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Biotic and abiotic drivers of plant redistribution under global change

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Padua, 29 September 2021 Costanza Geppert

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Summary

Understanding the drivers of species redistribution dynamics and determining the role of climate change, human disturbance and biotic interactions are fundamental challenges of ecology and conservation biology. In my PhD thesis, I addressed these issues in the European Alps, a highly biodiverse region among the most vulnerable to global change.

In the first part of the PhD thesis, I investigated the short-term effects of climate change, human disturbance and biotic interactions on plant establishment dynamics at the local scale. In the first study, we performed a semi-field experiment, where we disturbed the soil and manipulated drought, nitrogen fertilization and arthropod herbivory. Plant establishment was modulated by the combined action of biotic and abiotic factors, such as timing of soil disturbance and herbivory that are usually overlooked drivers. Results from this experiment stressed the need to incorporate herbivory effects and to adopt a multiple factor approach in global change studies. In the second study, I addressed similar questions by replicating the experiment under natural conditions in the European Alps along steep elevational gradients. Results from this field experiment highlighted the important role of arthropod herbivores, showing that natural herbivory pressure might amplify soil disturbance negative effects on resident native species and favour exotics. Along the same elevational gradients, in the third study, I investigated what drives the abundance and diversity of two key guilds of herbivorous insects with contrasting life-history traits. Thermophilic species such as grasshoppers will likely benefit from climate warming, while more specialised species such as leafhoppers are under threat by land-use change. With this study, I stressed that species will respond differently to global change based on their life-history traits.

In the second part of the PhD thesis, I explored the long-term effects of climate change and land-use on population and range dynamics of native and exotic species at the regional scale. In the fourth study, I compared the response to global change of regionally extinct, threatened and exotic plants. Exotic plants are spreading quickly from anthropized valleys to alpine areas, while threatened species are contracting their range. The highest concentration of extinct, threatened and exotic plants was found in the lowlands, where human pressure is at its highest and protection at its minimum. In the lowlands, exotic species might displace threatened plants with low competition ability. In conclusion, I stressed the urgent need to mitigate habitat deterioration and loss in the lowlands, thereby enabling the survival of threatened populations. Finally, in the fifth study, I analysed demographic trends and range dynamics over 28 years for about two-thirds of alpine orchid species. Abundance of most populations has declined and orchids were often unable to respond to climate warming and did not move from degraded and fragmented habitats. Results

suggest that climate change was not the only factor threatening orchid persistence, but that the interaction between climate change and land use change drove orchid declines.

In conclusion, three main messages emerged from these five studies. First, we should adopt a multiple factor approach when investigating global change impacts on species distribution. Most current research focuses on climate change impact, while a scenario where climate change is the only driver is highly unrealistic. Second, a better integration of multiple drivers should also incorporate the effects of biotic interactions. Here, I could stress the important role played by arthropod herbivores, but I could not integrate biotic interactions in long-term studies and many questions remain open. Finally, I advocate that considering species life-history traits should improve predictions of global change responses.

Riassunto

Nella mia tesi di dottorato ho cercato di comprendere come il cambiamento globale stia modificando la distribuzione delle piante vascolari studiando contemporaneamente il ruolo del surriscaldamento delle temperature e dei cambiamenti di uso del suolo. Oltre agli effetti diretti di questi fattori abiotici, ho indagato il ruolo degli insetti fitofagi nel modificare le comunità di piante native e esotiche.

Nella prima parte della tesi di dottorato, riporto tre studi a breve termine sull'effetto di cambiamento climatico, disturbo antropico e interazioni biotiche sulle dinamiche di insediamento delle piante a scala locale. Nel primo studio, ho condotto un esperimento in semi-campo, disturbando il suolo e manipolando la disponibilità di acqua, di azoto e la pressione degli insetti fitofagi. I risultati hanno mostrato come l'insediamento delle piante sia stato modulato dall'azione combinata di fattori biotici e abiotici solitamente poco considerati, come la tempistica della perturbazione del suolo e la fitofagia. Nel secondo studio, ho investigato le stesse tematiche replicando l'esperimento in condizioni naturali nelle Alpi Europee lungo ripidi gradienti altimetrici. I risultati hanno sottolineato nuovamente l'importanza degli insetti fitofagi, la cui pressione naturale è in grado di amplificare gli effetti negativi del disturbo del suolo sulle piante native, favorendo così quelle esotiche. Nel terzo studio, ho indagato lungo gli stessi gradienti altimetrici l'abbondanza e la diversità di due gruppi chiave di insetti fitofagi con tratti funzionali contrastanti, cavallette (Orthoptera) e cicaline (Rynchota, Auchenorrhyncha). È stato dimostrato che specie termofile, come le cavallette, saranno probabilmente favorite dal riscaldamento climatico, mentre gruppi più specializzati, come le cicaline, potrebbero essere minacciati dal disturbo antropico.

Nella seconda parte della tesi di dottorato, riporto due studi a lungo termine su scala regionale, con i quali sono stati esplorati gli effetti del cambiamento climatico e dell'uso del suolo sulle dinamiche di popolazione e sulla ridistribuzione di specie vegetali native ed esotiche. Nel quarto studio, ho confrontato le risposte al cambiamento globale di piante localmente estinte, a rischio ed esotiche. È emerso che le piante esotiche si stanno diffondendo rapidamente dalle valli, mentre le specie a rischio contraggono la loro distribuzione. La più alta concentrazione di piante estinte, a rischio ed esotiche si trova per tutti e tre i gruppi nelle valli, dove la pressione umana è più forte. Inoltre, laddove coesistono, le specie esotiche possono sostituire facilmente quelle native meno competitive. Di conseguenza, è emersa l'urgenza di proteggere le popolazioni di piante native presenti nelle valli. Nel quinto studio, ho analizzato le tendenze demografiche e la distribuzione di circa due terzi delle specie di orchidee alpine. La numerosità della maggior parte delle popolazioni è

diminuita e molte specie sono state incapaci di rispondere al riscaldamento climatico poiché si trovavano in habitat degradati e/o frammentati. Questi risultati hanno suggerito che l'interazione tra il cambiamento climatico e il cambiamento dell'uso del suolo è la causa principale del declino delle orchidee.

In conclusione da questa tesi sono emersi tre messaggi principali. In primo luogo, ho compreso che è cruciale adottare un approccio multifattoriale per indagare gli impatti del cambiamento globale sulla distribuzione delle specie. In secondo luogo, è risultata chiara l’importanza delle interazioni biotiche, ed in particolare della fitofagia, nel modificare le dinamiche di insediamento delle piante. Infine, ho visto come i tratti funzionali delle specie possano migliorare la nostra capacità di prevederne le risposte al cambiamento globale.

Introduction

Mountains have always been considered wild and pristine environments. For a long time, they have remained untouched because adverse to the settling of large human populations, although rich in natural resources. However, evidence is growing on the profound changes caused by human activities in mountain ecosystems (Catalan et al. 2017). Over the last decades, montane environments have emerged as particularly vulnerable to anthropogenic change. Mountains are prompt to shifts in climatic extremes and future projections predict temperature warming together with changes in annual precipitation and increasing frequency of drought events (Beniston et al. 2007). Besides altering the climate, humans are transforming the landscape from the valleys to the top of the mountains by building and creating new infrastructure, urban areas, ski facilities and agricultural fields (Tattoni et al. 2017). Moreover, the increased transport of goods and people facilitated the dispersal of all kinds of organisms to longer distances. As a result, mountains became exposed to exotic and invasive species and new diseases and pests (Pauchard et al. 2009). By now, three main drivers exert pressure on mountain biodiversity: climate change, land use change and biotic invasions. It is known that changes in abiotic conditions (e.g. climate and land use change) and in biotic interactions (e.g. species introductions) can all impact the abundances and geographical distributions of species (Ehrlén and Morris 2015). In a context of persistent change, it becomes fundamental to study the effect of multiple, simultaneous, and ongoing environmental changes on species' distributions. Knowing which of these changes are likely to be more important would allow us to focus on those factors when predicting species responses and when designing mitigation strategies.

Climate change and range shifts

In the European Alps, temperatures have increased with annual mean warming rates of 0.5 °C per decade from 1980 onwards (European Environment Agency 2009). This warming is associated to changes in the seasonality of precipitation and relative humidity, and to more intense precipitation extremes (Beniston et al. 2007; Gobiet et al. 2014). The study of climate impacts on species distribution, growth and survival has a rich history in the scientific literature (Parmesan 2006). Temperature may be the most widely acknowledged abiotic driver of species diversity and distribution, in particular in alpine ecosystems (Mod et al. 2016; Körner and Hiltbrunner 2018). Grinnell (1917) first elucidated the role of climatic thresholds in constraining the geographic boundaries of many species, followed by several works with a sharp increase in the number of publications each year (Parmesan 2006). Also drought events, that are predicted to increase in the next future, strongly affect the whole community, usually decreasing biodiversity (Chase 2007; Stampfli et al. 2018) and changing ecosystem functioning (Grossiord et al. 2013). Species responses to climate change have been summarised in: move, adapt, or die (Maggini et al. 2011; Corlett and Westcott 2013). Currently, among climate change responses, two key mechanisms had been reported: adapting by altering phenology and moving by shifting biogeographic ranges (Burrows et al. 2011). Both mechanisms allow species to accommodate spatial and seasonal changes in ambient temperature.

The redistribution of life on Earth in response to climate change, by now, is a fact and has far-reaching implications for ecosystem and human health (Lenoir and Svenning 2013). Expected distributional shifts in warming regions are poleward and upward range shifts. In the mountains, to follow changes in temperatures, plants are shifting upward to higher elevations (Lenoir and Svenning 2013). Species range shifts are the result of changes in population dynamics, because climatic conditions in a given location impact the individuals living there. For instance, plants sensitive to temperature may respond to a warmer climate through local changes in growth, colonization, and extinction rates (Lenoir and Svenning 2013). For montane plant species, warming temperatures should have different effects along the elevational gradient. On the one hand, locations at the leading margin of a species' range that were too cold and therefore less suitable, might become more suitable in a warmer climate. Thus, growth and colonization rates of the populations occurring in those peripheral sites should increase. On the other hand, locations at the rear margin or within the core area of a species' range might become too warm and therefore less suitable, resulting in populations with higher decline and extinction rates (Lenoir and Svenning 2013). The earliest detections of range shifts under climate change have come from work focused on range margins, documenting colonization and establishment events at the leading edge (Parmesan et al. 1999; Walther et al. 2005) or local extinction events at the rear edge (Parmesan et al. 1999; Lesica and McCune 2004). More subtle changes within the ranges of species are changes in species abundance, that can be considered as intermediate states in an ongoing shifting process or early signs of species range shifts (Maggini et al. 2011).

Research on range shifts observed a large variability between and within species across regions (Gibson-Reinemer and Rahel 2015; Freeman et al. 2018; Rumpf et al. 2019b). There are different types of range shifts, that can vary both in direction and magnitude. Besides the expected march upwards with expansion at the leading edge, shift of the optimum, as well as shift downward and overall decline across the existing range have been reported (Rumpf et al. 2019a). This idiosyncrasy in range shifts is not consistent with a scenario where temperature is the sole dominant factor driving species range distribution. More recently, a few novel studies investigated the source of variability in the responses to climate warming, highlighting how it can stem from multiple factors such as the interaction between climate change and land use change (Guo et al. 2018a; Hülber et al. 2020); differences in traits mostly related to dispersal and reproduction (Angert et al. 2011; Matteodo et al. 2013); topography and microclimate (De Frenne et al. 2013; Elsen et al. 2020), and biotic interactions (Alexander et al. 2015, 2016a). Even if the number of studies on range shifts has augmented enormously over the last decade, large research gaps still remain. This is mainly due to methodological constraints because most previous research is based on resurveys of permanent plots (Rumpf et al. 2018) or on species distribution modelling (Cotto et al. 2017a; Carboni et al. 2018). Resurveys mainly capture regionally common species, overlooking rare species that are under-represented due to their patchy distribution. Then, studies based on species distribution models usually work with a too broad spatial resolution to detect changes across heterogeneous mountain environments and often exclude land-use change effects. In addition, most of the previous studies has focused on high-elevation areas, while disturbed low elevation areas have been excluded (Gottfried et al. 2011; Steinbauer et al. 2018; Hülber et al. 2020). However, at the low-elevation edge of species distribution, the pressures of global change are likely to be stronger and the effects of climate warming are less predictable due to the co-occurrence of multiple drivers of plant distribution.

Human disturbance and local extinctions

Several studies predict that climate change impact on biodiversity might be superseded by land use change effects (Sala 2000; Díaz et al. 2019). Worldwide, terrestrial biodiversity has already experienced widespread large net losses due to changes in land use, mostly because of habitat conversion, alteration and fragmentation (Newbold et al. 2015). In the European alpine region, two large land use changes have occurred over the last decades. First, in the lowlands, settlement areas and areas devoted to agriculture increased. The increase in the amount of agricultural land has come with changes in management practices and intensity of production (Becker et al. 2007). In addition, agriculture expanded upwards from the lowlands to mid-elevations, for example, the leading edge of grape and apple cultivation has moved upwards in the past two decades (Monteiro et al. 2011; Eccel et al. 2016). The second major land use change consisted in the increase of forests at mid-elevation. Open areas have been naturally recolonized by forests as traditional agricultural and forest activities were reduced and reorganized (Sitzia et al. 2010). In the European Alps, the opening of extensive pasturing areas at mid elevations dates back to the Bronze Aegis. However, over the last decades, human population has decreased at mid and high elevations and has increased in the lowlands. The recent large demographic changes are closely linked to the abandonment of traditional farming. Due to land abandonment, forests increased downwards at the expense of open semi-natural areas approximately between 600 and 1500 m (Tattoni et al. 2017).

Among the ecological problems caused by natural reforestation and by the increase of urban and agricultural areas, the main one is the reduction of semi-natural open spaces. The reduction of open spaces results, at the local scale, in the loss of grasslands highly rich in plant species and in the loss of associated biodiversity, and, at the landscape scale, in the decrease of landscape heterogeneity (Gehrig-Fasel et al. 2007; Sitzia et al. 2010). Habitat loss and fragmentation are between the main drivers of local extinction worldwide (Sala 2000; Newbold et al. 2015). In the alpine region, removing and altering grassland vegetation led to the local extinction of plant species but also of arthropod consumers, such as grasshopper, butterfly and bee species (Marini et al. 2007, 2009a). Locally, transforming semi-natural areas to crop fields or forests may, for example, change the availability of resources (water, nutrients, light, prey, etc.), ambient conditions (e.g. microclimate, soil chemistry), disturbance regimes (e.g. fire, grazing, ploughing), and habitat structure (vertical structure, nesting sites, hiding places etc.) (Dullinger et al., 2021). These changes will force species unable to cope to vanish locally, or even regionally, and some of the vanishing species may become replaced by better adapted ones, mostly widespread generalists (Newbold et al. 2018). Besides the described local effects, population persistence and dynamics are determined by the spatial cohesion of habitat patches at the landscape scale (Hanski 1999; Opdam et al. 2003). The negative effects of habitat fragmentation on the conservation of species are well known, with rare species being disproportionately affected (Henle et al. 2004; Fletcher et al. 2018; Kormann et al. 2019). Less studied is the combined effect of land use and climate change. However, recent research highlighted that habitat fragmentation might exacerbate climate change effects, because species movement is largely constrained by habitat availability and connectivity (Opdam and Wascher 2004; Guo et al. 2018b).

Besides reducing semi-natural habitats, the expansion of agriculture has been accompanied by the intensification of management regimes. Traditional farming systems were characterized by lower degree of specialization and used more environmentally friendly farming practices than modern systems (Marini et al. 2011). Modern systems use chemical fertilizers and pesticides, irrigation technology, and agricultural machinery that have a detrimental effect on biodiversity (Dullinger et al. 2021). Moreover, over the last decades, in the European Alps, tourism has been growing replacing productive or extractive activities (Catalan et al. 2017). As a result, human disturbance such as construction of roads, buildings or ski facilities, has become more frequent across temperate mountain ecosystems with negative impacts on species abundance and diversity (Wipf et al. 2005).

Biotic interactions under global change

For centuries, ecologists and conservation biologists have studied how abiotic forces shape species distributions. However, besides abiotic drivers, also co-occurring organisms influence each other's survival, growth and reproduction. Lately, biotic interactions emerged as a fundamental driver of species distributions but for now their role is still overlooked (Alexander et al. 2015). In a changing environment, existing interactions between species are likely to be reorganized and novel interactions are likely to occur. In this PhD thesis, I focus on the role of interactions between arthropod herbivores and plants and on novel interactions with exotic plants in determining plant distribution under global change.

Herbivores influence plant communities through both direct consumption and many indirect effects that are usually difficult to disentangle (Maron and Crone 2006; Denyer et al. 2010; Bayliss et al. 2017; Tamburini et al. 2018). Overall, herbivores regulate plant biomass and community structure, and usually increase plant species richness and community evenness (Mortensen et al. 2018). They promote diversity by reducing light limitation, by negatively impacting dominant plants and by diminishing losses of slowly growing plants (Kaarlejärvi et al. 2017). Most research focused on vertebrate herbivores, but also arthropod herbivores are known to have a large impact on plant communities (Bale et al. 2002; Allan and Crawley 2011; Borgström et al. 2018). Herbivore effects are expected to change along environmental gradients (Rasmann et al. 2014). For example, increasing eutrophication can change herbivory pressure because high plant N content should result in a stronger impact of herbivores (Denyer et al. 2010; Allan and Crawley 2011; Borgström et al. 2017; Mortensen et al. 2018). In the context of climate change, recent experimental work has considered impacts of temperature warming and low water availability on plant-herbivore interactions. It emerged that herbivores may offset or magnify climatic change impact, and are thus one of the major sources of uncertainty in predicting future diversity changes (Kaarlejärvi et al. 2017). For instance, herbivores were found to maintain plant diversity in warming conditions compared to situations where herbivores were excluded (Eskelinen et al. 2017; Kaarlejärvi et al. 2017). In addition, under drought, herbivory can result in greater plant damage due to improved host plant quality (Castagneyrol et al. 2018; Souther et al. 2020). Besides modulating effects of climate change in local plant communities, biotic interactions can affect range boundaries (Bonebrake et al. 2018). For example, range-expanding plants might be favoured by a decrease in the ratio of plant pathogens to symbionts in the bacterial and fungal communities of the rhizosphere (Ramirez et al. 2019). By contrast, cold-adapted species might be poorly defended from warm-adapted herbivores shifting their range upwards into alpine ecosystems at a faster rate than their host plants (Descombes et al. 2020).

A fundamental aspect, that must be considered when studying herbivory, is herbivores' role in plant invasion dynamics. The enemy release hypothesis links non-native success in the newly invaded territories to the lack of specialised, co-evolved herbivores (Maron and Vila 2001; Dostál et al. 2013; Schultheis et al. 2015; Meijer et al. 2016). Previous studies indicate that invasive seedlings seem to be more tolerant to herbivory than natives (Rogers and Siemann 2002), and that this differential damage can alter community composition in the long-term (Relva et al. 2010; Barton and Hanley 2013). There is a growing body of evidence emphasizing the fundamental role of native vertebrate herbivores in promoting non-native plant invasions (Eskelinen et al. 2017; Averill et al. 2018; Christianen et al. 2019; Stokely et al. 2020), but also invertebrates can influence plant dynamics (Allan and Crawley 2011; Simberloff et al. 2013; Dostál et al. 2013).

Under global change, the increased transport of goods and people facilitated the dispersal of exotic plant species. Exotic establishment gives rise to novel interactions among species that did not previously co-occur. Besides forming novel links with herbivores and pollinators, exotic plants interact with the resident plant community. Most exotic plants possess traits associated with faster growth rate and resource acquisition (Van Kleunen et al. 2010). These traits enable them to quickly exploit resources at the expense of resident native species (Lembrechts et al. 2017; McDougall et al. 2018). Therefore, invasive exotic plants are usually strong competitors and threaten resident plant diversity and ecosystem functioning (Simberloff et al. 2013). For a long time, mountains were thought to be resistant to exotic invasion but recently exotic plants are increasing, establishing and spreading in mountain environments (Pauchard et al. 2009). As a matter of fact, human disturbance and temperature warming mostly promote exotic invasion (He et al. 2011; Pauchard et al. 2016), resulting in increasing negative effects on native plants (Simberloff et al. 2013; Alexander et al. 2016b).

Research objectives and thesis structure

The overall objective of this PhD thesis was to investigate biotic and abiotic drivers of plant distributions under global change. The European Alps are a highly biodiverse region among the most vulnerable to current human pressures and represent a natural laboratory for global change research. Mountain ecosystems capture in few meters of elevation an extremely large natural variation of abiotic and biotic factors that enable to explore the effect of multifactorial changes in the natural environment. Using a combination of different approaches with short term and long term studies, we could investigate the effects of climate change and human disturbance at both the local and regional scale and isolate the effect of arthropod herbivores at the local scale.

In the **first chapter**, we tested the hypothesis that climate change, human disturbance and the pressure from herbivorous insects interact in modifying the establishment dynamics of plant communities. With a factorial semi-field experiment, we performed soil disturbance in two seasons and manipulated drought, N deposition and herbivory.

In the **second chapter**, we explored interactions between climate change, human disturbance and the pressure from herbivorous insects. With a large field experiment along the elevational gradient, we followed the natural establishment under real field conditions of both native and exotic plants over one growing season

In the **third chapter**, with an observational study, we compared responses to climate change and human disturbance of two key herbivore groups with contrasting ecologies (Auchenorrhyncha and Orthoptera specialised in grassland environments).

In the **fourth chapter**, with a long-term study, we investigated responses to global change of locally extinct, threatened and exotic plant species in the European Alps. We calculated changes in their distribution, mapped hotspots of occurrence and assessed differences in plant ecological strategies.

