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The effect of forest ski-pistes on butterfly assemblages in the Alps

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## Abstract

The abandonment of man-made pastures below the tree line is 1. favouring natural reforestation in the European Alps. As such, the creation of forest ski-pistes might, paradoxically, be beneficial to butterflies. This study is the first to focus on the effects of forest ski-pistes on butterfly assemblages (Lepidoptera, Rhopalocera).

2. We sampled both butterflies and flowers on ski-pistes, in adjacent forests and in the nearest pastures at three sites in the Aosta Valley (north-western Italian Alps).

Transect counts showed that 3. butterflies were more abundant on ski-pistes (and forests) than in pastures. However, species richness and diversity were lower on ski-pistes than on nearby pastures. Flower abundance was higher, but flower richness and diversity were lower on ski-pistes than in pastures. Multivariate regression trees indicated that butterfly abundance was positively associated with flower abundance and butterfly diversity was positively associated with flower diversity.

We conclude that: 4. (i) butterfly abundance on ski-pistes was higher because in mid-summer these grassland strips were more abundant in flowers than nearby pastures and (ii) butterfly diversity was lower both because of the lower flower diversity and because of the higher isolation and/or smaller area of ski-pistes by comparison with pastures.

In the 5. Alps, several grassland butterfly species are of conservation concern. Ski-pistes are probably sub-optimal habitats for butterflies. Nevertheless, within a natural reforestation framework, they may be useful to butterfly conservation, on condition that they are completely re-vegetated and that grass cover of ski-pistes are favoured and maintained to facilitate their colonisation.

Keywords.

IndVal, Lepidoptera, multivariate regression trees, natural reforestation, Renyi diversity profile, Rhopalocera, ski-runs.

## Introduction

The severity of the impacts of pistes for downhill skiing in mountain environments changes in relation to the altitude. With increasing elevation, human impacts become more severe because many organisms, plants in particular, are subject to harsher climatic conditions (the vegetation period, for instance, decreases by about 1 week per 100 m of increasing elevation) and re-vegetation becomes therefore more difficult (Urbanska, 1997; Krautzer & Wittmann, 2006). Above the treeline, in prairies of the alpine belt, construction and machine-grading (i.e. the removal of soil and

vegetation by heavy machinery to create a smooth ground surface) of ski-pistes induce long-lasting impacts on vegetation, and on both chemical and physical soil properties (Wipf *et al.*, 2005; Roux-Fouillet *et al.*, 2011). Because of the serious damage to vegetation, both the diversity of birds and ground-dwelling arthropods are significantly lower in these linear habitats (Rolando *et al.*, 2007; Negro *et al.*, 2010; Caprio *et al.*, 2011).

Below the tree line, effects are less detrimental because of the milder climatic conditions. Nevertheless, the negative effects on soils and vegetation are still present and impacts on animal communities have been detected both on forest vertebrates and invertebrates. Ski-pistes in forests are not used by open habitat bird species and induce negative edge effects on forest birds, because forest edges have lower bird diversity than forest interiors (Laiolo & Rolando, 2005). Ski-pistes are avoided by small forest mammals and may function as semi-permeable ecological barriers (Negro *et al.*, 2009). Finally, the diversity of typical ground-dwelling forest arthropods (especially ground beetles) is usually very low on ski-pistes, which might also potentially prevent or reduce the movement of brachypterous species between adjacent forest patches (Negro *et al.*, 2009).

Contrary to the negative effects described so far, forest ski-pistes may present an opportunity for open habitat arthropods. Macropterous ground beetles and spiders are commonly found on ski-pistes, even though diversity is usually lower than on pastures at the same altitude. Ski-piste width and grass cover are the two principal ecological predictors of ground-dwelling arthropod diversity, which is positively related to both parameters (Negro *et al.*, 2009). Forest ski-pistes may also be used by butterflies (Lepidoptera, Rhopalocera), most species being dependent upon open or semi-open grassland habitats (van Swaay *et al.*, 2006) and all being heliothermic insects dependent on the sun's direct heat for flight activity (Merckx *et al.*, 2008). Serious conservation concerns for butterflies have arisen across the world in recent years as they are in severe decline in many countries (Van Dyck *et al.*, 2009; Dover *et al.*, 2011). Europe in particular is facing huge losses in butterfly diversity as its grassland butterflies have declined by over 70% in the last 20 years and many species are at risk (Butterfly Conservation-Europe 2010; van Swaay *et al.*, 2010). Land-use alteration, biotope destruction, the loss of certain species' habitats within surviving semi-natural biotopes due to changed land use (Thomas, 1995; Forister *et al.*, 2010) and climate change (Wilson & Maclean, 2011), have been established as leading causes of butterfly population declines. European mountain areas, and especially the Alps, represent important butterfly diversity hotspots (Kudrna *et al.*, 2011). The Alps house several endemic species ( $N = 41$ ; Tontini *et al.*, 2003) and some species of conservation concern. *Parnassius apollo* and *P. mnemosyne*, for instance, are listed under annex IV of the European Habitats Directive 92/43/CEE. Despite the conservation interest in alpine butterflies and their potential suitability as indicators (Brereton *et al.*, 2011), the relationships between alpine butterflies and ski-pistes have not yet been studied. Generally speaking, the construction of ski runs above the tree line has been considered detrimental to butterflies because it reduces large natural areas and leads to degraded grassland habitats (Pullin, 1995). Below the tree line, butterflies are highly threatened by land-use change and associated extensive habitat loss. In many alpine sectors, pastoral activities are declining and the abandonment of pastures is followed by shrub and tree encroachment, with a progressive enlargement of forested areas (natural reforestation) and a parallel decrease of open habitats (MacDonald *et al.*, 2000; Chemini & Rizzoli, 2003; Chauchard *et al.*, 2007; Tasser *et al.*, 2007). This trend may be deleterious for open-habitat animal species. It has been observed, for instance, that several alpine grassland bird species that are dependent upon grazed pastures have unfavourable conservation status, suggesting that large-scale abandonment of long-established pastoral habitats is detrimental in terms of bird conservation (Laiolo *et al.*, 2004). Consequences of pastoral abandonment are likely to be particularly adverse for alpine butterflies. It has been demonstrated, for example, that butterflies inhabiting grasslands may decline because of reforestation (Tae-Sung *et al.*, 2010). Within this framework, the creation of

long grassland strips within a forest matrix might be beneficial to butterflies, which could colonise forest ski-pistes from nearby grasslands and pastures.

Butterflies and flowering plants have life cycles which are closely linked. Butterflies are well known to depend on flowers for feeding (nectar sources). Therefore, to assess the effect of forest ski-pistes on assemblages of butterflies, we sampled both butterflies and flowers, in order to test if butterfly abundance and diversity co-vary with flower abundance and diversity. In addition to forest ski-pistes, sampling was also carried out in adjacent forests and in the nearest pastures.

