



Patterns of biodiversity in the northwestern Italian Alps: a multi-taxa approach

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Keywords: Animal diversity, Altitudinal gradient, Climate sensitivity, Community composition, Temperature.

Abstract: The current loss of biodiversity requires long-term monitoring of the distribution of living organisms, particularly in regions, such as mountains, which are highly sensitive to climatic and environmental changes. In 2007, three alpine parks in N-W Italy started a field program to determine the factors which influence animal biodiversity and identify the most appropriate methods for periodically repeatable monitoring. Twelve altitudinal transects (from montane to alpine belt) were chosen, each composed of 4-7 sampling units, for a total of 69 monitored plots. In each station, five taxonomic groups (carabids, butterflies, spiders, staphylinids, birds) were systematically sampled and topographic, environmental and micro-climatic variables were recorded. The aim was to assess the distribution of different taxa along altitudinal gradients and the relative influence of geographical, environmental and climatic factors. The data showed that species richness and community composition of invertebrates are mainly determined by altitude and microclimatic conditions, whereas birds are more sensitive to habitat structure. For invertebrates, the strong relationship with temperature suggests their potential sensitivity to climatic variations. The analysis of biodiversity patterns across vegetation belts indicated that the alpine belt hosts few species but a high percentage of endemic and vulnerable species, highlighting its importance for conservation purposes. This work offers a representative sample of the northwestern Italian Alps and it is a first step of a monitoring effort that will be repeated every five years to highlight the response of alpine biodiversity to climate and land-use changes.

Introduction

In the last few decades, species extinction and biodiversity decline have reached an alarming rate (Thomas et al. 2004, Butchart et al. 2010), indicating an urgent need to sort out and monitor factors that influence biodiversity variations and identify priority areas and sensitive taxonomic groups for conservation purposes (Yoccoz et al. 2001, Magurran et al. 2010).

In this framework, mountain ecosystems are of particular interest. Mountain landscapes, owing to their physical, topographic and climatic heterogeneity, create a mosaic of habitats along the altitudinal gradient (Körner 2000, Beniston 2003). Such heterogeneity determines high levels of biodiversity, usually higher than those recorded in adjacent lowland areas (Körner 2000, Theurillat et al. 2003). Compared to latitudinal variations, altitudinal gradients allow for investigating the relationships between biodiversity and abiotic/biotic parameters on a reduced spatial scale, where fauna and flora are often characterized by a similar biogeographical history (Rahbek 1995, Körner 2000).

Mountain habitats support some of the world's most rare and fragile ecosystems (Diaz et al. 2003, Pauchard et al.

2009). Populations at high elevations are usually small, isolated and prone to local extinction, are often poor dispersers and are characterised by high levels of endemism (McNeely 1990, Boggs and Murphy 1997, EEA 2010). Mountains are very sensitive to environmental changes and global warming (Huber et al. 2005, Beniston 2006) hosting a high number of species adapted to low temperature conditions (Pauli et al. 2004). Long-term records provide evidence for ongoing climate warming in mountain environments and in the Alps (Beniston 2006, Auer 2007, Rebetez and Reinhard 2008), that has already impacted the life cycle, pattern of activity, distribution and range size of various plant and animal species (Thuiller et al. 2005, Pauli et al. 2007, Bässler et al. 2010).

Mountains are outstanding heritage sites and their biodiversity is linked with the cultural patrimony of the people living therein. The European Alps have a long history of human presence and exploitation: during the last millennium, agropastoral activities determined a lowering of the treeline ecotone and shaped community composition of plants and animals (Theurillat and Guisan 2001, Chemini and Rizzoli 2003). Currently, high levels of recreational activities, as well the abandonment of traditional farming systems can

negatively affect mountain biodiversity (Patthey et al. 2008, Brambilla et al. 2010). Moreover the loss of more sedentary and specialized elements in favour of more vagile and tolerant species could determine an impoverishment of the biotic structure (e.g., Dirnböck et al. 2011).

For all these reasons, the identification of factors that determine biodiversity patterns has important implications on conservation and management decisions. Altitudinal gradients are particularly useful to test traits for their long-term adaptive nature, and allow for covering different belts along the vertical zonation of the vegetation pattern. Clearly, elevation must be seen as a proxy for the environmental conditions associated with it (Körner 2000). The knowledge of the relation with altitude becomes especially important in a time of global climate change, and it allows to assess which species will be more threatened by the temperature rise (e.g., Fleishman et al. 1998).

To gain a comprehensive understanding of biodiversity patterns, comparison of elevation trends between taxa and between different mountain ranges is necessary (Lomolino 2001). Information gained with a multi-taxa approach can be used as a primary tool to recognise areas of high natural value, to address management actions and to develop a more effective response to biodiversity loss than the standard ‘simply maintaining the site’s status quo’ (Hannah et al. 2002).

The present study represents the first attempt to develop a protocol for long-term monitoring of multiple taxa in the Italian Alps, and it is aimed at analyzing biodiversity changes along altitudinal transects encompassing three vegetation

belts (Montane, Subalpine and Alpine), in three non contiguous protected areas. Here we discuss the results of the first monitoring session of this effort, conducted in 2007, which allowed us to describe α - and β -diversity variations along the altitudinal gradient, to analyse the relative importance of geographical, environmental and climatic factors on biodiversity structure and community composition, and to assess if species of conservation concern follow patterns of distribution comparable to those of the other components of biodiversity.

Methods

Study area and sampling design

The study was carried out in three protected areas in the northwestern Italian Alps (Piedmont and Aosta Valley regions): Gran Paradiso National Park (720 km²; 44°25’N - 7°34’E), Orsiera Rocciavré Natural Park (110 km²; 44°75’N - 6°90’E) and Veglia Devero Natural Park (86 km²; 46°18’N - 8°13’E). All areas are characterised by mountain and alpine environments ranging from mixed forest to rocky meadows and glaciers. The three parks have similar mean elevation values and main vegetation characteristics, but display slight differences in terms of climatic regimes (highest monthly precipitation and lowest annual mean temperature in Veglia Devero Natural Park), offering a sub-sample of the natural variability in the northwestern Italian Alps.

