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**Climate and animal biodiversity: analysis of risk factors in western Alpine
protected areas**

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*A Zoe
che anche se è con noi da poco,
ha già stravolto il mio senso del tempo,
insegnandomi quali sono le cose davvero importanti...*

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Summary

Biodiversity, the variability among living organisms, beyond its intrinsic value, provides a huge quantity of ecosystem services that sustain life on earth and human society.

During the last century, decreases in biodiversity have been progressively more observed. The amount of species loss is greater now than at any time in human history, with extinctions occurring at rates hundreds of times higher than background extinction rates. This has seriously affected all biodiversity levels from genes to ecosystems and has reduced the benefits provided to human populations. Biodiversity is strictly linked to ecosystems' stability, resistance and resilience, factors that determine the ability to provide benefits.

Changes in the environment as a result of anthropogenic impacts are increasingly influencing animal and plant communities during the last decades. Major factors thought to be responsible for biodiversity modification are habitat loss, invasive species, pollution and nutrient load, overexploitation and unsustainable use and climate change.

Climate change seems to be the most serious threat especially in the ecosystems that are more vulnerable, like mountain systems. The organisms that inhabit these areas are adapted to survive at harsh conditions showing consequently high sensitivity to environmental changes.

Mountain ecosystems are considered "biodiversity hotspot" due to the huge quantity of endemic species and because they have already experienced exceptional loss of habitats and species.

As a result, alpine communities have been identified as being particularly at risk from predicted changes and alpine ecosystems are likely to show the effects of climate change earlier and more clearly than many others.

The ongoing and fast loss of alpine biodiversity underlines the need to monitor and identify the factors that influence its distribution.

In particular protected alpine areas could be suitable field station to identify conservation goals as well as to indicate the progress in conserving the world's remaining biodiversity.

In this framework take place my study that aimed to explore the relationship between animal biodiversity and climate in alpine protected areas, to evaluate the potential risk of biodiversity modification due to climatic changes.

To individuate the potential risk factors two different approaches have been adopted: a single species approach (1) to monitor the effects on population dynamic and a multi taxa approach (2) to evaluate effects of climate parameters on community structure.

In the single species approach (Chapter 2), we analyzed the effects of meteorological variability on the population dynamic of black grouse (*Tetrao tetrix*). Since this species is a habitat specialist with a large area requirement and a complex social system, it can be considered an umbrella species associated, with community complexity and so potentially an useful surrogate of biodiversity.

The Italian black grouse population has witnessed a constant decline in the last decades, similarly to most grouse populations in the western-central part of Europe. Analyzing fluctuations in population density is a key instrument to measure the effects of limiting factors on population dynamics and can provide a sound basis for conservation purposes. We investigated weather density and meteorological variables affected the growth rate and lek attendance of a black grouse population in the Orsiera-Rocciavè Park (Piedmont, Italy), in the western Alps, for the period 1991-2009. We detected a significant direct density dependence in the population growth rate of all the sub-populations in the three valleys of the Park, while we found no evidence of delayed density dependence. Population fluctuations were negatively affected by rainfall (or positively by temperature range) in early June, during the brooding-hatching period, and positively influenced by temperature range in December, likely affecting the probability of snow burrowing. The best model accounted for 82% of the variance. The proportion of solitary displaying males on the total counted males was negatively (albeit not significantly) related to male density, and was negatively affected by adverse weather conditions during late summer of the previous year (maybe preventing less experienced males to join leks in autumn and consequently in the following spring) and positively by temperature at the time of the census (as snowmelt could reduce the number of suitable areas for lekking). These results highlight the importance of climatic factors in controlling population fluctuations of black grouse. In particular rainfall during breeding and hatching period could have negative effect on population dynamic of black grouse that as ground nester, in case of heavy rainy periods could have problems with chicks or eggs survival.

The strong influence of meteorological variables in regulating the black grouse population dynamics, as revealed by this study, suggests that management actions should consider also climatic conditions.

In the multi taxa approach (Chapter 3), we described alpha and beta diversity variation of five different taxa along altitudinal gradients and analyzed the relative influence of geographical, environmental and climatic factors on biodiversity structure and community composition.

Data were collected in 2007 in three alpine parks located in N-W Italy (Gran Paradiso National Park, Orsiera-Rocciavrè Natural Park, Veglia-Devero Natural Park).

In the monitoring program, twelve altitudinal transects (from montane to alpine belt) were chosen. Each transect was composed of 4-7 sampling units separated by an altitude range of 200 meters, for a total of 69 monitored plots. In every station were collected data from 5 taxa (Lepidoptera, Aves, Staphylinidae, Carabidae, Araneae), census by standardized, repeatable and cheap methods. Each sampling station was characterized by parameters related to topography, environment (by in situ vegetation surveys) and micro-climate (by location of dataloggers). This study allows to assess the coherence in the distribution of different taxa along altitudinal gradients and the influence of geographical, environmental and climatic factors on biodiversity.

In particular the results show that gradients in species richness and in community composition are determined by altitude and microclimatic conditions. This is true for all the taxa pooled together and especially true for each invertebrates taxon while birds, as endothermic, are more related to habitat structure and composition.

The strong dependence of community composition of invertebrates on temperature suggest the potential sensitivity of these taxa to climatic variations.

Comparing species richness and community composition through vegetation belts, we observed that the alpine belt supports low values of species richness but a high percentage of endemic and vulnerable species, highlighting its importance for conservation purposes.

This kind of research can offer a representative sample of North-Western Italian Alps and it aims to be the first step of a monitoring program that is planned to be repeated every 5 years to highlight the response of alpine biodiversity to climate and land use changes.

Detailed information about biodiversity drivers and cause of vulnerability are essential, but still lacking in particular for invertebrates. Both these approaches lead to similar conclusion highlighting the influence of climatic factors on shaping alpine biodiversity patterns. In particular temperature seems to be the most important factor determining species richness and community composition of invertebrates while precipitation and temperature range play an important role in regulating the fluctuations of black grouse population dynamic. As umbrella species the black grouse presence would encompass the habitat requirements of a wide array of species from different taxonomic group, ensuring the presence of high levels of biodiversity. So, indirectly, this richness of species could suffer from climatic variability.

The dependence on weather conditions and the predicted climate change that will affect more seriously alpine areas make these ecosystems extremely vulnerable.

For all these reasons predicting species' future distributions and changes in community composition is necessary to evaluate the potential risk of biodiversity loss and to mitigate failure in ecosystem functions.

Mountain ecosystems are among the most threatened in the world because they host rare and fragile biota and they are expected to show more pronounced effects of climate change. Species distribution models represent essential tools to forecast impact of temperature changes and to develop adequate conservation strategies.

In this framework, we applied presence-only distribution models to data of species richness and community composition obtained in Chapter 3. Purpose of our work is to evaluate the effects of a moderate increase of temperature (three different scenarios) on multi-taxa distribution, described in term of alpha and beta diversity. We considered different level of environmental constraints, to compare only the effects of climate with those of other variables related to vegetation structure.

Our results show small changes in biodiversity patterns but different responses of species, depending on the taxonomic group and the degree of specialization. Models agree that changes in species richness may be particularly significant in alpine belt and particularly strong for endemic and vulnerable species. Community composition changes in a coherent way and becomes more similar to the low altitude ones. Nevertheless, the gradual but clear separation among vegetation belts is still retained after temperature increase scenarios.

Considering only temperature-related parameters, effects on biodiversity are enhanced. Moreover, we observed that minimum temperatures are more important in shaping species distribution, if compared to maximum and mean daily measurements.

Our model was able to highlight the relative role of different parameters on biodiversity patterns and to assess future vulnerability: even with a certain grade of uncertainty these predictions can be useful to assess the best conservation strategies.

Results of these approaches provide insights for future research. In particular land use changes should be considered both to analyse the effects on population dynamic of umbrella species, both to improve our predictive models in order to transfer the results even in space.

Future analysis are necessary, focused on the role of other meteorological variables, potentially important in shaping biodiversity and on the use of appropriate downscaling methodologies to hypothesize how the precipitation regime could vary in the next future.

Concerning conservation implication our results suggest that vulnerable species as well as umbrella species should be deeply monitored in the long term both for early warning signs of climate change and both as empirical tests of predictions. Moreover protected areas can be

used as a litmus test of any changes. To play this role parks need to share long term monitoring programmes that allow to measure biodiversity status (species richness, community composition and population dynamic), to underline the climatic and environmental factors that influence these patterns and to model the effects of climate and land use changes on these parameters.

Chapter 1 - Introduction

Biodiversity meanings

A definition of biodiversity that is altogether simple, comprehensive and fully operational is unlikely to be found.

Noss, 1990

The terms “biodiversity” originates from the contraction of two distinct words: biological diversity; it was born in the '80 to indicate the variability among living organisms from all sources, including, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part, It is not static, but constantly changing. A concept that emphasizes the interrelatedness of the biological world.

To obtain a broader definition we must include not only living organisms and their complex interactions, but also interactions with the abiotic (non-living) aspects of their environment.

A definition of biodiversity that is altogether simple, comprehensive and fully operational (i.e., responsive to real-life management and regulatory questions) is unlikely to be found. More useful than a definition, perhaps, would be a characterization of biodiversity that identifies the major components at several levels of organization (Noss, 1990).

To have a better understanding of what really is biodiversity we need to consider different organizational levels, all the functional aspects and also different spatial scales (Harrison et al., 2004). Moreover to delineate the multifaceted aspects of biodiversity for every levels or spatial scales we need to consider also three different dimensions: function, structure and composition (Franklin et al., 1981). The three attributes determine and in fact constitute, the biodiversity of an area. Composition has to do with the identity and variety of elements in a collection and includes species lists and measures of species diversity and genetic diversity. Structure is the physical organization or pattern of a system, from habitat complexity as measured within communities to the pattern of patches and other elements at a landscape scale. Function involves ecological and evolutionary processes, including gene flow, disturbances and nutrient cycling. (Noss, 1990). Ecosystem components, structures and functions are all interdependent.

The interactions between the individual organisms (*e.g.*, reproductive behaviour, predation, parasitism) of a population or community and their specializations for their environment (including ways in which they might modify the environment itself) are important functional aspects of biodiversity. These functional aspects can determine the diversity of different communities and ecosystems (Harrison et al., 2004) .

Organizational levels of biodiversity

Genetic diversity. This level of diversity refers to the variation of genes within species. It concerns the information represented by genes in the DNA of individual plant and animals (Wilson, 1994). It covers distinct populations of the same species or genetic variation within a populations. Each species is made up of many organisms and no two members of the same species are genetically identical. The genetic diversity enables a population to adapt to its environment and to respond to natural selection. Low values of genetic diversity means low resistance to stress factors (Lacy, 1997; Booy et al., 2000; Boulding and Hay, 2001). More individuals belong to the same population, greater the chance of genetic variation. This means for example that even if an endangered species is saved from extinction, it will probably have lost much of its internal diversity so that if that species is allowed to expand again, the new population created will be more genetically uniform than their ancestral populations. Genetic variation is the cornerstone of all biodiversity.

Species diversity. It refers to the variation in the number or phylogenetic diversity of species present in an area. World-wide more than 1.75 million species have been identified (Lecointre and Guyader, 2001) but estimates of the actual number vary from 5 million up to 100 million. This is probably the most frequently used level of biodiversity referring to species richness, the number of species occurring in a particular area or a combination of species richness and equitability, which is the degree of evenness in the species' relative abundances. Both of them are necessary to fully describe the structure and the composition of a community. Species diversity is also the most used level to indicate the total biodiversity probably because it is often positively related with diversity at other levels (Chiarucci et al., 2011; Bradshaw and Brook, 2010). So that more species richness means also more genetic diversity and more ecosystem diversity.

Ecosystem diversity. The variety of physical environments and biotic community over a landscape. An ecosystem can cover a large area, such as a whole forest, or a small area, such as a pond. The diversity of an ecosystem is dependent on the physical characteristics of the environment, the diversity of species present and the interactions that the species have with each other and with the habitat they live in. Not only the physical characteristics of an area will significantly influence the diversity of the species within a community, but also the

organisms can modify the physical characteristics of the ecosystem. This level of diversity contains also all the ecological process that affect an area.

Some definitions included also landscape diversity referring to the variation between landscape based on the different types of ecosystems they compose.

All levels are clearly connected and dependent upon the health of the others.

Spatial scales of biodiversity

Ecologists have also developed a distinction into 3 levels corresponding to different measurement scales, α , β and γ useful to characterize species diversity in a given area:

- Within-habitat diversity or alpha diversity is the diversity of organisms within a selected habitat or sample and is quantified by indices and by rank abundance models.

It refers to a group of organisms interacting and competing for the same resources or sharing the same environment (Whittaker, 1960, 1967; Fisher et al., 1943).

- Between-habitat diversity or beta diversity is an index of the rate of increase of alpha diversity as new habitats are sampled, so is a measure of the turnover of species along a spatial gradient. It refers to the response of organisms to spatial heterogeneity. High beta-diversity implies low similarity between species composition of different habitats. It is usually expressed in terms of similarity index between communities (or species turnover rate) between different habitats in same geographical area (often expressed as some kind of gradient). (Whittaker, 1960, 1967).

- Finally, geographical diversity or gamma diversity is the full diversity of an entire sampled landscape or gradient (Whittaker, 1960, 1972). The diversity of a landscapes is determined by the levels of both alpha and beta diversity, so by definition gamma diversity is a function of the alpha and beta diversity within the region. According to Hunter (2002) gamma diversity could be defined as "geographic-scale species diversity".

Alpha and gamma diversity are scalar quantities, i.e. may be represented by a single number while beta diversity is a vector with a directional component as well as a magnitude.

These three measures represent a partitioning of diversity across relative spatial scales so that a patch size that a mammal ecologist would consider to be one habitat (measuring alpha diversity) would be a mosaic of micro-habitats which a microbial ecologist might count as containing gamma diversity. Other factors can influence alpha and beta diversity such as the sample size, commonness and rarity, latitudinal or altitudinal gradients.

The spatial scales of biodiversity commonly refer to species richness, but analogues can be developed for the other organizational levels of biodiversity.

Biodiversity measures

Not everything that can be counted counts and not everything that counts can be counted

A. Einstein

Biodiversity, as a multidimensional concept, can be represented by a large variety of measures. Estimation of spatial and temporal pattern of biodiversity is an essential component both of adaptive management for nature conservation, both of the development of ecological theories. Adaptive management deals with the easy and quick quantification of effects of management intervention, e.g., reserve design, control harvest, restoring degraded habitats. This implies a first phase, estimating diversity at one point in time and in space, followed by a second phase, monitoring biodiversity, i.e., estimating diversity at the same location at more than one time period looking for changes (Wilson et al., 1996; Keith et al., 2011). General theories linked to ecological and historical explanation of biodiversity gradients are a central task in ecology and biogeography: from decades ecologists have described pattern of biodiversity, mostly using a community-based approach, looking for large pattern in group of species and trying to understand what caused them (e.g., MacArthur, 1969; Lomolino, 2001; Willig et al., 2003; Jones et al., 2011). But is not possible to look at how biodiversity is distributed, or how fast it is disappearing, without putting units on it (Purvis and Hector, 2000). As already outlined by Peet (1974), diversity is essentially defined by the indexes that measure it, but no single measure will capture all its aspects: at each level of biodiversity different units can be quantified. Consequently biodiversity studies require a clear and unambiguous classification of the subject, in order to choose the level to look into and the most appropriate metrics.

Different levels imply different measures

At the landscape level the identity, distribution and proportion of each habitat type and the distribution of species within those habitats, can be quantified. Components of landscape structure are important in shaping organisms distribution, in particular habitat area and isolation are essential elements of biodiversity (e.g., Magurran, 2004; de Bello et al., 2010).

At the ecosystem level measures of interest are the quantification of target ecosystem processes (e.g., primary production, soil formation, nutrient cycling) or properties (e.g.,

resilience, stability). Different ecosystem metrics are linked to different components of biodiversity: some services are associated with species diversity while other with the abundance of particular species (EASAC, 2005). For instance, primary productivity increases with species richness (e.g., Tilman, 2001) while ecosystem resilience and stability can be highly affected by species loss (e.g., McCann, 2000).

The species level is probably the most studied and analysed level in biodiversity assessment. Species are an obvious choice of unit when trying to measure diversity: most people have an idea what '*species*' means, many other units are less intuitive and species are also sensible units to choose from a biological perspective (Purvis and Hector, 2000).

At the genetic level, measurements of genetic and phylogenetic diversity offer a promising tool for conservation (Magurran, 2004; de Bello et al., 2010). As mentioned before (cfr. Cap1.1) genetic diversity provides information on population variability as a way to evaluate extinction risk (e.g., Vellend and Geber, 2005) and in many cases can be easily quantified in term of morphological variation. Phylogenetic diversity is measured in term of evolutionary lineages within a community: high values suggest the potential of future evolution, identifying area of high conservation interest (Magurran, 2004).

At each of the presented levels of complexity, biodiversity is characterised by three elements: variety, quantity and distribution (EASAC, 2005). Variety represents the number of different types (e.g., number of species in an area) in the level of interest. All types are assumed to be equally different and units assigned to a specific class are assumed equal. Quantity reflects how much there is of any one type, in term of numbers of entities or total biomass (e.g., population size of a species). Distribution is referred to the extent and nature of geographic spread of different types, it reflects where that attribute of biodiversity is located.

Summarizing measures

Summarizing, biodiversity can be quantified in many different ways and at many levels of biological organization, but obviously is not possible to measure exhaustively its status and trends. We are therefore required to simplify our measurements into tractable, quantifiable units that can be compared across time and space: biodiversity assessment methods must be optimized to the specific level of organization and spatial scale of interest (Chiarucci et al., 2011; de Bello et al., 2010; Bradshaw and Brook, 2010; EASAC, 2005). The simplest and perhaps easiest way to do this is to use organism-based metrics that count, in one way or another, number of '*distinct*' species: species diversity is one of the most widely adopted

measures and it is often positively related with diversity at other levels (e.g., Chiarucci et al., 2010; Bradshaw and Brook, 2010). Various indices and models have been developed to measure diversity within a community (Magurran, 2004). In general, three main categories of measures are used to assess species diversity: (1) species richness indices, which measure the number of species in a sampling unit, (2) species abundance models, which have been developed to describe the distribution of species abundances and (3) indices that are based on the proportional abundances of species such as the Shannon and Simpson indices (Magurran, 2004). The disadvantage of diversity indices is that they do not take into account the status of species, e.g., whether species are rare, endangered or even invasive (Magurran, 2004). So, even if species richness has become the ‘*common currency*’ in most biodiversity assessments, it can be complicated by adjusting for relative abundance, uniqueness, representativeness, spatial scale or evolutionary history (e.g., Bradshaw and Brook, 2010; Gaston and Spicer, 1998).

Even if bounded only at the species level, the complete diversity of a system is still impossible to determine (Margalef, 1974). However it is perfectly possible to characterise biodiversity through the use of surrogate measures and there is considerable experience worldwide in the development and application of biodiversity indicators (EASAC, 2005). Indicators, or surrogates, can estimate status and trends more efficiently, faster or at lower cost than more complete inventories: are therefore essential elements of strategies for managing biodiversity. The term indicator is used for any measurable variable that can help to estimate a particular component of biodiversity: the diversity within a reduced set of taxonomic groups is used as an indicator for the overall diversity (Noss, 1990; de Bello et al., 2010). A biodiversity indicator is a group of taxa or functional group, whose diversity can be used to make inference about the diversity of other taxa or habitat or the entire ecosystem in which they live. Moreover, in order to be useful, bioindicators should comply with *a priori* suitability criteria: easiness of sampling, cost-efficacy, taxonomic and basic ecological knowledge (Magurran and McGill, 2011). Hence, most studies limit their description of diversity (species richness and composition) only on particular, well-defined group of species, such as assemblages (i.e., group of taxonomically closely related species), guilds (i.e., groups of species within the same trophic level), communities (i.e., groups of population sharing the same habitat and interacting in various way), food webs (i.e., all the species involved in the transfer of energy, via feeding interaction in a particular area).

Biotic indicators of local diversity can be not only compositional, i.e., synthetic list of taxa and diversity indices, but even functional, i.e., referred to organismal traits that influence

ecosystem functioning (de Bello et al., 2010). Functional diversity is often measured to establish the mechanistic link between species and ecosystem functioning: differences in the way species use resources imply that they have different impacts on their environment and therefore different consequences for the functioning of ecosystem (Samways et al., 2010). The presence and abundance of a given set of functional traits (e.g., morphological, physiological and life history characteristics) may relate to the particular biodiversity level of interest and can be consequently used.

In calculating any species diversity metric, it is assumed (implicitly or not) that all of the species in a sample or dataset have been properly identified and represent comparable units; moreover sometimes the exact identification of species is not only difficult but time-consuming. Oliver and Beattie (1993) suggest an another approach: species richness of selected taxa (spiders, ants, polychaetes and mosses) could be estimated through recognizable taxonomic units (RTUs), i.e. taxa readily separated by morphological differences that are obvious to individuals with less training than professional taxonomists. They found that by using RTUs, there is little difference between classifications made by a biodiversity technician and those made by a taxonomy specialist, resulting in a considerable savings of time and money.

A further attempt of simplification in biodiversity assessment is represented by the use of limited suite of species that reflects the species richness of an entire biota (MacNally and Fleishman, 2004). In many cases, monitoring a given species indicates well the level of biodiversity (e.g., Maes and van Dyck, 2005). Target species need to be selected based on specific criteria: for example, rare species or species with red list status can be used to elucidate causes for the decline in species diversity (e.g., Duelli and Obrist, 2003). This individual/community coupling stands at the base of the concept of surrogate species (including indicator, umbrella, keystone and flagship species), that are often spatio-temporally associated with community complexity (Laiolo et al., 2011) and are considered an effective means of conservation planning.

In some cases surrogate species are effective, efficient and often the best (or only) way to proceed (Poiani et al., 2001; Brooker, 2002; Lambeck, 2002) obviously, the effectiveness should carefully assessed, both in order to verify the role of surrogate species, both to identify which mechanism are more important in determining spatially and temporal association between individual and communities performances (Laiolo et al., 2011).

Importance of biodiversity

For every third bite you take, you can thank a pollinator!

E.O. Wilson

Biodiversity has an intrinsic value because it is part of the natural world and the conservation of species, genetic resources and ecosystems is important for the maintenance of natural ecological processes. In addition, biodiversity performs a number of ecological services for humans, which implies economic, aesthetic and recreational values, representing arguments of human interest or anthropocentric arguments (Alho, 2008).

Intrinsic value

Biodiversity has an intrinsic value that is worth protecting because it has value in its own right regardless of its usefulness to humans (Callicot, 1986; Naess and Rothenberg, 1989). It is often based on considerations with respect to the autonomy, self-organization and self-directedness of nature (Callicot, 1997). In a quite philosophical sense could be identified as an inalienable right to the existence independently by economics values (Laverty et al., 2004)

This argument focuses on the conservation of all species, even if they are ecologically equivalent species because all species have an equal right to exist.

They are the product of a long history of continuing evolution by means of ecological processes and so they have the right to a continued existence. This ethical argument, stating that the protection of biological integrity is morally good, is based on the fact that most biodiversity loss nowadays is caused by human activities and disturbances, including, as a consequence, the recent extinction of species (Alho, 2008). Human responsibility toward other living things and obligations to future generations, provide strong grounds for conservation.

Anthropocentric values

It concerns all the biodiversity aspects that could be useful for human population: they can be summarized in the term Ecosystem services.

They are the direct and indirect benefits that biodiversity provides to sustain life on earth and human society (Daily, 1997; de Groot, 2002).

Biodiversity, encompassing genetic diversity, species, populations, communities and ecosystems and landscapes and regions, provides countless benefits to humans at all these

scales. It performs a number of ecological services that have economic, aesthetic or recreational value contributing to the social, economic, intellectual and spiritual development of society. Some benefits of biodiversity are represented in forms of goods that can be directly valued by the market and some are not because they are priceless.

On the basis of the need they satisfy four categories of ecosystem services are identified, also if many of these services are highly interlinked:

- provisioning, goods produced or provided by ecosystems such as food, fresh water, fuel wood, fiber, bio-chemicals, genetic resources;
- regulating, benefits obtained from regulation of ecosystem processes. climate, disease and flood controls, waste detoxification and decomposition, drought moderation;
- cultural, non-material benefits people obtain from ecosystems trough spiritual enrichment, cognitive development, reflection, recreation and aesthetic experience;
- supporting, those services that are necessary for the production of all the other ecosystem services and that maintain the conditions for life on earth. Pratical examples of these services are soil formation, nutrient and water cycling, pollination and seed dispersal, photosynthesis and primary production.

Approximately 60% (15 out of 24) of the ecosystem services evaluated in the Millennium Ecosystem Assessment are being degraded or used unsustainably. The alteration of ecosystem services often causes significant harm to human well-being and represents a loss of a natural asset or wealth of a country (MEA, 2005).

An estimated 40% of the global economy is based on biological products and processes (WEHAB, 2002) and yet these resources are being lost or severely damaged at an unprecedented rate.

Despite quite recent estimates that the Earth's ecological systems are worth about US\$33 trillion annually (Costanza et al., 1997), the comparatively low cost of maintaining the biological diversity that underpins these services is ignored (James et al.,1999). The cost and risks associated with biodiversity loss are expected to increase and to affect disproportionately populations who depend more heavily on local ecosystem services.

Link between biodiversity and ecosystem functioning

Biodiversity plays an important role in the way ecosystems function and in the services they provide: maintain biodiversity influence the key processes of ecosystem functioning.

All components of biodiversity, from genetic diversity to the spatial arrangement of landscape units, may play a role in the long-term provision of at least some ecosystem services (Diaz et al., 2006).

Each species performs an important role in maintaining a healthy ecosystem and plays a part in the cycling of materials and the transfer of energy. But the provision of tangible ecosystem services depends not only on species presence or absence but also on their abundance (Chapin et al., 2000).

Moreover also species' functional characteristics strongly affect ecosystem properties. Functional characteristics operate in a variety of contexts, including effects of dominant species, keystone species, ecological engineers and interactions among species (e.g., competition, facilitation, mutualism, disease and predation) (Hooper et al., 2005).

So, diversity could be considered a measure of the variation in species traits in an ecosystem (Tilman et al., 1997) and ecosystem processes depend on the range in those traits represented in the ecosystems (Tilman, 2001). Comprising different functional groups, the variety of species guarantees that if some species are lost others are available to fill their functional roles. Declining biodiversity simplifies ecosystems and potentially erodes this ecological insurance. If too many species or keystone species are lost, eventually it leads to the failure of ecosystem function (Estes and Duggins, 1995; Chapin et al., 2000, Hooper et al., 2005). So, functional diversity is likely to be the component of biodiversity most relevant to ecosystem functioning (Diaz and Cabido, 2001; Hooper et al., 2002; Naeem and Wright, 2003; Reich et al., 2004).

Therefore biodiversity is tightly intertwined with the ecosystem's stability and ability to withstand stress and disturbance.

As a matter of fact resilient ecosystems are characterized three distinctiveness:

- constancy that means lack of fluctuation;
- inertia or resistance to perturbation;
- renewal that means the ability to repair a damage.

Diversity leads to greater resilience and for a given ecosystem, because functionally diverse communities are more likely to adapt to changes than impoverished ones. As a matter of fact the most vulnerable systems would be the ones that are most exposed to perturbations, have limited capacity of adaptation and are least resilient (Liechenko and O'Brien, 2002).

Although it may be possible to augment or replace some ecosystem services—often at great cost, on a limited scale, or in constrained locations—the reliance of technology on functioning ecosystems often goes unrecognized (Brauman et al., 2007).

The capacity of ecosystems to provide services is determined by many human-induced factors that cause changes in an ecosystem. Direct drivers have a direct influence on ecosystem services, whereas indirect drivers operate indirectly, often by altering one of the more direct drivers (MA, 2003). The risk of biodiversity loss is evident if we continue to experience the current trend for predatory and unregulated exploitation of living natural resources (Alho, 2008).

