edge (Odum and Barret 2005). Forest/ski-piste zones are therefore typical ecotones, as are the typical forest/pasture zones derived from alpine pastoral activities. The two ecotone types are rather different because ski-pistes are linear, narrow landscape elements, whereas pastures are not. Moreover, forest/pasture edges are usually less abrupt than forest/ski-piste edges.

To assess the impact of forest ski-pistes on assemblages of spiders and carabids, we examined the structure of assemblages (expressed as abundance, species richness and Shannon diversity index) across forest/ski-piste ecotones by sampling at the edge and in each of the adjacent habitats. Forest/pasture ecotones were also considered to test whether assemblage diversity parameters were lower on ski-pistes than on pastures. Relationships between assemblages and environmental characteristics of ski-pistes

were analyzed to find out the best predictors of local diversity. In this study, pitfall trapping was not originally intended to catch small mammals. However, individuals found in traps were preserved in alcohol and identified *a posteriori*.

Material and Methods

Study areas

The study was carried out at two ski resort sites, i.e. Torgnon (45° 48' 39" N; 7°33'06" E) and Gressoney St. Jean (45°45'31" N; 7°49'50" E), located in Valtournenche and Gressoney Valley, respectively (two parallel valleys located in north-western Italian Alps, Aosta Valley). In Torgnon we surveyed ski-pistes (1700- 2000 m a.s.l, 30-70 m width) which cut coniferous forests dominated by larch *Larix decidua* and Norway spruce *Picea abies*. The understorey is sparse, mainly composed of juniper *Juniperus communis*, alpenrose *Rhododendron ferrugineum*, bilberry *Vaccinium myrtillus* and bearberry *Vaccinium uliginosum*. In Gressoney St. Jean (hereinafter simply indicated as Gressoney) we surveyed ski-pistes (1500-1900 m a.s.l, 40-70 m width) which cut coniferous forests dominated by fir *Abies alba*, larch and Norway spruce, with an under-storey mainly composed of bilberry.

In both study-areas, pastures and ski-runs are dominated by Gramineae grasses.

Sampling design

We selected 36 sampling plots at Torgnon (18 in forest/pastures ecotones and 18 in forest/ski-piste ecotones) and 50 at Gressoney St Jean (25 for each ecotone type). The exact location of plots was

established in the field by means of a Global Positioning System (GPS) Garmin eTrex® navigator. Each plot was located at a minimum distance of 100 m from the next nearest sampling plots. Nine pitfall traps were placed at each sampling plot: three (5 m apart) were placed in the forest, three in the ski-piste (or pasture) and three along the edge between the two habitats. Traps in forest and ski-piste (or pasture) were aligned in parallel with the edge, at a distance of 20 m from it. Pitfall traps were 7.5 cm in mouth diameter and 9 cm deep, filled with 150 mL of a standard mixture of wine vinegar and sodium chloride solution to preserve individuals. Traps were placed at the beginning of July 2006 and emptied after three weeks. Trapped arthropods were sorted and identified, whenever possible, to the species level using updated standard keys or specialists' works. Nomenclature follows Platnick (2008) for spiders and Audisio and Vigna Taglianti (2004) for ground beetles. A number of spider species were only present as juveniles, and could not be identified further than to genus level. In keeping with several authors (e.g. Krell 2004; Kapoor 2008), such individuals were included as morpho-species (hereinafter indicated with the name of the genus followed by spp.). Spiders can be collected by means of several sampling techniques: by using pitfall traps, we mainly detected wandering spiders.

Small mammals were identified using field guides (MacDonald and Barrett 1993; Spagnesi et al. 2002) and under the supervision of experts.

Environmental characteristics of ski-pistes were recorded at each plot. In circular areas of 20 m radius (centred on the second pitfall trap) we measured percentages of grass, soil and rubble cover (estimated by eye), mean grass height (ten measurements, in centimetres), aspect, altitude and width of the ski-piste (in metres).

Data analysis

For each sampling plot, samples from the three traps of each habitat type (forest, edge and ski-piste or pasture) were pooled and used in the analyses.

To compare species richness of the two study sites, rarefaction curves were calculated. Thereafter, to ensure valid inter-sites comparisons, these curves were rarefied to the lowest number of individual recorded.

At each study site we calculated three diversity parameters and tested for differences in species richness (S), abundance (N) and diversity (Shannon index: $H' = - \sum p_i \times \ln p_i$ where p_i is the relative frequency of species i) between the three habitats (or between pistes and pastures) by means of One-Way ANOVA. Least-squares deviation (LSD) post-hoc tests were used for pair-wise comparisons of habitat type means. To approach normality (checked by using normal probability plots), abundance and richness data were square-root transformed [$y = \sqrt{(x+0.5)}$], whereas diversity data were log transformed [$y = \log(x+1)$] (Sokal and Rohlf 1995). Ground beetle assemblages were composed of species with contrasting ecological requirements so that ecological patterns could not be revealed. Hence, carabids were divided into three main ecological groups based on their wing morphology: macropterous (full-sized wings), brachypterous (reduced wings or wingless) and wing-dimorphic (species with both winged and short-winged individuals). ANOVA and data transformation were performed using STATISTICA 6.0 package (StatSoft Inc. 2001).

Environmental characteristics of ski-pistes were analysed to find out the best predictors of local diversity. Since the environmental variables were correlated, much of the information in one or more of these can be redundant and thus the results of analyses based on these raw predictors might be ambiguous. Principal Component Analysis was chosen to minimize the effects of multicollinearity. However, PCA generated ambiguous derived components and we therefore examined all pairwise correlations to identify correlated pairs ($r > |0.7|$). Then, following Riitters et al. (1995), one variable was selected to

represent each group of highly correlated variables, selection criteria including the degree of normality and interpretability. This procedure identified grass cover, aspect, altitude and width of the ski-piste as independent variables.

To reveal relationships between diversity, abundance and richness of ground-dwelling arthropods and environmental variables of ski-pistes, we used generalized linear models (GLM). Data on species diversity were normally distributed and a normal distribution of error assumption with an identity link was applied. However, abundance and species richness attained a Poisson distribution; therefore a Poisson distribution of errors was assumed and the density of ground-dwelling arthropods was related to explanatory variables via a logarithmic link function (McIntyre and Lavorel 1994).

Akaike's information criterion (AIC, Akaike 1973) was used to select the most appropriate models, i.e. those fitting best the available data set. AIC is based on the principle of parsimony and helps to identify the model that accounts for the most variation and the fewest variables: the model that best explains the data is that with the lowest AIC. This information criterion is one of the most powerful approaches for model selection from a set of alternative plausible models and it solves the problems of stepwise model selection because no sequential statistical test is conducted (Burnham and Anderson 1998). Generalized linear models and AIC were calculated using the R package (Ihaka and Gentleman 1996; R Development Core Team 2005).