We selected twelve altitudinal transects, each composed of sampling units (plots with a radius of 100 m) whose cen-

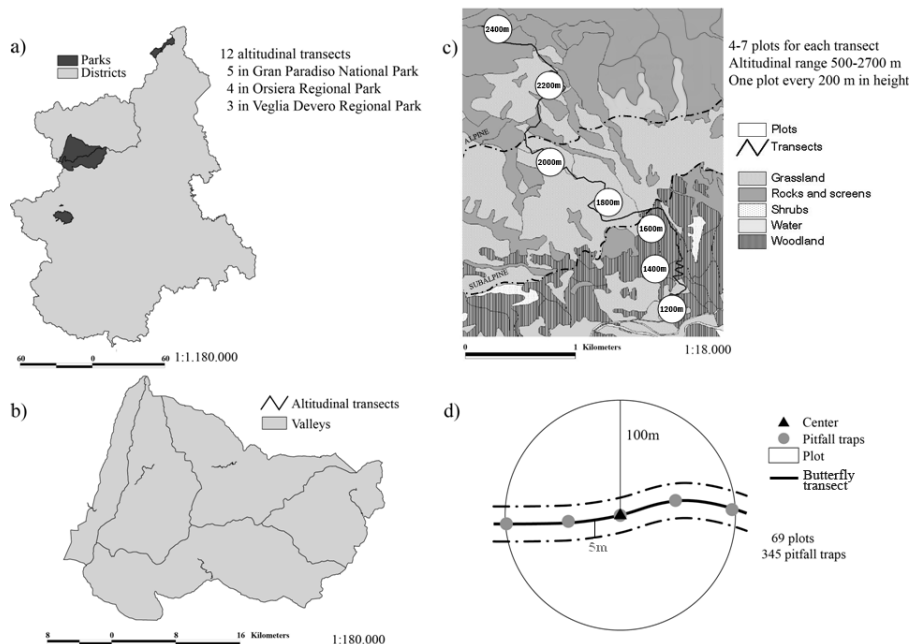


Figure 1. Description of sampling design. In 3 protected areas in the northwestern Italian Alps (a), data were collected along 12 altitudinal transects (b). Each altitudinal transect covers an altitudinal range of 800-1400 meters and three vegetation belts (boundaries are represented as dashed lines). Sampling areas are located every 200 m in height (c). The sampling unit is a circular plot, with horizontal radius of 100 m, where data on 5 different taxonomic groups have been collected. (d).

tres were separated by an altitude difference of 200 meters (Fig. 1).

Each plot was classified as belonging to one of three belts (Montane, Subalpine and Alpine), that are present in our gradient from the bottom to the top. We defined them as altitudinal sections characterised by a given vegetation and climate (Körner 1999, Theruillat and Guisan 2001, Grabherr et al. 2003, Körner et al. 2011) as follows: Montane, the zone below the timberline; Subalpine, the zone between the timberline and the tree species line (the line beyond which no adult tree occurs); Alpine, the zone above the tree species line. The sampling design included 22 plots in the Montane, 20 plots in the Subalpine and 27 plots in the Alpine belt.

Data collection

Data on Lepidoptera Rhopalocera, Aves and surface-active arthropods (Coleoptera Carabidae, Coleoptera Staphylinidae, Araneae) were collected in 2007 from April to October using, for each taxon, semi-quantitative census techniques, that were, as much as possible, easy to apply, standardized, cheap and repeatable.

Birds were recorded by means of point counts with infinite counting range (Bibby et al. 1992). Counts lasted 20 minutes and birds were identified using acoustic and morphological characteristics. Each plot was visited twice during the reproductive season. Early visits were especially useful for detecting low altitude species with a reduced optimal detection period, such as woodpeckers. Late visits allowed contacting long distant migrants reaching breeding grounds late in the season.

We sampled butterflies using linear transects along one of the diameters of the plot (200 m in length), walked at uniform speed. We recorded all butterflies seen within prescribed limits in an imaginary square of 5 m × 5 m, following Pollard (1977). Sampling was limited to sunny conditions, under calm to light wind. Each plot was visited once a month from June to September. Individuals were captured and released after specific identification, except for specimens of difficult identification, which were retained for subsequent determination.

We collected surface-active arthropods using pitfall traps (plastic cups, diameter of 7 cm, filled with 10 cc of white vinegar and some drops of detergent as surfactant). The traps were set along the diameter of each plot, in a single row of five traps at a distance of fifty meters from each other. The traps were emptied every two weeks from May to October, for a total of 10 to 12 samples per plot depending on the starting date. Individuals belonging to the selected taxa were determined at species level. In the case of Staphylinidae, we did not consider species belonging to the sub-family Aleocharinae, one of the largest and taxonomically most difficult lineages of staphylinid beetles (Ashe 2007), which makes it a scarcely useful indicator in the development of a long-term biodiversity monitoring program (Lindenmayer and Likens 2010).

For each plot we determined the percentage of ground covered by different structural layers (herbaceous layer, low shrubs - < 1 m, tall shrubs - between 1-5 m, trees, stone and bare ground cover), estimated by eye during field surveys using 10% classes and by using vegetation maps. We used vegetation layers to estimate structural diversity, defined as Shannon index on the value of herbaceous layer, shrub and tree cover, as often adopted in conservation studies to describe habitat heterogeneity (e.g., Marini et al. 2010, Oliver et al. 2011).

Microclimatic conditions in each plot were measured by data-loggers (Thermochron iButton, DS1922L, Maxim, Sunnyvale, CA, U.S.) that recorded air temperature every hour throughout the field season. They were located in the centre of each plot, at least 1 meter above ground and covered with a white shield. Daily temperatures were averaged among months (mean with the corresponding coefficients of variation) and then averaged to obtain seasonal values for each plot. Due to missing values for temperature in 7 sampling units, analyses involving this variable were performed using 62 plots.

Data analysis

To describe community structure and composition at each sampling site, we grouped data among temporal replicates.