The effects of species loss or changes in composition and the mechanisms by which the effects manifest themselves, can differ among ecosystem properties, ecosystem types and pathways of potential community change (Hooper et al., 2005).

Threats to Biodiversity

To keep every cog and wheel is the first precaution of intelligent tinkering.

A. Leopold

Extinction is a natural event and, from a geological perspective, routine, but the current extinction rates are likely occurring at 100 to 1000 times the normal background rates (Pimm, et al., 1995).

There have been five mass extinctions in the past 500 million years, the most recent about 65 million years ago (Raup and Sepkoski, 1982). Due to human actions we appear to be in the sixth in which species and ecosystems are threatened with destruction to an extent rarely seen in earth history.

Human alteration of the terrestrial biosphere has been significant for more than 8000 years. However, only in the past century has the majority of the terrestrial biosphere been transformed into intensively used lands with predominantly novel anthropogenic ecological processes. At present, even were human populations to decline substantially or use of land become far more efficient, the current global extent, duration, type and intensity of human transformation of ecosystems have already irreversibly altered the terrestrial biosphere at levels sufficient to leave an unambiguous geological record differing substantially from that of the Holocene or any prior epoch (Ellis, 2011).

Indeed, the Millennium Ecosystem Assessment (2005) reports that there has been a substantial and largely irreversible loss in the earth's biodiversity.

It's difficult to identify which are the causes of so biodiversity loss and the list of threats to the global biodiversity is quite lengthy; anyway by the Convention on Biological diversity (2010) five main threats to biodiversity are commonly recognized: habitat change, invasive

alien species, pollution and nutrient load, over-exploitation and unsustainable use and climate change. Some of them could act synergically and increase the effects on biodiversity.

Behind these direct drivers of biodiversity loss, there are a number of indirect drivers that interact in complex ways to cause human-induced changes in biodiversity. They include demographic, economic, socio-political, cultural, religious, scientific and technological factors, which influence human activities that directly impact on biodiversity.

Habitat change

This is an important cause of known extinctions (Sala et al. 2000).

Land-use changes and the associated habitat loss are a consequence of natural and human driven processes (Ojima et al., 1994; Pimm et al., 1995; Vitousek et al., 1997; Pimm and Lawton, 1998; Sanderson et al., 2002; Zebisch et al., 2004).

Habitat damage, especially the conversion of forested land to agriculture, has a long human history. The forests, for example, which have provided and continue to provide humanity with a wide range of products and services, have often been used wastefully (Hanski, 2005). For instance, by 1950 only about 30% of the Mediterranean forest biome remained and since then an additional 2.5% has been lost (Mace, 2005). Even higher rates of loss occur in the tropical biomes, where the current annual rate of forest loss is 0.6 to 0.8% (FAO, 2001). Where forest cover is not declining, such as in Northern Europe intensive forestry has turned natural forests into managed production areas. Such forests have lost most of the ecologically specialized species of animals and plants (Hanski, 2000). Also the conversion of primary forest in planted forests influence the survival of different taxa, including birds (Barlow et al., 2007a), amphibians and reptiles (Gardner, Barlow, Peres, 2007) and butterflies (Barlow et al., 2007b; Koh, 2007).

In addition to natural forests, the disappearance of wetlands has been dramatic over the last century, ranging from 60% in Denmark and Finland to 90% in Bulgaria (EEA, 2003).

Also the replacement of low-intensity farming systems, which support a high level of biodiversity (Bignal, McCracken; 1996), with industrial agroecosystems could affect ecosystems.

Finally, there are activities with significant impacts on marine ecosystems such as aquaculture (Naylor et al., 2000; Dalton, 2004), coastal engineering (habitat alteration) and past coastal habitat destruction (Airoldi, 2007)

Not only habitat loss, but also habitat fragmentation could seriously affect biodiversity. The habitat that remains generally is in small, isolated bits rather than in large, intact units and so it can sustain only small population. Environmental fluctuations, disease and other changing factors make these populations highly vulnerable to extinction.

Invasion of non-native species

Alien species introduction is an important and often-overlooked cause of extinctions. Of all documented extinctions since 1600, introduced species appear to have played a role in at least half, especially in the islands or in the more isolated areas. This phenomenon is enhanced by the domino effect that occurs when the addition of one species affects the entire biological system. Domino effects are especially likely when two or more species are highly interdependent, or when the affected species is a "keystone" species, meaning that it has strong connections to many other species.

So, a single species or functional group can strongly influence ecosystem properties (Mooney and Drake, 1986; Vitousek, 1986; Griffin et al., 1989; Vitousek and Walker, 1989; D'Antonio and Vitousek 1992; Alban and Berry, 1994; Gordon, 1998; Levine et al., 2003) and modifies ecosystem stability.

The success of alien species is due to the absence of diseases, competitors or predators that normally act as factors limiting the natural populations (Chitotti and Levi, 2001)

Pollution and nutrient load

Pollution from nutrients (nitrogen and phosphorous) and other sources is a continuing and growing threat to biodiversity in terrestrial, inland water and coastal ecosystems.

Modern industrial processes such as the burning of fossil fuels and agricultural practices, in particular the use of fertilizers, have more than doubled the quantity of reactive nitrogen - in the form that is available to stimulate plant growth - in the environment compared with pre-industrial times. In terrestrial ecosystems, the largest impact is in nutrient-poor environments, where some plants that benefit from the added nutrients out-compete many other species and cause significant changes in plant composition (CBD, 2010). Several studies concern the relation between N addition and biodiversity (Bobbink and Roelofs, 1995; Bobbink et al., 1998; Tilman, 1993; Thomas et al., 1999; Reich et al., 2001; Aerts et al., 2003, Wamelink et al., 2009) showing that a nitrogen addition leads to a biodiversity decrease. In particular,

increased N deposition results in a decrease of floristic diversity, at least in grassland and heathland communities (Aerts et al., 1990; Roem and Berendse, 2000; Stevens et al., 2004). Moreover, this threat, for many of the biodiversity hotspots (Myers et al., 2000) is expected to rise even further (Phoenix et al., 2006).

Overexploitation and unsustainable use

Overexploitation and destructive harvesting practices have brought several animal species to the brink of extinction and nowadays there has not been significant reduction in this pressure. Since prehistoric times humans have hunted wildlife for food. In more recent times hunting for food assumed less importance while poaching activities for skins, tusks or bones became more popular.

Hunting/trade activities impacted 29% of mammals, 28% of birds and 1% of plants (Hilton-Taylor, 2000) causing severe depletion in population of various species of animals including rhinos, tigers and elephants, thus making them vulnerable to extinction.

Overexploitation is the major pressure being exerted on marine ecosystems, with marine capture fisheries having quadrupled in size from the early 1950s to the mid 1990s (CBD, 2010).

The FAO estimates that more than a quarter of marine fish stocks are overexploited (19%), depleted (8%) or recovering from depletion (1%) while more than half are fully exploited.

Climate change

According to several authors climate change is the most severe problem that we are facing today (King, 2004; IPCC, 2007) and the major threat to biodiversity (Peters and Lovejoy, 1992; Thomas et al., 2004).

In almost all the scenarios delineated by IPCC climate change seems to be the major factor determining global biodiversity loss. It was estimated that 25% of the earth's species could disappear by 2050 due to global warming and habitat fragmentation (Thomas et al., 2004).

Climate change could affect biodiversity in many ways: from genetic (van Heerwaarden et al., 2009) to phenotypic evolution (Gienapp et al., 2008), from physiology (Portner and Farrell, 2008) to phenology (Roy and Sparks, 2000), from abundance (Merrill et al., 2008) to distribution (Root et al, 2003), from community composition (Tylianakis et al., 2007) to ecosystems functioning (Cramer et al., 2001). Furthermore global warming seem to affect

habitat very diverse from the sea level to the top of the highest mountains; from the desert to the polar.

There is very high confidence that a wide variety of ecological systems and taxa have changed in ways consistent with recent warming (Hughes, 2000; Walther et al., 2002; Parmesan and Yohe, 2003; Root et al., 2003; Menzel et al., 2006; Rosenzweig et al., 2007).

A surprising result is the high proportion of species responding to recent, relatively mild climate change (global average warming of 0.6°C) (Parmesan, 2006). The proportion of wild species impacted by climate change was estimated at 41% of all species (655 of 1598) (Parmesan and Yohe, 2003).

Thus, additional climate changes are likely to adversely affect many more species and ecosystems as global mean temperatures continue to increase. Each additional degree of warming increases disruption of ecosystems and loss of species. Individual ecosystems and species often have different specific thresholds of change in temperature, precipitation or other variables, beyond which they are at risk of disruption or extinction. Looking across the many ecosystems and thousands of species at risk of climate change, a continuum of increasing risk of loss of ecosystems and species emerges in the literature as the magnitude of climate change increases, although individual confidence levels will vary and are difficult to assess (Schneider et al., 2007).

Every single species can be expected to react in a unique way to climate change and thus no species will be affected in the same way as other species. Furthermore the effects of climate change on single species can lead to changes in all levels of biodiversity ranging from the genetic level to single species to communities to ecosystems. For many species, the primary impact of climate change may be mediated through effects on synchrony with that species' food and habitat resources. This potential mismatch between the life cycles of predators and their prey, herbivorous insects and their host plants, parasitoids and their host insects and insect pollinators with flowering plants is more crucial than any absolute change in timing of a single species (Harrington et al. 1999, Visser and Both, 2005; Parmesan, 2006).

As a result of mismatches, range shifts, invasion of alien species and so on ecosystems show new interaction in novel communities but not always this "new ecosystems" can act as the old providing all the benefits human need.

Alpine environment

Climb the mountains and get their good tidings. Nature's peace will flow into you as sunshine flows into trees.
J. Muir

A biodiversity hotspot

The Alps span eight countries, from the Mediterranean shores of Southern France to Slovenia, covering an area of about 200 000 km² are the most important mountain chain in Central Europe.

They exhibit an impressive variety of habitat and climatic conditions along reduced spatial scales, reflecting a complex physical history and have a long history of human presence and exploitation (Chemini and Rizzoli, 2003)

This complexity leads to a rich diversity of nature and landscape, which offers living place to a large number of plants and animals. They host about 30.000 animal species and 13000 plant species representing one of the most important regions for the preservation of biodiversity in central Europe (Theurillat et al., 2003).

A large part of the biodiversity of the Alps is therefore linked to artificial or semi-natural environments and to traditional land-use (Chemini and Rizzoli, 2003) that have shaped mountain ecosystems.

Recent changes in land-use systems have lead to intensification of exploitation in some areas and abandonment of traditional practices in other areas with serious effects on local biodiversity (Dirbonck et al., 2003; Laiolo et al., 2004; Martin and Possingham, 2005).

Because of the huge quantity of endemic species (Theurillat, 1995; Korner, 2002) and because they experience exceptional loss of habitat and species (Pauli et al., 2007) Alps are considered "biodiversity hotspot" (Myers, 1998; Ginsberg, 1999; Myers et al., 2000).

High mountain ecosystems are determined by low temperatures and are therefore considered to react sensitively to climate warming (Körner et al., 2005; IPCC 2007a,b; Pauli et al., 2007). They contains organisms highly specialised and that live close to the limits of their physiological tolerances showing consequently harsh sensitivity to environmental change.

As a result, alpine communities have been identified as being particularly at risk from predicted changes in climate (Grabherr et al., 2000; Walther et al., 2005) and alpine ecosystems are likely to show the effects of climate change earlier and more clearly than some other ecosystems (Grabherr et al., 2000; Pauli et al., 2004; Pickering et al., 2008).

Climate in the Alps

Mountain climates are governed by four major factors: continentality, latitude, altitude and topography (Barry, 1994; Beniston, 2006).

Climate variability in the Alps was influenced by North Atlantic weather systems, the Mediterranean Sea and the large Eurasian land (Wanner et al., 1997; Böhm et al., 2001; Beniston and Jungo, 2002; Begert et al., 2005; Auer et al., 2005). The North Atlantic Oscillation is the dominant climate mode for Europe and the Alps are situated in a band between northern and southern Europe, where the forcing of the NAO is amplified with distance north and south of the Alpine area (Beniston et al., 1994; Beniston and Jungo, 2002; Casty et al., 2005).

In addition to the influences of global climate change, which could affect both precipitation and temperature, regional effects can be particularly important in the mountain systems.

In these systems, snow cover and duration are a major controlling factor but the principal determinants of snow are temperature and precipitation; so climate changes, modifying temperature distributions and precipitation patterns, strongly influence snow amount and duration (Beniston et al., 2003). Comparing the global increase in temperatures of 0.7 °C observed during last century (Jones and Moberg, 2003) the temperature in the European Alps has increased since the late 19th century by 1.1–1.3 °C (Böhm et al., 2001). Long-term records provide evidence for an ongoing climate warming in mountain environments (Beniston, 2006) and in the Alps (Calmanti et al., 2007; Auer, 2007; Rebetez and Reinhard, 2008; Keiler et al., 2010). Moreover temperature and snow cover patterns are predicted to change seriously in the next future for alpine regions around the world (Hennessy et al., 2003; Pauli et al., 2007; IPCC, 2007). Regional studies of climatic change in Switzerland (Marinucci et al., 1995; Beniston et al., 1996; Rotach et al., 1996) suggest that Alpine temperatures could rise by as much as 3°C by 2050, with possibly increased precipitation in winter but a substantial decrease in summer (Beniston et al., 2003).

Any substantial changes in the mountain snowpack would have a significant impact on the flow of many major river basins, not only because of changes in the amount and timing of runoff, but also because of the potential for enhanced flooding, erosion and associated natural hazards (Beniston, 2006). These environmental changes are also resulting in the disappearance of glaciers: since 1850, 40% of the surface area of glaciers in the Alps and over 50% of their volume have disappeared as a result of climatic change (Haeberli, 1990).

Effects of climate change on Alpine biodiversity

Numerous studies provide evidence for the alpine biodiversity response to these changes.

In particular the vegetation at high altitudes seems to be particularly responsive because abiotic factors, especially climate, dominate over biotic factors (Beniston et al., 1996; Theurillat and Guisan, 2001).

As a matter of fact upward moving of alpine plants has occurred (Grabherr et al., 1994; Pauli et al., 2001), advances of treelines was well documented for several European mountain systems (Meshinev et al., 2000; Kullman, 2003; Moiseev and Shiyatov, 2003,) as well as for the Alps (Gherig-Fasel et al., 2007). As a result community composition has changed at high alpine sites (Keller et al., 2003) with an accelerating increase of species richness (Walther et al., 2005; Vittoz et al., 2006; Pauli et al., 2007).

But the enhance of species richness is presumably transitory (Theurillat and Guisan, 2001) because the decline of arctic-alpine species that go out of their distribution range will reduce alpine biodiversity (Lesica and McCune, 2004).

Moreover the timing of snow melt is strictly linked to the vegetation cycles of many alpine species (Keller and Körner, 2003) so, not surprisingly, flowering phenology has been advanced (Inouye and Wielgolaski, 2003) in the last years with possible consequences on pollinators due to mismatches.

More surprisingly earlier snowmelt has increased the frequency of frost damage to montane plants, with the loss of new growth on conifer trees, of fruits on some plants and of flower buds of other wildflowers (Inouye, 2007).

Less studies have investigated the effects of climate change on alpine fauna and the majority have focused on single taxon of invertebrates.

Some species of butterflies have risen their lower elevational limits of 7.0 m per decade responding to a 1.3 °C rise in mean annual temperature (Wilson et al., 2005; Ashton et al., 2009) and a recent altitudinal range expansion of 110-230 m upwards was found in 30 years for the pine processionary moth (Battisti et al., 2005).

Furthermore age of glacier retreat have already influenced spider species assemblages in the Alps of Northern Italy (Gobbi et al., 2006).

Changing in the vegetation and habitat characteristics of alpine environments could restrict taxa to progressively narrower alpine zones at the summit of mountains (Chapin and Körner, 1989). The reaction of any species to climate change depends on the position and breadth of the climatic niche of the species and the corresponding geographic position and the size of the

species range. Species restricted to cool will suffer most (Settele et al, 2008). Some butterflies change their phenology with a reduction of niche overlap with their host plant (Schweiger et al., 2008) and consequent disruption of the trophic interactions.

If glacial retreats continue, the species of arthropods tied to such environments will be at risk from habitat loss and, consequently, at risk from extinction (Gobbi, 2006).

Role of Alpine protected areas in conserving biodiversity

Protected areas are recognized as the most important core ‘units’ for *in situ* conservation and they are a valid, measurable indicator of progress in conserving the world's remaining biodiversity, or at least slowing the rate of loss (Chape et al., 2005).

Precise and detailed description of what is present in a protected area, referred to different taxonomic groups, selected as representative, is fundamental to identify conservation goals, both in term of ‘*sensitive areas*’ and ‘*representative taxa*’ (Hannah et al. 2002).

Behind the really significant contribute to the conservation that alpine protected areas offer ensuring a refuge for wildlife, their importance go over.

These areas include a large number of sites that are relatively not stressed by other factors and so the impact of global warming can be more readily and easily studied. Moreover the personal working there can carry out long-term monitoring activities offering their experience of linkage with the area investigated.

Finally the network of the alpine protected areas ensure the possibility to compare results obtained in different areas to gain a more comprehensive understanding of patterns of diversity and to validate the predicted biological effects of climate change.

Objectives and approach

Research goals

In our study we aimed to explore the link between animal biodiversity and climate in alpine protected areas in order to evaluate the potential risk of biodiversity modification in relation to climatic changes.

To individuate the potential risk factors two different approaches have been taken: single species approach (1) to monitor the effects on population dynamic and multi taxa approach (2) to evaluate effects of climate parameters on community structure.

Chapter 3 analyse the effects of climate parameters on the population dynamic of a single species that can potentially act as surrogate of biodiversity.

We choose black grouse (*Tetrao tetrix*) because in the Alps it is affected by many threats (Arlettaz et al., 2007; Patthey et al., 2008) and also because it is a species with narrow ecological needs and that could be considered an indicator of the health status of the entire ecosystem (Storch, 2007).

In particular in chapter 2, with a multi taxa approach, we describe alpha and beta diversity variation along altitudinal gradients analysing the relative influence of geographical, environmental and climatic factors on biodiversity structure and community composition.

The comparative study of species ecology along altitudinal or latitudinal transects/gradients may provide clues to the likely response of both species and communities to climate change at any one point over time (Hodkinson, 2005). Despite this, variation in diversity along altitudinal gradients is not well documented, specially comparing different taxa and different areas with standardized methods (Lomolino, 2001).

Moreover in order to evaluate the potential risk of biodiversity modification in relation to climatic and environmental changes in Chapter 4 we try to simulate the effect of temperature increase on species richness and community composition. The purpose is to predict in the short time and to validate the models obtained with field data collecting every five years.

Reliable predictions of the

likely effects of climate change on biodiversity are extremely useful for identifying the most robust and effective conservation strategies.

Chapter 5 include general conclusions and make recommendations for future research directions.

Data source

For the multi taxa approach data have been collected from 2007 until up to now in three different alpine protected areas (Gran Paradiso National Park, Orsiera Regional park and Veglia Devero Regional park) but for the preliminary analysis we use only one year (2007). Data of single species approach came only from one protected area where the temporal series, starting from 1991 until 2009, is longer than in the other parks and consequently more useful to analyse population dynamic relationship with climate parameters.

Concerning climate variables for the multi taxa approach microclimatic conditions of each sampling station were taken out by data loggers able to record air temperature every hour for all the field season.

The meteo-climatic data used for the single species approach came from stations that are part of the dense network of automatic meteorological stations managed by the Regional Agency for Environmental Protection (ARPA) of Piedmont, Italy.

Relevance of this study for biodiversity conservation

Results of this project have an immediate importance in terms of better knowledge of the biodiversity of the protected areas and in order to assess the risks factors for alpine biodiversity. Furthermore the individuation of the most sensitive habitat could be extremely useful in terms of planning and management choosing the areas that must be left free of any intervention and areas that could be modified without too much biodiversity loss. Indeed the research become more and more important as soon as there will be some repeated measures that allow to analyse biodiversity modification, to quantify the potential risk of biodiversity loss and to assess the right management strategies for protected areas. Moreover with caution due to the limitation of the predictive models they can be used not to guide, but as support in conservation and management decisions.

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Chapter 2 - Population dynamics of black grouse (*Tetrao tetrix*) in the western Italian Alps: climatic control and role of non-lekking males

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Abstract

The Italian black grouse population has witnessed a constant decline in the last decades, similarly to most grouse populations in the western-central part of Europe. Analyzing population density fluctuations is a key instrument to measure the effects of limiting factors on population dynamics and can provide a sound basis for conservation purposes. We investigated weather density and meteorological variables affected the growth rate and lek attendance of a black grouse population in the Orsiera-Rocciavre Park (Piedmont, Italy), in the western Alps, for the period 1991-2009. We detected a significant direct density dependence in the population growth rate of all the sub-populations in the three valleys of the Park, while we found no evidence of delayed density dependence. Population fluctuations were negatively affected by rainfall (or positively by temperature range) in early June, during the brooding-hatching period, and positively influenced by temperature range in December, likely affecting the probability of snow burrowing. The best model accounted for 82% of the variance. The proportion of solitary displaying males on the total counted males was negatively (albeit not significantly) related to male density, and was negatively affected by adverse weather conditions during late summer of the previous year (maybe preventing less experienced males to join leks in autumn and consequently in the following spring) and positively by temperature at the time of the census (as snowmelt could reduce the number of suitable areas for lekking). The strong influence of meteorological variables in regulating the black grouse population dynamics, as revealed by this study, suggests that management actions should consider also climatic conditions.

Keywords: Displaying cocks census, climate forcing, chicks survival, snow burrows, mating strategy

Introduction

The black grouse or blackgame (*Tetrao tetrix*) is a large bird in the family of tetraonids, that lives sedentarily in various parts of Eurasia. In Italy, the black grouse is found all over the Alps and it is hunted besides natural parks and nature reserves. The Italian population was recently estimated to be about 20.000-24.000 individuals in spring (Brichetti and Fracasso 2004) with a constant decline in the last 30 years, similarly to most grouse populations in the western-central part of Europe (Storch 2007).

In the Alps, the black grouse is considered an edge-species that prefers the ecotone between mountain forests with shrubs and the adjacent grassland vegetation. Owing to these specific environmental preferences and to the habit of spending most of the time during the winter in snow burrows where metabolic energy consumption is reduced (Marjakangas 1992), the alpine grouse populations are particularly threatened by habitat modification and disturbance through recreation, especially by winter outdoor activities which force the grouse to leave their hollows (Arlettaz et al. 2007, Patthey et al. 2008). Since the black grouse is a habitat specialist with a large area requirement and a complex social system, it can be considered as an umbrella species for timberline habitat (Angelstam et al. 2000, Kolb 2000, Storch 2007).

To understand the dynamics of these populations and estimate their fate in coming decades, a quantitative assessment of the main driving factors must be gained. Analyzing population density fluctuations is a key instrument to measure the effects of limiting factors on population dynamics and it is a central issue in theoretical and applied ecology (Ranta et al. 1998). Knowledge of the main factors driving population fluctuations can provide a sound basis for conservation purposes, for example by protecting the areas which are used in the most sensible periods for the species, or by considering environmental variations when planning management actions.

The effect of climate fluctuations on black grouse populations can be quite significant. In precocial birds, key-factors for population dynamics are related to losses during the breeding season, likely due to density-independent factors (Sæther et al. 1996). Black grouse chicks mortality is highest during the first 2 weeks after hatch, caused primarily by predation and exposure (see Hannon and Martin 2006 for a review). Owing to the inability to fully thermoregulate until they are 8–10 days old (Boggs et al. 1977), the young chicks are very

susceptible to cold and humidity. Inclement weather may also reduce availability of insects and foraging time, resulting in poor chick growth (Erikstad and Andersen, 1983), and may increase susceptibility to predation. Thus, the effect of weather conditions on survival seems to be particularly strong during the critical post-hatch period (Sæther et al. 2004).

Several studies underline the substantial effect of weather on the population dynamics of the “lowland populations” of black grouse, showing a negative effect of rain, and secondarily of lower temperatures, during the brooding and hatching periods (Loneux et al. 2003). Similar trends were found on the productivity of black grouse in Scotland (Summers et al. 2004) while the poor breeding success over the last 25 years of capercaillie (*Tetrao urogallus*), again in Scotland, seems to be linked to the delayed warming of temperatures in April (Moss et al. 2001). Data on black grouse’s leks from central Finland show that the onset of breeding and subsequent hatching is temperature dependent (Ludwig et al. 2006).

The effects of climatic conditions may differ geographically, according to altitudinal or latitudinal gradients (Sæther et al. 2004) and in mountain areas the influence of weather conditions could be stronger due to the larger and more extreme climate variability. Snowmelt and snow depth seem to be the most important regulating factors of the breeding success of rock ptarmigan (*Lagopus muta*) in the Pyrenees (Novoa et al., 2007) and white-tailed ptarmigan (*Lagopus leucurus*) in the Sierra Nevada (Clarke and Johnson 1992) while milder winter temperature negatively affect white-tailed ptarmigan in Colorado (Wang et al. 2002). This latter result was obtained also for different lowland black grouse populations in Europe (Loneux et al. 2000). Other, less significant, climatic effects on black grouse population dynamics are represented by the negative influence of high summer temperatures in Norway, through the effect on bilberry plants (Selås et al. 2011), and of autumn-winter total rainfall in Belgium (Loneux et al. 2003).

Less is known about the alpine black grouse populations, despite the fact that they inhabit one of the southernmost areas of the species range and are therefore more likely to be vulnerable to changes in global climate. Some observations in the canton of Grisons (Switzerland) suggest that long-term living conditions in winter are the key-factor for the dynamics of this alpine population (Matter 1985).

The aim of this paper is to investigate which factors affect the population growth rate of a black grouse population in the Orsiera-Rocciavrè Park (Piedmont, Italy), in the western Alps, whose displaying cocks were counted every spring in the period 1991-2009. Black grouse cocks, in fact, gather in spring in open areas (leks) where they play a very distinctive and well-recorded courtship ritual. Young birds are likely to be absent at the lek and tend to sing solitarily (Sutherland 1996).

Besides density dependence, we studied the effect of meteorological variables (precipitation, minimum and maximum temperature, and temperature range – a variable rarely considered in studies on animal population dynamics) averaged over 1-week, 15-days and 1-month. We also examined whether density or meteorological variables affect lek attendance (i.e. the proportion of solitary displaying males on the total counted males) and we discuss how this feature can influence, in turn, population dynamics.

Materials and Methods

Study area

The present study was carried out in the Orsiera-Rocciavrè Regional Park (Fig. 1), a natural protected area located in the western Alps (around 44°75'N - 6°90'E), with a surface of 11,000 ha and including three different valleys: Chisone, Sangone and Susa, with an elevation range from 1,000 to 2,880 meters a.m.s.l. In the park, hunting is forbidden. Outside the park, hunting of black grouse is allowed but severely regulated.

In this area, vegetation changes according to altitude and exposure: the montane belt is characterised mostly by the presence of beech (*Fagus Sylvatica*) and silver fir (*Abies alba*) in the northern part of the Park, while in the southern area (Val Chisone) the scots pine (*Pinus sylvestris*) dominates. At higher altitudes, independent of exposure, the vegetation distribution is dominated by the presence of larch (*Larix decidua*) and it is patched by shrubs (*Alnus viridis*, *Vaccinium myrtillus*, *Rhododendrum rhododendrum*). Higher up, the environment becomes the typical high-elevation mixture of rocks and grassland. The extension of permanent glaciers is rather limited in the park area.

Census methodology and black grouse data

Since 1991, singing black grouse cocks at the Orsiera-Rocciavrè park have been censused in spring, between the end of April and mid May, over a network of thirty sample areas (Fig.1), each covering about one hundred hectares (mean=103.75 ha; st.dev=41.40 ha). Each sample area was completely covered with transects or with fixed points, in order to count both the males singing in leks and the others males singing in the surroundings. Each census was carried out during a given morning, and all transects and fixed points were covered by park wardens or technical staff in radio contact with each other to avoid double counts.