## Materials and methods

### Study area

This study was carried out at three ski resort sites (i.e. Torgnon, Antagnod and Colle di Joux) located in the Tournanche and the Ayas valleys of the north-western Italian Alps, in the Aosta Valley region (Fig. 1). We surveyed ski-pistes (1600–2300 m a.s.l., 15–70 m width), adjacent coniferous forests and nearby pastures. Twenty transects for each habitat type (i.e. ski-pistes, coniferous forests and pastures) were established. Ski-pistes were at least 15 years old. However, we also conducted four additional transects in newly constructed ski-pistes, which had not been seeded, and were therefore long narrow strips of bare ground (Fig. 2).

All surveyed ski-pistes were equipped with snow-cannons for the production of artificial snow. Forests were dominated by *Larix decidua* and *Picea abies*. The forest understorey was sparse, and mainly composed of *Juniperus communis*, *Rhododendron ferrugineum*, and *Vaccinium myrtillus*. Pastures (1600–2200 m a.s.l.) and old ski-pistes were dominated by grasses (Poaceae). The most common flowering plants were those of the families Asteraceae (*Centaurea*, *Cirsium*, *Crepis*, *Chrysanthemum*, *Achillea*, *Arnica*, *Aster*), Rubiaceae (*Galium*), Campanulaceae (*Campanula*), Gentianaceae (*Gentiana*), Fabaceae (*Trifolium*) and Lamiaceae (*Thymus*). Cattle grazing occurred annually, although the intensity was higher on pastures than on ski-pistes, which were only occasionally used as pasture strips.

### Sample collection

Surveys were conducted from 20th July to 20th August 2010 using standardised transect counts (Pollard & Yates, 1993). Individual butterflies were counted along 300 m long/10 m wide transects during timed searches of about 30 min to provide data on both species presence and abundance. Where possible, butterflies were visually identified, or were collected with nets where required for species verification or identification. Taxonomy followed Balletto *et al.* (2005).

Given that transects were visited only once, and in order to control as much as possible for unwanted effects of weather conditions and time of day on sampling, surveys were carried out under standard conditions, specifically on sunny days with no wind and from 11:00 to 2:00 hours. Moreover, for each transect in ski-piste, one transect in the adjacent forest and one in the nearby pasture was carried out on the same day.

The number of potential nectar sources (flowers or inflorescences) was estimated for each transect and plants were identified to the genus level (Broglia *et al.*, 2008). Although these counts were not a direct measure of nectar quantity, a linear relationship between amount of nectar and number of inflorescences has been found, and it has been suggested that the effort needed to quantify sugar

production adds little additional information (Holl, 1995). Flower sampling took place within  $1 \times 1$  m randomly located squares along each transect. For each transect, a flower density index was obtained by dividing the total number of flowers or inflorescences by the number of sampled squares (20 squares for each transect). We also measured richness and diversity of vegetation and minimum and maximum grass height at each quadrat. The elevation for each transect was measured at half-length (150 m) by means of a Global Positioning System (GPS) Garmin eTrex navigator.

## Statistical analysis

Species richness estimators and diversity profiles. A completeness analysis of sampling was conducted in each habitat (forest, pasture and ski-piste) by preliminarily computing abundance-based estimates using two variants of extrapolated richness: Chao (unbiased variant) and ACE (Palmer, 1990; Colwell & Coddington, 1994). The inventory of completeness for each habitat was measured as the percentage of the total number of species predicted by the estimators that were actually recorded.

Butterfly assemblages in each habitat were described using several diversity parameters: Shannon diversity ( $\exp H'$  where  $H' = -\sum_{i=1}^S p_i \ln p_i$ ), Evenness ( $\exp H'/\exp H'_{\max}$  where  $H'_{\max}$  = the value of  $H'$  if all species had the same number of individuals) and Simpson's diversity ( $D = 1/\sum_{i=1}^S p_i^2$ ).  $p_i$  is the relative frequency of species  $i$  in the sample.

The Rényi diversity profile is a diversity ordering technique specifically designed to rank communities from low to high diversity (Kindt *et al.*, 2006).

Rényi diversity profile values ( $H_\alpha$ ) were calculated from the frequencies of each component species ( $p_i$ ) and a scale parameter ( $\alpha$ ) ranging from zero to infinity (Tóthmérész, 1995; Legendre & Legendre, 1998) as:

$$H_\alpha = \frac{\ln(\sum p_i)}{1 - \alpha}$$

It can be demonstrated that values of the Rényi profile at the respective scales of 0, 1, 2 and  $\infty$  are related respectively to species richness, the Shannon diversity index ( $\exp H'$ ), the Simpson diversity index and the Berger–Parker diversity index (Legendre & Legendre, 1998; Shaw, 2003).

Community A is more diverse than community B if the diversity profile for community A is above the diversity profile for community B at each value of  $\alpha$  (Kindt *et al.*, 2006). Communities that have intersecting profiles cannot be arranged in order of diversity. The fact that intersecting profiles (partial diversity ordering) can occur explains why ordering techniques such as the Rényi series are needed, since a single diversity index will not provide sufficient information. The values of the series for the various use-groups were calculated for the scales of: 0, 0.25, 0.5, 1, 2, 4, 8, 16, 32, 64,  $\infty$ .

Taxonomic diversity indices. We computed taxonomic diversity ( $\Delta$ ), taxonomic distinctness ( $\Delta^*$ ), average taxonomic distinctness ( $\Delta^+$ ) and variation in taxonomic distinctness ( $\Delta^+$ ). The first index, taxonomic diversity ( $\Delta$ ), is the average taxonomic distance between any two organisms, chosen at random from the sample. This distance can be visualised as the length of the path connecting these two organisms, traced through a Linnean classification of the full set of species involved (Clarke & Warwick, 1998).

Taxonomic distinctness ( $\Delta^*$ ), is the average path length between any two randomly chosen individuals, conditional on them being from different species (Clarke & Warwick, 1998). Average taxonomic distinctness ( $\Delta^+$ ) is the mean of all species-to-species distances through the classification tree for all pairs of species within a sample, and represents the taxonomic breadth of the sample (Clarke & Warwick, 2001). The variation in taxonomic distinctness ( $\Delta^+$ ) is the variation in branch lengths among all pairs of species and is a measure of the irregularities and divergences in the distribution of branch lengths within a sample (Clarke & Warwick, 2001).

Such indices quantify diversity as the taxonomic relatedness of the species within a sample, attempting to capture phylogenetic diversity rather than simple species richness. According to Clarke and Warwick (1998), taxonomic relatedness is more closely linked to functional diversity and, given their statistical properties (mainly robustness to sampling variation and independence from sampling effort) and their sensitivities to environmental degradation, they may represent useful parameters for biodiagnostic purposes (Clarke & Warwick, 1999, 2001). We tested for differences in mean taxonomic diversity indices ( $\Delta$ ,  $\Delta^*$ ,  $\Delta^+$  and  $\Lambda^+$ ) between the three habitat types (forest, ski-piste and pasture) by means of one-way anova.