In the **fifth chapter**, first, with an observational study, we evaluated the effect of land use and climate change on orchid population survival, and then, with a long-term study, we measured changes in abundance and range shifts for c. two-thirds of alpine orchid species over the last 28 years.

Chapter 1.

Drought, nitrogen deposition and arthropod herbivory modify plant establishment dynamics after soil disturbance

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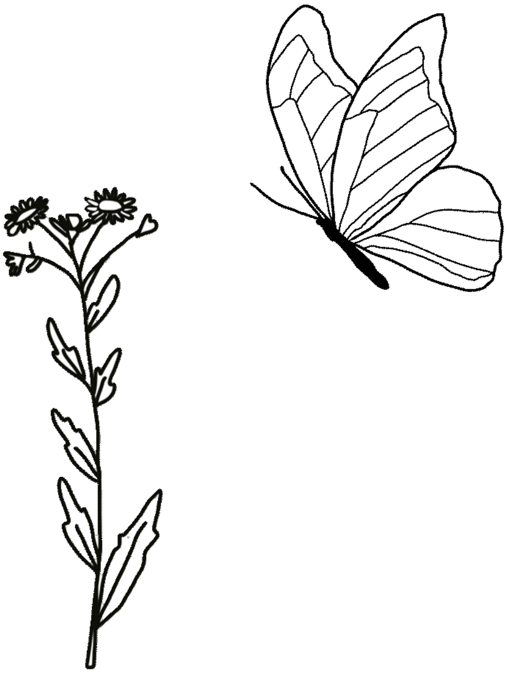

Abstract

Global change projections predict more recurrent and intense drought coupled with more frequent soil disturbance events and increased levels of N deposition related to intensive land-use. How these abiotic drivers interact with each other and with biotic drivers in determining plant community dynamics is still unclear.

Our study aimed to disentangle the roles of biotic and abiotic drivers in plant natural succession after soil disturbance. We carried out a factorial field experiment in which we performed soil disturbance in two seasons and manipulated drought, N deposition and herbivory. After each disturbance event, we monitored plant establishment dynamics.

The species composition of plant communities established after disturbance was different in the early and late season trial probably due to different phenology of species from the seed bank. Depending on the timing of disturbance, plant communities responded differently to drought and N. In particular, seedling emergence and growth appeared sensitive to water stress only in the late season trial. Irrespective of the other treatments, arthropod herbivores increased the number of plant species established after soil disturbance. N generally had a negligible effect on plant community dynamics. We only observed positive effects of N on plant biomass in in the late season trial when there was a high water availability.

Under future global change, we expect drought to affect plant establishment after soil disturbance by interacting with biotic and abiotic drivers. In particular, we showed that overlooked drivers such as timing of soil disturbance and arthropod herbivory will play an important role in shaping novel plant communities. Our results stress the critical need to adopt a multiple factor approach when assessing global change impacts on plant community diversity, composition and recovery ability.

Keywords (6): Climate change, insects, fertilization, natural succession, plant diversity, timing of soil disturbance.

Introduction

In natural ecosystems, the frequency of soil disturbance events is increasing due to common land use changes such as construction of infrastructure or conversion to agriculture (Sala 2000; Lembrechts et al. 2016). Many studies have indicated that soil disturbance is causing drastic changes in plant community composition by increasing the chances of seed germination and establishment of ruderal plants from the seed bank (Lembrechts et al. 2016; Corcos et al. 2020; Geppert et al. 2021; Orbán et al. 2021). Ruderal plant species are able to quickly exploit nutrients released by soil disturbance and are promoted by reduced competition with the pre-existing vegetation. However, it is still not clear how soil disturbance interacts with other biotic and abiotic drivers in determining plant community dynamics.

Vegetation ability to recover from disturbance is believed to lie mainly in the species pool contained in the seed bank (Luzuriaga et al. 2005). However, most previous studies on soil disturbance manipulated plant communities by sowing or transplanting species, thereby overlooking natural regeneration dynamics. A crucial phase of plant community dynamics is the establishment of seedlings that determines the potential for future replacement of adults (Lloret et al. 2009). As young seedlings are sensitive to resource availability and multiple stress factors, this phase is expected to be particularly vulnerable to environmental changes (Lloret et al. 2009; Ford and HilleRisLambers 2020). As a result of differential species' responses to nutrient or water availability, the composition of the seedling assembly may shift (Prober et al. 2005). First, under drought conditions, seedling emergence of several species is expected to change abruptly because of the strict water requirements for germination (Lloret et al. 2009). Second, increased soil nutrient content can favour the establishment of plant species with high competitive ability (Prober et al. 2005; Ford and HilleRisLambers 2020).

In addition to abiotic drivers such as drought or nitrogen (N) eutrophication, biotic drivers are also expected to affect seedling establishment. In particular, plant communities are expected to be influenced by arthropod herbivores through both direct consumption and many indirect effects that are usually difficult to disentangle (Maron and Crone 2006; Denyer et al. 2010; Bayliss et al. 2017; Tamburini et al. 2018). Overall, herbivores should increase plant species richness and evenness by negatively impacting dominant plants (Mortensen et al. 2018). However, herbivore impact is also expected to change along environmental gradients (Rasmann et al. 2014; Tamburini et al. 2018). Recent experimental work has mainly focused on how herbivory pressure changes along nutrient gradients, showing that high plant N content should result in a stronger impact of herbivores (Denyer et al. 2010; Allan and Crawley 2011; Borgström et al. 2017; Mortensen et al. 2018). In contrast, impacts of water availability have received less attention. However, drought usually reduces primary production and alters plant defences and nutrient concentration in plant tissues. Hence, drought should result in greater damage by herbivores due to improved host plant quality (Castagneyrol et al. 2018; Souther et al. 2020).

In Europe, climate change projections predict increased frequency and intensity of drought, while soil disturbance events and N deposition related to human activities are also expected to increase (Dentener et al. 2006; IPCC 2014; Stampfli et al. 2018). Even if N emissions have been reduced thanks to the Directive EU 2016/2284, this does not seem to result in the reduction of N deposition to natural ecosystems, mostly due to ammonia emissions from agriculture (Dirnböck et al. 2018; Serrano et al. 2019). In this context, it is of great importance to understand the role of drought and N in plant establishment dynamics after soil disturbance and how drought and N may interact with herbivory. To investigate the interactive effect of drought, N and arthropod herbivory on plant establishment after disturbance, we carried out a factorial field experiment under controlled conditions. In particular, we hypothesised that: 1) drought would have a negative effect on plant biomass and a positive effect on plant species richness and community evenness; 2) N would have a positive effect on plant biomass and negative effect on plant species richness and community evenness due to increased competition; 3) drought and N effects would modulate herbivore effects, i.e. herbivores are expected to promote plant species richness and evenness, in particular under drought conditions or N addition. In addition, to test the effect of timing of disturbances, we repeated the experiment twice in the growing season. First, different timing should expose plants to different climatic risks, with plots disturbed late in the growing season showing a slower recovery from soil disturbance (Li and Pennings 2017). Second, the timing of disturbance should have a considerable effect on the composition of the regenerating vegetation due to species specific emergence phenology (Crawley et al. 1999; Pakeman and Small 2005).

Materials and Methods

Study site and experimental design

An outdoor mesocosm experiment was set up in April 2019 at the Experimental farm "Lucio Toniolo" of the University of Padova (Northeast Italy, Legnaro; 45.8210N; 11.8580E; 6 m a.s.l.). In 2019, the mean annual temperature was 14.3°C, while the annual rainfall was 866.4 mm. We established 80 plots organized in 10 blocks (eight plots per block) (Fig. 1a). Each plot measured 1 × 1 m (1.5 m apart from each other) and was delimited and isolated from the surrounding soil by a concrete 10-cm wide wall dug 1 m into the ground. The concrete wall isolated the experimental plots for the surrounding soil reducing water run-off. A plastic roof in resin glass was mounted on the top of each plot to exclude precipitations. In each plot, we performed a mechanical soil disturbance twice: first in spring (19th April 2019) and then in summer (24th July 2019) by completely removing the existing vegetation and tilling the soil up to 20 cm. Hence, plots disturbed in April were disturbed only once, while plots disturbed in July were disturbed twice. The pre-existing vegetation was composed of species typical of mesic permanent grasslands such as *Holcus lanatus* L., *Festuca rubra* L., *Lotus corniculatus* L., *Trifolium repens* L., and *Plantago lanceolata* L., but several agricultural weeds were also present in the close surrounding. Soil fertility was measured in 2016 (available Olsen P: 16 mg kg−1), however, tilling the soil probably slightly enhanced N availability consistently in all plots (Tamburini et al. 2016). In each block, after each soil disturbance event, we performed three treatments: drought treatment, herbivory exclosure and N addition. We used a split plot design with herbivory exclosure nested within drought and N addition (Fig. 1 a, b). First, within each block, we randomly assigned the drought treatment (n = 40 plots). In these plots, precipitations were excluded, while control plots (n = 40 plots) were watered approximately once a week, simulating a total rainfall corresponding to the average amount of rainfall during the two trials over the last 10 years (2008-2018) in the study area: 155 mm of early season rainfall for the first trial and 126 mm of late season rainfall for the second trial (Table A S1). Second, in half of the plots (n = 40 plots), we simulated a N deposition of 40 kg ha $^{-1}$ corresponding to the maximum atmospheric N deposition in the study area. We added 1.5 g of urea (46 %) three times per trial corresponding to a total of 9 g. Third, we excluded arthropod herbivory in half of each plot by dividing the plot in two subplots (0.5 × 1 m^2) and setting up nylon cages (0.5 ×1 m^2) in one subplot (n = 80 subplots) (Fig. 1b). The cages were made of a light tulle with mesh size of 0.2 × 0.4 mm. We performed a pilot study for a month to measure the potential micro-climatic effects of the tulle and did not find any difference between inner and outer temperature (inner 27.60 °C ± 0.15, outer 27.82 °C ± 0.16 mean ± SEM, t = 1.142, df = 5481, p-value = 0.254).

Measurements

To assess the effects soil disturbance, drought, N and herbivory on the plant community, we monitored plant establishment over the two trials: May- beginning of July for the early season trial and August- beginning of October for the late season trial. In both trials, we identified plant species and estimated species cover at the biomass peak in each subplot (n = 160). In addition, we harvested the total above-ground biomass of each subplot for each trial: once in early July 2019 and once in early October 2019, without considering below-ground plant biomass. After the harvest of the total above-ground biomass of the early season trial, the disturbance event was repeated (Fig. 1c). Each cut corresponded to the peak of standing biomass. At harvest, plants were cut at 5 cm height above the soil surface. All removed plant material was collected, oven-dried at 65°C for 48 hr and then weighed. Hence, we measured total standing plant biomass in each enclosed community. Due to the size of the experiment (n = 160 subplots for two trials), we could not harvest plant species individually, therefore we do not have data on species biomass but on the total plant biomass of each subplot. However, we observed a positive correlation between total plant cover and total biomass (r = 0.77, p-value < 0.001) indicating that cover can be considered a good proxy.

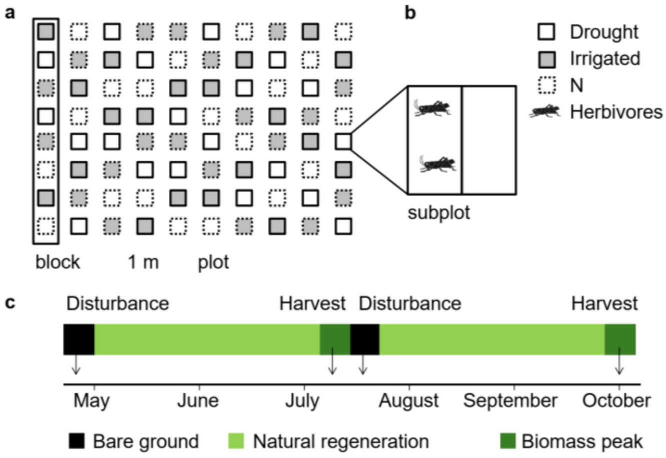

Figure 1: Representation of the sampling design a) mesocosms (1 × 1 m) organized in ten blocks, each of eight plots (n = 80 plots); b) subplots (1 × 0.5 m) where we performed our treatments: drought, N addition and herbivory exclosure (n = 160 subplots); c) time schedule of the experiment carried out over two treatments (early and late season trial) during the growing season.

Statistical analyses

Abiotic and biotic drivers of plant establishment

To test the effect of our treatments on plant species richness, we fitted a GLMM assuming a Poisson distribution with timing of soil disturbance (early and late season trial), drought, N and herbivory and their two- and three-way interactions as fixed factors and total species richness as response variable. The random structure of the GLMM consisted in plot ID nested within block ID. Second, we fitted a LMM with timing of soil disturbance (early and late season trial), drought, N and herbivory and their two- and three-way interactions as fixed factors using squared root transformed biomass as response variable. The random structure of the LMM consisting in plot ID nested within block ID took into account the split -plot design of the experiment. Third, we fitted the same LMM as above with ln-transformed evenness as response variable assuming a normal distribution. We calculated community evenness using the Evar index, as described by Smith & Wilson, 1996.

Dissimilarity in plant community composition

Based on cover data, we calculated temporal beta replacement, i.e. the replacement component of Jaccard dissimilarity indices between plant communities disturbed in the early and late season trial at the subplot level. Beta-diversity replacement component based on Jaccard dissimilarity indices was calculated following Baselga, 2010 as:

$$\frac{2 \times \min\ (bc)}{a + 2 \times \min\ (bc)}$$

where a = number of species common to both sites; b = number of species unique to the first site; c = number of species unique to the second site.

Then, we modelled if temporal beta replacement depended on drought, N addition or herbivory. We fitted a LMM with drought, N, herbivory and their two- and three-way interactions as fixed factors using temporal beta replacement as response variable. The random structure of the LMM consisted in plot ID nested within block ID.

As there are several methods to partition beta-diversity, we also calculated the replacement component of Sørensen index (Baselga, 2010; Baselga & Orme, 2012). Beta-diversity replacement component based on Sørensen dissimilarity indices was calculated following Baselga, 2010 as:

$$\frac{\min\ (bc)}{a + \min\ (bc)}$$

where a = number of species common to both sites; b = number of species unique to the first site; c = number of species unique to the second site. As the results of the two methods converged, we presented the Jaccard framework in the main text and the Sørensen framework in the supplementary materials (Table A S6).

Model selection and model diagnostics

Full models described above included all of the two-way and three-way interactions between the main effects. Starting from the full model, we used a backward deletion procedure, removing the interactions one-by-one if the p-value was higher than 0.05 and re-ran the model to avoid overfitting and to correctly interpret the main effects. All main effects were left even if not significant. Model assumptions were visually evaluated using diagnostic plots of model residuals. The final error distribution was selected based on the best outcome of model diagnostics. All analyses were run with R 3.5.1 (R Core Team 2017), using the package “lmer” to fit GLMMs (Bates et al. 2015).

Results

Abiotic and biotic drivers of plant establishment

Overall, we observed 42 plant species (Table A S2), with an average of three species per subplot (min = 0, max = 8 species). *Convolvulus arvensis* L. was the most abundant (n = 174) followed by *Sorghum halepense* (L.) Pers. (n = 130) and *Euphorbia helioscopia* L. (n = 123).

Plant species richness was affected by the interaction between drought and timing of soil disturbance (Fig. 2a, Table A S3). In the late season trial, drought reduced the number of species while in the early season trial the effect was neutral. In addition, irrespective of timing of disturbance, drought and N, plant species richness was affected positively by herbivore presence (Fig. 2b, Table A S3). Community evenness increased under drought conditions (Fig. 3a, Table A S4). In addition, community evenness decreased when N was added but only if herbivores were present (Fig. 3b) and it was higher in the late than in the early season trial without N addition (Fig. 3c).

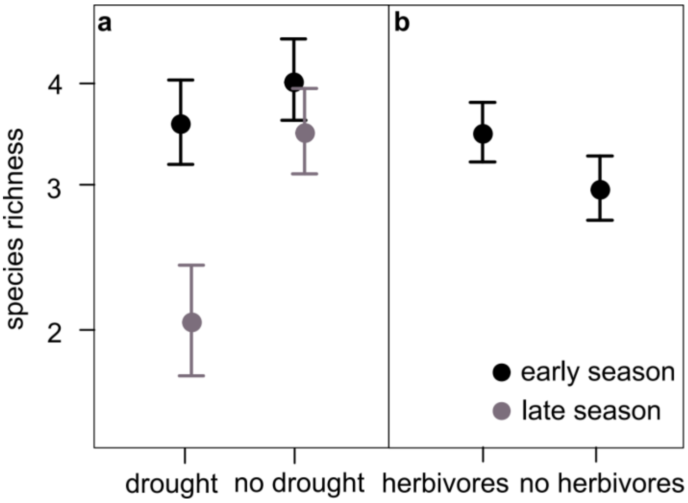

Figure 2: a) Effects of the interaction between drought and timing of disturbance (early vs. late season trial) on plant species richness; b) effects of herbivory on plant species richness.

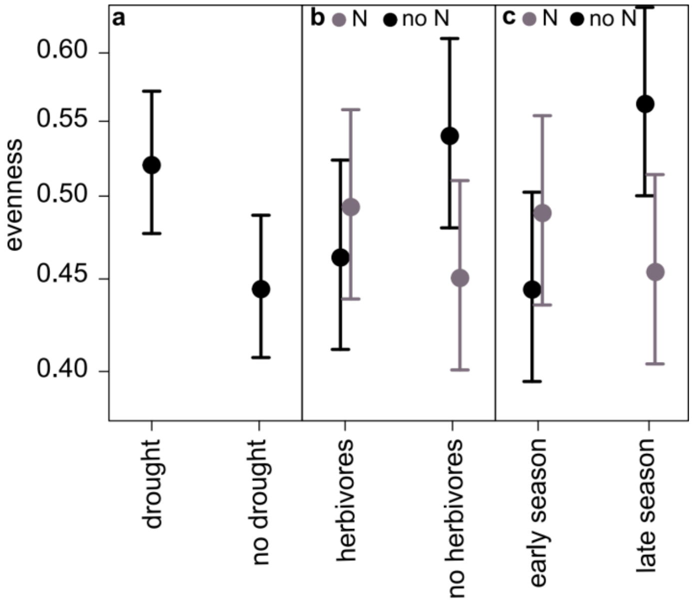

Figure 3: Effects of a) drought, b) the interaction between N and herbivory, and c) the interaction between N and timing of disturbance (early vs. late season trial) on community evenness (E_{var} index).

For biomass, we found a three-way interaction between timing, drought and N (Table A S5), i.e. plant biomass decreased under drought in the early season trial irrespective of N addition, while it reached its peak with N addition in the second trial (Fig. 4). More specifically, in the late season trial, in plots without drought and where N was added, plant biomass reached its maximum, while under drought conditions there was no difference between plant biomass of subplots with N and without N. Biomass did not respond to herbivore presence.

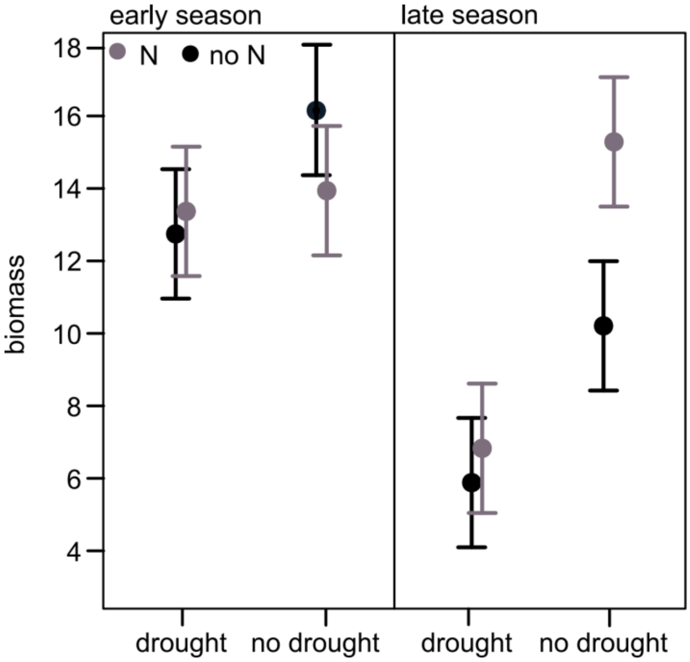

Figure 4: Effects of the three-way interaction between drought, N and timing of disturbance (early vs. late season trial) on root square-transformed biomass (g).

Dissimilarity in plant community composition

We found high temporal beta replacement between plant communities disturbed in the early season and in the late season trial ($\beta_{replacement}$ = 0.85 ± 0.21), showing that the vegetation established after the second disturbance was not a subset of the species pool already occurring after the first disturbance. In addition, we found that this dissimilarity was lower under drought conditions (Fig. 5, Table A S6).

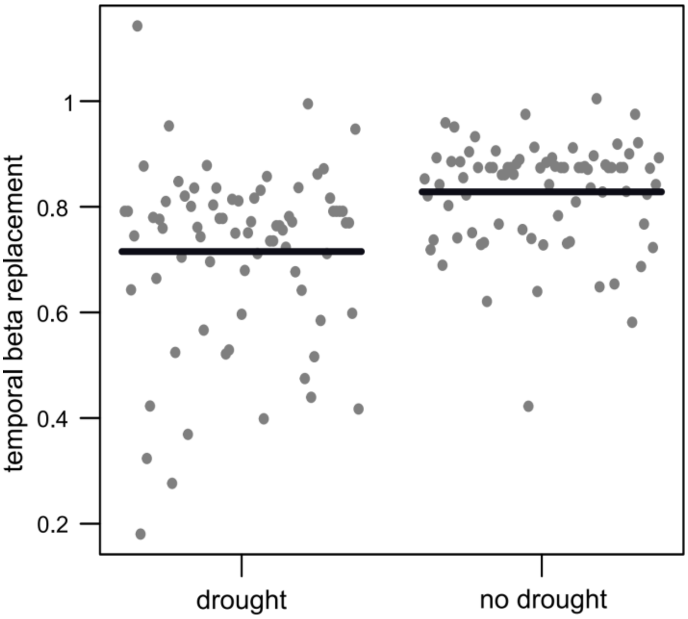

Figure 5: Effects of drought conditions on temporal beta replacement between early and late season trial. Temporal beta replacement was calculated using Jaccard index for each subplots (see Methods).