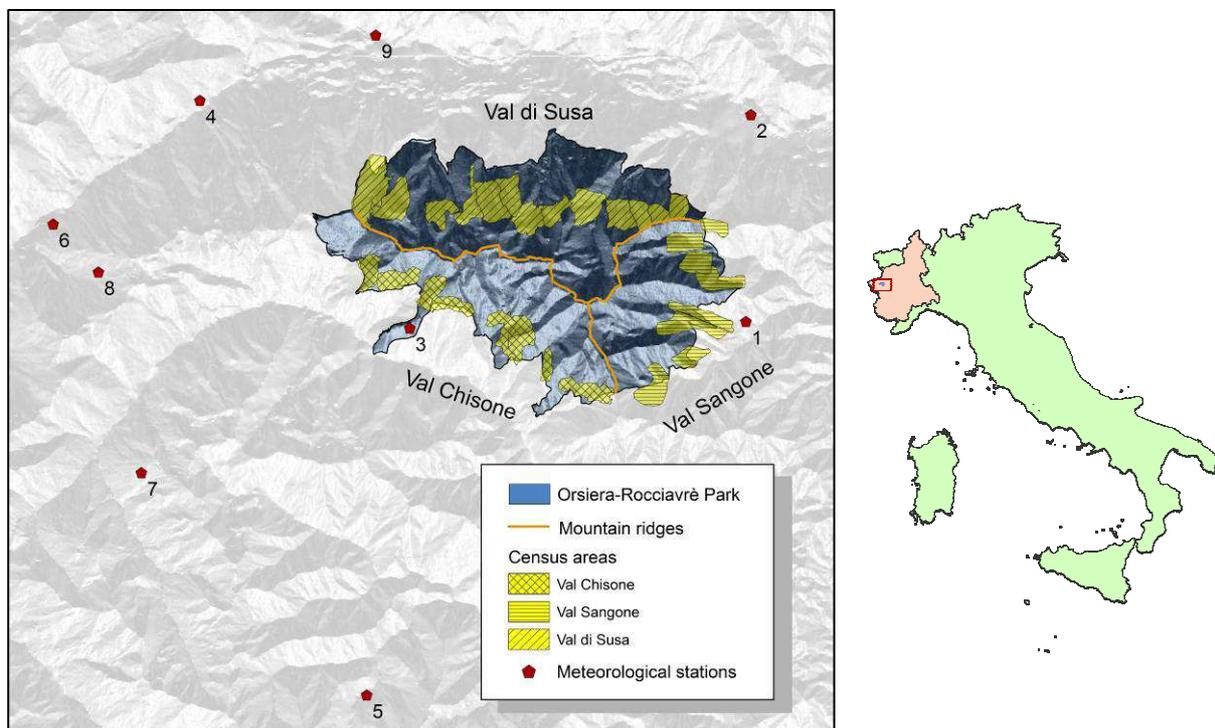


Figure 1. Study area: on the left, the Orsiera-Rocciavrè Park with census areas and meteorological stations (1-Coazze, 2-Borgone, 3-Pra Catinat, 4-Finiere, 5-Prali, 6-Graviere, 7-Pragelato, 8-Le Selle, 9-Pietrastretta); on the right, the position of the Park in the Piedmont region, Italy

Each valley and each sample area was censused twice every year, with about a week of delay between the two censuses. The largest count for each valley and each area was then kept as the annual count. The total area covered during the spring census was about 3,112.50 ha, corresponding to the 76% of the potential area (5,075.73 ha) of black grouse presence obtained from a suitability model (Viterbi R., unpublished data).

The census data included the number of leks (operationally, we define a lek as an area where at least two males sing at a distance of less than 50 meters), the number of males per lek, N_L , the number of solitary males, N_S , and the number of females, N_F . From these data, we obtained the number of males, $N=N_L+N_S$, and the fraction of males who were singing alone, $S=N_S/(N_L+N_S)$. The number of females was not considered in the analysis as the census methodology did not provide reliable information on the number of females. All data were recorded on a grid map with a sample unit of 2.5 ha. The male density was then computed as the total number of males divided by the census area. Fig. 2 shows the male density and the ratio of single males to total males, S , for the three valleys and for the total area of the park. Notice that the largest density was achieved in the Susa valley, while in the Sangone valley the black grouse density was generally lowest.

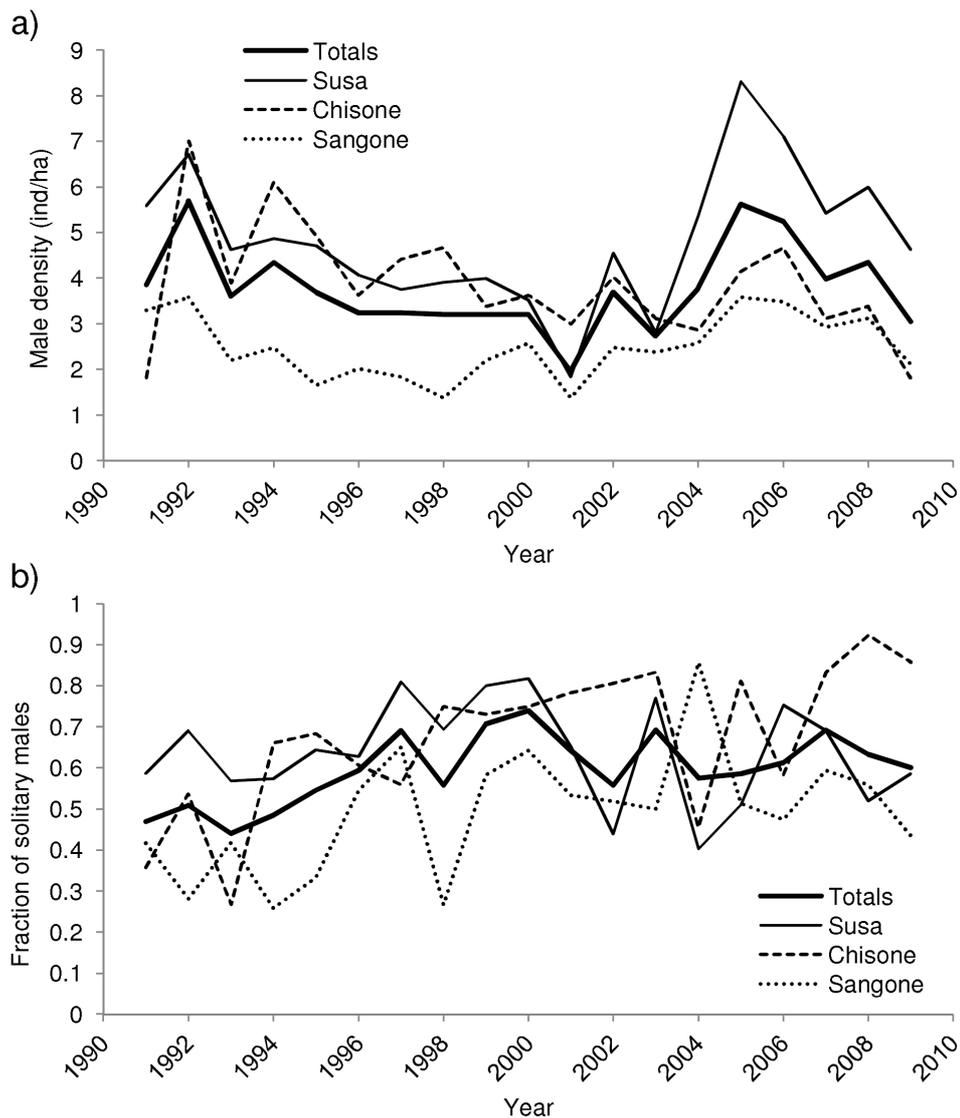


Figure 2. Density of black grouse males from spring counts (a) and ratio of males singing alone to total males (b), for the whole Orsiera-Rocciavrè park (Totals, bold solid curve) and for the three valleys of Susa, Chisone and Sangone.

No significant linear trend was detected in the density of the black grouse populations in any of the valleys or in the whole park. The strongest (albeit non-significant) trend was found in Chisone valley, where the population decline was 0.097 males/ha/yr ($p=0.07$). By contrast, the fraction of males singing alone displayed a significant growing trend with in the park totals (0.008/year, $p=0.01$), in Chisone valley (0.021/year, $p=0.001$), and in Sangone valley (0.012/year, $p=0.04$). In the Susa valley, the trend was not significant.

Meteoclimatic data

The meteoclimatic data used in this study were the maximum and minimum daily temperatures, T_{\max} and T_{\min} , and the daily cumulated precipitation, P , provided by 9 meteorological stations in the area of the park and in the immediate surroundings (Fig.1) from November 1990 to October 2009. These gauges are part of the dense network of automatic meteorological stations managed by the Regional Agency for Environmental Protection (ARPA) of Piedmont, Italy. From the maximum and minimum temperatures, we also obtained the value of the daily mean temperature, $T_{\text{mean}} = (T_{\max} + T_{\min})/2$, and the daily temperature range, $T_{\text{int}} = T_{\max} - T_{\min}$.

The correlation between daily values from any two stations of the ensemble was always larger than 0.88 for maximum temperature, 0.82 for minimum temperature and 0.67 for daily precipitation. When averaged over longer time scales (one week, two weeks or one month) the correlations became even larger. Given these high correlations, in the analysis we used the average of the standardized measurements over all stations, i.e., we used

$$C_j = \frac{1}{N_j} \sum_j \frac{C_{j,s} - \bar{C}_s}{\sigma_s} \quad (1)$$

where $C_{j,s}$ is the value of a climatic variable (T_{\max} , T_{\min} , T_{mean} , T_{int} or P) on day j and for station s , \bar{C}_s is the average of $C_{j,s}$ over the whole time period 1991-2009 for the station s , σ_s is the standard deviation and C_j is the average of the standardized values of the climate variable on day j . On each day, the average was performed on the number of stations N_j which were active on that day.

Meteorological fluctuations on daily scale are characterized by high variability and presumably are of limited relevance for the population dynamics of black grouse. For this reason and to avoid the effects of the high-frequency meteorological variability, in the following analysis we aggregated the daily values of meteoclimatic variables over 1-week, 15-days and 1-month averages.

During the study period, maximum and minimum daily temperatures displayed a weakly significant linear growing trend (for the annual averages, $p=0.10$ for T_{\min} and $p=0.09$ for T_{\max}) and precipitation showed a decreasing, albeit non-significant, linear trend ($p=0.13$). Analysis of monthly data indicated a significant, growing linear trend for minimum and maximum temperatures in June ($p=0.02$ and $p<0.01$ respectively) and an increase of minimum temperatures in October ($p=0.04$). The other monthly-averaged meteorological variables did not display a significant trend.

Some of the climatic variables considered here were correlated with each other. In particular, the 2-weeks averages for minimum and maximum temperatures were highly correlated with each other and with the mean temperature (the cross correlation of T_{\min} and T_{\max} never went below 0.81 and most of the time it was larger than 0.9). Interestingly, precipitation and the daily temperature range displayed a significant negative correlation with each other, especially in spring and fall, as shown in Fig. 3. This negative correlation is presumably related to the properties of the local radiation balance: when the sky is overcast and rain is recorded, during night the temperatures stays higher than in clear conditions, while daytime temperatures stay a little lower.

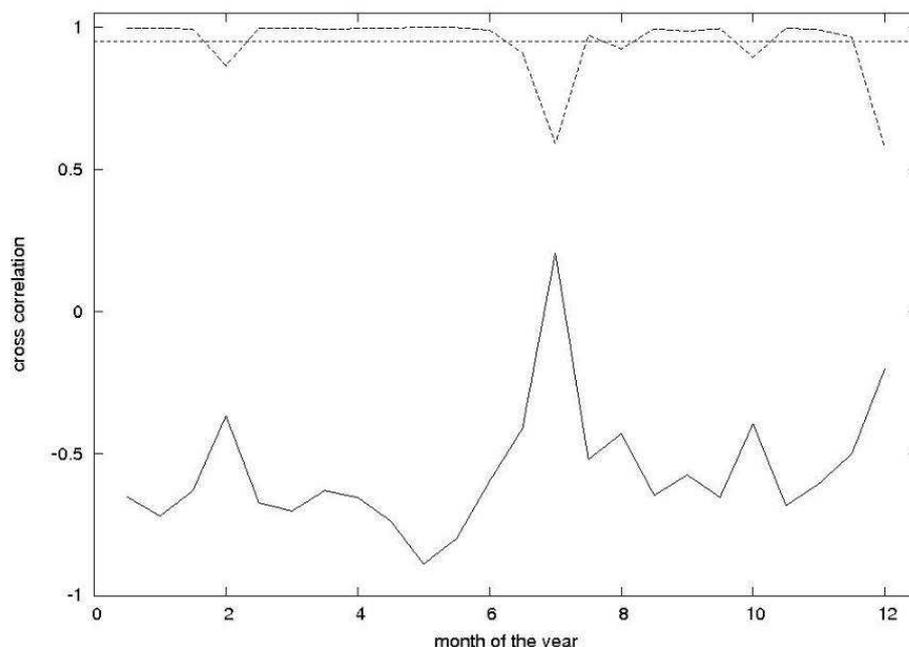


Figure 3. Cross-correlation between daily precipitation and daily temperature range, for the 15-days averaged data. The solid curve is the cross-correlation, the dashed curve represents the probability that the cross correlation is non-zero and the horizontal dotted line is the 95% confidence level.

Analysis methods

First we tested for direct and delayed density dependence (hereafter DD). To this end, we considered both the census data collected separately in the three valleys and the averages in the whole Park area, and focused on the total male population density and on the ratio of the number of males singing alone to the total number of males. To analyze population fluctuations, we define the annual relative increment, $y_t = \log(N_t / N_{t-1})$ where N_t is the population density in year t . The high values of the cross-correlations for y_t (see Tab. S1 in Supplementary materials) indicate a significant degree of coherence in the total population fluctuations in the different valleys, suggesting that some global factor could control, at least in part, black grouse population fluctuations in this area. By contrast, the logarithm of the ratio of the number of males singing alone to that of total males ($\log S_t$) did not display any significant correlation between different valleys (Tab. S1).

Table S1. Cross correlations of the population growth rate, y_t , and of the logarithm of the fraction of males singing alone, $\log S_t$ (in square brackets), between different valleys and between individual valleys and totals, for the Black Grouse population in the Orsiera-Rocciavrè Park, Piedmont (Italy). In round brackets, the probability that the corresponding cross correlation is zero.

	Susa	Chisone	Sangone
Totals	0.93 (<0.0001) [0.49 (0.03)]	0.73 (0.001) [0.66 (0.002)]	0.78 (<0.0001) [0.62 (0.004)]
Susa		0.47 (0.05) [0.14 (0.56)]	0.69 (0.001) [-0.11 (0.65)]
Chisone			0.41 (0.09) [0.08 (0.76)]

As explanatory variable, we used either the population density N_{t-j} (stochastic Ricker DD) or its logarithm, $X_{t-j} = \text{Log } N_{t-j}$ (stochastic Gompertz DD), in year $t-j$. The delay j is varied from $j=1$ (direct dependence on the previous year's population) to $j=4$. For direct DD, we tested also for models that included both a linear and a quadratic term.

To detect the effect of climate on the population dynamics of black grouse, we first tested the univariate contribution of each variable to the population growth rate, using the 1-week, 15-days and 1-month averages of meteorological variables of the whole year $t-1$, and those of the period January-April of year t (before the second census). With a similar approach we tested

the effect of meteo-climatic variables (from January of previous year, $t-1$, to April of the census year t) on the fraction of males singing alone.

For both DD and univariate tests for climatic control, we used a randomization technique to verify whether the regression coefficient was significantly different from zero (Jacobson et al. 2004). We generated a large number of surrogated data sets by shuffling the values of the explanatory variable while the dependent variable remained in the original order. We then compared the observed value of the b parameter in the least-square-fit with the distribution of b values obtained by the surrogate data set, rejecting the null hypothesis when less than 5% of the surrogate b values were equal or larger than the observed regression coefficient.

We next explored the joint effects of density dependence and climate control on the black grouse population at the Orsiera-Rocciavrè Park. We considered the bivariate regression of y_t versus a model containing a linear DD term (either of the Ricker or Gompertz type) and one meteo-climatic variable, with and without interaction between terms in the form $N_t C_t$ or $X_t C_t$ where C_t is a selected climatic variable. Finally, we built empirical stochastic models that included direct DD (on N or X) and the dependence on two meteo-climatic variables. This additive, stochastic, climate-driven Ricker model is written as

$$y_t = a + bN_{t-1} + cC_1 + dC_2 + \sigma W_t \equiv Y_t + \sigma W_t \quad (2)$$

and similarly for the Gompertz case. Here a , b , c and d are the parameters to be estimated, C_1 and C_2 are the selected climatic variables (at time $t-1$ or t), and W_t is a gaussian, zero-mean, temporally uncorrelated random variable.

In all regressions, we estimated the 95% confidence bounds on the regression parameters, to verify whether they include zero, and tested the characteristics of the model residuals. In particular, we tested whether the residuals, defined as $R_t = y_t - Y_t$ where Y_t is the deterministic part of the model, are Gaussian, have zero mean and are temporally uncorrelated. To this end, we used the REGRESS multivariate regression routine in MATLAB (ver. 7.4), which provided the fraction of outliers in the residuals (i.e., a residual whose expected distribution did not include zero at the 95% confidence level, called “outlier” in the following), and the fraction of the elements of the temporal autocorrelation function (ACF) of the residuals whose

absolute value exceeded the limit $\pm 1.96/\sqrt{N_{cor}}$ (where N_{cor} is the number of data points used in computing the ACF (called “excess” in the following)).

As a further test, we also estimated the explained variance for each model, defined as $R^2 = 1 - \sigma^2 / \sigma_{TOT}^2$ where σ^2 is the variance of the residuals and σ_{TOT}^2 is the variance of the measured values of y_t . To weight the model performance by the number of free parameters, for each model we also computed the value of the AIC parameter with finite sample correction (AICc, Burnham and Anderson 2002).

To validate the selected regression models and test their predictive ability, we used the “leave-one-out” cross validation (Michaelsen 1987), a kind of out-of-sample prediction which is particularly useful when the available time series of the predictand data is not very long. With this technique, models are repeatedly estimated using data sets of $n-1$ years, each time omitting one observation from the data set and using the estimated model to generate a predicted value for the discarded observation. At the end of this procedure, a time series of n predictions is compared with the observed predictand to compute validation statistics of model accuracy and error.

As a performance parameter, we used the sum of squares of validation error, which is the difference of the observed and predicted values. Allen (1974) called this validation statistic “PRESS”, acronym for “predicted residual sum of squares”:

$$PRESS = \sum_{i=1}^{n_v} (y_i - \hat{y}_{(i)})^2 \quad (3)$$

where n_v is the number of validation years (equivalent to the time series length in this case), and the notation (i) indicates that data for year i were not used in fitting the model that generated the prediction $\hat{y}_{(i)}$.

The root-mean-squared error of validation, $RMSE_v = \sqrt{PRESS / n_v}$

is a measure of the size of the prediction error in the original units of the predictant, whose calibration equivalent is the standard error of the estimate, s_e . The lower is the value of this parameter (and the difference between RMSE_v and s_e), the better the model is verified.

Finally, we calculated the Coefficient of efficiency (CE), conceived by Nash and Sutcliffe (1970) for hydrological modeling and defined as:

$$\text{CE} = 1 - \frac{\sum_{i=1}^{n_v} (y_i - \hat{y}_{(i)})^2}{\sum_{i=1}^{n_v} (y_i - \bar{y}_c)^2} \quad (4)$$

where \bar{y}_c is the calibration-period mean of the predictant. This measure (equivalent to the “Reduction of error” statistics elaborated by Fritts 1976) ranges from $-\infty$ to 1. A CE of 1 indicates perfect prediction (validation error = 0), while a value of 0 is reached when the square of the differences between measured and estimated values is as large as the variability in the measured data. Any positive value is accepted as evidence of a non-null prediction skill.

Results

Density dependence

The results of the analysis for density dependence in the population fluctuations (Tab. S2 in Supplementary materials, Fig. 4) indicate that there was a significant direct DD (at the 95% confidence level) in all valleys. The variance explained by density dependence was about 35% for the total population, and became as high as 56% for Chisone valley. In general, when only monivariate density dependence is considered, Gompertz-like models provided slightly better results than Ricker-like models. For direct DD, in most cases the residuals could not be considered to be temporally uncorrelated as the excess of the residual ACF values was higher than 5%. Only in the case of the Chisone valley, the residuals were uncorrelated. In all cases at least one residual was an outlier, i.e., its expected distribution did not include zero and thus the residual distribution was not fully compatible with a gaussian zero-mean distribution.

Table S2. Results from direct density dependence tests for the Black Grouse population growth rate in the Orsiera-Rocciavè Park, for the stochastic Ricker model (N) and the stochastic Gompertz model (X).

Column 1: valley; column 2: type of model (N for Ricker, X for Gompertz); columns 3: value of the DD exponent b (linear DD) and of the exponents b_1 and b_2 (squared DD, in brackets); columns 4 and 5: 95% lower and upper confidence limits on the value of b , b_1 and b_2 ; column 6: p value (obtained from random shuffling for linear DD); column 7: explained variance; column 8: AICc value; column 9: fraction of outliers in the residuals; column 10: fraction of ACF values that exceed the limit $\pm 1.96/\sqrt{N_{cor}}$. The values obtained from a density dependence model containing also a quadratic term are given in brackets.

See materials and methods of the manuscript for other explanations on statistical analyses.

	Type	b	b_{min}	b_{max}	p	R^2	AICc	Outliers	Excess
Totals	N	-0.18 (-0.62 ; 0.05)	-0.32 (-1.56 ; -0.06)	-0.04 (0.33 ; 0.17)	0.01 (0.04)	0.31 (0.35)	-43.9 (-42.1)	0.06 (0.06)	0.08 (0.08)
	X	-0.71 (-1.89 ; 0.46)	-1.23 (-5.31 ; -0.87)	-0.20 (1.54 ; 1.80)	0.01 (0.03)	0.35 (0.37)	-45.0 (-42.7)	0.11 (0.06)	0.08 (0.08)
Susa	N	-0.11 (-0.54 ; 0.04)	-0.23 (-1.08 ; -0.01)	0.0 (0.0 ; 0.09)	0.04 (0.04)	0.21 (0.34)	-34.1 (-34.5)	0.11 (0.11)	0.03 (0.25)
	X	-0.60 (-2.60 ; 0.72)	-1.08 (-5.07 ; -0.15)	-0.12 (-0.13 ; 1.59)	0.02 (0.02)	0.30 (0.42)	-36.4 (-36.8)	0.06 (0.11)	0.06 (0.25)
Chisone	N	-0.25 (-1.00 ; 0.08)	-0.40 (-1.71 ; 0.01)	-0.10 (-0.29 ; 0.16)	0.002 (0.001)	0.45 (0.59)	-34.0 (-36.4)	0.11 (0.06)	0.0 (0.0)
	X	-1.13 (-3.66 ; 0.97)	-1.66 (-6.33 ; -0.03)	-0.60 (-1.00 ; 1.97)	<0.001 (0.001)	0.56 (0.66)	-38.3 (-40.0)	0.11 (0.11)	0.0 (0.0)
Sangone	N	-0.24 (-1.22 ; 0.19)	-0.45 (-2.72 ; -0.10)	-0.04 (0.28 ; 0.49)	0.02 (0.03)	0.28 (0.36)	-41.3 (-40.6)	0.06 (0.0)	0.08 (0.25)
	X	-0.62 (-2.08 ; 0.90)	-1.09 (-4.61 ; -0.63)	-0.15 (0.45 ; 2.42)	0.01 (0.02)	0.32 (0.39)	-42.5 (-41.4)	0.06 (0.0)	0.08 (0.25)

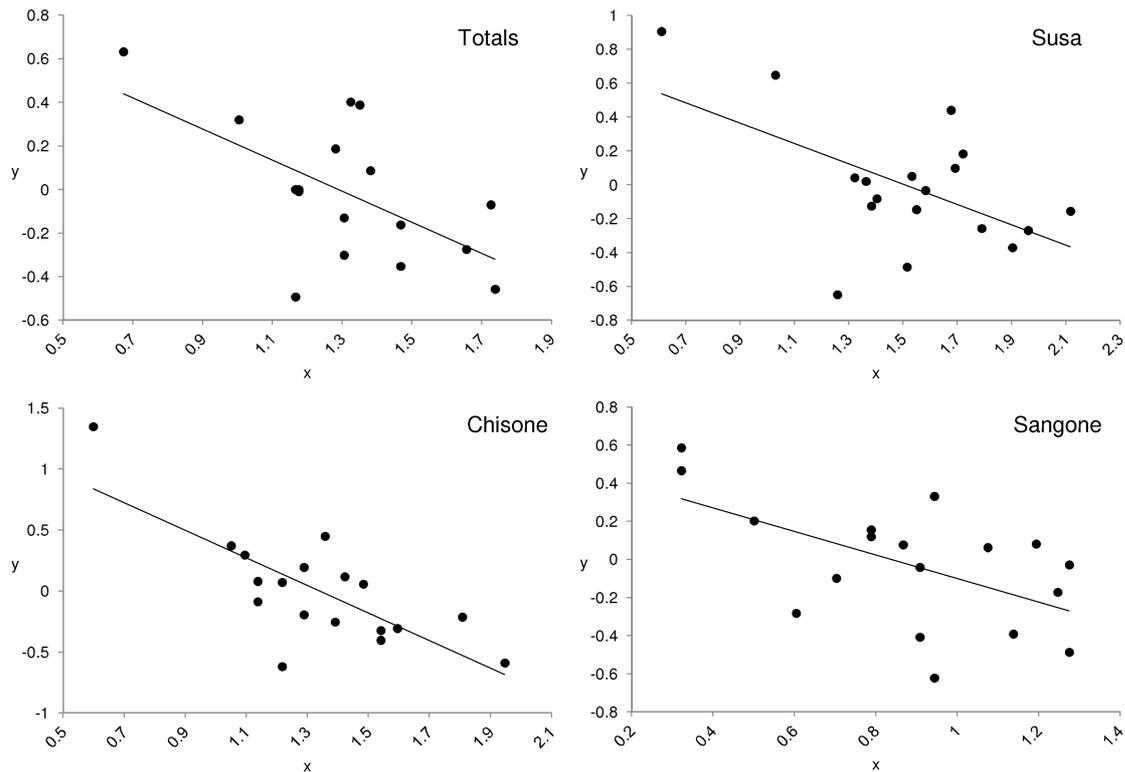


Figure 4. Dependence of the population log-increment, y_t , on the logarithm of density of the first census, X_{t-1} , for the total population of the Orsiera-Rocciavrè park (upper left panel) and for the valleys of Susa (upper right), Chisone (lower left) and Sangone (lower right).

The results for delayed DD, not reported here, indicated that the p value (from shuffling) never went below 5%, i.e., we did not detect any evidence for a significant delayed density dependence.

Testing for a model that includes both a linear and quadratic term in the direct DD resulted in an increase of the explained variance, with mixed results from the AICc (Tab. S2). While the quadratic models for the total population did not perform better (in AIC sense) than linear models, for the individual Susa and Chisone valleys the AICc value was slightly decreased by the inclusion of a quadratic term. For a quadratic model, the residuals appeared to have larger temporal autocorrelation (see the results for the Susa and Sangone valleys).

The values of detrended data on males singing alone (that is, $D_t = \log S_t - (A + B t)$, where t is the year and A and B are the parameters of a linear fit of $\log S_t$ versus time) on the whole Park area, were negatively and nearly significantly related to the density ($p=0.07$) or its logarithm ($p=0.06$) in the year of the census, while they did not display any significant dependence on density in any of the previous three years.

Climatic control

In the following, we report the results for the 15-days averages, which provided a good compromise between the need for filtering out short-term meteorological noise and the importance of keeping a sufficient temporal resolution. The results obtained by using 1-week and 1-month averages (not shown) are very similar.

