

Biodiversity gradients in the Alps: the overriding importance of elevation

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Abstract Land abandonment is causing woodland expansion and loss of open habitats in the Alps, coupled with a shift in forestry practices from coppice management to high forest. Despite such rapid large-scale changes, there has been very little investigation of the environmental predictors of biodiversity in the Alpine landscape. We assessed the richness of amphibians, reptiles and breeding birds ($n = 189$ species), used as a surrogate of biodiversity, in 58 quadrats of 100 km², located within a well surveyed area of the province of Trento (central-eastern Italian Alps). The surrogates were then related to a series of environmental variables by means of stepwise multiple regression. Depending on the surrogate analysed, species richness declined linearly or quadratically with elevation, and increased with habitat heterogeneity and the availability of grassland and arid-rocky habitats. The same results were obtained when incorporating a measure of species threat into the biodiversity estimates. Different surrogates were positively inter-correlated, probably because of a common response to the same factor, namely elevation, which was the only variable to enter all models. Such elevational gradient produced a clear biodiversity peak in low-elevation areas, generating potential conflict between efficient biodiversity conservation and economic interests linked to human development, a scenario which probably applies to many mountain regions worldwide. The current network of protected areas was quite satisfactory in terms of area covered but biased towards high-elevation areas, of high scenic beauty but relatively low in animal biodiversity value. Low-elevation reserves were small and isolated. Proposed conservation targets include the establishment of corridors increasing the connectivity of low-elevation reserves and the promotion of incentives for the extensive management of grassland, an agro-ecosystem of high historical and biological value.

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Introduction

In recent decades, the worldwide rapid loss of biodiversity has promoted new approaches to conservation, with two main emergent trends. Firstly, the traditional focus on single species conservation has been increasingly questioned and replaced with broader biodiversity-driven targets (e.g. Franklin 1993; Tucker and Evans 1997; Entwistle and Dunstone 2000). Secondly, there is increasing consensus that, for biodiversity preservation to be effective, the establishment of protected areas should be more integrated with the maintenance of hospitable environments within the unprotected matrix of managed landscapes (e.g. Shafer 1994; White et al. 1997; Norris and Pain 2002). This is especially important considering that land-use practices have been identified as the single major cause of biodiversity loss in recent years (Soulé 1991). The above cited trends have caused a high interest in databases reporting biodiversity estimates over large areas. In this context, atlas data on species distribution have become a valuable tool to derive spatial estimates of species richness (frequently employed as a surrogate of biodiversity, Purvis and Hector 2000) subsequently used for conservation planning (e.g. Boone and Krohn 2000; Wessels et al. 2000; Underhill and Gibbons 2002).

In Europe, the Alps represent a large expanse of natural and semi-natural habitats, which may function as important sources of colonizers for the surrounding intensively cultivated lowlands. Despite such strategic importance and the fact that mountain systems are generally regarded as hotspots of biodiversity (Lomolino 2001; Korner and Spehn 2003), the alpine landscape is currently going through a series of profound changes with unknown biodiversity consequences. Firstly, as in other mountainous areas of Europe, the declining profitability of agro-pastoral activities is causing widespread land abandonment, with consequent woodland expansion into previously cultivated areas (Cernusca et al. 1999) and negative impacts on species of open habitats (e.g. Laiolo et al. 2004). In particular, woodland extent is increasing through natural regeneration by 0.5–1% per year, almost exclusively at the expense of abandoned pastures (e.g. PAT 1995; Barbaro et al. 2001; CIPRA 2001; Dirnböck et al. 2003). Such change can be decomposed into two simultaneous processes: (1) at medium-low elevations, land abandonment causes the loss of grassland fields originally managed for fodder production in association with the once flourishing livestock industry, an agro-pastoral system which dates back to 6,000 years ago (Lichtenbergen 1994; Dirnböck et al. 2003); (2) at higher elevations, the rapidly declining utilization of alpine pastures for livestock rearing is causing an upward shift of the tree-line, originally lowered by human action so as to increase the surface available for grazing (Dirnböck et al. 2003). Both processes promote a temporary increase in shrub vegetation, which ultimately develops into woodland, leading to long-term loss of alpine grassland and pastures, and declines in landscape heterogeneity. Secondly, the above cited woodland expansion is accompanied by a rapid change in forestry practices. Much of the low-elevation broadleaved woodland, once managed by stool-shoot regeneration (coppice management, Matthews 1989), is being converted to high forest, a process favoured by incentives from local administrations and from the Common Agricultural Policy of the European Union (e.g. IPLA 2000). Such radical, large-scale changes impose an urgent need for investigations of their potential biodiversity impact. To date, there has been few comprehensive investigations of the potential landscape-level determinants of biodiversity in the Alpine