Discussion

Using a manipulation experiment, we tested the effect of drought, N deposition, and herbivory pressure on natural plant establishment dynamics after disturbance. We observed that timing of disturbance changed plant responses to N and drought and shifted plant community composition. During the establishment phase, arthropod herbivores increased plant species richness irrespective of the other treatments and modified community evenness responses to N, while they did not affect total biomass. Our study provides further support for the prediction that under current global change, novel plant communities are shaped by the interaction between biotic and abiotic drivers of plant establishment.

Timing of disturbance modifies the effect of drought and N but not the effect of herbivores

Depending on the timing of disturbance, plant communities responded differently to our treatments. Herbivore effects on plant species richness did not change between the two manipulations, while the effects of drought and N addition were greater in the late than in the early season trial. This is probably due to differences in climatic conditions and due to the shorter time available in the growing season after the late disturbance for plant species to recover (Crawley et al. 1999; Pakeman and Small 2005). Drought reduced plant species richness as well as biomass production (Van Ruijven and Berendse 2010; Stampfli et al. 2018). In temperate areas, seedling emergence and survival appear extremely sensitive to water stress during the first summer (Lloret et al. 2009). In accordance with this finding, in our experiment, the negative effects of drought on both species richness and biomass were exacerbated by warmer temperatures in the late season trial. In addition, probably due to the reduced competition with the dominant plants, plots under drought conditions sustained more even plant abundance distribution than the plots that received the average rainfall. Other studies have shown that increasing water availability favours fast-growing species at the expense of stress-tolerant species better adapted to drier conditions, leading to lower diversity and evenness (Kardol et al. 2010; Smith et al. 2016; Liu et al. 2017). In our experiment, drought probably disadvantaged fast-growing species and favoured more drought resistant species, increasing the establishment of these less competitive species and ultimately increasing plant community evenness. Depending on the timing of disturbance, biomass production also responded differently to N deposition. N increased biomass production when water was available only in the late season trial. Plant responses to N pulses depend on when the pulses occur in relation to environmental conditions (Bilbrough and Caldwell 1997; Lu et al. 2016). This means that drought can limit the response of plants to N, showing that the water availability acted as main driver of plant productivity (Tulloss and Cadenasso 2016). In our experiment, we did not find a negative effect on plant species richness of the current maximum level of N deposition in the study area, but the increase in biomass induced by N could potentially lead to increased competition and result in fewer species in the long term (Tulloss and Cadenasso 2016).

In addition to changes in diversity, we found that species composition in the early season trial was extremely different from species composition in the late season trial, i.e. different pools of species established depending on the timing of soil disturbance. A large proportion of the species (48 %) only occurred after the first disturbance but not after the second. These species might have been driven to local extinction because their seed banks were small (Crawley 2004) or the differences in composition might have been due to species' differences in timing of germination and phenology. Because of multiple germination requirements such as water, light, and temperature, species are likely to increase in abundance when the timing of disturbance matches their preferred recruitment time (Crawley 2004). Overall, these temporal changes in species composition were less pronounced under drought. Many studies demonstrated that drought can cause dominance shifts by allowing only a subset of species to persist (Hoover et al. 2014; Griffin-Nolan et al. 2019). Here, drought probably acted as the main environmental filter, enhancing community evenness and reducing differences in composition caused by the timing of disturbance.

Herbivore pressure increases plant species richness without affecting total biomass

Plant - herbivore interactions emerged as a fundamental driver of plant community dynamics, with arthropod herbivores promoting higher species richness after disturbance. There is a general consensus on the positive effects of herbivores on plant diversity (Scherber et al. 2010a; Descombes et al. 2017; Mortensen et al. 2018). Generally, herbivores feed primarily on the dominant plants and, as a result of their pressure, resources, in particular light availability, increase and competition decreases, promoting seedling establishment of less competitive species (Mortensen et al. 2018; Descombes et al. 2020). Under current global change, this positive effect of herbivores on plant diversity becomes particularly important as maintaining and promoting plant diversity can support ecosystem resilience to environmental change (Scherber et al. 2010a; Mariotte et al. 2013; Souther et al. 2020). Contrary to our hypotheses, the positive effect of herbivores on plant diversity remained constant in the early and late trial, with and without drought or N addition. Drought and N addition should result in increased concentration of nutrients in leaves of the plants (Stampfli et al. 2018). Although we expected both treatments to exacerbate herbivore impact (Borgström et al. 2017; Stampfli et al. 2018; Tamburini et al. 2018; Brambila et al. 2020), we found that the positive effect of herbivore on plant diversity was constant across treatments. However, herbivores and N interacted in determining community evenness. The expected negative effect of N on community evenness was reduced by herbivores. This might be due to the higher pressure exerted by herbivores on plants with high nutrient concentration. As herbivores feed preferably on dominant plants (Carson and Root 2000; Allan and Crawley 2011; Mortensen et al. 2018), this higher pressure under N addition might have superseded N negative effect on community evenness. Finally, herbivores did not decrease plant biomass. This might be related to the low natural herbivory pressure exerted in the study area that was embedded in a mostly urban and agricultural landscape. In a similar experiment carried out in more remote areas, a strong decrease of biomass (c. -20 %) was observed in plots where herbivores were not excluded (Geppert et al. 2021).

Study limitations

Due to technical limitations, we tested only for linear responses of plant communities to timing of disturbance, drought, N and arthropod herbivory. However, plant diversity and biomass responses to the considered drivers might involve non-linear effects and may vary depending on the environmental context and species identity (Holmgren et al. 2012; Boch et al. 2021; Compagnoni et al. 2021). In addition, we repeated the second disturbance in the same plots that were disturbed in the early season. Therefore, plots disturbed in the late season trial were disturbed twice. Before we harvested plant biomass and tilled the soil for the second time, plants had reached maturity and we manipulated the soil in the same way during the first and second disturbance, removing plant material and tilling the soil up to c. 20 cm. However, we cannot exclude that the observed timing effect (i.e. difference between first and second trial) might include some disturbance legacy effects. Finally, we did not take into account the effects of the considered drivers on below-ground plant biomass as we collected only above-ground plant material.

Conclusions

After soil disturbance, drought emerged as the dominant driver of plant establishment dynamics, affecting both diversity and biomass of plant communities, while N deposition had generally smaller effects. Drought effects were particularly strong under warm temperatures, conditions that are expected to be more frequent in the future. In addition, arthropod herbivores played an important role in shaping novel plant communities, promoting species coexistence, and increasing plant diversity. Our results indicate that adopting a multiple stressor approach is of outmost importance when assessing global change impact on plant community diversity, composition and recovery ability after soil disturbance.

Acknowledgments

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Chapter 2.

Contrasting response of native and non-native plants to disturbance and herbivory in mountain environments

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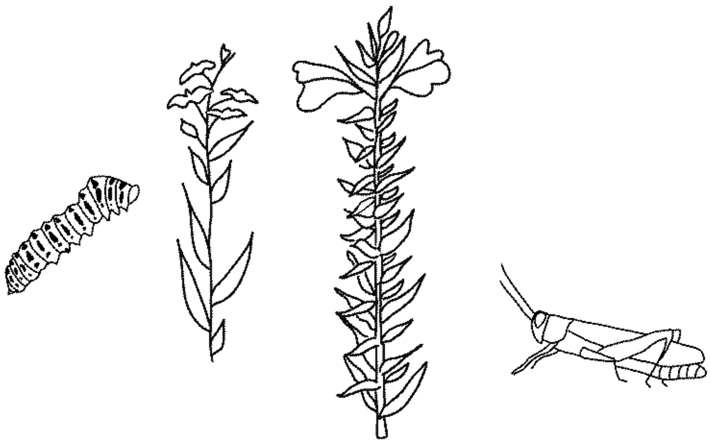

Abstract

Aim: Climate warming and increasing human disturbance are expected to promote non-native plant invasions in mountain ecosystems. Although biological invasions are also expected to be modulated by biotic interactions, it is still not clear how invertebrate herbivores can affect plant invasion dynamics. Using a large manipulative experiment, we aimed at testing: 1) the effect of soil disturbance and elevation on native and non-native plant communities, and 2) the effect of plant-herbivore interactions, nitrogen deposition, and elevation in driving plant establishment after soil disturbance.

Location: European Alps, NE Italy

Taxon: Vascular plants

Methods: We selected remote, uninvaded dry semi-natural grasslands along the core elevational range of non-native plants in the European Alps (0-1330 m) and manipulated soil disturbance, nitrogen deposition, and invertebrate herbivory. Then, we followed the natural establishment under real field conditions of both native and non-native plants over one growing season. We used generalized mixed-effects models to test the effects of the experimental treatments.

Results: Native and non-native species showed contrasting responses to soil disturbance and elevation. Low elevations and disturbance promoted non-native success, while affecting native species diversity negatively. Two-thirds of the experimental sites acquired novel non-natives after disturbance. Most of the observed non-natives were not present in the surrounding vegetation as mature plants, indicating that propagules were able to reach even remote natural areas. While current N deposition levels did not affect plant establishment, we found that after disturbance invertebrate herbivory might play an important role in facilitating non-native invasions by reducing native cover.

Main conclusions: Our findings show that highly resistant ecosystems such as continuous grasslands can be easily invaded once the resident vegetation has been removed, and that natural herbivory pressure from invertebrates might amplify the negative effects of disturbance on resident native species irrespective of elevation. Together, these results indicate increasing risks of future plant invasions on mountains under global change.

Key-words: Alien invasions, Altitude, Exotic plants, Herbivory, Nitrogen addition

Introduction

Native plants inhabiting temperate mountains are currently under threat by multiple global change stressors (Alexander et al., 2018; Dirnböck, Dullinger, & Grabherr, 2003; Engler et al., 2011). First, climate-induced extinction risks appear to be large, even under moderate scenarios of temperature warming (Thuiller, Lavorel, Araújo, Sykes, & Prentice, 2005). Second, increasing human disturbance associated with habitat loss and intensive land-use is expected to further reduce plant diversity (Gerstner, Dormann, Stein, Manceur, & Seppelt, 2014). By contrast, the same drivers are expected to promote non-native plant establishment and spread (He, Yu, & Sun, 2011; Liu et al., 2017), resulting in increasing invasions across mountains worldwide (Pauchard et al., 2009). Species' responses to these drivers should be modulated by biotic interactions (Alexander, Diez, & Levine, 2015), but it is still not clear how biotic interactions across trophic levels affect plant invasion. As these invasions pose additional potential threats to resident plant diversity and ecosystem functioning (Alexander, Lembrechts, et al., 2016; Simberloff et al., 2013), it is crucial to understand how abiotic and biotic drivers might interact and favour non-native plants over natives (Sorte et al., 2013).

In the last decades, soil disturbance related to the construction of roads, ski-slopes and other infrastructures has become more frequent across temperate mountain ecosystems (Wipf, Christian, Fischer, Schim, & Stoeckli, 2005). Disturbance (through the removal of existing vegetation) decreases competition for light and increases the chances of seed germination and establishment of ruderal plants and species present only in the seed-bank (Corcos et al., 2020; Haeuser, Dawson, & van Kleunen, 2017; Lembrechts et al., 2017; McDougall et al., 2018). Besides the direct effects on plants, disturbance also affects key soil properties such as nutrient and water content. In particular, soil disturbance is often coupled with nutrient leaching and high nitrogen (N) deposition (Davis, Grime, & Thompson, 2000). Soil eutrophication usually reduces plant diversity, enabling fast-growing plants to outcompete slow-growing, stress-tolerant species (Stevens et al., 2010). Since most non-natives are fast-growing plants, high N levels coupled with soil disturbance are usually predicted to facilitate invasive plants compared to local natives in and out of mountain regions (He et al., 2011; Lembrechts et al., 2016).

Plant invasions lead to novel interactions across trophic levels, and are themselves likely driven by ecological interactions (Alexander et al., 2018; Grassein, Lavorel, & Till-Bottraud, 2014; Morriën, Engelkes, Macel, Meisner, & Van der Putten, 2010; Richman, Levine, Stefan, & Johnson, 2020; Waller, Callaway, Klironomos, Ortega, & Maron, 2016). For instance, the enemy release hypothesis (ERH) links non-native success in the newly invaded territories to the lack of specialised, co-evolved herbivores (Dostál et al., 2013; Maron & Vila, 2001; Meijer, Schilthuizen, Beukeboom, & Smit, 2016; Schultheis, Berardi, & Lau, 2015). Previous studies indicate that invasive seedlings seem to be more tolerant to herbivory than natives (Rogers & Siemann, 2002), and that this differential damage can alter community composition in the long-term (Barton & Hanley, 2013; Relva, Nuñez, & Simberloff, 2010). Native vertebrate herbivores have been demonstrated to promote non-native plant invasions (Averill et al., 2018; Christianen et al., 2019; Stokely, Kormann, & Betts, 2020), but also invertebrates can influence plant dynamics through both direct consumption and many indirect effects that are often difficult to disentangle (Denyer, Hartley, & John, 2010; Maron & Crone, 2006; Tamburini, Dani, Bommarco, & Marini, 2018). However, the interaction between invertebrate herbivory and other drivers of plant invasion has been poorly investigated so far (Dostál et al., 2013; Simberloff et al., 2013). Given the likely emergence of complex interactions between biotic and abiotic drivers under global change, there has been a call to develop experimental approaches under realistic field conditions, to advance our understanding of plant invasion dynamics (Alexander, Diez, Hart, & Levine, 2016). However, most of the few previous experimental studies on non-native establishment manipulated propagule pressures through seeding (Lembrechts et al., 2016), while studies evaluating natural succession are rare (but see Corcos et al., 2020).

Here, to disentangle the role of soil disturbance, invertebrate herbivory, N deposition and their potential interactions in explaining plant establishment dynamics of both native and non-native plants, we set up an experiment along the elevation extent of non-native invasion in the Alps (c. 0-1300 m). In mountainous areas, both abiotic and biotic drivers (e.g. temperature, human disturbance, and herbivory pressure) are expected to vary with elevation and to potentially interact in determining non-native success. First, we tested the hypothesis that conditions at low elevations should favour non-native plant establishment compared to high elevations. At low elevations, we expected warmer temperatures coupled with soil disturbance to be beneficial for non-native establishment over natives, as non-native plants are generally ruderal, warm-adapted species introduced in the lowlands (Marini et al., 2013). Second, we tested whether the combined effect of warmer temperatures, N addition and herbivory pressures on native plants (Zuo, Moses, West, Hou, & Brown, 2012) promotes non-native establishment and success after soil disturbance.

Materials and Methods

Study area and experimental design

The study area was located in the Julian Prealps in the province of Udine (Friuli Venezia Giulia region, NE Italy). The area is mainly covered in mountains and climate depends primarily on elevation. During the field season (from May to August 2019), mean temperature at the minimum elevation in the study area (100 m a.s.l.) was 20.7°C, and 11.3°C at the maximum elevation in the study area (1630 m a.s.l.). The mean annual precipitation is ca. 1500-2300 mm. We selected 15 dry semi-natural grasslands regularly mowed once per year along the elevational extent of non-native invasion in the study area (0 - 1330 m a.s.l.) (Fig. 1a). Selected grasslands received no fertilizer, were found on shallow, well-drained soils rich in bases, and hosted rich floristic communities dominated by *Brachypodium rupestre*, *Bromopsis erecta* and *Festuca* spp. Selected sites were located in remote areas (cover of urban areas in a 500 m buffer: mean= 6.4%, SD= 13.7%), they were little invaded by non-natives and presented a continuous vegetation cover (Table B S1). For each site, we also quantified the distance to the nearest paved road as a proxy for non-native propagule pressures (Dainese et al., 2017). Dry semi-natural grasslands are considered very resistant to non-native plant invasions due to the high competition of resident native species (Boscutti, Sigura, De Simone, & Marini, 2018). At each site, we identified a block of 12 m × 3 m, where we performed a mechanical soil disturbance by removing completely the existing vegetation and tilling the soil up to 20 cm (Fig. 1b, Fig. B S1). Even if mixing together soils might affect differentially soil microbiota (Reinhart & Rinella, 2016), the scale of our experimental treatment was comparable to the scale of real disturbance events (e.g. road construction). We excluded vertebrates from the block by fencing the disturbed block with a nylon net (mesh: 4 x 4 cm). In the disturbed block, we performed two treatments: N addition and herbivory exclosure. Herbivory exclosure was nested within N addition, nested within the disturbed block. Each block included 4 plots (2 m × 2 m) separated by 1 m and divided in 4 subplots (1 m × 1 m) (N= 15 × 4 × 4= 240 subplots). First, we fertilized half of the plots adding N in the form of urea CH_4N_2O pellets, spreading them evenly and leaving them to be dissolved by rain. The amount of added N corresponded to 20 kg ha^{-1} (4 g/m^2, urea 46%). In the Alps, N total deposition rate ranges from 10 to 23 kg ha^{-1} year^{-1}. Second, we excluded invertebrate herbivory in half of the subplots by setting up nylon cages (1 m×1 m) (Fig. 1c, Fig. B S1). The cages were made of a light tulle with mesh size of 0.2 × 0.4 mm. We performed a pilot study to measure for a month the potential micro-climatic effects of the tulle and did not find any difference between inner and outer temperature (t = 1.142, df = 5481, p-value= 0.254). In the study area, natural seed release mostly occurs in late summer-autumn. Hence, the exclusion cages -installed in spring- did not prevent the seed rain to reach the soil. In each site, we further identified two undisturbed control subplots (1 m × 1 m) where no treatment was performed (Fig. 1c). We did not cross all treatments for the controls since the focus of the experiment was on the vegetation dynamics after disturbance. In addition, to measure local temperature, we installed five data-loggers at 1.5 m from the ground in five sites along the elevational gradient at 110, 429, 650, 850 and 1330 m a.s.l. Temperature and elevation were strongly correlated in the study area (Pearson correlation *r* = -0.95; p-value < 0.001), while distance to the nearest road and elevation were not correlated (Pearson correlation *r* = -0.07, p-value = 0.229).

Moreover, to study which invertebrate herbivores were excluded using our treatments, we sampled in each site for the whole duration of the experiment herbivore communities using pitfall traps and sweep-netting (Table B S9). Herbivore abundance did not vary with elevation, although there was a trend for a negative effect of temperature on several groups (Table B S9).

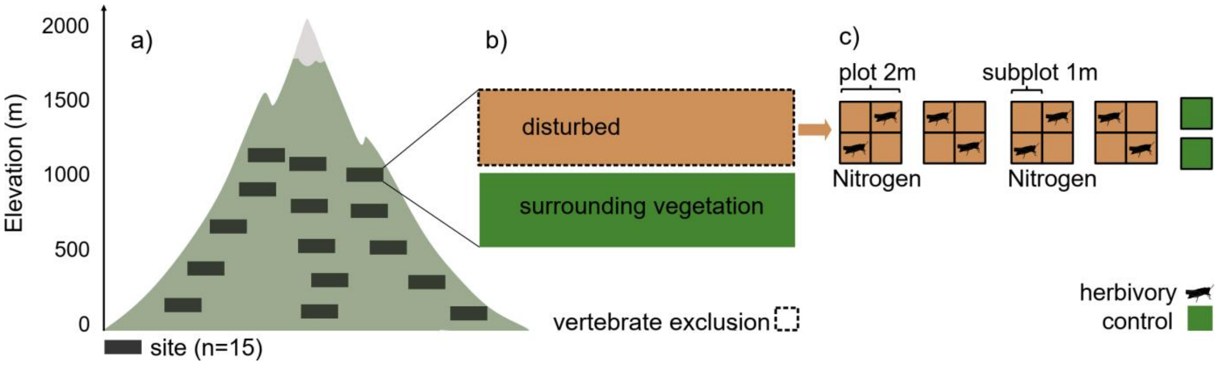

Figure 1: a) Experimental design showing the 15 sites selected along the elevational gradient in Friuli (Northeast Italy). The experimental sites were spread over multiple mountain ranges within an area of c. 140 km^2; b) in each site, we carried out soil disturbance on a block of 12 × 3 m; c) within the disturbed block, we created 4 plots (2 × 2 m), each plot was divided in 4 subplots (1 × 1 m) for a total of 16 disturbed subplots per site. We installed cages to exclude arthropod herbivores and added N in half of the disturbed subplots. In addition, we defined two control undisturbed subplots per site where no treatment was performed. Plant establishment dynamics has been monitored over one growing season.

Plant data collection

To study natural plant establishment dynamics, we carried out a floristic survey both inside and outside the disturbed blocks (Fig. 1b). In each of the 15 sites, to characterize the surrounding vegetation, we recorded all plant species and we visually estimated their cover in a 12 m × 3 m plot outside the disturbed block. We classified plants as native or non-native according to Poldini (2002). We considered as non-native species that are established in the study area irrespective of their invasiveness. During the entire growing season (from May to August) every two weeks, we monitored plant establishment inside the disturbed blocks by taking pictures of each 1 m^2 subplot with a digital camera (DSC-W330 Sony) (Fig B S2). To study plant dynamics, we quantified bare ground and species cover at four different times (2, 4, 6 and 14 weeks after disturbance) for each subplot using ImageJ (Schneider, Rasband, & Eliceiri, 2012). When vegetation biomass peaked, after c. 100 days since the disturbance, we recorded all plant species and cover in each disturbed subplot and in the two control subplots, and we harvested total aboveground plant biomass. We oven-dried and weighed biomass after keeping the samples at 60 °C for 72 hours. Due to the size of the experiment and the high plant diversity (n= 264 species), the species could not be harvested individually. Hence, to compare the native vs. non-native response, we used plant cover obtained from the pictures. As the plant cover did not reach 100% at the end of the experiment (mean 69.4 ± 30.8 SD %), species cover can be considered a good proxy per biomass. Total plant biomass and total plant cover per subplot were highly correlated (Pearson correlation r= 0.75, p-value < 0.01).