Before analysing α -diversity, we tested whether the methodologies adopted in our study allowed for obtaining comparable results, in terms of sampling design efficiency, for the different habitats and taxonomic groups. To estimate the effectiveness of the sampling effort for each taxon in different belts, we used plot-based rarefaction curves (Gotelli and Colwell 2001, Chiarucci et al. 2008). The rarefaction pattern that we obtained, where the last quartile of the taxon/taxon ratio curves become constant, indicates that the sampling effort gives the same amount of information for each taxon allowing a comparison among them (Appendix S1).

We computed species richness (S), Shannon-Wiener index (H'), Simpson index, corrected for a finite community and expressed as its reciprocal $1/D$, and abundance (N), the number of recorded individuals for each taxon and for all taxa pooled together.

We observed that species richness was strongly correlated with the Shannon index ($0.629 < \rho < 0.947$, all p-values < 0.0001), and presented a weaker but always significant correlation with the Simpson index ($0.320 < \rho < 0.857$, all p-values < 0.01) and abundance ($0.412 < \rho < 0.790$, all p-values < 0.0001). Consequently, further analyses were based only on species richness, an effective measure of biodiversity which is easier to interpret.

To assess the conservation value of single elements, each species was characterised by habitat preferences, climate requirements and morphological characteristics, which determine potential vulnerability and/or sensitivity to environ-

mental and climatic change (Appendix S2.1). Percentages of endemic and vulnerable species were obtained for each plot and correlated with each other to explore for similar patterns of variation and consequently to identify areas of high conservation concern.

To explore how species richness changes along the altitudinal gradient, we performed locally weighted regression scatterplot smoothing (LOWESS regression). To quantify the relationship between species richness and altitude we applied a generalized linear model assuming a negative binomial distribution, using a log-link function, in the MASS library (Venables and Ripley 2000), to determine the best fit between a first, second or third order equation. To choose among polynomial equations we used the likelihood ratio test and the AICc criterion. To quantify the relationship between proportion of species of conservation concern and altitude, we applied a generalized linear model assuming a quasibinomial error distribution and using a logit function. To choose among polynomial equations, we used an analysis of deviance and the qAICc criterion.

In both cases, as a measure of goodness of fit, we calculated the adjusted D^2 (D^2_{adj} , see Guisan and Zimmermann 2000) and we applied a leave-one-out cross-validation estimate of prediction error. The coefficient of correlation (Spearman ρ) between the jack-knife-predicted and the observed values of the response variable was computed (Davison and Hinkley 1997).

We analysed the variables determining α -diversity patterns into a variation partitioning framework (Borcard et al. 1992), following the approach suggested by Borcard et al. 2011 and Legendre and Legendre 2012 (Appendix S2.2). This approach allowed for analysing non-independent explanatory variables and it is designed to identify the portions of explained variability that are uniquely determined by the different sets of predictors. Consequently, we divided explanatory variables into four groups: altitude (up to a third order degree), temperature (up to a third order degree), vegetation (percentage of vegetation cover and structural diversity), geographic location (UTM latitude and longitude). All the variables were standardized, to allow for comparison between dimensionally heterogeneous variables.

To assess if vegetation belts differed in term of diversity pattern, species richness and percentage of endemic and vulnerable species per plot were compared using a Kruskal Wallis test.

To visualise the main trend in the compositional gradient of the five taxonomic groups, we first performed a correspondence analysis (CA), one for each taxon and one for all taxa pooled together. This multivariate technique is preferred when unimodal patterns along the ecological gradient are expected (Palmer 2007) and when data are dimensionally homogeneous and characterized by non-negative numbers (Borcard et al. 2011). The appropriateness of these methodologies and the data transformation applied before the Correspondence Analysis are described in the Supplementary Ma-

terial (Appendix S2.3). To analyze the possible effect of one species in determining the plot ordering along the first axis, we performed CA removing from the data one species at a time, and correlated the first axes obtained in this way.

To estimate a first influence of the predictor variables on the main gradient, we analysed them *a posteriori*, through the correlation of the scores obtained along the first axes and each single predictor (Spearman rank correlation test); significance levels were corrected using a sequential Bonferroni procedure (Rice 1989).

To assess if community composition significantly changed between belts, we compared sites scores along the first axes with Kruskal-Wallis test. Site scores for the first axes were plotted against altitude and the plots were examined for discontinuities with respect to those gradients, using LOWESS regression and applying a linear model. A linear relationship between scores on the first axis and an environmental variable would indicate constant change in the species composition of sites along the gradient (Jankowski et al. 2009).

To relate changes in species composition to specific variables and to decompose the variability in community composition among the groups of predictors (altitude, temperature, vegetation, geographic location), we analysed the species-by-sample matrices using canonical correspondence analysis (CCA) in a variation partitioning framework, following the same steps and obtaining the same fractions already described for α -diversity (Appendix S2.2). Such analyses were conducted with the program Varcen version 1, which adjusted for bias in R^2 (Peres-Neto et al. 2006). Prior to partitioning the effects of different groups of predictors, we selected the variables that significantly contribute to the variation in species data by forward selection, using the *ordstep* function in the vegan R package (Oksanen et al. 2012). In this analysis altitude and temperature were considered only in their first degree, because we were mainly interested in linear effect on community composition. This function achieves automatic stepwise model building for constrained ordination methods, using AIC and permutation tests (999 permutations).

To analyse the structure of β -diversity among sites, we further applied a distance approach (Tuomisto and Ruokolainen 2008), exploring the relationships between pairwise dissimilarities in community structure and pairwise differences in predictor variables through simple and partial Mantel Test (Anderson et al. 2011). The simple Mantel test (Mantel 1967) was used to verify whether distances in community composition (community dissimilarity matrices) correspond to distances in geography, temperature, altitude and vegetation. Partial Mantel's test allowed us to decompose the relative importance of each matrix of the predictor variables, controlling for the effects of the others (Smouse et al. 1986, Anderson and Legendre 1999).

