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Synergy between habitat fragmentation and climate change: implications for biodiversity in Alpine ecosystems

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"We should preserve every scrap of biodiversity as priceless while we learn to use it and come to understand what it means to humanity"

E. O. Wilson

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Declaration

I hereby declare, as the author of this thesis, that material here contained is a presentation of original research work performed by me under the guidance and advice of my faculty supervisors, and has not been submitted in any form for another degree or diploma at any university or other institute. All contributions of others are involved, every effort is made to indicate this clearly in the text, with due reference to the literature.

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Abstract

An increase in global temperature accompanied by rapid fragmentation of habitats will lead to greater pressure on biodiversity, with more dramatic impacts expected on high mountain ranges. A new wave of extinction is likely to occur as the ability of species to migrate toward new cooler suitable areas will be hampered by altered landscapes, also the magnitude of species loss will in part depend on species traits, or phenotypic plasticity of individuals which will have to adapt to the changed environmental conditions.

In this PhD thesis, I included different models employing altitudinal gradient as a surrogate, to understand how effects determined by climatic variation might or might not exacerbate the negative impact of landscape changes on carabid communities (eastern Italian Alps). *Chapter I* contains a brief overview of the current body of scientific literature on the main ecological impacts of habitat fragmentation and climate change, and the emerging research related to the response of organisms to the synergistic impacts of these two threats.

The aim of *Chapter II* is to determine whether the effects of rising temperature might enhance the impact of habitat fragmentation on beetle diversity and community structure. *Chapter III* describes an attempt to assess the existence of simultaneous effects generated by habitat fragmentation and climate change on variation of morphological traits (fluctuating asymmetry and body length) in natural populations of forest-dwelling species *Haptoderus unctulatus.*

Finally, *Chapter IV* explores if species' sensitivity to landscape modification and altitude might be maximized or not by a combination of life history traits of ground beetles. In

summary, data of carabid assemblages suggest that the impact of rising temperature acting in synergy with land use pressure will move up along the mountainside, inflicting more serious negative impact on species composition, and causing changes in morphological traits of beetle populations particularly accentuated at lowlands. Also, interaction between these two drivers of change will exert a selective pressure on species with certain functional traits, which will result in a greater impact on the beetle assemblages of Alpine ecosystems than either driver acting individually.

Chapter I

Background

1.1 Alps and development of conservation network

The presence of several high peaks which reach an elevation of 4000 m, incised by longitudinal valleys and the vast system of European glaciers, make the Alps one of the most important biodiversity hot spots and the greatest mountain chains in Europe (Fig.1) (Pedrotti and Gafta, 2003). This mountain system with an area of 180,000 km^2, extends from the Mediterranean sea to the Vienna basin placed between the Eurosiberian and the Mediterranean biogeographic regions is divided into four major sectors: the Western, Central, Eastern, and Southern Alps (Shoumatoff and Shoumatoff, 2001). The Alps are a relatively young Tertiary belt largely shaped in the Cenozoic era (ca.1-12 million years BP),

Figure 1 A satellite image of the Alps (Data source: http//earthobservatory.nasa.gov/GlobalMaps/)

as a result of subduction and collision events (Mani, 1968; Froitzheim *et al.*, 2008). Their origin is the result of a long and complex geological history, due to convergence between the European and African plates during the Oligocene and Miocene epochs.

Subsequent Pleistocene glaciations have repeatedly covered the Alpine chain with ice (only a small area in the southeast and south west remained ice-free) thereby shaping their profile. Different geological substrates (Pedrotti and Gafta, 2003), soil horizons, and cryological processes in combination with a mixture of climatic conditions, topography and altitude are directly responsible for both the biological richness and high habitat diversification in the Alps (Nagy *et al*., 2003).

About a third of the European flora species, and approximately 30’000 animal species inhabit the Alps (Table 1) (WWF, 2004). A large number of endemic species are constrained to this mountain range as a consequence of the geographic isolation of the area which has acted as a barrier to the migrations of the post glacial period (Nagy *et al.* 2003; Schmitt, 2009). Despite a long-term human presence along the Alpine territory, there is still a high degree of naturalness which is reflected by the existence of about 200 habitat types located along the valleys, subalpine forests, and in the alpine zone (Arduino *et al.*, 2006).

In order to preserve this natural heritage, different strategies have been developed, which included classical approaches such as political instruments, the institution of protected natural areas, and international organizations (CIPRA, 2009). Specifically:

- CIPRA (International Commission for the Protection of Alps) works to promote sustainable forms of development in the Alpine regions.

- ALPARC (Network of Alpine Protected Areas) established in 1995 with the purpose of promoting exchange between the alpine protected areas, institutions, researchers, and local actors.

- ISCAR (International Scientific Committee for the Alpine Research), officially instituted in 1999 by research institutions in order to provide scientific research and international co-operation in the Alps.

Additionally, in November 1991 the Alpine Convention was established with the purpose of promoting the strengthening of synergies on a political level (Fig.2) (Arduino *et al*., 2001). This first multilateral accord between Alpine countries (Austria, France, Italy, German, Liechtenstein, Switzerland, Slovenia) and the EU, is applied by means of “protocols of

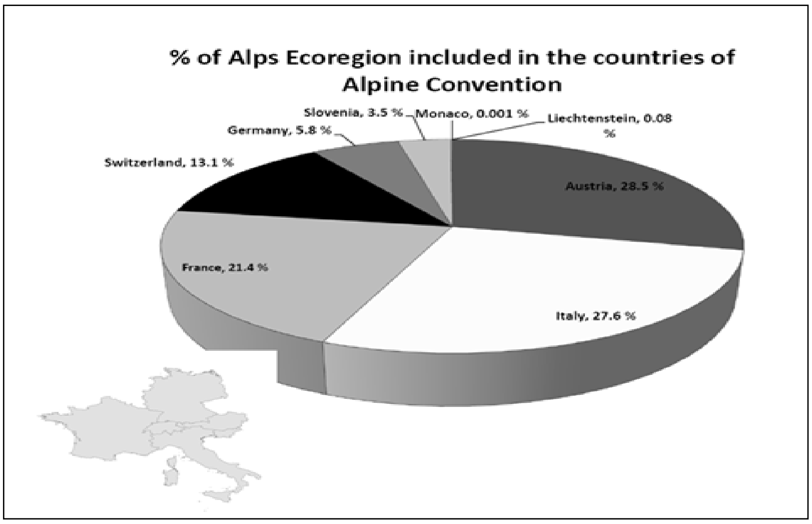

Figure 2 Percentage of the Alpine territory included within the border of the eight states of the Alpine Convention of 1991 (bases on data from Arduino et al., 2001)

Implementation" visualized by 12 sectors which refer to various aspects of sustainable development (e.g. nature conservation, landscape, forestry and agriculture, tourism, society, transit traffic etc). The Alps are part of the Alpine biogeographic region designated by the EU and included in the network NATURE 2000, created under the Habitats Directive (CE/92/43) (Fattorini, 2004; Sundscth, 2006), with a total of 62 ZPS (Zones of Special Protection) in the Italian boundary.

Table 1 Estimates of the number of species from different taxonomic groups occuring in the Alps (Data source: WWF, 2004)

Taxonomic group	**Species**
Fauna	ca 30,000
Invertebrates	ca. 20,000
Bird	ca. 400
Mammal	ca. 80
Freshwater Fish	ca. 80
Amphibian	21
Reptile	15
Flora	13,000
Fungi	over 5,000
Vascular plants	ca. 4,500
Lichens	ca. 2,500
Mosses	ca. 800

Currently, about 20-25% of the entire territory included in the Alpine Convention is protected through the creation of a network of national and regional parks, nature reserves, biosphere reserves and natural world heritage sites (14 National Parks, 70 Regional Parks, 300 Nature reserves, 10 Biosphere reserves, 3 UNESCO World Natural Heritage sites, 2 Geological reserves) (Arduino *et al.*, 2006). The Alpine arc is also listed as one of the “Global 200 Ecoregions” (Lassen and Savoia, 2005), and, most recently, included 9 areas covering 141,903 ha in the Dolomites (North Italy) listed as World Heritage Sites on 26th June 2009 (UNESCO, 2011).

This protected area network, which involves national and international legislative tools, could offer the possibility to initiate long-term conservation plans based on complex ecological and socio-economic scenarios for the Alps.

1.2 Fragmentation in modified alpine ecosystem

There is a consensus among researchers that fragmentation and loss of habitats represent the major global menaces to biodiversity (Fahrig, 2003; Laurance *et al*., 2007), affecting a large proportion of the land surface throughout the world (Foley *et al.*, 2005). Fragmentation takes place where unaltered contiguous habitat is broken up into patches of variable size and separated by a matrix of different vegetation or land use (Fischer & Lindernmayer, 2007; Collinge, 2009).

Modifications to the spatial configuration and structure of forests generate a series of well-known “edge effects”, or changes in the abiotic and biotic components inside and outside the fragments (Fahrig, 2003; Ewers and Didham, 2006; Piessens *et al.*, 2006). Abiotic effects include a perceivable altered microclimatic condition (e.g. moisture, temperature, wind flux) in remnant forest patches as a consequence of tree coverage loss (Chen *et al.*, 1993; Asbjornsen *et al.*, 2004; Pinto *et al.*, 2010). Apart from that, changes of spatial attributes of landscape imply modification on population dynamics and community structure. For example, many studies have reported the negative influence of habitat fragmentation on population density (Holland and Bennett, 2010), and dispersal ability (Alados *et al.*, 2010). Modified landscapes can also adversely affect community composition (Banks-Leite *et al.*, 2010), cause species' morphological changes (Tyler, 2008), disrupt interactions among species (Ness and Morin, 2008), and alter their reproductive rates (Twedt *et al.*, 2010). Overall, an impoverishment of habitat quality and the decline of its availability reduces the ability of individuals to persist in fragmented ecosystems making them more prone to extinction (Opdam and Wascher, 2004). Habitat fragmentation has clear repercussions for tropical, boreal and temperate forests (Lindenmayer and Franklin, 2002; Wright, 2005).

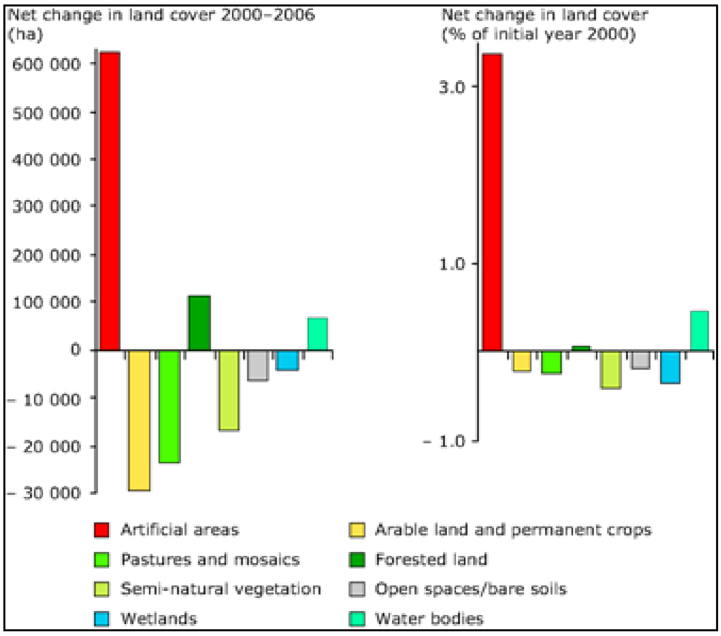

Figure 3 (left) total area ha, (right) percentage of land use changes occured in Europe between 2000-2006. (Data source EEA, 2010)

Between the decade 2000-2010, the total area of forest lost globally was about 5.2 million hectares per year (FAO, 2010). In developed regions, land-use has changed over the centuries through a reduction of forest cover over the past to a current opposite trend of agricultural land abandonment, and to an expansion of secondary successions (Goldewijk, 2001; EEA, 2010; Sitzia *et al*., 2010) (Fig.3).

Figure 4 Images showing landscape in the Alps mountains located within Stelvio National Park's boundaries (north-east of Italy), (a) example of regeneration of Norway spruce forest within the remant grassland patches in the subalpine belt (b) abrupt forest-edge created for skin-runs which represent a more recent anthropic impact located mainly at higher altitude (O. Pilia)

This phenomenon is particularly evident along the mountain regions in Europe, and has increased markedly in the last century leading to a considerable loss of semi-natural grassland areas (Maurer *et al.,* 2006). In the Alps, human-induced disturbances date back to the Late Neolithic (Motta, 2002; Schmidl, 2005), with grazing and summer pasturing occuring in many subalpine and alpine areas since at least medieval times (Bätzing, 2003). Conversely, there has been a progressive decline of the agricultural landscape starting from last century (Grabherr, 2009), largely due to changes such as agricultural intensification, specialization, combined with depopulation in many mountain regions (MacDonald *et al.*, 2000). After abandonment of traditional forms of land-use, forests and shrubs are gradually re-invading previous pastures and meadows, and this natural regeneration process of wooded areas is mostly observable in the southern side of the European Alps (Tasser *et al.*, 2007, Lingua *et al.*, 2008) (Fig.4).

The replacement of old managed grassland by secondary forest has resulted in a spatial pattern termed "perforation" (Lindenmayer and Fischer, 2007; Collinge, 2009), whereby tracts of individual trees develop with the creation of openings of variable size within the continuous forests (Forman, 1995) (Fig.5). Currently, perforation is one of the dominant fragmentation patterns across the Alps, but it also been recognized in forests of North and South America (Salvador-Van Eysenrode *et al*., 2000; Leupin *et al.*, 2004; Riitters and Coulston, 2005). Despite its prevalence in the Alps, the literature investigating the effect of perforation on biodiversity is very limited. If commonly, as time passes, perforation is followed by a progressive increase of open areas' surface, creation of forest patches and gradual increasing isolation between them. In the Alps, however, this pattern of fragmentation involves an inverse process with more complex features. For example, if once continuous forests have been eliminated on areas on which they formerly existed, now the impact of land abandonment (following the decline of traditional farming practices), and forest cover expansion are leading to decline and disappearance of many semi-natural grassland areas (Gellrich *et al.*, 2007), which appear as fragmented patches dispersed within a matrix of forest cover. These open habitats have been recognized as important ecosystems in supporting the existence of a high level of species diversity, and are included in the list of protected habitat type in the annex of the EU Habitat Directive (Calaciura and Spinelli, 2008). As Bowen et al. (2007) argue, understanding the spatial redistribution of flora and fauna communities in relation to re-growth-forests will be challenging, mainly because it will be likely to differ not only among species, but also will be related to the history of the landscape. While some species already benefitted from the new expanding forests, many others of subalpine and alpine grasslands do not and tend to be more at risk (Kampmann *et al.*, 2008). This recent spatial configuration has been a determinant for the presence of high densities of wild ungulates (Motta, 1998), and also positively affected woodland bird diversity (Laiolo *et al.*, 2004).

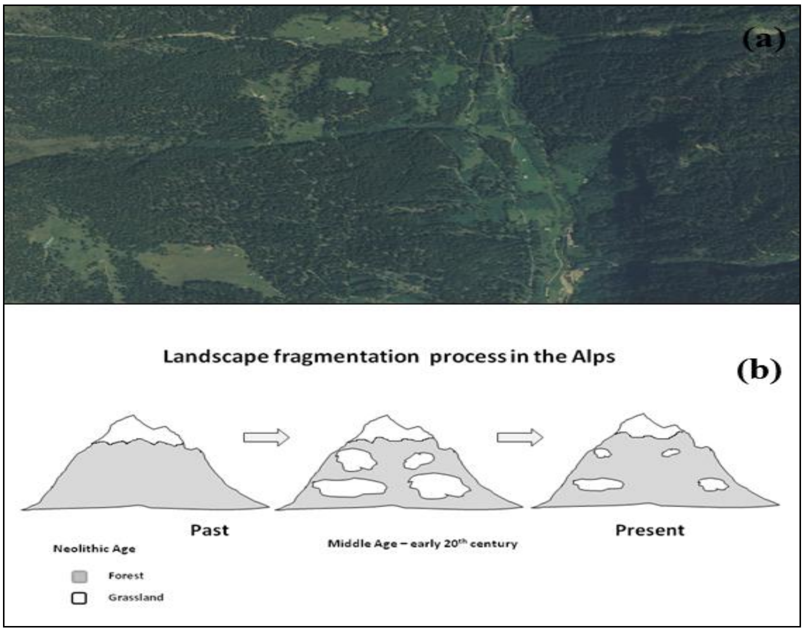

Figure 5 Fragmented landscape in the Alps (a) image illustrating grassland patches surrounded by forested matrix, (b) changes of forest cover in the Alps through time (O.Pilia)

Many studies have, however, provided evidence of a decline of species of different taxa associated with grassland habitats in the Alps, and most examples involve vascular plants (Spiegelberger *et al.*, 2006), insects (Marini *et al.*, 2009), and birds (Signorell *et al.*, 2010). In this view, there is a real concern that a vanishing heterogeneity within the landscape can pose a severe threat to the persistence of biodiversity in alpine ecosystems.

1.3 Global warming and prospective scenarios for the Alps

Climate change is affecting all ecological systems worldwide (Hannah *et al*., 2005). Over the last three decades, global average temperature has risen by about 0.2 °C (IPCC, 2007) (Fig.6), and a further increase of 1.5-2.5 ° C (as a result of major carbon dioxide in emissions the atmosphere) could put 15-37 % of plant and animal species at risk of extinction (Thomas *et al.*, 2004). Almost 30 years of global warming have produced noticeable changes in the phenology and physiology of organisms, shifts of their geographic distribution, and alteration to the composition and dynamics of ecological communities (Hannah *et al.,* 2002; Walther *et al*., 2002; Root et al., 2003).

Species' distributions are expected to move poleward in latitude and upward in altitude as a result of higher temperatures (Lenoir *et al.*, 2008; Hu *et al.*, 2011), with corresponding contractions in lower altitudinal and latitudinal species' range limits (Menendez, 2007). For example, analysing 35 species of non migratory European butterflies, (Parmesan *et al*., 1999) provided the first evidence of a large scale northward shift in response to climatic factors during this century. Likewise, Wilson et al., (2005) documented an upward shift in the elevational ranges of 16 butterfly species of the Sierra de Guadarrama (Spain) over a 30 year period.

Similar responses to climate change seem likely for organisms such as beetles, grasshoppers, rodents and frogs with discrete populations and limited power of dispersal (Parmesan & Yohe, 2003). In the Alps, climate change is expected to generate increased temperatures and considerable summer warming (Beniston, 2006). Here, the most substantial climate change occurred at the end of the Ice Age (approximately 11,000 years BP) (Ortu *et al.*, 2008), with a drastic increase of minimum temperatures by up to 2° C during the 20th century (Beniston, 2005). Since the 80s, this warming trend appears to be more accentuate in the Alps compare to the global average (Beniston, 2005; Casty *et al.*, 2005). Simultaneously long term precipitation patterns observed during 1901-2000 show a minor decline in average annual precipitation (Casty *et al.*, 2005).