Statistical analyses

Response of natives and non-natives to disturbance under natural conditions

First, we investigated the effects of soil disturbance and elevation on native and non-native species richness under natural conditions, i.e. we only considered the disturbed subplots where herbivores were present (no exclusion cages) and with no N addition, and the control subplots where the soil was not disturbed (Fig. 1c). For native and non-native species separately, we fitted a generalised linear mixed-effects model (GLMM) assuming a Poisson distribution with species richness as response variable and elevation, disturbance and their interaction as fixed effects. Both models included as random structure plot ID nested within site ID.

Second, we compared the whole disturbed block with the surrounding vegetation (Fig. 1b). Based on presence/absence community data, we calculated Jaccard dissimilarity between disturbed and undisturbed plant communities, separately for native and non-native plants. We used the function “betadiver” of the R-package “vegan” (Oksanen et al., 2019), to calculate beta-diversity using the Jaccard index and its replacement and richness components (Legendre, 2014). These analyses tested whether the vegetation established after disturbance was a subset of the species pool already occurring in the existing vegetation or whether disturbance released species mostly present in the seed-bank from competition (i.e. high species turnover). As there are several methods to partition beta-diversity, we also calculated Sørensen index using the function “betapair” of the R-package “betapart”, and partitioned the total beta-diversity in turnover and nestedness components (Baselga, 2010; Baselga & Orme, 2012). As the results of the two methods converged, we presented the Jaccard index in the main text and the Sørensen index in the supplementary materials (Table B S2).

Response of natives and non-natives to N addition and herbivory exclosure after disturbance

We analysed the effect of the experimental treatments on plant establishment in the 240 disturbed subplots of the experiment, excluding the control subplots. First, we fitted a LMM with elevation, herbivory exclosure, N addition and their two- and three-way interactions as fixed factors and ln-transformed total biomass as response variable. The random structure of the LMM consisted in plot ID nested within site ID. Second, we fitted a LMM with elevation, herbivory exclosure, N addition, status (native or non-native) and their two- and three-way interactions as fixed factors using ln-transformed species richness as response variable. The random structure of the LMM consisted in subplot ID nested in plot ID nested within site ID. Third, we analysed the effects of the experimental treatments on bare ground cover over time. We considered the first 6 weeks of the experiment and the final measurement before cutting the aboveground biomass (measurements were taken at the second week after disturbance, fourth, sixth and fourteenth week). As fixed factors we fitted elevation, herbivory exclosure, N addition, time (ln-transformed week of the experiment), and their two- and three-way interactions. We used as random structure subplot ID nested within plot ID nested in site ID. Finally, we tested for the effect of the experimental treatments on native and non-native plant cover over time. To improve the linearity and residuals distribution, we used square root transformed plant cover as response variable. We used elevation, herbivory exclosure, N addition, status (native or non-native), time (ln-transformed week of the experiment), and all the two-way and three-way interactions. We included as random structure subplot ID nested in plot ID nested within site ID.

Model selection procedure

Full models described above included all of the two-way and three-way interactions between the fixed factors and main effects. Starting from the full model, we used a backward deletion procedure, removing one-by-one the interactions if the p-value was higher than 0.05 and re-ran the model to avoid overfitting and to correctly interpret the main effects. All main effects were left even if not significant.

Multi-model inference

To evaluate model selection uncertainty, we also performed a multi-model inference analysis. With our information-theoretic approach, we compared the fit of all possible candidate models nested within each of the full models presented above. In a set of n models, each model i can be ranked using its difference in AICc with the best-fitting model ($\Delta AICc_i = AICc_i - AICc_{MIN}$). A model in a set can be considered plausible if its ΔAICc is below 2. Multi-model inference analyses were performed with the MuMIn package (Barton, K., & Barton, 2015; Burnham, Anderson, & Huyvaert, 2011). Final models selected according to the backwards stepwise deletion were consistent with the ranking of the plausible models based on AICc (Tables B S3-7). Hence, we presented the results of the reduced models from the backward deletion procedure in the main text and reported the multi-model inference analyses only in the supplementary materials.

Model diagnostic

In all models, to assess possible collinearity issues between fixed effects, we estimated variance inflation factors (VIFs). VIF values were always close to 1, indicating very little collinearity among predictors (Akinwande, Dikko, & Samson, 2015). Model assumptions were visually evaluated using diagnostic plots of model residuals. All analyses were run with R 3.5.1 (R Core Team, 2017), using the package "lmer" to fit GLMMs (Bates, Mächler, Bolker, & Walker, 2015).

Results

Response of natives and non-natives to disturbance under natural conditions

Overall, we recorded 251 native plant species and 14 non-natives (Table B S8). Soil disturbance had a negative effect on native richness and a positive effect on non-native richness (Fig. 2a, 2b; Table 1). Moreover, increasing elevation negatively affected non-native richness (Fig. 2b, Table 1), while native richness tended to be affected positively by increasing elevation (Table 1).

Table 1 Effects of disturbance and elevation on native and non-native species richness. Coefficients are estimated from final GLMM assuming a Poisson distribution. Models only contained subplots under natural conditions: disturbed subplots where herbivores were present (no exclusion cages) and with no N addition, and the control subplots where soil was not disturbed (n = 60 disturbed subplots and 30 control subplots).

Response variable	Fixed factors	Estimate	SE	df	z	p
a) *Native species richness*	disturbance (yes)	-0.400	0.059	29	-6.63	<0.001
	elevation	0.145	0.074	13	1.95	0.051
b) *Non-native species richness*	disturbance (yes)	0.742	0.352	29	2.109	0.035
	elevation	-1.438	0.454	13	-3.168	0.002

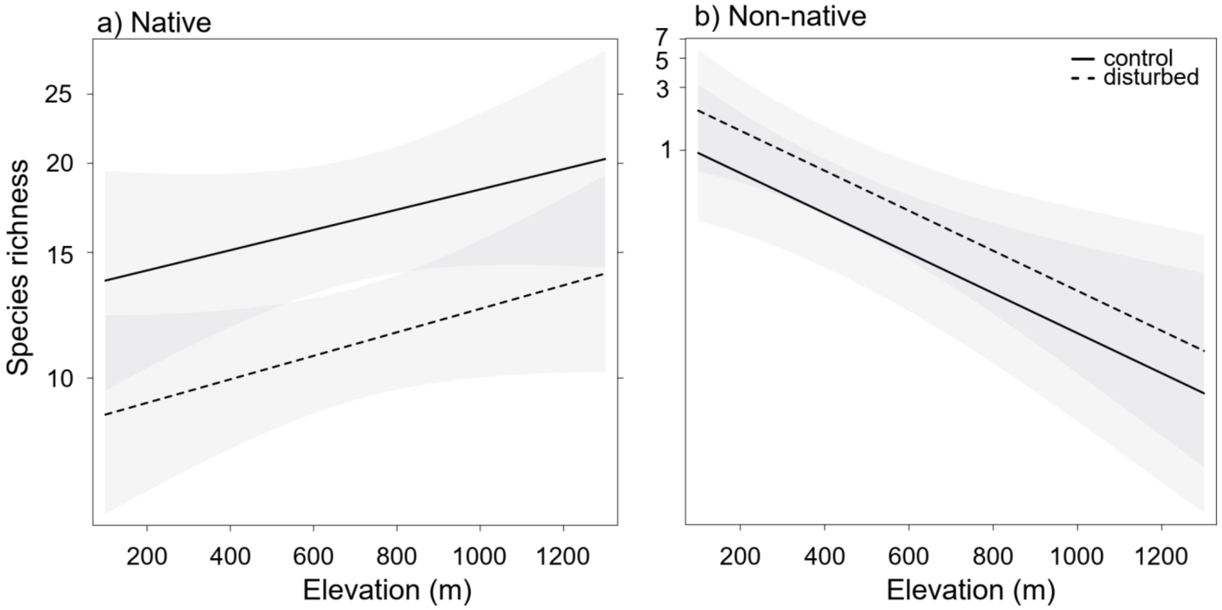

Figure 2: Effects of soil disturbance and elevation on a) native and b) non-native plant species richness along the elevational gradient in Friuli (Northeast Italy). For native species richness, the effect of elevation was marginal (p-value= 0.051). Models only contained subplots under natural conditions: disturbed subplots where herbivores were present (no exclusion cages) and with no N addition, and the control subplots where soil was not disturbed (n= 60 disturbed subplots and 30 control subplots).

Both native and non-native communities showed high beta-diversity between disturbed communities and undisturbed surrounding vegetation ($\beta_{Jaccard}$>0.70) (Fig. 3). For native plants, total beta-diversity was mostly due to species replacement ($\beta_{replacement}$ = 0.58 ± 0.03; $\beta_{richness}$ = 0.17 ± 0.03), i.e. in disturbed blocks, most of the emerging native seedlings were novel species (mean = 60 %, SD = 11 %). For non-native plants, total beta-diversity was mostly related to species richness difference ($\beta_{replacement}$ = 0.07 ± 0.04; $\beta_{richness}$ = 0.73 ± 0.08). In 67 % of the sites, several non-native species occurring after disturbance were not observed in the close surrounding as adult plants (Tables B S1-2).

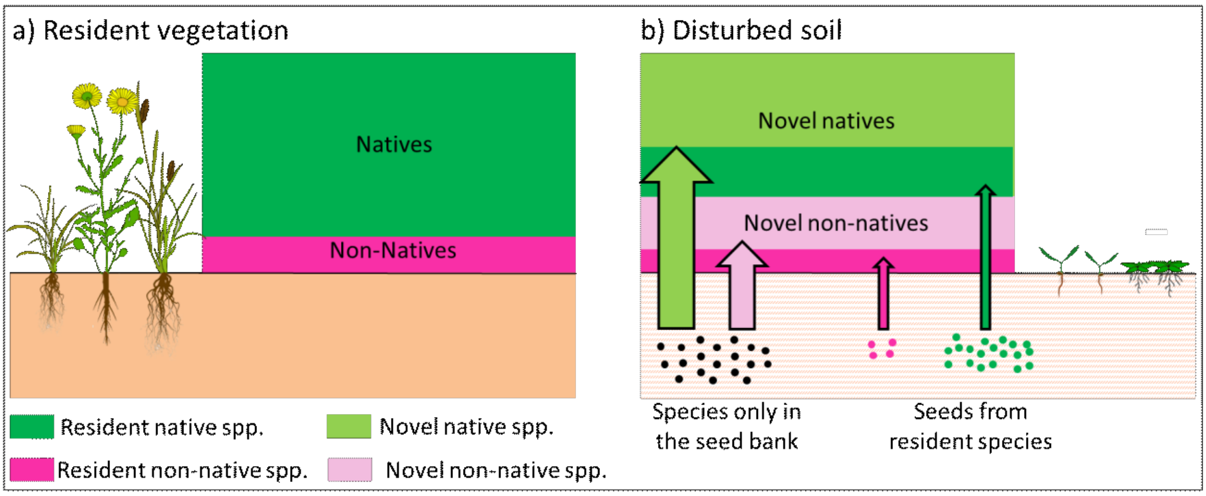

Figure 3: a) In the study area (Northeast Italy), the resident vegetation consisted mainly of native species and only a few non-natives; b) in disturbed soils, species mainly emerged from the seed-bank resulting in novel species communities. Rectangles represent species pools and their size is proportional to the mean number of plant species per site, while arrow size is proportional to the contribution of the seed bank.

Response of natives and non-natives to N addition and herbivory exclosure after disturbance

In each subplot, we recorded an average of 12 species (min= 2, max= 22). The most frequent species were: *Plantago lanceolata* L. (native, n= 127), *Erigeron annuus* L. (non-native, n= 99), *Peucedanum oreoselinum* (L.) Moench (native, n= 89), and *Trifolium pratense* L. (native, n= 89).

Total biomass was not affected by elevation and N deposition, while we observed a significant effect of herbivory exclosure (Table 2a), i.e. when herbivores were present biomass decreased by c. 20 % (Fig. 4).

Figure 4: Effect of herbivore presence on total plant biomass of each subplot harvested at the peak vegetative development after soil disturbance. Models contained disturbed subplots (n= 240).

For species richness, we found an interaction between status and elevation (Table 2b), i.e. species richness of native plants was higher than species richness of non-native plants and it was affected by elevation positively, while non-native richness decreased with elevation (Fig. B S3). Herbivory exclosure and N addition did not have any effect on overall species richness (Table 2).

Table 2: Effects of a) herbivores, elevation and N addition on ln-transformed biomass, and b) herbivores, elevation, N addition, status and the interaction between elevation and status on ln-transformed species richness. Coefficients are estimated from final LMMs. Besides main effects, we tested two-way and three-way interactions and removed them when p-value > 0.05.

Response variable	Fixed factors	Estimate	SE	df	t	p
a) Biomass	herbivores (yes)	-0.276	0.051	179	-5.363	<0.001
	elevation	-0.057	0.182	13	-0.305	0.765
	N (yes)	-0.024	0.071	44	-0.344	0.733
b) Species richness	herbivores (yes)	-0.013	0.018	179	-0.733	0.465
	elevation	0.121	0.044	13	2.734	0.017
	status (non-native)	-1.296	0.018	238	-73.720	<0.001
	N (yes)	-0.006	0.018	44	-0.329	0.744
	elevation x status (non-native)	-0.265	0.018	238	-15.054	<0.001

By analysing the temporal dynamics of bare ground cover, we found an interaction between time and herbivores and between time and elevation (Table 3a). First, bare ground declined with time but more strongly when herbivores were excluded (Fig. 5a), i.e. herbivores kept the vegetation more open. Second, bare ground declined more slowly over time at high elevations than at low elevations (Fig. 5b). Bare ground cover did not respond to N addition.

Table 3: Effect of a) herbivores, time (week), elevation, and N addition on bare ground cover, and b) herbivores, time (week), elevation, N addition and status on root squared-transformed plant cover. Coefficients are estimated from final LMMs. Besides main effects, we tested two-way and three-way interactions and removed them when p-value > 0.05.

Response variable	Fixed factors	Estimate	SE	df	t	p
a) Bare ground cover	herbivores (yes)	-2.555	2.576	792.019	-0.992	0.322
	time	-38.319	1.125	793.444	-34.065	<0.001
	elevation	-0.440	3.228	17.528	-0.136	0.893
	N (yes)	-1.983	1.518	45.193	-1.306	0.198
	herbivores (yes) x time	5.042	1.558	791.875	3.236	0.001
	elevation x time	2.562	0.803	794.782	3.191	0.001
b) Plant cover	herbivores (yes)	-0.379	0.088	1337.245	-4.291	<0.001
	status (non-native)	-0.232	0.233	1347.897	-0.999	0.318
	time	3.526	0.064	1337.093	55.133	<0.001
	elevation	-0.200	0.290	16.665	-0.689	0.501
	N (yes)	0.165	0.118	39.088	1.399	0.170
	herbivores (yes) x status (non-native)	0.339	0.156	1353.680	2.172	0.030
	status (non-native) x time	-2.228	0.122	1337.032	-18.276	<0.001
	status (non-native) x elevation	0.135	0.244	1352.720	0.555	0.579
	time x elevation	0.147	0.060	1337.191	2.451	0.014
	status (non-native) x time x elevation	-0.470	0.134	1337.076	-3.507	<0.001

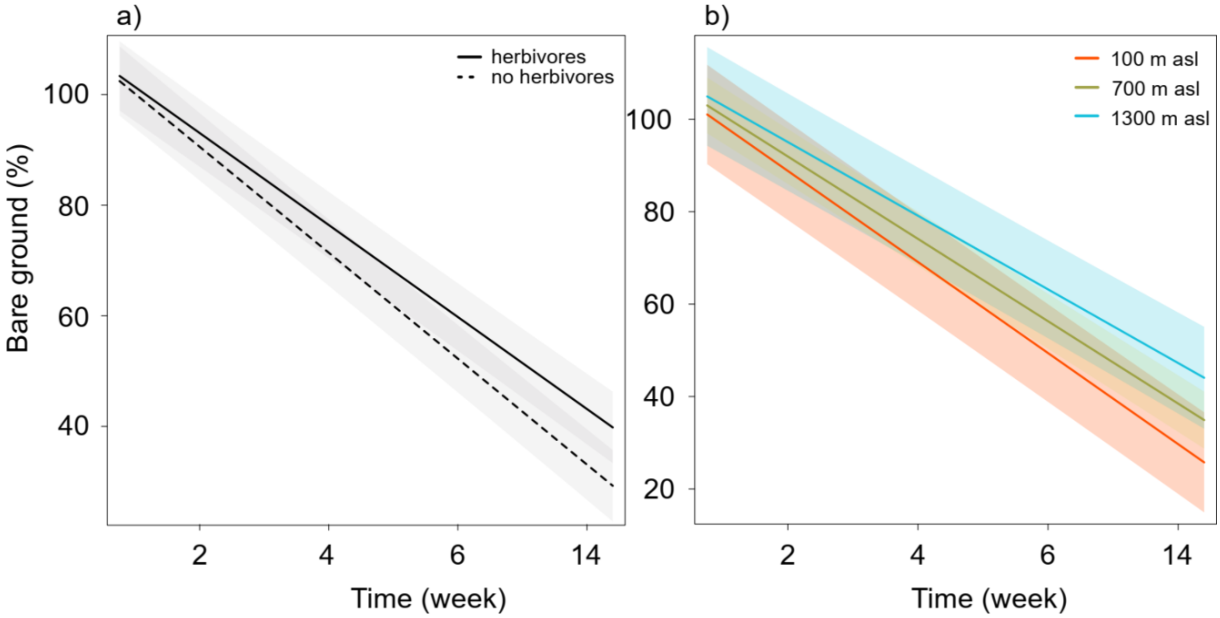

Figure 5: Effect of the interaction a) between herbivore presence and time (week of the experiment) and b) between elevation and time (week of the experiment) on bare ground (percent cover) of each subplot. Models contained disturbed subplots (n= 240).

For plant cover, we found an interaction between status and herbivores (Table 3b), i.e. plant cover of natives decreased in presence of herbivores, while non-native cover did not respond to herbivory exclosure (Fig. 6a). We also found a three-way interaction between time, status and elevation (Table 3b), i.e. non-native cover increased more over time at lower than at higher elevations (Fig. 6 b, Table 3b). All plant cover did not respond to N addition.

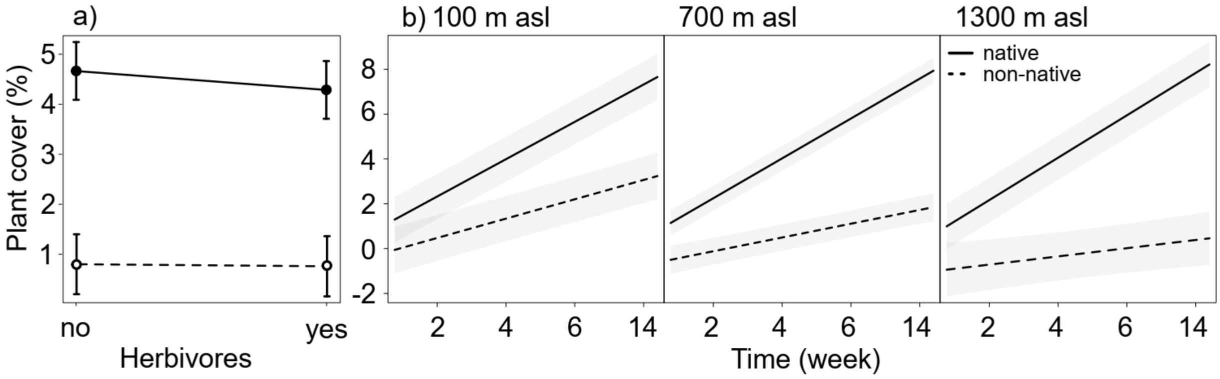

Figure 6: Effect of the a) two-way interaction between herbivore presence and plant species status (native vs. non-native) and b) three-way interaction between time (week of the experiment), elevation and plant species status (native vs. non-native) on squared root transformed plant cover. Models contained disturbed subplots (n= 240).

Discussion

With a large manipulative experiment under realistic field conditions, we investigated the potential interactions between elevation, N deposition, and invertebrate herbivory in driving plant establishment dynamics after soil disturbance. Native and non-native species showed contrasting responses to these drivers. Irrespective of elevation, soil disturbance increased non-native plant success, while it affected native species diversity negatively. Moreover, native species richness increased with elevation while non-native richness decreased at high elevations. Similar to the effects observed for large herbivores (Averill et al., 2018; Relva et al., 2010; Stokely et al., 2020), we found that invertebrate herbivory might play an important role in plant establishment dynamics by feeding preferentially on native plants. Current levels of N deposition in the Alps seemed to have little effect on both native and non-native species. Altogether our results confirm the high risks of future plant invasions in mountains under warming temperature and increasing human disturbance, and point to the need of incorporating plant-herbivore interactions in future invasion studies.