Community dissimilarity matrices for each taxon were based on the complement of Jaccard estimator index, pro-

posed by Chao (Chao et al. 2005) and calculated with EstimateS 8.0 (Colwell 2005). Differences in temperature between plots were calculated as Euclidean distances, obtained using monthly values (mean and coefficient of variation) derived from the data-logger located in each plot. The geographical distance matrix was obtained using plot midpoint coordinates and calculated with ArcView 3.2, using the Animal Movement Analyst Extension (Hooge and Eichenlaub 2000). Differences in vegetation were quantified using a matrix (called belt matrix), in which distances between plots were scored 0 for samples belonging to the same belt, 2 for samples belonging to non-consecutive belts (pair Montane-Alpine), and 1 in all the other cases. Altitude matrices were built using the altitudinal differences among plots.

Simple and partial Mantel tests were performed using the Zt software with Mantel tester GUI (Bonnet and Van de Peer 2002). The significance level was assessed using 100,000 randomisations, through permutation of the residual of the null model. The level of significance was set to $\alpha = 0.01$, to reduce the risk of significant results by chance due to the large number of tests performed on the same data set.

Except when indicated, all statistical analyses were performed using R 2.15.1 (R Core Team 2012).

Results

Species richness

We recorded 663 species: 101 carabids, 134 butterflies, 245 spiders, 119 staphylinids and 64 birds.

The LOWESS regression showed a hump-shaped dependence of total species richness versus altitude. The relationship between species richness (S) and altitude (Alt) was better described by a quadratic function, as shown in Fig. 2a for all taxa pooled together ($S = \exp(2.841 + 0.002 \text{ Alt} - 6.420e^{-07} \text{ Alt}^2)$; $D^2_{\text{adj}} = 0.425$; $p < 0.0001$; Appendix S3), with a peak in species richness at medium elevations. A simi-

lar quadratic relationship has been recorded for almost all individual taxa, except for butterflies, where we found a linear decrease along the altitudinal gradient, and for carabids, where we found no clear relationship with altitude (Appendix S3).

Percentages of vulnerable and endemic species were related ($\rho = 0.568$, $N = 69$, $p < 0.0001$) and both increased in a monotonic way along the altitudinal gradient (*logit* (proportion of vulnerable species) = $-5.701 + 0.002 \text{ Alt}$, $D^2_{\text{adj}} = 0.535$, $p < 0.0001$; *logit* (proportion of endemic species) = $-3.388 + 0.001 \text{ Alt}$; $D^2_{\text{adj}} = 0.277$; $p < 0.0001$; Fig. 2b; Appendix S3).

As reported in Table 1, the most important variables in determining Species richness were altitude and temperature, while the variables related to vegetation structure played a lesser role. These results held for the Species richness of all taxa pooled together, for the proportion of vulnerable and endemic species and for the individual taxonomic groups, with the exception of carabids and butterflies. For these two latter taxa, variables related to vegetation explained the highest proportion of variance. In the case of carabids such influence was determined by the extent of the herbaceous layer, while for butterflies both the structural diversity and the extent of herbaceous layer determined an increase in species richness.

A negative influence of rock coverage was observed, in particular for staphylinids, spiders, birds and all taxa pooled together, while a significant influence of structural diversity was observed not only for butterflies, but even in the case of birds and all taxa pooled together (Table 1).

Temperature displayed a quadratic relationship for all taxa pooled together and for the individual taxonomic groups, with a peak at intermediate temperatures. Only the proportion of endemic species clearly decreased along the temperature gradient, while the proportion of vulnerable species decreased with temperature, not in a monotonic way, but better described by a quadratic function with a positive coefficient of the second order term.

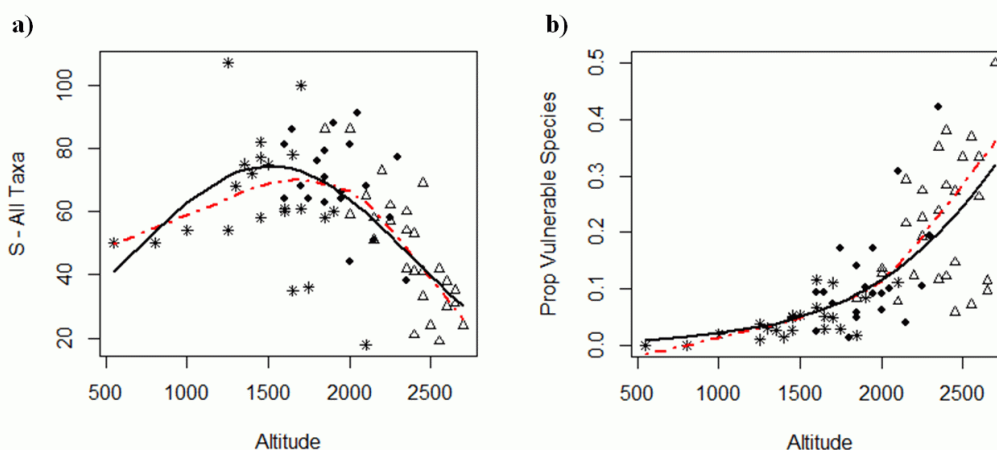


Figure 2. Scatterplots of the total species richness per site for all taxa pooled together (a) and of the proportion of vulnerable species (b) along the altitudinal gradient. The LOWESS regression curve is represented as a dashed line, while the significant regression curve is represented as a solid line. Montane belt (*), Subalpine belt (●), Alpine belt (△).