chain, most of the studies focusing on “restricted” groups of species in specific components of the landscape (e.g. birds in grassland habitats, Laiolo et al. 2004).

Here, we: (1) assess the richness of terrestrial vertebrate species in an area of the central-eastern Italian Alps; (2) investigate the potential environmental predictors of biodiversity level; (3) examine the inter-correlation among different biodiversity estimates; (4) assess the potential biodiversity impact of the ongoing landscape changes; (5) identify hotspots of vertebrate diversity and compare them with the location of the local reserve network; and (6) propose conservation guidelines aimed at the long-term preservation of biodiversity in the modern alpine landscape.

Methods

Study area

Vertebrate species were surveyed in a 6,300 km² plot coinciding with the administrative province of Trento, located in the central-eastern Italian Alps (45° N, 11° E, Fig. 1). Elevation of the study area ranged from 65 to 3764 m a.s.l. Thirty-one percent of the land lay below 1,000 m, twenty-eight percent at an elevation between 1,000 and 1,500 m, 22% between 1,500 and 2,000 m, 13% between 2,000 and 2,500 m, and 6% at an elevation >2,500 m. The natural tree line is at 1,800–1,900 m, but has often been lowered by human activities and sheep grazing. The landscape is characterized by intensively cultivated valley floors, mountain slopes covered by forests interspersed with sparse pastures and vineyards at lower elevation, by managed grassland at middle elevation, and by montane grassland, rocky outcrops and permanently snow-covered ground above the tree line. In particular, 52% of the area was covered by woodland, 18% by montane grassland and pastures, 6% by

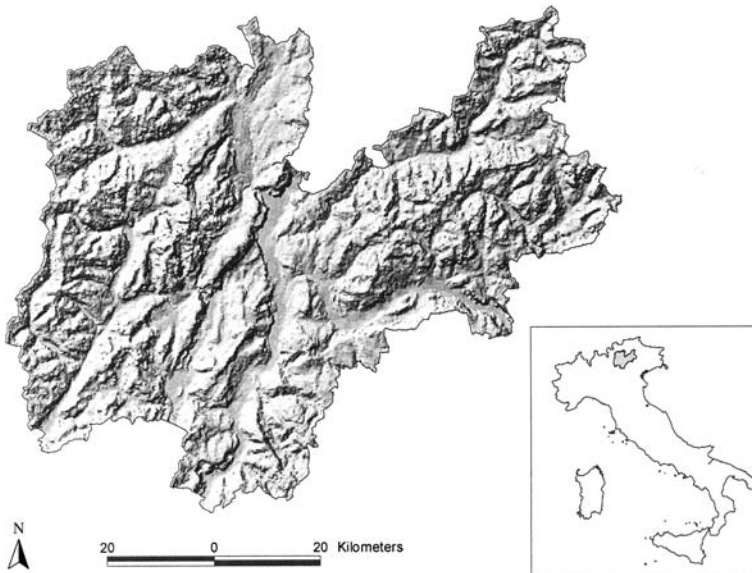


Fig. 1 Relief map of the Administrative Province of Trento. The inset shows the location of the study area in the Italian peninsula