Least-squares deviation (LSD) post-hoc tests were used for pair-wise comparisons of the means. To achieve normality (checked by using normal probability plots), data were log transformed [ $y = \log(x + 1)$ ] (Sokal & Rohlf, 1995).

Species turnover. Species turnover between sample units (habitats) was described by using a ternary plot (Koleff *et al.*, 2003). We considered the presence/absence of species in a focal habitat compared with each neighbouring habitat in turn. The number of species that are present in both habitats is the pairwise matching component  $a$ . The number of species that are present only in the neighbouring habitat is  $b$ , while the number present only in the focal habitat is  $c$  (Raes *et al.*, 2007). The total number of species for the pair of habitats is therefore  $a + b + c$ ; in percentage terms, this is  $a' + b' + c' = 100\%$ . Whittaker's beta diversity was calculated for each pair of habitats.

Regression trees and indicator value analysis. The Univariate regression trees (URT) method was used to identify the interactions between environmental variables (in our case habitat type, elevation, abundance, richness and diversity of vegetation and minimum and maximum grass height) and butterfly Shannon diversity (Ripley, 2009). This method performs a binary recursive partitioning of the dataset and offers the opportunity to identify the influential explanatory variables (Crawley, 2007; Gall  t *et al.*, 2011).

The variation in assemblage structure was evaluated by considering species abundance and using multivariate regression trees (MRT; De'ath, 2002). This method is an extension of URT with multivariate responses. MRT identifies groups defined by environmental variables. The result is presented as a tree of dichotomies. Each dichotomy is chosen to minimise the dissimilarity within each branch. The size of the tree was selected based on the minimum tree size that fell below 1 SE of the minimum cross-validation estimate (Breiman *et al.*, 1998; De'ath, 2002). We combined MRT with indicator value calculations (IndVal; Dufr  ne & Legendre, 1997) for the species falling into the MRT branches. The IndVal evaluates the presence/absence and abundance of a given species among transects of a given MRT branch with those of the other end branches. For each branch, each species included gets a value that varies from 0 (not present in a given group of transects) to 100 (perfect indicator; present in all samples within a given group of transects but completely absent from all the other groups). The statistical significance of the maximum indicator value was evaluated by a Monte Carlo randomization test (1000 runs). All analyses were carried out on R 2.1.0 with *vegan*, *mvpart*, *agricolae* and *labdsv* packages (R Development Core Team, 2010).

## Conservation concerns and managing implications

The Italian Alps, and the western Alps in particular, are hotspots of biodiversity, both for butterflies and a number of other vertebrate and invertebrate taxa (Balletto *et al.*, 2010). Many grassland butterfly species occurring in the Alps need conservation measures. Laws exist to protect *Parnassius apollo* in many countries, and this species in particular is also listed in the Annex II of the Convention on International Trade in Endangered Species. *P. apollo* and *P. mnemosine* are listed under the Annex IV of the European Habitats Directive, together with *Erebia christi* (Annexes II, IV). *Erebia calcaria* (also protected under Annexes II and IV) is severely threatened by habitat fragmentation and overgrazing (De Groot *et al.*, 2009). Several other species are not protected but still need conservation measures. *Maculinea rebeli*, among a number of other species, is threatened in the Alps by the destruction of habitats caused by holiday houses and tourism (Bonelli *et al.*, 2011). Ski-resorts considered in this study house some species of conservation interest. *P. apollo* occurred at several sites in both valleys; we also sampled individuals of *Erebia mnestra* and *Coenonympha gardetta*, which are two species endemic to the Alps.

Ski-pistes may have a significant conservation effect upon butterflies because in the Alps they extend for thousands of kilometres (Rolando *et al.*, 2007) and the area affected is still increasing (Abegg *et al.*, 1997; Elsasser & Messerli, 2001; Wipf *et al.*, 2005). Our results have demonstrated that forest ski-pistes were consistently used by many butterflies but, despite the prediction of the “edge effect principle”, diversity, richness and mean taxonomic diversity were lower than in pastures. The reproduction of butterflies in these anthropogenic habitats might be disturbed by the negative effects of snow compression and artificial snowing on overwintering caterpillars or chrysalises. Therefore, ski-pistes are probably sub-optimal habitats for butterflies. Nevertheless, in a reforestation framework, they may be useful to butterfly conservation, on condition that they are completely re-vegetated, as newly constructed ski-pistes without any grass-cover were completely avoided. After re-vegetation, grass (and flower) cover of ski-pistes should therefore be favoured and maintained to facilitate colonisation. We recommend, in keeping with previous studies on ground-dwelling arthropods (Negro *et al.*, 2009, 2010) that new, biodiversity-friendly ways of constructing and managing pistes are urgently developed and adopted. After tree clearing, only the roughest ground surfaces should be levelled, in order to preserve as much soil and natural vegetation as possible. Restoration techniques based upon the use of site-specific seeds and reduced fertilisation may now lead to stable, enduring and ecologically adapted plant communities, especially on ski-pistes below the tree line, where climatic conditions are milder (Krautzer & Wittmann, 2006). Once natural re-vegetation is achieved, management should avert any further disturbances and the vegetation cover should be preserved without compromising the safety of ski-runs. Grass and scrub can be kept low, if required, through direct vegetation removal without machine-grading. These are simple measures, but they are rarely applied. It should be mentioned, for instance, that 1 year after our surveys (i.e. in summer 2011), taking advantage of an allowance for felling trees to enlarge pre-existing tracks, three old ski-pistes of Torgnon were intensely machine-graded and completely deprived of grasses and flowers.

## Results

### Species richness estimators and diversity profiles

A total of 54 species and 2952 individual butterflies were recorded in the three habitats. Twenty species and 1060 individuals were recorded in forests, 45 species and 759 individuals in pastures and 42 species and 1133 individuals on ski-pistes. The complete list of species and the habitats in which they were found is given in the Appendix.

Completeness of species recorded ranged from 74% to 88%, irrespective of the estimator employed, which suggests that the sampling effort was sufficient in order to correctly describe the local assemblages of butterflies in each habitat.

In assessments of butterfly assemblages containing species flying at forest canopy level, there is a high probability that surveys will lead to diversity and abundance underestimates in forest habitats. Nevertheless, all species considered in this study are known to fly at ground level, which suggests that both abundance and species richness reported from coniferous forest habitats have been correctly estimated.

Species observed on ski-pistes came from nearby pastures, but also from adjacent forests. *Erebia euryale* was the dominant species, mostly observed in forests and on ski-pistes (Table 1). Ski-pistes of recent construction (without grass-cover) were completely avoided by butterflies (only three individuals observed). The number of butterflies was higher on ski-pistes than in pastures. In contrast, butterfly diversity was higher on pastures (Table 1).

The number of flowers or inflorescences was higher on ski-pistes than in pastures, whereas species richness and diversity were higher in pastures. Flower composition was clearly different in the three habitats. *Thymus* (*T. serpyllum*), in particular, was almost exclusive to ski-pistes (Table 2).