High specificity and fidelity of every species within habitats were explored by the IndVal (Indicator Value) procedure (Dufrêne and Legendre 1997). The indicator value is maximum (100) when all individuals of a species are found in a single habitat (high specificity) and when the species occurs in all samples of that habitat (high fidelity). The statistical significance of the maximum indicator value was evaluated by a Monte Carlo randomization test (1000 runs). IndVal analyses were run using PC-Ord software (McCune and Mefford 1999).

The effect of ski-pistes on small mammals was tested comparing observed frequencies in the three adjacent habitats and expected ones under the assumption of an equal use of the three habitats (chi-square test for goodness of fit). Individuals collected on forest/pasture ecotones were very few and they were therefore excluded from analyses.

Results

A total of 171 ground-dwelling arthropod species (corresponding to a total of 12,053 individuals) were collected altogether (Table 1, appendices 1 and 2). Spiders were dominated by wandering species (95.3% of the capture), whereas ground beetles were mostly represented by brachypterous (60%) and macropterous species (24%) and, to a lesser extent, by wing-dimorphic species (16%). Despite the proximity between the two study areas (only 22.3 kilometres in straight line), species composition was rather different: percentages of shared species were 37% for spiders and 25% for ground beetles. Rarefaction procedure suggested that species richness of the two study sites areas was quite similar (Table 1).

Three small mammal species were sampled in both study areas: the bank vole *Myodes glareolus* (Schreber 1780), the common shrew *Sorex araneus* Linnaeus, 1758 and the pygmy shrew *Sorex minutus* Linnaeus, 1766. In this case, given the low number of trapped individuals, data of the two study sites were merged into a single sample for each species.

Ski-piste mean grass cover was lower at Torgnon than at Gressoney (67.5 vs. 85.0%, $F_{1,37} = 3.3$, $P < 0.05$).

Differences between habitat types

Mean abundance, species richness and diversity of spiders were significantly different between the three habitat types, and increased from the forest interior to the open habitats (ski-piste or pasture). A noticeable exception to this pattern regarded the forest/ski-piste ecotone at Torgnon, where species richness and diversity were significantly lower on ski-pistes than at the edge (Table 2, Fig. 1). Mean abundance, species richness and diversity of macropterous ground beetles showed the same general pattern as spiders (Table 3, Fig. 1). In contrast to macropterous, mean values of brachypterous parameters significantly decreased from the forest interior to the open habitat (Table 3).

Individuals of wing-dimorphic species were few (mostly short-winged) and no significant variation between habitat types was evidenced. Hence, this guild was excluded from subsequent statistical analyses.

Small mammals were virtually absent from ski-pistes. Observed frequencies in the three adjacent habitats were significantly different from expected ones for the bank vole and the pygmy shrew (Fig. 2).

Differences between ski-pistes and pastures

Differences between ski-pistes and pastures might depend on differences between plots. Hence, data were standardized by calculating the ratio of the value of each diversity parameter (abundance, species richness and diversity) of the open habitat (ski-piste or pasture) to the average value of the same parameter at each plot (the average among the three habitats). This enabled us to measure the relative contribution of the open habitat to the mean diversity of each plot. Mean ratios of abundance, species richness and diversity of macropterous ground beetles were usually higher on pastures than on ski-pistes (Gressoney H': $F_{1,29} = 5.3$ $P < 0.05$; Torgnon N: $F_{1,39} = 7.0$ $P < 0.05$, S: $F_{1,39} = 10.0$ $P < 0.01$, H': $F_{1,39} = 12.2$ $P < 0.01$) and the same pattern was also observed for spiders at Torgnon (S: $F_{1,40} = 4.2$ $P < 0.05$, H': $F_{1,40} = 4.0$ $P < 0.05$). This indicates that the relative contribution of ski-pistes to the mean diversity of plots was lower

than that of pastures. The relative decrease of species richness on ski-pistes in comparison with pastures is apparent in Fig.1 (black arrows). The only exception to this pattern was the mean ratio of abundance of spiders, which was significantly higher on ski-pistes than on pastures at Gressoney ($F_{1,27} = 5.3$ $P < 0.05$).

Relationship between arthropod assemblages and ski-pistes

Results of Generalized Linear Models (GLM) of spider and macropterous carabid abundance, species richness and diversity on environmental predictors are shown in Table 4. Ecological parameters were positively associated with grass cover in six selected models out of nine (diversity of spiders at both sites, abundance and species richness of spiders at Torgnon, abundance of macropterous at Gressoney) and with width of ski-pistes in three out of nine (abundance of spiders at Torgnon, abundance and species richness of ground beetles at Gressoney).

Species identity

Spiders and ground beetles which were indicators of open habitats are shown in Appendix C. In general, species that significantly preferred ski-pistes were less numerous than those preferring pastures, especially at Torgnon. Only three species were exclusive indicators of ski-pistes (i.e. they were never classed as indicator of any other habitat): *Pardosa blanda*, *Drassodes* spp. (spiders) and *Agonum sexpunctatum* (ground beetle). IndVal analysis also detected species which positively selected coniferous forests: five spider species (*Pardosa ferruginea*, *Malthonica silvestris*., *Coelotes* spp. at Gressoney; *Micaria* spp. and *Alopecosa aculeata* at Torgnon) and six ground beetle species (*Pterostichus flavofemoratus*, *Pterostichus apenninus*, *Carabus depressus* at Gressoney; *Calathus micropterus*, *Pterostichus multipunctatus*, *Notiophilus biguttatus* at Torgnon).

Discussion

All studies regarding the impact of ski on mountainous areas agree on defining the establishment of ski districts as a general threat to the environment. This is rather worrying in the Alps because the area affected by ski-pistes is still increasing (Abegg et al. 1997; Elsasser and Messerli 2001; Wipf et al. 2005). Below the tree line, grass colonization of ski-runs is faster than above the tree line because the success of revegetation declines with altitude (Urbanska 1997a). Nevertheless, the impact is severe because in most cases the construction of ski-pistes requires the permanent elimination of the forest from the track. The construction of ski-pistes in the montane belt induces forest loss and fragmentation, potentially inducing severe impacts on animal communities. However, apart from a study on bird communities living in forests crossed by ski-runs (Laiolo and Rolando 2005), no other research on the effects of ski-pistes below the tree line has been carried out. Further studies on other animal taxa are thus particularly needed.