agricultural crops (mainly vineyards and apple groves) and 3% by human development (GIS analysis on CEC 1993). Forest composition varied from deciduous to coniferous depending on elevation, slope orientation, and local microclimate. With increasing elevation, woodland tended to be dominated respectively by *Quercus pubescens*, *Quercus-Tilia-Acer* spp., *Fagus-Abies* spp., *Picea excelsa* and *Larix decidua-Pinus cembra* (PAT 1995). Eighty-two percent of the woodland area was managed for wood production; 73% of this woodland was managed as high forest and 27% as coppice (PAT 1995). The network of protected areas is composed of three large parks (Stelvio National Park, Adamello-Brenta Regional Park and Paneveggio-Pale di San Martino Natural Park) and by 65 smaller reserves (“biotopi provinciali”, PAT 1997) (Fig. 3).

Distributional data

The distribution of terrestrial vertebrate species has been recorded in the study area since 1987, as part of different atlas projects (Caldonazzi et al. 2002; Pedrini et al. 2005), and expressed as the presence-absence of each species in the 10 km × 10 km quadrats of the national 1:25000 cartography. Intensive field surveys were conducted year-round between 1987 and 1996. The data collected in this period showed that species richness increased linearly with sampling effort, reaching a plateau above 20–25 visits per quadrat. Therefore, between 1996 and 2001, under-sampled quadrats were surveyed until all quadrats had received a minimum of 25 visits. Further details on field procedures can be found in Caldonazzi et al. (2002) and Pedrini et al. (2005). For the purpose of this study, we only included in the analyses the quadrats which were included for > 85% of their surface in the study area ($n = 58$ quadrats), so as to avoid the potential sampling biases associated with area-effects (Gaston 1996a). For these 58 quadrats, none of the biodiversity estimates was significantly related to the percentage of each quadrat included in the Trento administrative province ($r = 0.16$, $P > 0.24$).

Statistical and GIS analyses

To investigate the potential effect of environmental factors on biodiversity, for each quadrat we: (1) calculated the richness of amphibian, reptile and avian species and their cumulated richness (hereafter “vertebrate richness”), and used them as surrogate measures of biodiversity (Table 1); (2) measured the environmental variables reported in Table 1 by accessing GIS land-use maps (CEC 1993; Servizio Foreste 1999) or by digitising 1 m-resolution, aerial colour-photographs (courtesy of Provincia Autonoma di Trento, “Permit IGM n.278 of 30 June 2000”); and (3) employed stepwise multiple regression with a generalised linear model procedure (GLM, Crawley 1993) to relate the biodiversity estimates to the environmental variables of Table 1. Because high species richness does not necessarily equate to high conservation priority or level of threat (Gaston 1996b), we also calculated for each quadrat the richness of bird species classified as vulnerable by Tucker and Heath (1994) (i.e. cumulative richness of species classified as SPEC 1, 2, and 3; Table 1), and employed it as a dependent variable in an additional multiple regression. No similar analysis was conducted for amphibians and reptiles because the vulnerability status of such species is less known.

In all regressions, we added to the set of explanatory variables a quadratic term for elevation (calculated on the untransformed variable), because species richness was shown to peak at intermediate elevations in some previous studies (Rahbek 1997; Brown 2001). No direct estimates of climate could be included among the explanatory variables because of a