The total time series of population fluctuations displayed significant positive dependence on the daily temperature range in the first half of June and on the daily temperature range in December of the previous year (with a larger explained variance for the conditions in the first half of December) (Fig. 5; see also Tab. S3 in Supplementary materials). Owing to the strong negative correlation between daily temperature range and precipitation in June, there was also a significant negative dependence of population fluctuations on precipitation in the first half of June. We detected also a weaker dependence on the maximum temperature in the first half of June of the previous year and on the maximum temperature in the first half of April on year t . For the individual valleys, the strongest dependences paralleled those found for the total counts, with some variations from one valley to another owing to local climatic characteristics: for example, the dependence on spring precipitation (or, equivalently, on the daily temperature range) was anticipated to the second half of May on year $t-1$ in the southernmost Chisone valley. In most cases, however, there were outliers in the residuals and more than 5% of the residual ACF were larger than the correlation threshold.

Table S3 - Results from the analysis of univariate meteorological effects on Black Grouse population growth rate in the Orsiera-Rocciavrè Park. Only significant ($p < 0.05$) effects are showed.

Column 1: valley; column 2: meteorological variable (P: precipitation, T_{min} and T_{max} : minimum and maximum temperature; T_{int} : temperature range); column 3: 2-week period, (1) means the first half of the month, (2) the second half and the subscripts $t-1$ and t indicate that is a month in the year of the first and second census, respectively; column 4: value of the exponent c ; columns 5 and 6: 95% lower and upper limits on the value of c ; column 7: p value; column 8: explained variance; column 9: AICc value; column 10: fraction of outliers in the residuals; column 11: fraction of ACF values that exceed the limit $\pm 1.96/\sqrt{N_{cor}}$.

See materials and methods of the manuscript for other explanations on meteorological variables and statistical analyses.

	Variable	Period	c	c_{min}	c_{max}	p	R^2	AICc	Outliers	Excess
Totals	T_{max}	June $_{t-1}$ (1)	0.59	0.04	1.15	0.038	0.24	-42.2	0.11	0.42
	T_{int}	June $_{t-1}$ (1)	0.67	0.25	1.01	0.004	0.41	-46.8	0.06	0.17
	P	June $_{t-1}$ (1)	-0.45	-0.77	-0.12	0.011	0.34	-44.8	0.11	0.17
	T_{int}	Dec $_{t-1}$ (1)	0.55	0.20	0.91	0.004	0.40	-46.6	0.06	0.33
	T_{int}	Dec $_{t-1}$ (2)	0.58	0.18	1.00	0.008	0.37	-45.4	0.0	0.33
	T_{max}	April $_t$ (1)	-0.55	-1.02	-0.07	0.028	0.27	-42.8	0.0	0.42
Susa	T_{int}	June $_{t-1}$ (1)	0.81	0.28	1.34	0.005	0.40	-38.9	0.11	0.33
	P	June $_{t-1}$ (1)	-0.50	-0.92	-0.08	0.023	0.28	-35.8	0.06	0.42
	T_{min}	August $_{t-1}$ (1)	0.93	0.21	1.66	0.015	0.32	-36.7	0.06	0.25
	T_{max}	August $_{t-1}$ (1)	0.77	0.17	1.36	0.014	0.32	-36.8	0.06	0.42
	T_{mean}	August $_{t-1}$ (1)	0.82	0.18	1.46	0.015	0.32	-36.7	0.06	0.42
	T_{min}	October $_{t-1}$ (1)	1.04	0.09	1.98	0.034	0.25	-35.0	0.0	0.33
	T_{int}	Dec $_{t-1}$ (1)	0.63	0.18	1.09	0.009	0.35	-37.7	0.06	0.58
	T_{int}	Dec $_{t-1}$ (2)	0.58	0.03	1.13	0.039	0.24	-34.8	0.11	0.58
Chisone	T_{int}	March $_{t-1}$ (1)	-1.21	-2.16	-0.26	0.016	0.31	-30.1	0.06	0.0
	P	March $_{t-1}$ (1)	1.09	0.57	1.61	<0.001	0.55	-37.7	0.06	0.17
	P	March $_{t-1}$ (2)	1.28	0.35	2.20	0.010	0.35	-31.1	0.06	0.0
	T_{min}	May $_{t-1}$ (1)	-1.26	-2.23	-0.29	0.014	0.32	-30.3	0.06	0.0
	T_{max}	May $_{t-1}$ (1)	-1.02	-1.87	-0.18	0.021	0.29	-29.6	0.06	0.08
	T_{mean}	May $_{t-1}$ (1)	-1.21	-2.16	-0.26	0.016	0.31	-30.1	0.06	0.0
	T_{int}	May $_{t-1}$ (2)	0.81	0.29	1.34	0.005	0.40	-32.6	0.06	0.0
	T_{int}	Dec $_{t-1}$ (1)	0.73	0.17	1.28	0.014	0.32	-31.2	0.06	0.0
	T_{int}	Dec $_{t-1}$ (2)	0.98	0.43	1.53	0.002	0.47	-34.7	0.06	0.0
	T_{max}	April $_t$ (1)	-0.74	-1.46	-0.02	0.045	0.23	-28.0	0.06	0.0
	T_{int}	April $_t$ (2)	0.82	0.11	1.52	0.026	0.27	-29.1	0.06	0.0
	Sangone	T_{int}	June $_{t-1}$ (1)	0.67	0.23	1.14	0.005	0.39	-44.4	0.11
P		June $_{t-1}$ (1)	-0.38	-0.76	-0.01	0.044	0.23	-40.1	0.11	0.08
T_{int}		June $_{t-1}$ (2)	0.80	0.18	1.42	0.014	0.32	-42.4	0.06	0.25

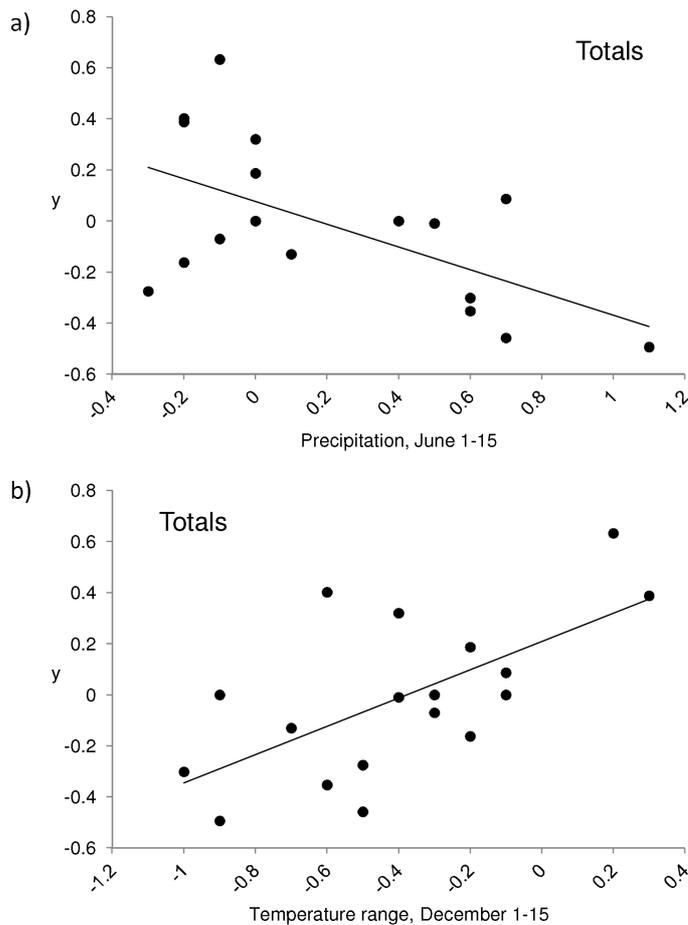


Figure 5. Dependence of the population log-increment, y_t , on precipitation in the first half of June (a) and on the daily temperature range in the first half of December (b) on year $t-1$, for the total population of the Orsiera-Rocciavè park. Meteorological variables were standardized and then averaged over the whole set of nine stations and over 15-days periods.

The negative dependence of y_t on precipitation and the positive dependence on the daily temperature range in early June presumably described the same effect, owing to the strong negative correlation between precipitation and daily temperature range during spring months. However, the dependence on the daily temperature range in December was presumably generated by a different effect, as the mutual correlation between T_{int} in the first half of June and T_{int} in the first half of December was low ($r=0.28$, $p=0.25$) and the explained variance of the bivariate fit of the total series on both variables (0.63) was much larger than that associated with a model where the variables are taken individually (0.41 for either variable). Thus, these climatic factors presumably affected the population dynamics in different ways. However, also in the case of a model including both climatic effects, there were outlier

residuals (frequency of outlier residuals: 0.06) and the residuals cannot be considered to be uncorrelated (excess of the residual ACF values: 0.25).

The fraction of males singing alone displayed significant dependence on some meteorological variables, although the picture that emerged in this case was less coherent than for population fluctuations (see Supplementary material, Tab. S4). In the whole Park area, the (detrended) fraction of males singing alone, D_t , displayed a significant ($p < 0.05$) positive correlation with the amount of rainfall in the first half of August in the year preceding the census (i.e., year $t-1$). A positive dependence on precipitation in the first half of August, together with a negative dependence on temperature in the whole month, was detected also in the Susa valley, while in Chisone the negative dependence on temperature was anticipated to the second half of July. This implies that colder and wetter conditions in late summer tended to induce a larger fraction of lone singers in the following spring. In addition, all valleys displayed a positive dependence on temperature in the first half of May of the census year (t), i.e., on the weather condition at the time of the census, and the total time series is also negatively affected by the precipitation in April of the same year.

Table S4 - Results from the analysis of univariate meteorological effects on detrended fraction of Black Grouse males singing alone (the residuals $D_t = \log S_t - (A + B t)$, where t is the year and A and B are the parameters of a linear fit of $\log S_t$ versus time) in the Orsiera-Rocciavè Park, Piedmont (Italy). Only significant ($p < 0.05$) effects are showed.

The definition of variables and statistics is the same as in Tab. S3.

	Variable	Period	c	c_{min}	c_{max}	p	R^2	AICc	Outliers	Excess
Totals	P	August _{t-1} (1)	0.29	0.02	0.56	0.036	0.25	-95.1	0.06	0.25
	T _{int}	August _{t-1} (1)	-0.13	-0.25	-0.002	0.047	0.22	-94.6	0.0	0.08
	P	April _t (1)	-0.11	-0.21	-0.01	0.029	0.26	-95.5	0.06	0.25
	T _{int}	April _t (1)	0.07	0.004	0.15	0.041	0.24	-94.9	0.06	0.33
	T _{min}	May _t (1)	0.21	0.02	0.40	0.034	0.25	-95.2	0.06	0.0
Susà	P	August _{t-1} (1)	0.49	0.02	0.95	0.041	0.24	-75.7	0.0	0.33
	T _{min}	August _{t-1} (1)	-0.26	-0.51	-0.02	0.038	0.24	-75.8	0.06	0.33
	T _{max}	August _{t-1} (1)	-0.26	-0.44	-0.07	0.010	0.35	-78.5	0.11	0.42
	T _{mean}	August _{t-1} (1)	-0.27	-0.47	-0.06	0.014	0.32	-77.9	0.06	0.50
	T _{int}	August _{t-1} (1)	-0.23	-0.44	-0.03	0.027	0.27	-76.5	0.0	0.25
	T _{min}	August _{t-1} (2)	-0.36	-0.66	-0.06	0.020	0.29	-77.0	0.0	0.33
	T _{max}	August _{t-1} (2)	-0.32	-0.56	-0.08	0.012	0.33	-78.1	0.0	0.25
	T _{mean}	August _{t-1} (2)	-0.35	-0.66	-0.05	0.026	0.27	-76.6	0.0	0.58
	T _{int}	August _{t-1} (2)	-0.26	-0.50	-0.02	0.036	0.25	-75.9	0.06	0.33
	T _{int}	Sept _{t-1} (1)	-0.19	-0.33	-0.04	0.014	0.32	-77.8	0.0	0.25
	T _{min}	May _t (1)	0.44	0.14	0.74	0.007	0.38	-79.3	0.11	0.17
	T _{max}	May _t (1)	0.28	0.04	0.52	0.027	0.27	-76.5	0.0	0.33
	T _{mean}	May _t (1)	0.33	0.04	0.63	0.028	0.27	-76.4	0.06	0.25
Chisone	T _{min}	Feb _{t-1} (2)	0.17	0.01	0.32	0.034	0.25	-73.4	0.11	0.0
	T _{mean}	Feb _{t-1} (2)	0.16	0.01	0.32	0.043	0.23	-72.9	0.11	0.0
	P	May _{t-1} (1)	0.13	<0.01	0.26	0.049	0.22	-72.7	0.06	0.08
	T _{min}	July _{t-1} (2)	-0.32	-0.64	-0.01	0.044	0.23	-72.9	0.06	0.08
	T _{mean}	July _{t-1} (2)	-0.32	-0.63	<0.01	0.050	0.22	-72.6	0.06	0.0
	T _{int}	August _{t-1} (1)	-0.23	-0.46	-0.01	0.042	0.23	-73.0	0.06	0.0
	P	Dec _{t-1} (1)	-0.25	-0.44	-0.05	0.017	0.31	-74.8	0.11	0.0
	T _{min}	May _t (1)	0.48	0.17	0.80	0.005	0.39	-77.2	0.06	0.08
	T _{max}	May _t (1)	0.30	0.05	0.56	0.024	0.28	-74.1	0.11	0.17
	T _{mean}	May _t (1)	0.40	0.09	0.70	0.014	0.32	-75.2	0.06	0.08
Sangone	T _{max}	June _{t-1} (1)	0.26	0.02	0.50	0.033	0.25	-72.5	0.0	0.17
	T _{max}	May _t (1)	-0.28	-0.55	-0.01	0.044	0.23	-72.0	0.0	0.17
	T _{int}	May _t (1)	-0.22	-0.44	-0.01	0.043	0.23	-72.0	0.06	0.17

Interplay of density dependence and climate in population fluctuations

Tab. 1 reports the results of the bivariate regressions (y_n versus a linear DD term and one meteorological variable, aggregated over all stations and the 15-days period) for the four valleys. For simplicity, we report only those cases which have both an explained variance larger than 60% (except for the Sangone valley where we show also the first two models with $E < 0.6$) and a AICc value that is lower than the smallest between the AICc values obtained from the univariate (linear or quadratic) DD or the corresponding univariate meteorological dependence.

In the bivariate fits, the most important meteorological variables turned out to be the precipitation in the first half of June and the daily temperature range in December. For the total time series, the model containing density dependence and precipitation in the first half of June explained about 68% of the variance, and had the lowest AICc value. The two explanatory variables, N (or X) and early June precipitation (all on year $t-1$) were uncorrelated with each other ($r_N=0.01$, $p=0.96$; $r_X=0.04$, $p=0.85$). The model with a Gompertz-like DD performed slightly better in terms of explained variance, but the model with a Ricker-like DD scored better in terms of reducing residual correlation. The models including the daily temperature range in the first half of June (which performed better when taken as a univariate dependence) explain less variance than those including precipitation. Models that included DD and the daily temperature range in the first or second half of December of the previous year also explained more than 60% of the variance; however, they had a high fraction of the residual ACF components that exceeded the correlation limit (correlation between variables, first half Dec: $r_N=-0.13$, $p=0.61$; $r_X=-0.19$, $p=0.46$; second half Dec: $r_N=-0.02$, $p=0.94$; $r_X=-0.10$, $p=0.70$). In general, the results for the individual valleys were consistent with those obtained for the total time series, except for the fact that in Sangone valley, in the first half of June daily temperature range provides a slightly better fit than precipitation.

Table 1. Results from the analysis of the additive effects of density dependence and meteorological variables. Column 1: valley; column 2: variables (N: Ricker-like model, X: Gompertz-like model; P: precipitation, T_{\min} and T_{\max} : minimum and maximum temperature; T_{int} : temperature range); column 3: 15-days period for the meteorological variable, (1) means the first half of the month, (2) the second half and the subscript $t-1$ indicates that is a month in the year of the first census; column 4: p value; column 5: explained variance; column 6: AICc value; column 7: fraction of outliers in the residuals; column 8: excess of ACF elements. In brackets, we report the results when the model includes a bilinear term representing the product of density (either N or X) and the meteorological variable under examination.

	Variables	Period	p	R^2	AICc	Outliers	Excess
Totals	X, T_{int}	June _{$t-1$} (1)	< 0.001 (< 0.001)	0.60 (0.69)	-50.9 (-54.9)	0.11 (0.06)	0.08 (0.0)
	N, P	June _{$t-1$} (1)	< 0.001 (< 0.001)	0.66 (0.71)	-53.6 (-52.9)	0.06 (0.06)	0.0 (0.17)
	X, P	June _{$t-1$} (1)	< 0.001 (< 0.001)	0.68 (0.71)	-54.6 (-53.3)	0.06 (0.06)	0.08 (0.0)
	N, T_{int}	Dec _{$t-1$} (1)	< 0.001 (< 0.001)	0.63 (0.63)	-52.4 (-49.0)	0.06 (0.06)	0.50 (0.50)
	X, T_{int}	Dec _{$t-1$} (1)	< 0.001 (0.002)	0.64 (0.64)	-52.5 (-49.3)	0.06 (0.06)	0.42 (0.42)
	N, T_{int}	Dec _{$t-1$} (2)	< 0.001 (0.01)	0.66 (0.66)	-53.8 (-50.5)	0.06 (0.06)	0.83 (0.92)
	X, T_{int}	Dec _{$t-1$} (2)	< 0.001 (0.001)	0.65 (0.66)	-53.3 (-50.3)	0.11 (0.11)	0.75 (0.83)
Susa	X, P	June _{$t-1$} (1)	< 0.001 (< 0.001)	0.61 (0.70)	-43.9 (-45.4)	0.06 (0.0)	0.33 (0.33)
Chisone	X, T_{int}	May _{$t-1$} (2)	< 0.001 (< 0.001)	0.73 (0.83)	-44.3 (-49.3)	0.11 (0.06)	0.08 (0.0)
	X, P	May _{$t-1$} (2)	< 0.001 (< 0.001)	0.74 (0.82)	-44.8 (-48.0)	0.06 (0.06)	0.08 (0.17)
	X, P	June _{$t-1$} (2)	< 0.001 (0.001)	0.67 (0.67)	-40.2 (-36.9)	0.06 (0.06)	0.0 (0.0)
	X, P	July _{$t-1$} (2)	< 0.001 (< 0.001)	0.67 (0.73)	-40.3 (-41.0)	0.11 (0.06)	0.08 (0.25)
	X, T_{int}	Dec _{$t-1$} (1)	< 0.001 (< 0.001)	0.66 (0.69)	-40.0 (-38.1)	0.06 (0.06)	0.08 (0.08)
	X, P	Dec _{$t-1$} (1)	< 0.001 (< 0.001)	0.68 (0.70)	-41.1 (-38.6)	0.11 (0.06)	0.0 (0.0)
	X, P	Dec _{$t-1$} (2)	< 0.001 (< 0.01)	0.68 (0.71)	-41.0 (-39.1)	0.06 (0.06)	0.25 (0.08)
Sangone	X, T_{int}	June _{$t-1$} (1)	0.002 (0.002)	0.57 (0.63)	-47.6 (-47.3)	0.06 (0.06)	0.0 (0.0)
	X, T_{int}	Dec _{$t-1$} (2)	< 0.001 (0.003)	0.60 (0.61)	-49.2 (-46.2)	0.06 (0.06)	0.33 (0.33)
	X, P	June _{$t-1$} (1)	0.003 (0.012)	0.53 (0.53)	-46.2 (-45.9)	0.06 (0.06)	0.0 (0.0)

To test whether there is evidence for the interaction of density dependence and climatic control, we have also considered a model including a bilinear term with the product of density (either N or X) and a meteo-climatic variable. The results (Tab. 1) indicate that the interaction of climate and density (represented by the bilinear term) did not play a relevant role in the population dynamics of the black grouse at the Orsiera Park, as the AICc of the models containing the bilinear term was usually larger than that of the model without the interaction term. In the few cases when the addition of the interaction term lowered the AICc, the effect was anyway rather small. These findings indicate that density dependence and climate control in this population can be considered as independent effects.

Finally, we considered the results obtained with a model that includes direct DD (on N or X) and the dependence on two meteo-climatic variables. To this end, we have considered only the meteo-climatic variables reported in Tab. 1, which have been shown to be significant in the analysis of the interplay of density and climate in at least one of the valleys. Tab. 2 reports the results of the four models with the lowest AICc for each valley. Models including both precipitation (or daily temperature range) in early June and the daily temperature range in December (either the first or the second half) of the previous year explained up to 82% of the variance and on average performed better (in the AIC sense) than models including just one meteo-climatic effect. All four models for Chisone valley and one for Sangone included the temperature range (or precipitation) of May on year $t-1$ instead of those of June. No clear preference for a Ricker-like or Gompertz-like model emerges from the analysis results.

Table 2. Results from the analysis of the additive effects of density dependence and two different meteorological variables (four best models for each valley). The definition of variables and statistics is the same as in Tab. 1.

	Model ID	Variables	p	R^2	AICc	Outliers	Excess
Totals	Tot1	N (X), T_{int} - June $t-1$ (1)	< 0.001	0.79	-58.7	0.11	0.25
		T_{int} - Dec $t-1$ (1)	(< 0.001)	(0.78)	(-58.3)	(0.11)	(0.17)
	Tot2	N (X), T_{int} - June $t-1$ (1)	< 0.001	0.82	-61.8	0.11	0.33
		T_{int} - Dec $t-1$ (2)	(< 0.001)	(0.80)	(-60.3)	(0.11)	(0.42)
Tot3	N (X), P - June $t-1$ (1)	< 0.001	0.78	-58.1	0.06	0.33	
	T_{int} - Dec $t-1$ (1)	(< 0.001)	(0.78)	(-58.1)	(0.06)	(0.33)	
Tot4	N (X), P - June $t-1$ (1)	< 0.001	0.80	-59.6	0.06	0.42	
	T_{int} - Dec $t-1$ (2)	(< 0.001)	(0.79)	(-58.7)	(0.06)	(0.67)	
Susa	Su1	N (X), T_{int} - June $t-1$ (1)	< 0.001	0.70	-45.3	0.0	0.33
		T_{int} - Dec $t-1$ (1)	(< 0.001)	(0.73)	(-46.9)	(0.06)	(0.50)
	Su2	N (X), T_{int} - June $t-1$ (1)	< 0.001	0.69	-44.6	0.06	0.50
		T_{int} - Dec $t-1$ (2)	(< 0.001)	(0.70)	(-45.4)	(0.06)	(0.50)
Su3	N (X), P - June $t-1$ (1)	< 0.001	0.67	-43.4	0.06	0.25	
	T_{int} - Dec $t-1$ (1)	(< 0.001)	(0.70)	(-45.5)	(0.06)	(0.33)	
Su4	N (X), P - June $t-1$ (1)	0.002	0.65	-42.6	0.0	0.42	
	T_{int} - Dec $t-1$ (2)	(< 0.001)	(0.68)	(-44.0)	(0.06)	(0.50)	
Chisone	Ch1	N (X), T_{int} - May $t-1$ (2)	< 0.001	0.78	-44.1	0.06	0.25
		T_{int} - Dec $t-1$ (1)	(< 0.001)	(0.81)	(-47.3)	(0.0)	(0.17)
	Ch2	N (X), T_{int} - May $t-1$ (2)	< 0.001	0.75	-41.9	0.06	0.33
		T_{int} - Dec $t-1$ (2)	(< 0.001)	(0.78)	(-44.2)	(0.0)	(0.33)
Ch3	N (X), P - May $t-1$ (2)	< 0.001	0.76	-42.5	0.06	0.17	
	T_{int} - Dec $t-1$ (1)	(< 0.001)	(0.80)	(-46.4)	(0.0)	(0.17)	
Ch4	N (X), P - May $t-1$ (2)	< 0.001	0.75	-42.4	0.06	0.33	
	T_{int} - Dec $t-1$ (2)	(< 0.001)	(0.79)	(-45.1)	(0.0)	(0.42)	
Sangone	Sa1	N (X), T_{int} - May $t-1$ (2)	0.003	0.62	-46.8	0.06	0.33
		T_{int} - Dec $t-1$ (2)	(0.002)	(0.65)	(-47.8)	(0.06)	(0.33)
	Sa2	N (X), T_{int} - June $t-1$ (1)	0.003	0.62	-46.8	0.06	0.0
		T_{int} - Dec $t-1$ (1)	(0.002)	(0.64)	(-47.7)	(0.06)	(0.0)
Sa3	N (X), T_{int} - June $t-1$ (1)	< 0.001	0.70	-51.0	0.06	0.08	
	T_{int} - Dec $t-1$ (2)	(< 0.001)	(0.72)	(-52.2)	(0.06)	(0.0)	
Sa4	N (X), P - June $t-1$ (1)	0.002	0.64	-47.4	0.06	0.08	
	T_{int} - Dec $t-1$ (2)	(0.001)	(0.66)	(-48.6)	(0.06)	(0.08)	

Model validation

The leave-one-out validation statistics described in the section on materials and methods are shown in Tab. 3. The coefficient of efficiency (CE) was always positive and higher than 0.40 (0.59 for the whole Park), indicating a good prediction skill for all the selected models. Models including the temperature range of the first half of December showed the best performance for Susa and Chisone valley, while for Sangone and the average growth rate of the whole Park the temperature range of the second half of December fitted better. No preference for precipitation or temperature range in June (or May) emerged. Ricker- and Gompertz-like models showed a similar fit. Note that the choice of the best models by validation statistics was often different from the ones selected by AICc (see Tab. 2), however several models had very close values within the same valley, and could be considered virtually identical in prediction ability. Fig. 6 offers a visual evaluation of the fit of the two best performing models, accounting for Ricker and Gompertz DD, for the population of the whole Park area (Ahnert et al. 2007).

Table 3. Leave-one-out validation statistics for the selected regression models (the Model ID is the same as in Table 4). PRESS: predicted residual sum of squares; RMSE_v: root-mean-squared error of validation; CE: coefficient of efficiency. In brackets, we report the results for a Gompertz-like (X) density dependence. The model that best fits, according to each statistics, is represented in bold.

	Statistic	Regression models			
	Model ID	Tot1 - N (X)	Tot2 - N (X)	Tot3 - N (X)	Tot4 - N (X)
Totals	PRESS	0.67 (0.69)	0.54 (0.62)	0.57 (0.58)	0.54 (0.57)
	RMSE _v	0.19 (0.20)	0.17 (0.19)	0.18 (0.18)	0.17 (0.18)
	CE	0.59 (0.58)	0.67 (0.62)	0.65 (0.65)	0.67 (0.65)
	Model ID	Su1 - N (X)	Su2 - N (X)	Su3 - N (X)	Su4 - N (X)
Susa	PRESS	1.43 (1.29)	1.38 (1.27)	1.37 (1.23)	1.48 (1.31)
	RMSE _v	0.28 (0.27)	0.28 (0.27)	0.28 (0.26)	0.29 (0.27)
	CE	0.42 (0.48)	0.44 (0.49)	0.45 (0.51)	0.40 (0.47)
	Model ID	Ch1 - N (X)	Ch2 - N (X)	Ch3 - N (X)	Ch4 - N (X)
Chisone	PRESS	1.36 (1.15)	1.77 (1.59)	1.75 (1.19)	1.62 (1.48)
	RMSE _v	0.27 (0.25)	0.31 (0.30)	0.31 (0.26)	0.30 (0.29)
	CE	0.62 (0.68)	0.50 (0.55)	0.51 (0.67)	0.54 (0.58)
	Model ID	Sa1 - N (X)	Sa2 - N (X)	Sa3 - N (X)	Sa4 - N (X)
Sangone	PRESS	1.02 (1.00)	1.04 (0.99)	0.81 (0.82)	1.08 (1.03)
	RMSE _v	0.24 (0.24)	0.24 (0.23)	0.21 (0.21)	0.24 (0.24)
	CE	0.44 (0.45)	0.43 (0.46)	0.56 (0.55)	0.41 (0.43)

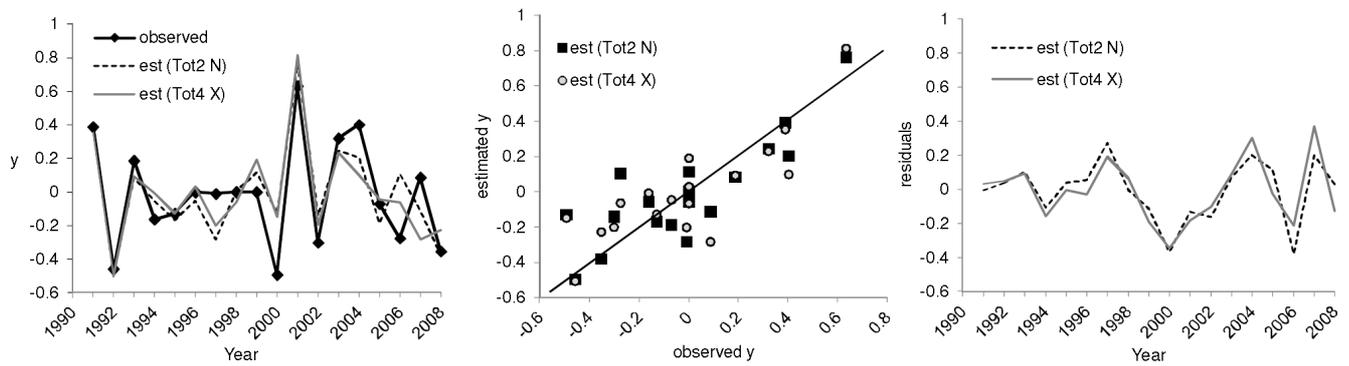


Figure 6. Leave-one-out predicted values of the two best performing models (Tot2-N and Tot4-X) for the whole Park. Left: goodness of fit of the two models; middle: scatter plot with observed data; right: plot of validation errors.