Table 1. Results of variation partitioning for all taxa pooled together, for each taxonomic group and for the percentage of vulnerable and endemic species. Mod represents the single variables selected for each group, after forward selection procedures and linear regression models. Variations in species composition are explained by four group of variables: altitude (Alt), temperature (Temp), vegetation (Veg), geography (UTM); Unex represents the unexplained variance; Exp the total variance explained by each group of variable and Pure the unique effect of each group. The sign of the interaction is represented in brackets. Significance values of each fraction have been calculated by using 999 random permutations. ns = not significant; ° = $p < 0.10$; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$. Code for variables are the following: altitude (Alt), temperature (Temp), structural diversity (Str Div), trees (Tree), tall shrubs (TShr), low shrubs (LShr), herbaceous layer (HerbL), stone (Rock), UTM longitude (x), UTM latitude (y).

| | Carabids | Butterflies | Spiders | Staphylinids | Birds | All | Endemic | Vulnerable |
|------|----------|-------------|---------------------------------|---------------------------------|---------------------------------|---------------------------------|---------------------------|---------------------------------|
| Alt | Mod | NA | (-) Alt, (-) Alt ² | (-) Alt, (-) Alt ² | (-) Alt, (-) Alt ² | (-) Alt, (-) Alt ² | (+) Alt | (+) Alt |
| | Exp | NA | 9.7* | 23.6*** | 42.0*** | 35.0*** | 40.9*** | 44.6*** |
| | Pure | NA | 1.9 ^{ns} | 1.5 ^{ns} | 9.6* | 0.0 ^{ns} | 0.0 ^{ns} | 0.0 ^{ns} |
| Temp | Mod | NA | (+) Temp, (-) Temp ² | (-) Temp, (-) Temp ² | (+) Temp, (-) Temp ² | (-) Temp, (-) Temp ² | (-) Temp | (-) Temp, (+) Temp ² |
| | Exp | NA | 23.5*** | 20.9** | 30.6*** | 37.5*** | 45.3*** | 31.9*** |
| | Pure | NA | 8.7* | 0.0 ^{ns} | 0.0 ^{ns} | 0.5 ^{ns} | 1.3 ^{ns} | 0.0 ^{ns} |
| Veg | Mod | (+) HerbL | (+) Str Div, (+) HerbL | (-) Rock | (-) Rock, (+) Tree | (-) Rock, (+) Str Div | y = (-) Rock, (+) Str Div | (+) Rock, (-) Str Div |
| | Exp | 12.1** | 30.1*** | 13.3** | 26.8*** | 32.4*** | 34.1*** | (+) Rock, (-) Tree, (-) TShr |
| | Pure | 12.1** | 11.7* | 1.0 ^{ns} | 1.0 ^{ns} | 3.8 ^{ns} | 1.9 ^{ns} | 36.8*** |
| UTM | Mod | NA | NA | NA | NA | NA | NA | (+) x |
| | Exp | NA | NA | NA | NA | NA | NA | 20.5*** |
| | Pure | NA | NA | NA | NA | NA | NA | 6.0* |
| Unex | 87.85 | 60.71 | 77.10 | 57.74 | 58.66 | 53.53 | 62.07 | 29.23 |

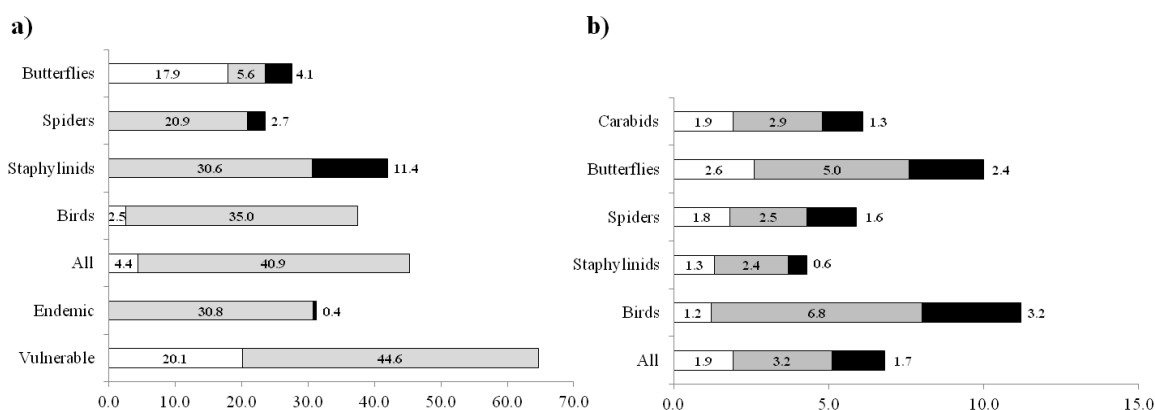


Figure 3. Variation partitioning of species richness (a) and community composition (b) into the independent effect of temperature (white), altitude (black) and their shared effect (grey).

By further exploring variation partitioning between altitude and temperature, we observed that, in all cases except butterflies, the highest amount of their explained variation is shared. In the case of butterflies, birds, all taxa pooled together and vulnerable species, temperature presented a higher pure effect (Fig. 3a).

The Subalpine belt had the highest total species richness per plot and the alpine belt the lowest. Considering single taxa, these results held in particular for butterflies and birds, where we observed large differences between the subalpine and alpine belts. For spiders and staphylinids differences were nearly significant, with lowest values in the alpine belt, while no differences have been recorded in carabids. Endemic and vulnerable species displayed significant differences between belts, clearly increasing from the montane to the alpine belt (Fig. 4). Detailed results of such analyses are shown in Appendix S4.

Community composition

The site ordination for all taxa, as obtained by correspondence analysis is shown in Fig. 5a. Percentage of inertia explained by the first axis ranged between 6.914 for spiders to 13.882 for birds and was 7.499 in the case of all taxa pooled together.

Along the first CA axis we found a clear distinction between sites of the Montane and the Alpine belts, while the plots of the Subalpine belt were intermediate between the two (Fig. 5c). Differences in plot scores among belts along the first axis were significant for all taxa pooled together (Kruskal-Wallis test: $N = 62$, $df = 2$, $H = 38.902$, $p < 0.0001$) and for the individual taxa (Appendix S5). Moreover, we observed a gradual change along the altitudinal gradient in almost all cases (Fig. 5b; Appendix S5).