Pastures showed consistently higher Rényi profiles than ski-pistes and these in turn showed consistently higher profiles than forests (Fig. 3). In particular, measures related to species richness ( $\alpha = 0$ ) Shannon ( $\alpha = 1$ ), Simpson ( $\alpha = 2$ ) and Berger–Parker ( $\alpha = \infty$ ) diversity indices were always higher in pastures, followed by ski-pistes and forests.

Forests, ski-pistes and pastures also showed significant differences in terms of taxonomic diversity ( $\Delta$ ), taxonomic distinctness ( $\Delta^*$ ), average taxonomic distinctness ( $\Delta^+$ ) and variation in taxonomic distinctness ( $\Delta^+$ ) (Table 3; Fig. 4). Pastures presented the highest values of taxonomic diversity indexes, whereas forests supported the lowest. Differences between forests and pastures or between forest and ski-pistes were always significant, whereas those between pastures and ski-pistes were never significant (Table 3).

### Species turnover

For species turnover, the ternary graph showed that the percentage of species present both in pasture and ski-piste ( $a'$ ) was rather high (i.e. low turnover), whereas the percentage of species present both in the forest and in open habitats was lower (high turnover) (Fig. 5). This pattern was confirmed by Whittaker's beta, with high turnover rates between forest and pasture or between forest and ski-piste ( $\beta_w = 0.51$  and  $0.52$ , respectively), and low turnover between ski-piste and pasture ( $\beta_w = 0.19$ ) (Fig. 5).

### Regression trees and IndVal

In the URT, built considering butterfly Shannon Diversity, the basal dichotomy separated forest transects (mean value of diversity equal to 1.43) from open grassland habitats (pasture and ski-piste transects). The second split regarded open habitat transects (ski-pistes and pastures) and separated a

group of 16 transects showing lower flower diversity ( $\text{expH} < 3.93$ ) from those with higher flower diversity ( $\text{expH} \geq 3.93$ ). The last dichotomy separated the latter transects (with high flower diversity) into two groups (number of transects equal to 21 and 3, respectively) according to altitude (elevation  $< 2175$  m a.s.l. vs.  $\geq 2175$  m), and indicated that the highest butterfly diversity (8.36) was found in high altitude assemblages (Fig. 6). This suggests that the best predictors of butterfly diversity are habitat type (open vs. closed habitats), flower diversity and elevation, in decreasing order of importance.

The MRT built considering species abundances was a two-node tree indicating abundance of flowers and elevation (first and second ranking, respectively) as the best predictors of butterfly assemblage structure (Fig. 7). The basal dichotomy separated 48 transects with a lower number of flowers ( $< 271.3$ ) from transects with a higher number of flowers ( $\geq 271.3$ ).

These flower-abundant transects were split according to elevation ( $< 1892$  m a.s.l. vs.  $\geq 1892$  m). The analysis of indicator species (IndVal) showed that several species preferred flower-rich transects; seven species (*Lycaena virgaureae*, *Melitaea athalia*, *Melitaea phoebe*, *Boloria titania*, *Polyommatus coridon*, *Aricia agestis* and *Colias phicomone*) significantly selected higher altitude sites, whereas two species preferred lower altitude sites (*Melanargia galathea* and *Maniola jurtina*) (Fig. 7).

## Discussion

This study is the first to focus on relationships between butterflies and ski-pistes. Two opposite patterns emerged: one regarding total abundance and one regarding species richness and diversity.

### Total abundance

Transect counts showed that butterflies were more abundant on ski-pistes (and forests) than in pastures and, analogously, vegetation surveys showed that flower abundance was higher on ski-pistes than in pastures. The high abundance of flowers on ski-pistes may result from two factors: (i) a delay in flowering on ski-pistes, (ii) removal of most of the flowers from pastures due to cattle grazing. During winter, snow compaction by snow-grooming vehicles and skiers causes decreased insulation of the ground below the snow. Soil freezing leads to a delayed development of plants in spring after snow melt, even if the actual thaw is not delayed (Rixen *et al.*, 2008). In many ski resorts of the Alps, as in those we surveyed, the production of artificial snow has gradually been intensified (Keller *et al.*, 2004). Artificial snow also postpones the melt in spring and early summer by a mean of two to three weeks (Rixen *et al.*, 2004). The final result is that in mid-summer, flowers on ski-pistes are still in bloom, whilst those of prairies and pastures may not be. Cattle arrived at pastures in late June; after 1–2 months of grazing activity, pastures were therefore partially deprived of flowers, whereas ski-pistes were not, being little used by livestock.

### Species richness and diversity

Butterfly species on ski-pistes came from nearby pastures, but also from adjacent forests. This mixing of species was expected to enhance local species richness and diversity, in keeping with the notion of a positive edge effect (the “edge effect principle”, *sensu* Odum, 1971). However, Rényi diversity profiles showed that butterfly diversity and species richness were significantly lower on ski-pistes than on nearby pastures. The same trend was also shown by taxonomic complexity indices, that decreased, although not significantly, from pasture to ski-pistes.

Analogously, vegetation surveys showed that flower richness and diversity were lower on ski-pistes than in pastures. Effects on butterfly diversity are in keeping with those regarding macropterous ground beetles and spiders. Both groups were able to colonise forest ski-pistes, but the diversity of both was significantly higher in nearby pastures (Negro *et al.*, 2009). Ski-piste width and ski-piste grass cover were the two principal ecological predictors of ground dwelling arthropod diversity, which increased with increases in both parameters (Negro *et al.*, 2009).

Multivariate regression trees analyses represented an explanatory synthesis because they revealed that butterfly abundance was significantly associated with flower abundance, while butterfly diversity was associated with flower diversity. Finally, transect counts also showed that newly constructed ski-pistes, devoid of grass cover and flowers, were completely avoided by butterflies.

The results commented on above, taken together, show therefore that the structure of butterfly assemblages largely co-varies with that of flower assemblages. We deduce that: (i) butterfly abundance on ski-pistes was higher because in mid-summer these grassland strips contained more flowers than nearby pastures and (ii) butterfly species richness and diversity were lower because of their lower flower diversity. Low butterfly species richness and diversity of ski-pistes, however, may also depend on their higher topographical isolation and smaller area by comparison with pastures. Ski-pistes are long and narrow corridors that cut the forest matrix. They are colonised by individual butterflies that, coming from the open pastures, follow the track which penetrates the coniferous forest matrix. This may be easy for large nymphalids and papilionids (A. Rolando, pers. obs.) which are long-distance fliers, but may be more difficult for smaller species such as some satyrines or lycaenids which fly shorter distances. Colonisation may also be difficult because open-habitat butterflies cannot arrive at the ski-pistes by crossing coniferous forests, which represent a relatively impermeable ecological barrier. It is known, for instance, that in the Rocky Mountains of North America one consequence of forest encroachment into the alpine zone is the fragmentation of meadows; as a consequence, encroaching forests decouple alpine butterfly population dynamics, producing more and smaller independent populations (Roland & Matter, 2007). The positive relationship between the area of a patch and the number of species (the so called SA curve) is well known in metapopulation ecology (Hanski, 1999). The effect of patch area and isolation also reflects upon single species, generating possible conservation consequences. In the endangered butterfly *Lycaena helle*, for instance, patch occupancy was primarily determined by patch size and isolation (Bauerfeind *et al.*, 2009). The area occupied by forest ski-pistes, because of their reduced width (15–70 m in areas considered in this study), is usually smaller than that occupied by pastures: this may also partly explain why the butterfly diversity of pastures was higher than that of ski-pistes.