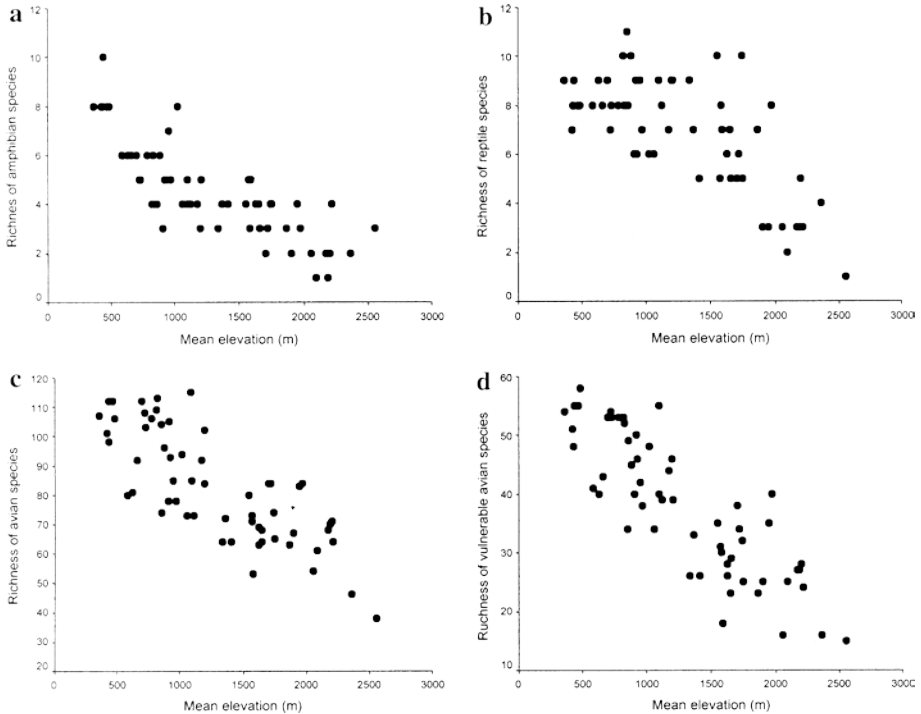


Fig. 2 Elevational decline in species richness for amphibians (a), reptiles (b), birds (c) and vulnerable birds (d)

low number of weather-recording stations with long-enough time-series, However, we assigned each quadrat to a climate-category reflecting the climatic zonation proposed by Odasso (2002) on the basis of soil characteristics and phytosociological community type (Table 1). Furthermore, climate can be adequately estimated through topographical surrogates (e.g. elevation) when: (1) the extent of the study area is relatively small; (2) climate remains relatively constant over the study area; and (3) the lapse rate of temperature with increasing elevation is constant through the study plot (Gandolfo and Sulli 1993; Austin 2002). The three conditions apply to this study.

All multiple regressions (GLMs with Poisson errors and a logarithmic link function) were built by a backward stepwise procedure following Crawley (1993): all explanatory variables were fitted to the model, extracted one at a time from such maximal model and the associated change in model deviance assessed by a χ^2 test. Overdispersion was checked following Crawley (1993). To reduce collinearity and the number of variables presented to the multivariate models, we employed a modification of the method of variable reduction proposed by Green (1979) and commonly employed in habitat selection studies (e.g. Austin et al. 1996; Sergio and Bogliani 2000; Sergio et al. 2004 and references therein). In this method, pairs of strongly intercorrelated, explanatory variables ($r > 0.6$) are considered as estimates of one underlying factor. Only one of the two is retained for analysis, usually the one considered as more biologically relevant in terms of the investigated relationship. Of the remaining variables, only those that were significantly related to the dependent variable in univariate correlations were retained as explanatory variables.

The relationship among different biodiversity surrogates was assessed by means of univariate correlations (Sokal and Rohlf 1981). To examine whether the current network of

Table 1 Biodiversity estimates and environmental variables measured at 58 quadrats of 100 km² (Trento region, central-eastern Italian Alps)