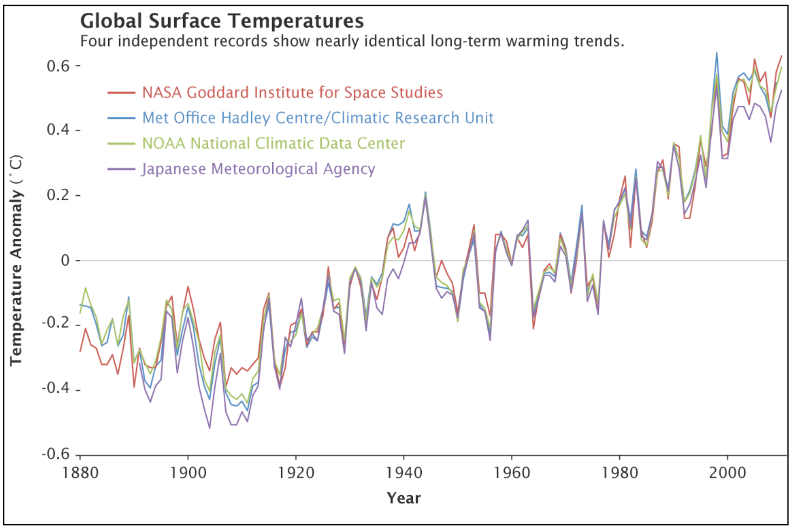

Figure 6 Increasing global temperature from the 19th century (Data source: http://www.giss.nasa.gov)

Future climate change projections for the European Alps indicate temperature will increase by 0.3 to 0.45° C per decade by 2100 (Déqué, 2007), and as Beniston, (2006) suggests, increasing temperature will be more pronounced in the summer and autumn season.

Global retreat of glaciers is an indicator of warming climates (Oerlemans, 2005; Diolaiuti and Smiraglia, 2010), and this trend has been occurring across the Alps from the end of the Little Ice Age in 1650 until now (Zemp *et al.*, 2006). In the south-eastern Swiss Alps, ice volume of 20 glaciers has decreased by 47% since the 1900s (Huss *et al.*, 2010), whereas, Cannone et al. (2008) have documented a decrease of Sforzellina glacier surface (northern Italy) of nearly 14% between 2002 to 2006. The effects of climate change on the biotic components of alpine ecosystems have now been recognized from the level of individual species (Johnson *et al.*,

2010) to communities (Maggini *et al.*, 2011). Over the last 50 years, altitudinal limits of alpine and nival plant species appear to be modified, with a gradual upward shift of vegetation at a rate of about 8-10 m per decade (Walther *et al.*, 2005). For instance, in the North-Eastern calcareous Alps (Austria), a significant reduction of available habitat for alpine plants is likely to be a consequence of treeline conifer Pine shrubs (*Pinus mugo*) expansion into the Alpine zone, as a result of increased temperature (Dirnbock *et al.*, 2003; Dullinger, 2004).

In the case of insects, it is expected that a more rapid reaction to climatic change will occur since their life-cycles are strongly dependent on temperature (Bale and Hayward, 2010). Alteration in phenological patterns, changes in habitat selection, and shifts of geographic and altitudinal distribution might all be possible responses (Menendez, 2007), although, it is likely that their responses will appear dissimilar and not always occur in a linear way (Bale *et al.*, 2002).

Phenological responses are likely to be wide spread within all groups of insects, especially at higher latitudes and elevations where temperature has increased and is predicted to increase more than in other parts of the world (IPCC, 2007). Higher temperature can influence the developmental stages of insects interfering, for example, with systems of induction and duration of diapause (Bale and Hayward, 2010). Species characterized by fast development rates, with no diapause or whose diapause is not temperature induced, will be likely to expand their distribution as a consequence of warming. On the contrary, range contraction will likely occur for boreal and mountain species of the northern hemisphere which need low temperatures to induce diapause (Bale *et al.*, 2002). It must, however, be considered that there is great difficulty in detecting species declines (Menendez, 2007), and that insects' responses are related to the magnitude of climate warming (Estay *et al.*, 2009). In fact, only a small number of species characterized by adaptable life cycles will react positively to slight or moderate warming, but a significant increase in temperature will be more likely to have an impact on other ecological groups or species (Musolin, 2007).

1.4 Combined effects of habitat fragmentation and climate change on biodiversity

Indubitably, there is still uncertainty about the independent effects generated by global warming and habitat fragmentation on biodiversity, but the potential consequence of the simultaneous influence of these two global drivers of environmental change represents a greater source of concern (Sala *et al.*, 2000; Novacek and Cleland, 2001; Brook *et al.*, 2008).

Over the past few years, a small number of studies have been undertaken in that direction, with different approaches which included simulation models (Jetz *et al.*, 2007; Scheller & Mladenoff, 2008; Asner *et al.*, 2010) under different land-use and climate change scenarios or, for example, the use of field experiments manipulating temperature directly in ecosystems (Honnay *et al.,* 2002; Mora *et al.*, 2007). Most of these studies have involved different latitude, spatial scale, and taxa. All their results appear clearly unidirectional, revealing that these two threats acting simultaneously can amplify their combined negative effects on biodiversity, above and beyond the individual effects they might induce separately.

What is expected is that fragmented landscapes might pose a barrier to distributional shift of species which track changing bioclimatic conditions (Opdam and Wascher, 2004). At a global level, deforestation, logging and warming temperature might jointly affect tropical forests causing significant vegetation changes by the year 2100 (Asner *et al.*, 2010). In their projection models, Asner et al. (2010) indicate also that the effects resulting from this synergy will be likely to be particularly severe in the Amazon with a rearrangement of plant functional types in 57-81% of the region. Restriction of tree expansion in fragmented mesic forests in Wisconsin (USA) (Scheller and Mladenoff, 2008), and a larger decline in extent for 18 *Banksia* spp. in western Australia (Yates *et al*., 2010) is also anticipated in spatial models including multiple scenarios of increasing temperature together with land transformation. Even studies emerging from Europe do not seem encouraging.

Using deciduous forest successional stages as a surrogate of time series to predict the migration rate of 203 plants of fragmented landscapes in Belgium, Honnay et al (2002) found that even after about 40 years, all plants had a low chance of colonizing new forests both in fragmented or highly connected landscapes. The influence of climate change in synchrony with habitat fragmentation will be expected to put a pressure on the persistence of fox squirrel populations which occupy forest patches on the Delmarvia Peninsula in USA (Hilderbrand *et al.,* 2007).

Recently, Foufopoulos et al., (2011) presented evidence of past reptile population extinctions occurring during late Holocene in the Aegean islands (Greece). Key to their study, based on data from 35 reptile species, is that the rate of extinction was higher for those populations with a northern distribution among those islands. In fact, species from cooler regions were more inclined to extinction as a result of habitat loss that took place in the context of shrinkage of island due to rising sea level. Species will however, be likely to be affected differentially by these dual forces; habitat specialists will face higher rate of extinction than generalist species which will appear to dominate in the communities (Warren *et al.,* 2001, Leimu *et al.,* 2010).

All these studies clearly demonstrate that changes in species distribution, abundance and community structure will be inevitable, although the knowledge of how habitat fragmentation and increasing temperature might intervene causing intra-specific variation (life-history, trophic-level, and morphology) is still relatively limited. In the case of insects, association among these two threats are expected to affect dramatically fecundity, therefore influencing population persistence. For example, in the specialist herbivore butterfly *Cupido minimus*, stressful climatic conditions and a severe decline of its host plant, *Anthyllis vulneraria,* have caused not only a reduction of population size, but also an alteration of rates of egg deposition (Piessens *et al*., 2009). By comparing fitness of woodland butterfly populations *Pararge aegeria* from continuous and open highly fragmented agricultural landscape, Karlsson & Dyck, (2005) found that a variation of lifespan, number of eggs laid, and egg weight were visibly associated with increasing temperature. Egg-laying patterns of populations linked to continuous forests were negatively affected by higher thermal profile. Modifications in individual morphology may also result from these driving changes. For example, Silva et al. (2009) reported increasing levels of small random deviations from perfect symmetry of bilateral traits (fluctuating asymmetry) in Euglossa pleosticita populations (Euglossine bee) living in semi-deciduous tropical forests. In this work, where seasonal variation of temperature were used as a surrogate to predict climate change, bees collected during the hot season on the forest border were more asymmetric than individuals sampled inside the forests in the cold season. Some fields, however, still remain unexplored, and in this context, given the actual landscape fragmentation and the accelerated rate of global warming, clearly a body of work focused on the interacting threats is critically needed.

1.5 Altitudinal gradient as surrogate for changing climate

Experimental approaches aiming to determine the impact of global warming on ecosystems can involve the use of natural gradients as surrogate, which are manipulated in the laboratory or directly in the field (Andrew and Hughes, 2004; Mora *et al.*, 2007; Silva *et al.*, 2009). As Körner (2003) states, natural difference among different sites may indicate the long-term consequences of climatic changes, and thus be used to design "space for time/warming experiments".

Altitude can be used as a surrogate gradient to efficiently represent models of climate change (Körner, 2007a), particularly at local scale where the lapse rate of temperature with increasing elevation is relatively homogeneous within or all over a territory (Sergio and Pedrini, 2007). The steepest thermal variation on earth is exhibited along the mountainsides, with a lapse rate in temperature of approximately 0.5° C every 100 m. of increasing altitude, (Rolland, 2003; Shoo *et al.*, 2005) (Fig.7).

Seasonal changes and slope can cause fluctuations in climatic pattern (Rolland, 2003; Tang and Fang, 2006). Since, these gradients in air temperature are an environmental key factor for organisms living at higher elevations (Körner, 2007b), high mountain ecosystems represent an ideal model system because climatic parameters such as temperature, precipitation and seasonality are mainly responsible for the spatial distribution of numerous taxa and communities within compressed thermal life zones (Grabherr *et al.*, 2000; Theurillat and Guisan, 2001). In view of the fact that organisms inhabiting mountains are adapted to occupy specialized niches with narrow distributions in relation to geographic or climatic factors (Williams *et al.*, 2007) , any shift of their spatial distribution along the altitudinal

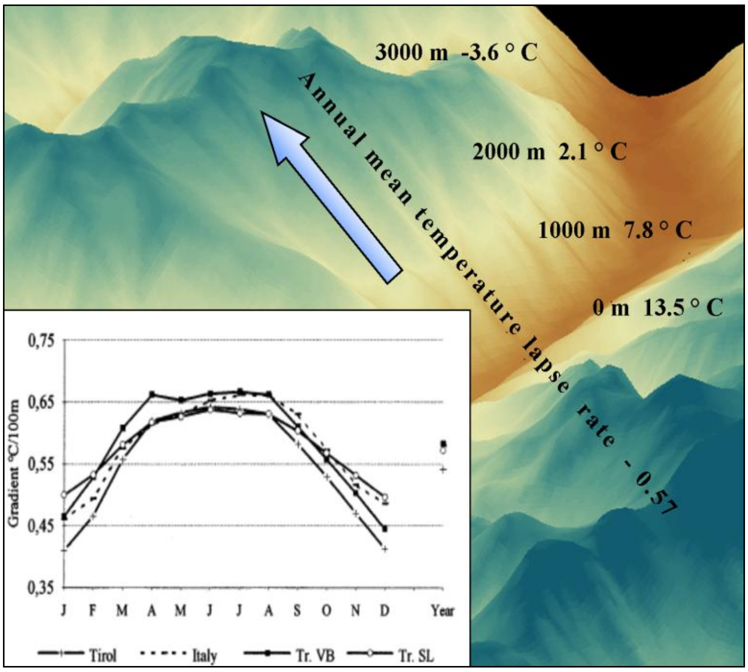

Figure 7 Lapse rate of mean temperature, and the difference between the mean annual temperature in the valley and up on the top of the mountain (figure based on datasets from Rolland (2002), using stations from northern Italy (269), Tyrol (205), Trentino-Upper A Adige (166). (bottom left) Graph showing seasonal variation of lapse rates in mean temperatures, (source: Rolland, 2002)

gradient can provide information about their temporal distribution associated with climatic change.

1.6 Ground beetles and their role on environmental studies

Ground beetles were selected as a suitable taxon to assess the biological impacts of interactions between fragmentation and global warming, in view of their role as a bioindicator taxon in several previous studies (Niemelä, 2001, Rainio and Niemela, 2003; Pearsall, 2007) (Fig.8). Carabids have often been used in experimental work, being a group with a well-known taxonomy and ecology, global distribution, and which are easy to capture

(Thiele, 1977; Desender *et al.*, 1994; Lövei and Sunderland, 1996). What makes this group particularly appropriate is that carabid communities are known to be distributed in relation to environmental factors such as habitat quality and land use (Maleque *et al*., 2009). Much literature has been produced from studies on carabids in different habitats as diverse as boreal temperate forests (Abildsnes and Tømmerås, 2000), glaciers (Gobbi *et al*., 2007), grasslands (Grandchamp *et al.,* 2005), different level of anthropogenic disturbance (Lövei and Cartellieri, 2000; Kotze and O'Hara, 2003; Ewers *et al.*, 2007), climate change (Butterfield, 1996; Ashworth, 2001; Gonzalez-Megias *et al.*, 2008), whether in the northern or in the southern Hemisphere (Davies and Margules, 1998; Xiao-Dong Yu, 2006).

Figure 8 *Carabus hortensis* (Linnaeus, 1758), European species localized in the Alps, and in the North and Central Europe. (O.Pilia)

Ground beetles are profoundly sensitive to habitat fragmentation (Barbaro and Van Halder, 2009), although, frequently, contrasting results have emerged (Niemelä, 2001). For instance, in terms of edge effects, beetle species richness can decrease from forest fragments to clear-cut (Xiao-Dong Yu, 2006) or be positively correlated with distance from interior forest resulting in higher species richness along the habitat matrix-edge (Heliola *et al.,* 2001).

Fragment isolation and patch size can also negatively affect beetle species richness (Ewers *et al.*, 2007), or alternatively, the number of species may not be influenced by the size of forest remnants (Gaublomme *et al.*, 2008). Differences in ground beetle community composition occurs also in fragmented areas (Ewers and Didham, 2008), with characteristic beetle assemblages associated with different habitats such as woodland or more open habitats (Elek and Tóthmérész, 2010). Examining ground beetle assemblages from 22 sampling sites located in the Picos de Europa National Park (Spain), Gutiérrez *et al.* (2004) found a strong dependence of species composition on vegetation structure, especially for those species linked with more open habitats. Interesting research has also been focused on carabids in relation to climate change. Based on the fossil record, Ashworth (2001) suggested that beetles have responded to Quaternary paleoclimatic variation, mostly thanks to their ability to disperse.

Butterfield (1996) reinforced this theory, suggesting that some carabid life-cycles can appear too complex to adapt to climate variation, and shifting of carabid communities is more likely to occur in view of future warming. Dormann *et al.* (2008), however, infer that including only climate parameters might overestimate the effects of climate change on ground beetles responses. What emerges from the literature is the necessity to apply more sophisticated models that contain a combination of environmental parameters in order to improve predictions of future carabid distributions (Eyre *et al.*, 2005; Gonzalez-Megias *et al.*, 2008). Specifically, research focused on combining data derived from fragmentation and altitudinal parameters is still scarce but needed, as the threat of habitat fragmentation, concomitantly with global warming, will be more likely to affect negatively carabid communities in the near future.

Chapter II

Climate gradients magnify the impact of habitat fragmentation on ground beetle communities in the Italian Alps

2.1 Abstract

Considered globally as a key biodiversity hotspot, the Italian Alps are threatened with a changing climate combined with simultaneous land abandonment leading to the fragmentation of semi-natural grasslands. In this study, we used climate variation along altitudinal gradients as a surrogate to predict the consequence of combined effects of temperature increases and habitat fragmentation on the composition and diversity of carabid communities. More than 12,000 ground beetles from 50 species were sampled using 410 pitfall traps placed along both horizontal and vertical transects in habitats that included alpine grassland patches and coniferous forests. We found a differentiated and well-structured carabid community, with assemblages changing along gradients of distance to patch edges, patch size and altitude. Gradients of altitude and habitat fragmentation had a synergistic impact on ground beetle communities, with more pronounced effects of grassland patch area edge effects on carabid communities at low than at high altitude. We argue these patterns are the result of microclimatic changes that were also synergistically impacted by altitudinal and fragmentation gradients. Our findings indicate that future climate change will magnify the impact of habitat fragmentation, impacting communities more than would be expected from simple additive effects of the two global change drivers operating in unison.

Keywords: *Carabidae (Coleoptera), climate change, fragmented landscapes, habitat perforation, high-altitude ecosystems.*

2.2 Introduction

Habitat loss and fragmentation are considered among the most influential factors affecting wildlife populations, making them more vulnerable to extinction (Baille *et al.,* 2004). At a global level, all ecosystems are facing profound alterations as a consequence of modern agricultural systems, forest management and progressive urbanization, all of which gradually modify landscapes (Fischer and Lindernmayer, 2007). Species in fragmented landscapes may however, also suffer from further threats that could intensify the impacts of fragmentation (Ewers and Didham, 2006).

Species within remnant patches may be more vulnerable to pressures from outside the system (Novacek and Cleland, 2001), including climate change (Travis, 2003), pollution (Weathers *et al*., 2001) or invasive species (Didham *et al.,* 2007). Most studies into the biodiversity impacts of land-use change on biodiversity focus on what happens when habitat is lost (Fahrig, 2003; Cushman, 2006), but a frequent condition in Europe is the regeneration of habitat as a result of agricultural land abandonment (Flinn and Vellend, 2005).

In the case of the European Alps, high mountain ecosystems have been strongly modified since the sixteenth century, when many forests and shrublands were replaced by pasture to promote the expansion of agriculture and livestock grazing (Dullinger *et al.,* 2003). These practices declined sharply during the middle of the 19th century, leading to land abandonment and a consequent expansion of forest and shrubby ecotones in those areas once occupied by cattle and crops (Theurillat and Guisan, 2001). As a result, most of the subalpine and alpine zones are now characterized by a type of fragmentation pattern described as “perforation”, in which there are many small clearings of anthropogenic land use embedded within a largely continuous matrix of native forest (Fischer and Lindernmayer, 2007). In the Alps, the process leading to this pattern is more complex than most perforated landscapes, since forest was the original land-cover type which had first been largely removed before subsequently expanding back across the landscape through reforestation (Rammig *et al.*, 2006). Habitat perforation does not imply there has been a loss of continuity of native habitats, which is an important issue commonly associated with habitat fragmentation, where patches of natural habitat become progressively isolated from each other (Collinge, 2009).

This expansion of native forest cover in the Italian Alps has been beneficial for some species such as forest-dwelling wild ungulates, whose populations have increased in some areas as a consequence of reforestation (Motta, 2003). On the other hand, however, forest expansion has negatively affected several grassland species, reducing their abundance and changing their distributional ranges (Chemini and Rizzoli, 2003; Giupponi *et al*., 2006).

Negative impacts of grassland abandonment have been documented for invertebrates such as dung beetle communities in the north-western Italian Alps (Macagno & Palestrini, 2009), and for avian species such as Scops Owl *Otus scops* (Sergio *et al.*, 2009) and the Golden Eagle *Aquila chrysaetos* (Pedrini and Sergio, 2001). Certainly, land-use change represents one of the most important anthropogenic impacts in the Alps (Sala *et al.*, 2000; Dirnbock *et al*., 2003; Körner, 2007a), although empirical evidence indicates that climate change is also inducing biodiversity changes in this region (Körner, 2007b).

For example, in the Swiss Alps, the minimum annual temperature has increased by 2 ºC during the twentieth century, with a perceptible rise occurring since the early 1980s (Dirnbock *et al*., 2003) that has altered mountainside vegetation communities (Keller *et al.*, 2000). Upward altitudinal shifts in species distributions as a result of climate change have also been observed for species such as the pine processionary moth *Thaumetopea pityocampa* in the Italian Alps (Battisti *et al.*, 2005), and for *Pinus mugo* in Austria (Dullinger, 2004). The Alpine belt is home to a heterogeneous system of natural protected areas, but even these are not exempt from pressures exerted by climate change (Sala *et al.,* 2000). Changes in temperature and precipitation patterns could exacerbate ecophysiological stresses on species inhabiting protected sites (Halpin, 1997), and ongoing land use change means that many reserves are destined to become isolated “habitat islands” (Ewers and Rodrigues, 2008).