Multivariate regression trees also showed that altitude is a significant predictor of both the diversity and abundance of butterflies. Butterfly abundance, in particular, seems to increase with altitude. The IndVal analysis associated with the MRT for the butterfly abundance revealed a high number of species ( $n = 7$ ) which were significantly associated with the flower-rich grasslands at high elevations.

The ternary plot of Whittaker's beta diversity showed that species turnover between pastures and ski-pistes was low. These slight differences may be due to flower composition on ski-pistes differing from those on pastures. *Arnica montana* was abundant on ski-pistes (and in forests) but very scarce in pastures, *Thymus serpyllum* was abundant and exclusive to ski-pistes: both were consistently visited by butterflies (A. Rolando, pers. obs.). Different vegetation composition was also detected above the tree line, where two ecological plant groups can be affected by changed soil conditions: species that are characteristic of windy ridges (e.g. *Elyna myosuroides* and *Loiseleuria procumbens*) become more frequent (Wipf *et al.*, 2002), whereas early-flowering species (e.g.

*Crocus albiflorus*, *Soldanella pusilla*) are reduced on ski-pistes in comparison to control plots next to pistes (Wipf *et al.*, 2005; Roux-Fouillet *et al.*, 2011). Alternatively, the slight difference in composition between pastures and ski-pistes may also depend on the fact that ski-pistes were used by typical forest species when they moved from a forest patch to another, whereas pastures were not.

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Paola Rolando and Federico Riva greatly helped with fieldwork. We are also grateful to Angela Roggero, who prepared genitalia for the study and identification of doubtful butterfly specimens. Dan Chamberlain revised the English text.

#### Appendix

List of butterfly species observed or collected along transects on ski-pistes (SP), pastures (PA) and coniferous forests (CF). Taxonomy following Balletto *et al.* (2005) and Kudrna *et al.* (2011).

#### Family HesperIIDae:

*Hesperia comma* (Linnaeus, 1758) (SP, PA)

*Pyrgus alveus* (Hübner, [1803]) (SP, PA)

*Pyrgus carthami* (Hübner, [1813]) (PA)

*Thymelicus lineola* (Ochsenheimer, [1808]) (SP, PA)

*Thymelicus sylvestris* (Poda, 1761) (SP, PA)

#### Family PapilionIDae:

*Parnassius apollo* (Linnaeus, 1758) (PA)

*Papilio machaon* (Linnaeus, 1758) (PA)

#### Family PierIDae:

*Aporia crataegi* (Linnaeus, 1758) (SP, PA)

*Colias alfacariensis* (Ribbe, 1905) (SP, PA)

*Colias phicomone* (Esper, [1780]) (SP, PA)

*Pieris brassicae* (Linnaeus, 1758) (SP)

*Pieris bryoniae* (Hübner, [1806]) (SP)

*Pieris rapae* (Linnaeus, 1758) (SP, PA)

#### Family LycaenIDae:

*Aricia agestis* ([Schifferrmüller], 1775) (SP, PA)  
*Aricia nicias* (Meigen, 1830) (SP, PA)  
*Lycaena alciphron* (Rottemburg, 1775) (SP)  
*Lycaena virgaureae* (Linnaeus, 1758) (SP, PA, CF)  
*Plebejus argus* (Linnaeus, 1758) (SP, PA)  
*Polyommatus coridon* (Poda, 1761) (SP, PA)  
*Polyommatus damon* ([Schifferrmüller], 1775) (SP, PA)  
*Polyommatus dorylas* ([Schifferrmüller], 1775) (SP, CF)  
*Satyrrium spini* (Fabricius, 1787) (SP, PA)

Family Nymphalidae:

*Argynnis adippe* ([Schifferrmüller], 1775) (SP)  
*Argynnis aglaja* (Linnaeus, 1758) (SP, PA, CF)  
*Argynnis niobe* (Linnaeus, 1758) (SP, PA, CF)  
*Argynnis paphia* (Linnaeus, 1758) (PA)  
*Boloria titania* (Esper, [1789]) (SP, PA, CF)  
*Issoria lathonia* (Linnaeus, 1758) (SP, PA)  
*Melitaea athalia* (Rottemburg, 1775) (SP, PA, CF)  
*Melitaea cinxia* (Linnaeus, 1758) (SP, PA)  
*Melitaea didyma* (Esper, [1778]) (SP, PA)  
*Melitaea phoebe* (Goeze, 1779) (SP, PA)  
*Melitaea trivialis* (Schifferrmüller, 1775) (PA, CF)  
*Melitaea varia* (Meyer-Dür, 1851) (SP, PA)  
*Polygonia c-album* (Linnaeus, 1758) (PA)  
*Vanessa cardui* (Linnaeus, 1758) (PA, CF, SP)

Family Satyridae:

*Coenonympha darwiniana* (Staudinger, 1871) (SP, PA)

*Coenonympha gardetta* (de Prunner, 1798) (SP, PA)  
*Coenonympha pamphilus* (Linnaeus, 1758) (SP, PA, CF)  
*Erebia aethiops* (Esper, [1776]) (CF)  
*Erebia alberganus* (de Prunner, 1798) (SP, PA, CF)  
*Erebia carmenta* (Fruhstorfer, 1909) (SP, PA, CF)  
*Erebia epiphron* (Knoch, 1783) (SP, CF)  
*Erebia euryale* (Esper, [1805]) (SP, PA, CF)  
*Erebia melampus* (Fuessly, 1775) (SP, PA)  
*Erebia mnestra* (Hübner, [1804]) (PA)  
*Erebia montana* (de Prunner, 1798) (PA)  
*Hyponophele lycaon* (Kühn, 1774) (SP, PA, CF)  
*Hipparchia semele* (Linnaeus, 1758) (PA, CF)  
*Hipparchia fagi* (Scopoli, 1763) (CF)  
*Kanetisa circe* (Fabricius, 1775) (CF)  
*Lasiommata maera* (Linnaeus, 1758) (SP, PA, CF)  
*Maniola jurtina* (Linnaeus, 1758) (SP, PA, CF)  
*Melanargia galathea* (Linnaeus, 1758) (SP, PA)