The site ordination along the first axis was similar for the five groups, and it was strongly correlated with the site ordi-

Table 2. Spearman correlation coefficient between each environmental variable and the extracted scores of the first dimension of correspondence analysis for the five taxa and all taxa pooled together. ScoreAx1 = scores of the sampling sites along the first CA dimension. * = $p < 0.05$; ** = $p < 0.01$, after sequential Bonferroni procedure. For abbreviations see Table 1.

| | Alt | Temp | StrDiv | Tree% | TShr% | LShr% | HerL% | Rock% | x | y |
|-------------------------------|----------|----------|----------|----------|----------|---------|--------|--------|---------|----------|
| ScoreAx1_{car} | 0.581** | -0.624** | -0.396* | -0.321 | -0.424** | -0.264 | 0.085 | 0.033 | 0.607** | 0.774** |
| ScoreAx1_{but} | -0.863** | 0.883** | 0.487** | 0.606** | 0.619** | 0.197 | -0.248 | -0.030 | -0.381* | -0.477** |
| ScoreAx1_{spi} | -0.821** | 0.850** | 0.398* | 0.490** | 0.580** | 0.170 | -0.134 | -0.135 | -0.325 | -0.461** |
| ScoreAx1_{sta} | -0.516** | 0.618** | 0.089 | 0.227 | 0.188 | -0.086 | 0.205 | -0.077 | -0.215 | -0.310 |
| ScoreAx1_{bir} | 0.912** | -0.852** | -0.589** | -0.788** | -0.678** | -0.371* | 0.377* | 0.219 | 0.226 | 0.257 |
| ScoreAx1_{all} | 0.891** | -0.919** | -0.470** | -0.560** | -0.600** | -0.214 | 0.188 | 0.128 | 0.346 | 0.481** |

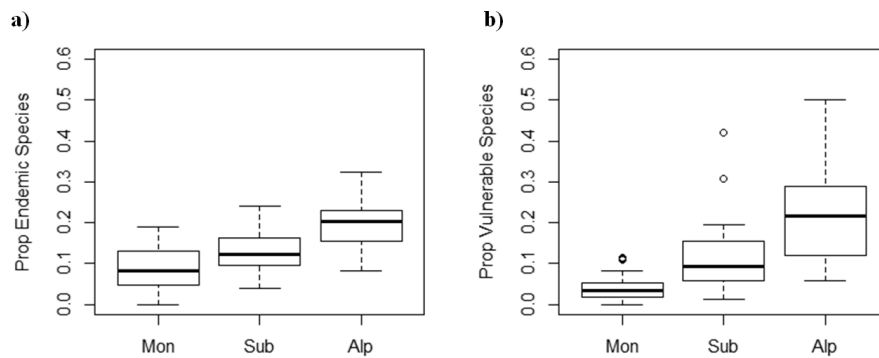


Figure 4. Percentage of species of conservation concern, endemic (a) and vulnerable (b) species, in the different belts. The boxes show median, first and third quartile, whiskers represent minimum and maximum values and outliers are plotted as circles. Montane belt (Mon), subalpine belt (Sub), alpine belt (Alp).

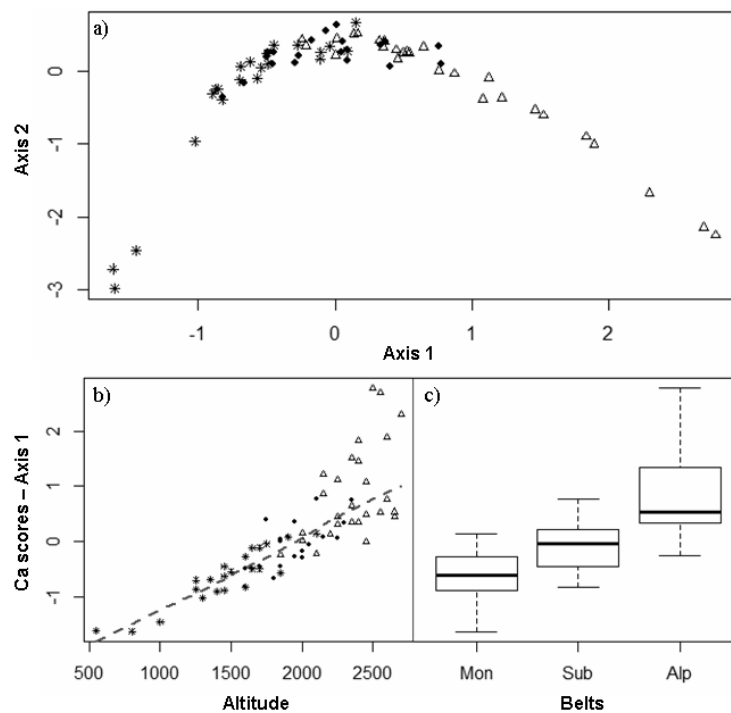


Figure 5. a) Correspondence analysis for the 69 sampling sites, based on data from all taxa pooled together. Montane belt (*), Subalpine belt (●), Alpine belt (△). b) Scatterplot between site scores along the first axis of the CA with all taxa pooled together and altitude. The LOWESS regression is represented as a dashed line. c) Box-plot of site scores among vegetation belts. Montane belt (Mon), subalpine belt (Sub), alpine belt (Alp).

Table 3. Results of simple and partial Mantel Tests. For the simple test, correlations are presented as r-values; n.s. = not significant; * = $p < 0.01$; ** = $p < 0.001$; *** = $p < 0.0001$. The results of the simple Mantel test are shown in the diagonal with grey background colour. Number of plots = 62, owing to missing temperature values in 7 plots.

| | Temperature | Altitude | Belt | Geography | |
|--------------|-------------|----------|----------|-----------|-----------------------------|
| Carabids | 0.228*** | (n.s.) | * | *** | Controlling for Temperature |
| Butterflies | 0.390*** | * | *** | *** | |
| Spiders | 0.316*** | (n.s.) | ** | *** | |
| Staphylinids | 0.245*** | (n.s.) | * | *** | |
| Birds | 0.398*** | *** | *** | (n.s.) | |
| Carabids | *** | 0.178*** | (n.s.) | *** | Controlling for Altitude |
| Butterflies | *** | 0.350*** | *** | *** | |
| Spiders | *** | 0.255*** | * | *** | |
| Staphylinids | *** | 0.204*** | (n.s.) | *** | |
| Birds | (n.s.) | 0.523*** | *** | ** | |
| Carabids | *** | ** | 0.149*** | *** | Controlling for Belt |
| Butterflies | *** | *** | 0.354*** | *** | |
| Spiders | *** | ** | 0.221*** | *** | |
| Staphylinids | *** | ** | 0.149*** | *** | |
| Birds | *** | *** | 0.594*** | ** | |
| Carabids | *** | *** | *** | 0.305*** | Controlling for Geography |
| Butterflies | *** | *** | *** | 0.285*** | |
| Spiders | *** | *** | *** | 0.237*** | |
| Staphylinids | *** | *** | *** | 0.164*** | |
| Birds | *** | *** | *** | 0.110* | |

nation obtained with all taxa pooled together ($0.763 < \rho < 0.967$, all with $p < 0.001$). By leaving out one species at a time, we still obtained the same ordering of the plots (Spearman rank correlation between $0.999 < \rho < 1.000$).