This study focused for the first time on ground dwelling arthropods and small mammals. The two areas, despite their relative proximity, greatly differed in arthropod species composition, due to environmental and historical events (Casale and Vigna Taglianti 1993). Nevertheless, the results were similar at two sites and showed that mean abundance, species richness and diversity of spiders and macropterous carabids increased from the forest interior to the open habitat (ski-piste or pasture). Both assemblages were characterized by open habitat species capable of colonizing new habitats (wandering spiders, small body size, winged carabids). Contrarily to macropterous, diversity of brachypterous carabids significantly decreased from forest interior to open habitat. These ground beetles are medium-large body size species, wingless or with reduced wings, hence incapable of long movements or dispersal

by flight (den Boer 1970; Negro et al. 2007, 2008). The relationship between brachyptery and endemic status of montane forest dwelling carabids in the Alps has been examined closely in Brandmayr (1991).

Our results also showed that bank voles and pygmy shrews virtually avoided ski-pistes. Both are typical forest species (MacDonald and Barrett 1993; Alibhai and Gipps 1991), which may be affected by the construction of ski-pistes because movements and abundance of small mammals are influenced by habitat loss and fragmentation (Diffendorfer et al. 1995; Bentley et al. 2000; Laakkonen et al. 2001).

Although both open habitats (pastures and ski-pistes) were positively selected by spiders and macropterous carabids, comparisons between the two habitats suggested that ski-pistes were less attractive than pastures, in particular for carabids. IndVal analyses strengthen these conclusions because the number of typical pasture species were usually higher than that of ski-piste species. GLM analyses suggested that the local degree of grass cover of ski-pistes can significantly affect spider and macropterous ground beetle diversity, which increased with increasing of the grass cover. This explains why at Torgnon, where the desolation of ski-pistes (in terms of scarce grass cover) was great, species richness and diversity were significantly lower on ski-pistes than on the edge. Ski-piste width was another predictor of ground-dwelling arthropod diversity, which increased with increasing width. We believe both predictors concur to explain why ski-pistes are less attractive to macropterous carabids and spiders than pastures. On one hand, migration to ski-pistes is more difficult because they are perceived as narrow pastures enclosed in the forest matrix, on the other colonization is more difficult because of the lower grass availability.

Despite the general low attractiveness of ski-pistes, a few species in the study areas were significantly associated with this habitat. This was the case of the spider *Pardosa blanda* and the ground beetle *Agonum sexpunctatum*. *P. blanda*, in particular, was much more abundant in ski-pistes than in pastures, especially at Gressoney (where the local mean abundance was higher on ski-pistes than on pastures just

because of its prevalence). This species might have found better environmental conditions on ski-pistes than on pastures (micro-habitat and/or competitive conditions).

Carabids and spiders may show fairly similar responses to environmental disturbances (Rushton et al. 1989; Alaruikka et al. 2002; Öberg and Ekblom 2006; Pearce and Venier. 2006). Our study confirmed that spiders and ground beetles may be usefully simultaneously considered to monitor environmental man-induced changes. However, it also emphasized that when/where assemblages are heterogeneous (ground beetles, in this study), distinct ecological guilds and species identities should be considered.

Open habitat arthropods were usually common. However, some spider species, caught occasionally on ski-pistes, were of conservation interest because rare and endemic to the Alps (*Coelotes rudolfi*, *Cybaeus intermedius*, *Berlandina nubivaga*, *Metopobactrus schenkeli*). Our results suggested that the poor grass cover of ski-pistes is a serious hindrance to optimal colonization of macropterous ground beetles and spiders. From this point of view, retaining the ground-dwelling fauna of these anthropogenic open habitats is likely to involve developing environmentally friendly ways of constructing pistes. After tree clearing, only the roughest ground surfaces should be levelled, in order to preserve as much soil and natural vegetation as possible. Where necessary, ski-pistes should be restored through management to promote the recovery of local vegetation. Transplants of wild species (Urbanska 1997b; Conlin and Ebersole 2001; Ebersole et al. 2002) are particularly promising methods. Once natural revegetation is achieved, vegetation cover should be preserved without compromising the safety of the ski-runs. Grassy and shrubby vegetation, for instance, can be kept low through cattle-grazing and direct pruning without applying ground levelling.

Our results also suggested that typical forest species (both brachypterous carabids and small mammals) may be heavily damaged from ski-piste construction because they are unable to colonize these open habitats. For these species, forest removal along narrow strips can cause habitat loss and habitat fragmentation, both potentially exerting negative effects on animal diversity (Hanski 1999; Odum and

Barrett 2005). Ski-pistes might potentially prevent or reduce movements between adjacent forest patches. This is of particular concern in the case of carabid endemic species, such as *Pterostichus flavofemoratus*, *P. muntipunctatus*, *Carabus depressus* (all identified by IndVal as typical forest species), which were precinctive to more or less restricted alpine areas (Negro et al. 2007). Certain carabids and spiders rarely cross large roads (Mader 1984, Koivula and Vermeulen 2005), which are known to lead to significant intraspecific genetic differentiation in flightless carabids (Keller I et al. 2004). Movements of forest small mammals are also known to be constrained by the presence of open habitats as fields (Wegner and Merriam 1979) or roads (Oxley et al. 1974; McGregor et al. 2008). Home ranges of the bank vole are usually between 0.1 and 0.2 ha in deciduous woods (Alibhai and Gipps 1991) and those of the pygmy shrew between 0.05 to 0.2 ha (Churchfield 1991). Hence, in theory, for these species most ski-pistes might be too large to be crossed.

All in all, specific studies on animal movements across ski-pistes should be carried out to ascertain whether they operate as true barriers to movements between forest patches.

To make movements between forest patches easier, a possible management intervention could be that of restoring the gradual transition from forest to open habitat by enhancing a partial shrub colonization of ski-pistes. It has been demonstrated that the presence of shrubs facilitate the movements of the ground beetle *Carabus olympiae*, which likely uses shrubs as shelter and protection from predators (Negro et al. 2007, 2008). Moreover, shrub cover may increase the amount of prey available to carabids and may provide a more uniform resource distribution in time (Niemelä and Spence 1994; Magura 2002). Shrubs and fencerows are also known to be used by small mammals (Wegner and Merriam 1979). The bank vole, in particular, favours dense shrubby cover (Alibhai and Gipps 1991; Tattersall et al. 2002).

Finally, it is worth mentioning that all the managing measures here proposed have a broader ecological significance because they may simultaneously be useful to preserve forest bird diversity (Laiolo and Rolando 2005).

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Appendices

Appendix A. List of spider species and morpho-species collected at Torgnon (T) and Gressoney (G).