Discussion

As expected, density dependence is an important factor driving the fluctuations of black grouse populations in the alpine area under study. Density-dependence in birds is often associated to losses during the non-breeding season (Sæther et al. 2004). Higher densities enhance parasite infections, which in turn reduce host breeding production and survival (Hudson et al. 1992b); moreover, density affects predation rate, and there is also an interaction between these two effects, as predators selectively remove heavily parasitized individuals (Hudson et al. 1992a). However, no evidence for delayed density dependence was found in any of the valleys, suggesting that any delayed effects of young body conditions, parasite burden, or of predator density can be considered negligible. Lack of delayed density dependence was found also in black grouse dynamics in Finland (Lampila et al. 2011).

Given the little information on the dynamics of alpine populations, in this study we investigated the effect of climatic variables all year round. Spurious correlations were avoided by using a randomization procedure and by following a step-by-step approach, i.e. including in each model level only the most significant relations present in the simpler models. The resulting critical periods (brooding-hatching time and winter) for the effect of climate on the dynamics of this alpine population were not surprising.

Adverse weather conditions during late brooding and hatching is known to negatively affect recruitment in black grouse populations (Summers et al. 2004, Ludwig et al 2010). In particular, heavy rain could wash away the eggs of ground-nesting birds such as grouse, and cause thermoregulation problems to chicks just after hatching (Hannon and Martin 2006). In addition, precipitation affects the availability of insects in summer (Thacker et al. 1997), influencing chick food provisioning.

Despite lowland black grouse populations are mainly driven by climatic conditions during breeding period, a significant effect of winter weather is well demonstrated for different populations (Loneux et al. 2000) in the sense that milder temperatures, likely preventing snowfall, negatively affect population growth rates. However the interpretation of the temperature range effect is less straightforward. Wider daily ranges of temperatures, translating in clear-sky, sunny and dryer days, resulted favourable to population growth rate in the Orsiera-Rocciavrè Park. Two mechanisms explaining this observed effect are possible. First, the temperature range is negatively correlated with precipitation, at least in the second half of December (see Fig. 3). A negative effect of precipitation in winter was found in other black grouse populations (Loneux et al. 2003) and snowfall associated to milder winters was found to be the main factor affecting the ruffed grouse (*Bonasa umbellus*) population in Minnesota (Zimmerman et al. 2008); this effect could be relevant also for the alpine black grouse populations studied here. Notice, however, that measured precipitation in December does not seem to directly affect the growth rate of this population, as shown by the monivariate tests. Nevertheless, it is known that rain gauges can have troubles in correctly estimating solid precipitation in mountain areas, especially in the presence of strong winds (Goodison et al. 1998), and the temperature range could perhaps be considered a more reliable proxy for snowfall than direct rain gauge measurements.

Secondly, the temperature range is strongly correlated with solar radiation (Bristow and Campbell 1984), that can affect winter survival both directly (under sunny conditions, birds may reduce requirements for regulatory thermogenesis by “sunbathing”, Whittow 2000, p. 365) and indirectly, being one of the variables affecting snow compaction (Gray and Male 1981, p. 326). Black grouse, in fact, must survive winter months by reducing heat losses (Andreev 1999) roosting in snow burrows, where ambient temperature usually exceeds their lower critical temperature (Marjakangas et al. 1984); moreover, there are evidences that snow burrows have also an important anti-predator function (Marjakangas 1990, Spidsø et al.

1997). Snow burrowing has therefore a primary importance for winter survival, and could be favoured by compact snow, as Blanchette et al. (2007) showed for ruffed grouse in Québec.

The analysis of climate trends in north-western Italy in the last 50 years indicates the absence of significant precipitation trends in any season and a positive trend for winter temperatures, which is larger for maximum daily temperatures and lower for minimum temperatures (Ciccarelli et al. 2008). This suggests an increase in the daily temperature range in winter, at variance with the results reported by Beniston (1994) for the whole alpine range. On the other hand, snow depth measurements at selected stations indicate a strong decrease of the average snow depth in the last twenty years, associated with increased temperatures (Jacobson et al. 2004). Future projections at regional scale indicate a continuing growing trend for temperatures and a decreasing trend for snow cover (Beniston 2003). The best-performing model derived here, which included the effects of density dependence, early June rainfall and December temperature range, could be driven by the output of a regional climate model and used to estimate future trends in black grouse populations in this area.

While models explaining changes in population abundance are well defined, we failed to detect key factors affecting lek attendance by males. In promiscuous grouse species, males typically do not breed as yearlings, because young males cannot compete effectively for mates with more experienced males (Wittenberger 1978). Beside age, choosing between alternative mating strategies is mostly driven by population density (and we found a weak negative correlation with male density), but in particular by mate density (Kokko and Rankin 2006). The fraction of males singing alone should therefore be more affected by female density, rather than density of competing males: the higher the number of females attending leks, the stronger the stimulus to display and fight on leks. The reason why, at lower female densities, less experienced males renounce to lek is easily explained by the far higher spring mortality of adult territorial cocks compared with that of non-territorial males, due to weight loss and exposure to predation (Angelstam 1984).

The main climatic effects affecting lek attendance were detected in August of the previous year and in May. Black grouse males are known to attend leks also in autumn, and males that established their territories in the previous autumn or earlier are more successful in obtaining copulations during next spring (Rintamäki et al. 1999). It is possible that adverse weather conditions during late summer negatively affect the chances of less experienced males to

succeed in fighting, preventing them to join leks in autumn and consequently in the following spring. On the contrary, the positive effect of temperature at the time of census on the fraction of males singing alone is harder to justify. One possibility is that higher temperatures in May are associated with reduced snow cover and correspondingly reduced availability of suitable areas for leks. This is confirmed by the negative dependence on precipitation in April.

The positive trend in the fraction of solitary males during the study period cannot be explained with changes in population density or with trends in climatic factors. The reason of a lower lek attendance should possibly be sought in habitat modifications that occurred in the area, such as shrinking of the ecotone and of the size and number of open areas used as leks, due to shrub encroachment induced by rising temperatures and abandonment of high pastures. The scarcity of suitable display sites can in fact induce males to a non-lekking mating strategy (Höglund and Stöhr 1997). This hypothesis will be verified in a forthcoming analysis using satellite and airplane data on the vegetation conditions.

Some remarks can be made on non-lekking males. The census methodology adopted here based on transects, not focused only on leks, allowed to identify and count solitary males in the population. Given the numerical importance and the trend observed in the fraction of solitary males, ignoring them (as done in traditional, lek-based census methods) could introduce a non-negligible bias in the calculation of male density. In addition, the fraction of males singing alone should be regarded as a symptom of poor health of the population, either as a result of a decreasing female density or of suitable habitat. In any case, a larger fraction of solitary males can cause lower genetic diversity (Svobodová et al. 2011), threatening the existence of the population on the long-term.

As other European grouse species, black grouse has specialised habitat needs and it is susceptible to environmental variations, as also demonstrated by this paper. Although the species is listed as “least concern” in the Red List of threatened species (IUCN 2011), conservation efforts for declining populations should be a priority objective, as they will be likely beneficial to other animal species with similar (or less specialised) needs within the same habitat (Storch 2007). This is particularly true in the southern part of the range of the species, and in extreme habitats such as mountains.

The strong influence of meteorological variables in regulating population dynamics resulting from this study, suggests some amelioration in the management strategies to help the persistence of black grouse populations in the western Alps. In particular, one should promote the conservation of breeding and wintering habitat, limiting disturbing activities in years of unfavourable weather conditions. Moreover, management actions should consider also climatic conditions, when for example defining hunting quotas.

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Chapter 3 - Patterns of biodiversity along altitudinal transects in north western Italian Alps: a multi-taxa approach

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Abstract

The current loss of biodiversity underlines the need to monitor and to identify what influence its distribution. In 2007, three alpine parks in N-W Italy started a project to determine factors influencing animal biodiversity and the most appropriate methods for a periodically repeatable monitoring programme.

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 were systematically sampled 5 taxonomic groups (Lepidoptera, Aves, Staphylinidae, Carabidae, Araneae), and collected topographic, environmental and micro-climatic parameters. Aim of the work is to assess the coherence in the distribution of different taxa along altitudinal gradients and the influence of geographical, environmental and climatic factors on biodiversity pattern.

Our results show that species richness and community composition are mainly determined by altitude and microclimatic conditions. In particular for invertebrates, whereas birds are more related to habitat structure. The strong relationship between community composition of invertebrates and temperature suggest their potential sensitivity to climatic variation.

Comparing species richness and community composition through vegetation belts, we observed that the alpine belt supports low values of species richness but a high percentage of endemic and vulnerable species, highlighting its importance for conservation purposes.

This kind of research can offer a representative sample of North-Western Italian Alps and it aims to be the first step of a monitoring program that should be repeated every 5 years to highlight the response of alpine biodiversity to climate and land use changes.

Keywords: biodiversity, multi-taxa approach, temperature, altitude, climate sensitivity

Introduction

In the last few decades, species extinction and biodiversity decline have reached an alarming rate (Pimm et al. 1995; Thomas et al. 2004; Butchart et al. 2010), indicating an urgent need to sort out and monitor factors that influence biodiversity variability and identify priority areas and sensitive taxonomic groups. Characterising and following the changes of biota in space and time is a crucial conservation tool to prevent degradation and further decrease of biodiversity (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, are among the most spatially heterogeneous environments in the world, creating a mosaic of habitats along an altitudinal gradient (Haslett 1997; Beninston 2003; Körner 2000). Such level of heterogeneity determines high levels of biodiversity, usually higher than that recorded in adjacent lowland areas (Körner 2000; Theurillat et al 2003). Compared to latitudinal gradients, altitudinal gradients allow for investigating the relationships between biodiversity distribution and abiotic/biotic parameters on a reduced spatial scale, with fauna and flora characterized by a similar biogeographical history (Rahbek 1995; Körner 2000). Moreover, mountains provide valuable ecosystem services for lowland human settlements (e.g., water supply, recreation; Körner 2005).

On the other hand, mountain habitats support the world's most rare and fragile ecosystems (Diaz et al. 2003; Nogues-Bravo et al. 2007; Pauchard et al. 2009). Populations at high elevations are usually small, isolated and often prone to local extinction, comprise specialised elements, are often poor disperser and are characterised by high levels of endemism (McNeely 1990; Boggs and Murphy 1997; EEA 2010). Mountains are particularly sensitive to global environmental change (Huber et al. 2005), notably global warming, as they are generally characterized by adaptations to low temperature conditions (Pauli et al. 2004). Long-term records provide evidence for an ongoing climate warming in mountain environments (Beninston 2006) and in the Alps (Calmanti et al. 2006; Auer 2007; Rebetez and Reinhard 2008; Keiler et al. 2010) that has already impacted the life cycle, pattern of activity, distribution and range size of various plant and animal species (Thuiller et al. 2005; Rull and Vegas-Vilarrúbia 2006; Pauli et al. 2007, Bassler et al. 2010).

Mountains are also outstanding natural heritage sites, where biodiversity is linked with the cultural patrimony of the people living therein. The European Alps, in particular, have a long history of human presence and exploitation (CBD 2003; Chemini and Rizzoli 2003). Touristic

and recreational activities, if not properly controlled, can negatively affect mountain biodiversity (Pickering et al. 2003, Patthey et al. 2008) but even the abandonment of traditional farming systems can be detrimental (Brambilla et al. 2010). During the last millennia, agro-pastoral activities determined a lowering of the treeline ecotone and profoundly shaped community composition both of plants and animals (e.g., Chemini and Rizzoli 2003; Theurillat and Guisan 2001). Abandonment of traditional farming systems has been recorded at least from the beginning of 1900 (Bätzing et al. 1996): consequences have been shown to be negative for some taxa and the effects may cumulate with those due to climate warming. Therefore, in the Alps there appears to be a significant risk of an impoverishment of the biotic structure, due to the loss of more sedentary and specialized elements in favour of more vagile and tolerant species (e.g., Giupponi et al. 2006; Dirnböck et al. 2011).

For all these reasons, the identification of factors that determine biodiversity patterns has important implications for conservation and management decisions, and exploring the causes of species distributions and community composition in mountains is an urgent task. To this end, altitudinal gradients are particularly useful to test traits for their long-term adaptive nature. Clearly, it is not elevation in itself that exerts a selective pressure, rather elevation must be seen as a proxy for the environmental conditions associated with it (Körner 2007). The communities of organisms change along environmental gradients, and one of the central aims of community ecology is to uncover the mechanisms responsible for such changes in community structure and diversity (Brehm et al. 2003). Despite this, variation in diversity along altitudinal gradients is not well documented, especially comparing different taxa and different areas with standardized methods (Lomolino 2001). The use of altitudinal gradients also ensures the possibility of covering different vegetational belts, as the climate variations associated with topography determine a vertical zonation of the vegetation pattern. The knowledge of the link with altitude becomes especially important in time of global climate change, as it allows to predict which species will be more threatened by the ongoing and future temperature rise (Fleishman et al. 1998).

To gain a more comprehensive understanding of the biodiversity patterns, comparison of elevational trends among taxa and among different mountain ranges is crucial (Lomolino 2001; Ellis et al. 2007). In general, focusing on any single biodiversity component is insufficient to gain information on the conservation status of the other components (Bonn and Gaston 2005). Information gained with a multi-taxa approach along altitudinal gradients can thus be used as a primary tool to recognise areas of high natural value and address

coordinated management actions, to develop a more useful response to biodiversity losses than the standard 'simply maintaining the site's *status quo*' (Hannah et al. 2002).

In this framework, the present study represents the first attempt to develop and evaluate a long-term multi-taxa monitoring programme protocol for the Italian Alps, and it is aimed at analysing changes of biodiversity in space and time along altitudinal transects encompassing the three vegetation belts present in our altitudinal gradient, in three, non contiguous, protected areas. In the following we discuss the results of the first monitoring session of this effort, conducted in 2007, which allowed us to describe alpha and beta diversity variations along an altitudinal gradient in the Alps and to analyse the relative influence of geographical, environmental and climatic factors on biodiversity structure and community composition.

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 Rocciavrè Natural Park (110 km²; 44°75'N - 6°90'E) and Veglia Devero Natural Park (86,2 km²; 46°18' N - 8°13' E). All areas are characterised by mountain and alpine conditions with a vegetation 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 regime (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 (one for each valley for each of the three parks), starting from the altitude of 550 m and reaching 2700 m a.s.l. Each transect is composed of 4-7 sampling units separated by an altitude range of 200 meters, to allow for independence of sampled data, for a total of 69 monitored plots. The sample unit is a circular plot with a radius of 100 meters, labelled as belonging to one of the three belts distributed along the altitudinal gradient (Montane, Subalpine and Alpine), identified considering both altitude and potential vegetation, as suggested by Körner (1999) and Grabherr et al. (2003). The study includes 22 plots in the Montane, 20 in the Subalpine and 27 in the Alpine belt.

Data collection

Data about 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 are, as much as possible, easy to apply, standardized, cheap and repeatable.

Birds were census 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.

We sampled butterflies using walking transects along the diameter of the plot (200 m in length), walked at uniform speed. We recorded all butterflies seen within prescribed limits in an imaginary 5 x 5 m square, following Pollard (1977). Sampling was limited to sunny condition, 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, retained for further determination.

We collected surface-active arthropods using pitfall traps (plastic cups, diameter of 7 cm, filled with 10 cc of white vinegar). For each plot, the traps were set along the diameter, in a single row of five traps at a distance of fifty meters from each other. The traps were collected and refilled 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 to 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 tool in the development of a long-term biodiversity monitoring programme.

For each plot we determined the percentage of ground covered by different structural layers, estimated by eye during field surveys: herbaceous layer, low shrubs (< 1 m), tall shrubs (between 1-5 m), trees, stone and bare ground cover. We used vegetation layers to estimate structural diversity, defined as 1 - Simpson Index on the value of the herbaceous layer, shrub and tree cover, as often adopted to describe vegetation complexity in conservation studies (e.g., Kati et al. 2010).

Microclimatic conditions of each plot were measured by data-loggers (Thermochron iButton, DS1922L, Maxim, Sunnyvale, CA, U.S.), able to record air temperature every hour throughout the field season. Data of daily, monthly and seasonally temperature (Mean, Maximum, Minimum Temperature with relative coefficients of variation) were calculated for each plot.

Data analysis

To describe community structure and composition at each sampling site we grouped data among temporal replicates. We computed Species richness (S), Simpson Index (corrected for a finite community and expressed as the reciprocal 1/D to represent the diversity of the assemblage) and Abundance (N, number of individuals recorded) for each taxon and for all taxa pooled together.

Each species was characterised by habitat and climate requirements and morphological characteristics, that could determine potential vulnerability and/or sensitivity to environmental and climatic changes. We defined as vulnerable: species of carabidae with short wing (brachiptera, as suggested by Brandmayr et al. 2005); bird species included in Annex I of the European Directive 2009/147/EC, SPEC species (following Birdlife International 2004) or species depicted as 'particularly protected' by the Italian Law 157/92; butterfly species with low altitudinal tolerance (found in only one or two adjacent vegetational belts, following the classification of Balletto and Kudrna 1985) and depicted as SPEC (following van Swaay and Warren 1999); species of staphylinidae and araneae with low altitudinal tolerance (as suggested by expert taxonomists). Percentages of endemic and vulnerable species were obtained for each plot and correlated to underscore similar patterns.

The linkage between community indexes and environmental parameters was assessed by Spearman rank correlation test. Bonferroni corrections were used to correct for multiple comparisons (α/n , with $n=48$). Relationship with altitude was explored using the LOWESS regression technique and further evaluated with a polynomial regression (McDonald 2007), to determine the best fit among a first-order (linear), a second-order (quadratic) and a third-order (cubic) equation. We used plot-based rarefaction curves to estimate the effectiveness of the sampling effort among taxa and habitats (Gotelli and Colwell 2001; Chiarucci et al. 2008). Curves were obtained by EstimateS (Version 8.0 for Windows 1985-2005). The ratios between the species rarefaction curves of pairs of taxa were calculated within each belt to evaluate congruence of rarefaction patterns: in case of similarity between taxa the curve is expected to be horizontal (Chiarucci et al. 2005). For each belt we selected the last quartile of the taxon/taxon ratio curves to assess whether they became horizontal in their last portion. To identify the peculiarities of each vegetation belt, data on community parameters and percentage of endemic and vulnerable species were compared using a Kruskal Wallis test. To identify similarities in the compositional gradients of the five taxonomic groups in the 69

plots, we performed correspondence analysis (CA) ordinations: one for each group and one for all taxa pooled together. The abundance of each species was expressed as the natural logarithm, ($\ln(n+1)$).

To remove undue effects of rare species on the CA analysis (Gauch 1982) we eliminated species occurring in only one sampling site. To analyze the possible effect of one species in determining the order of plot 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. Scores obtained along the first axes were used to test for correlation (Spearman rank correlation test) with environmental and topographic variables. The Mantel test (Mantel 1967) was used to assess congruence between community composition of different taxa. The influence of geographical, environmental and climatic factors on community composition was evaluated using Simple and Partial Mantel's Test (Smouse 1986; Anderson and Legendre 1999). Partial Mantel's test allows to quantify the relationship between two matrices while controlling for the effects of a third one.

Community dissimilarity matrices for each taxon were based on the complement of Jaccard Estimator Index, proposed by Chao (Chao et al. 2005) and calculated with software EsimateS. 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 software ArcView 3.2, applying Animal Movement Extension. A belt matrix was created as a model matrix, in which distances between plots are scored as 0 for samples belonging to the same belt, as 2 for samples belonging to non-consecutive belts (pair Montane-Alpine), as 1 in all the other cases. All matrices were estimated using 62 plots, due to missing values for temperature in 7 sampling units.

Simple and partial Mantel tests were performed using Zt software with Mantel tester GUI. The significance level was assessed using 100 000 randomisations, through permutation of the residual of a null model (Bonnet E. and Van de Peer Y. 2002). The level of significance was set to $\alpha=0.01$, owing to the high number of tests performed on the same data set. Except when indicated, all statistical analysis were performed using Statistica 6.0.

Results

Species richness

We recorded 663 indigenous species: 64 Birds, 134 Butterflies, 101 Carabidae, 119 Staphylinidae, and 245 Araneae. Species richness was strongly correlated with Shannon index ($0.629 < \rho < 0.947$, all p -values < 0.0001), and presented a weaker but always significant correlation with Simpson index ($0.320 < \rho < 0.857$, all p -values < 0.01) and Abundance ($0.412 < \rho < 0.790$, all p -values < 0.0001). Further analyses were thus based only on Species richness, an effective measure of biodiversity which is easier to interpret.

The LOWESS regression shows a hump-shaped dependence of the total Species richness versus altitude. The relationship between Species richness (S) and Altitude (Alt) is better described by a quadratic equation, as shown in Fig.1 for all taxa pooled together ($S = -3.37 + 0.1003 Alt - 3e^{-05} Alt^2$; $r^2=0.44$; $p < 0.01$).

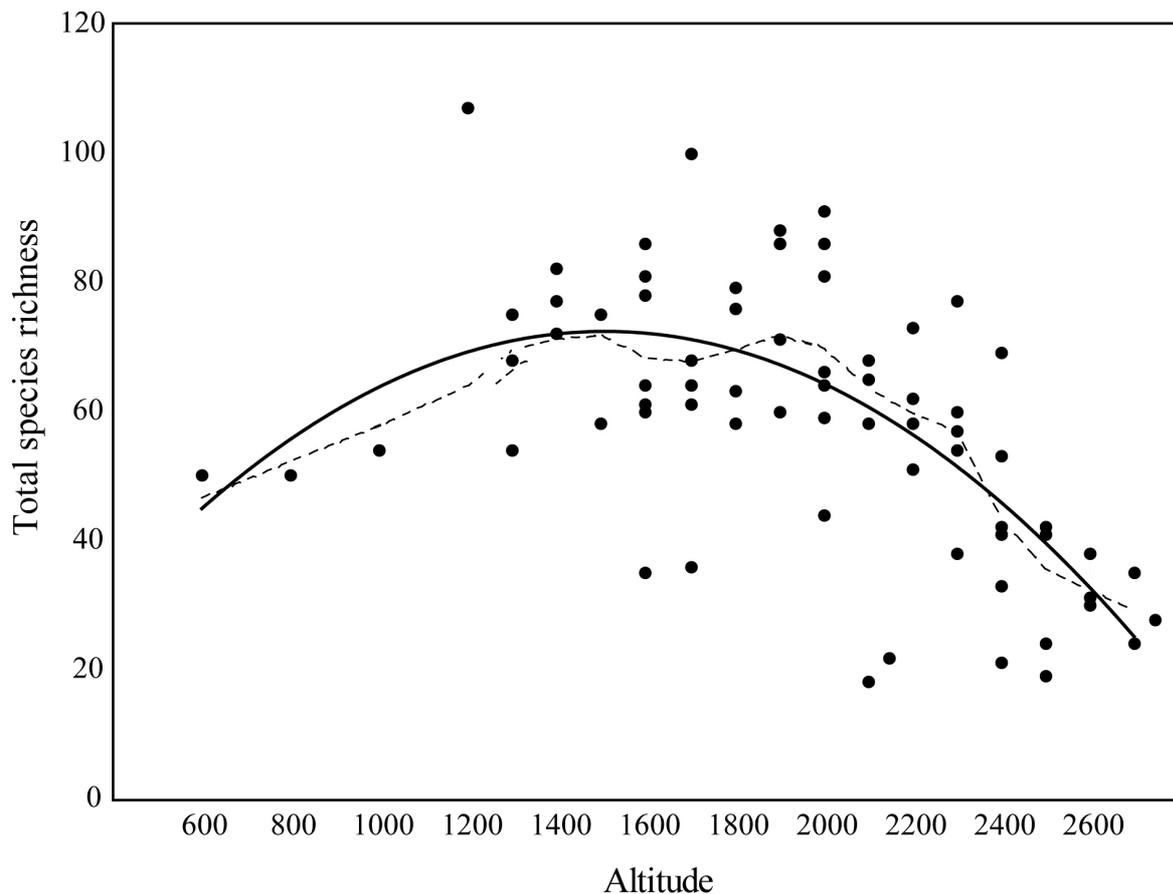


Fig. 1. Scatter plot of the total Species richness (all taxa pooled together) in each site along the altitudinal gradient. The LOWESS regression curve is represented as a dashed line, while the quadratic regression curve is represented as a solid line. The quadratic regression is statistically significant ($r^2=0.44$; $p < 0.01$).

As reported in Table 1, the most important parameters in determining Species richness appear to be Altitude and Temperature, while the vegetation structural characteristics play a lesser

role. These results hold for the Species richness of all taxa pooled together and for the individual taxonomic groups, with the exception of Carabids where the extent of the herbaceous layer is the most important, although not significant, explanatory variable.

Table 1. Significant relationships expressed as Spearman correlation coefficients among environmental variables and species richness (S). Bonferroni corrected p-values: * $p < 0.05/48$; ** $p < 0.01/48$. Legend: S_{sta} (S Staphilinidae), S_{car} (S Carabidae), S_{bir} (S Aves), S_{but} (Lepidoptera), S_{ara} (Araneae), S_{tot} (Overall species richness); altitude (Alt), temperature (Temp), structural diversity (Str Div), trees (Tree), tall shrubs (TShr), low shrubs (LShr), herbaceous layer (HerbL), stone (Rock).

	Alt	Temp	Str Div	Tree%	TShr%	LShr%	HerbL%	Rock%
S_{sta}	-0.435**	0.415*	0.147	0.374	0.154	0.273	0.028	-0.509**
S_{car}	-0.208	0.198	0.009	-0.232	0.061	-0.145	0.373	-0.225
S_{bir}	-0.566**	0.565**	0.289	0.428**	0.326	0.248	-0.111	-0.367
S_{but}	-0.409**	0.485**	0.313	0.306	0.386*	0.318	-0.007	-0.054
S_{ara}	-0.449**	0.451**	0.089	0.289	0.246	0.284	0.048	-0.422**
S_{tot}	-0.519**	0.562**	0.192	0.302	0.270	0.272	0.104	-0.406*

Rarefaction curves were used to estimate the effectiveness of the sampling effort for each taxon in the three vegetation belts (Montane, Subalpine, Alpine). Neither of the curves reaches a horizontal asymptote and for different taxa does not always show a similar pattern within the same belt. Some (41.2%) ratio curves (such as surface arthropods to any other taxon or birds to butterflies) are horizontal while the others display a large variability that is constant in the vegetation belts. Variation of ratio values ranges from 0.01 for Staphylinidae/Araneae to 0.75 for Aves/Carabidae (Fig. 2). But for all the calculated ratios, the last part of the curve, i.e. last quartile of the pooled samples, becomes horizontal (range always less than 0.05) suggesting similar gradients at the end of the sampling effort. These results may suggest that a lower sampling effort cannot be considered as representative of the belt and the taxa.