Understanding how organisms will cope with future climatic scenarios within fragmented landscapes may represent a key issue for conservation. For example, fragmented landscapes can act as barriers to species dispersion, limiting their ability to undergo range shifts in response to climate change and thereby causing their decline (Leimu *et al.*, 2010). This effect has been investigated for the Virginia pine *Pinus virginiana* in the eastern United States (Iverson *et al*., 1999) and for a number of butterfly species in the Sierra Nevada Mountains of California (Forister et al., 2010). At the same time, but at a much reduced spatial scale, climatic warming could alter microclimatic conditions within habitats (Harte *et al.,* 1995), reducing their suitability for a wide range of species.

Microclimate is also heavily affected by habitat fragmentation (Laurance, 2004), with forest edges typically being hotter and drier than forest interiors (Chen *et al.*, 1993; Davies-Colley *et al.*, 2000). Altered microclimatic conditions is thought to be one of the primary causes of invertebrate species responses to habitat fragmentation, with many forest-dependent species having reduced abundance near forest edges (Grimbacher *et al.,* 2006). Increasing temperatures under climate change may magnify the microclimatic changes observed at forest edges, thereby accentuating the level of stress for organisms and the biodiversity impacts of land use change. This is likely to exert a particularly strong impact on ectotherms, which are more sensitive than endotherms to fluctuating thermal conditions (Piessens *et al.*, 2009).

Altitudinal gradients can be used to determine the impact of future climatic change on species (Moser *et al.*, 2009), since changes in temperature with elevation can simulate long-term changes of temperatures produced by global warming (Körner, 2007a). In the Swiss Alps, air temperature decreases by around 0.5 ° C for every 100 m of altitude (Moser *et al*., 2009), so altitudinal gradients of 800 m represent a viable model for determining likely species responses to expected temperature increases of up to 4 ° C by the year 2100 (Raible *et al*., 2006).

Here, we used an altitudinal gradient in the Italian Alps to explore the simultaneous influence of fragmentation and climate change on species diversity, abundance and assemblage structure of ground beetles (Coleoptera: Carabidae). Specifically, we examined: (1) how environmental gradients of habitat area, habitat edges and temperature affect the spatial variability of carabid communities; and (2) whether there is any evidence for habitat fragmentation and climatic gradients interacting with each other to either magnify or minimise their individual effects on ground beetle assemblages.

2.3 Methods

2.3.1 Study Area

This study was conducted in the Peio Valley in Stelvio National Park, eastern Italian Alps. The study site (46°21’N,10º41’E) covers an area of approximately 9,191 ha and an altitude range from 1,253 to 2,200 m. a.s.l. (Fig.1). The Peio Valley is a characteristic U-shaped valley that originated when the glacier withdrew during the last glaciations of the Pleistocene, and has been intensely modified by alluvional erosion and landslide events (Sitzia, 2001). The geological substrate is mainly composed of metamorphic rock such as gneiss, granite, and mica-shist formations (Viola *et al*., 2003).

Climatic conditions are temperate-humid, with average annual temperature around 6.8 °C (-0.6°C during winter and 15.6°C in the summer) and annual precipitation of 861 mm (Sitzia, 2001; Provincia Autonoma di Trento, 2009). The valley is mostly covered by coniferous forest. Norway spruce (*Picea abies*) in association with European larch (*Larix decidua*) dominate from 1400 to 1900 m. Broadleaved trees (*Alnus viridis*, *Alnus incana*, *Alnus glutinosa*, *Betula pendula*, *Populus tremula*) also occur, but with a fragmented distribution at the valley floor. At higher altitudes, Norway spruce is gradually replaced by Alpine stone pine (*Pinus cembra*), which gives way above the treeline to the shrubs, snowrose (*Rhododendrum ferrugineum*) and common juniper (*Juniperus communis*) (Sitzia, 2001).

Similarly to the rest of the Alps, the natural landscape in Peio Valley has been heavily modified by human activity over the past four centuries. Exploitation of magnetite mines and deforestation initially led to a reduction of the forest cover, which reached its minimum extension at the end of the 18th century (Colaone, 1980). Only during the last few decades has the opposite process of forest regeneration occurred due to a gradual abandonment of traditionally managed grassland throughout the valley (Sitzia and Viola, 2009). Hence, at present, the existing landscape is characterized by a network of grassland patches embedded in a matrix of continuous forest. Some of the grassland patches have been abandoned, whereas others are still used for grazing, albeit less intensely than in the past.

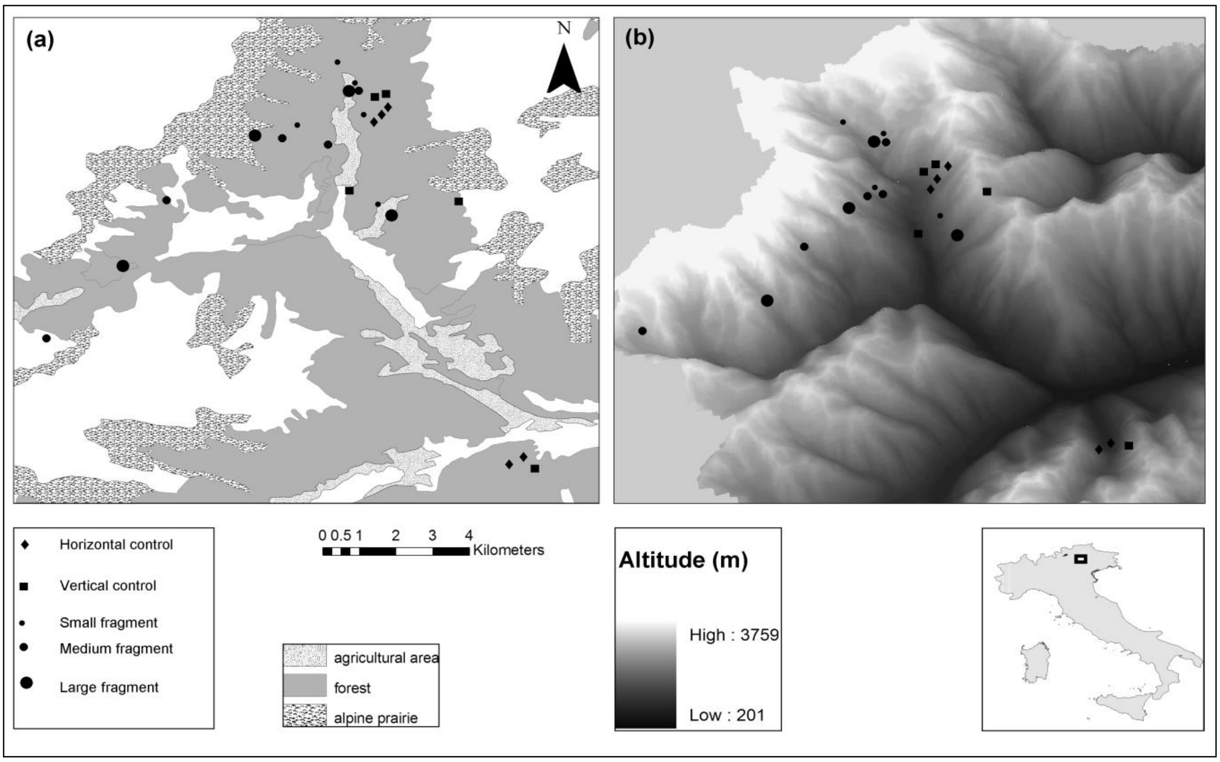

Figure 1 Maps showing (a) land-use pattern, and (b) 3D elevation perspective of the study area located in Val di Peio and Val di Sole (Trento, Italy). Points represent the different forest fragments as well as the location of control transects

2.3.2 Experimental design and sampling of ground beetles

Carabid communities were sampled using pitfall traps located at 410 sites along 24 linear transects during the June to September period in both 2008 and 2009. To investigate the combined effects of fragmentation and climatic gradients on the ground beetle assemblage, we established a total of 24 transects divided into three groups. First, we established 14 horizontal edge transects running from the centre of a grassland patch, across the grassland-forest edge and into the forest interior. Transects ran at an equal altitude and extended 90 m into the forest. Patches were chosen on the basis of their size, altitude and accessibility. They ranged in size from 0.16 to 10.11 ha, and the transects running across patch edges were located at altitudes ranging from 1385 to 1839 m.

Importantly, patches were selected to ensure there was no confounding correlation between log-transformed patch size and altitude (Pearson correlation $r = 0.24$, $N = 14$, $p = 0.40$, Appendix 1a). Second, we established a set of five horizontal control transects located in continuous forest. These transects each ran a distance of 190 m at equal altitude, and were established at five different altitudes (1382, 1620, 1685, 1781 and 1840 m) to provide information on naturally occurring spatial heterogeneity in beetle communities. Finally, we established a further five vertical transects to evaluate natural patterns of community composition changes along altitudinal gradients; three transects running in the interior of forest, one running from the grassland on the valley floor into the forest, and the last across the forest- alpine prairie edge.

Traps were positioned at 10 m intervals along all transects, and emptied fortnightly over the three-month period. Some trap samples were lost due to trampling by mammals, and several traps inadvertently captured small mammals which prevented invertebrates from being captured, so we had a final total of 14,783 trap-days sampling effort across the two years.

Pitfall traps consisted of plastic cups (70 mm diameter) that were partially filled with a solution of vinegar mixed with salt. This mixture was considered a more environmentally friendly option over other more toxic options, preventing harmful effects for vertebrates that could be attracted by it (e.g. cows, deer and small mammals) (Hall, 1991). Carabid beetles were removed from the samples, transferred to 70 % alcohol solution for storage, and identified to species using standard identification keys (Porta, 1923; Hurka, 1996) and following the correct and updated nomenclature for this group (Fauna Europaea, 2010).

2.3.3 Microclimate

Microclimate data (soil temperature, air temperature and relative humidity) were collected at each of the 410 sampling sites to assess patterns of spatial variation in relation to the three main gradients of patch area, patch edges and altitude. All data were recorded using a digital hygro-thermometer equipped with a pt100 sensor (Ø 26x170 mm, accuracy: ±0.3 °C, ±1 % RH) (Delta OHM HD2301.0). Air temperature and relative humidity were measured in the air at the height of 120 cm above, and soil temperature at a depth of 8 cm below, the ground surface. At each sampling point, measurements were taken on two separate days (07 July - 24 August 2009) and all were collected between the hours of 0900 and 1200.

2.3.4 Statistical analysis

To test the effectiveness of the altitudinal gradient as a surrogate for climate change, we performed a simple linear regression between altitude and each of the three microclimate variables, using data collected solely from the three vertical transects located entirely within forest. We used multiple linear regressions to explore the simultaneous influence of altitude, edge, and area effects on microclimate. Microclimate data were log-transformed (ln + 1) to meet assumptions of normality and constant variance. All beetle samples collected at a given trap within one sampling season were pooled, giving a total of 820 samples for analyses. We used Detrended Correspondence Analysis (DCA) to detect broad patterns of variation in ground beetle community composition. Ordination analyses were conducted using data on the relative abundance of species (number of individuals per trap-day), with samples combined for the two sampling years at each of the 410 sample sites. The abundance, diversity and composition of carabid assemblages were quantified with a range of response metrics.

For each sample site, we used observed number of individuals (*N*), observed species richness (*S*), the Shannon-Weiner index (*H'*), and the Berger-Parker dominance index (*D*) to reflect different aspects of community abundance, diversity and structure, whereas the scores from the first two DCA axes were used to reflect variation in community composition (DCA Axis 1 and DCA Axis 2). To correct for potential biases related to small variations in sampling effort among locations, data on species richness and abundance were standardised by including the total trap effort (number of trap-days) per sample as an offset to models. All response variables were tested for normality with the Shapiro-Wilk test prior to analysis and transformed as required.

Variation in the abundance, diversity and composition of carabid assemblages across gradients of patch size, patch edges and altitude, and all their interactions, were tested using standard analytical procedures accounting for the particular error distributions of different response variables. Generalized linear mixed effect models (GLMM) specifying a log link function with poisson distribution were used for species richness and the number of individuals, while linear mixed effect models were used to analyse patterns in community composition (DCA Axis 1), log-transformed Shannon-Weiner index, and log-transformed Berger-Parker index. In all models, year was added as a random effect. Minimum adequate models were selected by sequentially removing variables from the full models, and the best model was chosen using Akaike's information criterion (AIC) values (Burnham and Anderson, 2002).

The software package Species Diversity & Richness 4.0. (Seaby and Henderson, 2006) was used to calculate diversity indices. All other analyses were performed with R software (R Development Core Team 2008), using the libraries 'nlme' and 'lme4' for mixed effect models, and 'vegan' (Oksanen *et al.*, 2009) for ordination analysis.

2.4 Results

2.4.1 *Microclimatic gradients*

Temperature decreased significantly with increasing altitude (Table 1), with the strongest relationship observed with soil temperature (R^2 = 0.78). Relative humidity did not significantly change along the altitudinal gradient. Mean air temperature exhibited a gradient of 5.5 ˚C, ranging from 21.1 ˚C at low altitude to 15.6 ˚C at high altitude (Fig. 2a). Microclimate also exhibited strong, but complex, patterns along the gradients of patch size, patch edge and altitude (Table 1).

Air temperature displayed much variation along the edge gradient, being significantly higher in grassland than in the forest habitat (Fig. 2c). Patch size had weak interaction effects with both patch edges and altitude, in that edge temperature gradients were more pronounced in large than in small patches, and the decrease in air and soil temperature with increasing altitude was detected in small but not in large patches (Fig. 2d).

2.4.2 *Ground beetle composition*

A total of 12,588 individuals from 50 carabid species were collected (see Appendix 1b for a complete list of species). *Carabus hortensis* (Linnaeus 1758) and *Pterostichus multipunctatus* (Dejean 1826) were the most frequently caught species, comprising 27 and 29 % of all individuals respectively.

Other common species included *Haptoderus unctulatus* (Duftschmid 1812) and *Calathus melanocephalus* (Duftschmid 1812) (10 and 5 % of individuals respectively). Four of the 50 captured species have a geographic distribution constrained to the Alps; *Carabus depressus* (Bonelli 1810), *Cychrus angustatus* (Hoppe & Hornschuch 1825), *Cychrus attenuatus*

(Fabricius 1775), and *Thricotinus laevicollis* (Duftschmid 1812) (Magistretti, 1979). We also collected 19 individuals of the Italian endemic species, *Cychrus italicus* (Bonelli 1810), and a single female of the canopy predator *Calosoma sycophanta* (Linnaeus 1758). The first two axes from the DCA explained 43 and 23 % of the variance in carabid community composition respectively (axis 3 16.89 %, axis 4 16.70 %; eigenvalues 0.73, 0.39, 0.28, 0.29 for axes one to four respectively) (Fig. 3).

DCA Axis 1 reflected strong turnover in community composition along a gradient from the forest to the grassland. Forest assemblages were characterised by species such as *C. micropterus* (Duftschmid 1812), *P. multipunctatus* (Dejean 1826), *H. hunctulatus* (Duftschmid 1812), *C. hortensis* (Linnaeus 1758), and *Notiophilus palustris* (Duftschmid, 1812). Several forest specialist species such as *C. attenuatus* (Fabricius 1775), and *C. angustatus* (Hoppe & Hornschuch 1825) were mostly restricted to deeper forest habitats and were detected at relatively low abundances. By contrast, grassland habitats were dominated mainly by generalist macropterous species in the genus *Amara*, complemented with some flightless beetles such as *Cymindis humeralis* (Geoffroy in Fourcroy 1785), *Carabus germarii* (Sturm 1815), and *Carabus convexus* (Fabricius 1775). DCA Axis 2 revealed a pattern of species turnover along the altitudinal gradient. Species such as *Carabus problematicus* (Herbst 1786), and *N. biguttatus* (Linnaeus 1758) occurred only at high altitude and near the timberline, whereas the low altitude assemblages were dominated by *C. depressus* (Bonelli 1810), *Pterotichus burmesteri* (Herr 1838), *Abax parallelepipedus* (Piller & Mitterpacher 1783), and the endemic *C. italicus* (Bonelli 1810).

Table 1 Modelled variation of microclimate variables in relation to (a) altitude along vertical transects inside forest, and (b) along ecological gradients of patch size, patch edges, altitude and their interactions. Variables not retained after model simplification are omitted from the table.

		Air temperature		**Soil temperature**		**Relative humidity**	
		F	**p**	**F**	**p**	**F**	**p**
(a)Vertical transect	Altitude	81.12	**<0.001**	213.72	**<0.001**	0.23	0.628
Model R^2		0.57		0.78		0.004	
(b)Fragments	Altitude	3.89	0.049	1.30	0.254	14.57	<**0.001**
	Area	63.90	**<0.001**	61.81	**<0.001**	11.12	**<0.001**
	Edge	137.48	**<0.001**	202.66	**<0.001**	71.78	**<0.001**
	Area x Edge	3.29	0.070	5.91	**0.015**	3.67	0.056
	Altitude x Edge	0.01	0.891	0.81	0.368		
	Area x Altitude	15.00	<**0.001**	13.75	<**0.001**		
	Altitude x Area x Edge	3.02	0.083	2.30	0.130		
Model R^2		0.54		0.60		0.34	

Table 2 Summary results of mixed effect models for the independent and interactive effects of distance from edge, grassland patch area and altitude on species richness, two diversity indices, abundance, and community composition parameters (DCA Axis1), respectively. Variables not retained after model simplification are omitted from the table.

	Species richness*		**Shannon-Wiener index‡**		**Berger-Parker index‡**		**Abundance***		**DCA1‡**	
	z	p	F	p	F	p	z	p	F	p
Area	-3.00	**0.003**					-11.76	**<0.001**	0.003	0.956
Altitude	-1.83	0.067					-9.95	**<0.001**	32.12	**<0.001**
Edge	3.01	**0.002**	6.22	**0.013**	12.82	**0.0003**	2.00	**0.045**	354.75	**<0.001**
Altitude x Area	2.81	**0.005**					11.46	**<0.001**		
Altitude x Edge							-2.30	**0.021**	8.39	**0.004**
Model R^2		0.33[†]		0.05		0.05		0.77[†]		0.54

[*] **Generalized linear mixed effect models with the Poisson likelihood**

[‡] **Linear mixed effect models**

[†] **Pseudo R^2value**

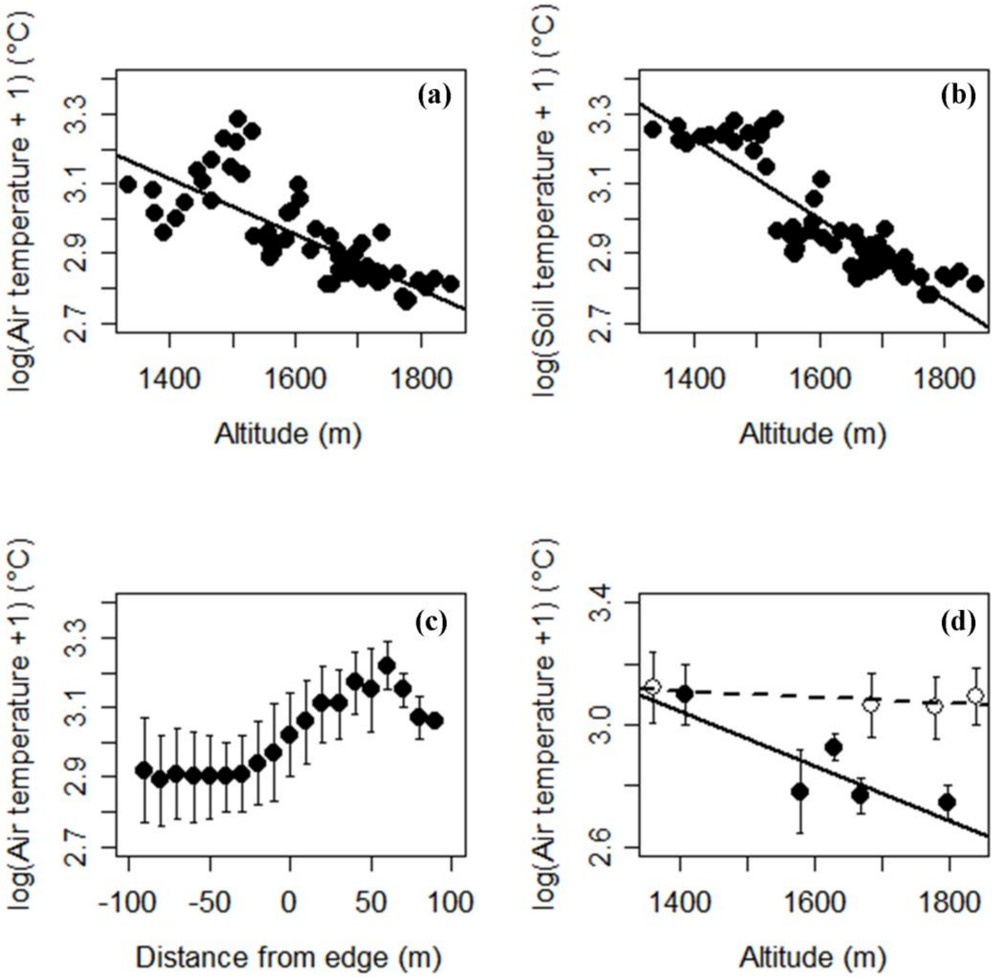

Figure 2 Microclimatic patterns across altitude and fragmentation gradients in the Italian Alps. Altitudinal variation in (a) air temperature and (b) soil temperature. (c) Variation in air temperature along transects extending from forest (negative edge values) to grassland (positive values) habitat. (d) The interactive effect of altitude and grassland patch area on air temperature. For clarity, we only present values from small (solid circles) and large (open circles) grassland patches. Values presented in panels c and d are the mean ± 95% confidence interval.