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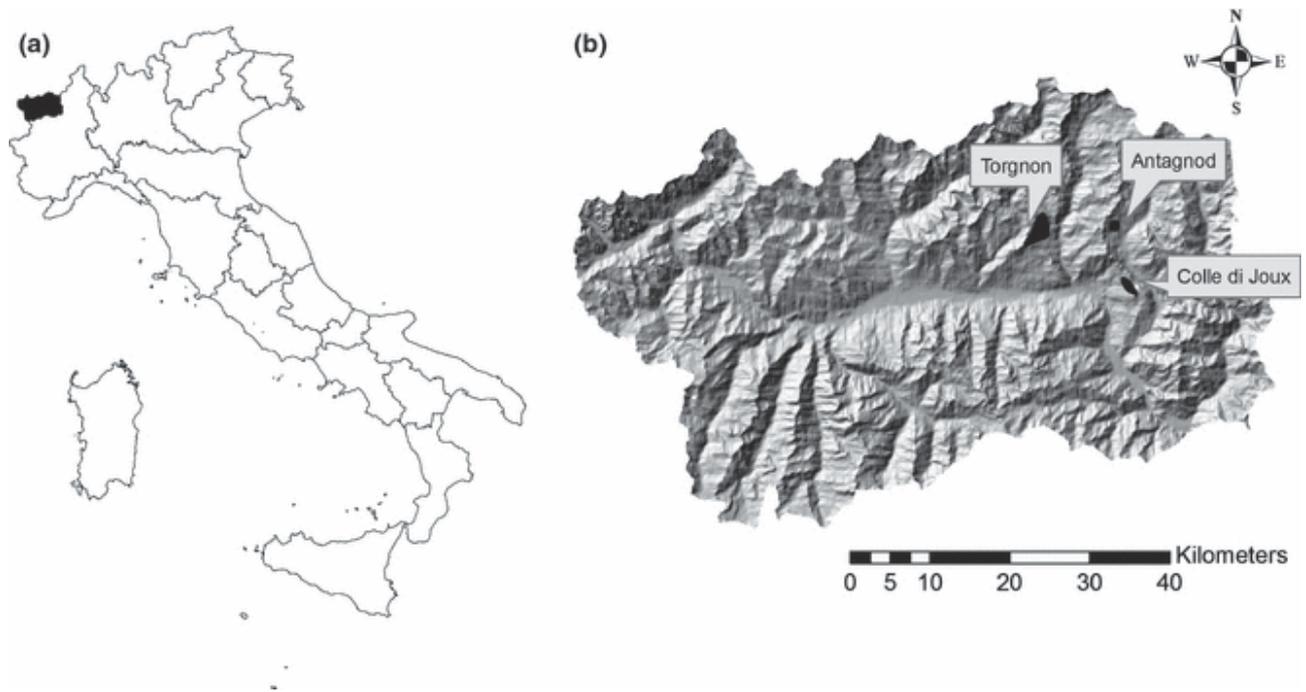


Figure 1.

Map of the three ski resort sites (b) located in the Aosta Valley region (a), north-western Italian Alps.

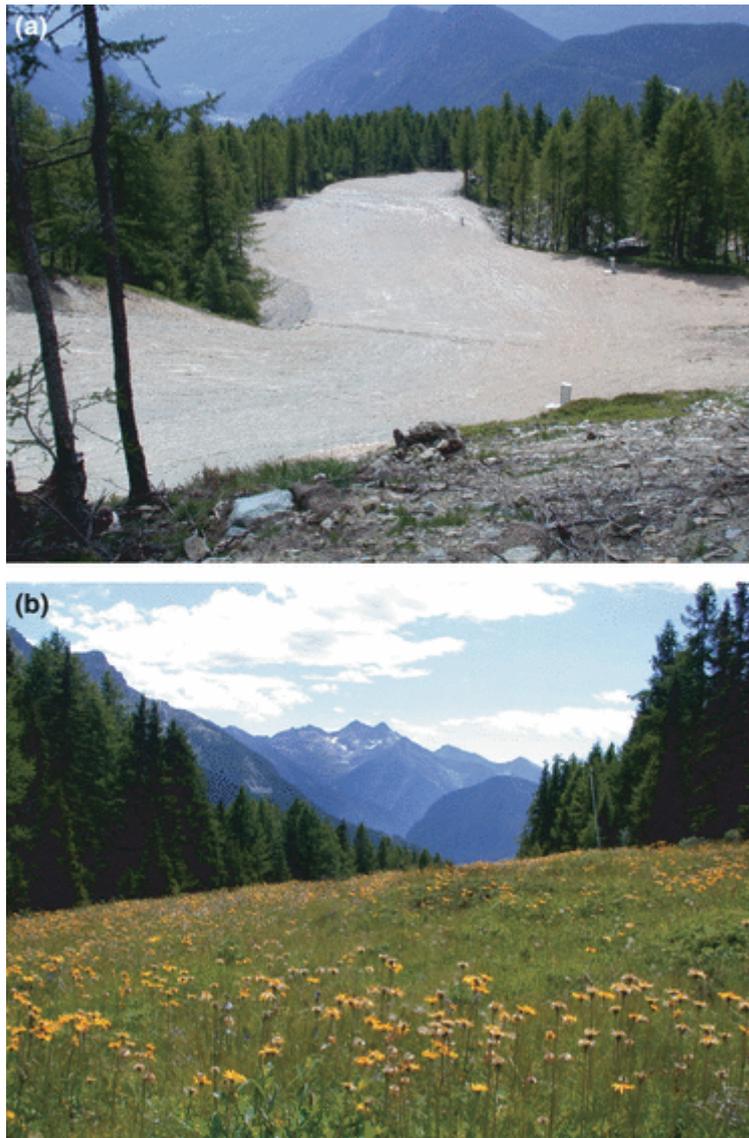


Figure 2

A newly-constructed ski-piste at Torgnon (a), compared with an old ski-piste at Antagnod (b). Pictures were taken on 2 August 2010. The flowers in the foreground are mountain arnicas (*Arnica montana*).

Table 1. Numbers of individuals, species estimates (chao1 and ACE), sample completeness and diversity parameters (Shannon diversity, Evenness, Simpson's Dominance) for the three habitats studied.

Table 1. Numbers of individuals, species estimates (chao1 and ACE), sample completeness and diversity parameters (Shannon diversity, Evenness, Simpson's Dominance) for the three habitats studied.