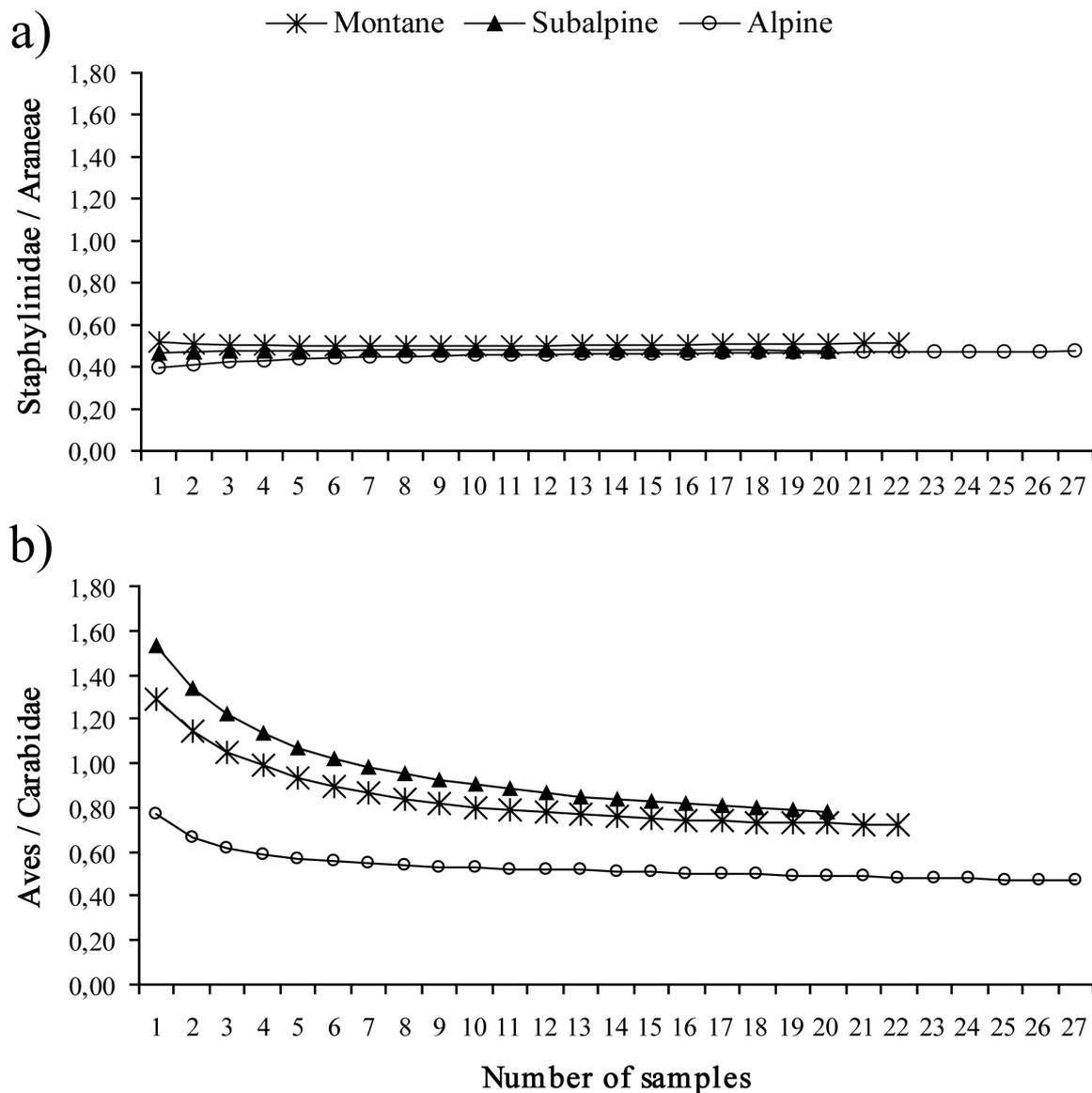


Fig. 2. Ratios between plot-based rarefaction curves for Staphylinidae/Araneae (a) and Aves/Carabidae (b) in the three belts. The curve in (a) reaches a clear horizontal asymptote. The curve ratios in (b) are the less horizontal which we found.

The distribution of species richness in the different plots in each vegetation belt shows that the Subalpine belt is the most speciose, while the Alpine belt displays the lowest values (mean \pm SE: $S_{\text{montane}} = 63.1 \pm 4.3$, $S_{\text{subalpine}} = 68.9 \pm 3.2$, $S_{\text{alpine}} = 48.7 \pm 3.6$; Kruskal-Wallis test: $N=69$, $H = 14.114$, $p=0.001$). Percentages of vulnerable species and endemisms are related ($\rho=0.568$, $N=69$, $p<0.0001$): both increase along the altitudinal gradient ($\rho_{\text{endemic}}=0.542$, $\rho_{\text{vulnerable}}=0.762$ for both $p<0.0001$), increase with decreasing temperature ($\rho_{\text{vulnerable}}=-0.801$, $\rho_{\text{endemic}}=-0.531$, for both $p<0.0001$) and display significant differences between belts (endemic species, Kruskal-Wallis test, $N=69$, $H=30.085$, $p=0.0001$; vulnerable species, Kruskal-Wallis test, $N=69$, $H=34.633$, $p=0.0001$), clearly increasing from the Montane to the Alpine belt (Fig. 3).

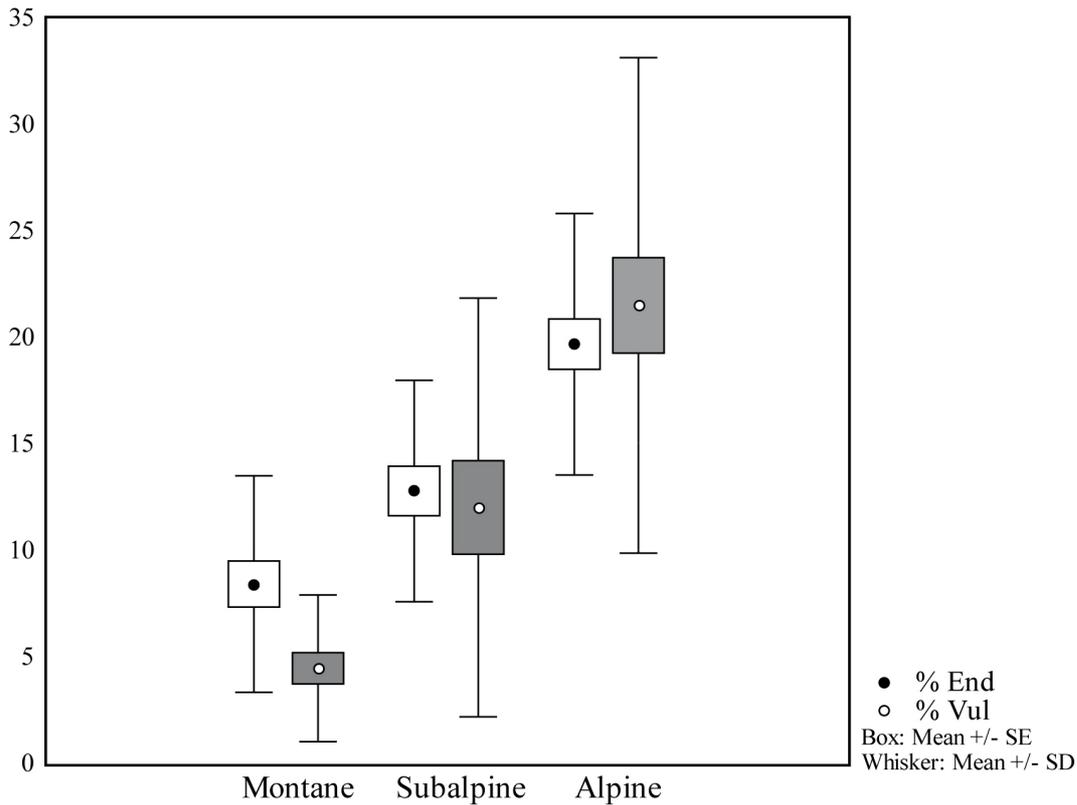


Fig. 3. Percentages of species of interest in the different belts. End: endemic species (white boxes); Vul: vulnerable species (grey boxes).

Community composition

The site ordination for all taxa, as obtained by Correspondence Analysis (CA), is shown in Fig. 4. Along the first CA axis there is a clear distinction between sites of the Montane and Alpine belts, while the results for the Subalpine belt are intermediate between these two.

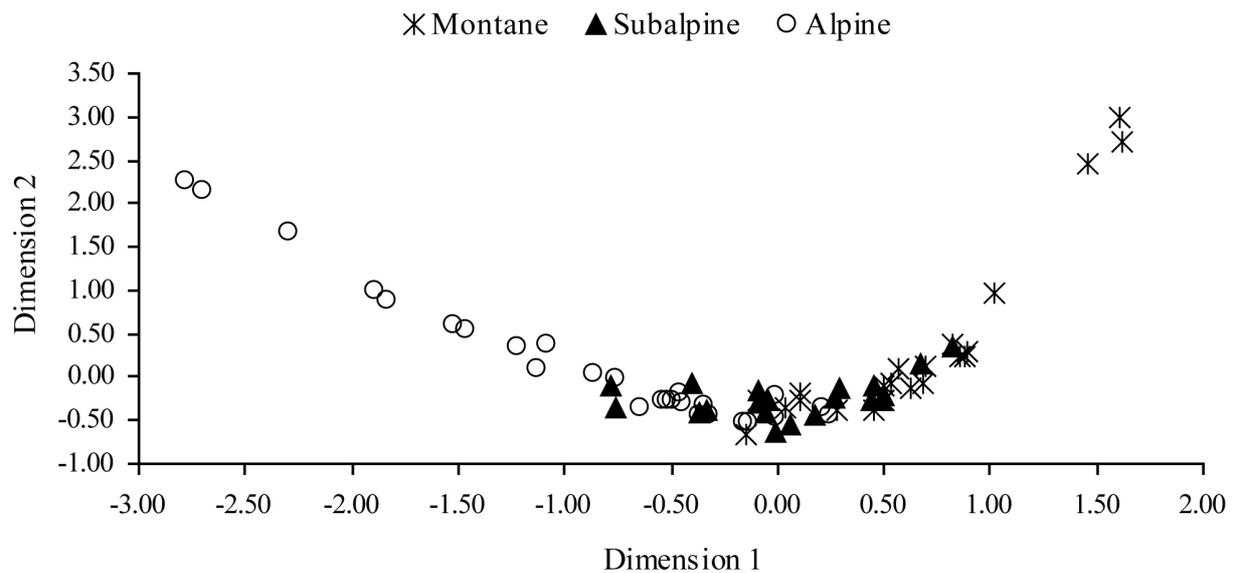


Fig. 4. Correspondence Analysis (CA) for the 69 sampling sites, based on data from all the taxa pooled together. Montane belt (*), Alpine belt (○), Subalpine belt (▲).

The site ordination along the first axis is similar for the five groups, and it is strongly correlated with the site ordination obtained with all taxa pooled together ($0.763 < \rho < 0.967$, all with $p < 0.001$). By leaving out one species at a time, one still obtains the same ordering of the plots (Spearman rank correlation between $0.999 < \rho < 1.000$). The results of the analysis indicate that the main compositional gradients are determined mainly by Altitude and Temperature (Table 2).

Table 2. Spearman correlation coefficient between each environmental variable and the extracted scores of the first dimension of CA ordinations for the five taxa and all taxa pooled together. Score Ax1=scores of the sampling sites along the first CA dimension. Bonferroni corrected p-values: * $p < 0.05/48$; ** $p < 0.01/48$. Legend: altitude (Alt), temperature (Temp), structural diversity (Str Div), trees (Tree), tall shrubs (TShr), low shrubs (LShr), herbaceous layer (HerbL), stone (Rock).

	Alt	Temp	Str Div	Tree%	TShr%	LShr%	HerbL%	Rock%
Score Ax 1	0.567**	0.657**	0.328	0.232	0.326	0.049	0.037	0.058
Score Ax 1	0.574**	0.623**	0.293	0.328	0.418*	0.261	0.112	0.026
Score Ax 1	0.911**	0.852**	0.430**	0.800**	0.674**	0.377*	0.388*	0.234
Score Ax 1	0.860**	0.882**	0.353	0.610**	0.612**	0.191	0.276	0.043
Score Ax 1	0.818**	0.849**	0.400**	0.500**	0.581**	0.171	0.158	0.117
Score Ax 1	0.889**	0.918**	0.399*	0.569**	0.600**	0.214	0.212	0.138

The congruence of the community composition for the five taxa was partially confirmed by a Simple Mantel Test for the five “taxon dissimilarity matrices” based on the complement of the Jaccard Estimator Index ($0.193 < r < 0.416$, but in all cases $p < 0.0001$). All these results suggest the presence of a similar way of responding to environmental variations at community level. The correlations, of β -diversity with topographic and environmental variables, estimated with the Mantel’s Test, are weak but significant in all cases (Table 3). In almost all cases, temperature shows the highest value of correlation and geography the lowest. The results of the Mantel Test on topographic and environmental variables shows that distances in temperature and altitude are strongly related ($r = -0.737$, $p < 0.0001$) while geography shows almost no link with the others variables. The different belts are influenced both by altitude ($r = 0.560$, $p < 0.0001$) and temperature ($r = 0.357$, $p < 0.0001$). The results of the partial Mantel test allowed us to decompose the relative importance of these factors, controlling for the effects of other factors in determining the β -diversity of individual taxa.

The relationship between compositional dissimilarity and altitude, conditional on temperature or distance among sites, loses significance for all groups except birds, while temperature still accounts for significant variation in compositional dissimilarity for all taxonomic groups

(not including birds). The variance explained by geographical distance cannot be attributed to any other factor (Table 3).

Table 3. Results of Simple and Partial Mantel Tests. For the Simple test, correlations are presented as r-values; Bonferroni corrected p-values: * = p < 0.01; ** = p < 0.001; *** = p < 0.0001; n.s. = not significant. Simple Mantel tests are shown in the diagonal with grey background colour. Number of plots = 62, due to temperature missing values in 7 plots.

	Temperature	Altitude	Belt	Geography	
Carabidae	0.228***	(n.s.)	*	***	Controlling for Temperature
Lepidoptera	0.390***	*	***	***	
Araneae	0.316***	(n.s.)	**	***	
Staphylinidae	0.245***	(n.s.)	*	***	
Aves	0.398***	***	***	(n.s.)	
Carabidae	***	0.178***	(n.s.)	***	Controlling for Altitude
Lepidoptera	***	0.350***	***	***	
Araneae	***	0.255***	*	***	
Staphylinidae	***	0.204***	(n.s.)	***	
Aves	(n.s.)	0.523***	***	**	
Carabidae	***	**	0.149***	***	Controlling for Belt
Lepidoptera	***	***	0.354***	***	
Araneae	***	**	0.221***	***	
Staphylinidae	***	**	0.149***	***	
Aves	***	***	0.594***	**	
Carabidae	***	***	***	0.305***	Controlling for Geography
Lepidoptera	***	***	***	0.285***	
Araneae	***	***	***	0.237***	
Staphylinidae	***	***	***	0.164***	
Aves	***	***	***	0.110*	

Discussion

Species richness

Our results suggest that, for the altitudinal gradient explored here, species richness decreases with elevation in a non-monotonic way. The curve of the overall species richness is hump-shaped, with a peak in richness at intermediate elevations and a stronger decline at increasing elevations. Similar patterns have already been observed in other studies for various taxonomic groups, e.g. vascular plants (Grytnes 2003), insects (Fleishman et al. 1998), birds (Kessler et al. 2001) and small mammals (Rickart 2001; Sanchez-Cordero 2001). Different explanations have been advocated for this biodiversity pattern, such as trends in primary productivity

(Rosenzweig and Abramsky 1993; Rosenzweig 1995; Waide et al. 1999; Wimp et al. 2010), hard boundaries (Colwell and Lees 2000) and/or the influence of the altitudinal range of individual species (Rapoport's rule) (Stevens 1992; Fleishman et al. 1998). In the sampling sites analysed here, the lower-elevation portion of the curve is strongly influenced by xeric conditions (3 plots in the Orsiera Rocciavrè Parks) and by higher level of human impacts, compared to the belts at higher altitude. The plots at lower altitude are mainly located at the boundaries of the protected areas. These areas can properly act as buffer zones but do not possess high conservation value, not only in terms of the number of species found, but especially in the amount of elements with conservation and biogeographical interest.

In principle, altitudinal gradients relate to a large number of intercorrelated variables that can potentially affect organismic diversity (Brhem et al. 2003). In our study, temperature appears to be the most important factor determining this gradient (Oomen and Shanker, 2005) while environmental variables are of lesser importance. This holds for almost all taxonomic groups and for the overall species richness. Only carabids show a slightly different pattern, as they are more influenced by environmental factors such as grass coverage. 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).

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; Oomen and Shanker 2005). As observed in the analysis of community composition, in the subalpine belt species which are exclusive of this area are present together with species shared with the surrounding belts. Some authors suggest that ecosystem response in mountain environments should be stronger at ecoclines/ecotones, owing to possibly different trends in adjacent habitats (Guisan et al. 1995; Beniston 2003). A general trend of reforestation in the mountains of Europe has already been observed, as reported by different sources (e.g., Falcucci et al. 2007, Brambilla et al. 2010; EEA 2010; FAO 2010). When coupled with a warmer climate, this trend could reduce the surface and the connectivity of subalpine and alpine areas. In the long term, this can lead to impoverished fauna in mountain ecosystems, not only as a result of the loss of localised and specialised elements in the high altitude belt, but also because of possible difficulties for new colonisations from lower elevations. Obviously, these considerations concern mainly invertebrates and small vertebrates, while the effects of reforestation could be beneficial to some large vertebrates (e.g., Falcucci et al. 2007).

As a general trend, we observed a significantly higher proportion of vulnerable and endemic species in the Alpine belt. The high altitude belt thus emerges as a priority area, containing the highest number of sensitive species for all taxonomic groups. Endemic and vulnerable species often present very narrow ranges and their peaks of presence are not necessarily coherent with species richness, but often shifted to higher altitudes (Schmitt 2009; Vetaas and Grytnes 2002; Colwell and Lees 2000; Bhattarai and Vetaas 2006). In addition, the Alpine belt is characterized by significant environmental constraints (severe climatic conditions, short summer periods, slope, natural hazards) and by the importance of direct and indirect effects of climatological factors, in particular low temperatures (Beniston 2003; Pauli et al. 2004; Körner et al. 2011).

Many species inhabiting alpine habitats are highly specialized and have a finely-tuned physiology for coping with pronounced changes in temperature, air density and oxygen partial pressure (Marchand 1996; Dillon et al. 2006; Altshuler and Dudley 2006). Altitudinal belts can thus constrain physiological capacity and mountain zones can act as islands in a sea of unsuitable habitat (Brown 1971). Consequently, many species are isolated at high elevation; in contrast, lowland communities can occupy climatic niches which are spread over wider latitudinal belts (e.g., Beniston 2003). In the Alps, there is a large number of endemisms of typical 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 experience higher levels of threat and to be vulnerable to climatic and environmental changes (Manne and Pimm 2001; Parmesan 2006).

To fully describe habitat vulnerability our results indicate that species richness, that consider all species in the same way cannot be used as the only indicator, particularly in mountain ecosystems. Number of species, dominance relationships and ecological characteristics of single elements must be analysed at the same time, to identify which areas are important for the different conservation purposes (Rey Benayas and de la Montaña 2003; Orme et al. 2005). We also tested whether the methodologies adopted in our study allow to obtain comparable results, in term of sampling design efficiency, for the different habitats and taxonomic groups. The three vegetation belts investigated here differ in their rarefaction curves, and none of the taxonomic groups reached an asymptote. Thus, they do not allow for drawing general consideration in term of γ -diversity for each belt as a whole.

The ratio of rarefaction curves can be used to compare the way species richnesses of different taxa increase as a function of the number of sampled specimens. This method is often used to compare the category/subcategory ratio in biogeography surveys (Gotelli and Colwell 2001) and only recently it has been applied to the comparison of rarefaction curves between focal species versus all species in biodiversity surveys (Chiarucci et al. 2008) or to analyse cross-taxon congruency (Chiarucci et al. 2007). In our results, the ratio of couples of taxon-specific rarefaction curves displayed some variability, but for all tested pairs the last part of the curve became constant, suggesting similar pattern at least at the end of the sampling effort. The sampling effort for the different vegetation belts and taxa turned out to be sufficient to reach a comparable description of all taxa, allowing to compare diversity indices among taxa and habitats.

Community composition

As already observed for species richness, temperature and elevation play a dominant role in shaping community composition, at the level of individual taxonomic groups and when all taxa are pooled together. However, the low percentage of inertia explained by the first two axes of the Correspondence Analysis indicates that the pattern of community composition is more complex and cannot be easily summarized in a space with reduced dimensionality. Our description of coenosis variation along the first CA axes must, in fact, be aware of these limitations and of the possible presence of explaining variables which are not measured by our sampling design.

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

Results from the Mantel Test partly confirmed what was observed with CA, showing, in almost all taxonomic groups, a strong influence of altitude and temperature on community composition.

We observed that, when the effect of temperature was removed, altitude lost any significance for all taxonomic groups excepts birds. On the contrary, when the effect of altitude is removed first, temperature still remains 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 strongly affect the community composition of the invertebrates studied here, in keeping with the fact that ectothermic organisms are particularly

sensitive to climate (Huey and Stevenson 1979; Frazier et al. 2006). 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 has been observed for birds: since they are endothermic, they are less affected by temperature for their metabolic activities, and the composition of their assemblages seems to be less influenced by climate and more by habitat structure and complexity (Kessler et al. 2001). Some past studies found no clear bird response to temperature trends along altitudinal gradients, probably due 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 remain significant, even when controlling for the other factors. These results underline that, in terms of invertebrate communities, each protected area presents peculiarities that cannot be explained by other factors than their geographical characteristics and distance from the others. Thus, each protected area is important in terms of conservation purposes. The reason can possibly be found in historical factors: the Alps have a high number of endemics and many of them are more or less local endemics in some restricted area (Schmitt 2009). Endemisms are surely important but ecological factors and local climatological circumstances may play a role in shaping present 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 alpine areas, climate could act as the main force driving species richness and community composition across all taxa. The dominant role played by temperature in determining species richness, distribution of vulnerable species and community composition emphasizes the potential vulnerability of mountain ecosystems to climate warming. In particular, the Alpine belt

emerges as an habitat characterised by a peculiar fauna and by a limited number of species which are exclusive of high altitude regions and highly sensitive to environmental changes.

An added value of this work is the successful attempt to coordinate a monitoring programme among different Natural Reserves in the N-W Italian Alps. The results of the programme indicated that each protected area, even if covers a similar altitudinal gradient and has a similar succession of environments, has its own peculiarities in terms of community composition as whole 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 are based on the establishment of long-term monitoring programmes, 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 along these lines for the Italian Alps, creating the baseline against which to assess future changes on the basis of a long term monitoring programme that is planned to be repeated every five years.

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Chapter 4 - Effects of temperature increase scenarios on multitaxa distribution in mountain ecosystems

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Abstract

Mountain ecosystems are among the most threatened in the world because they host rare and fragile biota and they are expected to show more pronounced effects of climate change. Detailed information about biodiversity drivers and cause of vulnerability are essential, but still lacking in particular for invertebrates. Species distribution models represent essential tools to forecast impact of temperature changes and to develop adequate conservation strategies.

In this framework, we applied presence-only distribution models to real field data, coming from a systematic survey of 5 taxonomic groups (birds, butterflies, carabids, spiders, staphylinids) collected along altitudinal gradients, from the montane to the alpine belt.

Purpose of our work is to evaluate the effects of a moderate increase of temperature (three different scenarios) on multi-taxa distribution, described in term of alpha and beta diversity. We considered different level of environmental constraints, to compare only the effects of climate with those of other variables related to vegetation structure.

Our results show small changes in biodiversity patterns but different responses of species, depending on the taxonomic group and the degree of specialization. Models agree that changes in species richness may be particularly significant in alpine belt and particularly strong for endemic and vulnerable species. Community composition changes in a coherent way and becomes more similar to the low altitude ones. Nevertheless, the gradual but clear separation among vegetation belts is still retained after temperature increase scenarios. Considering only temperature-related parameters, effects on biodiversity are enhanced. Moreover, we observed that minimum temperatures are more important in shaping species distribution, if compared to maximum and mean daily measurements.

Our model was able to highlight the relative role of different parameters on biodiversity and to assess future vulnerability.

Key-words: mountain ecosystems, temperature increase, predictive models, biodiversity, multi-taxa approach

Introduction

The evidence of global change and the potential risk of species loss have increased the emphasis on understanding the factors that influence biodiversity patterns and on forecasting how these patterns may vary in the future (Thomas et al. 2004, Araujo and Rahbek 2006, Fitzpatrick et al. 2008, Fitzpatrick et al. 2011). Among the world's environments, mountains are particularly sensitive to the effects of global change (Huber et al., 2005) in particular climate warming, because they are mainly characterized by low temperature conditions (Pauli et al., 2004) and because they support rare and fragile ecosystems (Diaz et al., 2003; Nogues-Bravo et al., 2007).

The Alps, in particular, are under threat, both because they are "biodiversity hotspots" (Ginsberg, 1999; Myers et al., 2000), hosting high level of endemic species (Korner, 2002; Schmitt, 2009), both because they have already experienced exceptional loss of habitat and species (Pauli et al., 2007). Moreover, long-term records in mountain environments (Beniston, 2006) and in the Alps provide evidence for a warming of the climate that is greater than the global average (Calmanti et al., 2007; Auer, 2007; Rebetez and Reinhard, 2008; Keiler et al., 2010) and the projected temperature increase for the 21st century is still higher than observed for the last one (Nogues-Bravo et al., 2007).

The alpine biodiversity has already responded to these changes, as shown in particular for the alpine flora. Uphill shifts of alpine plants (Grabherr et al., 1994; Pauli et al., 2001) and the advance of treeline are documented for several European mountain systems (Meshinev et al., 2000; Kullman, 2003; Moiseev and Shiyatov, 2003) as well as for the Alps (Gherig –Fasel et al., 2007). As a result, community composition has changed at high alpine sites (Keller et al., 2003) with an accelerating increase of species richness (Walther et al., 2005; 2006; Pauli et al., 2007). But this enhance of species richness is presumably transitory (Theurillat and Guisan, 2001) because the decline of arctic-alpine species that go out of their distribution range will reduce alpine biodiversity (Lesica and McCune, 2004).

The number of studies investigating the effects of climate change on alpine fauna is consistently lower, in particular at community level and on a multi-taxa approach, due to the lack of widespread long term monitoring projects. But some clear ecological responses are already recorded, such as uphill shifts of single species due to temperature increase (e.g., Wilson et al., 2005; Battisti et al., 2005), and invertebrates assemblages strongly shaped by climate warming consequences (Gobbi et al., 2006).

Assessing species vulnerability to climate change allow to identify potential risk of biodiversity loss, but requires at the same time good knowledge of current spatial patterns in biodiversity (Botkin et al. 2007) and also the ability to project it into the future. Predictive distribution models, even if with some limitations, are unique and useful tools for predicting species response to climate change and to assess the sensitivity and potential adaptability or resilience of species, habitat and ecosystems (Elith and Leathwick, 2009; Franklin, 2009). Reliable predictions of the likely effects of climate change on biodiversity are extremely useful for identifying the most robust and effective conservation strategies (Mokany and Ferrier, 2010).