Response of natives and non-natives to disturbance under natural conditions

Native and non-native plants showed contrasting responses to soil disturbance. As expected, the removal of resident vegetation and the creation of bare ground through soil disturbance promoted non-native establishment (Lembrechts et al., 2016). This confirms that an invading species must have access to resources such as light, nutrients, and water, and that it will have greater success in invading a community if it does not encounter intense competition for these resources from resident species (Davis et al., 2000). Most non-natives possess traits associated with faster growth rate and resource acquisition (Van Kleunen, Weber, & Fischer, 2010). These traits probably enabled them to quickly exploit the resources released by soil disturbance at the expense of resident native species (Lembrechts et al., 2017; McDougall et al., 2018). Consistently, we found a negative effect of disturbance on native species richness, indicating that only a small subset of native species was able to colonize the disturbed soil.

Second, elevation affected native and non-native plants, oppositely. Non-native species richness peaked at low elevations where human activities are more intense and temperatures are warmer (Haider et al., 2018; Marini et al., 2013; Pauchard et al., 2009; Seipel, Alexander, Edwards, & Kueffer, 2016). This confirms that climate can be a fundamental barrier for the establishment of warm-adapted non-native plants (Alexander et al., 2011; Lembrechts et al., 2016; Marini et al., 2013). However, it was not possible to disentangle the effects of temperature and human activities, i.e. in addition to warmer conditions, also a higher propagule pressure can contribute to explain non-native success in the lowlands. At low elevations, the probability of introducing species is higher than at high elevations, creating a larger species pool of potential invaders (Alexander et al., 2011; Boscutti et al., 2018; Marini et al., 2013). By contrast, native diversity showed a trend for increasing with elevation. Probably, the truncated elevation gradient of the study (100-1330 m) prevented us to see the hump-shaped pattern that is often reported for native plant diversity (Haider et al., 2018; Marini et al., 2013; Nogués-Bravo, Araújo, Romdal, & Rahbek, 2008).

Besides the effect on species richness, soil disturbance has been identified as a key driver of plant community composition (Corcos et al., 2020; Haider et al., 2018). Beta-diversity between disturbed and resident vegetation was high, indicating that a large proportion of established species did not occur in the surrounding vegetation but only in the seed-bank (Fig. 3). Disturbance released from competition several native and non-native species naturally present in the seed-bank, allowing them to germinate and establish. For native plants, this high replacement was due to several annual ruderal species that were able to colonize the soil after disturbance (see also Corcos et al., 2020). For non-natives, very few species occurred in the undisturbed vegetation. After disturbing the soil, in addition to the few non-native species already present in the surrounding vegetation, several others emerged, showing that propagule pressure in the soil was relatively high. Ten sites out of fifteen acquired novel non-native species after disturbance, while the only four sites where no non-native species occurred, were located at mid or high elevations confirming the expected negative effect of increasing elevation on propagule pressure (Alexander et al., 2011).

Response of natives and non-natives to N addition and herbivory exclosure after disturbance

Invertebrate herbivores emerged as a potential driver of plant establishment after soil disturbance. They removed overall around 20 % of the total biomass and increased bare ground by 10 % compared to situations where herbivory was excluded. We found herbivores to have a negative effect on native plant cover but a neutral effect on non-natives. Through biomass reduction, increase in bare ground and/or reduction in the rate of resource capture by the resident vegetation (Davis et al., 2000; Meineri, Klanderud, Guittar, Goldberg, & Vandvik, 2020), herbivores may release resources, thereby favouring the establishment of fast growing species such as most non-natives (McDougall et al., 2018; Van Kleunen et al., 2010). After soil disturbance, herbivory, and especially seedling herbivory, may become a crucial driver of vegetation dynamics and it can be determinant in facilitating non-native success (Relva et al. 2010). Although our results showed that herbivores hindered native establishment and did not affect non-natives, we could not confirm findings of less herbivore damage on non-native than on native plants (Cappuccino & Carpenter, 2005; Huang et al., 2020; Liu, Stiling, & Pemberton, 2007). In addition, we cannot exclude that the lower susceptibility of non-natives might also arise from a 'sampling effect' (Loreau, 2000); i.e. the lower number of introduced species compared to resident natives might possess a particular suite of traits associated to higher herbivore resistance (Lemoine, Burkepile, & Parker, 2016). Surprisingly, herbivory effect did not change under N addition nor with elevation. We expected herbivory to increase at elevated N due to a higher nutrient content (Borgström, Strengbom, Marini, Viketoft, & Bommarco, 2017). However, we did not find any direct or indirect effect of N on plant establishment. Similar to other studies (Potter & Bowman, 2020), the lack of N effect can be related to the low amount of N (average deposition rate in the Alps) or to co-limitation of multiple resources (Kaspari & Powers, 2016). At high elevations where temperatures are colder, we expected that invertebrate herbivory decreases in intensity (Bale et al., 2002; Moreira, Abdala-Roberts, Rasmann, Castagneyrol, & Mooney, 2016; Zuo et al., 2012). Probably, our elevation gradient (100-1330 m) was too short to capture the expected variation in herbivore pressure (Silvestre, Aguilar, Seoane, & Azcárate, 2019; Sohn, Kim, & Choi, 2019). Moreover, while native cover increased irrespective of elevation over the course of the experiment, non-native cover grew at a much slower rate at high than at low elevations. This might confirm the negative effect of cold temperatures on non-native plants. Finally, more soil remained bare at higher elevations than in the lowlands, creating potential opportunities for invasion. These results point at high risks of future invasion in mountains under warming climate.

Conclusions

Using a large experiment under realistic field conditions, we showed that the joint effects of warm temperatures and human-induced disturbance favoured non-native plant establishment over natives, suggesting that global change will probably promote the further spread of non-native plants in mountain environments (Pauchard et al., 2009). We also showed for the first time that during the establishment phase, invertebrate herbivory might play a role in shifting competition hierarchies between natives and non-natives. As global change is reshuffling ecological interactions across trophic levels, it is fundamental to incorporate the effects of biotic interactions to fully understand plant redistribution dynamics (Alexander et al., 2018; Alexander, Diez, et al., 2016). Although the magnitude of herbivore effect was expected to increase under warm temperatures (Zuo et al., 2012) and high resource availability (Olff & Ritchie, 1998), we found no interaction between herbivory and abiotic drivers. Our results show that even highly resistant ecosystems such as continuous semi-natural grasslands (Boscutti et al., 2018) can be easily invaded once the resident vegetation is removed. Therefore, besides human-related disturbance, also natural phenomena such as land-slides or small erosion events might be associated with plant invasions due to the existing high propagule pressure observed in most of the seed-banks. Decreasing soil disturbance regime, in particular where propagule pressure is high, appears as a top priority to reduce the probability of invasions of non-native plants across temperate mountains.

Ackowledgments

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Chapter 3.

Effects of temperature and plant diversity on orthopterans and leafhoppers in calcareous dry grasslands

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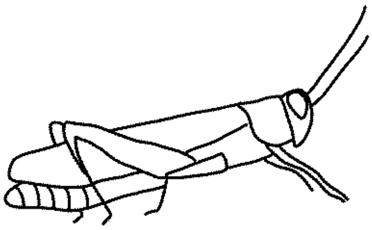

Abstract

In mountains, current land-use changes are altering plant communities of semi-natural grasslands with potential cascading effects on associated herbivores. Besides vegetation changes, temperature is also a key driver of insect diversity, and in the European Alps is predicted to increase by 0.25°C per decade. Understanding herbivore responses to temperature and plant composition changes in mountain environments is of increasing importance.

Our study aims at investigating the response to temperature and plant diversity and composition of two key herbivore groups (orthopterans and leafhoppers) belonging to contrasting feeding guilds (chewers vs. sap-feeders). We hypothesized that orthopteran diversity would be driven by temperature while leafhoppers by plant community composition. We selected 15 dry calcareous grasslands ranging from 100 to 1330 m a.s.l. along two independent gradients of plant diversity and temperature. We sampled orthopteran and leafhopper species richness and abundance by sweep-netting.

Consistent with their low feeding specialisation, orthopteran species richness and community composition were only driven by temperature. By contrast, leafhopper species richness was not affected by temperature nor by plant diversity but leafhopper community composition was strongly influenced by plant species composition. This response can be explained by the higher host feeding specialisation of many leafhopper species. Species rarity and mobility did not change the response of the diversity of both groups, but orthopteran abundance increased with temperature only for highly mobile species.

Altogether, our results suggest that future responses of grassland herbivores to vegetation changes and temperature warming are highly variable and depend on the feeding strategy and specialisation of the focal herbivore group.

Introduction

In the last decades, the loss and deterioration of species-rich, semi-natural grasslands has been a major conservation problem throughout Europe (van Dijk 1991; Poschlod and WallisDeVries 2002; Hodgson et al. 2005). In the European Alps, traditionally managed grasslands host highly diverse communities of flora and fauna but are also increasingly under threat by global changes such as management intensification, abandonment of low-intensity grazing, landscape simplification and climate change (Tasser and Tappeiner 2002; Dirnböck et al. 2003; Humbert et al. 2009; Monteiro et al. 2011; Hinojosa et al. 2016; Tattoni et al. 2017). In mountains, many plant species respond to climate warming by moving to higher elevations reshuffling local plant communities (Lenoir et al. 2008). Both climate and local management changes often result in shifts in plant community composition and in the loss of plant diversity (Marini et al. 2009a) with potential cascading effects on associated insect diversity (Van der Putten et al. 2010).

A large body of research reports a strong bottom-up effect of plant composition and diversity on herbivore communities (Deraison et al. 2015; Moreira et al. 2016). Highly diverse plant communities are often more productive than species-poor communities and should provide a greater diversity of shelter and reproduction sites as well as food resources, thereby favouring a larger number of consumers (Moreira et al. 2016). Consequently, altering grassland vegetation and reducing plant richness can lead to the loss of arthropod consumers, such as grasshopper, butterfly and bee species (Kruess and Tscharntke 2002; Marini et al. 2007, 2009b). However, plant-herbivore diversity relationship does not follow a general pattern but also depends on herbivore specialisation and feeding guild (Joshi et al. 2008; Rodríguez-Castañeda et al. 2010; LaRose et al. 2020). Low-mobile and specialised herbivores are more likely to be strongly affected by changes in plant composition, whereas the diversity of generalists should exhibit weaker responses because they are less limited to feed on specific host plants (Koricheva et al. 2000; Jactel and Brockerhoff 2007).

In montane ecosystems, besides vegetation diversity and composition, temperature is one of the main factors influencing insect herbivore diversity (Bale et al. 2002; McCain and Grytnes 2010). Low temperatures may directly affect species distribution by limiting physiological processes or indirectly constrain population size via reduced plant productivity (Bale et al. 2002). Hence, the rapid temperature changes over short geographical distances associated with elevational gradients are expected to influence arthropod species community and diversity (Körner 2007; Sundqvist et al. 2013). Herbivore species richness is generally expected to decline with elevation (Bale et al., 2002). However, due to the interdependence of moisture, temperature, exposition and altitude, the observed elevational patterns in species richness are complex and may vary among feeding guilds, taxonomic groups and regions (Bale et al. 2002; Hodkinson 2005; Rodríguez-Castañeda et al. 2010). As in the European Alps, a 1.5°C warming (0.25°C per decade) is expected in the first half of the 21st century (Gobiet et al. 2014), understanding herbivore response to temperature is of increasing importance.

Besides the environmental pressures explained above, species traits are also expected to influence species' sensitivity to environmental changes such as climate and land-use change

(Matenaar et al. 2015). First, mobility appears as a strong predictor of success or decline of insect populations (Kotiaho et al. 2005), as varying mobility might affect how the species respond to variations in habitat area and quality (Shen et al. 2009). In general, poor dispersers seem to be more prone to extinction and range contractions imposed by several human-induced pressures such as fragmentation or eutrophication (Reinhardt et al. 2005; Marini et al. 2010). Second, also rarity may influence species' sensitivity as species that have narrower range are expected to be lost more frequently as a result of land-use change compared with species with broader habitat affinities and range (Sykes et al. 2020).

In this context, our study aims to investigate the response to temperature and plant diversity and composition of two key herbivore groups (Auchenorrhyncha, hereafter referred to as leafhoppers; and Orthoptera specialised in grassland environments, hereafter referred to as orthopterans) in dry calcareous grasslands. We selected them as model organisms because they both play an important role in grassland ecosystems (Deraison et al. 2015) and due to their ecological differences. Leafhoppers are a very abundant and diversified group of sap-feeders showing different degrees of host plant specialisation from strictly monophagous to polyphagous species (Biedermann et al. 2005). In contrast, orthopteran species are generalist chewers able to feed on many plant species, and are a fundamental component of arthropod communities in grasslands (Branson et al. 2006; Alignan et al. 2018). In addition, in Europe, Orthoptera are often thermophilic and are expected to be particularly sensitive to temperature changes (Willott and Hassall 1998; Fontana 2002; Schmitz et al. 2016). Hence, they represent a good model group to study the effect of temperature. By selecting 15 dry calcareous grasslands under the same extensive management, similar rainfall conditions and surrounding land-use, but along two independent gradients of plant diversity and temperature we addressed the following questions: (1) Does herbivore diversity increase with temperature? (2) Do shifts in plant composition and diversity explain variation in herbivore communities? (3) Do the two taxa belonging to contrasting feeding guilds exhibit a common response to these drivers? (4) Do herbivore responses to the considered drivers change depending on their regional rarity and mobility?

Materials and Methods

Study area

The study was carried out during spring-summer 2019 in the Natisone Valleys (Julian Prealps), in the South-Eastern Alps in Friuli Venezia Giulia region (NE Italy). In this area, the landscape is dominated by mixed broadleaf forests and, in lower proportion, by semi-natural grasslands within traditional agricultural landscape. Semi-natural dry grasslands in the study area are mowed once per year and host floristic communities with a high richness of sub-endemic and alpine species at the limit of their distribution range (Poldini 1995). Mean annual temperature at the lowest elevation in the study area is 12.46 °C (at 138 m a.s.l.) and 4.40 °C at the highest (1630m a.s.l.), mean annual precipitation is ca. 1500-2300 mm.

Sampling design

We selected 15 sites ranging between 100 to 1330 m a.s.l. (Table C S1, Figure C S1). As the upper altitudinal limit for semi-natural calcareous dry grasslands is set at approximately 1300 m a.s.l., the selected range corresponded to the elevational distribution of this habitat (*Festuco-Brometalia*, Natura 2000 priority habitat, code 6210). The 15 selected grasslands laid on flat ground, were cut once a year and received no fertilizer applications. The lack of a management gradient allowed us to isolate the effect of different plant diversity across sites that did not differ in their management. All selected sites were dominated by *Brachypodium rupestre*, *Bromopsis erecta* and *Festuca* spp and characterized by a wide diversity of grasses and herbs. Along the elevational gradient, we placed data loggers at 1.5 m from the soil, to record air temperature every 30 min. Air temperature was recorded approximately over 12 weeks (from mid-June to August) along the altitudinal gradient. Mean temperatures over the whole duration of the experiment ranged from c. 25.2 °C at the lowest elevation (100 m a.s.l.) to 17.1 °C at the highest elevation (1330 m a.s.l.). The selection of the sites was performed to keep statistical independence between plant diversity and temperature. Temperature and elevation were strongly correlated (Pearson correlation r = -0.95; $p < 0.001$), whereas temperature and plant species richness were not (Pearson correlation r = 0.27; $p = 0.322$) as well as elevation and plant species richness (Pearson correlation r = -0.274; $p = 0.323$).

As both herbivore groups are expected to be affected by the composition of the surrounding landscape (forest cover, Marini et al., 2009 and Walcher et al., 2017; landscape connectivity Rösch, Tscharntke, Scherber, & Batáry 2013), we quantified the proportion of forest cover (dominant habitat in the study area) in a buffer of 500 m (diameter) around each sites. This variable was not related to both temperature (Pearson correlation r = 0.04; $p = 0.889$) and plant diversity (Pearson correlation r = -0.40; $p = 0.112$). In preliminary analyses, we tested this variable and found no effect on both groups. Hence, we only present the effect of our local factors in the main text.

Plant surveys

In each site, we performed a floristic survey at the end of May, before the mowing. It consisted in the assessment of all vascular species and their cover present in a 12 m × 3 m plot. Plant species nomenclature followed Poldini, Oriolo and Vidali (2001). In the selected sites, overall 175 plant species occurred ranging from a minimum of 22 to a maximum of 53 species per site (Table C S2).

Herbivore surveys

Around the plot used for the plant surveys, insects were sampled approximately every two weeks starting from mid-May until the end of August, for a total of six rounds of sampling, in order to collect species with different phenology. We chose the sweep netting as sampling method, because it is widely adopted, quick and provides reliable estimates of relative abundance and species composition of both orthopteran and hemipteran communities in grasslands (Gardiner et al. 2005; Doxon et al. 2011). In each site, we sampled along two transects 25 m long, distant from each other about 6 m. We performed 25 sweeps per transect, for a total of 50 sweeps per site. Surveys took place during the warmer hours of the day (between 10:00 and 18:00) on sunny days that did not follow a day of rainfall, and were carried out always by the same person (GLB). We preserved collected specimens into 70% ethanol and identified them at the species level in the laboratory. We followed Biedermann & Niedringhaus (2009); Della Giustina (2019); Vidano (1965); and Wagner (1951) for leafhoppers identification and nomenclature. Orthopterans were identified using Fontana (2002), we identified and counted only adult specimens. Based on Fontana (2002), we included only orthopteran species that are known to be specialized for grassland habitats. We excluded 10 Ensifera species for a total of 33 individuals. For each taxonomic group, the species richness referred to the pooled number of species. Following Matenaar et al. (2015), we assessed for each species two traits: mobility and regional rarity. These categories were chosen because likely associated with extinction risk for both herbivore groups (Öckinger et al. 2010; Marini et al. 2012; Rösch et al. 2013). Mobility was defined based on wing development, we classified both taxa in two categories: “macropterous” and “non-macropterous”. For orthopterans, non-macropterous species consisted in apterous, squamipterous and brachypterous species, while for leafhoppers only in brachypterous ones. Rarity was calculated based on species occurrence in the study sites, following Matenaar et al. (2015), a species was considered “rare” when present in less than 3 sites, “intermediate” in more than 2 and less than 4 sites, and “common” in more than 4 sites.

Statistical analyses

Diversity patterns of orthopteran and leafhopper communities

All analyses were conducted with the Software R version 3.6.1 (R Core Team 2017). We used linear models to estimate the effects of temperature and plant species richness on orthopteran and leafhopper communities. For each taxon, models included as response variables the pooled number of species and abundance observed during the six sampling rounds. In addition, we used linear models to test if the two taxa responded differently to temperature and plant species richness depending on their mobility and rarity. First, for each taxon, we tested the effect of temperature and plant species richness separately for rare, intermediate and common species, using the pooled number of species and then, their abundance as response variables. Second, for each taxon, for macropterous and non-macropterous species separately, we tested the effect of temperature and species richness on their pooled number of species and abundance. For all models, to improve the linearity and residuals distribution, all response variables were log-transformed. Normality of the residuals was visually evaluated with q-q plots using the “car” package (Fox et al. 2012). Although our response variables were counts, we did not present the results from generalized linear models (both Poisson and negative binomial distribution) due to the poor outcome of model diagnostics compared to linear models. For each model, we tested for spatial correlation in the residuals using Moran’s I and we did not find any significant spatial autocorrelation.

Plant composition effects on orthopteran and leafhopper communities

To investigate the effects of temperature and plant community composition on the composition of orthopteran and leafhopper communities, we performed multiple regression on distance matrices (Lichstein 2007). First, based on presence/absence matrices, we calculated for each taxon (i.e. plants, orthopterans, leafhoppers) a distance matrix using Jaccard dissimilarity index (Legendre 2014), with the “vegdist” function in the “vegan” package (Oksanen et al. 2019). Second, we generated a temperature distance matrix using the “vegdist” function with Euclidean distance. Then, we performed regressions on distance matrices using the “MRM” function in the “ecodist” package (Goslee and Urban 2007), and tested the effects of plant dissimilarity and temperature distance on leafhopper and orthopteran dissimilarity, separately. We also calculated Bray-Curtis dissimilarity matrices using the “vegdist” function based on leafhopper and orthopteran abundance and on plant cover but, as results were consistent with the one obtained using presence absence matrices, we do not present them in the text.

To visualize the relationship between temperature and single species of orthopterans and leafhoppers, we run a principal component analysis (PCA). We performed a PCA using the function “prcomp” on abundance matrices transformed using logarithmic transformation as suggested by Anderson et al., (2006).

In preliminary analyses, using a Mantel test with the function “mantel” in the “vegan” package (Oksanen et al. 2019), we tested whether dissimilarity in orthopteran or leafhopper composition varied with increasing geographical distance. For both groups, we found no effect of distance (for orthopterans r = -0.253, $p = 0.980$, for leafhoppers r = 0.094, $p = 0.226$).

Results

Orthopteran communities

Overall, we found 31 species of orthopterans, ranging from 4 to 12 species per site, and 940 individuals (918 individuals identified to the species level, Table C S3). The most abundant species was *Micropodisma salamandra* (43% of total abundance) followed by *Chorthippus parallelus* (13%). Results of the linear model revealed that temperature was the only driving factor of orthopteran species richness (Figure 1, Table 1). We found a linear positive relationship between species richness and temperature. Orthopteran abundance did not respond to temperature nor to plant species richness (Table 1).