AGELENIDAE		<i>Zelotes apricorum</i> (L. Koch, 1876)	G
<i>Histopona italica</i> Brignoli, 1977	G	<i>Zelotes</i> spp.	G,T
<i>Malthonica silvestris</i> (L. Koch, 1872)	G,T	<i>Zelotes subterraneus</i> (C. L. Koch, 1833)	G,T
		<i>Zelotes talpinus</i> (L. Koch, 1872)	G,T
AMAUROBIIDAE		HAHNIIDAE	
<i>Coelotes mediocris</i> Kulczyn'ski, 1887	G	<i>Cryphoeca silvicola</i> (C. L. Koch, 1834)	G,T
<i>Coelotes rudolfi</i> (Schenkel, 1925)	G	<i>Hahnina nava</i> (Blackwall, 1841)	T
<i>Coelotes</i> spp.	G		
		LINYPHIIDAE	
ARANEIDAE		<i>Agyneta conigera</i> (O. P.-Cambridge, 1863)	T
<i>Parazygiella montana</i> (C. L. Koch, 1834)	T	<i>Asthenargus paganus</i> (Simon, 1884)	G
		<i>Centromerita bicolor</i> (Blackwall, 1833)	G
CLUBIONIDAE		<i>Centromerus brevivulvatus</i> Dahl, 1912	T
<i>Clubiona alpicola</i> Kulczyn'ski, 1882	G	<i>Centromerus subalpinus</i> Lessert, 1907	T
<i>Clubiona diversa</i> O. P.-Cambridge, 1862	T	<i>Ceratinella scabrosa</i> (O. P.-Cambridge, 1871)	G,T
<i>Clubiona neglecta</i> O. P.-Cambridge, 1862	T	<i>Collinsia inerrans</i> (O. P.-Cambridge, 1885)	G,T
<i>Clubiona reclusa</i> O. P.-Cambridge, 1863	G	<i>Diplocentria bidentata</i> (Emerton, 1882)	T
<i>Clubiona</i> spp.	G,T	<i>Diplocephalus latifrons</i> (O. P.-Cambridge, 1863)	G
		<i>Diplostyla concolor</i> (Wider, 1834)	G,T
CYBAEIDAE		<i>Erigone dentipalpis</i> (Wider, 1834)	G
<i>Cybaeus intermedius</i> Maurer, 1992	G	<i>Gonatium rubens</i> (Blackwall, 1833)	T
		<i>Incestophantes frigidus</i> (Simon, 1884)	G
DYSDERIDAE		<i>Mansuphantes prope pseudoarciger</i> Wunderlich, 1985	G,T

<i>Dysdera crocata</i> C. L. Koch, 1838	T	<i>Meioneta prope orites</i> (Thorell, 1875)	G,T
		<i>Metopobactrus schenkeli</i> Thaler, 1976	T
GNAPHOSIDAE		<i>Micrargus apertus</i> (O. P.-Cambridge, 1871)	G,T
<i>Aphantaulax trifasciata</i> (O. P.-Cambridge, 1872)	T	<i>Minyriolus pusillus</i> (Wider, 1834)	G
<i>Berlandina nubivaga</i> (Simon, 1878)	T	<i>Neriene peltata</i> (Wider, 1834)	G
<i>Callilepis nocturna</i> (Linnaeus, 1758)	G,T	<i>Palliduphantes pallidus</i> (O. P.-Cambridge, 1871)	T
<i>Drassodes cupreus</i> (Blackwall, 1834)	G,T	<i>Pelecopsis elongata</i> (Wider, 1834)	G,T
<i>Drassodes lapidosus</i> (Walckenaer, 1802)	G	<i>Pelecopsis radicola</i> (L. Koch, 1872)	T
<i>Drassodes pubescens</i> (Thorell, 1856)	G,T	<i>Peponocranium orbiculatum</i> (O. P.-Cambridge, 1882)	G,T
<i>Drassodes</i> spp.	G,T	<i>Pityohyphantes phrygianus</i> (C. L. Koch, 1836)	T
<i>Drassyllus praeficus</i> (L. Koch, 1866)	G	<i>Porrhomma microphthalmum</i> (O. P.-Cambridge, 1871)	G
<i>Drassyllus pusillus</i> (C. L. Koch, 1833)	G,T	<i>Tapinocyba pallens</i> (O. P.-Cambridge, 1872)	T
<i>Drassyllus</i> spp.	G,T	<i>Tenuiphantes flavipes</i> (Blackwall, 1854)	G
<i>Gnaphosa badia</i> (L. Koch, 1866)	G,T	<i>Tenuiphantes tenuis</i> (Blackwall, 1852)	G
<i>Haplodrassus aenus</i> Thaler, 1984	T	<i>Tiso vagans</i> (Blackwall, 1834)	G
<i>Haplodrassus signifer</i> (C. L. Koch, 1839)	G,T	<i>Trichopterna cito</i> (O. P.-Cambridge, 1872)	T
<i>Haplodrassus</i> spp.	G,T	<i>Walckenaeria alticeps</i> (Denis, 1952)	G,T
<i>Haplodrassus umbratilis</i> (L. Koch, 1866)	G,T	<i>Walckenaeria atrotibialis</i> (O. P.-Cambridge, 1878)	G
<i>Micaria aenea</i> Thorell, 1871	G,T	<i>Walckenaeria furcillata</i> (Menge, 1869)	G
<i>Micaria alpina</i> L. Koch, 1872	G	<i>Walckenaeria nodosa</i> O. P.-Cambridge, 1873	T
<i>Micaria fulgens</i> (Walckenaer, 1802)	G,T	<i>Walckenaeria obtusa</i> Blackwall, 1836	T
<i>Micaria pulicaria</i> (Sundevall, 1831)	G,T		
<i>Micaria</i> spp.	G,T	LIOCRANIDAE	
<i>Zelotes electus</i> (C. L. Koch, 1839)	T	<i>Agroeca cuprea</i> Menge, 1873	T
<i>Zelotes latreillei</i> (Simon, 1878)	T	<i>Scotina celans</i> (Blackwall, 1841)	T
LYCOSIDAE			
<i>Alopecosa aculeata</i> (Clerck, 1757)	G,T	<i>Robertus truncorum</i> (L. Koch, 1872)	T
<i>Alopecosa cuneata</i> (Clerck, 1757)	G,T	<i>Steatoda phalerata</i> (Panzer, 1801)	G,T