2.4.3 Interactions between fragmentation and altitude

One or more of the patch size, patch edge and altitude gradients had significant effects on all measures of beetle species richness, diversity and abundance, and community composition (DCA Axis 1) (Table 2). Overall, ground beetle diversity increased along the gradient from forest to grassland habitats. Much of the variation in community composition was explained by the gradients of patch size, patch edge and altitude, accounting for 54% of the variation in DCA Axis 1 (Table 2), although the changes in community composition across habitat edges depended on the altitude at which they were measured (Fig. 4a, Table 2).

Species assemblages changed distinctly with edge gradients, with higher axis 1 score for species in grassland sites, and decrease along the altitudinal gradient being more evident in forested habitats located at high altitude. Abundance patterns were dominated by significant two-way interactions of altitude with both distance from edge and patch size. In general, the number of individuals decreased across the forest to grassland gradient. However, that pattern was more marked at low than at high altitudes (Fig 4 b). Altitude also modified the patch size effect, with small patches supporting a higher number of carabid species and individuals at low than at high altitude (Fig. 4 c,d).

Consequently, the apparently negative effect of increasing grassland patch area on ground beetle diversity at low altitude was absent at high altitude where both the number of species an individuals was approximately equal in large and in small grassland patches.

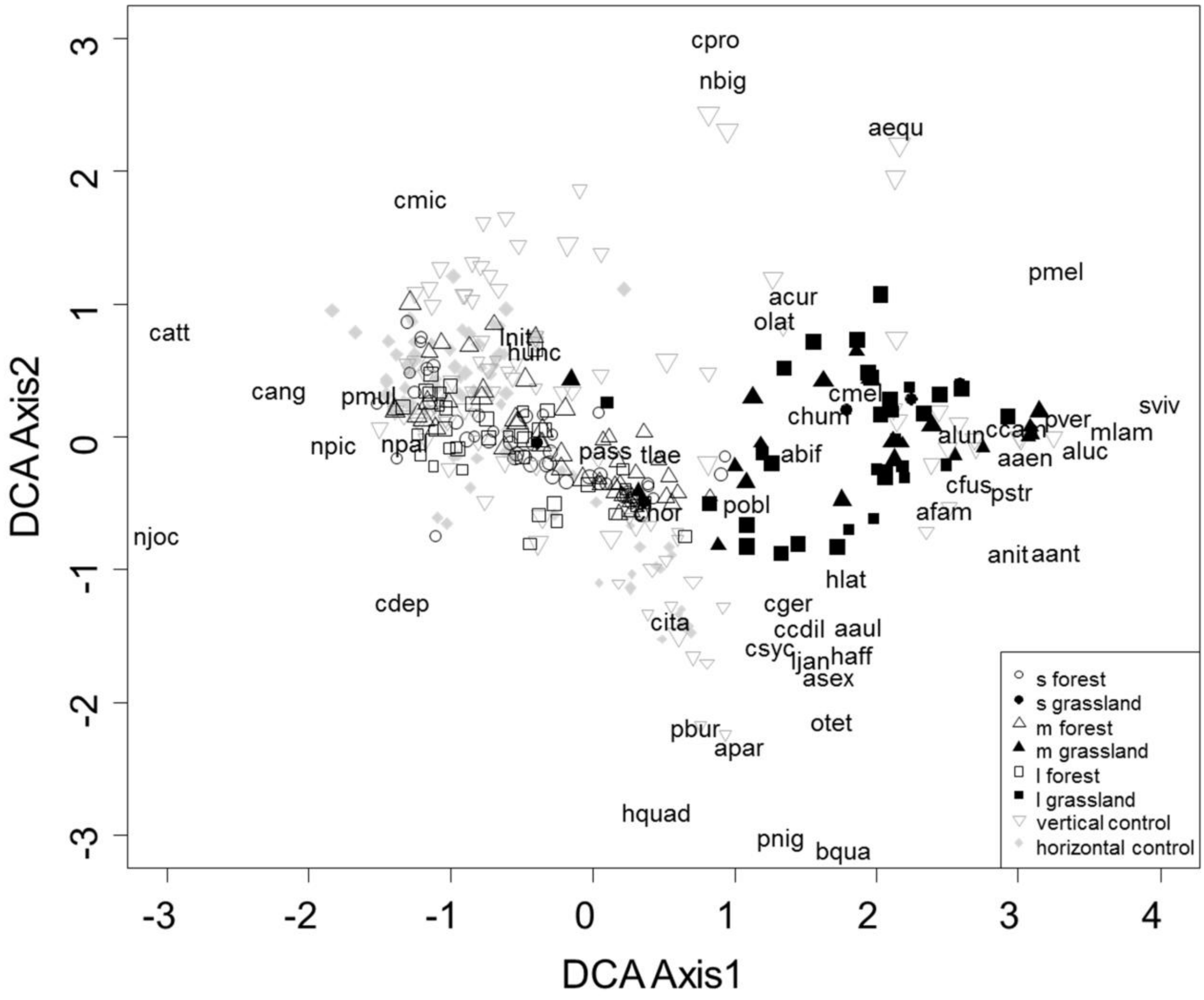

Figure 3 Ordination diagram showing how carabid community composition in the Italian Alps varies with habitat type, fragment area and altitude. Increasing symbol size reflects a gradient from low to high altitude (reflecting an altitudinal range of 1200 to 2100 m). Sites located on transects crossing forest edges are classified according to two habitat categories (forest or grassland) and three patch size categories (small [s], medium [m] and large [l] patches). In addition, samples were collected from control transects located within forest and which extended either horizontally along, or vertically up, the mountainside. Species are represented by a four letter code consisting of the first letter of its genus and first three letters of its species name (see Appendix 1b for species abbreviation).

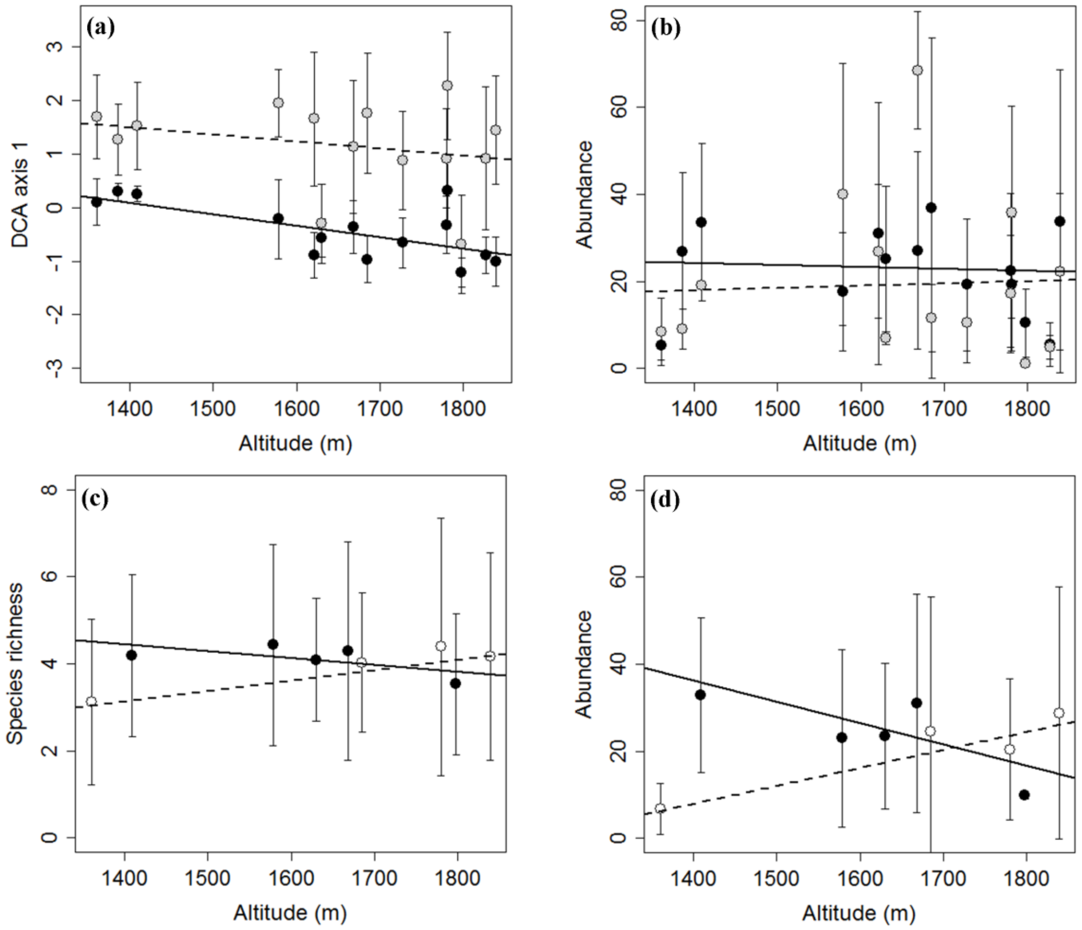

Figure 4 (a) DCA axis 1 scores and (b) abundance in relation with altitude and distance from edge (gray circles-grassland sites; black circles-forest sites), as results from the mixed effects models (Table 2). Models illustrating the two-way interactions between the slope of mean species richness (with 95% CI) (c), and abundance (d) on altitudinal gradient respectively for small (solid circles), large (open circles) grassland patches. Plots are based on results from the mixed effect models displayed on Table 2.

2.5 Discussion

Our data show that the effects of habitat fragmentation on biodiversity may be magnified by climate change to exert a much stronger total impact on ground beetle communities. Previous authors have suggested that the combination of habitat loss and global climate change could have strong and negative impacts on biodiversity (Thomas *et al.* 2004; Piessens *et al*., 2009), although the negative effect on biodiversity of a heavily fragmented landscape is expected to predominate over the consequences of increasing temperature (Warren *et al*., 2001).

Here, however, we have shown that not only do the two global change drivers impact biodiversity at the same time, as highlighted recently by Forister et al (2010) on Californian butterfly communities, but that one can magnify the effect of the other. Many fragmentation impacts on carabid communities that we detected at low altitude were not detected at high altitude. Consequently, as climate change increases air temperatures and forces species to move up the mountainside, fragmentation impacts are likely to also move up the mountainside.

The implication is that a larger proportion of the region will be impacted by habitat fragmentation than is currently impacted, meaning that climate change will magnify the impacts of fragmentation on this group of species. In line with previous European studies (Elek et *al*., 2010), we found that the number of carabid species tended to increase with increasing distance from forested sites into grassland patches. Conversely, we detected a higher abundance of individuals in forest than in grassland, a pattern similar to that described by (Koivula *et al.*, 2004) along forest-farmland edges in southern Finland. This pattern could be attributable to higher levels of productivity at ecotonal zones, which can lead to an increased number of prey available for generalist forest predators such as carabids and thereby directly affect their density (Magura *et al.,* 2001). The combination of reduced species richness and high abundance inside forest ensures that the Berger-Parker index, a measure of community dominance by the most abundant species, was greatest inside forest than in grassland. The effect of patch size on beetle richness and abundance was marked at low altitude and absent at high altitude (Fig. 4).

The observed decline of beetle richness and abundance in larger grassland patches at lower altitude could be due to a combination of higher temperature and the impact of anthropogenic activity that has traditionally been concentrated in the lowlands (Grandchamp *et al*., 2005). At local scales, beetle richness and abundance is strongly affected by microclimate conditions (Baker, 2006; Roslin *et al.,* 2009), and larger grassland patches might be responsible for impacting the microclimate inside the forest to a greater extent than small patches, as indicated by a significant interaction between patch size and distance to edge on soil temperature (Table 1).

Temperatures are higher immediately inside forest edges than deep inside forest (Barbosa *et al.,* 2010), and our data indicate that that edge effect increases in magnitude when forest edges are adjacent to large rather than small grassland patches. The approach of using temperature variation along altitudinal gradients to understand the effect of climate change has been previously used in field experiments (Whittaker and Tribe 1998). Our results indicated that the altitudinal gradient in temperatures in our study area was in line with projected climate scenarios of a more than 4 ° C temperature rise by 2100 (IPCC, 2007). Air and soil temperature both declined with altitude, but that altitudinal gradient was modified by habitat fragmentation. Temperature exhibited steeper altitudinal declines in small than in large patch sizes (Fig. 2), indicating that elevation is not the sole determinant of microclimate in mountainous landscapes. Rather, microclimatic changes are caused by the simultaneous and interacting effects of altitude and land-cover change (Vanwalleghem and Meentemeyer, 2009).

The microclimatic impacts of forest fragmentation have been documented numerous times (Barbosa *et al.*, 2010; Godefroid *et al*., 2006; Suggitt *et al.*, 2010), although these studies almost invariably consider what happens to the microclimate of forest patches inside an anthropogenic matrix whereas we studied the reverse. Studies such as that by Barbosa et al. (2010) highlighted a negative correlation between air temperature and forest fragment area. Here, we found a consistent but opposite pattern, in which large grassland patches in a forested matrix had higher temperatures than small patches.

Both results have the same implication that habitat fragmentation alters forest microclimate, but our data go one step further and show that the fragmentation impact is more accentuated at higher altitudes. Lowlands absorb a higher proportion of solar radiation compared to higher altitudes (Iziomon and Mayer, 2002), and we found the expected pattern of decreasing temperatures with altitude (Beniston, 2006). However, that pattern was detected in the forest and in small grassland patches, but not in large grassland patches (Fig. 2). We suggest this effect is due to differences in the heat capacity of large compared to small openings. Small grassland patches capture little direct sunlight and heat diffusion models suggest they will be greatly impacted by the cooler temperatures of the surrounding forest (Malcom, 1998), which decreases with altitude (Fig. 2). By contrast, larger grassland patches at high altitude are likely to absorb and retain more heat from the sun than small patches, helping maintain air and soil temperatures which are higher than the temperatures in the surrounding forests. We found that this highly modified alpine landscape hosted a diverse pool of carabid species, with a substantial differentiation of beetle assemblages across the fragmentation and elevation gradients. A number of species exhibited consistent associations with particular habitat types, resulting in strong edge gradients in community composition across forest-grassland edges.

Typically, forest sites supported a community which mainly included large-bodied and smaller brachypterous species. On the other hand, grassland patches were inhabited by a carabid community with more varied traits, including eurythotic species with good flight capability, dimorphic species as well as several wingless species. Changes in altitude were also associated with shifts in species’ composition, indicating that few species are able to tolerate the entire variety of habitats and range of temperatures encountered along the altitudinal gradient (Hodkinson, 2005; Moret, 2009). The combined impacts of habitat fragmentation and climatic variation will likely affect beetle species in different ways (Menendez, 2007; Barbaro and Van Halder, 2009).

Some forest or grassland species will be able to expand their range at upper altitude as a response to warmer conditions and anthropic impacts, but others are inevitably destined to have shrinking distributions (Menendez, 2007). There are some life-history traits that can potentially act as surrogates to predict the response of different species to these different threats (Magura *et al.*, 2006). For example, flightless large-bodied beetles are more prone to decline in highly modified habitats (Kotze and O'Hara, 2003), and species that are both rare and specialised are more likely to suffer population declines in fragmented landscapes (Davies *et al.*, 2004). Further contractions of distribution ranges might be also expected for a range of other wingless species that are associated with grassland habitats, as a consequence of the progressive abandonment of meadows and their subsequent recolonisation by conifer forests.

2.5.1 Conclusion

This study shows how the joint effects of fragmentation and climatic gradients influence carabid communities at a local scale in the Italian Alps. Our findings highlighted that, although the landscape has been characterized by a complex history, this alpine territory has a varied carabid composition, with spatial turnover in the composition determined by the preferences of individual beetles species to particular habitat types and along altitudinal gradients.

We found evidence that the effect of habitat fragmentation on ground beetle communities will become more accentuated as global temperatures rise. The magnitude of this synergy is likely to vary among species, with specialist and brachypterous species most at risk. Efficient conservation planning methods should be focused on maintaining the heterogeneity of the landscape in order to enhance ground beetle diversity in both forest and grassland habitats. Maintaining diversity in this region will require the maintenance not only of old-growth coniferous stands, but also the maintenance of post-abandonment secondary forests and the preservation of exiting subalpine and alpine grassland patches. These patches should, ideally, be linked via the creation of ecological semi-corridors (vegetation with a mixture of shrub and woodland) (Eggers *et al.*, 2009) that establish dispersal routes among patches at all elevations.

Chapter III

Interacting effects of habitat fragmentation and altitude on body size and fluctuating asymmetry of *Haptoderus unctulatus* (Carabidae) in the Italian Alps

3.1 Abstract

Human-induced disturbance in ecosystems might act as a potent selective force which can affect the phenotypic quality of individuals, inducing variations in their morphology such as fluctuating asymmetry and body size. Here, we investigated the simultaneous impacts of habitat fragmentation and climate change on variation of morphological traits in the forest-dwelling *Haptoderus unctulatus* (Coleoptera: Carabidae), using altitudinal gradients in the Eastern Alps (Italy) as a surrogate for climate change. We measured the body length and fluctuating asymmetry of elytra and femurs on individuals collected across gradients of altitude, distance from grassland edges, and the area of grassland patches. We detected significant interaction effects between altitude and fragmentation on both body length and fluctuating asymmetry. Individuals adjacent to large grassland patches had larger body size at low, but not high, altitude, and the edge × area interaction on fluctuating asymmetry changed in nature with increasing altitude with edge effects detected adjacent to large grassland patches at high, but not low, altitude. Overall, our results indicate that habitat fragmentation, acting in concert with increasing temperatures from climate change, might be expected to increase both body size and levels of fluctuating asymmetry in the *H. unctulactus* population, thereby increasing the level of morphological variation in this species.