Variable	Description
<i>Biodiversity estimates</i>	
Richness of amphibians	Number of amphibian species recorded as present in the quadrat
Richness of reptiles	Number of reptile species recorded as present in the quadrat
Richness of birds	Number of bird species recorded as present in the quadrat
Richness of vertebrates	Cumulative number of amphibian, reptile and bird species in the quadrat
Richness of SPEC 1–4	Number of vulnerable ^a bird species recorded as present in the quadrat
<i>Environmental variables</i>	
Mean elevation (m)	Mean elevation within the quadrat ^b
Range of elevation (m)	Range of elevation within the quadrat ^b
Mean slope	Mean slope angle within the quadrat ^b
Mean ruggedness index	Mean of the ruggedness indices ^c of each of all the 1-km ² quadrats included within the 100-km ² quadrat
% urban	% extent of urban areas ^d
% grassland	% extent of managed grassland ^d
% alpine pastures	% extent of alpine grassland above the tree line ^d
% vineyards	% extent of vineyards ^d
% apple groves	% extent of apple groves ^d
% farmland	% extent of intensive farmland (excluding vineyards and apple groves) ^d
% arid	% extent of rocky outcrops and xerophytic vegetation ^d
% shrubs	% extent of shrubs ^d
% shrubs in evolution	% extent of shrubs evolving into woodland vegetation after land abandonment ^d
% broadleaved forest	% extent of broadleaved forests ^d
% conifer forest	% extent of conifer forests ^d
% mixed forests	% extent of mixed broadleaved and conifer forests ^d
% water	% extent of aquatic habitats ^d
% roads	% extent of the road-network ^{d,e}
% total grassland	Sum of: % grassland + % alpine pastures
% total farmland	Sum of: % vineyards + % apple groves + % farmland
% total shrubs	Sum of: % shrubs + % shrubs in evolution
% total woodland	% extent of woodland ^d
% coppice woodland	% extent of coppice-managed woodland ^f
% high forest	% extent of mature forest ^f
River length (km)	Length of rivers ^f
No. of wetlands	Number of wetlands (<0.5 ha) ^g
Habitat diversity	Shannon index of land-use diversity (Krebs 1998)
Phyto-climatic factor	Dichotomic factor discriminating between warm, dry sites on carbonatic soils (1) and other areas (2) (based on the zonation by Odasso 2002)

^a Species classified as SPEC 1, SPEC 2 or SPEC 3 by Tucker and Heath (1994)

^b Calculated from a 10 m-resolution digital elevation model

^c Number of 10-m contour lines crossed by two N–S and W–E transects of 1 km, crossing in the centre of the 1-km² quadrat

^d Recorded by accessing GIS land-use maps (CEC 1993) and, when necessary, by digitising 1 m-resolution, aerial colour-photographs

^e Assuming a 10-m buffer along all asphalted roads

^f Recorded by accessing GIS land-use maps (Servizio Foreste 1999) or by digitising 1 m-resolution, aerial colour-photographs

^g Digitised from 1 m-resolution, aerial colour-photographs

protected areas is efficient at preserving biodiversity, we: (1) defined as biodiversity hotspots the 12 quadrats in the upper quintile of the values of vertebrate richness (Harcourt 2000) and compared their distribution with the location of the main local reserves; and (2) used univariate correlations to relate the biodiversity surrogates to the percentage of each quadrat which was under some sort of protection. Means are given \pm 1 SE, tests are two-tailed, and statistical significance was set at a $\alpha = 0.05$. Prior to parametric tests, variables were logarithmically, square-root or arcsin square-root transformed as necessary in order to achieve a normal distribution or normalise the standardised residuals or multiple regressions. When multiple tests were performed on the same data set, the sequential Bonferroni correction was used to adjust the significance level (Rice 1989).