<i>Alopecosa accentuata</i> (Latreille, 1817)	T	<i>Ozyptila trux</i> (Blackwall, 1846)	G
<i>Alopecosa</i> spp.	G,T	<i>Xysticus audax</i> (Schrank, 1803)	G,T
<i>Arctosa figurata</i> (Simon, 1876)	T	<i>Xysticus bifasciatus</i> C. L. Koch, 1837	G
<i>Arctosa renidescens</i> Buchar & Thaler, 1995	G,T	<i>Xysticus erraticus</i> (Blackwall, 1834)	G,T
<i>Pardosa amentata</i> (Clerck, 1757)	G	<i>Xysticus gallicus</i> Simon, 1875	G,T
<i>Pardosa bifasciata</i> (C. L. Koch, 1834)	T	<i>Xysticus kochi</i> Thorell, 1872	T
<i>Pardosa blanda</i> (C. L. Koch, 1833)	G,T	<i>Xysticus ninnii</i> Thorell, 1872	T
<i>Pardosa ferruginea</i> (L. Koch, 1870)	G,T	<i>Xysticus</i> spp.	G,T
<i>Pardosa lugubris</i> (Walckenaer, 1802)	G,T		
<i>Pardosa mixta</i> (Kulczyn'ski, 1887)	T	ZORIDAE	
<i>Pardosa palustris</i> (Linnaeus, 1758)	G,T	<i>Zora spinimana</i> (Sundevall, 1833)	G,T
<i>Pardosa riparia</i> (C. L. Koch, 1833)	G,T		
<i>Pardosa</i> spp.	G,T		
<i>Trochosa ruricola</i> (De Geer, 1778)	G		
<i>Xerolycosa nemoralis</i> (Westring, 1861)	G,T		

PHILODROMIDAE

<i>Philodromus cespitum</i> (Walckenaer, 1802)	G,T
<i>Philodromus collinus</i> C. L. Koch, 1835	T
<i>Philodromus</i> spp.	G,T
<i>Philodromus vagulus</i> Simon, 1875	G,T
<i>Thanatus formicinus</i> (Clerck, 1757)	T
<i>Tibellus oblongus</i> (Walckenaer, 1802)	T

PISAURIDAE

<i>Pisaura mirabilis</i> (Clerck, 1757)	T
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SALTICIDAE

<i>Aelurillus v-insignitus</i> (Clerck, 1757)	G,T
<i>Heliophanus cupreus</i> (Walckenaer, 1802)	G,T
<i>Pellenes tripunctatus</i> (Walckenaer, 1802)	T
<i>Phlegra fasciata</i> (Hahn, 1826)	G,T
<i>Sitticus saxicola</i> (C. L. Koch, 1846)	T

SEGESTRIIDAE

<i>Segestria senoculata</i> (Linnaeus, 1758)	T
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TETRAGNATHIDAE

<i>Pachygnatha listeri</i> Sundevall, 1830	G
<i>Pachygnatha degeeri</i> Sundevall, 1830	T

THERIDIIDAE

<i>Enoplognatha thoracica</i> (Hahn, 1833)	T
<i>Euryopis flavomaculata</i> (Keyserling, 1891)	T
<i>Robertus lividus</i> (Blackwall, 1836)	G
<i>Robertus negelctus</i> (O. P.-Cambridge, 1871)	G
<i>Robertus</i> spp.	G

Appendix B. List of ground beetle species collected at Torgnon (T) and Gressoney (G) grouped by wing morphology.

CARABIDAE

Brachypterous

Wing-dimorphic

<i>Abax exaratus</i> (Dejean, 1828)	G	<i>Calathus erratus</i> (C.R. Sahlberg, 1827)	T
<i>Calathus fuscipes</i> (Goeze, 1777)	T	<i>Calathus melanocephalus</i> (Linné, 1758)	G,T
<i>Calathus micropterus</i> (Duftschmid, 1812)	G,T	<i>Leistus nitidus</i> (Duftschmid, 1812)	T
<i>Carabus depressus</i> Bonelli, 1810	G,T	<i>Metallina lampros</i> (Herbst, 1784)	G,T
<i>Carabus nemoralis</i> O.F. Müller, 1764	G,T	<i>Notiophilus biguttatus</i> (Fabricius, 1779)	G,T
<i>Carabus problematicus</i> Herbst, 1786	T	<i>Notiophilus palustris</i> (Duftschmid, 1812)	G
<i>Laemostenus janthinus</i> (Duftschmid, 1812)	G	<i>Poecilus lepidus</i> (Leske, 1785)	G
<i>Licinus hoffmanseggii</i> (Panzer, 1803)	G	<i>Synuchus vivalis</i> (Illiger, 1798)	G,T
<i>Pterostichus apenninus</i> (Dejean, 1831)	G	<i>Trichotichnus laevicollis</i> (Duftschmid, 1812)	G,T
<i>Pterostichus cribratus</i> (Dejean, 1828)	G	<i>Trichotichnus nitens</i> (Heer, 1838)	G
<i>Pterostichus flavofemoratus</i> (Dejean, 1828)	G		
<i>Pterostichus multipunctatus</i> (Dejean, 1828)	T		
<i>Pterostichus spinolae</i> (Dejean, 1828)	G		

Macropterous

<i>Agonum sexpunctatum</i> (Linné, 1758)	G
<i>Amara aenea</i> (De Geer, 1774)	T
<i>Amara aulica</i> (Panzer, 1796)	T
<i>Amara bifrons</i> (Gyllenhal, 1810)	T
<i>Amara convexior</i> Stephens, 1828	G
<i>Amara curta</i> Dejean, 1828	T
<i>Amara equestris</i> (Duftschmid, 1812)	G,T
<i>Amara erratica</i> (Duftschmid, 1812)	G,T
<i>Amara lunicollis</i> Schiödte, 1837	G,T
<i>Amara nitida</i> Sturm, 1825	G
<i>Amara ovata</i> (Fabricius, 1792)	T
<i>Amara praetermissa</i> (C.R. Sahlberg, 1827)	T
<i>Amara similata</i> (Gyllenhal, 1810)	T

<i>Bembidion quadrimaculatum</i> (Linné, 1761)	G
<i>Cymindis cingulata</i> Dejean, 1825	G,T
<i>Cymindis humeralis</i> (Geoffroy in Fourcroy, 1785)	T
<i>Cymindis scapularis</i> Schaum, 1857	T
<i>Cymindis vaporariorum</i> (Linné, 1758)	T
<i>Harpalus affinis</i> (Schrank, 1781)	T
<i>Harpalus honestus</i> (Duftschmid, 1812)	T
<i>Harpalus rubripes</i> (Duftschmid, 1812)	T
<i>Harpalus rufipalpis</i> Sturm, 1818	T
<i>Harpalus solitarius</i> Dejean, 1829	T
<i>Limodromus assimilis</i> (Paykull, 1790)	G
<i>Ocydromus bualei</i> (Jacquelin du Val, 1852)	T
<i>Ocydromus incognitus</i> (G. Müller, 1931)	G,T
<i>Ocydromus tetracolus</i> (Say, 1823)	G
<i>Ophonus laticollis</i> Mannerheim, 1825	G
<i>Ophonus puncticollis</i> (Paykull, 1798)	T
<i>Panagaeus bipustulatus</i> (Fabricius, 1775)	G
<i>Poecilus versicolor</i> (Sturm, 1824)	G,T
<i>Pseudoophonus rufipes</i> (De Geer, 1774)	G
<i>Pterostichus oblongopunctatus</i> (Fabricius, 1787)	G
<i>Pterostichus strenuus</i> (Panzer, 1796)	G