***Key words**: body size, Carabidae, climate change, fluctuating asymmetry, habitat fragmentation.*

3.2 Introduction

Stressful conditions in the environment can impact the morphological characteristics of organisms at an intra-specific level (Weller and Ganzhorn, 2004; Lagisz, 2008), with individuals under high stress conditions having a sub-optimal body size or high levels of asymmetry in some traits (Tomkins and Kotiaho, 2001; Berggren, 2008). Small random differences in normally bilaterally symmetrical traits, termed fluctuating asymmetry (FA), can arise during the development stages of an individual (Graham *et al*., 2010).

There is a growing body of evidence showing that FA can arise in response to the impact of environmental stress (Söderman *et al.*, 2007; Almeida *et al.*, 2008; Henríquez *et al*., 2009, Maia *et al*., 2009). Forest fragmentation disrupts the continuity of forests, changes the abiotic and biotic conditions of a forest, and thereby imposes severe pressure on populations inhabiting the fragmented remnants (Fahrig, 2003, Ewers and Didham, 2006).

Habitat fragmentation is known to impact the morphology, including the body size and degree of FA, of a range of organisms (Tomkins and Kotiaho, 2001; Henríquez *et al.*, 2009). For example, individuals confined to smaller forest fragments can experience fluctuations in morphological traits as a result of reduced food availability (Kaiser and Lindell, 2007), or display increased FA levels due to loss of genetic variability (Anciaes and Marini, 2000; Băncilă *et al*., 2010). Fragmented landscapes in Puerto Rico have led to a general reduction in the body length of two endemic amphibian populations (Delgado-Acevedo and Restrepo; 2008), and higher FA in the tarsus length of birds was found in populations associated with severely fragmented afro-tropical ecosystems (Lens *et al.,* 1999). Climatic gradients have also been linked to morphological changes in species, although literature on this topic is rather scarce (Graham *et al.*, 2010). For example, a number organisms display a gradual reduction in body size that is correlated with increasing altitude, a common surrogate for decreasing temperature (Guevara and Aviles, 2007; Ciplak *et al.*, 2008; Lu *et al*., 2009; Liao *et al*., 2010).

Increasing FA levels in the forewings of the orthopteran *Chorthippus parallelus* with increasing altitudes has been reported (Jentzsch *et al.*, 2003), as has a similar trend for mountain birch leaves in northern Norway (Hagen *et al.*, 2008). By contrast, controlled experiments that have manipulated temperature have reported a positive correlation between increasing temperature and FA in insects (Vishalakshi and Singh, 2008), isopods (Savage and Hogarth, 1999), and fish (Lucentini *et al.*, 2010).

Species inhabiting fragmented landscapes will be simultaneously impacted by global warming over the coming decades. Understanding how patterns of morphological change will be influenced by the interplay of habitat fragmentation and climate change will be a challenging task, but there is evidence to suggest that the two drivers of global change will interact to additively or synergistically impact the morphology of species. For example, Silva et al. (2009), showed that no significant variation in body asymmetry of individuals was induced by temperature and fragmentation acting independently, but when combined together, these two environmental stresses increased the level of asymmetry in the Euglossine bee *Euglossa pleosticta.*

Here, we investigated how the simultaneous influence of habitat fragmentation and climate change might interact to impact intra-specific morphological variation. We used an altitudinal gradient in the Italian Alps as a surrogate for changing temperature, and investigated the morphology of the forest ground beetle *Haptoderus unctulatus* (Carabidae: Pterostichinae)

(Duftschmid 1812). Ground beetles are commonly regarded as effective bioindicators (Pearce and Venier, 2006), and are also known to display variation in morphological traits associated with reduced habitat quality (Marianski, 2002; Weller and Ganzhorn, 2004; Lagisz, 2008; Henriquez *et al.* 2009). However, it is not currently known whether the impacts of habitat fragmentation and climate change will impact these species in an additive manner, or whether one global change driver might magnify the effect of the other. Consequently, we aimed to determine if the combined effects of climatic variation and habitat fragmentation might intensify levels of intra-specific variation in morphological traits of *H. unculactus*, and if there are gender differences in this potential synergy.

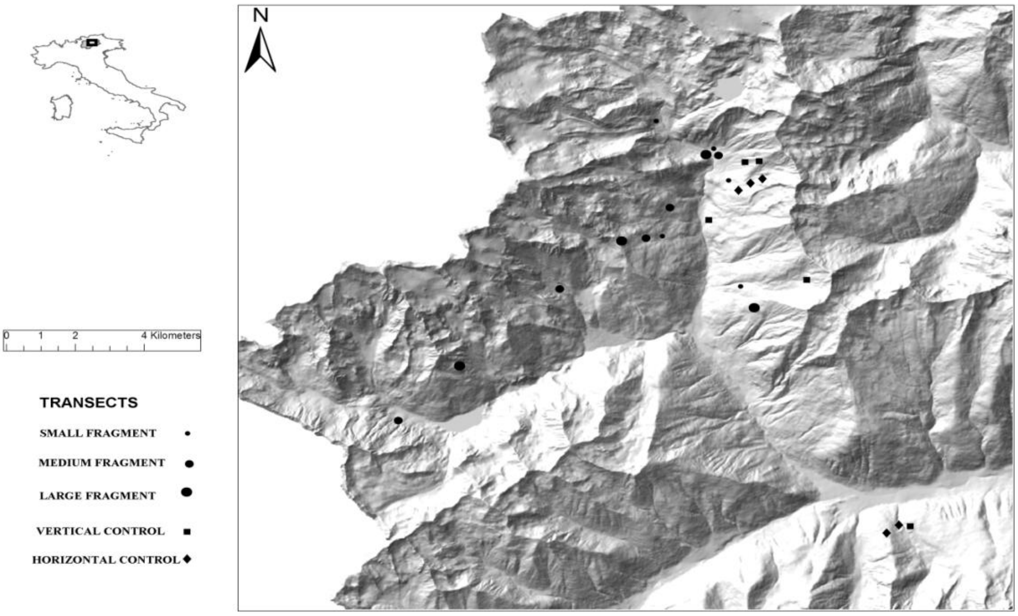

Figure 1 Map of the study area in the eastern part of Italian Alps showing the location of transects where *H. unctulatus* specimens were collected.

3.3 Material and methods

3.3.1 Study site

This study took place within Stelvio National Park in the eastern Italian Alps, where the topography consists largely of U-shaped valleys and mountains up to 3764 m.a.s.l. Mean daily maximum and minimum temperatures during mid-summer (July) are 19° C and 8° C respectively, and 0° C and -8° C in mid - winter (January).

There is also an altitudinal gradient in annual rainfall, ranging from 855 mm at the valley floors (1580 m) to 1300 mm at higher altitudes (2400 m). The vegetation is primarily Norway spruce *(Picea abies)* that extends from the valley floor to the upper limit of subalpine belt, where it is gradually replaced by Larch *(Larix decidua)* and Swiss stone pine *(Pinus cembra),* and dwarf-shrubs at higher altitudes. Some broadleaved trees are present but are mostly restricted to the lower limit of forest vegetation close to the valley floor.

The landscape comprises remnant pastures and meadows of different size that are embedded in a landscape matrix of old growth and younger secondary succession of coniferous forests that have expanded as a result of historical silvo-pastoral activities along the mountainsides. Intense exploitation of forests during the last three centuries saw forest cover reduced to its minimal extent during the 1800s, but these have progressively expanded since then as a consequence of agricultural abandonment (Sitzia, 2009). Land abandonment, which is a widespread phenomenon in the European Alps (Gellrich, 2007), has resulted in the decline of grassland areas at higher elevation, and is associated with simultaneous intensification of human activities and settlements at lower altitudes (Sitzia, 2009).

3.3.2 Sampling scheme

Specimens were collected from a total of 410 pitfall traps, consisting of a plastic cup sunk into the ground and partially filled with a solution of vinegar and salt. All pitfall traps were spaced 10 m apart along three sets of 24 linear transects: (1) 14 horizontal transects, running from inside the forest matrix (90 m inside a forest) across a forest-grassland edge and into the centre of grassland patches that ranged in size from 0.16 to 10.11 ha.

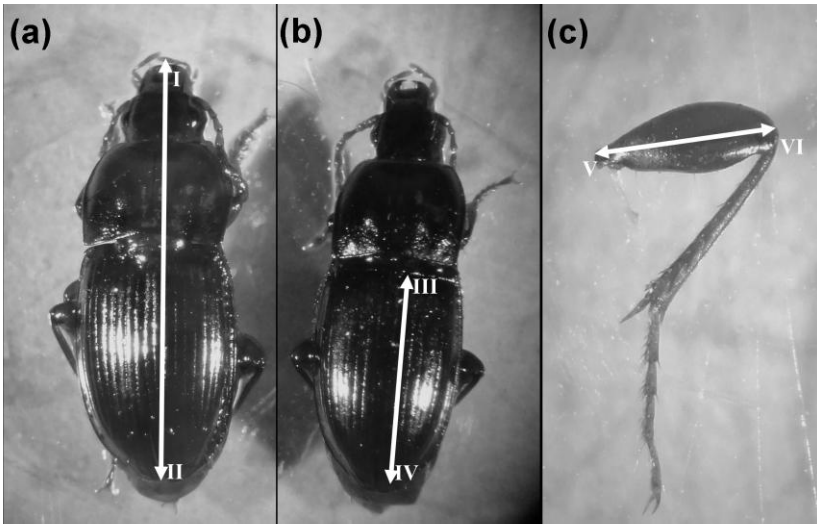

Figure 2 Morphometric traits measured in adults of *H. unctulatus* individuals. Body length seg. I-II from the peak of the mandibulae to the elytrae apex (a), elytron length seg.III-IV measured from the base of scutellum to the apex of elytron (b), meta femur length seg.V-VI measured without including the articulation segments (c).

Patches were located across an altitudinal range of 1385 to 1839 m, with patches chosen to ensure that log-transformed patch size was not confounded with altitude ($r = 0.24$, $N = 14$, $p = 0.40$), making it possible to discern their independent effects on dependent variables; (2) five vertical transects running up the valley wall, including three transects set inside the forest, one crossing from grassland on the valley floor and extending into the forest above, and the last extending from the forest across the upper timberline and into the alpine grassland; and (3) five horizontal control transects, each one 190 m long and located in the continuous forest matrix at different altitudes (1382, 1620, 1685, 1781 and 1840 m). Pitfall-traps were emptied fortnightly from June to September 2009. Specimens were preserved in 70 % ethanol, and identified to species using systematic keys (Porta, 1923, Hurka, 1996).

3.3.3 Species and morphometry

We collected detailed morphometric measurements on individuals of *Haptoderus unctulatus* (Carabidae: Pterostichinae). This species was selected because it is an abundant forest species that occurred at all altitudes in the study area. Its distributional range extends across Central and Eastern Europe, and it is widespread along the Alpine chain (Grandscamp, 2005). *H. unctulactus* is a small, stenotopic brachypterous species (size around 6 mm), with a preference for acidophilous spruce forest habitats (Hurka, 1996; Grandschamp 2005).

This species has been shown to be particularly susceptible to habitat fragmentation (Nitzu *et al.*, 2008; Šustek, 2007), but its potential response to climate change is not known. Both males and females were collected and preserved in 70% ethanol until they were sexed and measured.

Before the measurements, each individual was dried in order to reduce optical distortion, and subsequently measured using three types of morphometric measures with definite landmarks: (1) body length, defined as the distance from the peak of the mandibulae to the apex of elytra (Fig. 2a); (2) elytron length, defined as the distance from the base of the scutellum to the apex of the elytra (Fig. 2a); and (3) hind femur length, excluding the articulation joints (Fig. 2b).

Each femur was removed from the hind coxa and mounted on glass slides for measurement. Measurements were taken always by the same observer with a stereomicroscope (model LEICA MS5, total magnification 2× to 320×) using an eyepiece graticule. To estimate FA, we measured the left and right side elytron and femur of each individual. Measurement error can impact estimates of FA, so it has been recommended that all measurements should be repeated multiple times (Palmer, 1994).

We repeated our measurements of all individuals two times. In order to reduce any error attributable to insect positioning measurement, each of the individuals was removed after the first measurements and replaced under the microscope for the second measurement. To further quantify the potential for measurement error to influence our results, we randomly selected a subsample of 12 individuals, repeating the measurements four times on each individual.

Repeated measurements were made with an interval of at least 24 hours between measurements, and were conducted in a blind manner with no reference to earlier measurements or to sample identification codes (Palmer, 1994).

3.3.4 Statistical analysis

Preliminary analysis of asymmetry in femur and elytron traits: We conducted a series of preliminary procedures following the protocol of Palmer (1994) to estimate the presence of measurement error (ME) and other patterns of asymmetry that might invalidate the FA indices and thus prejudice further analysis (DA – directional asymmetry, and AS – anti-symmetry). Measurement error was evaluated with a two-way mixed effect model performed separately for each trait on the subsample of 12 individuals.

Two factors and their interaction were entered in the models: (a) SIDE, using the side of the body (right and left) as a fixed effect; (b) INDIVIDUAL as a random effect; and (c) the interaction term SIDE × INDIVIDUAL as a fixed effect. This test allowed us to divide the variance into two fractions (difference between side among and within individuals), thus determining if the amount of ME is insignificant compared to the observed FA between side (this is given by a significant SIDE × INDIVIDUAL interaction term) (Palmer, 1994; Merila and Biorklund, 1995).

Directional asymmetry (DA) arises when a specific trait has a consistently different size on one or other side of the body (Tomkins and Kotiaho, 2001). Traits that exhibit DA should not be considered in an FA study as it is thought to have a genetic basis (Palmer, 1994). The presence of DA would show up in the two-way mixed ANOVA as a significant effect of SIDE. Fluctuating asymmetry is calculated as the difference in a trait between the left and right side, and we used a *t*-test together with skewness and kurtosis coefficients to test for any deviations from normality and whether the distribution of the signed or relative FA had a mean that was significantly different to zero.

These analyses were performed to reveal the occurrence of anti-symmetry (AS), which implies a large variation in a trait on a particular side of the body relative to the variation on the other side. Finally, Pearson’s correlation coefficient between unsigned FA (|R–L|) and the mean trait size ([R+L]/2) was used to test for covariance in character size and FA for each of the FA indices. These tests were repeated separately for individuals collected on each of the three groups of sampling transects (forest-grassland, horizontal controls and vertical controls).

The effects of habitat fragmentation and altitude on body length and FA: All morphological data were checked for normality with the Shapiro-Wilk test and, due to unequal variances, were transformed using a square-root transformation. We used linear mixed effect models to test for the simultaneous effects of altitude, grassland patch area, and edge gradients on variation of body size and fluctuating asymmetry in *H. unctulactus* populations. Altitude, area and edge were included as covariates in the models, and to detect any intersexual differences we included SEX as a factor in the model.

We controlled for the variation among individuals by adding INDIVIDUAL as a random effect, thus using all FA measures from the original dataset. Mixed effects models were also used to assess if altitudinal gradients (using only data for three vertical transects running inside the forest habitat, and four horizontal controls) were associated with variation in body size and FA (specifying sex as factor, altitude as a covariate, and INDIVIDUAL as a random effect). All models were simplified using manual backwards stepwise selection, retaining models with the lowest Akaike's Information Criterion (AIC) as the best model (Burnham & Anderson, 2002). The R statistical software (R Development Core Team 2008) was used for all analyses.

3.4 Results

We collected 263 individuals of *Haptoderus unctulatus* (139 females and 124 males). *H. unctulatus* individuals were abundant at all altitudes. This species showed a strong preference for forest habitats, being caught exclusively in sampling points located in the forest, so we omitted all grassland samples from further analyses. Of the 263 individuals, 156 were captured in the edge transects adjacent to grassland patches, 23 were captured in the horizontal control transects located in continuous forest, and the remaining 84 were captured in the vertical control transects.

3.4.1 Preliminary analyses of asymmetry

Results from two-way mixed effect ANOVA on repeated measures for each traits revealed a highly significant SIDE × INDIVIDUAL interaction (femur, $F_{1,92}$=12.13, p<0.001; elytra, $F_{1,92}$=17.09, p<0.001). This suggested that the magnitude of ME was insignificant relative to the levels of FA. We found no evidence for DA in the samples, illustrated by a non-significant SIDE term for femur ($F_{1,92}$=2.62, p=0.10) and elytra ($F_{1,92}$=0.49, p=0.48). Moreover, we found no evidence that asymmetry means (distribution of the right minus left trait values) diverged significantly from expected values of zero, thus suggesting an absence of AS. Finally, values of unsigned asymmetry and mean femur and elytron size were not correlated (Appendix 1).

Table 1 Summary of linear mixed effect models examining the association of altitude, distance from edge, grassland patch size, and gender on the body length and fluctuating asymmetry of *H. unctulatus* individuals. Only variables that were retained after model simplification are presented. Significant *p*-values (<0.05) are shown in bold.

Trait	**Variable**	**MS**	***F***	***p***
Body Size	Altitude	0.006	2.116	0.147
	Area	0.003	1.084	0.299
	Edge	0.008	2.651	0.105
	Sex	0.058	19.173	**<0.001**
	Area x Altitude	0.021	7.005	**<0.01**
Femur	Edge	0.036	6.494	**0.012**
Elytron	Altitude	0.005	1.069	0.302
	Area	0.001	0.219	0.640
	Edge	0.114	21.71	**<0.001**
	Sex	0.012	2.410	0.122
	Sex × Altitude	0.029	5.560	**0.019**
	Sex × Edge	0.000	0.140	0.708
	Area × Altitude	0.002	0.522	0.471
	Area × Edge	0.000	0.006	0.936
	Edge × Altitude	0.002	0.450	0.503
	Sex × Area	0.010	1.996	0.160
	Sex × Edge × Area	0.007	1.395	0.239
	Altitude × Area × Edge	0.033	6.330	**0.013**

Based on these initial results, we concluded that the value |R-L| was an appropriate index of FA for further analysis.

3.4.2 Effects of habitat fragmentation and altitude on beetle morphology

We detected significant main and interaction effects of habitat fragmentation and altitude on body size and all FA indices, as well as significant effects of gender (Table 1). Dimorphism in body size was detected among *Haptoderus unctulatus* individuals, with female individuals being significantly larger than males (♀, 7.24 ± 0.03; ♂, 7.08 ± 0.04) (Fig. 3a). We detected a consistent increase in fluctuating asymmetry as a response of distance from edge for both femur and elytra FA, with individuals tending to be more asymmetric the closer they were to the forest-grassland edge (Fig. 3b, c). However, we also detected significant interaction effects between the fragmentation variables and altitude that impacted the morphology of *H. unctulatus* (Table 1). First, we found that at low and medium elevation, individuals tended to increase in body length when they were adjacent to grassland patches of increasing area, whereas no significant trend was found for high-altitude sites (Fig.4).

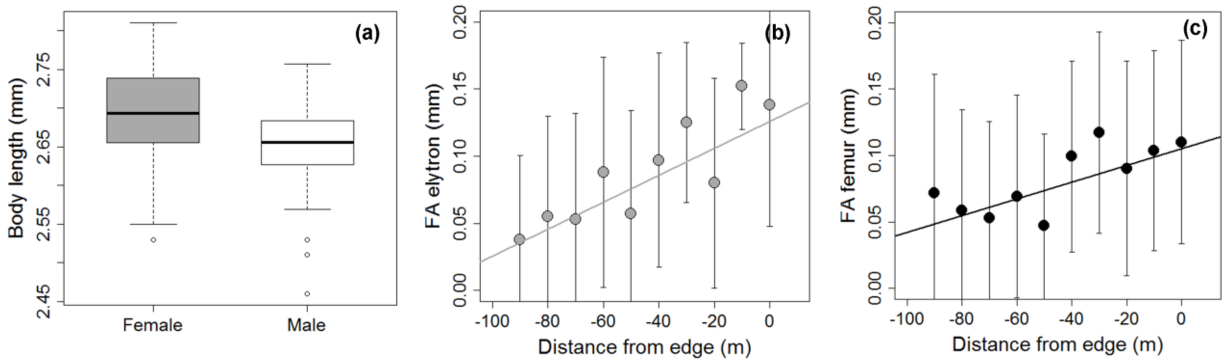

Figure 3 (a) Differences in the body length distribution of male and female adults of the carabid beetle *Haptoderus unctulatus*. (b,c) Spatial variation in fluctuating asymmetry along forest-grassland edge gradients for (b) elytra, and (c) femur. Values for FA represent the mean ± 1 SE. Negative edge distances represent sampling points that are inside the forest habitat.