Spearman rank correlation between scores along the first CA axis and environmental variables indicated that the compositional gradients were mainly correlated with altitude and temperature (Table 2). Even if with a lower importance, variables related to vegetation, i.e. structural diversity, tree and tall shrubs coverage, are still significant, in particular for birds and butterflies (Table 2).

The analysis of variation partitioning applied to a CCA showed that all the fractions explained only low amount of variation (Appendix S6), suggesting a highly complex succession of species along the ecological gradients under study. Temperature was the most influencing variable in the case of carabids and staphylinids, while spiders, birds, butterflies and all taxa pooled together were mainly affected by variables related to vegetation structure.

The analysis of the relative role of altitude and temperature showed that the temperature effect is highly shared with altitude, but presented a pure effect which is larger than altitude, in all cases except for birds (Fig. 3b).

The correlations of α -diversity with topographic and environmental variables, estimated with the Mantel's Test, were weak but significant in all cases (grey boxes in Table 3). In almost all cases, temperature showed the highest correlation and geography the lowest. Partial Mantel test shows that the relationship between compositional dissimilarity and

altitude, conditional on temperature, was still significant for birds. On the opposite, when conditional on altitude, temperature accounted for significant variation in compositional dissimilarity for all invertebrates. The variance explained by geographical distance cannot be attributed to any other factor (Table 3).

The results of the Mantel test on topographic and environmental variables showed that distances in temperature and altitude were strongly related ($r = -0.737$, $p < 0.0001$) while geography showed almost no link with the other variables. The belt matrix was significantly correlated with both altitude ($r = 0.560$, $p < 0.0001$) and temperature ($r = 0.357$, $p < 0.0001$).

Discussion

Species richness

Our results suggest that, for the altitudinal gradient explored here, the curve of the overall species richness was hump-shaped, with a peak in richness at intermediate elevations and a stronger decline at increasing elevations. Similar patterns have been observed in other studies for various taxonomic groups, e.g. vascular plants (Grytnes 2003), ferns (Bhattarai et al. 2003), insects (Fleishman et al. 1998), birds (Kessler et al. 2001) and small mammals (Rickart 2001, Sanchez-Cordero 2001). In the sampling sites analysed here, the lower-elevation portion of the curve was strongly influenced by xeric conditions (3 plots in the Orsiera Rocciavre Parks) and by higher levels of human impact, compared to the belts at higher altitude. The plots at lower altitude were

mainly located at the boundaries of the protected areas. These areas can properly act as buffer zones but do not possess high conservation value, neither in terms of the number of species nor in the amount of elements with conservation and biogeographical interest.

In principle, altitudinal gradients are a proxy for a large number of interrelated variables that can potentially affect biological diversity (Brehm et al. 2003). As observed in other studies (e.g., Oommen and Shanker 2005), we found that temperature was the most important variable associated with altitude. This held for almost all taxonomic groups and for the overall species richness. Only butterflies and carabids showed a slightly different pattern, as they were more influenced by environmental variables. In the case of butterflies, higher structural diversity and higher amount of herbaceous layer positively influenced species richness, while in the case of carabids the major driver was the amount of herbaceous layer. Presumably, this is due to the fact that carabids are extremely sensitive to grassland management (Grandchamp et al. 2005), and also because carabid species richness is not clearly related to habitat characteristics (Gobbi et al. 2007). In the case of butterflies, higher structural diversity means higher availability of different habitats at a local scale, allowing for the coexistence of a higher number of species (e.g., Weibull et al. 2000, Kraus 2003).

We found the highest levels of species richness in the Subalpine belt, as could be expected from the fact that this is a transition area where different habitats coexist (Lomolino 2001, Oommen and Shanker 2005). As observed in the analysis of community composition, the Subalpine belt was characterized by the presence of both species which are exclusive to this area and species shared with the surrounding belts. Some authors suggest that responses in mountain ecosystems should be stronger at ecotones, owing to the possibility of different trends in adjacent habitats (Guisan et al. 1995, Beniston 2003). Consequently, the Subalpine belt is one of the most endangered, because its peculiar community composition could be disrupted. Both the general trend of reforestation in the mountains of Europe (e.g. EEA 2010) and a warmer climate could determine an increase of species from lower altitude and a decrease of species shared with the Alpine belt.

We observed a significantly larger proportion of vulnerable and endemic species in the Alpine belt, which thus emerged as a priority area. Moreover, we observed that vulnerable species were the ones with the greatest explained variance (more than 50%): their richness was clearly influenced by the shared effect of temperature and altitude. Endemic and vulnerable species often present very narrow ranges and their abundance peaks are not necessarily coherent with species richness, being often shifted to higher altitudes (Kessler 2002, Vetaas and Grytnes 2002, Fu et al. 2006, Schmitt 2009). In addition, the Alpine belt is characterized by environmental constraints (severe climatic conditions, short summer periods, slope, natural hazards) and by the importance of direct and indirect effects of climatological fac-

tors, in particular low temperatures (Beniston 2003, Pauli et al. 2004, Körner et al. 2011).