Appendix C. Indicator Species Analysis (IndVal). Species which significantly indicate open habitat (i.e. ski-piste or pasture) are shown. Maximum indicator value (Max. obs.) and mean expected indicator value (mean exp.) are given. Statistical significance obtained by Monte Carlo randomization test (1000 runs). * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Site	Open	IndVal	IndVal
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	habitat type	Species	Max. obs.	Mean exp.	P	Species	Max. obs.	Mean exp.	P
		Ground beetles				Spiders			
Gressoney	ski-piste	<i>Amara erratica</i>	53.8	17.6	***	<i>Pardosa blanda</i>	79.0	28.5	***
		<i>Metallina lampros</i>	38.5	18.9	*	<i>Drassodes spp.</i>	59.3	35.6	***
		<i>Agonum sexpunctatum</i>	28.6	10.7	*	<i>Xysticus gallicus</i>	35.7	13.3	***
						<i>Pardosa palustris</i>	28.6	11.1	*
	pasture	<i>Poecilus versicolor</i>	64.7	19.2	***	<i>Pardosa riparia</i>	74.9	28.2	***
		<i>Ophonus laticollis</i>	49.7	25.9	***	<i>Pardosa palustris</i>	48.9	15.6	***
		<i>Amara lunicollis</i>	38.9	11.5	***	<i>Drassylus spp.</i>	26.0	11.9	*
		<i>Amara erratica</i>	20.4	9.4	*				
		<i>Pseudophonus rufipes</i>	19.4	10.3	*				
	Torgnon	ski-piste	<i>Metallina lampros</i>	44.9	12.7	***	<i>Pardosa blanda</i>	52.9	35.6
<i>Amara erratica</i>			18.5	7.5	*	<i>Pardosa palustris</i>	30.4	10.0	***
pasture		<i>Amara equestris</i>	29.2	9.8	***	<i>Pardosa mixta</i>	75.4	17.9	***
		<i>Calathus fuscipes</i>	27.7	13.4	*	<i>Steatoda phalerata</i>	61.1	13.0	***
		<i>Amara lunicollis</i>	22.1	10.5	*	<i>Alopecosa cuneata</i>	50.6	17.1	***
		<i>Poecilus versicolor</i>	20.1	10.0	*	<i>Pardosa palustris</i>	40.9	15.4	***
		<i>Metallina lampros</i>	17.9	8.4	*	<i>Xysticus gallicus</i>	30.2	9.9	***
		<i>Amara curta</i>	16.7	6.5	*	<i>Xysticus ninni</i>	30.1	14.3	*
		<i>Harpalus rubripes</i>	15.6	8.1	*	<i>Zelotes spp.</i>	30.1	16.4	*
					<i>Pardosa bifasciata</i>	21.8	12.5	*	

<i>Philodromus spp.</i>	20.1	8.3	***
<i>Caccilepis nocturna</i>	19.2	8.1	*
<i>Arctosa figurata</i>	17.70	8.80	*

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Fig.1 Differences in species richness of spiders and macropterous carabids between habitats (viz. forest interior, edge and open habitat, from the left to the right for each three-bars histogram). Error bars are \pm standard errors. Black arrows indicate cases of apparent decrease of species richness in ski-pistes.

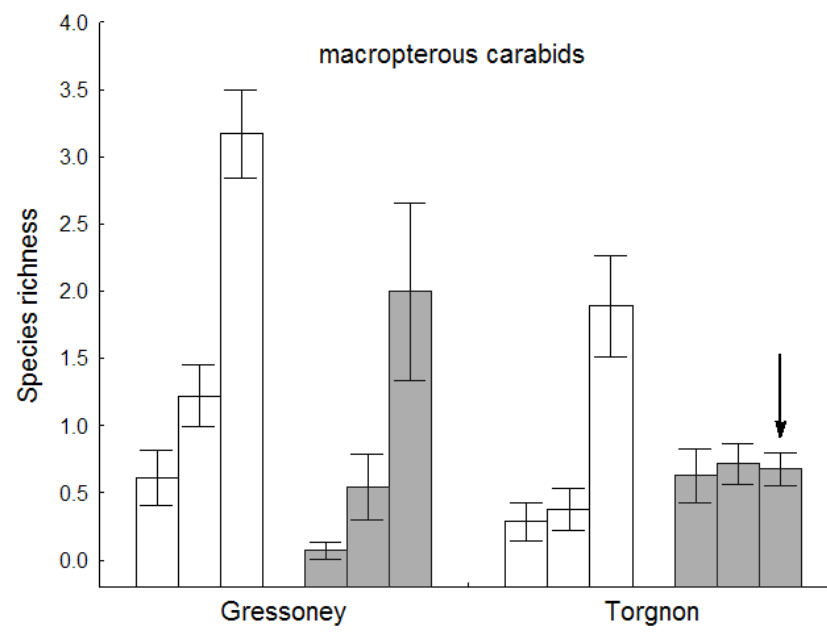
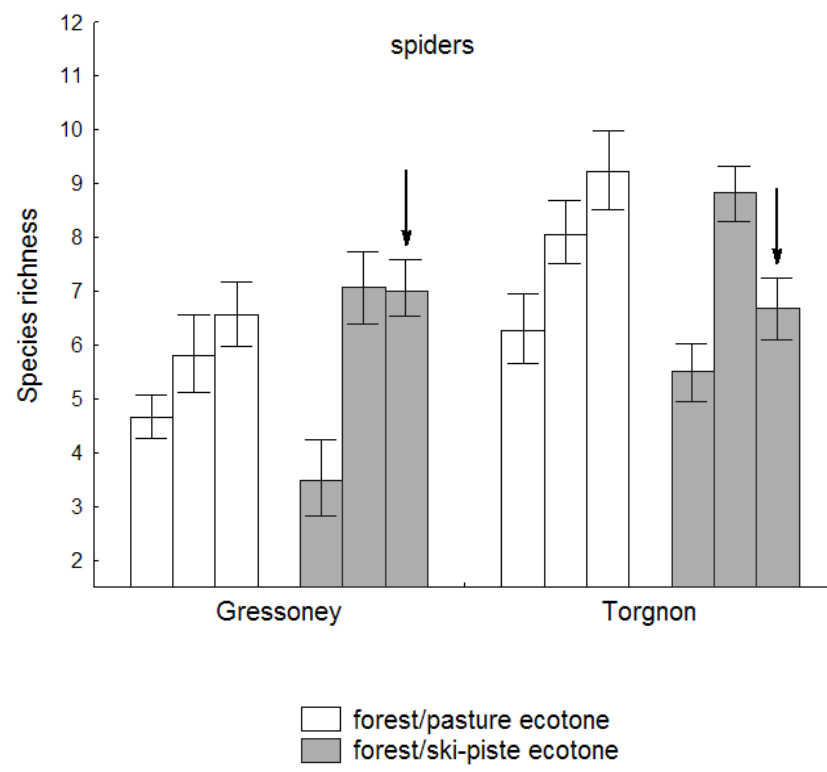