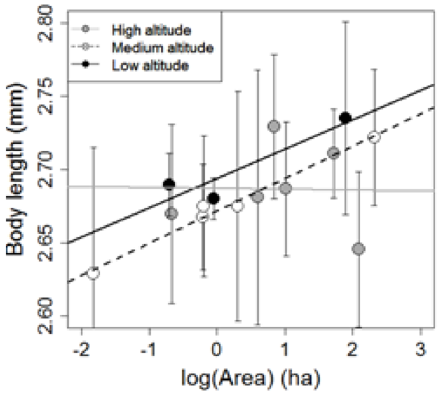

Figure 4 Interaction effects of grassland patches size and altitude on the body length of *Haptoderus unctulatus*. For clarity, altitude is categorised into low (1360-1409 m), medium (1578-1685 m) and high (1727-1839 m), but all analyses treated it as a continuous variable. Values for body length represent the mean ± 1 SE.

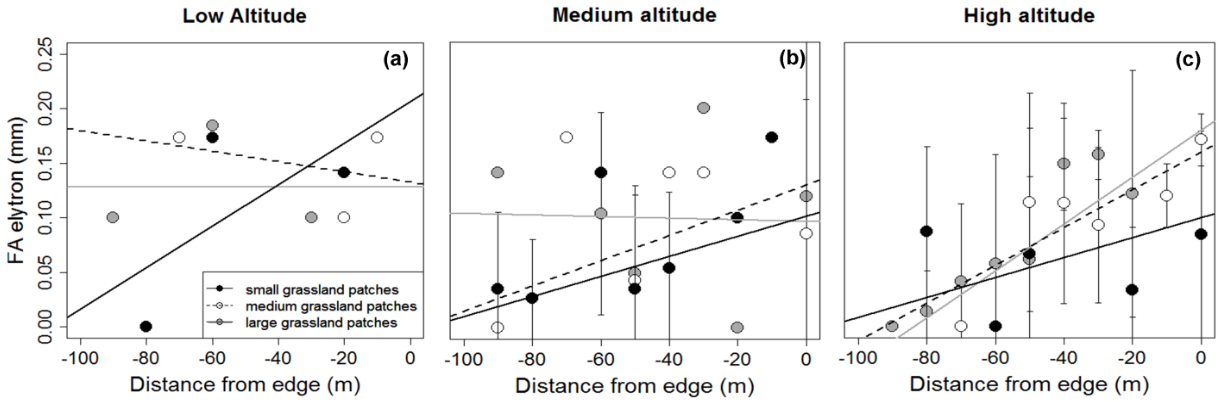

Figure 5 Models illustrating the three-way interaction of altitude, patch area and distance to patch edge on the elytra fluctuating asymmetry of the carabid beetle *Haptoderus unctulatus*. Panels show the interaction between two fragmentation variables, patch area and distance to patch edge, at (a) low, (b) medium, and (c) high altitude. For clarity, altitude is categorised into low (1360-1409 m), medium (1578-1685 m) and high (1727-1839 m), and patch area is categorised into small (0.162-0.822 ha), medium (0.941-2.761 ha) and large (5.576-10.114ha). All analyses treated both altitude and patch area as continuous variables. Values for FA represent the mean ± 1 SE. Negative edge distances represent sampling points that are inside the forest habitat.

Second, there was a significant three-way interaction between the edge, area, and altitude gradients on elytra FA. There was an altitudinal transition in a way that habitat fragmentation impacted elytra FA, with the edge effect at low altitude being apparent on transects adjacent to small grassland patches, but at high altitude the edge effect was apparent adjacent to small medium and large grassland patches (Fig.5). There were no significant patterns in body length and FA indices along the vertical transects, indicating no direct effect of altitude on *H. unctulatus* morphology. Similarly, we detected no significant patterns of morphological variation along the horizontal control transects, indicating that the detection of edge effects was not due to naturally occurring spatial variation in beetle morphology.

3.5 Discussion

This study suggests that climatic changes may accentuate the effects of habitat fragmentation on the morphology of *Haptoderus unctulactus*. As temperatures increase over the coming decades, we expect to see habitat fragmentation impacts on body size and fluctuating asymmetry that are present at low altitude to gradually move up the mountainsides.

The qualitative outcome of these synergistic effects for the species is difficult to predict, as it depends on the balance between increasing fecundity with body size and decreasing fitness with increasing FA. Consistently to previous studies conducted on different carabid species (Desender 1989; Sota *et al*. 2000a; Tyler, 2008), we detected significant sexual dimorphism in body size of *H unctulactus* individuals with females being larger-bodied than males. However, we also found that body size was further impacted by an interaction effect between grassland patch area and altitude. At low altitudes, increasing grassland patch area appeared to have beneficial impacts, with individuals in forest adjacent to large patches having larger body lengths. It is generally recognized that the increases in mean temperature and nutritional resources available at lower altitudes might influence the developmental rates of insects, and can result in an increased body size of individuals (Hodkinson, 2005; Dillon *et al*., 2006; Rodriguez-Jimenez and Sarmiento, 2008).

The increased body size of individuals living in forest close to a large grassland patch at lower elevation could, then, be explained by increased microclimate temperatures near forest-grassland edges. The same process may explain the lack of a patch size effect at high altitude, assuming that microclimate gradients across high altitude forest edges are reduced. This may be the case if grassland patches at high altitude do not heat up as much as those in the warmer, low altitude zones. Increasing altitude has previously been linked to reductions in the body size of beetles (Krasnov *et al.,* 1996; Sota *et al.,* 2000b). Similarly, habitat fragmentation has been linked to declines in carabid body size (Niemela, 2001; Barbaro and Van Halder, 2008), although patterns in body length variation might be species-specific responses to environmental stress with different species exhibiting different patterns (Garbalińska and Skłodowski 2008).

Our data, however, go further and show a complex synergy between altitude and fragmentation which, in the case of *H. unctulactus*, suggests that individuals simultaneously experiencing climate change and habitat fragmentation may increase in body size. We also detected strong interactions between expected rising temperature due to climate change and habitat fragmentation that may lead to greater levels of fluctuating asymmetry in *H.unctulactus* populations. Habitat fragmentation is widely associated with increasing FA in a variety of taxa, including birds (Lens and Eggermonth, 2008), mammals (Marchand, *et al.*, 2003), amphibians (Gallant and Teather, 2001), and ground beetles (Weller and Ganzhorn, 2004). Furthermore, a recent study in Brazilian forests suggested that rising temperatures together with habitat fragmentation might impose more severe changes on Euglossine bee morphology (Silva *et al*. 2009), and interaction effect that is similar to the one we detected for *H. unctulactus*.

The spatial patterns in fluctuating asymmetry observed in *H. unctulactus* could be the result of spatial variation of climatic conditions along the mountainsides. Particularly, at low elevation where temperatures are higher, the presence of grassland patches might directly cause a rising of temperature inside the adjacent forests (Barbosa *et al.*, 2010), but this effect may be dampened at higher altitudes where grassland patches heat up less. The higher levels of FA at low altitude forest edges could be the result of accentuated differences in ground soil temperature between forest and grassland sites, and grassland habitats are known to have higher seasonal oscillations in soil temperature than forest habitats (Sharrat 1998).

Given that the development of carabid beetles is known to be strongly dependent on ground condition (Lövei and Sunderland, 1996), it seems likely that fragmentation-induced changes to forest microclimate may be interfering with the developmental stability of *H. unctulactus*, with that effect mediated by microclimate. At high altitude, increasing temperatures may mean that small patches begin to heat up to the same extent as small patches at low altitude in the present-day climate.

This, in turn, means that the impacts of high-altitude fragmentation on FA that currently only occur adjacent to large grassland patches may begin to appear adjacent to small patches as well, leading to an increase in the spatial area impacted by habitat fragmentation under climate change. Body size is positively correlated with fecundity in carabid beetles (Juliano, 1985; Östman, 2005), suggesting that the fragmentation × climate interaction will be positive for the species. Yet there is also a negative correlation between asymmetry and fitness components such as the growth, fecundity and survival of individuals (Møller, 1996; Møller, 1999; Andersen *et al*., 2002; Lens *et al.*, 2002), which indicates that the fragmentation × climate interaction will negatively affect the species.

We expect that increasing temperatures under climate change will lead to a simultaneous increase in average body size and fluctuating asymmetry in the *H. unctulactus* population, so it will be the balance of these two influences on fitness that will determine whether the net outcome of this synergistic interaction will be positive, neutral or negative. Our study examined a single ground beetle species, and because we know that the morphological responses to environmental stress are species-specific in carabids (Garbalińska and Skłodowski 2008), it is unclear to what extent our results can be generalised to other species. To obtain a cohesive picture of the interacting impacts of climate change and habitat fragmentation will require a larger number of studies that explore the phenotypic plasticity of a wider range of organisms in response to these two major drivers of global environmental change.

Chapter IV

Similar life history trait combinations interact to determine species' sensitivity to habitat fragmentation and climate change

4.1 Abstract

The life history traits of species are known to be associated with species vulnerability to anthropogenic disturbances such as habitat fragmentation and climate change. Species with certain traits are more likely to persist within altered ecosystems than others, but the sensitivity of species to these two global changes may also depend on the covariance among traits, with certain trait combinations likely to elevate the extinction risk for particular species. Here, we tested this hypothesis using data on 32 species of ground beetle (Coleoptera: Carabidae), collected from 300 pitfall traps in a mountain forest landscape in the eastern Italian Alps. We detected significant interaction effects among species traits that determined their sensitivity to gradients of habitat fragmentation (patch size and edge effects) and altitude (a surrogate for climate change). In line with expectations, we found that large-bodied species with restricted dispersal and specialised diets were most susceptible to environmental change. We also found that dimorphic and macropterous forest specialist species, together with smaller wingless open habitat specialists were negatively affected by increasing grassland patch areas. Importantly, we found a positive correlation between species susceptibility to habitat fragmentation and climate change, indicating that the two environmental changes acting simultaneously may exert stronger combined effects on biodiversity than either change acting independently.

Keywords: *Carabid beetle community, elevational range, fragmented landscapes, global warming, life history traits, mountain ecosystems.*

4.2 Introduction

As the destruction of habitats and rising temperatures continue to alter the global environment in the near future (Pimm *et al.*, 1995; Travis, 2003; Keith *et al*., 2008), the ability of organisms to persist is likely to be determined by the intricate interplay between their life history traits and the altered habitats in which they occur (Vandewalle *et al.*, 2010). Not only will species need to respond to the simultaneous influence of these two global environmental changes, but their responses will likely depend on the interactions among, and covariance between, different life history traits. Worryingly, there are particular trait sets that can elevate the level of extinction risk that a species faces (Davies *et al*., 2004; Fréville *et al.*, 2007).

Moreover, simultaneous changes to multiple aspects of the environment may have larger impacts on species persistence than changes to a single aspect alone. Piessens et al. (2009) showed that specialist butterfly *Cupido minimus* that exist in small, isolated populations were more vulnerable to habitat fragmentation when they are simultaneously impacted by extreme weather events, a result similar to that of McLaughlin et al., (2002) who showed that the interaction between habitat loss and changing precipitation regimes led to the extinction of populations of the checkerspot butterfly *Euphydryas editha bayensis* in California. In another study from Spain, Stefanescu et al., (2011) found the diversity of butterflies was most heavily reduced in locations with both high temperature (lower altitudes) and low levels of habitat availability.

Predicting the impacts of global environmental change on biodiversity is further complicated by the fact that species might respond differently to the same environmental changes. For example, in a recent study based on a 23-year data series on moth assemblages, Kadlec et al. (2009) found that generalist species were more sensitive to climate changes than habitat specialists, which in turn appeared to be more affected by land use changes.

Differences in the biological traits of species ensure that some organisms are more susceptible to changing environments than others, a result that has been shown repeatedly for a large number of taxa (Ward and Masters, 2007; Barbaro and Van Halder, 2008; Pueyo *et al.*, 2008; Jiguet *et al.*, 2010; Kennedy et al., 2010; Ockinger *et al.*, 2010). For example, species with a high power of dispersal are more favoured in fragmented landscapes where the geographical isolation between habitat patches is increased (Öckinger *et al.*, 2009), whereas those with narrow feeding niches are more likely to be compromised as the size of habitat patches decreases (Cagnolo *et al.*, 2009). As a general rule, habitat specialists are more sensitive to habitat loss and fragmentation than generalist species with wider distributions (Krauss *et al.*, 2003; Ewers and Didham, 2006; Devictor *et al.*, 2008; Brückmann *et al.*, 2010). Perhaps surprisingly, the same species traits that predict species sensitivity to habitat loss may also be associated with sensitivity to other forms of environmental disturbance (Williams *et al.*, 2010).

Directional trends in terms of species sensitivity associated with climate variability, with positive responses expected for widespread habitat generalists than specialist species in the face of global warming (Menendez *et al.*, 2006). Rising temperature might also induce a strong dispersal process in the case of fully developed winged individuals within polymorphic species (Hochkirch and Damerau, 2009), while a high incidence of brachyptery has been associated with higher altitudes or colder temperature conditions (Hodkinson, 2005). Based on a chronosequence of an Italian Alpine glacier foreland as a spatio-temporal approach for study on climate change, Gobbi *et al.* (2007) found that communities in older stages of the chronosequence were dominated by short-winged species, whereas larger bodied species were mostly associated with the younger sites near the glacier. Moreover, particular trait sets might act synergistically to magnify their relative importance and lead to much greater population reductions than expected from the two traits acting independently. For example, Davies et al. (2004) showed that beetles that were both rare and specialised were particularly vulnerable to habitat fragmentation.

If such synergies are common, then more local extinctions might be expected to occur than are apparent from predictions based on single traits, potentially leading to a gradual process of life history trait homogenisation within communities (Smart *et al.,* 2006; Ekroos *et al.,* 2010). Here, we focused on the cosmopolitan family of ground beetles (Coleoptera: Carabidae) to examine how species with different combinations of life history traits respond to gradients of habitat fragmentation and altitude in the Italian Alps, with the latter gradient used as a surrogate measure for climatic change. Carabids are important bioindicators across a wide range of terrestrial ecosystems (Pearce and Venier, 2006), based on their marked associations with environmental conditions that lead to distinct beetle assemblages that characterize different habitats (Lövei and Sunderland, 1996; Niemelä, 2001; Koivula, 2011).

In this study, we used data on the wing form (a proxy for dispersal ability), body size, habitat preference and diet of ground beetles to investigate the possibility that life history traits might interact in a non-additive manner to affect species sensitivity to land use and climate change. We expected the strongest responses to be detected in species characterized by low mobility, large body sizes and narrow habitat requirements, and that the species most susceptible to fragmentation would likely also be the most susceptible to climate change. However, we had no *a priori* expectation about which trait combinations might interact to exacerbate the impacts of fragmentation and climate.

4.3 Methods

4.3.1 Study site and sampling design

The study was carried out along the mountainsides of the Peio Valley and Val di Sole in the eastern Italian Alps (46°21'N, and 10º41'E) (Fig. 1). This mountain range is characterized by semi-natural grassland habitats of variable size embedded within old-growth and secondary succession forests that have expanded as a consequence of land abandonment (Sitzia, 2009).

Carabid beetles were sampled using a total of 300 pitfall traps located on 19 linear transects. Removable pitfall traps (plastic cups: 70 mm diameter x 70 mm depth) were dug into the soil, separated along transects by 10 m intervals, and half filled with a solution of vinegar and salt (6%). The 19 transects were divided into two groups. In the first group, 14 transects extended from 90 m inside the forest interior, across the forest-grassland edge and out into the centre of grassland patches. Patches ranged in area from 0.16 ha to 10.11 ha, and were located at altitudes ranging from 1386 to 1839 m.a.s.l.

Patches were selected to ensure there was no correlation between log-transformed patch size and altitude (Pearson correlation $r = 0.24$, $N = 14$, $p = 0.40$), ensuring the absence of potential confounding effects of collinearity between predictors. The second group comprised five horizontal transects (190 m long), each having 20 pitfall traps and placed in continuous forests at five different altitudes (1382 to 1840 m). Fieldwork was carried out between June and September of 2008 and 2009, during the peak of ground beetle activity in the study area. At each sampling point, pitfall traps were emptied and beetles were collected every two weeks for a period of three months in both years.

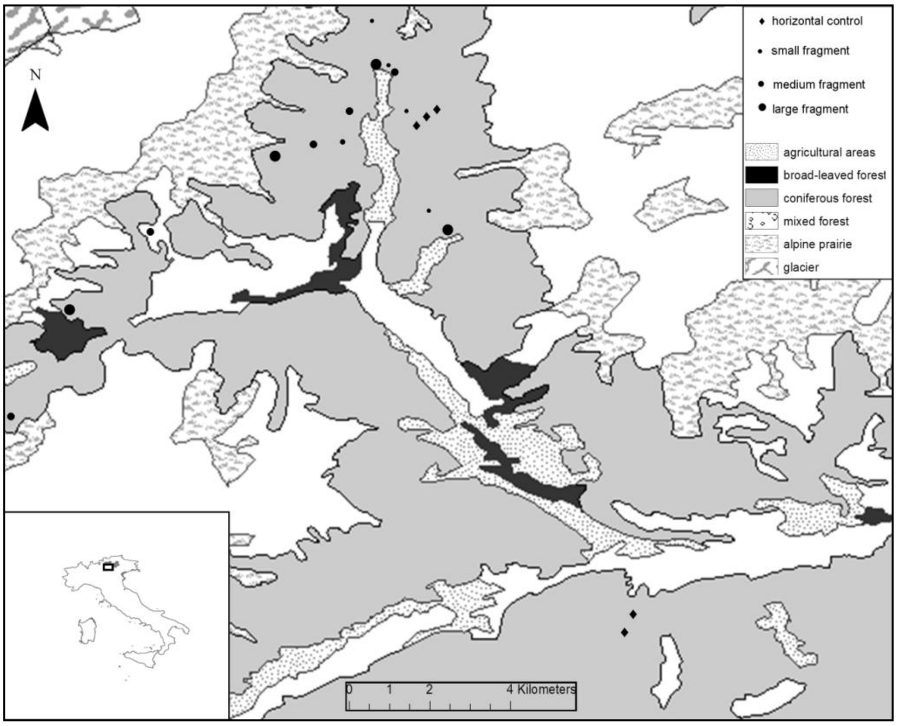

Figure 1 Map showing the position of the 19 transects along the altitudinal profile of the Stelvio National Park

4.3.2 Ground beetle functional traits

A set of four ground beetle life-history traits were selected for analysis: (1) flight ability, (2) trophic guild, (3) habitat preference, and (4) body length (see Appendix I for a full list of species and traits). First, based on the literature (Hurka, 1996), carabids were classified into three categories according to the degree of functional wing development: brachypterous (species with reduced wings, not able to fly), macropterous (with fully developed wings and high dispersal potential), or dimorphic (individuals of the same species with both short and long wing forms). Second, we assigned each carabid species to one of three trophic levels: zoophagous (generalist predator on different organisms), specialized zoophagous (with a restricted diet consisting mainly of a specific type of prey), or phytophagous (mainly herbivore or granivore). Data on trophic specialization were extracted from Thiele (1977), Koivula et al., (2004), Luff (2007).