Results

Richness of amphibian, reptile and bird species

Data were available for 13 amphibian species, 12 reptile species and 164 avian species. The richness of amphibian species was only related, linearly, to elevation (Table 2a, Fig. 2a). The richness of reptile species showed a quadratic decline with increasing elevation

Table 2 Effect of environmental variables on the richness of vertebrate species recorded in 58 quadrats of 100 km² (Trento region, central-eastern Italian Alps)

Variable	Parameter estimate \pm SE	Z ²	P	% deviance explained
(a) Effect on: richness of amphibian species^a				
Mean elevation	$\hat{\beta}$ 0.051 \pm 0.004	10.31	<0.01	65.5
Constant	2.894 \pm 0.205	–	–	
(b) Effect on: richness of reptile species				
Mean elevation	0.003 \pm 0.002	1.70	>0.05	59.2
Mean elevation ²	$\hat{\beta}$ 0.002 \pm 0.000	8.10	<0.02	
Constant	7.325 \pm 1.050	–	–	
(c) Effect on: richness of bird species				
Mean elevation	$\hat{\beta}$ 0.022 \pm 0.023	0.98	>0.05	63.6
Mean elevation ²	$\hat{\beta}$ 0.015 \pm 0.001	9.10	<0.01	
Habitat diversity	1.287 \pm 0.138	8.88	<0.01	
Constant	$\hat{\beta}$ 52.63 \pm 57.53	–	–	
(d) Effect on: richness of vertebrate species^b				
Mean elevation	$\hat{\beta}$ 0.011 \pm 0.007	1.83	>0.05	75.0
Mean elevation ²	$\hat{\beta}$ 0.002 \pm 0.001	10.71	<0.01	
% total grassland ^c	0.377 \pm 0.177	5.84	<0.05	
% arid ^d	0.591 \pm 0.153	11.21	<0.001	
Constant	6.182 \pm 0.291	–	–	
(e) Effect on: richness of vulnerable bird species				
Mean elevation	$\hat{\beta}$ 0.037 \pm 0.032	3.78	<0.05	73.4
Mean elevation ²	$\hat{\beta}$ 0.025 \pm 0.011	6.48	<0.05	
% total grassland ^c	0.882 \pm 0.123	7.30	<0.02	
% arid ^c	0.812 \pm 0.224	8.32	<0.001	
Constant	7.311 \pm 0.221	–	–	

^a Variable log_e transformed

^b Cumulative richness of amphibians, reptiles and bird species

^c Variable arcsin square-root transformed

(Table 2b, Fig. 2b). The richness of bird species declined quadratically with elevation and increased with habitat heterogeneity (Table 2c, Fig. 2c). The richness of all vertebrate species showed a quadratic response to elevation and increased with the availability of grassland and arid-rocky habitats (Table 2d). The same variables entered the model with the richness of vulnerable bird species as the dependent variable (Table 2e, Fig. 2d).

Inter-correlation among biodiversity surrogates

The inter-correlation among the richness of amphibians, reptiles and birds was positive and significant in all cases ($r \geq 0.60$, $n = 58$, $P < 0.0001$). The richness of the three vertebrate classes was also positively correlated with the richness of vulnerable bird species (in all cases $r \geq 0.62$, $n = 58$, $P < 0.0001$). Finally, the richness of vulnerable bird species was positively correlated with the richness of non-vulnerable bird species ($r = 0.85$, $n = 58$, $P < 0.00001$).

Biodiversity hotspots and the protected area network

All the 12 quadrats identified as hotspots were located along the main valley floors of the region (Fig. 3), as to be expected on the basis of the results outlined above. Most of the quadrats were poorly protected (Fig. 3). The percentage of each quadrat included in any type of protected area increased with the mean elevation of the quadrat ($r = 0.37$, $n = 58$,