	<b>Forest</b>	<b>Pasture</b>	<b>Ski-piste</b>
1. Only species with more than 1% of individuals sampled were reported. Inventory completeness is observed richness as a percentage of total Chao and ACE expected richness.			
<i>Hyponphele lycaon</i> (Rottemburg, 1775)	2	21	34
<i>Maniola jurtina</i> (Linnaeus, 1758)	5	57	17
<i>Melanargia galathea</i> (Linnaeus, 1758)	0	149	8
<i>Coenonympha pamphilus</i> (Linnaeus, 1758)	4	53	35
<i>Erebia euryale</i> (Esper, [1805])	980	160	622
<i>Argynnis niobe</i> (Linnaeus, 1758)	4	57	48
<i>Argynnis aglaja</i> (Linnaeus, 1758)	1	31	59
<i>Boloria titania</i> (Esper, [1793])	6	10	30
<i>Melitaea didyma</i> (Esper, 1779)	0	17	13
<i>Polyommatus coridon</i> (Poda, 1761)	0	23	56
<i>Lycaena virgaureae</i> (Linnaeus, 1758)	4	3	40
Other species (43)	54	178	171
Observed richness	20	45	42
Chao1	27.00	52.86	47.60
ACE	26.69	56.79	47.32
Completeness chao1 (%)	74.07	85.14	88.24
Completeness ACE (%)	74.93	79.24	88.75
Shannon diversity	1.56	16.27	7.99
Evenness	0.03	0.30	0.15
Simpson's diversity	1.17	9.41	3.18
Total numbers	1060	759	1133

Table 2. Numbers of flowers or inflorescences, sample completeness and diversity parameters (Shannon diversity, Evenness, Simpson's dominance) for the three habitats studied.

Table 2. Numbers of flowers or inflorescences, sample completeness and diversity parameters (Shannon diversity, Evenness, Simpson's dominance) for the three habitats studied.

	<b>Forest</b>	<b>Pasture</b>	<b>Ski-piste</b>
1. Only genera with more than 1% of individuals sampled were reported. Inventory completeness is observed richness as a percentage of total Chao and ACE expected richness. Systematics follow Broglio <i>et al.</i> (2008). Richness is expressed in terms of the number of genera observed.			
<i>Achillea</i>	6	1028	275
<i>Arnica</i>	216	32	114
<i>Calluna/Erica</i>	201	75	246
<i>Campanula</i>	235	82	182
<i>Centaurea</i>	277	249	618
<i>Cirsium</i>	16	157	289
<i>Crepis</i>	715	175	1330
<i>Epilobium</i>	0	10	71
<i>Gallium</i>	0	600	36
<i>Leucanthemum</i>	32	45	345
<i>Potentilla</i>	19	342	218
<i>Prunella</i>	0	325	32
<i>Trifolium</i>	11	121	424
<i>Thymus</i>	0	8	1694
Other genera (12)	16	158	32
Shannon diversity	5.46	9.52	8.67
Evenness	0.21	0.37	0.33
Simpson's diversity	4.14	6.47	6.18
Total numbers	1742	3406	5905
Richness	14	24	18

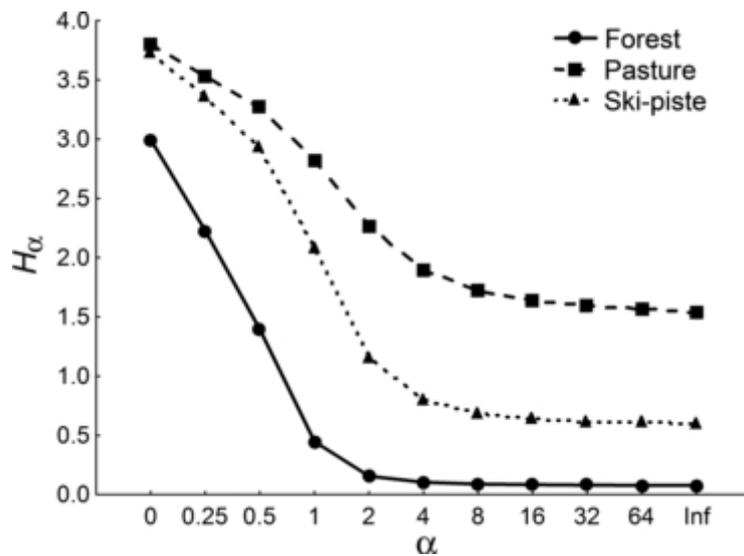


Figure 3

Rényi diversity profiles for the different habitat types. H-alpha ( $H_\alpha$ ) is the Rényi diversity index. Alpha ( $\alpha$ ) is a scale parameter ranging from zero to infinity.

Table 3. Mean  $\pm$  SE of taxonomic diversity ( $\Delta$ ), taxonomic distinctness ( $\Delta^*$ ), average taxonomic distinctness ( $\Delta^+$ ) and variation in taxonomic distinctness ( $\Lambda^+$ ) per habitat type.

Table 3. Mean  $\pm$  SE of taxonomic diversity ( $\Delta$ ), taxonomic distinctness ( $\Delta^*$ ), average taxonomic distinctness ( $\Delta^+$ ) and variation in taxonomic distinctness ( $\Lambda^+$ ) per habitat type.

	Forest (1)	Ski-piste (2)	Pasture (3)	Inter habitat differences	Significant pair-wise comparisons at $P < 0.05$
1. Inter-habitat differences were tested with one-way anova. Least-squares deviation (LSD) post-hoc tests were used for pair-wise comparisons of means.					
2. * $P < 0.05$ ; ** $P < 0.01$ ; *** $P < 0.001$ .					
$\Delta$	8.1 $\pm$ 2.1	45.7 $\pm$ 5.3	56.5 $\pm$ 2.8	F 2,57 = 30.98***	(1) vs. (2); (1) vs. (3)
$\Delta^*$	44.6 $\pm$ 6.9	73.3 $\pm$ 5.8	78.6 $\pm$ 2.5	F 2,57 = 5.34**	(1) vs. (2); (1) vs. (3)
$\Delta^+$	47.7 $\pm$ 7.3	74.9 $\pm$ 5.9	82.9 $\pm$ 1.2	F 2,57 = 5.23**	(1) vs. (2); (1) vs. (3)
$\Lambda^+$	153.9 $\pm$ 62.3	420.8 $\pm$ 43.9	527.1 $\pm$ 29.2	F 2,57 = 27.99***	(1) vs. (2); (1) vs. (3)

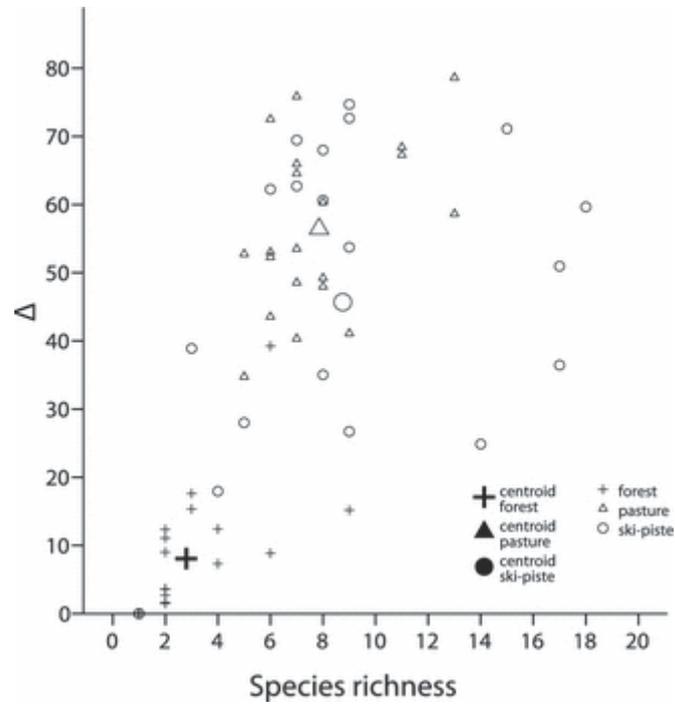


Figure 4

Values of Taxonomic Diversity ( $\Delta$ ) for the butterfly assemblages, plotted against the number of species. The empty symbols represent individual transects and the full symbols represent centroids for each habitat.