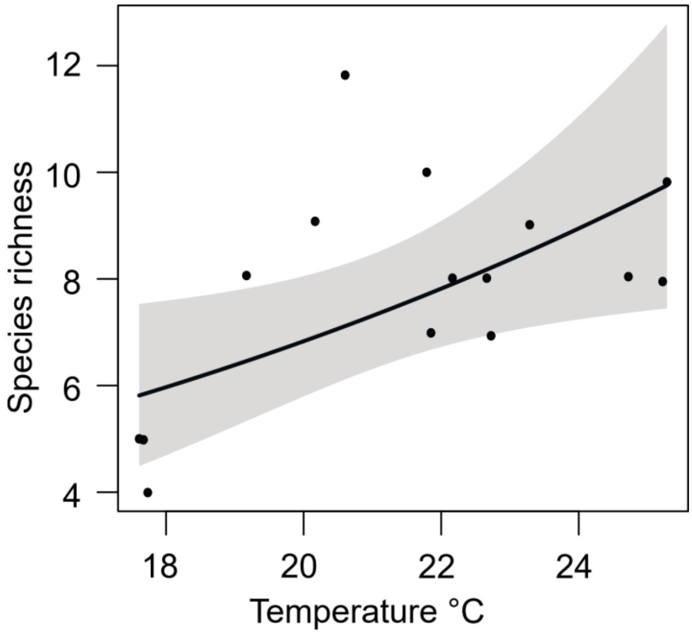

Figure 1: Effect of temperature on orthopteran species richness. Line indicates model predicted values, shading shows 95% CI.

Responses of abundance and species richness to both considered drivers did not change based on orthopteran rarity (Table C S5). Responses of species richness did not change based on orthopteran mobility but the abundance of macropterous species increased with temperature, while the abundance of non-macropterous species did not (Table C S6). Multiple regression on distance matrices showed that temperature distance affected orthopteran community dissimilarity, while plant community dissimilarity did not have any effect (Figure 2a, Table 2). The PCA analysis extracted 33.23, 19.27, and 11.22% of the variance with the first three components, respectively (Figure 3a). *Micropodisma salamadra* most contributed to the first principal component, while *Chorthippus parallelus* to the second. *Omocestus rufipes, Euchorthippus declivus* and *Glyptobothrus mollis* were more closely associated with warmer temperatures. By contrast, *Gomphocerippus rufus* and *Mecostethus parapleurus* were related to colder temperatures.

Table 1: Results from linear models testing the effects of temperature and plant species richness on species richness and abundance of a) orthopterans and b) leafhoppers.

Response variable		Estimate	SE	t	p
a) Orthopterans					
Species richness	temperature	0.067	0.026	2.555	0.025
	plant species richness	0.001	0.007	0.113	0.914
Abundance	temperature	0.060	0.075	0.794	0.443
	plant species richness	0.030	0.022	1.276	0.226
b) Leafhoppers					
Species richness	temperature	0.042	0.049	0.870	0.401
	plant species richness	-0.009	0.015	-0.638	0.536
Abundance	temperature	0.139	0.084	1.644	0.126
	plant species richness	0.008	0.025	0.302	0.768

Table 2: Results from multiple regression models on distance matrices testing the effects of temperature distance and plant composition dissimilarity on composition dissimilarity of orthopterans and leafhoppers. Distance matrices for plants, orthopterans and leafhoppers were calculated using Jaccard dissimilarity index (Legendre, 2014), while temperature distance using Euclidean distance.

Response variable	Explanatory variables	R^2	Estimate	p
Orthopteran dissimilarity	temperature distance	0.159	0.025	0.006
	plant dissimilarity		0.080	0.721
Leafhopper dissimilarity	temperature distance	0.261	0.008	0.112
	plant dissimilarity		0.462	0.001

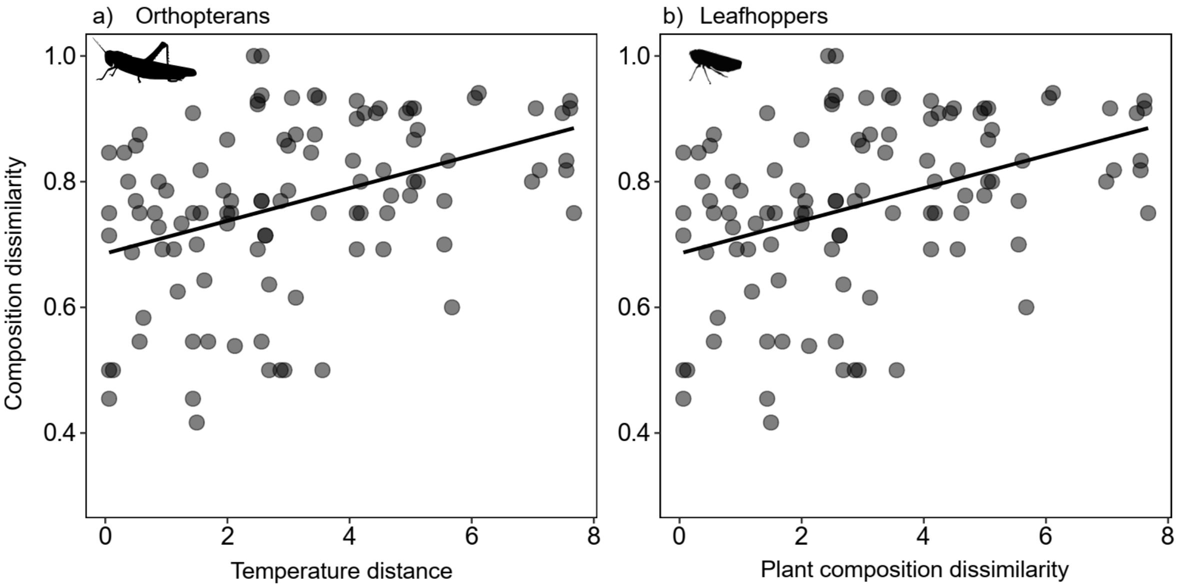

Figure 2: Effect of (a) temperature distance on orthopteran dissimilarity and (b) plant community dissimilarity on leafhopper dissimilarity. Composition dissimilarity was calculated using Jaccard index (Legendre 2014). Regression lines are estimated from multiple regression models on distance matrices, only significant results are shown.

Leafhopper communities

Overall, we found 82 species and 2468 individuals of leafhoppers (2405 individuals identified at the species and at the genus level and the remaining at the family level, Table C S4). Most common species were *Jassargus obtusivalvis* (19%) and *Philaenus spumarius* (9%). Neither leafhopper species richness nor abundance responded to temperature or plant species richness (Table 1). In addition, responses of species richness and abundance to both considered drivers did not change based on leafhopper mobility nor rarity (Tables S5 and S6). Moreover, multiple regression on distance matrices indicated strong differences in leafhopper community composition among sites with dissimilar composition of plant communities, while temperature distance had no effect (Figure 2b, Table 2). Results from the PCA analysis show that 22.85, 17.71, and 16.25% of the variation is explained by the first three axes, respectively, for a cumulative total of 56.81% of variance explained (Figure 3b). *Jassargus flori* most contributed to the first principal component while *Adarrus multinotatus* to the second. *Dicranotropis hamata* and *Forcipata citrinella* showed a closer association to warmer temperatures.

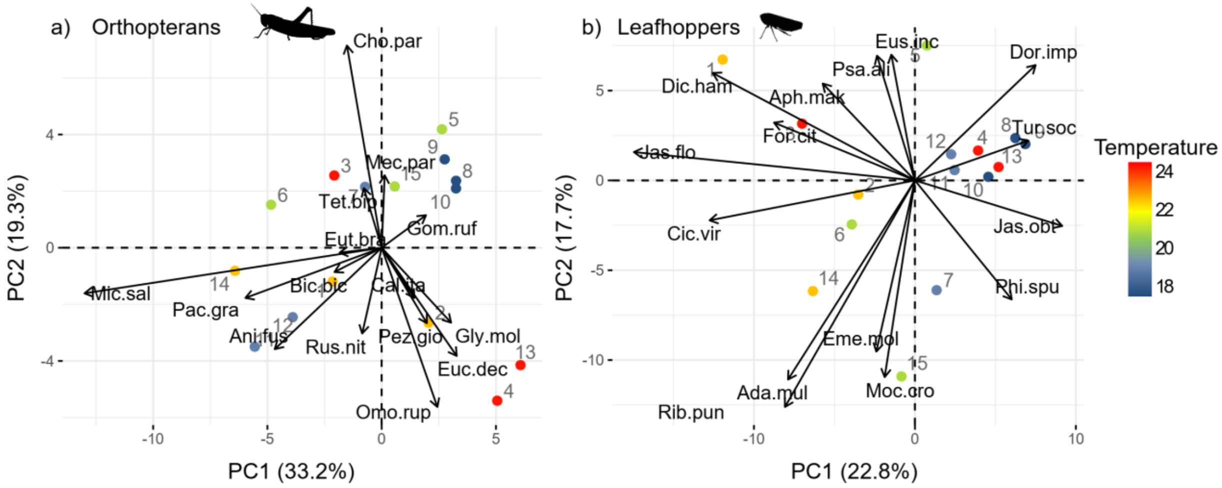

Figure 3: Results of the Principal Component Analysis (PCA) carried out on the 15 sites (a) on orthopteran and (b) on leafhopper species. Only the fifteen species with a large value of cos^2 and therefore contributing the most to the construction of the axes are shown (Kassambara and Mundt 2017). To enable a clearer visualization, species names are abbreviated showing only the first three letters of genus and species names. Full names are available in Tables S3 and S4.

Discussion

In dry calcareous grasslands, we investigated the effects of temperature, plant species richness and composition on two key herbivore groups with different specialisation and belonging to contrasting feeding guilds. We found that orthopteran species richness as well as species composition were driven by temperature, while leafhopper richness was affected neither by temperature nor by plant diversity. However, leafhopper community composition was strongly influenced by plant composition. Species rarity and mobility did not change the response of the diversity of both groups, but orthopteran abundance increased with temperature only for highly mobile species. Altogether, our results show that herbivore responses to shift in plant composition and temperature are highly variable and depend on the feeding specialisation of the focal herbivore group.

Orthopteran communities

Orthopteran species richness increased with increasing temperatures. Moreover, as sites became more dissimilar in terms of temperature (i.e. low vs high elevation sites), orthopteran communities became also more dissimilar in terms of species composition. These results are consistent with other studies reporting detrimental effects of colder temperatures on orthopteran diversity along elevational gradients (Kati et al. 2012; Descombes et al. 2017). Most orthopteran species are thermophilic and low temperatures limit all their key physiological processes, thus determining a reduced performance and fitness (Willott and Hassall 1998; Schmitz et al. 2016). In particular, *Omocestus rufipes*, *Euchorthippus declivus* and *Glyptobothrus mollis* were more closely associated with warmer temperatures. The latter two species are xerophilous, typical of dry grasslands, while *O. rufipes* is a more generalist termophilous species (Fontana 2002). By contrast, *Gomphocerippus rufus* and *Mecostethus parapleurus* that were related to colder temperatures, are usually found in colder and wetter environments. We cannot exclude that temperatures were also associated with moisture, that plays a fundamental role in the embryonic development and hatching of orthopterans (Powell et al. 2007). Moreover, temperature affected orthopteran abundance differently depending on their mobility. We found that the abundance of mobile species increased with increasing temperature, while sedentary species' abundance did not respond to temperature. Highly mobile species are expected to be less affected by barriers, because they are better at occupying suitable habitats compared with sedentary species (Marini et al. 2012). This result supports other studies where mobility appears as a strong predictor of widespread success of insect populations (Kotiaho et al. 2005). Contrary to temperature, plant diversity and plant composition did not affect orthopteran species richness, abundance or community composition. Orthoptera are generally associated with vegetation characteristics, such as vegetation structure and plant nutrient contents (Unsicker et al. 2010; Miao et al. 2018). In fact, vegetation structure determines the availability of microsites for oviposition, shelter to escape from natural enemies and food resources (Zhu et al. 2017). However, as they are generalist chewers, orthopterans depend more on the amount of resources than on plant identity (Perner et al. 2005). Therefore, plant richness or composition seem to be weak predictors of orthopteran diversity, while other factors such as temperature but also vegetation structure, management intensity, vegetative litter amount and soil type might act as drivers of their distribution (Torrusio et al. 2002; Kruess and Tscharntke 2002; Nickel and Hildebrandt 2003; Marini et al. 2007; Schirmel et al. 2011; Helbing et al. 2014; Löffler and Fartmann 2017; Walcher et al. 2017; Miao et al. 2018).

Leafhopper communities

We did not find any effect of temperature and plant species richness on leafhopper communities. Leafhoppers responded only to plant community composition indicating a strong link between plant and leafhopper species identity. Most leafhoppers are specialist sap-feeders that show a strong dependency on their host plants (Nickel and Hildebrandt 2003). Therefore, it is the plant species identity that determines which leafhopper species can occur in a site (Perner et al. 2005; Taft and Dietrich 2017). Leafhopper dependency on vegetation composition emerged also from other studies showing a positive relationship between host plant and leafhopper species richness (Koricheva et al. 2000; Scherber et al. 2010b; Rösch et al. 2013). Here, different plant communities also provided different microclimatic conditions and sites for shelter, oviposition or overwintering, hence favouring a more diverse number of consumers (Helbing et al. 2017). Altogether these results suggest that habitat quality and, in particular, plant species composition (i.e. the identity of plant species in a community) might play a more important role than temperature in driving patterns of species composition of specialist herbivores such as leafhoppers (Koricheva et al. 2000; Everwand et al. 2014; Helbing et al. 2017; Chisté et al. 2018; Poniatowski et al. 2018). In fact, except for some species as the thermophilous *Dicranotropis hamata*, leafhopper species showed a weak association with temperature. An alarming consequence of leafhopper reliance on vegetation composition is that any management practice such as fertilization, mowing or grazing, that modifies vegetation composition and, in particular, intensive practices, will have a strong negative effect on leafhopper communities (Biedermann et al. 2005; Kőrösi et al. 2012; Helden et al. 2015).

Conclusions

In dry calcareous grasslands, insect herbivores exhibiting different feeding specialisation showed contrasting responses to temperature and shifts in plant species composition. For the persistence of specialist sap-feeder insects, the relevance of habitat quality and, in particular, of plant community composition clearly emerged (Anthes et al. 2003; Biedermann et al. 2005; Samways and Lu 2007; Bauerfeind et al. 2009; Löffler and Fartmann 2017; Münsch et al. 2019). Our results show that, even with no loss of plant diversity, shifts in plant composition strongly modified the assembly of leafhopper species communities. This suggests the importance of studying variation in species composition besides the more common approach of only considering species richness. By contrast, orthopterans, that are generalist chewers, were not affected by plant composition but were limited by colder temperatures (Schmitz et al. 2016; Descombes et al. 2017). Any management actions affecting plant composition should consider these differential responses driven by the feeding specialisation of the focal herbivore group (Vehviläinen et al. 2007). Moreover, in the context of climate change, we expect leafhoppers to be particularly sensitive to potential climate-induced shifts in vegetation composition, while orthopterans are expected to respond directly to temperature warming due to their relaxed association with plant community diversity and composition.

Acknowledgments

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Chapter 4.

Global change promotes exotic invasions and increases native extinction risk in the low elevation areas of the European Alps

Costanza Geppert, Alessio Bertolli, Filippo Prosser, Lorenzo Marini

Abstract

Mountain ecosystems are exposed to multiple anthropogenic pressures that are currently reshaping the distribution of plant populations. Here, using a unique dataset consisting of 1,153,161 occurrence records from the foothill to the snow alpine belt, we could reconstruct the response to global change of c. half of the species pool of the European Alps. While exotics are quickly spreading upwards expanding their elevational range, threatened natives are experiencing a strong erosion of their rear margins, contracting their range. In the lowlands, we observed high spatial congruence in the distribution of exotic, threatened, and extinct species, suggesting that these areas are those more vulnerable to global change pressures. Extinction risk was higher for warm-adapted species and was negatively correlated with the competitive ability to exploit resources, indicating that intensive land-uses might be more important drivers of extinction than temperature warming in mountain ecosystems, at least in the short-term.

Introduction

Mountain ecosystems are exposed to multiple anthropogenic pressures that are currently reshaping the distribution and abundance of plant populations (Guo et al. 2018a; Nomoto and Alexander 2021). On the one hand, climate warming has induced a rapid upward range shift of native plants, in particular warm-adapted species, whereas species inhabiting high elevations often decreased their population size and contracted their range (Rumpf et al. 2018; Geppert et al. 2020). While climate-induced extinctions have been still seldom reported (Wipf et al. 2013; Nomoto and Alexander 2021), land-use changes have already triggered the decline of rare, specialised native plants, in particular at low elevations, where agriculture and urbanization have caused the loss and deterioration of natural habitats (Foley et al. 2005; Sykes et al. 2020; Geppert et al. 2020). On the other hand, exotic invasive plants are quickly spreading from the disturbed lowlands to higher elevations due to a combination of temperature warming and increased soil disturbance, with potential negative effects on resident biodiversity (Matthies et al. 2004; Dullinger et al. 2012a; Dainese et al. 2017; McDougall et al. 2018; Geppert et al. 2020; Nomoto and Alexander 2021).

Despite a growing body of empirical research on the effects of global change on plant redistribution dynamics in mountain ecosystems, there has been no attempt to compare simultaneously the response of threatened, common and exotic species. This is mostly due to methodological constraints of the previous studies that have mainly used resurveys of permanent plots (Rumpf et al. 2018) or species distribution modelling (Cotto et al. 2017b; Carboni et al. 2018).

Resurveys usually capture regionally common species while threatened species are often underrepresented due to their patchy distribution. In contrast, studies based on species distribution models work with a too broad spatial resolution to detect changes across heterogeneous mountain environments and usually exclude land-use change effects. In addition, most previous research has focused on high-elevation areas, while disturbed low elevation areas have been often disregarded (Gottfried et al. 2012; Pauli et al. 2012; Steinbauer et al. 2018; Hülber et al. 2020).

Here, using a unique dataset consisting of 1,153,161 plant records sampled along a complete elevational gradient from the foothill to the snow alpine belt, we could reconstruct the response to global change of c. half of the plant species pool of the European Alps. First, we tested whether threatened native, common native and exotic plants show different range dynamics by estimating their vertical shift rate at both rear and leading edge. Species that are classified as threatened in the IUCN Red Lists are mostly rare species, with narrow ecological niches and small geographical ranges, and face the highest risk of extinction (Pimm et al. 1988; McKinney 2003; Clavel et al. 2011; Slatyer et al. 2013). Second, using spatially-explicit occurrence data we could test for spatial congruence in extinction, threatened species occurrence and exotic invasions with a *hotspot analysis*. Third, using species traits, we elucidated the ecological mechanisms beyond the different responses of regionally extinct, threatened and exotic species to the compounded effect of climate warming and land use.

Materials and Methods

Study area

Plants were sampled throughout the Trento Province, NE Italy (6’207 km^2, elevation range 66–3’769 m; Supplementary Figure D 1). The region is located in the centre of the European Alps and hosts c. half of the total species pool of the European Alps including species whose geographic ranges are Alpine, central and northern European and Mediterranean (Aeschimann et al. 2004). Climate in the region depends primarily on elevation: it is alpine at high elevations and continental in the lowlands. Maximum annual temperature between 1980 and 2010 was 17.5 °C and minimum 7.8 °C (at 200 m a.s.l.) (Di Piazza, A., & Eccel 2012). Between 1981 and 2010, mean temperatures increased by c. 0.75 °C (Di Piazza, A., & Eccel, 2012). The most recent meta-analysis on range shifts indicated that worldwide species moved their elevational range upward on average of 1.22 m year^{-1} (Chen et al. 2011), but a previous study in the European Alps reported higher velocities (2 m year^{-1} at the leading edge, and 8 m year^{-1} at the rear edge) (Rumpf et al. 2019b). Mean annual precipitation over the past 40 years was 1050 mm. Annual precipitation slightly increased between

1981 and 2010 (+2 %), but decreased in winter (−6 %). The study area has experienced major land-use changes in recent decades. First, agricultural land increased, became more intensive and expanded upwards from the lowlands to mid-elevations (up to c. 900 - 1000 m) (Monteiro et al. 2011). Second, forests increased downwards at the expense of open semi-natural areas at mid-elevations (approximately between 600 and 1500 m) due to land abandonment (Tattoni et al. 2017). Third, human settlements (urban, industrial and roads) increased, especially in the lowlands (Monteiro et al. 2011).

Plant data

Plant data were collected from 1990 to 2019 for a total of 1’153’161 plant occurrence records over an elevation gradient spanning from 66 to 3’500 m a.s.l. The sampling campaign was coordinated by FP and AB and carried out by a group of botanists that systematically covered the study area. To aid a systematic sampling of the area, the province was divided in 228 quadrants (c. 7 km × 5 km) following the standard central European floristic cartography (Messtischblatt 1: 25’000). The aim of the sampling was to map a detailed point-based distribution atlas of all the species. Each species population was localized with a global positioning system (GPS). We excluded from the original data subspecies, hybrids, and aggregates of species with difficult taxonomy, for a total of 2’092 species.

In addition, we analysed a smaller historical dataset comprising 570 records from 1823 to 1973 of 52 species that are currently considered regionally extinct. These records are based on the first printed Florae and Herbaria of the Trento province and were later collected and revised by FP and AB. The dataset included all the known local populations with the date of last observation of the species that went extinct in the last century. Before 1990, there was no coordinated floristic inventory in place and the sampling effort in the study area. Hence, it was not possible to reconstruct the date of extinction of the species that could have occurred between the last of observation and 1990.

Ecological characterization of plant species

Plant status. We classified plant species in four groups according to their origin and conservation status: regionally extinct species (n = 53), threatened native species (n = 619), common native species (n = 1’339), and exotic species (n = 134). Threatened species included species listed in the regional IUCN Red List (Prosser et al. 2019), belonging to the threat categories: near-threatened (NT), vulnerable (VU), endangered (EN), or critically endangered (CR). Data deficient species were removed from the analyses since they mostly included species with difficult and uncertain taxonomy (e.g. *Hieracium*, *Alchemilla* and *Rubus* sp.) Common native species were all native species not included in the Red List. Exotic species comprised established species introduced accidentally or deliberately by humans in the European continent after 1500 AD.