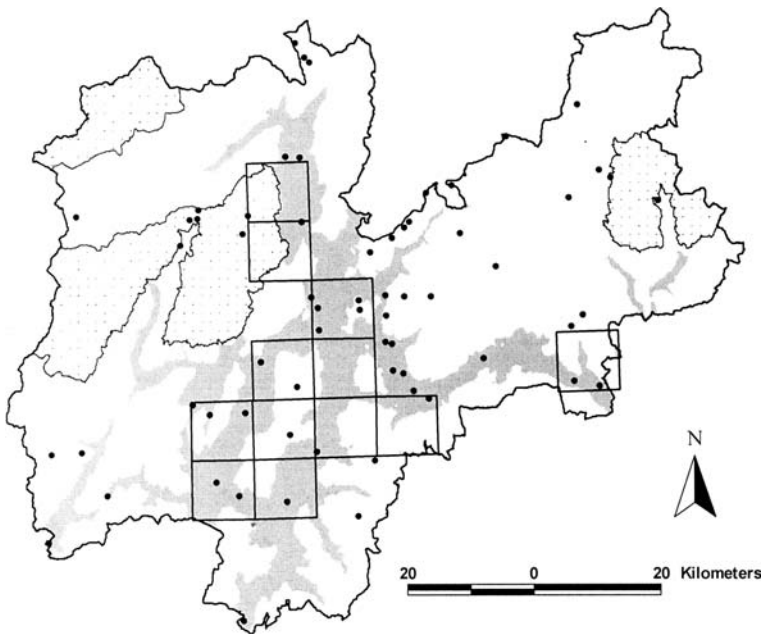


Fig. 3 Biodiversity hotspots and protected areas in the Trento region of the central-eastern Italian Alps. The stippled polygons represent the three large parks of the region (Stelvio, Adamello-Brenta and Paneveggio-Pale di San Martino), the black points represent the “biotopi provinciali” (smaller reserves). Grey patches depict areas below 800 m of elevation and the large quadrats are the 12 hotspots identified in our dataset on the basis of the cumulative richness of all vertebrate species (see Methods)

$P = 0.03$) and was negatively related to all the biodiversity surrogates (all $r < -0.18$), though only the relationship with reptiles was significant ($r = -0.33$, $n = 58$, $P = 0.05$).

Discussion

The richness of the vertebrate species employed in this study was related to elevation, habitat heterogeneity and the availability of two land-cover types. At the spatial scale analysed, topography, elevation in particular, was the single most important variable, entering all models and explaining alone a large part of the variation in species richness, as commonly reported in previous studies (review in Gaston and Williams 1996). In agreement with recent reviews (Rahbek 1997; Gaston and Williams 1996; Brown 2001), species richness declined both linearly or quadratically with elevation, depending on the taxa considered. In contrast, we did not observe the biodiversity peak at medium elevations reported by some authors (e.g. Brown 2001), the richness estimates usually declining steadily, though curvilinearly, all along the elevation gradient (Fig. 2). The biodiversity decline with increasing elevation is probably caused by three non-exclusive factors. Firstly, climate becomes progressively colder with increasing elevation, temperature usually declining at a lapse rate of $7^{\circ}\text{C}/\text{km}$ increase in elevation (Wallace and Hobbs 1977; Beniston 1994). The lower temperature at higher elevation, frequently accompanied by higher rainfall and snow cover, results in a progressively more hostile and less energy-rich environment for most species, thus promoting the decline in species richness (e.g. Boone and Krohn 2000). Secondly, the elevational biodiversity decline may be an artefact related to the three dimensional surface-decline with increasing elevation typical of mountain systems (Gaston and Williams 1996; Lomolino 2001). The increase in species richness with available area is a long recognized pattern in ecology (species-area curve, review in Rosenzweig 1995). Thirdly, the above cited larger area, more favourable climate and higher available energy at lower elevations may promote high habitat heterogeneity, which is often a direct determinant of species richness (e.g. Owen 1990; Lomolino 2001). In our study, the best explanation (climate-driven elevational decline in species richness) was supported by the fact that ectothermic species seemed to respond solely to elevation while endothermic species responded to elevation as well as to other factors.

Besides the effect of elevation, bird richness was also positively related to habitat diversity. A higher availability of different habitat types probably implies a higher number of potential niches, ultimately promoting higher species richness (Hutchings et al. 2000; Tilman 2000). A similar relationship has been reported in other previous studies (e.g. Miller 1994; review in Gaston 1996b; Hansen and Rotella 1999) and habitat diversity has even been proposed as a surrogate of biodiversity (reviews in Wessels et al. 1999; Margules and Pressey 2000; Purvis and Hector 2000).