Fig. 2 Habitat use of small mammals (bank vole *Myodes glareolus*, pygmy *Sorex minutus* and common shrew *S. araneus*) in the forest/ski-piste ecotone. No bank vole and no common shrew were trapped in ski-piste. χ^2 test for goodness of fit. Single classification, expected frequencies based on hypothesis extrinsic to the sampled data, i.e. assuming an equal use of the three habitats. * $P < 0.05$; ** $P < 0.01$; N.S.= not significant.

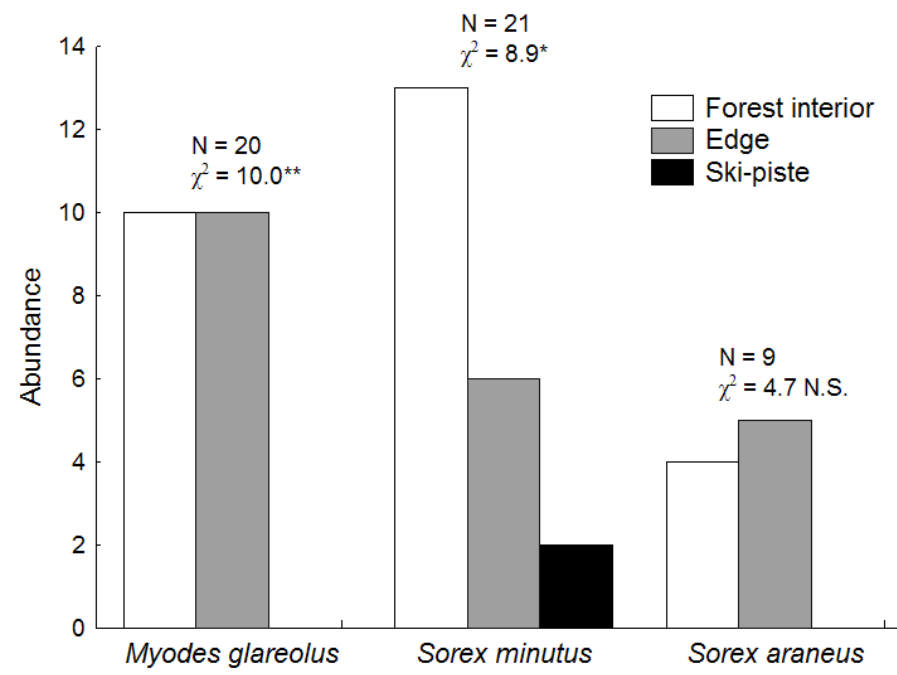


Table 1 Number of plots (n), abundance of individuals (N) and species richness (S) of ground beetles and spiders at the two study sites. Site exclusive species in brackets. Rarefied species richness was obtained by rarefying the most abundant sample down to the less abundant one (\pm standard deviation).

Study site	n	N	S	S (rarefied)
Carabids				
Torgnon	46	1108	36 (22)	36
Gressoney	32	1971	35 (21)	34.1 \pm 1.4
Spiders				
Torgnon	46	5790	84 (42)	69.7 \pm 2.8
Gressoney	32	3184	72 (30)	72

Table 2 Mean \pm SE spider abundance (N), species richness (S) and diversity (H') in the three habitat types (viz. forest interior, edge and open habitat) at each plot (One-way ANOVA). LSD posthoc tests were used for pairwise comparisons of means. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Par.= diversity parameter.

Site	Ecotone type	Par.	Forest interior	Edge	Open habitat	F	Significant pair-wise comparisons
Gressoney	forest/ski-piste	N	8.1 \pm 1.6	38.6 \pm 10.7	68.5 \pm 9.2	$F_{(2,38)} = 22.2^{***}$	(1) vs (2); (1) vs (3); (2) vs (3)
		S	3.5 \pm 0.7	7.1 \pm 0.7	7.1 \pm 0.6	$F_{(2,38)} = 11.7^{***}$	(1) vs (2); (1) vs (3)
		H'	0.9 \pm 0.2	1.4 \pm 0.1	1.2 \pm 0.1	$F_{(2,38)} = 4.1^*$	(1) vs (2)
	forest/pasture	N	16.5 \pm 3.4	32.2 \pm 6.7	39.6 \pm 6.3	$F_{(2,49)} = 5.4^{**}$	(1) vs (3)
		S	4.7 \pm 0.4	5.8 \pm 0.6	6.6 \pm 0.6	$F_{(2,49)} = 2.6^*$	(1) vs (3)
		H'	1.1 \pm 0.1	1.2 \pm 0.1	1.3 \pm 0.1	$F_{(2,49)} = 1.8$	
Torgnon	forest/ski-piste	N	24.7 \pm 4.0	64.9 \pm 8.6	52.1 \pm 9.8	$F_{(2,71)} = 9.2^{***}$	(1) vs (2); (1) vs (3)
		S	5.5 \pm 0.6	8.8 \pm 0.5	6.7 \pm 0.6	$F_{(2,71)} = 9.4^{***}$	(1) vs (2); (2) vs (3)
		H'	1.3 \pm 0.1	1.6 \pm 0.1	1.2 \pm 0.1	$F_{(2,71)} = 4.0^*$	(1) vs (2); (2) vs (3)
	forest/pasture	N	22.6 \pm 3.3	48.4 \pm 8.6	39.6 \pm 4.7	$F_{(2,58)} = 6.5^{**}$	(1) vs (2); (1) vs (3)
		S	6.3 \pm 0.6	8.0 \pm 0.5	9.2 \pm 0.8	$F_{(2,58)} = 6.0^{**}$	(1) vs (2); (1) vs (3)
		H'	1.4 \pm 0.1	1.5 \pm 0.1	1.7 \pm 0.1	$F_{(2,58)} = 3.6^*$	(1) vs (3)

Table. 3 Mean \pm SE ground beetle abundance (N), species richness (S) and diversity (H') in the three habitat types (viz. forest interior, edge and open habitat) at each plot (One-way ANOVA). LSD posthoc tests were used for pairwise comparisons of means. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Par.= diversity parameter.