Habitat preference. We assigned each species to one habitat preference category following Flora del Trentino (Prosser 2020). Habitat categories were non-overlapping among species and consisted in: 1) alpine, cold-adapted species growing in alpine open areas above the tree-line; 2) semi-natural dry grassland, species specialised in open grasslands with shallow, well-drained soils rich in bases below the tree line; 3) forest, species occurring in shrubland, broadleaf or conifer forests; 4) grassland, species growing in mown meadows, abandoned grasslands, grass margins, from low elevations to alpine habitats; 5) rocky, species specialised in rocky soils and cliffs; 6) ruderal, species growing in highly disturbed areas such as abandoned agricultural fields, road or field margins, railways, urban areas or quarries; 7) wetland, species occurring in fens, mires, ponds and aquatic species.

Landolt's indicator for temperature. Global change will likely increase temperature favouring warm-adapted species (Rumpf et al. 2018). For each species, we defined the preferred temperature level using the ordinal scale (1–5) from Landolt et al., (2010) (from alpine: 1 to very warm: 5).

Grime C-S-R strategy. We classified species according to Grime C-S-R strategy in seven categories (Grime 1979): competitor (c), competitor ruderal (cr), competitor stress-tolerator (cs), competitor stress-tolerator ruderal (csr), ruderal (r), stress-tolerator (s), stress-tolerator ruderal (sr) (Klotz and Durka 2002). Competitor species are primarily composed of plants with high relative growth rate and high allocation to leaf construction. Stress-tolerant species are usually found under extreme environmental conditions with low disturbance. Due to the low resources available, growth and reproduction are usually reduced. Ruderals usually inhabit habitats with high disturbance regimes (i.e. tillage, mowing) and allocate their resources mainly to seed reproduction, being often annuals or short-lived perennials. Due to the correlation between the three scores, we only used the competitor score that can assume the following values: 0 (r, s, sr), 0.33 (csr), 0.5 (cr, cs) and 1 (c).

Range shift

We computed rates of shift in the elevational distribution of species, i.e. changes at the rear (low-elevation) and leading (high-elevation) edge using density distribution of the elevation of occurrence (Rumpf et al. 2019b; Geppert et al. 2020). To quantify the shift between the recent historical (hereafter 'historical') and current range, we split the data set into two periods of 15 years (1990–2004 and 2005–2019). For each species, with at least 30 records per period, we estimated a density distribution of the elevation of occurrence for the first and second period, separately (54 exotic, 112 threatened, and 1339 common species). The rear edge was calculated as the 10 % quantiles of the density distribution, and the leading edge as the 90 % quantile of the density distribution. The shift was measured by subtracting historical (1990–2004) from current (2005–2019) quantiles. We divided the total shift by 15 years to obtain an annual rate. We also calculated rear and leading edges as the 5 and 95 % quantiles of the density distribution. Shift rates at rear and leading edges as the 5 and 95 % quantiles were highly correlated with shift rates at rear and leading edges as the 10 and 90 % (Pearson's correlation $r = 0.93$, $p < 0.001$). To account for potential non-random sampling effort across the study region (Aikio et al. 2010), we visually checked the elevational distribution in each period for all records (Supplementary Figure D2). As no biased emerged, i.e. botanists surveyed sites at the same elevations in the two periods, we used the raw data with no correction (Geppert et al. 2020).

Hotspot analysis

To understand whether exotic invasions in the last 30 years occurred in sites where threatened and regionally extinct native species are also concentrated, we run a spatially-explicit hotspot analysis based on extinct, threatened and exotic species occurrence. We imposed over the entire study area three regular grids one with the resolution of 2 × 2 km, one of 4 × 4 km and one of 7 × 5 km. We chose a 2 × 2 km grid as the smallest scale because a smaller grid would have created a very patchy system with too many empty cells, whereas we used as the largest grid a 7 × 5 km grid corresponding to the quadrants used in the original sampling because for each quadrant we have the complete census of occurring plant species. In our analyses, we included only those cells where at least 100 records were reported, for a total of 99.96 % of the surveyed cells. As the occurrence of both threatened and exotic species depends also on the sampling effort, we corrected the occurrence data for exotic and threatened species hotspots at 2 km and 4 km resolution with the total number of occurrence records of common species per grid cell (Sussman et al. 2019). The total number of records of common species is a good proxy of the sampling effort for the single cell. The effort-corrected count consisted in the number of observations per grid cell divided by the natural logarithm of the total number of common species occurrence records for that grid cell. We used the natural logarithm of occurrence records because in our study few cells had been sampled extensively compared to the others (Supplementary Figure D2). Results with no sampling effort correction yielded similar results. By contrast, threatened and exotic species occurrence at quadrant resolution were analysed without effort corrections as there was no potential sampling bias. For regionally extinct species, we used the raw count of the populations of regionally extinct species per grid cell at 2 km, 4 km and 5 × 7 km resolution. We did not correct the raw number because we have all records of occurrence of these species in the study area.

We performed hotspot analyses using the Getis-Ord Gi* statistic, that detects hotspots while also indicating the statistical significance of those hotspots by examining each grid cell within the context of the neighbouring cells. We built a neighbour list for all grid cells using the Queen case contiguity (contiguity between each focal cell and the 8 neighbouring cells around it) and then used the neighbour list to calculate a row-standardized spatial weights matrix. The matrix informs every grid cell relationship to all other cells in the neighbourhood. We used the counts and the spatial weights matrix to calculate the Gi* for each grid cell. Gi* produces a z-score for each grid cell, where high positive values are statistically significant and indicate the possibility of a local cluster of high species abundance (i.e. a hotspot) that is unlikely due to random chance. We performed Getis-Ord Gi* analysis and all subsequent analyses at 2 km, 4 km, and quadrant resolution, but as they were highly consistent, we present here only results from the most accurate resolution (2 km).

In addition, we performed hotspot analyses for regionally extinct, threatened and exotic species using a kernel density estimation. This estimation converts point data into a continuous surface grid reflecting relative densities across all grid cells. We used R stats density function to estimate regionally extinct, threatened and exotic species density. We selected a Gaussian kernel with a 2-km bandwidth for kernel smoothing based on the geographic extent of the data. Results were consistent with the hotspot analysis using the Getis-Ord Gi* statistic.

Finally, using the Zonal statics tool in QGis (QGis 3.4.14 Madeira), for each grid cell used in the hotspot analyses we calculated several environmental metrics: mean elevation based on an elevation raster (25 × 25 m), rate of soil consumption between 2012 and 2019 based on the oldest and most recent available data (10 × 10 m) (ISPRA 2021) and the area covered by urban elements and crops based on the CORINE land cover map (2003) (1:100,000) (Büttner et al. 2004). The latter was used as a proxy for intensive land-use.

Statistical analyses

Range shift statistical analysis

We tested if threatened native, exotic, and common native species differed in their range shift. We used shift rate as response variable and range margin (rear vs. leading), and plant status (threatened native vs. exotic vs. common) and their interaction as fixed effects. A significant interaction between range margin and status would indicate that plants are moving at different speed at the rear vs. leading edge of their distribution. We added species as random effect (random intercepts). Because shift rates had non-normal errors, the significance of the difference for all models was computed using a resampling approach (non-parametric permutation test) with the ezPerm function of the ez R package (Lawrence & Lawrence, 2016). Bootstrapping (n = 1'000) was used to estimated 95% CIs around the mean. We compared results from non-parametric tests with results from LMMs after excluding shift rates comprised between -0.3 and 0.3 m× year $^{-1}$ and transforming the response variable (shift rate) as follow: sign(shift)*ln(abs(shift)) to obtain normal errors. Results from bootstrapping and LMMs were consistent (Supplementary Table D1).

Hotspot statistical analysis

First, we tested for spatial congruence in the hotspots using Pearson's correlation. We considered correlations between natural logarithmic transformed regionally extinct, threatened and exotic Gi* statistics at 2 km, 4 km and quadrant-level (Supplementary Figure D 3). We transformed the Gi* statistics using the natural logarithmic scale to linearize the relationship. Second, to visualize a potential overlap in the elevation range distribution of the hotspots, we estimated the density distribution of the mean elevation per cell (2 km^2) of hotspots of extinction, threatened species occurrence, exotic invasion and of protected areas. Finally, we tested for correlations between mean elevation of each grid cell and agricultural land, broadleaf forest, conifer forest, alpine grassland, managed grassland, urban area and wetland (Supplementary Figure D4). All statistical analyses were performed with R 3.5.1.

Results & discussion

To capture on-going changes in the distribution of montane plants, we quantified elevational range shifts at both rear and leading edges. Over the last thirty years, common species (i.e. those not included in the regional IUCN Red List) have shifted upwards on average by 2.9 m year^{-1}at the rear edge and 2.2 m year^{-1} at the leading edge. This almost symmetric shift at both edges indicated that the large majority of plant species moved their elevation range upwards according to climate change direction and speed. However, when we compared this symmetric range shift with range dynamics of threatened and exotic species, striking contrasting patterns emerged (Figure 1).

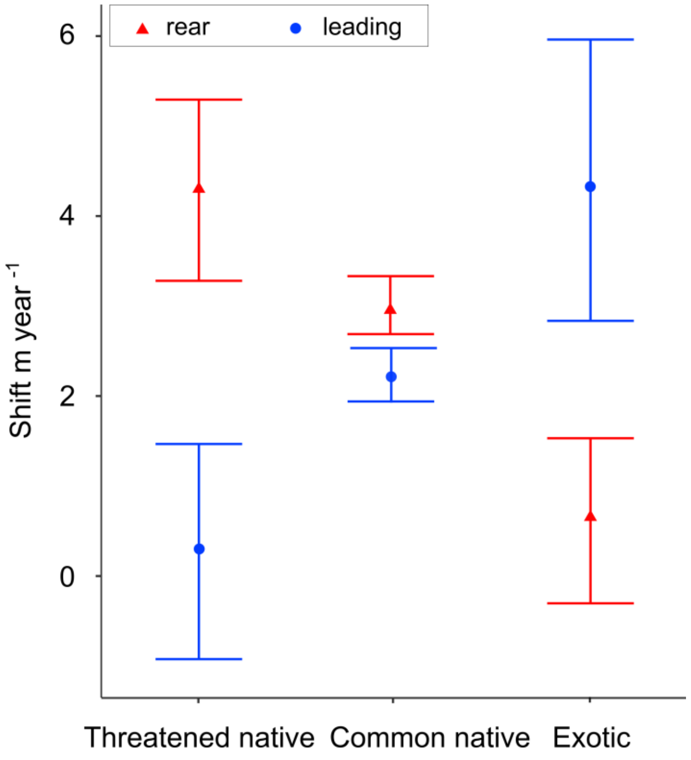

Figure 1: the effect of plant status (exotic, threatened native and common native) on shift rate (m / year) at the rear (red) and leading (blue) edge over the last 30 years (1990 - 2019).

Exotic plants expanded their elevational range marching upwards at the leading edge, while keeping their rear edge almost still. Leading edges of exotic species' distributions moved even above the average speed of climate warming in the region (Dainese et al. 2017). This suggests that under climate warming exotic species can still tolerate increasing temperatures at the rear margin, while they can effectively track temperature warming at the leading edge (Alexander et al. 2011; Dainese et al. 2017). This is consistent with the directional ecological filtering hypothesis claiming that elevational distributions of exotic species are a result of the sequential filtering of species with progressively broader climatic niches along a gradient of increasing temperature severity (Alexander et al., 2011). Accordingly, the large majority of exotic species in our study area were thermophilic species (Landolt's Thermophilic index = 4.4 ± 0.04 mean ± SE). Moreover, as exotic introductions often occur in the lowlands (Marini et al 2013), exotic species might require several years to expand their range up to their potential cold thermal limit (Alexander et al. 2009). Finally, the reported rapid expansion might also be related to human-assisted dispersal associated with soil disturbance events and the presence of roads and rails that are known to facilitate exotic spread (Alexander et al. 2011; Dainese et al. 2017; Geppert et al. 2021).

For threatened species, we found an opposite trend, i.e. species contracted their elevational range, with their rear edge moving upwards almost four times faster than their leading edge (Figure 1). This slow range expansion at the leading edge might be caused by several mechanisms including dispersal limitation (Gonzalez-Varo et al. 2021), slower population dynamics at cold temperatures (Rumpf et al., 2018) or lack of suitable habitats beyond historical leading edge (Guo et al. 2018b; Platts et al. 2019). Threatened plants often possess narrow ecological niches, making them adapted to a small range of environmental conditions (McKinney 2003; Clavel et al. 2011; Slatyer et al. 2013). Therefore finding the suitable environment along the elevational gradient might be particularly challenging for them compared to more generalist species (Geppert et al. 2020; Mi et al. 2021). Consistent with this hypothesis, amongst threatened plants, specialists of wetlands and semi-natural dry grasslands were overrepresented in our species pool (Figure 2).

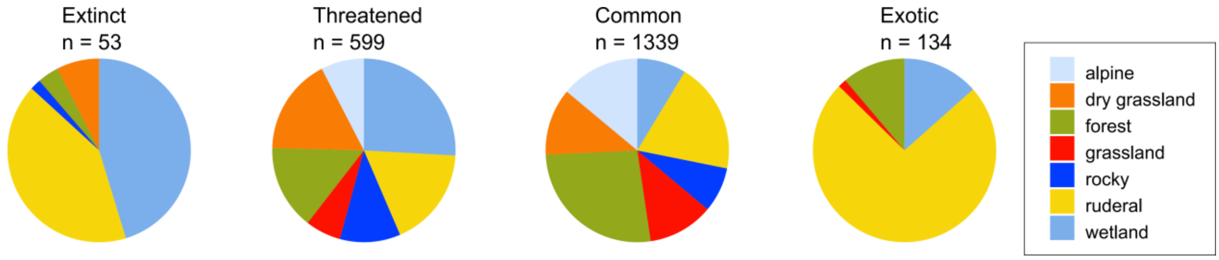

Figure 2: number of species belonging to each habitat preference category for extinct, threatened, common, and exotic species.

In addition, populations at the leading edge may also lag behind climatic changes in terms of growth and fitness compared to populations at low elevations, because demographic processes are usually slower at high elevations (Rumpf et al. 2018). Contrary to leading shift, rear edges of the distribution of threatened species moved quickly upwards. Besides temperature warming, land-use changes in the more intensive lowland areas might have also contributed to the erosion of the rear margin populations (Geppert et al. 2020). Moreover, local extinctions at the rear margin can also be driven by competitive replacement by warm adapted species that are fostered by climate change (Pauli et al. 2007; Alexander et al. 2015, 2018). The combination of warming, intensive land-uses, and potential interactions with novel species might jointly contribute to declines of rear edge populations (Nomoto and Alexander 2021). Therefore, novel species such as invading exotics might accelerate the local extinctions of threatened native plants caused by warming and land use changes. To test this hypothesis, we performed a spatially explicit hotspot analysis and identified whether hotspots of threatened species occurrence and historical regional extinction events coincided with hotspots of exotic species invasions.

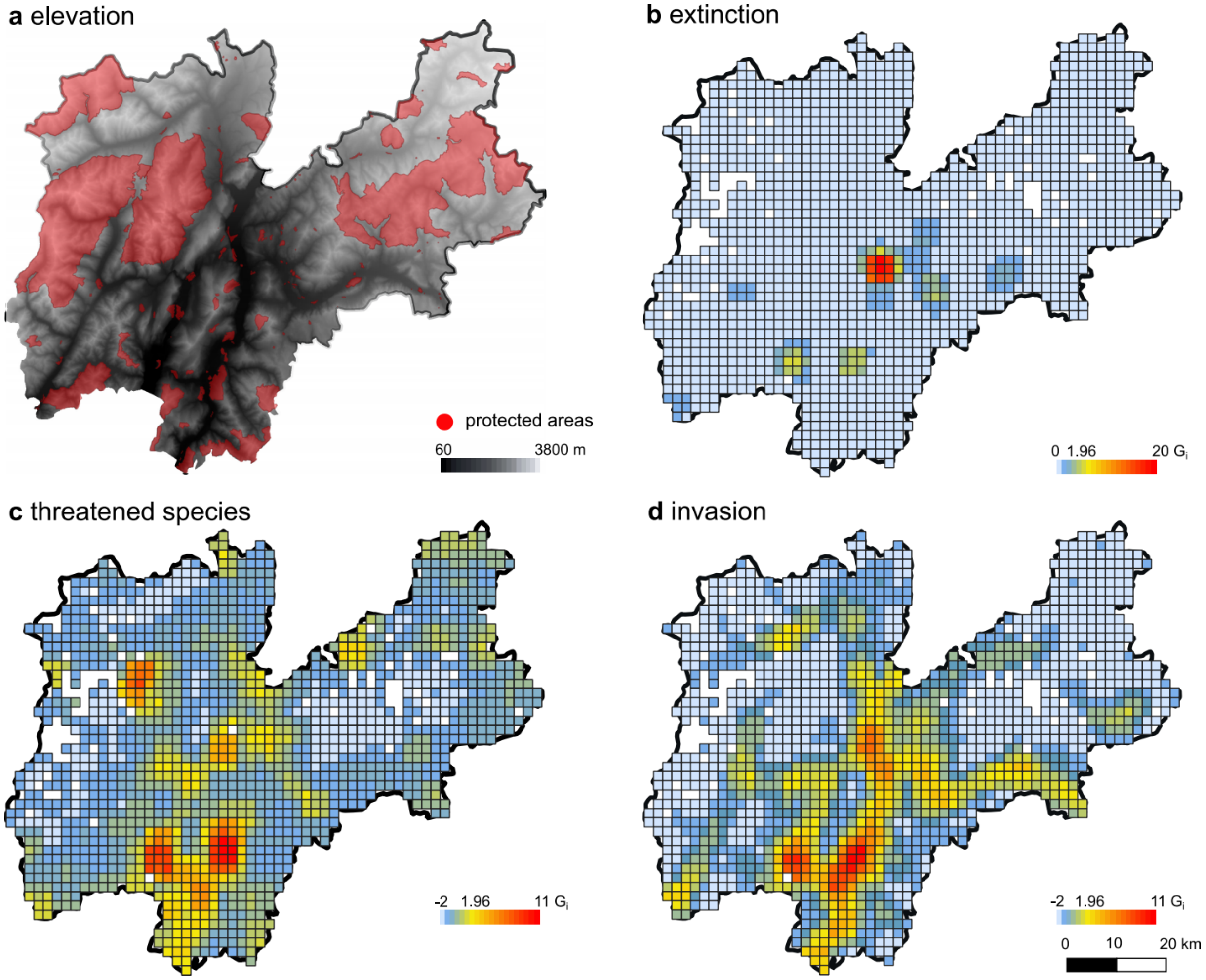

Figure 3: a) Digital elevation model (25 × 25 m^2) for the study area (Province of Trento, NE Italy); hotspot maps (2 × 2 km^2) for b) regionally extinct species, c) threatened species occurrence and d) exotic species occurrence. Colours show different values of the Getis-Ord G_i statistic from low (light blue) to high values (red). Getis-Ord G_i statistic values higher than 1.96 are considered statistically significant ($p < 0.05$).

Populations of regionally extinct, threatened and exotic species were mostly clustered in the same geographical locations (Figure 3). In particular, hotspots of historical extinctions and invasions of exotic species showed the highest spatial congruence (Pearson's correlation: $r = 0.60$; $p < 0.001$, Supplementary Figure D3). Most of the hotspots were associated with highly urbanized, low elevation areas, while intermediate and high elevations were usually characterized by a low concentration of extinct, threatened and exotic species (Figure 4). In particular, all hotspots sharply disappeared above 1000 m a.s.l. The only exception was for threatened species that showed secondary hotspots above 2500 m a.s.l. The latter consisted of hotspots of rare endemic species adapted to the harsh conditions of Alpine calcareous mountains. The spatial overlap between extinction risk and exotic invasions is likely related to a response to common drivers, while we could not identify a causal relationship between the two processes. In our study area, elevation can be considered a good proxy for intensive land-uses. In particular, we found a negative correlation between elevation and agricultural land (Pearson's correlation r = -0.57, $p < 0.001$), and urban areas (Pearson's correlation r = -0.52, $p < 0.001$). We also found that the rate of soil loss in the last two decades was higher in hotspots than in the remaining areas (Mann-Whitney test $p < 0.001$ for regionally extinct, threatened and exotic species), indicating an on-going intensifying use of low elevation areas.

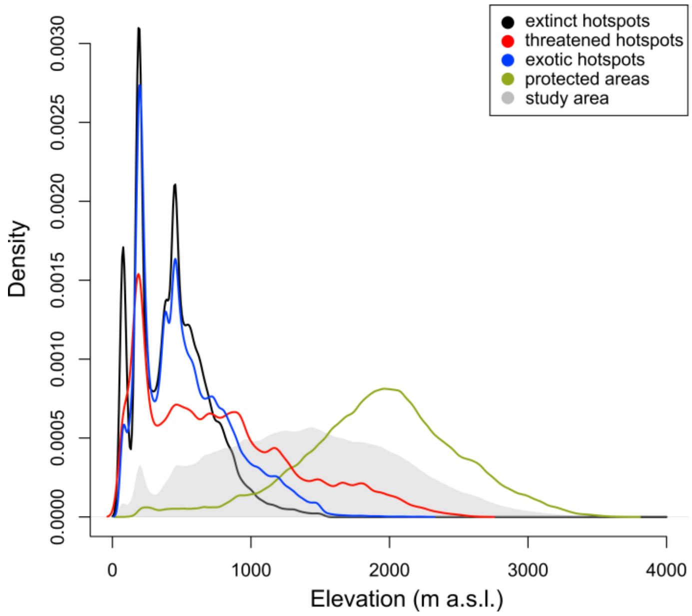

Figure 4: Density function at the regional scale of the elevational distribution of hotspots for extinct (black), threatened (red), exotic (blue) species, protected areas (green) and the whole study area (grey). Data on protected areas come from regional land-use maps (see Methods).