Third, beetles were assigned one of three habitat preference categories: open habitat (species common in dry, grassland areas), forest generalist (including all eurytopic species living in forest-grassland edges), and forest specialist (species restricted to closed-canopy forest sites), based on our field data and previous published information acquired by Brandmayr and Zetto, (1988), Hurka (1996). In the case of ambiguous or contradictory information about specific traits, we used the traits presented in the most recent published source.

Finally, we determined the body length of each species, included as a continuous variable in our analyses. Due to the large number of individuals collected in the field we did not take a measurement of each individual, but rather estimated an average body size for each species by measuring a minimum of 3 specimens.

4.3.3 Data analysis

For each individual pitfall trap, we pooled the untransformed data of beetle species abundances from the years 2008 and 2009, and corrected for small differences in sampling effort by dividing the number of individuals by the number of sampling days. These abundance data were used to derive three indices to quantify species sensitivity to patch area, edge effects and altitude respectively. Species with less than five individuals were excluded from all analyses, meaning that our analyses were restricted to a total of 32 species. For each species, we calculated the three sensitivity indices using log ratios, indicating directional species preferences in response to area, edge and altitude gradients. To avoid the problem of obtaining an infinite log ratio value for species which had a value of zero for the denominator, we added the arbitrary, small amount of 1×10^{-7} to all estimates of mean species abundance.

Species sensitivity to the two fragmentation variables were based on data collected from the transects running from forest into grassland patches. (1) To estimate area sensitivity, we subsetted our data to include only transects running across the edges of small (0.162 to 0.822 ha, N = 5 transects) and large (5.576 to 10.114 ha, N = 4 transects) grassland patches. Beetle responses to patch area were calculated as the log ratio of mean beetle abundance in transects adjacent to large grassland patches relative to mean beetle abundance in transects adjacent to small grassland patches. Directional area sensitivity was, then, calculated as:

$$DS_{Area} = log\left[\bar{N}_{large}/\bar{N}_{small}\right].$$

This index can be explained as proportional measure of change of abundance of a species as a consequence of increasing grassland patch area. Species with positive values of DS_{Area} are more abundant in large grassland patches, species with negative value are more abundant in small grassland patches, and species with a value of zero are insensitive to patch area. (2) To estimate directional edge sensitivity, we calculated the log ratio between the mean beetle abundance within forest sites relative to the mean beetle abundance in grassland sites, using the formula:

$$DS_{Edge} = log\left[\bar{N}_{forest}/\bar{N}_{grassland}\right].$$

Values greater than zero indicate a preference for forest habitat, values less than zero indicate a preference for grassland habitat, and values of zero indicate no habitat preference and therefore no sensitivity to the gradient across forest-grassland edges (3) Finally, directional altitude sensitivity was calculated using samples from the horizontal transects located inside the continuous forest matrix at different altitudes. We considered only sites at low and high altitude (two linear transects situated at 1382 m, 1840 m). Altitude sensitivity was obtained by calculating the log ratio of average beetle abundance in high altitude sites divided by average beetle abundance in low altitude sites using the formula:

$$DS_{Altitude} = log\left[\bar{N}_{high}/\bar{N}_{low}\right].$$

Indices with positive values represent species associated with higher altitude, species with negative values were associated with low altitude, and species with a value of zero were insensitive to altitude.

The indices described above retain information on the direction of the sensitivity, meaning that a species that is sensitive to patch area and associated with large patches has a different value to an area-sensitive species that is associated with small patches. In this example, both species may be equally sensitive to patch area, so to quantify this 'absolute' sensitivity, we used the absolute values from the three directional indices described above. Species exhibiting large values of the absolute sensitivity indices are more sensitive to the gradients of area, edge, and altitude than species with low absolute sensitivity values. We computed Pearson correlations to investigate the correlation between beetle species' sensitivity to the three gradients of area, edge and altitude.

We used analysis of covariance (ANCOVA) to test for the effects of the four life history traits and all of their interactions on both the directional and absolute sensitivity of beetle species to the gradients of area, edge and altitude. Full models were simplified using backward stepwise regression, with the best model determined by using Akaike's Information Criterion (AIC) (Burnham and Anderson, 2002). Body length data, and all absolute sensitivity scores (*AS)* were log-transformed to achieve normality of model residuals. Directional species sensitivity scores (*DS*) exhibited a leptokurtic distribution, so positive values were transformed to log(x+1) and negative values to –log (|x| +1) (Ewers, 2006). All statistical analyses were performed using R software (R Core Development Team, 2008).

4.4 Results

We collected individuals from a total of 50 species, from which we were able to calculate at least one sensitivity index for 32 species (accounting for 8,773 of 12,588 individuals collected) and were used for analysis. Within the subset of 32 species, 12 species were brachypterous (N = 6,853), followed by 13 macropterous species (N = 1,124) and seven dimorphic species (N = 796). A total of 16 species (N = 1,654) were open habitat species, while 12 species (N = 6,845) were forest specialists, and four species (N = 274) were forest generalists. Most species were zoophagous (S = 18, N = 7,635), just seven species were phytophagous (N = 955), and only four species (N = 183) were zoophagous with restricted diets.

Beetle body lengths ranged from 4 to 29 mm (11.92 ± 6.80 mm). We were able to estimate area sensitivity for 32 species, edge sensitivity for 32 species, and altitude sensitivity for 13 species. Directional area sensitivity was negatively and significantly correlated with directional edge sensitivity scores (r = -0.52, df = 30, p = 0.0024), indicating that species that were more abundant in forest than grassland were also more abundant in small than large grassland patches (Fig 2 a). There was also a strong positive correlation between the absolute sensitivity of beetle species to area and altitude (r = 0.57, df = 11, p = 0.039) (Fig. 2 b).

Table 1 Summary of general linear models (analysis of covariance) testing for the effect of species traits on species sensitivity to gradients of area, edge and altitude. Species sensitivity is modelled separately for (a) directional and (b) absolute sensitivity, and only parameters retained in the final minimum adequate models are presented. Values in bold indicate significant parameters with $P < 0.05$.

(a) Directional sensitivity	***F***	**d.f.**	***p***	***R^2***	**(b) Absolute sensitivity**	***F***	**d.f.**	***p***	***R^2***
Area					**Area**				
Habitat	7.55	2	**0.003**	0.69	Trophic group	5.64	2	**0.009**	0.52
Trophic group	1.85	2	0.181		Flight ability	8.48	2	**0.001**	
Flight ability	5.44	2	**0.012**		Residuals		26		
Habitat x Flight	4.72	4	**0.007**						
Residuals		21							
Edge					**Edge**				
Habitat	153.7	2	**<0.001**	0.94	Habitat	1.99	2	0.163	0.46
Trophic group	4.49	2	**0.024**		Trophic group	0.95	2	0.405	
Flight ability	0.02	2	0.972		Flight ability	2.68	2	0.090	
Body length	0.14	1	0.711		Body length	0.007	1	0.931	
Body length x Flight	0.08	2	0.918		Body length x Flight	1.58	2	0.230	
Body length x Trophic group	4.83	4	**0.019**		Body length x Habitat	0.96	2	0.400	
Residuals		20			Residuals		19		
Altitude					**Altitude**				
Trophic group	0.89	1	0.380	0.78	Flight ability	5.93	2	**0.026**	0.73
Flight ability	2.37	2	0.173		Body length	5.88	1	**0.041**	
Body length	10.4	1	**0.017**		Body length x Flight	4.15	1	0.075	
Body length x Flight	2.10	1	0.197		Residuals		8		
Body length x Trophic group	3.25	1	0.121						
Residuals		6							

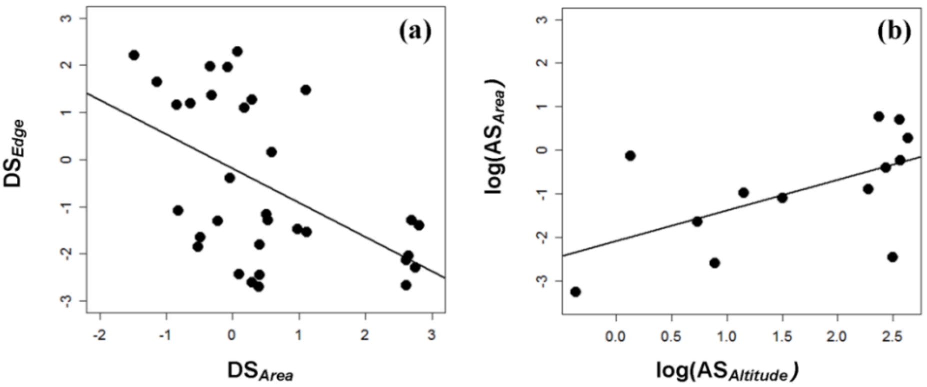

Figure 2 (a) Correlation between directional edge and area sensitivity of ground beetle species. (b) Correlation between the absolute sensitivity of ground beetle species to patch size and altitude.

Models of species sensitivity in relation to the effects of habitat and altitude accounted for at least 46 % of the variance, with models of directional sensitivity generally having higher explanatory power than models of absolute sensitivity (Table 1).

We detected a significant interaction between flight ability and habitat preference that influenced species' directional sensitivity to patch area (Table 1, Fig. 3 a), in which dimorphic and brachypterous forest generalist, and dimorphic open habitat species were more abundant in large grassland patches. By contrast, flightless open habitat species, together with dimorphic and macropterous forest specialist beetles were most abundant in small grassland patches. There was also a significant interaction effect between flight ability and habitat preference on absolute sensitivity to patch area.

However, this interaction was caused by the only macropterous and forest generalist species (*Pterostichus oblongopunctatus*) and had an unusually low absolute sensitivity value. Removing this one species from the analysis removed the interaction effect, but significant effects of trophic group and flight ability remained, with dimorphic species and generalist zoophagous species being most sensitive to gradients of grassland patch area (Fig 4 a, b). Directional edge sensitivity was strongly, and self-obviously, affected by habitat preference with forest specialists having a strong preference for sites located in the interior forest, and *vice versa* for open habitat species that were associated with grassland areas.

More interestingly, there was a significant interaction between beetle body length and trophic group on directional edge sensitivity (Fig. 3b). Grassland patch areas were dominated by small phytophagous species whereas specialized zoophagous species were heavily associated with forests. Both generalist and specialist zoophagous species tended to weakly increase in body size with smaller species in pasture and larger species in forest, but the opposite was true of phytophagous species. Both altitudinal sensitivity indices were strongly influenced by life-history traits (Table 1).

There was a strong, negative relationship between directional altitude sensitivity and body length, indicating that smaller bodied species were more abundant at high altitude and larger species were more abundant at low altitude (Fig 3c). In addition, beetle body length was strongly positively related to the absolute altitude sensitivity index, with large bodied species much more sensitive to the altitudinal gradient than smaller ones, regardless of the direction of their sensitivity (Fig. 4c). Brachypterous species also had very high absolute sensitivity to altitude (Fig. 4d).

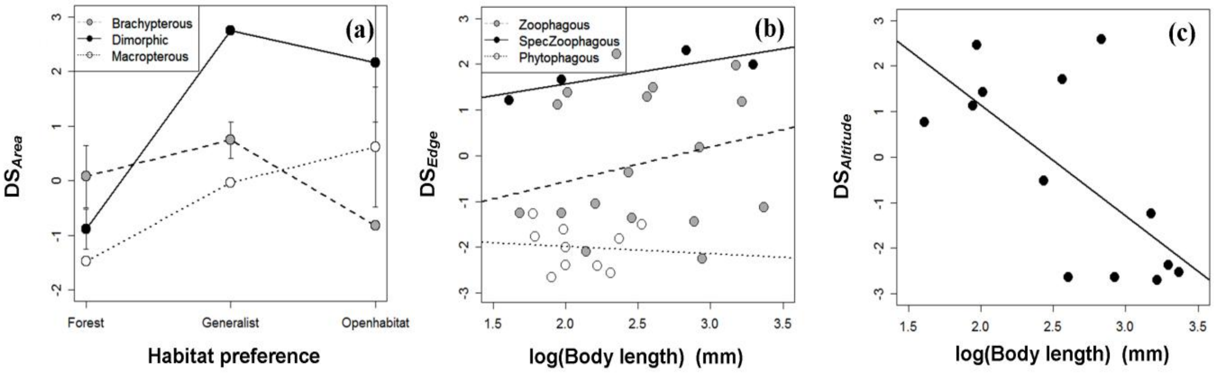

Figure 3 (a) Interaction effect between habitat preference and dispersal ability of carabid beetles that determines their directional sensitivity to patch size. (b) Directional edge sensitivity of ground beetles in relation to combined effects of trophic group and body length. (c) Directional altitude sensitivity of ground beetles in relation to body length.

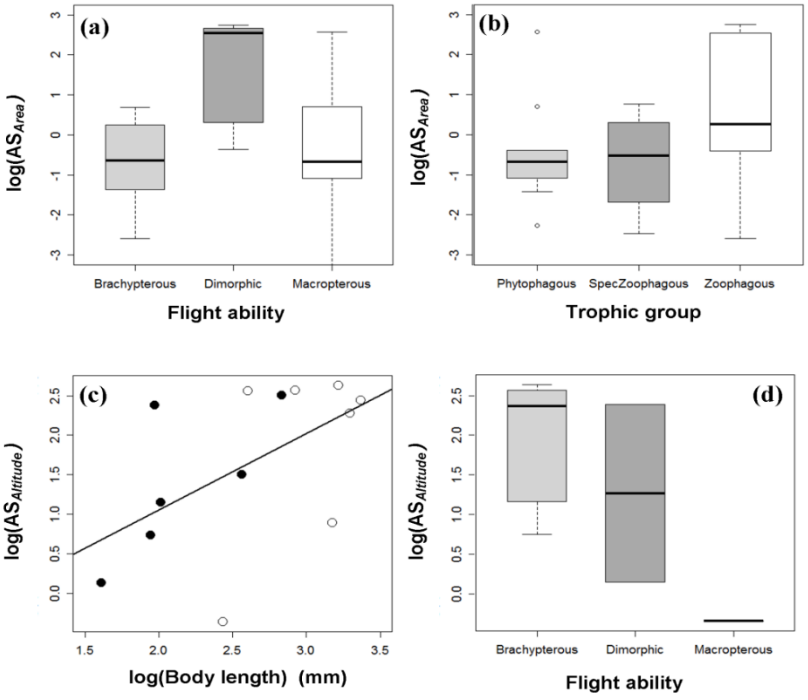

Figure 4 The absolute sensitivity of ground beetles to patch size as a function of habitat preference (a) and trophic group (b). The absolute sensitivity of ground beetles to altitude in relation to body size (c) and (d) flight ability. Filled and open circles in (c) represent species that exhibited a preference for high and low altitude respectively.

4.5 Discussion

Increasing temperature, together with land use change, is likely to have very complicated impacts on the persistence and distribution of species in mountainous regions (Forister et al., 2010). Our findings indicate that the species that are most sensitive to habitat fragmentation tend to also be the most sensitive to climate change.

Moreover, we found that there are certain combinations of traits that appear to amplify the level of species sensitivity to these two drivers of global environmental change, making some species particularly vulnerable. We found strong effects of life history traits on species sensitivity to habitat area and edge effects, two measures of habitat fragmentation. In line with Banks et al. (2010), species sensitivity to patch area and edge effects were strongly correlated. Our study differs from that of Banks et al. (2010) in that we investigated grassland patches inside a forest matrix rather than forest patches inside an agricultural matrix, meaning the correlation we detected between area and edge sensitivity was negative rather than positive. However, this is consistent in that edge sensitive species with a preference for forest tended to be more abundant near small than large patches, whereas edge sensitive grassland species also had a preference for large grassland patches.

Our results were also consistent with a large literature that has hypothesised that specialist and less mobile species are more sensitive to disturbance and habitat fragmentation than generalist and mobile species (Futuyma and Moreno 1988; Heino and Hanski, 2001; Magura *et al.*, 2001; Gaublomme *et al.,* 2008; Jelaska and Durbesic, 2009; Tóthmérész *et al.*, 2011). Similarly to Taboada et al., (2010), we found that the boundary between forest and grassland appeared to act as a barrier for open habitat species which were seldom collected in forest sites. Species such as the small brachypterous *Cymindis humeralis* (Geoffroy in Fourcroy 1785) that had a strong preference for small grassland areas, may struggle to persist in these landscapes over the long term due to the progressive disappearance of grassland habitats.

During the last few decades, land use change in the Alps has primarily been caused by the abandonment of pastures and meadows, leading to forest encroachment on these habitats and the consequent fragmentation of many semi-natural subalpine and alpine grasslands (Tasser *et al*., 2007). Many individual life-history traits of species have been linked to vulnerability to global environmental change (Lövei and Magura, 2006; Jiguet *et al.*, 2007; Kadoya *et al.*, 2008; Öckinger *et al.*, 2009), but our data suggest that there are particular combinations of traits that interact to magnify species' vulnerabilities.

For example, the combination of large body size and a specialised diet increased species vulnerability to edge effects and tended to be restricted to interior forest habitats. By contrast, the smaller, phytophagous carabids were also highly vulnerable to edge effects, but in the opposite direction in that they were restricted to grassland patches. This latter pattern probably reflects the increasing availability of food resources for plant and seed eaters that are present in grassland areas (Thiele, 1977). Interestingly, our findings indicate that the species that are most susceptible to changes in land use appeared to also be the most susceptible to the altitudinal gradient, a commonly used spatial surrogate for climate change (Körner, 2007a). These species tended to be brachypterous or dimorphic species of large body size and high trophic level. The Italian Alps represent a dynamic landscape with ongoing, directional land use change that is progressively altering the spatial patterning of forests and semi-natural grasslands (Tasser *et al*., 2007), and has also experienced recent temperature increases due to global climate change (Cannone *et al.*, 2008). The fact that these two environmental changes are occurring simultaneously, and that both changes appear to impact the same set of species, suggests that global environmental change may have a particularly severe impact on the carabid community in this region. It is important to note that species' susceptibilities are directional, meaning that two species that have the same absolute susceptibility to environmental change may have very different outcomes to that change, with some species likely to benefit and others to suffer. The ongoing process of upland abandonment followed by forest cover expansion will be likely to cause severe contractions in the range of small, wingless, open habitat specialist species that are associated with semi-natural grassland remains.

Yet that same process is likely to benefit the less mobile, larger bodied forest specialists as a result of forest expansion. The most severe impacts due to increasing temperature will be felt by rare forest specialists with narrower feeding niches and patchy distributions that are confined to higher altitudinal bands, but small species with good dispersal powers, together with some species that are poor dispersers but widespread habitat generalists, will likely have a high degree of resilience to future environmental change and may increase in abundance.

Our results reinforce the importance of considering multiple functional traits and their combinations when trying to predict species responses to environmental change. Importantly, we found that life history traits might act either independently or synergistically to amplify species sensitivity to habitat fragmentation or climate change, and that while some species will undoubtedly suffer negative impacts from ongoing environmental change, others will likely benefit.

Chapter V

Summary and prospects

5.1 Discussion

Overall, the emphasis in this PhD thesis is to provide some important insights into the way that habitat fragmentation and climate change impacts might jointly affect ground beetle assemblages of the Alpine ecosystems, both at the community, and population level. This local scale study, carried out in the eastern Italian Alps, has been based on a new sampling approach which involved the use of transect designs across an altitudinal (as surrogate for climate change) and land-use gradients.