The number of techniques currently available is large and increasing (Elith et al. 2006, Heikkinen et al. 2006; Elith and Leathwick, 2009),but among the vast array of possible approaches species distribution models have probably been the most widely used in ecology (Heikkinen et al. 2006; Elith and Leathwick, 2009).

Although species are likely to respond individualistically to climate change, the overall consequences of these changes will be at community and ecosystem level (Menéndez et al., 2006; Kattwinkel et al., 2009). Furthermore, conservation planning and management for biodiversity requires the adoption of multispecies or community approaches (Margules and Pressey 2000; Kattwinkel et al., 2009).

Therefore strategies in which species are initially modelled individually to produce single species predictions and then analysed at the community level ('predict first, assemble later', sensu Ferrier and Guisan, 2006) are particularly useful to study climate change impacts and establish conservation priorities. Nevertheless their potential and even if many recent studies have modelled large numbers of species, few of this have proceeded to community-level analysis of resulting distributions (Ferrier and Guisan, 2006).

Moreover, up to now, there have been few attempts to sum information from community-level modelling of alpha- and beta-diversity (Mokany et al.,2011) especially in order to make climate change predictions.

In 2007 started a multi-taxa monitoring project in the Italian Alps, aimed to analyze in the long term changes of biodiversity in space and time along altitudinal transects, in three protected areas. Results of first monitoring step (unpublished data) have shown that both species richness and community composition of invertebrates are highly related to temperature and altitude. These linkage highlight the potential vulnerability of alpine species and communities to climate change.

In this framework, aim of this work is to assess the risk of alpine animal biodiversity modification in relation to climate change. In particular we would like to simulate the effect of temperature increase on species richness and community composition using a multi taxa approach and assessing effects on alpha and beta diversity, after individually modeling of single species.

Methods

Biodiversity inventory: data sources and species information

The Biodiversity Monitoring Project N-W Italian Alps has been established in 2007 in three protected areas in North-Western Italian Alps: Gran Paradiso National Park, Orsiera Rocciavre Natural Park and Veglia Devero Natural Park. We chose twelve altitudinal transects, starting from the altitude of 550 m and reaching 2 700 m asl with sampling units separated by an altitude range of 200 meters, to allow for independence of sampled data. Sample unit is a circular plot with a radius of 100 meters, labelled as belonging to one of the three belts distributed along the altitudinal gradient (Montane, Subalpine and Alpine), for a total of 69 monitored plots.

In each plot were collected data about 5 taxa: butterflies (Lepidoptera Rhopalocera), birds (Aves), staphylinids (Coleoptera Staphylinidae), carabids (Coleoptera Carabidae), spiders (Arachnida Araneae), census by standardized and cheap methods for a total of 663 species.

Each species was classified as endemic and as vulnerable for the following characteristics: carabids with short wing (brachiptera); birds with an altitudinal optimum above 1500 m; butterfly species with low altitudinal tolerance; species of staphylinids and spiders with low altitudinal tolerance.

Microclimatic conditions were measured by data-loggers (Thermochron iButton, DS1922, Maxim, Sunnyvale, CA, U.S.), located in each sampling plot, programmed to record air temperature every hour throughout the field season (June-September). Raw data were used to calculate following parameters: mean, maximum, minimum and standard deviation of daily measurements. Daily data were aggregate to obtain seasonal mean values for each parameters. Each sampling unit was further characterised by: mean altitude, geography (categorical variable, indicating the park) and percentage of ground covered by different structural layers, estimated by eye during field surveys: herbaceous layer, low shrubs (< 1 m), tall shrubs

(between 1-5 m), trees, stone/bare ground cover and an index of structural diversity (1-Simpson Index built on percentage values of herbaceous layer, shrubs and trees cover).

Model simulation: current conditions and temperature change scenarios

Seven plots were excluded because of temperature missing values and 359 species were excluded because present in less than 4 plots. We selected 4 as threshold value below species' occurrence is considered only accidental and not enough detailed for further estimations.

Consequently, for modelling purposes a data-matrix of 304 species and 62 plots was available.

Each species was modelled individually. We performed species distribution models based on presence-only data using Maxent software version 3.3, developed by S. Phillips and colleagues (freely available at <http://www.cs.princeton.edu/~schapire/maxent>).

We favoured presence-only instead of presence/absence analysis to reduce problems related to unreliable absence records and to focus attention on environmental predictors, chosen as important, reducing the effect of varying detectability of species from site to site and reducing the influence of confounding factors, e.g., human disturbance, in determining observed distribution (Jimenez-Valverde et al., 2008).

Maxent models the species distribution directly by estimating the density of environmental covariates conditional on species presence: it gives a logistic output format, that estimates probability of presence, given the environment (see Phillips et al., 2006 and Elith et al., 2011 for a detailed explanation of methodology).

This model is robust with small datasets, because it is not a regression, but a density estimation method (Phillips and Dudík, 2008; Franklin, 2009) and it is more stable when correlated variables are used (Elith et al., 2011), allowing us to analyse simultaneously temperature-derived parameters and altitude.

We used the default parameterisation of Maxent with 62 points of background that are our monitored plots, because predictions are limited to the set of sampling units, in which all data are collected at the same scale.

As environmental predictors, we chose the variables that define micro-climate, altitude, geographic position and vegetation cover conditions, measured in each plot (see 2.1). We combined them in three different ways, to obtain models with an increasing number of environmental constraints (from here called Environmental Conditions):

- Temp, that consider only temperature-derived parameters and altitude to model species distribution;
- Tempark, that consider temperature-derived parameters, altitude and geography;
- All, that consider temperature-derived parameters, altitude, geography and vegetation cover conditions.

To project species distribution, at each model (TEMP, TEMPARK, ALL) we applied three different scenarios of temperature change:

- 1Degree, in which minimum, mean and maximum temperature are all equally increased by 1° C;
- 1.5Min, in which, minimum temperature is increased by 1.5° C, maximum by 0.5° and mean by 1°;
- 1.5Max, in which minimum temperature is increased by 0.5°, mean by 1°, maximum by 1.5°.

Available literature about temperature trend in the alpine areas during the last century support our choice, in particular Beniston (2006), which observed a larger increase of minimum temperature, and Ciccarelli et al. (2008), which detected the same increase but for maximum temperature.

We evaluated each single model using the area under the curve (AUC) of the receiver-operating characteristic plot (ROC) with resubstitution method, i.e. using the same data for training and for testing the models. This measure tends to provide optimistic values of prediction success (Fielding and Bell, 1997), but we consider this less important in order to assess potential effects of temperature changes on species distribution. Species with an $AUC < 0.6$ were considered as stable through temperature scenarios.

On these assumptions logical thinking of our models was to evaluate effects of temperature increase on current species distribution assessing the role of environmental predictors in determining species and habitat vulnerability (Fig. 1).

Model output analysis

We transformed model output in presence/absence data using as decision threshold the minimum training presence logistic value. It allows to identify like present sites at least as suitable as real presence.

After running all the models for every single species, accounting for individual responses, we calculate the parameters of alpha and beta diversity in order to evaluate differences from the current situation following the recommendations of Olden et al. (2006).

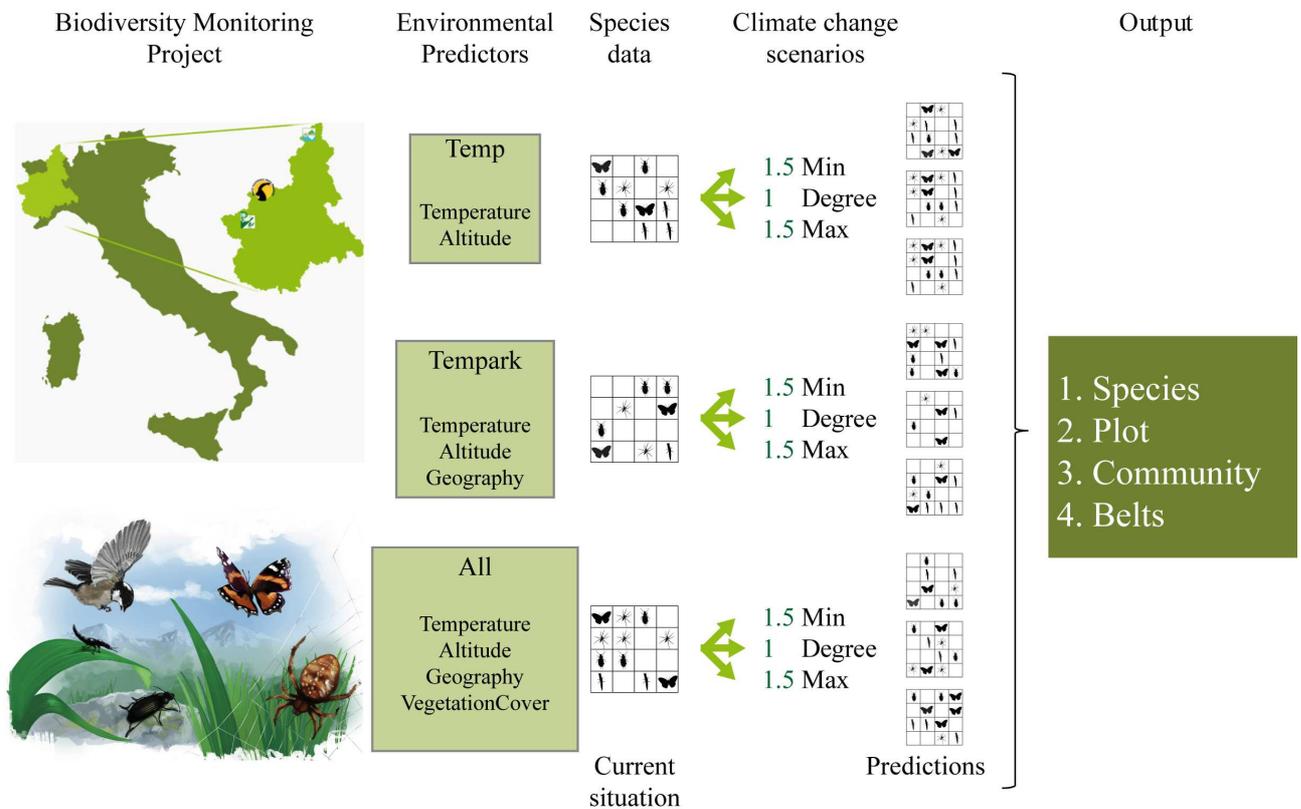


Fig. 1. Conceptual model idea

Alpha diversity

For each environmental condition, we compared every scenario to the current distribution, both in term of species richness per plot, both in term of number of occupied plots per species. Differences are tested with Wilcoxon Rank Sum Test, applied at first to all the dataset and then to subsets of species (taxonomic groups, endemic and vulnerable species) and plots (vegetational belt).

To see if the three scenarios and the three environmental conditions significantly differ in affecting species distribution, we applied Friedman ANOVA Test both to number of plots per species and to species richness per plot. Then we evaluate the differences between taxa in the number of plots gained or lost in the future predictions (Kruskal Wallis test). The same test was used to compare differences in the number of species gained or lost in each vegetation belts. Moreover we highlighted differences in the number of plot gained or lost for endemic and vulnerable species compared with the others (Mann Whitney Test).

We classified species in 3 categories of change based on the number of plots gained or lost in each scenario and environmental condition: above III quartile, below I quartile, between these two values (extremes included). To analyse taxa vulnerability, we applied χ^2 on contingency tables of number of species per taxa among these three groups. Therefore the marginal proportions were compared with McNemars test. Due to small sample size, we computed exact probabilities (p-values), using binomial probability distribution (Agresti 2007), in order to identify species that significantly increase or decrease their number of plots.

Beta diversity

We used Mantel Test on Jaccard Index, calculate from presence/absence data to highlight significant relationships between similarity structure of observed and predicted communities (significance level assessed after 999 permutations).

To evaluate the effects of temperature increase on community structure, we applied CA (Correspondence analysis) to presence/absence data, for each taxon and for each environmental condition, comparing one scenario per time with the corresponding current baseline. We analysed pairs of plots in a reduced space of two axes. Significance of axes was tested comparing explained variance with a random distribution of 999 data matrices, changing presence of species across plots, while keeping prevalence constant.

To interpret axes in terms of environmental factors, we used Pearson correlation coefficient between plot scores and environmental parameters.

The significance of temporal shift in species composition was tested (Wilcoxon Rank Sum Test) as well as differences in amount of change among vegetation belts (Kruskal Wallis Test). To look for community homogenization after temperature increase scenario, we calculate, in each two- dimensional CA, distance from centroid, both for projected, both for current plot and compare them with t-test for paired samples (significance level assessed after 999 randomizations, following Legendre, 1998).

To compare amount of changes among taxonomic groups, environmental constraints and scenarios, we calculated Jaccard Indexes between species composition in each modeled plot and the corresponding baseline and compared them with Friedman ANOVA Test.

Statistical analysis were performed using Statistica 6.0 and R 2.14.1.

Results

Current models description

All analyses were based on 304 species: 45 Carabidae, 80 Lepidoptera, 99 Araneae, 40 Staphylinidae and 40 Birds. Among them, 42 were endemic and 87 vulnerable.

For each species we run three Maxent models (Temp, Tempark, All) for a total of 912 current distribution datasets. Only in 35 cases single models were inadequate ($AUC < 0.6$), 29 in Temp, 6 in Tempark and 0 in All; in these cases, species presence was considered constant in the temperature increase scenarios.

Species richness per plot obtained using Maxent models for estimate current distribution is, in almost all cases, much higher than field data (min=+2, max=+171). This increase is different among environmental conditions: in particular All shows lower values (mean 87.5 ± 3.19 s.e.) if compared with Temp (mean 119.39 ± 2.99 s.e.) and Tempark (mean 125.82 ± 2.42 s.e.).

Number of occupied plots is highly variable from species to species, even reaching an increase of 58 plots. Mean values per environmental conditions follow the same patten as species richness, with highest values in Tempark (25.66 ± 0.81), followed by Temp (24.06 ± 0.71) and All (17.84 ± 0.70).

Alpha diversity

For each environmental condition, we run three different scenarios, for a total of 2736 future distribution outputs.

Comparisons between each scenario and the corresponding baseline (current distribution of the same environmental condition) show high variability in species' response to temperature increase.

The majority of species show no variation (42%), some others show an increase (32%), whereas the lower percentage a decrease in number of occupied plots (27%). On the opposite, considering only endemic and vulnerable species, in both cases, the percentage of decreasing species is higher (44% for endemics; 42% for vulnerable species) and the percentage of increasing is lower (28% for endemics; 23% for vulnerable ones) (Fig.2).

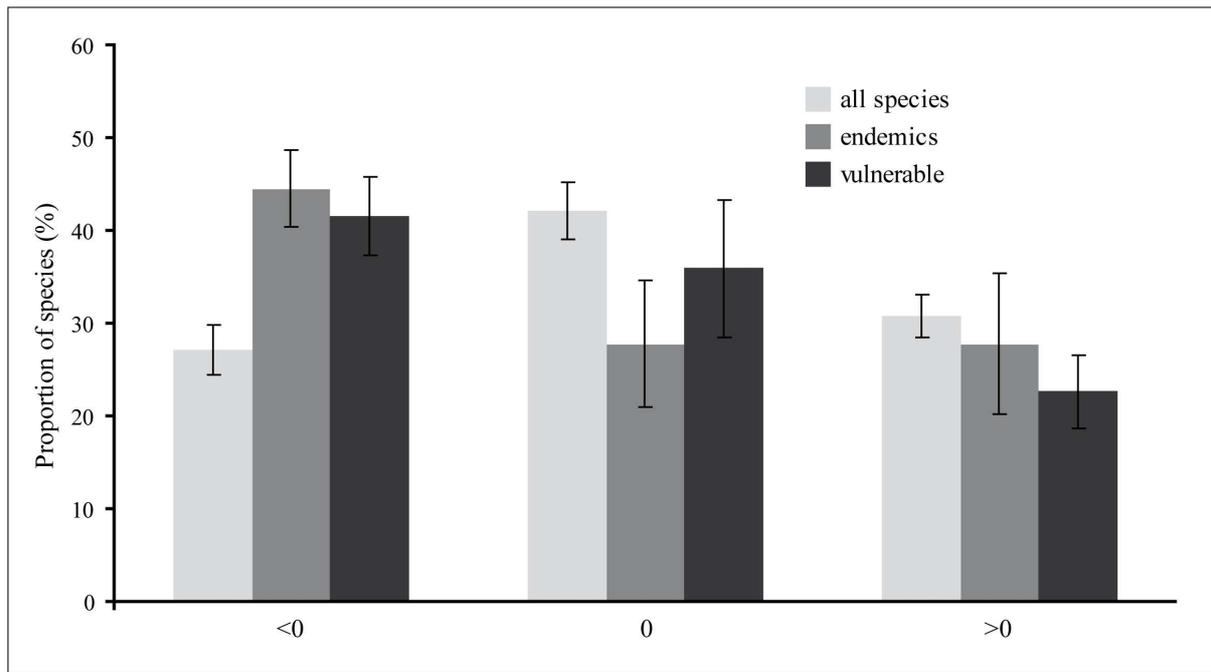


Fig. 2. Percentage of species that show no variation (0); increase of area occupied (>0) or decrease (<0). Bar charts represent mean percentage and error bars the standard deviation among environmental conditions and scenarios.

Considering species that show some variation, the amount of change is usually low: 31.7% of changing species presents small variation (1 or 2 plots in both direction). Moreover, results from marginal homogeneity test show that the highest amount of species are ‘stable’ (241.44 ± 7.65 , among environmental conditions and scenarios), meaning that the number of acquired plots is not significantly different from the number of lost one and viceversa. The proportion of taxonomic groups among categories of change (below the I quartile, above the III quartile, in between) present significant differences only in two cases (Tempark, 1Degree: $\chi^2=17.508$, p-value=0.028; All, 1.5Max: $\chi^2=17.947$, p-value=0.024), but butterfly presents always the highest proportion within the increasing species (I quartile: 25.09 ± 0.93 , III quartile: 36.46 ± 0.77), while spiders the lowest (I quartile: 36.47 ± 0.74 , III quartile: 22.83 ± 0.89).

Differences are detected comparing species richness between each scenario and the corresponding baseline, in particular among taxonomic groups and environmental conditions. Carabids do not show significant differences in any comparison. Butterflies display an increase in species richness per plot, in particular considering the alpine belt. For spiders results show the opposite trend, with current species richness significantly higher in almost all cases. Staphylinids and birds show different results when considering different environmental conditions. The overall species richness shows a significant decrease considering only ‘temp’ or ‘tempark’ conditions both in all the study area and both in the montane and subalpine belts.

On the opposite considering all the variables the species richness in the total area seems to significantly increase (Table 1)

Table 1. Results of Wilcoxon T test of all plot and the three vegetation belts for the three different scenarios (1.5Max, 1.5Min, 1Degree) under different environmental conditions (Temp,Tempark, All) for each taxon (car= Carabidae, lep= Lepidoptera, ara= Araneae, staf=Staphilinidae, bir=Aves, all= all taxa together). NS= not significant, += significant increase of species respect to the actual, -= significant decrease of species. P-values= *p<0.05, **p<0.01, ***p<0.001.

		All plot			Montane belt			Subalpine			Alpine		
		1.5Max	1.5Min	1Degree	1.5Max	1.5Min	1Degree	1.5Max	1.5Min	1Degree	1.5Max	1.5Min	1Degree
Temp	car	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
	lep	+***	+	+**	NS	NS	NS	NS	NS	NS	+***	+***	+***
	ara	-.***	-.***	-.***	-.***	-.***	-.***	-.***	-.***	-.***	NS	NS	NS
	staf	-.*	NS	NS	-.**	-.*	-.*	-.*	NS	NS	NS	NS	NS
	bir	-.*	NS	NS	NS	NS	NS	-.*	NS	NS	NS	NS	NS
	all	-.**	-.**	-.**	-.**	-.**	-.**	-.***	-.***	-.***	NS	NS	NS
Tempark	car	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
	lep	NS	NS	NS	NS	NS	NS	NS	NS	NS	+++	+++	+++
	rag	-.**	-.***	-.***	-.**	-.**	-.**	-.**	-.***	-.**	NS	NS	NS
	staf	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
	ucc	NS	-.*	NS	NS	NS	NS	NS	+	+	NS	+	NS
	all	NS	NS	NS	NS	-.*	-.*	-.**	-.*	-.*	NS	NS	NS
All	car	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
	lep	+***	+***	+***	NS	NS	NS	NS	+	NS	+++	+++	+++
	rag	-.**	NS	-.*	-.*	NS	NS	NS	NS	NS	NS	NS	NS
	staf	NS	+***	+**	NS	+	NS	NS	NS	NS	NS	+	NS
	ucc	+	+***	+**	NS	NS	NS	NS	+	NS	+	+	+
	all	NS	+***	+***	NS	+++	NS	+	NS	NS	NS	+++	+

The number of species gained or lost with respect to the current modelled situation is significantly different between vegetation belts. In general alpine belt seems to be positively influenced by temperature increase for butterflies, spiders and overall species richness and in some of these cases the subalpine belt loses an higher number of species. Only for staphylinids and for one scenario montane belt loses more species than the others (e.g. Fig. 3).

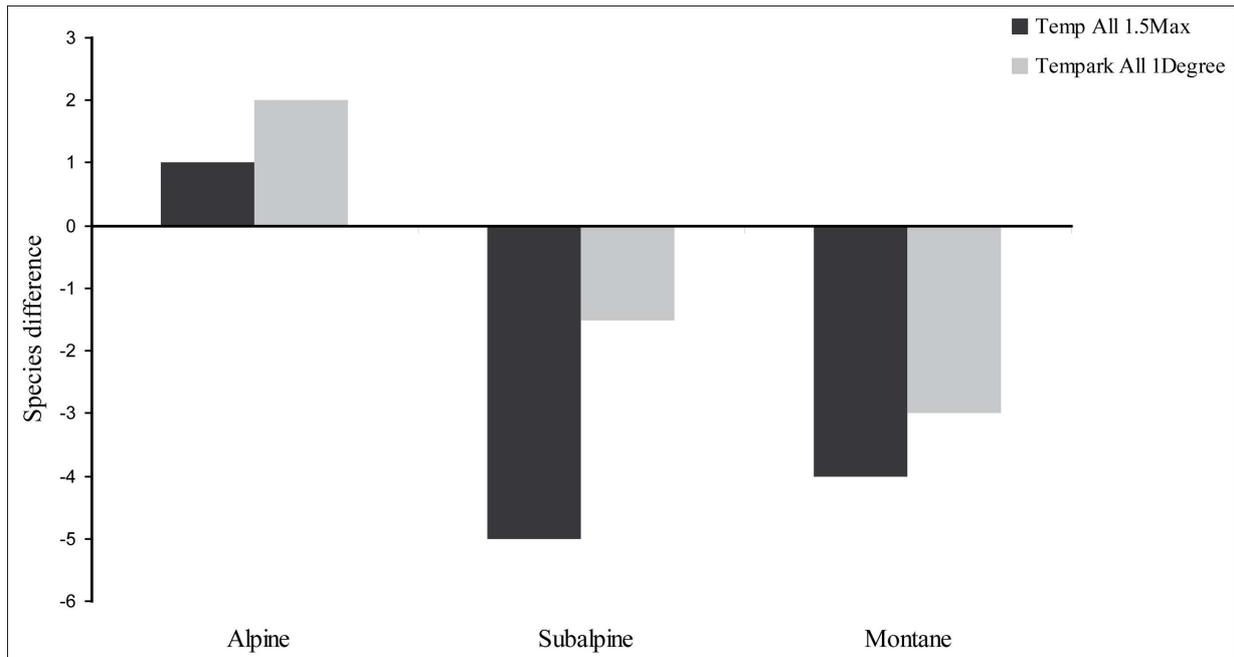


Fig. 3. Bar chart of the difference between current and projected species per plot in the three vegetation belts for all taxa pooled together in Temp environmental condition, 1.5Max scenario (grey) and in Tempark environmental condition, 1Degree scenario (light grey).

The comparisons performed considering for all species the number of plots gained or lost show almost no difference with the current situation except for butterflies where we detected a significant increase of number of plots considering all the environmental variables. Concerning only endemic species we found a significant decrease of plots for all taxa in two out of the three scenarios under tempark environmental conditions. Moreover vulnerable species of butterflies and spiders such as all the vulnerable species show for all the scenario and the three different environmental conditions a significant decrease in the number of plot (Wilcoxon T test, $p < 0.05$).

No difference between the taxonomic group was found in terms of number of plots gained or lost respect to the current situation (K-W test, ns). On the opposite endemic species always gains less plots than the others for the three scenarios and in two out of three environmental conditions (Tempark and All, Mann Whiney tests with all p-values < 0.05). Also vulnerable species for all scenarios and conditions gains significantly less plots than non vulnerable ones with all p-values < 0.01 (e.g Fig. 4).

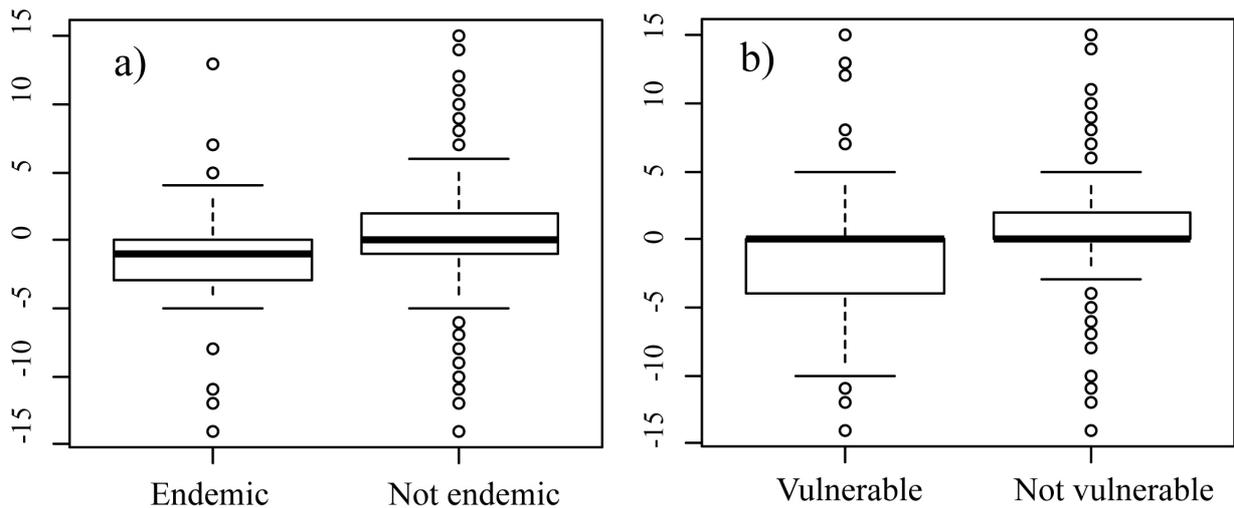


Fig.4. Box plot of the number of plots gained or lost for endemic and vulnerable species in Tempark environmental condition, 1.5Min scenario. The box shows median, first and third quartile, whisker represent minimum and maximum values and outliers are plotted as circle.

Environmental conditions and scenarios

Some interesting results came when comparing the three environmental conditions.

We observed that the number of ‘increasing’ and ‘decreasing’ species is lower with a higher number of environmental variables. In particular the ‘decreasing’ change from STemp=46.67, STemPark=32.33 to SAll=18.67, and the ‘increasing’ from STemp=40.67, STemPark=27.33 to SAll=22.00. ‘Decreasing’ species are higher than the ‘increasing’ ones with Temp and TemPark, while lower with All.

None of the three environmental conditions differs from the others in the number of plot gained or lost neither for each taxonomic group and neither for all the taxa pooled together. In terms of species the three conditions are different and when all environmental variables are considered the predicted species richness is always lower than the other two conditions (Friedman ANOVA tests, always $p < 0.000001$). On the opposite the number of species gained or lost is always significant different from the others and higher when all the environmental variables are taking into account while the conditions with only temperature constraints gains always less species than the others, this is true for all the taxonomic group except carabids and for almost all the scenarios (Tab.2 and Fig. 5).