Site	Ecotone type	Par	Forest interior	Edge	Open habitat	F	Significant pair-wise comparisons
Macropteros							
	forest/ski-piste	N	0.1 \pm 0.1	1.3 \pm 0.7	11.4 \pm 6.0	$F_{(2,39)} = 6.3^{**}$	(1) vs (3); (2) vs (3)
		S	0.1 \pm 0.1	0.5 \pm 0.3	2.0 \pm 0.7	$F_{(2,39)} = 8.1^{**}$	(1) vs (3); (2) vs (3)
		H'	0.0 \pm 0.0	0.1 \pm 0.1	0.4 \pm 0.1	$F_{(2,39)} = 4.3^*$	(1) vs (3)
Gressoney	forest/pasture	N	1.1 \pm 0.4	3.3 \pm 1.1	16.5 \pm 2.9	$F_{(2,51)} = 31.5^{***}$	(1) vs (3); (2) vs (3)
		S	0.6 \pm 0.2	1.2 \pm 0.2	3.2 \pm 0.3	$F_{(2,51)} = 24.2^{***}$	(1) vs (2); (1) vs (3); (2) vs (3)
		H'	0.1 \pm 0.1	0.3 \pm 0.1	0.8 \pm 0.1	$F_{(2,51)} = 14.8^{***}$	(1) vs (3); (2) vs (3)
	forest/ski-piste	N	1.1 \pm 0.4	1.2 \pm 0.3	1.4 \pm 0.4	$F_{(2,71)} = 0.4$	
		S	0.6 \pm 0.2	0.7 \pm 0.2	0.7 \pm 0.1	$F_{(2,71)} = 0.3$	
		H'	0.2 \pm 0.1	0.1 \pm 0.1	0.1 \pm 0.0	$F_{(2,71)} = 0.7$	
Torgnon	forest/pasture	N	0.5 \pm 0.3	0.5 \pm 0.2	3.6 \pm 1.5	$F_{(2,57)} = 8.5^{***}$	(1) vs (3); (2) vs (3)
		S	0.3 \pm 0.2	0.4 \pm 0.2	1.9 \pm 0.4	$F_{(2,57)} = 13.2^{***}$	(1) vs (3); (2) vs (3)
		H'	0.1 \pm 0.1	0.1 \pm 0.1	0.5 \pm 0.1	$F_{(2,57)} = 12.3^{***}$	(1) vs (3); (2) vs (3)

Brachypterosus

		N	17.0 ± 3.4	20.7 ± 5.1	6.2 ± 2.0	$F_{(2,39)} = 3.7^*$	(1) vs (3); (2) vs (3)
forest/ski-piste	S		3.0 ± 0.3	3.5 ± 0.5	2.1 ± 0.3	$F_{(2,39)} = 1.5$	
	H'		0.8 ± 0.1	0.8 ± 0.1	0.5 ± 0.1	$F_{(2,39)} = 1.1$	
<hr/>							
Predictor			β	SE	p		
<hr/>							
forest/pasture	N		20.8 ± 3.8	13.1 ± 2.1	6.8 ± 1.5	$F_{(2,51)} = 6.9^{**}$	(1) vs (3); (2) vs (3)
	S		3.1 ± 0.3	2.4 ± 0.3	1.4 ± 0.2	$F_{(2,51)} = 9.1^{***}$	(1) vs (3); (2) vs (3)
	H'		0.7 ± 0.1	0.5 ± 0.1	0.2 ± 0.1	$F_{(2,51)} = 8.6^{***}$	(1) vs (3); (2) vs (3)
forest/ski-piste	N		9.7 ± 2.4	7.5 ± 4.0	1.2 ± 0.6	$F_{(2,71)} = 8.1^{***}$	(1) vs (3); (2) vs (3)
	S		1.4 ± 0.2	1.2 ± 0.2	0.4 ± 0.1	$F_{(2,71)} = 12.9^{***}$	(1) vs (3); (2) vs (3)
	H'		0.3 ± 0.1	0.2 ± 0.1	0.0 ± 0.0	$F_{(2,71)} = 7.0^{**}$	(1) vs (3); (2) vs (3)
Torgnon							
forest/pasture	N		7.6 ± 2.4	1.6 ± 0.7	1.0 ± 0.4	$F_{(2,57)} = 9.4^{***}$	(1) vs (2); (1) vs (3)
	S		1.2 ± 0.2	0.5 ± 0.1	0.4 ± 0.1	$F_{(2,57)} = 6.1^{**}$	(1) vs (2); (1) vs (3)
	H'		0.2 ± 0.1	0.1 ± 0.0	0.0 ± 0.0	$F_{(2,57)} = 3.5^*$	(1) vs (2); (1) vs (3)

Spiders – Gressoney

Diversity

Grass cover 0.02 0.00 <0.05

AIC = 20.57

Abundance

North-East 0.31 0.10 <0.001

AIC = 286.92

Richness

North-Ovest 0.50 0.20 <0.05

AIC = 66.92

Spiders – Torgnon

Diversity

Grass cover 0.01 0.00 <0.05

AIC = 42.15

Abundance

Grass cover 0.01 0.00 <0.001

North -0.82 0.10 <0.001

South -0.80 0.11 <0.001

East 0.81 0.11 <0.001

Width of ski-piste 0.01 0.01 <0.05

AIC = 657.15

Richness

Grass cover 0.01 0.00 <0.001

AIC = 120.78

Macropterous carabids - Gressoney

Diversity		spiders		
Altitude		0.00	0.00	<0.05
AIC = 14.88				
Abundance				
Grass cover		0.11	0.02	<0.001
Width of ski-piste		0.10	0.02	<0.001
North		-2.02	0.43	<0.001
Altitude		0.01	0.00	<0.05
AIC = 136.80				
Richness				
Grass cover		0.05	0.03	<0.05
Width of ski-piste		0.08	0.02	<0.01
AIC = 43.93				

Table 4 Generalized linear models of abundance, species richness and diversity of spiders and macropterous ground beetles in relation to environmental predictors of ski-pistes [grass cover, width of ski-pistes, altitude and geographical aspect (North, North-East, North-West at Gressoney and North, South, East, South-East at Torgnon)]. Only significant variables included in the best model (i.e. those minimizing AIC) are shown. Variables added sequentially. No model significantly predicted the diversity of macropterous ground beetles at Torgnon.