Consequently, many species are isolated at high elevation; in contrast, lowland communities can occupy climatic niches which are spread over wider areas (e.g., Beniston 2003). In the Alps, there is a large number of endemism among high altitude species, some of which are widespread through the entire region, while others are strictly localized (Schmitt 2009). High altitude biota are consequently poorer and more fragile: localized and strongly adapted elements are prone to higher levels of threat and are vulnerable to climatic and environmental changes (Manne and Pimm 2001, Parmesan 2006, Dirnböck et al. 2011).

Our results indicate that α -diversity indices, which weight all species in the same way or consider only their relative abundances, are not enough to describe habitat vulnerability and to identify conservation priority areas, particularly in mountain ecosystems. The number of species and the ecological characteristics of single elements must be taken into account, to identify which areas are important for the different conservation purposes (e.g., Orme et al. 2005, Samu et al. 2008).

Community composition

The analysis of community composition showed the presence of a less clear pattern: this is confirmed by all three approaches that we adopted in analysing the species-per-site matrices.

The low percentage of inertia explained by the first two axes of the correspondence analysis indicated that the pattern of community composition was more complex and cannot be easily summarized in a space with reduced dimensionality. In any case, temperature and elevation were highly correlated with the first dominant gradient found from CA.

Species distribution along the first CA axis displayed a smooth transition, leading to a large separation at the extremes of the gradients (Brehm et al. 2003). Different belts showed no clear-cut separation, but led to very different community composition.

Variation partitioning applied to the CCA showed that a high percentage of variance remained unexplained: community composition, inside our gradient, followed patterns that are not directly determined by the measured variables.

Both these results imply that different species change along the altitudinal gradient in a non-coherent way, but at the same time significantly different communities are found at the extremes of the gradient. Results from the distance-based approach (the Mantel test) confirmed these considerations. We observed, in almost all taxonomic groups, an influence of altitude and temperature on differences in community composition.

Partialling out the effect of temperature, altitude lost significance for all taxonomic groups except birds. On the contrary, when the effect of altitude was removed first, tempera-

ture still remained important, even though caution should be adopted when interpreting the results from partial Mantel tests (Raufaste and Rousset 2001). All these results indicate that temperature differences affected the community composition of the invertebrates studied here, in keeping with the fact that poikilothermic and ectothermic organisms are particularly sensitive to climate (Huey and Stevenson 1979, Hodkinson 2005). Changes in temperature have already been observed as a main factor driving life cycles, physiological responses and assemblage composition for different taxonomic groups of invertebrates (e.g., Parmesan 2006, McGeoch et al. 2006, Hassal et al. 2007, Wilson et al. 2007). A different pattern was observed for birds: since they are endothermic, they are less affected by temperature for their metabolic activities, and the composition of their assemblages was less influenced by climate and more by habitat structure and complexity, as already observed for example by Kessler et al. (2001). Some past studies found no clear bird response to temperature trends along altitudinal gradients, probably owing to a stronger effect of land use changes than of climate warming (e.g., Archaux 2004, Popy et al. 2010).

We observed that, for all invertebrate groups, the role of geographic distance in shaping community composition remained significant, even when controlling for the other factors. These results indicate that, in terms of invertebrate communities, each protected area presents peculiarities that cannot be explained by factors other than geographical characteristics and distance from each other. The reason can possibly be found in historical factors: the Alps have a high number of endemism and many of them are local endemic in a restricted area (Schmitt 2009). Endemism is surely important but ecological and climatic factors at local scale may have played a role in shaping the current distribution of terrestrial insects along altitudinal gradients (e.g., Hodkinson 2005).

Conclusion

The study presented here allowed for assessing the pattern of congruence and diversity in the distribution of five taxonomic groups along altitudinal gradients and determining the relative role of geographical, environmental and climatic factors.

When the role of environmental constraints is low, the standard expectation is that different taxonomic groups respond in a different way to local habitat and landscape composition. However, in harsher environmental conditions, such as those encountered in mountain areas, climate could act as the main force driving species richness and community composition across all taxa. The role played by temperature in determining species richness, distribution of vulnerable species and partially community composition, as observed in this study, emphasizes the potential vulnerability of mountain ecosystems to climate warming. In particular, the Alpine belt emerged as a habitat characterised by a peculiar fauna and by a limited number of species which are exclusive to

high altitude regions and are highly sensitive to environmental changes.

An added value of this work is the attempt to coordinate a monitoring program among different Natural Parks in the N-W Italian Alps. The results of the program indicated that each protected area, even if it covers a similar altitudinal gradient and has a similar succession of environments, has its own peculiarities in terms of community composition and it is important for conservation purposes. Precise and detailed descriptions of what is present in these protected area, considering different representative taxonomic groups, is thus fundamental to identify conservation goals, both in term of sensitive areas and representative taxa.

The strategies for research activities in mountain ecosystems should be based on the establishment of long-term monitoring programs, in different mountain regions and organised along altitudinal gradients (Becker and Bugmann 2001, Lomolino 2001, Beniston 2003). The work reported here represents a first step for the Italian Alps, creating the baseline against which to assess for future changes with a long term monitoring program that is planned to be repeated every five years.

Acknowledgements: We are grateful to the park Directors, M. Ottino, L. Castagneri, I. De Negri for funding, logistic support and data availability, and to all park wardens and students for their fundamental help during the field work. We thank the expert taxonomists G. Allegro, A. Zanetti, S. de Angelis, A. Fantoni, P. Palmi, R. Sindaco, P. Savoldelli and A. Perrone for the identification of the huge amount of collected specimens. This work was partially funded by the Project of Strategic Interest "NextData" of the Italian Ministry of Education, University and Research.

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Received September 4, 2012
Revised November 15, 2012
Accepted February 5, 2013

Supplementary Material

Appendix S1: Rarefaction curves and ratio

Appendix S2: Data Analysis

Appendix S2.1: Species vulnerability

Appendix S2.2: Variation Partitioning

Appendix S2.3: Correspondence Analysis

Appendix S3: Regression with altitude - GLM results

Appendix S4: Comparison among belt - α -diversity

Appendix S5: CA scores - Relationships with altitude

Appendix S6: Variation Partitioning applied to CCA

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