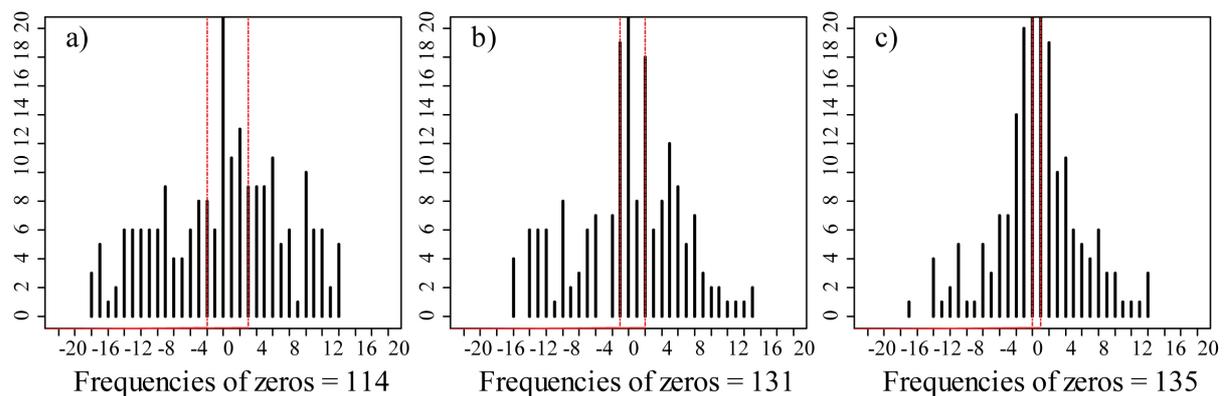


Fig. 5. Frequency distribution of number of plots gained or lost per species for all the taxa pooled together, 1.5Min scenario in Temp (a), Tempark (b), All (c). Red lines indicate first and third quartile. Number of species with no variation (zeros) are shown until 20, real frequencies are written under the graphs.

Comparing scenarios, we observed a higher number of non ‘stable’ species with 1.5Min and a lower one with 1.5Max, showing a higher impact of minimum daily temperature in species distribution.

Table 2. Friedman ANOVA tests between the three environmental conditions for the three scenarios (Sig. env.) and viceversa (Sig.scenario). In bold are significant test results. Values indicate the mean number of species gained or lost per plot comparing with the current situation.

Scenario	Environmental condition	car	lep	ara	staf	bir	all
1.5Min	Temp	0.290	1.129	-1.935	0.177	-0.161	-1.903
	Tempark	-0.065	0.387	-1.500	-0.016	0.355	-0.839
	All	0.032	1.258	-0.565	0.565	0.516	1.806
	Sig.env.	<i>NS</i>	<i>NS</i>	<0.01	<0.05	<0.001	<0.001
1.5Max	Temp	0.274	1.710	-1.677	-0.468	-0.403	-1.968
	Tempark	0.097	0.581	-1.032	-0.081	0.145	-0.290
	All	0.032	1.097	-0.839	0.290	0.258	0.839
	Sig.env.	<i>NS</i>	<0.01	<i>NS</i>	<0.05	<0.001	<0.001
1Degree	Temp	0.274	1.403	-1.710	-0.194	-0.306	-1.935
	Tempark	-0.113	0.403	-1.419	-0.016	0.258	-0.887
	All	0.129	1.242	-0.581	0.468	0.371	1.629
	Sig.env.	<i>NS</i>	<i>NS</i>	<0.01	<0.05	<0.01	<0.001
Sig.scenario	<i>Temp</i>	<i>NS</i>	<i>NS</i>	<i>NS</i>	<0.001	<i>NS</i>	<i>NS</i>
	<i>Tempark</i>	<i>NS</i>	<i>NS</i>	<i>NS</i>	<i>NS</i>	<i>NS</i>	<i>NS</i>
	<i>All</i>	<i>NS</i>	<i>NS</i>	<i>NS</i>	<i>NS</i>	<0.05	<0.05

No difference was detected between the three scenarios in the number of plots gained or lost while considering number of species except for carabids and butterflies we found some peculiarities. The 1.5Max scenarios loses more species than the others for spiders in the montane belt and for the overall species richness in the total area. 1.5Min scenario gains more species for staphilinidae and birds in total area and for birds in two out of the three vegetation belts. A more marked situation were found for staphilinidae in the subalpine and alpine belts where 1.5Min gains more species than the others and 1.5Max less. In only one case (Staphilinidae in the subalpine belt considering temperature and geography) 1Degree scenario gains more species than the others (Table 2).

Beta-diversity

Mantel Test results show high values of correlation coefficients: they are always highly significant (all p-values<0.001) and above 0.9, with values comprise between 0.923, for carabids, with All variables, in the 1degree scenario, and 0.991 for all taxa pooled together, with All variables, in the 1.5Max scenario. Even if plots are grouped among vegetation belts (montane, subalpine, alpine belts), the correlation coefficients are always highly significant (all p-values<0.001), and comprise between 0.857, for carabids in the Alpine Belt, with Temp variables, in the 1.5Min scenario, and 0.991, for all the taxa pooled together in the Alpine Belt, with All variables, in the 1.5Min scenario.

First and second CA axes are always significant ($p < 0.001$, after 999 randomizations), for each taxonomic group and for all the taxa pooled together. In each taxonomic group and within the same environmental conditions, the amount of explained variance do not present high differences among scenarios (0.217 ± 0.041 mean percentage difference with 1degree as baseline for the first axis and 0.127 ± 0.020 for the second).

On the opposite, concerning environmental conditions, the common trend in all taxonomic groups is that the highest amount of explained variance, for the first axis, is with Temp (mean values among scenarios, from 42.51% for Staphylinids to 52.36% for Birds), followed by TempPark (mean values among scenarios, from 26.23% for Staphylinids to 44.45% for Birds) and All (mean values among scenarios, from 19.68% for Staphylinids to 36.70% for Birds). For the second axis, the highest amount of explained variance has been found, for all the taxonomic groups, with TempPark (mean values among scenarios, from 13.32% for Birds to 23.14% for Carabids).

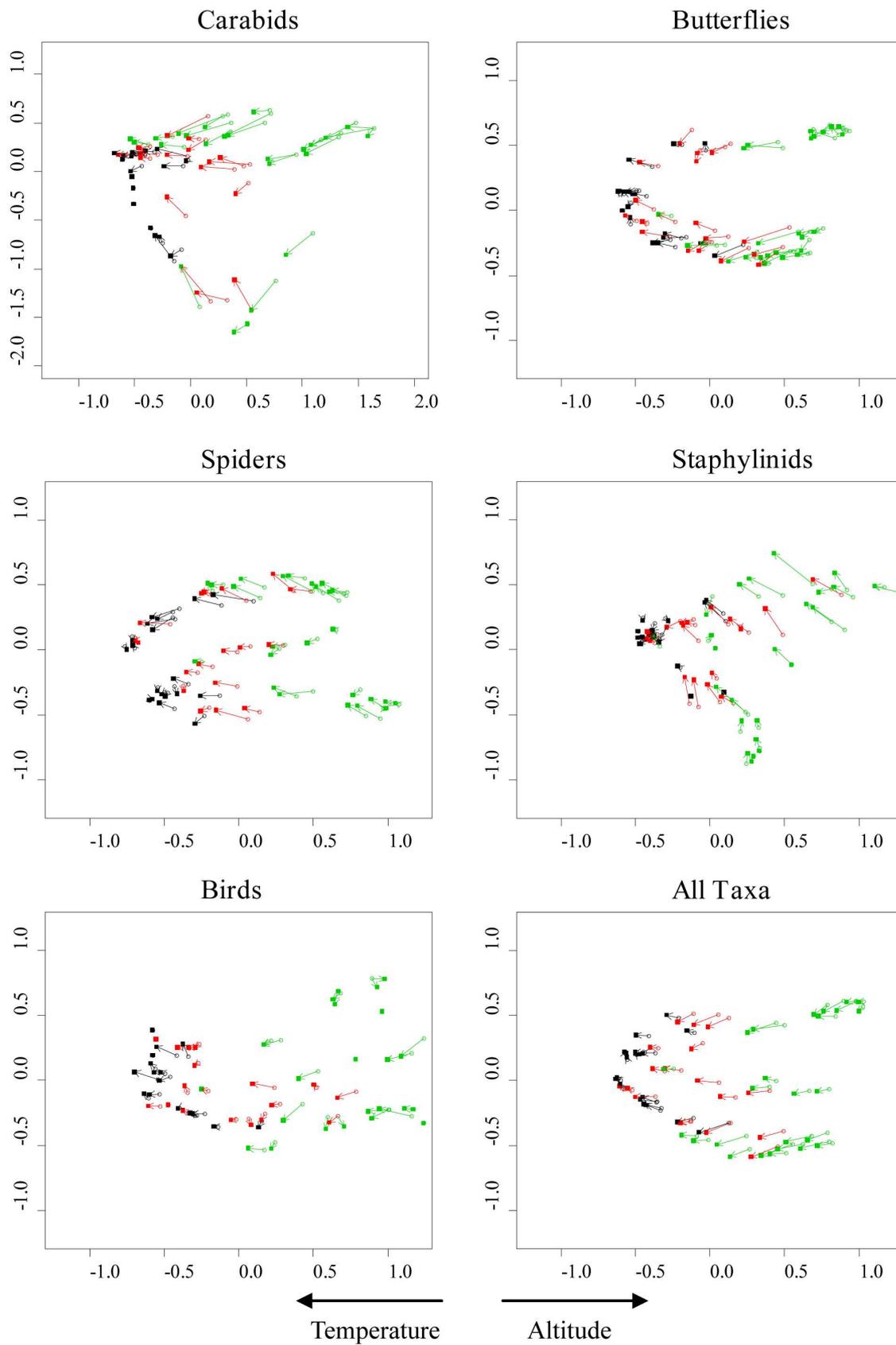


Fig. 6. Correspondence Analysis (CA) with TemPark environmental condition in the 1.5Min scenario, for each taxon and all taxa pooled together. Open circles indicate present situation, while filled square the projected one. Arrows indicate shift of each plot. Different colours mean different vegetation belt (green=alpine, red=subalpine, black=montane). First axes are all positive correlated with altitude and negative with minimum temperature.

First axis (Fig. 6) is determined by altitude (Pearson correlation coefficient above 0.7 in 54 cases to 54, ranging in absolute values from 0.81 to 0.93), T_{\min} (54 to 54, from 0.70 to 0.88) and T_{mean} (51 to 54, from 0.71 to 0.92). No clear and common environmental trend has been found for the second axis: only in 10 cases we found a correlation above the fixed threshold, always with T_{sd} (from 0.68 to 0.75). Plot are distributed from the montane to the alpine belt along the first axis, with significant differences in plot scores among belts (Kruskal-Wallis test, $df = 2$, all $p < 0.0001$) that are still retained in the projected plots (Kruskal-Wallis test, $df = 2$, all $p < 0.0001$).

Spearman Rank Correlation coefficients of coordinates of present vs projected plots are always high in all tested CA, both for the first axis ($0.978 < \rho < 0.998$), both for the second ($0.894 < \rho < 0.997$).

The median change in plot scores from present to projected is significantly different from zero along the first axis in 53 cases (Wilcoxon signed rank test with $p < 0.01$ in all cases except one, Staphylinids with All variables, 1.5Max scenario). Along the second axis, results are less coherent: significant results (Wilcoxon signed rank test with $p < 0.01$) have been observed in 35 cases to 54.

Differences between pairs of plot (present minus projected) among vegetational belts along the first axis show an interesting pattern. They are significant for carabids (Temp and Tempark, all scenarios) butterflies (Temp, all scenarios; Tempark, 1.5Min, 1Degree; All, 1.5Max), staphilinidae (only Tempark, 1.5Min and 1Degree) and all species richness (all env. constraints and scenarios) showing the lowest values (around 0) for the montane belt (e.g. Fig. 7).

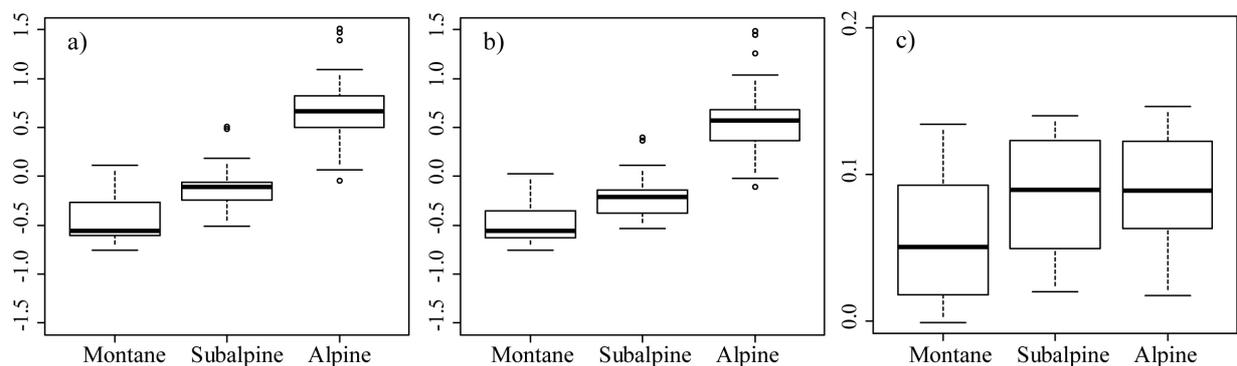


Fig. 7. Analysis of plot scores along the first axis, obtained from CA of all taxonomic group pooled together with All as selected environmental condition in the 1.5Min scenario. Plots are grouped on the base of their vegetational belt (Mon=Montane Belt, Sub=Subalpine Belt, Alp=Alpine Belt). Values for plot scores are represented separately for the present situation (a) and the projected one (b). Differences between present and projected scores are drawn to show differences in rate of change among belts (c). The box shows median, first and third quartile, whisker represent minimum and maximum values and outliers are plotted as circle

Mean euclidean distance from centroid in the first two dimensions, compared between present and projected plots is always higher in present situation, but not all differences are significant (29 to 54 $p < 0.05$ after 999 randomizations).

We observed that in all environmental conditions and scenarios Jaccard Indexes values are low, near to 0, but they always significantly differ among taxonomic groups (Friedman ANOVA Test, all p -values < 0.0001), reaching the highest values in carabids ($J=0.138$, as mean values of all comparisons) and the lowest in birds ($J=0.067$). Considering all the taxa pooled together, we observed significant differences among scenarios ($p < 0.0001$), with the lowest values in 1.5Max, and among environmental constraints ($p < 0.0001$), with the highest values with Temp.

Discussion

Maxent approach allow us to consider even rare and localized species and to combine species distribution models in term of alpha and beta diversity in order to deep investigate the role of temperature in shaping biodiversity of mountain ecosystems.

Our results confirm that, even if with a conservative increase of temperature, species richness and community composition of taxa studied show some modifications.

We detected an high variability of reaction in each species considered. This may depend on the position and breadth of the climatic niche of the species, the corresponding geographic position and the size of the species range.

Differences are not uniform among groups of species or sites. The majority of modeled species do not show any differences, but, as a general pattern, we observed that endemic and vulnerable species are more affected, in term of number of plots lost. Even inside our altitudinal gradient, these species are highly specialized and restricted to a limited range of temperature.

Other studies, both on modelling approach, both on real data, have observed that endemic species will be particularly affected by climate variations also because the rate of change is likely to exceed the migration capacity of many range-restricted species (e.g., Pearson, 2006; Dirnböck et al., 2011).

Vulnerable species that are habitat specialists and poor dispersers, selected for traits advantageous

under stable environmental conditions (e.g. brachyptery and loss of flight dispersal) can be negative influenced by environmental changes (Zera and Denno, 1997).

Moreover the probability of extinction under climate change reflects the species' ability to shift with suitable habitats (Pearson, 2006; Engler et al., 2009; Ozinga et al., 2009) and species restricted to cool will suffer most (Settele et al., 2008) due to less availability of habitats.

There are some differences of reaction between taxonomic groups. Carabids collected inside our monitoring programme did not show any relationship with temperature (unpublished data). Consequently, they do not display great changes under our scenarios. Butterflies feel the effects of temperature increase showing for all the scenarios and environmental conditions a higher proportion of plot occupied and are the taxa with the highest proportion of increasing species. Butterflies are strictly heliothermic and their distribution is highly determined by temperature. A small increase in temperature should effectively determine a transient increase in species richness. But at the same time species more linked to high altitude are negatively affected.

On the contrary spiders seem to suffer from temperature variation showing a decrease in the number of areas occupied. In our monitoring spiders were highly localized and most species present in a small number of plots; therefore, variation of microclimatic conditions can reduce the areas of occurrence.

In terms of community composition, we observed significant modifications in all cases (environmental conditions, scenarios, taxa), meaning that plot composition changes in a coherent way and that the differences among vegetation belts are retained even after temperature change scenarios.

As already showed by other studies both with modelling approach, both with real data focused on plants (Walther et al. 2005; Vittoz et al., 2009; Jurasinski and Kreyling, 2007) we observed the rise from below of species belonging to bioclimatic belts at lower altitudes, with consequent increase of species richness in the alpine belt.

According to our simulation, meadow potentially could experience the greatest changes in fauna under climate change with a pattern robust for butterflies, staphylinids, spiders and all taxa pooled together. But the enhance of species richness is presumably transitory (Theurillat and Guisan, 2001) because the decline of arctic-alpine species that go out of their distribution range will reduce alpine biodiversity (Lesica and McCune, 2004).

In the subalpine belt species lost outweighs species gains, in almost all scenarios and environmental conditions as a signal that species shifts is greater from subalpine to alpine than from montane to subalpine belt. In several studies this belt is used as a fingerprint of

climate change because ecotones are considered particularly sensitive to altered temperature regimes (e.g. Theurillat and Guisan 2001).

Montane belt almost never gains species, because in our study it represents the inferior limit of the gradient. But some plots show temperature values lower than the ones in the subalpine, due to the choice of the belts, based both on altitude and potential vegetation (Körner, 1999; Grabherr et al., 2003) and this leads to an increase of species number. As a mirror of the changes in species richness in the montane belt community composition seems to be more stable while the subalpine and alpine belts show the high turnover due to species shifts. These species forge new ecological relationships with each other and with current species and the character of species interactions as well as fundamental ecosystem processes stands to become transformed in unforeseen ways (Walther et al., 2002; Schmitz et al., 2003).

Due to the sources of uncertainty about the land use changes (Dirnböck et al., 2003) we did not simulate them but to partial out the relative importance of temperature rather than environmental and geographical variables we modelled different levels of constraints.

We found a slight overall increase in potential species richness with increasing of the environmental variables considered. In models run under 'all' condition the effects of temperature variations are minimized resulting in less species lost because also the others variables affect the probability of occurrence buffering microclimatic changes. More pronounced effects on species turnover are found when only variables linked to temperature are considered: this environmental condition seems to enhance the simulated effects of temperature increase.

Considering that the direction of the temperature parameters changes are not consistent between different studies (Beninston,2006; Ciccarelli, 2008) we simulated three scenarios with different levels of increase in minimum and maximum daily temperature.

We observed that 1.5Min displays the higher variation and 1.5Max the lower. In particular under 1.5Min scenarios we found the major gain of species suggesting that minimum daily temperature can limit species distribution (Coulson et al., 1995; Sykes et al., 1996). Considering that minimum temperature have increased at a faster rate than maximum temperature during the latter half of the 20th century (Easterling et al.,1997; Vose et al.,2005), variations in biodiversity pattern greater than the one predicted by our models can occur.

In conclusion, although it cannot be known definitely how species richness and community composition will change, present results suggest that even moderate temperature increase has the potential to influence the distribution of animal biodiversity in N-W Italian Alps.

In particular marked increases in species richness is likely to occur in cool areas like alpine ones and for some taxa, while it is probably a decrease in the number of endemic and vulnerable species with a consequent change in community composition. Predictive models are always affected by sources of uncertainty but are helpful to explore biodiversity patterns especially when few occurrence data are available (Elith and Leathwick, 2009). Even with caution due to the limitation of these models they can be used as support in conservation and management decisions. Space for time substitution used to simulate next future patterns must be validate. Our conservative approach allow us to compare in the next future real changes in species responses using repetitions (every 5-years) of the same monitoring programme. Long term field data are essential for revising and fine-tuning these predictions in order to design effective conservation strategies.

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Chapter 5 - Conclusions

Main results

In this thesis, the relationship between climate and alpine biodiversity was explored by using both a single taxa approach (Chapter 2) and both a multi taxa approach (Chapter 3).

Moreover in order to assess potential risk for biodiversity we modelled the species richness and community composition described in Chapter 3 simulating effects of temperature increase through different scenarios (Chapter 4).

The results underline the tight influence of climate parameters on biodiversity.

In Chapter 2 in particular we analysed how density and meteorological variables affected the growth rate and lek attendance of a black grouse population in one Alpine protected area of the Western Alps. We choose this approach because population dynamic could be considered a fundamental unit of measure of species health and because black grouse has particular habitat requirements. Consequently his presence and the status of his populations are highly correlated with presence of other species (Angelstam et al., 2002). Managing the habitat for “umbrella species” that act as surrogate of biodiversity, can successfully maintain favourable conditions for several species.

The best-performing model, which included the effects of density dependence, early June rainfall and December temperature range, could be driven by the output of a regional climate model and used to estimate future trends in black grouse populations in this area.

While models explaining changes in population abundance are well defined, we failed to detect key factors affecting lek attendance by males. The reason of a lower lek attendance in the last years should possibly be caused by habitat modifications that occurred in the area, such as shrinking of the ecotone and of the size and number of open areas used as leks, due to shrub encroachment induced by rising temperatures and abandonment of high pastures. The scarcity of suitable display sites can in fact induce males to a non-lekking mating strategy (Höglund and Stöhr, 1997).

Also multi taxa approach used in chapter 3 highlight the influence of climate on biodiversity structure. Temperature, in particular, seems to be the most important factor affecting species richness and community composition of ectotherm species with patterns coherent for different taxonomic groups. It was also possible to individuate the most vulnerable species and the most fragile habitats. The strong link with temperature highlights the potential sensitivity of alpine biodiversity to climate variations.

Climate change disproportionately threatens species with small or isolated populations or distribution sizes, narrow habitat requirements, and poor dispersal abilities. These traits increase the risk that climate variation will result in decline in population size and local extinctions, whilst reducing the ability of species to exploit novel resources or colonize climatically suitable locations (Wilson, 2009). Mountain ecosystems represent, at the same time, areas where many species present such vulnerability and where the exposure to climate change is extreme.

In this framework this study represents a good starting point to evaluate future changes. This mostly because were employed different taxa to gain a more comprehensive image on the effects on biodiversity. Moreover the use of altitudinal transects ensure the possibility to cover a broader set of habitats and vegetation belts, increasing the probability to individuate the more vulnerable ones. Value of the monitoring project delineated here will further increase in the future, as soon as time series will be available, and community data will be compared with variation in climatic parameters.

It will be possible to compare the different sites in a more rigorous way, and further investigate possible gradients and outliers in the patterns of diversity.

Finally because loss of biodiversity is commonly characterised by species extinction rates and by depletion of single populations, that could determine substantial changes in biodiversity pattern, in Chapter 4 we try to predict how species richness and community composition determined in Chapter 3 could react to temperature increase scenarios. Our results suggest that current climatic change has the potential to influence the distribution of animal biodiversity in N-W Italian Alps. Models agree that changes in species richness and community composition may be particularly significant in alpine belt and particularly strong for endemic and vulnerable species.

Future research

Results from both the single species (Chapter 2) and the multi taxa approach (Chapter 3) suggest that even other parameters could be important in shaping observed patterns.

Considering the multi-taxa approach, deeper analyses focused not only on mean summer temperatures but also on other meteorological variables are strongly desirable.

Moreover longterm records on vegetation changes obtained using satellite and airplane images can provide useful information about the habitat suitable for these species. These data can be also used to integrate models of black grouse population dynamic and to explain

non-lekking mating strategy of males. The same data on vegetation changes represent a starting point to predict future land cover modifications. Changes in land use and land cover are widely regarded as one of the main drivers of global change affecting mountain ecosystems (e.g., Bugmann et al., 2007; Zierl and Bugmann, 2007; Batllori and Gutierrez, 2008). For these reasons such data should be integrate also in our predictive models (Chapter 4) in order to obtain a broader sensitivity and accuracy and to try to export our models to other areas. The results of our predictions should be improved also increasing the number of the possible scenarios, to identify the temperature threshold beyond which the risk of biodiversity loss will be extremely elevated. There is high confidence that a warming above 3°C will cause further disruption of ecosystems and extinction of species (IPCC, 2007). Although most scenarios agree regarding the warming of mountains, the future development of precipitation is often unclear. But to have an idea on how a modification of precipitation regime could influence population dynamic of some sensitive species (e.g. black grouse) we need confidence about the magnitude and direction for future changes also in this parameter. Downscaling meteorological data could be really useful (e.g., Benestad, 2002; Steinacker et al., 2006; Qian, 2010), even though challenging because these systems are characterised by extreme small-scale heterogeneity (Ihse, 2007; Pape et al., 2009). Finally, because mountain ecosystems are a source of environmental capital for local populations, whose economies are mainly based on direct exploitation of natural resources, we need to assess the impact of climate and land use modifications on human well-being and to evaluate the risk due to the loss of ecosystem services. Moreover, the loss of mountain services can have serious repercussion on the lowland (Köllner, 2009).

Conservation implication

Our results provide useful implication for conservation purposes. Some of them have a local value while others can be exported in a broader context.

First of all, the identification of the most vulnerable species and habitats, highlight the need to take into account these information in developing management strategies. It is the only way to avoid the addition of others disturbing factors on species or habitats already sensitive to climate change effects. Moreover our results imply that vulnerable species as well as umbrella species should be deeply monitored in the long term, both for early warning signs of climate change and both as empirical tests of predictions.

The strong influence of meteorological variables in regulating population dynamics of black grouse resulting from this study, suggests some amelioration in the management strategies to

help the persistence of this species in the western Alps. In particular, the conservation of breeding and wintering habitat and the limitation of disturbing activities in years of unfavourable weather conditions should be promoted. Moreover, management actions should consider not only biological data but also climatic parameters, when for example defining hunting quotas.

The fact that centres of species richness are expected to shift or even to contract (Erasmus et al., 2002) in response to climate and habitat changes, will have severe consequences for conservation efforts. Currently, international conservation efforts focus on areas with many endemic or threatened species. With the predicted changes in ranges it can be expected that many threatened species move out of the areas that receive highest conservation efforts. The new ranges might then be placed in areas with high human population density or areas with conflicting land-use (Erasmus et al., 2002). Moreover such changes in climate are likely to be disproportionately great in areas that are currently most fully protected (Wiens et al., 2011). This because normally protected areas already occur in extreme environments, at high elevations or in places with low productivity (Scott et al., 2001) and because species with small ranges disproportionately occupy places with “rare climates” (Ohlemüller et al., 2008). Protected areas are fixed in space, but the environments they contain change over time, altering the conservation value of such areas (Wiens et al., 2011). Under these conditions, future management and conservation may need to be especially nimble. Shifting the management focus from individual species to broader assemblages or ecosystem properties, together with using adaptive management in an anticipatory rather than a reactive mode, may be necessary (Lawler et al., 2010).

On a broader point of view while mitigation of climate change is necessary to meet many conservation targets, we need to develop effective strategies to promote the resilience of ecological systems and aid in their adaptation to novel and changing climates (Hannah et al., 2002a; Hannah et al., 2002b; Hansen et al., 2003; Hannah et al., 2007). This promotion of resilience must concretize in actions that protect appropriate places, limit non-climatic stressors and manage adaptively (Al-Khafaji, 2008). In this sense protected areas can be used as a litmus test of any changes. To play this role parks need to share long term monitoring programmes that allow to measure biodiversity status (species richness, community composition and population dynamic), to underline the climatic and environmental factors that influence these patterns and to model the effects of climate and land use changes on these parameters.

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