Finally, the richness of all vertebrates and of vulnerable bird species was positively related to the availability of grassland and of arid and rocky habitats. Extensive agro-ecosystems are well known for their biological richness and many species are strictly dependent on such habitats in the Alps (e.g. Pain and Pienkowski 1997; Tucker and Evans 1997; Laiolo et al. 2004). Arid habitats are frequently located in sites with a rugged topography, scarce human access and alteration, and often show particularly warm micro-climates, thus favouring the persistence of many "Mediterranean" species typical of warmer areas (e.g. Marchesi and Sergio 2005). In a way, grassland and arid patches are frequently the main features which stand out of the regional woodland matrix, thus providing an essential contribution to landscape heterogeneity (Forman 1995).

Conservation implications

The positive inter-correlation among the different biodiversity surrogates, including those incorporating a measure of species vulnerability, simplifies any prioritisation strategy because sites with high species richness for one taxon will also show high richness for other taxa. Such spatial concordance was probably promoted by the common response of all the taxa analysed to the local elevational gradients, as confirmed by the fact that the inter-correlation among the surrogates disappeared when controlling for the effect of elevation through a partial correlation analysis (all $r < 0.17$, $P > 0.22$). On the contrary, the biodiversity peak at low elevation may generate conflict between the implementation of efficient conservation and human development, which also peaks at low elevation. In particular, the current reserve network in the Trento region is dominated by three large parks and a series of smaller “biotopi” (Fig. 3). The three parks cover almost exclusively high elevation areas (Fig. 3), while most of the biotopi-reserves coincide with low elevation wetlands, but, despite their obvious value, their size is always too small to allow the persistence of most vertebrate species (mean area = 0.51 ± 0.07 km², $n = 65$). Therefore, the system is characterized by a relatively satisfactory amount of protected land (17% of the area), but also by a bias towards the preservation of unproductive, high-elevation, biodiversity “poor” sites, a condition which typifies many developed countries (e.g. Sutherland 1998; Margules and Pressey 2000). Considering that the economic value of the lowlands for agriculture and for urban development makes the planning of large lowland reserves unrealistic, a more rewarding conservation strategy could focus on two targets: (a) utilize the biotopi-reserves as stepping stones and attempt to connect them through corridors; and (b) strive to make the unprotected matrix of the lowlands as hospitable as possible for wildlife. The above scenario is likely to be common to many mountain systems worldwide (see Hansen et al. 1999 for similar conflicts).

As for the habitat changes currently occurring in the alpine landscape, our results suggest that forest expansion per se and the conversion of coppice woodland to high forest may not be necessarily detrimental to biodiversity conservation, unless they imply a large-scale decline in landscape heterogeneity. This is in agreement with the conclusions from previous studies on various species (e.g. Sergio et al. 2003, 2005; Marchesi et al. 2006). On the contrary, the declining availability of grassland could cause long-term biodiversity declines and should be urgently tackled through subsidies for extensive farming, aimed at halting the ongoing land abandonment. In conclusion, our data provide a first, coarse-level assessment of landscape-level gradients in vertebrate species richness. Because regional-levels of biodiversity set the upper limit attainable by local communities (e.g. Cornell and Lawton 1992), this study provides a large-scale framework for more detailed future studies. For example, amphibian richness is probably better modelled at the finer-scale pond-level, so as to incorporate the effect of variables such as pond isolation, internal characteristics of the pond (e.g. underwater vegetation, fish presence) and hospitability of the habitats surrounding the pond (e.g. Ray et al. 2002; Bosch et al. 2004). Similarly, many avian and reptile species may respond to environmental factors acting at a finer-grained scale than the one employed in our analyses.

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