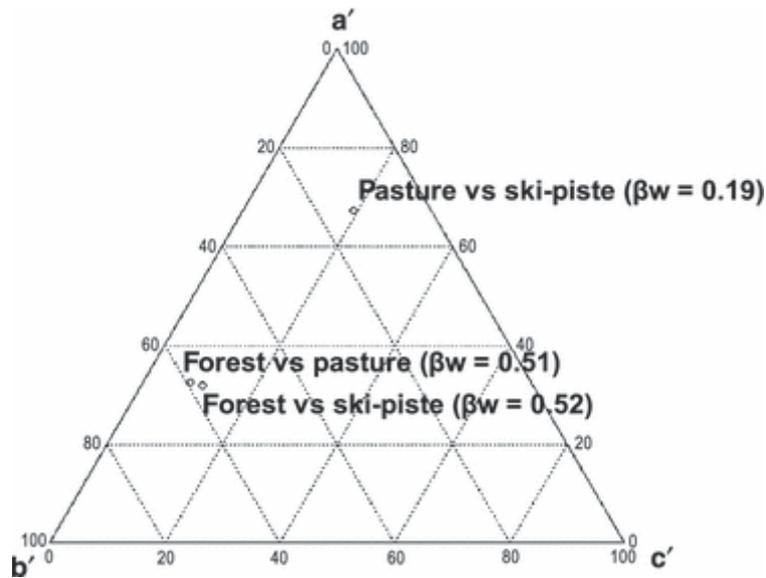


Figure 5

Ternary plot representing species turnover between pairs of habitats. Triangle vertices are as follows:  $a'$  is the percentage of species that are present in both habitats,  $b'$  is the percentage of species that are present only in the neighbouring habitat (the second of the pair), while  $c'$  is the percentage of species present only in the focal habitat (the first of the pair). The  $\beta$  value of Whittaker index is given in brackets.

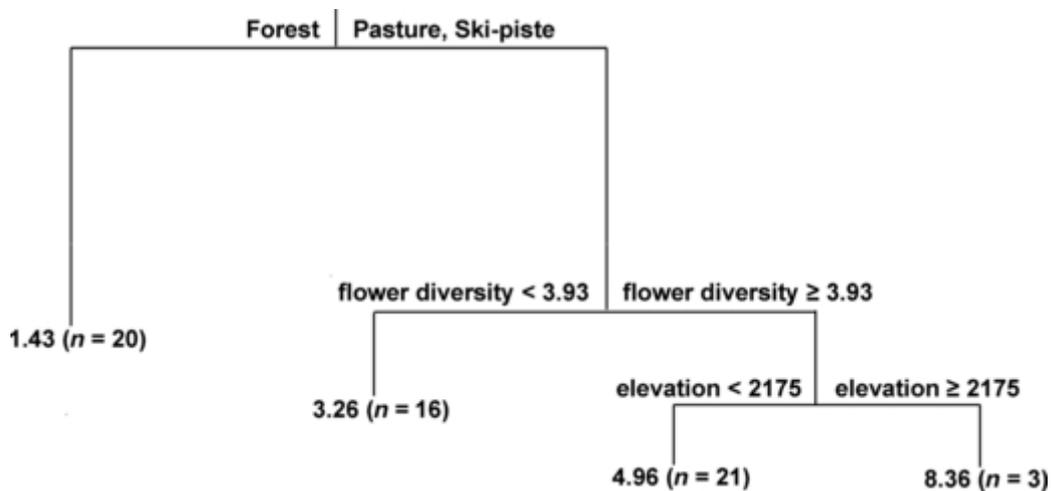


Figure 6

Univariate regression trees for butterfly Shannon diversity. The number below each end branch shows the mean value of Shannon diversity;  $n$  = the number of transects.

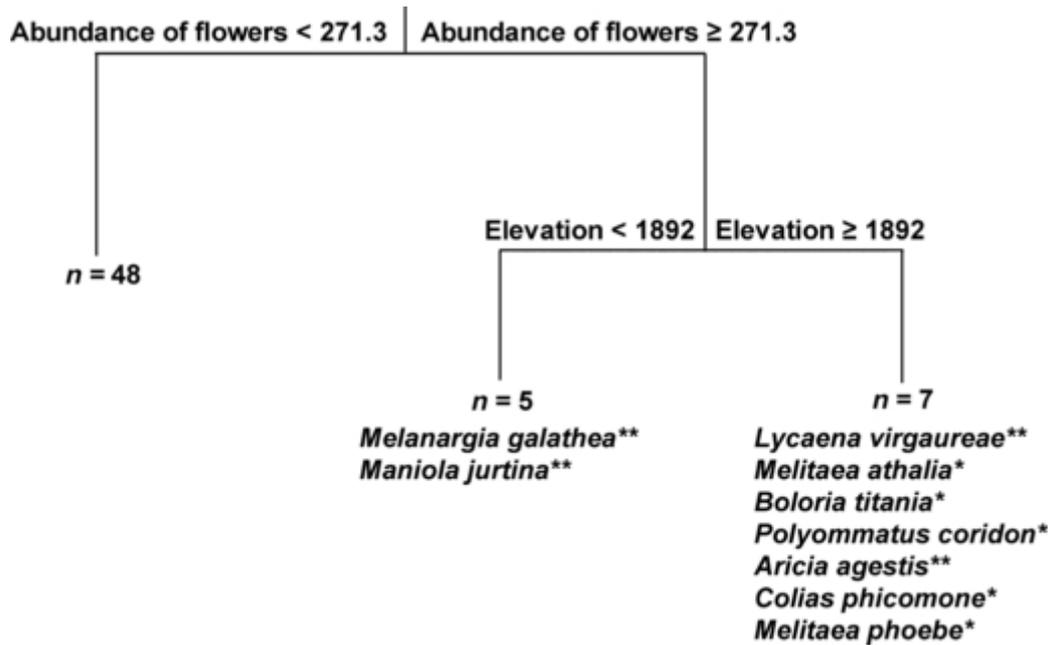


Figure 7

Multivariate regression tree for butterfly abundance. Only species which are significantly associated with one of the branches are shown;  $n$  = number of transects. Statistical significance was obtained by Monte Carlo randomization test (1000 runs): \* $P < 0.05$ ; \*\* $P < 0.01$ .