The results emerging from this research project suggest that synergies between habitat degradation and climatic variation are expected to induce multi-faceted threats, ranging from (a) more substantial differences in the spatial distribution and patterning of beetle communities along the mountainside, (b) exerting combined selective pressure on species, with particularly strong impacts on species with certain combinations of ecological traits, and (c) enhancing changes to the morphological traits of species.

Past and more recent anthropogenic impacts in the Alps have resulted in dramatic changes of landscape structure, and future threat attributed to climate change will be likely to produce a new warming trend in the Alpine climates (Beniston, 2006), leaving them considered as a very vulnerable ecosystem (EEA, 2009). The upward migration of species associated with higher temperatures has been documented in the Alpine ecosystems (Battisti *et al.,* 2005, Walther *et al.,* 2005), with altitudinal shifts of species occurring at a median rate of 29 m per decade (Lenoir *et al.,* 2008) (Fig.1).

However, species ability to track new climatically suitable habitat will be limited within fragmented landscapes (Opdam and Wascher, 2004). Results presented in *Chapter II* suggest that climate change and habitat fragmentation together will be likely to magnify each other's influence on beetle community structure, so that future migration upward of beetle species range due to rising temperature will have to take into account the direction of effects imposed by habitat modification, which in turn will vary along the mountainsides. In *Chapter II* of this thesis, I found strong responses to habitat fragmentation in beetle assemblages located at all altitudes along the mountainsides, with beetle community composition showing substantial differences along the edge, area, and altitudinal gradients. However, the magnitude of patch area-effects differed considerably along the mountainside, being stronger in sites at lower altitude, and causing lower species richness and abundance in larger grassland patches at low altitudes.

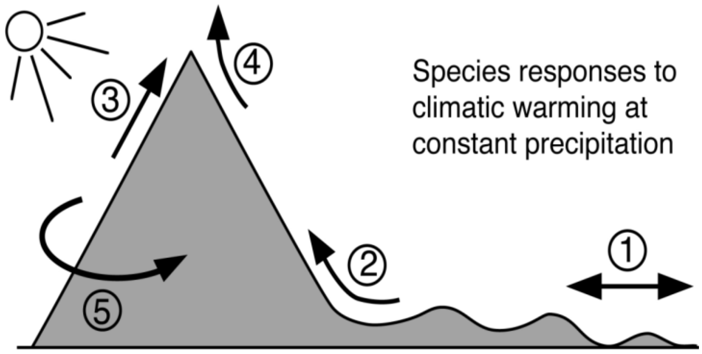

Figure 1 Models of species migrations as a result of increasing temperature respectively for (1) species at low altitudes, (2) valley floor species (3) high elevation species, (4) summit species (5) species at medium elevation (From Körner, 2009)

Here, the general idea is that increasing temperatures caused by global warming and land use changes might alter microclimatic alteration at very small scales (IPCC, 2007). Invertebrate and plants that are associated to soil condition will be directly affected, with consequent changes to community structure. This hypothesis has been previously tested in a study on Orthopthera assemblages in the Austrian Alps, where species abundance and rate of development were particularly affected by changes in microclimate conditions caused by altered habitats (Illich and Haslett, 1994).

Here, I suggest that this same mechanism underlies the patterns of community compositions that I detected in *Chapter II*. Additional support for this hypothesis comes from my own data, which indicated that spatial variation of microclimate is related to both the altitudinal gradient and the influence of landscape fragmentation. Changes in canopy structure attributable to land use change (e.g hay meadow, pastures, abandonment grassland) are known to strongly influence evapotranspiration rates and soil respiration, altering microclimate conditions of ground surface (Tappeiner and Cernusca, 1998).

However, the effects of habitat fragmentation on the forest matrix become more noticeable at higher altitude than lowlands as we expected. This result makes the direction of the combined effects of these global change on microclimate condition more difficult to interpret. Thus, there is a need for more studies to focus on variation of microclimate conditions related to the potential influence of human land use practices and climate change on mountainsides. In a general view, however, we can infer that under the menace of future climate change, the upward shift of lowland species might be restricted if the rate of habitat modification is faster than the ability of species to track their climatic niche through time.

Species constrained at high altitude sites will, ultimately, be likely to experience severe loss being less capable of coping with upslope shift as a result of habitat loss in the summit regions (Dinbörk *et al*, 2011). However, even if species will be able to adapt or shift, some set of functional traits might act individually or synergistically to each other, mediating the effects of climatic variation and fragmentation. Evidence from *Chapter IV* reveals that there is not a common species' response in relation to these global environmental changes. I found that species with some combinations of functional and morphological traits are predisposed to be more sensitive to pressure resulting from fragmentation.

By contrast, other species appear more tolerant and better equipped to survive within mountain landscapes that are affected by land abandonment at higher altitudes and larger anthropic disturbances localized in the lowlands (Tasser and Tappenier, 2002). Traits including body size, dispersal ability, trophic group and habitat preference are commonly identified as powerful indicators of species sensitivity to habitat fragmentation (Henle *et al.*, 2004), but if they act together the vulnerability of species to extinction in modified habitats might increase strongly. My results showed that the intensification of edge and area effects from increasing habitat fragmentation might lead to higher loss among species with larger body and specialized diet, macropterous and dimorphic forest specialists.

Interestingly, the same traits appeared to mediate species sensitivity to both drivers of change, suggesting that the combined impact of these two drivers may exacerbate the pressure being exerted on this subset of species, likely resulting in a greater impact on the beetle assemblage of these sensitive mountain landscapes than either driver acting alone. This is particularly the case of specialized predators, including brachypterous species with large body sizes, and smaller dimorphic species restricted to higher altitude.

Those species that are not able to colonize new areas with better climes as a consequence of fragmentation, will need to adapt *in situ* to survive in their changing environments. Species may also show individualistic morphological responses to disturbance, which may act as an early warning signal of population decline (Tsubaki, 1998). Moreover, signals of developmental instability such as fluctuating asymmetry underline the incapability of organisms to cope with environmental disturbance (Markow, 1995). According to the results of *Chapter III*, it can be expected that climate change might enhance fragmentation-induced changes in beetle morphology, with the direction of these effects moving upward along the mountainsides.

I found that individuals of *H. unctulactus* associated with habitat fragmentation at lower altitude have higher levels of fluctuating asymmetry, which might indicate that individuals in the low altitude forests are more stressed than their conspecifics living at higher altitude. Also, body size was influenced by the interaction between gradients of altitude and patch area, resulting in larger-bodied individuals in forest adjacent to larger grassland patch at lower and medium altitudes.

Spatial variation in microclimate might in part determine the patterns of morphology that I detected. The role of temperature has been found to be a crucial determinant of phenotypic size, with increasing temperature directly associated with higher growth rate in insects (Chown and Gaston, 2010). Higher temperature may also favour change in the variability of some morphometric traits in *Drosophila* (Savić *et al.*, 2008).

The ultimate success of species will be at least partly determined by their capability to maintain optimal phenotypes under ever-changing environmental conditions. My models presented in *Chapter III*, however, do not directly indicate how these global changes might interact to promote species declines. To make that link will require more research focused on the possible connection between among-individual morphological differences and among-individual fitness (e.g fecundity, survival). Overall, the results from my thesis reveal that a rapidly changing climate, in conjunction with habitat fragmentation, are likely to impose more dramatic changes on ground beetle communities of high mountain ecosystems than either driver acting alone. Severe pressure from these dual threats will cause significant declines to local beetle diversity that will be more evident at low altitude, and simultaneously amplify patterns of morphological variation among natural populations. The impacts will likely be focussed on a relatively small number of species that have particular combinations of functional traits that can either amplify their vulnerability, or determine their resilience, to global environmental change

5.2 Future work

Following the main findings highlighted in this PhD thesis, there are some further research directions that should be considered in the future. Overall, based on the use of altitudinal transects designs, and my results that show climate change might exacerbate the negative impact of land use changes on beetle communities in alpine ecosystems, I suggest that observational studies investigating the concurrent effects of drivers of global environmental change should be expanded, taking into consideration, for example, species responses from

different taxonomic groups, and expanding this approach to larger scale field-studies (e.g on regional scale) that might include mountain systems at different latitudes.

This is in order to acquire more information about the combined magnitude of impacts of habitat fragmentation and climate variation on a wide range of species. There is also a need to conduct further study on changes in species interactions (e.g. prey-predator, plant-herbivore) in response to multiple drivers of environmental change. For example, it would be interesting to gain more data on variation in predation rates along gradients of altitude and habitat fragmentation. Finally, in order to generate and validate predictions made about the direction of species changes, empirical analyses should be coupled with modelling studies, these latter ideally including information about past, present and future environmental conditions. Results from models that integrate the impact of potential future changes to climate and habitat fragmentation, can ultimately provide a powerful tool to develop comprehensive long term management plans in different mountain systems worldwide.

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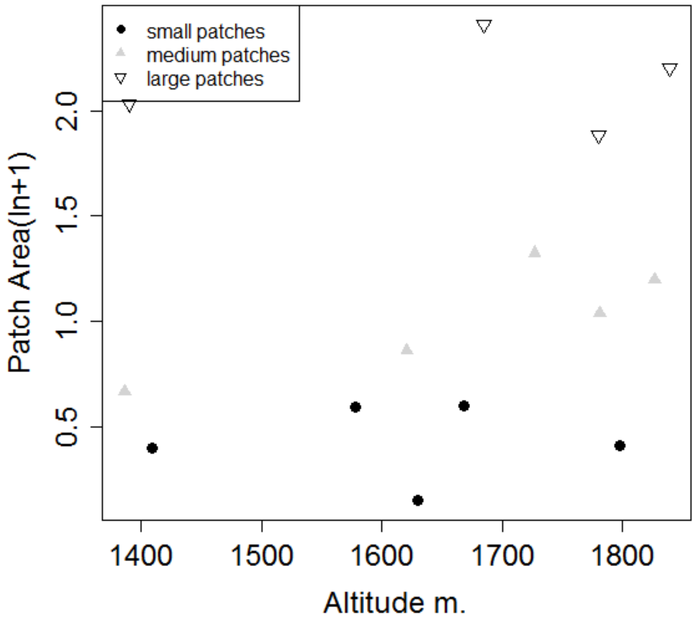
Appendix

APPENDIX 1a (Chapter II). Relationship between patches area and altitude.



APPENDIX 1b (Chapter II). Species list of carabid beetles (Coleopetera: Carabidae) collected as part of the study. Species codes are the same as presented on Fig. 3.

Species Code	Genus	Species	Authority
csyc	*Calosoma*	*sycophanta*	(Linnaeus 1758)
cger	*Carabus*	*germarii*	(Sturm 1815)
chor	*Carabus*	*hortensis*	(Linnaeus 1758)
cdep	*Carabus*	*depressus*	(Bonelli 1810)
ccdil	*Carabus*	*convexus dilatatus*	(Fabricius 1775)
cpro	*Carabus*	*problematicus*	(Herbst 1786)
cita	*Cychrus*	*italicus*	(Bonelli 1810)
cang	*Cychrus*	*angustatus*	(Hoppe & Hornschuch 1825)
catt	*Cychrus*	*attenuatus*	(Fabricius 1775)
npic	*Nebria*	*picea*	(Dejean 1826)
njoc	*Nebria*	*jockischii*	(Sturm 1815)
pmul	*Pterostichus*	*multipunctatus*	(Dejean 1826)
pobl	*Pterostichus*	*oblongopunctatus*	(Fabricius 1775)
pbur	*Pterostichus*	*burmeisteri*	(Herr 1838)
apar	*Abax*	*parallelepipedus*	(Piller&Mitterpacher 1783)
cfus	*Calathus*	*fuscipes*	(Goeze 1777)
cmel	*Calathus*	*melanocephalus*	(Linnaeus 1758)
cmic	*Calathus*	*micropterus*	(Duftschmid 1812)
pver	*Poecilus*	*versicolor*	(Sturm 1815)
pass	*Platynus*	*assimilis*	(Paykull 1790)
ljan	*Laemostenus*	*janthinus*	(Duftschmid 1812)
haff	*Harpalus*	*affinis*	(Schrank 1781)
hlat	*Harpalus*	*latus*	(Linnaeus 1758)
olat	*Ophonus*	*laticollis*	(Mannerheim 1825)
aaen	*Amara*	*aenea*	(De Geer 1774)
aaul	*Amara*	*aulica*	(Panzer 1797)
abif	*Amara*	*bifrons*	(Gyllenhal 1810)
acur	*Amara*	*curta*	(Dejean 1826)
aequ	*Amara*	*equestris*	(Duftschmid 1812)
aluc	*Amara*	*lucida*	(Duftschmid 1812)
alun	*Amara*	*lunicollis*	(Schiödte 1837)
afam	*Amara*	*familiaris*	(Duftschmid 1812)
anit	*Amara*	*nitida*	(Sturm 1815)
aant	*Amara*	*anthobia*	(A.Villa & G.B.Villa 1833)
hunc	*Haptoderus*	*unctulatus*	(Duftschmid 1812)
npal	*Notiophilus*	*palustris*	(Duftschmid 1812)
lnit	*Leistus*	*nitidus*	(Duftschmid 1812)
tlae	*Trichotichnus*	*laevicollis*	(Duftschmid 1812)
sviv	*Synuchus*	*vivalis*	(Illiger 1798)
asex	*Agonum*	*sexpunctatum*	(Linnaeus 1758)
mlam	*Metallina*	*lampros*	(Herbst 1786)
bqua	*Bembidion*	*quadrimaculatum*	(Linnaeus 1758)
otet	*Ocydromus*	*tetracolus*	(Say 1823)
chum	*Cymindis*	*humeralis*	(Geoffroy in Fourcroy 1785)
nbig	*Notiophilus*	*biguttatus*	(Linnaeus 1758)
ccam	*Cicindela*	*campestris*	(Linnaeus 1758)
pmel	*Pterostichus*	*melanarius*	(Illiger 1798)
hquad	*Harpalus*	*quadripunctatus*	(Dejean 1826)
pstr	*Pterostichus*	*strenuus*	(Panzer 1797)
pnig	*Pterostichus*	*nigrita*	(Paykull 1790)

APPENDIX 1 (Chapter III). Summary of statistics for femur and elytron FA indices to evaluate the frequency of directional symmetry (DS), presence of anti-symmetry (AS), and the correlation among trait size (R+L)/2 and unsigned asymmetry (|R-L|).

					Anti-asymmetry		Unsigned asymmetry	Correlation trait-size	
Habitat type	**Trait**	**t-test**	***p***	**Mean ± SE**	**Skew**	**Kurtosis**	**Mean ±SE**	**r**	***p***
	Femur								
Fragments		-1.51(130)	0.13	-0.002 ± 0.001	-0.04	0.97	0.011 ± 0.001	-0.09	0.31
Horizontal Control		0.19 (23)	0.84	0.0004± 0.002	-0.09	-0.06	0.007 ± 0.001	-0.10	0.63
Vertical Control		-0.69 (76)	0.48	-0.001 ± 0.001	-0.12	0.52	0.008 ± 0.013	-0.11	0.30
	Elytron								
Fragments		-0.39(149)	0.69	-0.0006 ± 0.001	-0.22	0.99	0.012 ± 0.001	-0.05	0.49
Horizontal Control		-0.89 (23)	0.38	-0.0017 ± 0.002	0.01	0.62	0.006 ± 0.001	-0.20	0.34
Vertical Control		-1.02 (83)	0.30	-0.0023 ± 0.002	0.13	0.92	0.001 ± 0.001	-0.06	0.56

APPENDIX 1 (Chapter IV). List of the carabid species on investigated sites during the years 2008-2009. Legends: dispersal ability (B-brachypterous, M-macropterous, D-dimorphic species), habitat preferences (F-forest specialists, G-generalists, O-open habitat species), trophic group (P-phytophagous, Z-zoophagous, S-specialized zoophagous) and mean body sizes in mm. (Species in bold were excluded from the statistical analysis due to low abundance, n. individuals < 5.

Species	**Dispersal ability**	**Habitat preference**	**Trophic group**	**Body Size *(mm)***
Calosoma sycophanta (Linnaeus 1758)	M	F	S	30
Carabus germarii (Sturm 1815)	B	G	Z	29
Carabus hortensis (Linnaeus 1758)	B	F	Z	25
Carabus depressus (Bonelli 1810)	B	F	Z	24
Carabus convexus dilatatus (Fabricius 1775)	B	G	Z	18
Carabus problematicus (Herbst 1786)	B	F	Z	28
Cychrus italicus (Bonelli 1810)	B	F	S	27
***Cychrus angustatus* (Hoppe & Hornschuch 1825)**	B	F	S	22.5
Cychrus attenuatus (Fabricius 1775)	B	F	S	17
***Nebria picea* (Dejean 1826)**	B	O	Z	10.7
***Nebria jockischii* (Sturm 1815)**	M	O	Z	11.5
Pterostichus multipunctatus (Dejean 1826)	B	F	Z	13
Pterostichus oblongopunctatus (Fabricius 1775)	M	G	Z	11.4
Pterostichus burmeisteri (Herr 1838)	B	F	Z	13.5
Abax parallelepipedus (Piller&Mitterpacher 1783)	B	F	Z	18.6
Calathus fuscipes (Goeze 1777)	D	O	Z	11.7
Calathus melanocephalus (Linnaeus 1758)	D	O	Z	7.2
Calathus micropterus (Duftschmid 1812)	B	F	Z	7.5
Poecilus versicolor (Sturn 1815)	M	O	P	10.7
Platynus assimilis (Paykull 1790)	M	F	Z	10.5
Laemostenus janthinus (Duftschmid 1812)	D	G	Z	19
***Harpalus affinis* (Schrank 1781)**	M	O	P	10.3
Harpalus latus (Linnaeus 1758)	M	O	P	9.2
***Ophonus laticollis* (Mannerheim 1825)**	M	O	P	10.2
Amara aenea (De Geer 1774)	M	O	P	7.4
Amara aulica (Panzer 1797)	M	O	P	12.5
***Amara bifrons* (Gyllenhal 1810)**	M	O	P	6.1
Amara curta (Dejean 1826)	M	O	P	5.9
Amara equestris (Duftschmid 1812)	M	O	P	10.1
Amara lucida (Duftschmid 1812)	M	O	P	6.7
Amara lunicollis (Schiödte 1837)	M	O	P	7.3
Amara familiaris (Duftschmid 1812)	M	O	P	6
Amara nitida (Sturm 1815)	M	O	P	7.4
***Amara anthobia* (A .Villa & G.B.Villa 1833)**	M	O	P	6.4
Haptoderus unctulactus (Duftschmid 1812)	B	F	Z	7
Notiophilus palustris (Duftschmid 1812)	D	F	S	5
Leistus nitidus (Duftschmid 1812)	D	F	S	7.2
***Trichotichnus laevicollis* (Duftschmid 1812)**	D	F	P	7.1
***Synuchus vivalis* (Illiger 1798)**	D	G	P	6.5
Agonum sexpunctatum (Linnaeus 1758)	M	O	Z	8.5
Metallina lampros (Herbst 1786)	D	O	Z	3.9
Bembidion quadrimaculatum (Linnaeus 1758)	M	O	Z	3.6
Ocydromus tetracolus (Say 1823)	D	O	Z	5.4
Cymindis humeralis (Geoffroy in Fourcroy 1785)	B	O	Z	9.1

Notiophilus biguttatus (Linnaeus 1758)	D	F	S	5
Cicindela campestris (Linnaeus 1758)	M	O	Z	14.5
***Pterostichus melanarius* (Illiger 1798)**	D	G	Z	15,7
***Harpalus quadripunctatus* (Dejean 1826)**	M	F	P	9.6
***Pterostichus strenuus* (Panzer 1797)**	D	G	Z	5.6
***Pterostichus nigrita* (Paykull 1790)**	M	G	Z	11

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