After identifying the hotspots, we overlaid the existing network of protected areas to verify the current degree of regional protection. A large extent of total hotspot area of threatened species (53%) resulted to be under protection. However, the existing network of protected areas covered only 5% of extinct species hotspots, suggesting that there might be a potential conflict between biodiversity conservation and economic development (Enquist et al. 2019). On the one hand, intensive land-uses such as agriculture and urban areas are expected to threaten native species due to habitat loss and deterioration (Pimm et al. 1988; Sala et al. 2005; Geppert et al. 2020). On the other hand, the same processes are known to favour exotic invasions mainly through soil disturbances (Tattoni et al. 2017; Rumpf et al. 2019b). The observed high spatial congruence of exotic invasions and native extinctions suggests that the lowlands are experiencing a rapid species turnover. In the last two centuries, we observed 53 regional species extinctions and 133 exotic naturalization of species mostly in agricultural lands and wetlands (Figure 2).

To gain insights into the potential causes leading certain species to become threatened or to become successful invaders, we first applied the Grime's C-S-R strategy classification and used the Grime’s competitor component that measures the ability of plant species to thrive under high resource conditions by outcompeting neighbouring plants (see Methods for details on the classification) (Grime 1979; Pierce et al. 2017). If competition was a key driver of species decline and exotic success, the competitor component should covary with the extinction risk (i.e. red-list categories). As a benchmark, we also estimated the average competitor score of common native species. Extinct species showed the lowest competitor score (Figure 5a). By contrast, exotic species were characterized by the highest competitor score probably due to the combination of several traits enabling them to rapidly use resources, such as high relative growth rate, short leaf-life, and high allocation to leaf construction (Van Kleunen et al. 2010). Threatened species exhibited intermediate competitor scores that, however, were lower than those of common and exotic species. We also found a trend for increasing competitor scores with declining levels of extinction risk, suggesting that competitive interactions might play a fundamental role in determining species success under global change (Lembrechts et al. 2015; Alexander et al. 2015). Species with poor competitor abilities usually thrive in unproductive habitats with severe environmental conditions such as shortage of light, water, or nutrients, while a strong competitor strategy becomes advantageous when habitats are rich in resources. Hence, plants with a low competitor score are expected to be particularly vulnerable to anthropogenic land use change (Prévosto et al. 2011; Sykes et al. 2020).

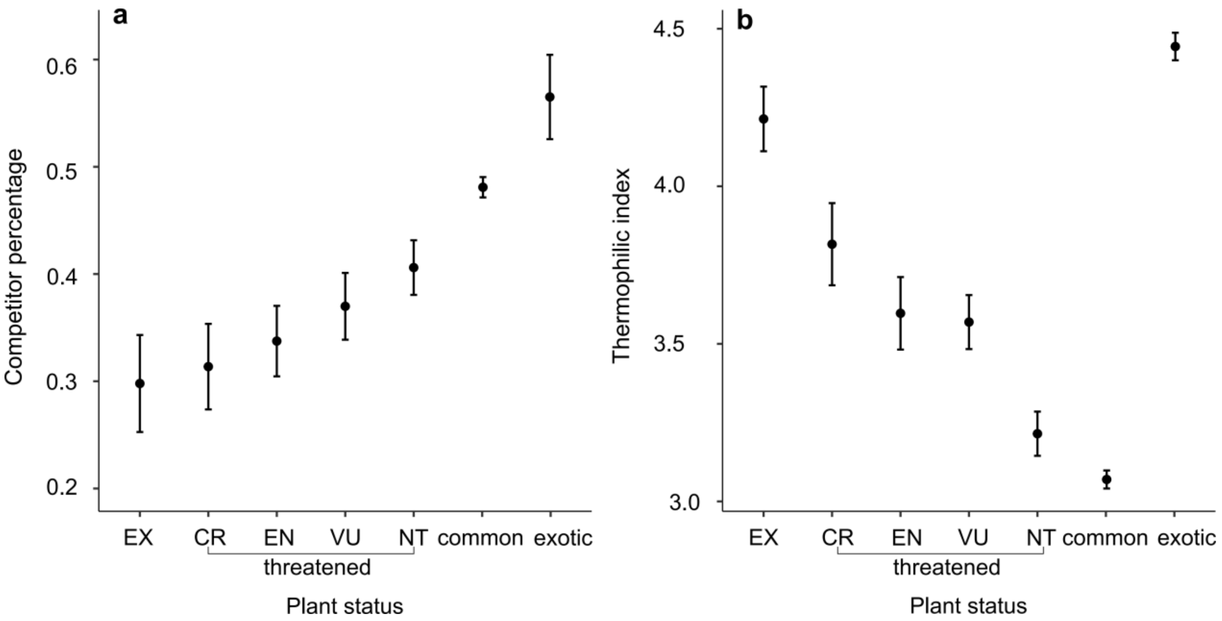

Figure 5: a) Grime competitor score and **b)** thermophilic index for extinct, threatened, and common native and for exotic species (mean ± SE). Grime competitor score varies between 0 (very poor competitor) and 1 (strong competitor). Thermophilic index varies between 1 (alpine-nival plants) and 5 (very warm-colline species). Red list categories are EX (extinct species), CR (critically endangered species), EN (endangered species), VU (vulnerable species), NT (near-threatened species

Second, if climate warming was a key driver of species extinction risk, cold-adapted species should be overrepresented among the red-list categories with the highest extinction risks. However, we found an opposite pattern with a negative relationship between extinction risk and thermophilic index (Figure 5b). Extinct species resulted to be the most warm-adapted species, while species listed as near threatened and common species were adapted to colder conditions. As expected, exotic species exhibited the highest thermophilic index. Theoretically, climate warming should favour warm adapted species, but here, besides exotic plants, the most thermophilic species were also the most threatened. This pattern might indicate that land use superseded climate change effects (Sala 2000; Díaz et al. 2019). Habitat destruction and land-use changes, mainly induced by urbanization and agriculture, are indicated as the major causes of plant extinction worldwide (Roux et al. 2019). Here, especially at low elevations, where human activities are at their highest, habitat alteration, fragmentation and loss threaten with extinction species that are not able to quickly exploit resources and to compete with their neighbours.

Conclusions

Here, we showed for the first time a spatial explicit analysis of the response to global change of both threatened native and exotic plants in a diversity hotspot of the European Alps. We found that exotic species are spreading upwards, while threatened native species are experiencing a strong erosion of their rear margins. Native plant species at low elevations resulted to be those more at risk of extinction mainly due to on-going land use changes. In accordance with recent studies (Roux et al. 2019; Díaz et al. 2019), our results suggest that increased disturbance and eutrophication induced by intensive land-use might be more important drivers of extinction than temperature warming in the short-term. In addition, in the lowlands, exotic species might displace some threatened plants with low competition ability, while invasive impact is milder at mid and high elevations because exotic plants are still strongly associated with areas below c. 1000 m a.s.l. We found that a large share of hotspot area of threatened species is under protection compared to hotspots of extinction events and invasions. However, currently, around 80 % of protected areas in the study region are established at elevations above 1500 m a.s.l. (Figure 3). We advocate that protection should also move to the lowlands to curb habitat deterioration and loss, thereby enabling the survival of threatened populations. However, conflicts with economic development exist, because most income generating activities in the European Alps are confined to low elevation areas. In contrast to the lowlands, the combined action of protection, less frequent human activities and colder temperatures makes high elevation areas a safer place for native plants. Even if in the future endemic alpine plants might be increasingly threatened by climate warming (Gottfried et al. 2012), they do not appear to be at immediate risk and, therefore, we should prioritize the lowlands for implementing more urgent conservation measures. Finally, one should bear in mind that plants usually exhibit large extinction debts, therefore effects of invasions, climate change and landscape transformations by agriculture and urban development could last for hundreds of years (Dullinger et al. 2012a; Catford et al. 2018; Roux et al. 2019). Hence, it is crucial to preserve relict populations of threatened plants in the lowlands areas and to implement mitigation measures outside the current network of protected areas to reduce potential plant extinctions in the future.

Chapter 5.

Consistent population declines but idiosyncratic range shifts in Alpine orchids under global change

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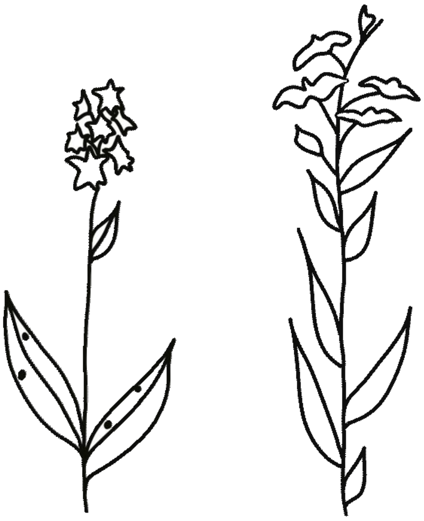

Abstract

Mountains are plant biodiversity hotspots considered particularly vulnerable to multiple environmental changes. Here, we quantify population changes and range-shift dynamics along elevational gradients over the last three decades for c. two-thirds of the orchid species of the European Alps. Local extinctions were more likely for small populations, after habitat alteration, and predominated at the rear edge of species' ranges. Except for the most thermophilic species and wetland specialists, population density decreased over time. Declines were more pronounced for rear-edge populations possibly due to multiple pressures such as climate warming, habitat alteration, and mismatched ecological interactions. Besides these demographic trends, different species exhibited idiosyncratic range shifts with more than 50% of the species lagging behind climate warming. Our study highlights the importance of long-term monitoring of populations and range distributions at fine spatial resolution to be able to fully understand the consequences of global change for orchids.

Introduction

Mountain ecosystems harbour a high rate of endemic and rare plant species that are considered particularly vulnerable to climate change (Gottfried et al. 2012). While a large body of research has elucidated how plants respond to temperature warming by shifting their range(Kelly and Goulden 2008; Dainese et al. 2017; Lamprecht et al. 2018), significant knowledge gaps still remain. First, there is growing evidence that range shifts can lag behind climate change for several decades due to the ability of plants to persist under unfavourable conditions, dispersal limitation, or lack of suitable habitats (Bertrand et al. 2011; Dullinger et al. 2012b; Rumpf et al. 2019a). Declines in population density stemming from changes in mortality and fecundity rates are expected to precede range shifts (Pauli et al. 2007; Cannone and Pignatti 2014) and even when demographic changes are dramatic, they may often go undetected due to the lack of long-term monitoring data (Pounds et al. 1997; Beaugrand et al. 2003). Second, current methodological approaches such as resurveys of permanent sites or species distribution modelling are often limited to common and abundant taxa, overlooking the response of rare species (Rumpf et al. 2019a). Third, previous research has mostly focused on population dynamics at mountain tops, where warm-adapted species are expanding their distributions but cold-adapted species tend to decline in abundance or to go extinct due to climate warming (Lehikoinen et al. 2019). There is also an urgent need to consider the dynamics of species at the rear, low-elevation edge of their distributions (Lenoir and Svenning 2013; Rumpf et al. 2018), where the pressures of global change are likely to be stronger and the effects of climate warming are less predictable due to the co-occurrence of multiple drivers of plant distribution (Nogués-Bravo et al. 2008).

Besides climate warming, mountain ecosystems have experienced rapid habitat transformations such as forest expansion, increased urbanization and invasion of exotic species (Dainese et al. 2017; Carboni et al. 2018), with potentially negative consequences for resident plant communities. In the European Alps, a major trend is the abandonment of remote and less productive areas at mid-elevations and above (Tattoni et al. 2017). Human activities directly shape the elevational distribution of habitats, often irrespective of the direction and speed of climate change (Nogués-Bravo et al. 2008; Mair et al. 2014). As a result, climate warming may cause a spatial mismatch between suitable climatic conditions and habitat availability (Opdam and Wascher 2004; Troia et al. 2019; Elsen et al. 2020). Under these circumstances, habitat distribution and quality are expected to play a central role in explaining local population dynamics and climate–induced range shifts (Lenoir and Svenning 2015; Guo et al. 2018b; Freeman et al. 2018; Platts et al. 2019; Dullinger et al. 2020), in particular for specialist, rare, and threatened species whose range shift dynamics are likely to be most sensitive to the elevational distribution of suitable habitats.

Here, we analysed population survival, trends in population size, and range-shift dynamics of Alpine orchids over 28 years across the whole elevational range (66-2970 m) in one of the plant diversity hot-spots of Europe (Italy, Trentino) (Fig. 1). Orchids are one of the most threatened groups of plants, and population declines are well documented worldwide (Kull and Hutchings 2006; Wraith and Pickering 2019; Phillips et al. 2020; Wraith et al. 2020) (but see (van der Meer et al. 2016) for a positive effect of warming on orchid populations). These declines are usually associated with land-use intensification or habitat loss (Vogt-Schilb et al. 2015, 2016), coupled with the loss of mutualistic interactions with mycorrhizal fungi and pollinators (Wraith and Pickering 2019). Moreover, plant species in the southern European Alps are expected to shift upwards with a rate of 3.8-5.5 m year^{-1} to keep track of recent rates of warming (Dainese et al. 2017). We used multiple datasets containing a very large number of both occurrence records and population data for taxa that are normally disregarded due to their rarity and scattered geographical distribution. First, we combined historical data with a field re-survey campaign to elucidate the mechanisms underpinning orchid population persistence under global change. Second, we quantified both orchid demographic trends and shifts in the optimum, rear and leading edge of species' elevational ranges. Here, we show that orchid populations at the rear edge and in sites undergoing habitat alteration were more likely to suffer local extinctions. Similarly, population size declined at the rear edge of the elevation range in most habitat types, contributing to increased local extinction risk. Besides these consistent population declines, different species exhibited idiosyncratic range shifts with upward, downward and no movement, suggesting that temperature was not the sole factor driving range dynamics. Despite some upward shifts, the interspecific variability in range dynamics meant that most species did not shift their range uphill as fast as rates of warming.

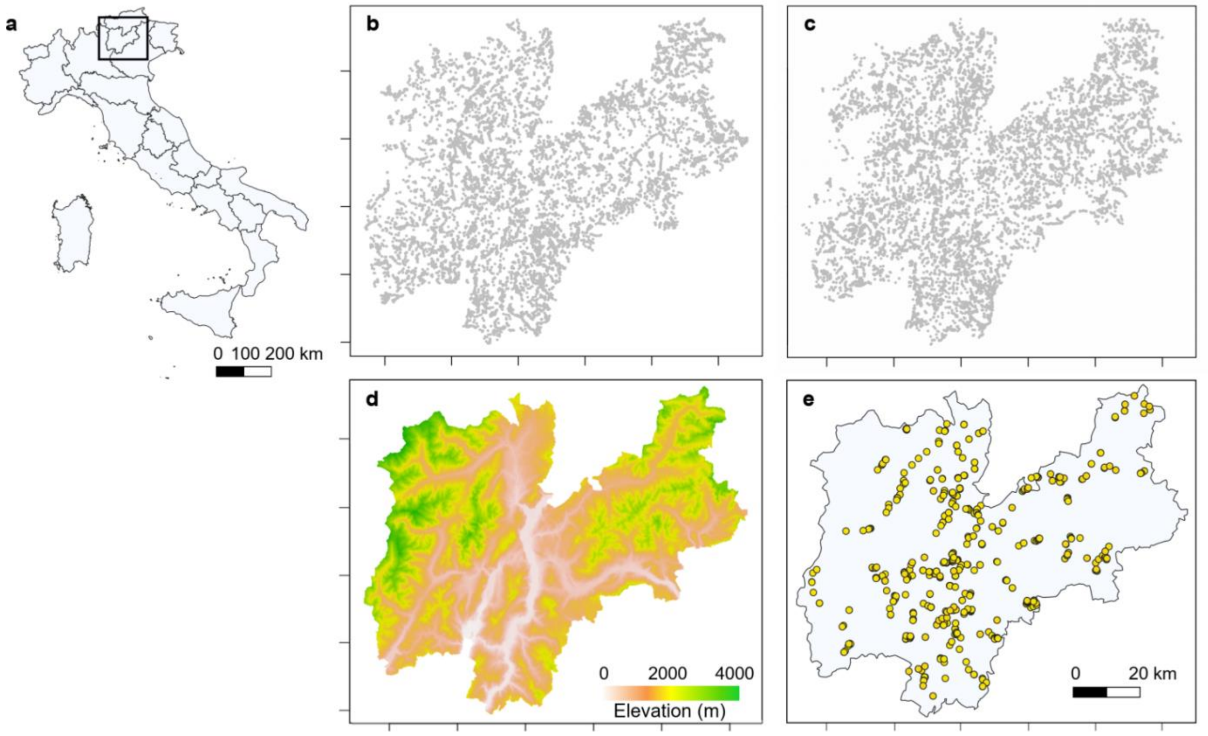

Figure 1: Geographical description of the datasets a) Location of the study area; b) geographical distribution of the sites (grey dots) over the first period (1990-2003: n = 10,293) and c) the second period (2004-2017: n = 11,308); d) digital elevation model of the study area (resolution: 25 x 25 m); and e) location of the 463 resurvey sites (yellow points).

Materials and Methods

Study area

Orchid populations were sampled throughout the Trento Province, NE Italy (6207 km^2, elevation range 66-3769 m) (Fig.1). The region is located in the centre of the European Alps, and represents a hot-spot of plant species diversity, including species whose geographic ranges are Alpine, central and northern European, and Mediterranean (Aeschimann et al. 2004).

Climate change

Climate in the region depends primarily on elevation: it is alpine at high elevations and continental in the lowlands. Maximum annual temperature between 1980 and 2010 was 17.5 °C and minimum 7.8 °C (at 200 m a.s.l.) (Di Piazza, A., & Eccel 2012). In Trentino, mean temperatures increased by ca. 0.75°C between 1981 and 2010 (Di Piazza, A., & Eccel 2012). A stronger temperature increase was measured during the growing season (spring and summer). A previous study in the region indicated that a vertical spread rate from 3.8 m year^{-1} to 5.5 m year^{-1} is necessary for species to be able to fully track climate warming (Dainese et al. 2017). Precipitation is abundant throughout the year, and mean annual precipitation over the last 40 years was 1050 mm. Annual rainfall slightly increased between 1981 and 2010 (+2%), but decreased in winter (-6%) (Di Piazza, A., & Eccel 2012).

Land-use

The availability of the major habitat types for orchids is influenced by land-use at different elevations. To describe the current elevational distribution of these major habitat types, we used the most accurate land-use maps available. We used data from the 2009 regional land-use map for alpine habitats, forests and wetlands (2009). For the extent of semi-natural grasslands in 2009, we used a detailed map provided by the Rovereto Museum (provided by FP and AB). We converted vectorial layers of each habitat into a raster layer with a grain of 50 x 50 m. Then, for each habitat layer we extracted the elevation of each pixel (50 x 50 m) and created a density plot in order to evaluate the regional availability of each habitat type over the elevational gradient (Supplementary Fig. E1). The lowlands were dominated by urban elements and intensively cultivated areas with fragmented semi-natural grasslands (extensively-managed or recently-abandoned meadows). These habitats historically replaced the native forest vegetation at lower elevations. At mid-elevations, forests interspersed with managed grasslands covered mountain slopes. Above the tree line (1800-2000 m a.s.l.), the landscape was characterized by subalpine grasslands and rocky and snow-covered ground. Wetlands did not exhibit any clear elevational distribution patterns. The study area has experienced two major land-use changes in recent decades. First, forests increased downwards at the expense of open semi-natural areas at mid-elevations (approximately between 600-1500 m) due to land abandonment (Tattoni et al. 2017). Currently, forests cover c. 60% of the territory. The abandonment of traditional agriculture is closely linked to demographic changes: human population has decreased above 600 m, and has increased in the lowlands. Second, agriculture expanded upwards from the lowlands to mid-elevations (up to c. 850 m): the leading edge of grape (c. 750-850 m) and apple cultivation (c. 1000-1100 m) moved upwards in the last two decades (Monteiro et al. 2011; Eccel et al. 2016). These two ongoing changes, of increased direct anthropogenic pressure at low elevations, and reduced pressure (abandonment) at mid-elevations, each imposed direct increasing constraints on habitat availability for orchids associated with open areas.

Historical orchid surveys (1990-2017)

In total, the historical database included 50,074 records belonging to 60 orchid species spanning an elevational gradient from 66 to 2,970 m over 28 years (1990-2017) (Fig. 1). However, we present results from analyses of 21,601 sites and 49,303 records for 44 species that meet our criteria for inclusion in the study, i.e. at least 30 records in the first 14 years (1990-2003) and last 14 years (2004-2017) of the historical dataset. Giorgio Perazza (GP) and collaborators collected data by sampling the 21,601 sites, systematically covering the whole area of Trento Province. Each site was visited only once. Having identified a potentially suitable area in the field (i.e. natural or semi-natural habitats corresponding to open grassland, wetland or the woodland understorey), using a GPS they marked the site (point), recorded all the orchid species occurring in the close surroundings (c. 50 m), and counted the number of individuals per species. The general small size of orchid populations and the patchy distribution of individuals allowed estimates of population size in the field with relatively low uncertainty. The only exception was when populations were very large. However, the frequency of populations with size above 100 individuals was only 4%. The aims of the sampling were to describe the regional orchid species distributions at a very fine spatial resolution, and to provide a network of sites to investigate orchids' population dynamics. The sites were not physically marked as true permanent plots but the centre of each site was georeferenced using a GPS (c. 5-10 m precision) and high-resolution topographical maps. The average density of sample sites was c. 4 per km^2, including in the count areas where no orchids are usually found (e.g. industrial areas, urban fabric, roads, construction sites, water bodies, cliffs etc.) (Fig.1). The database is unique in describing the regional distribution of a rare, highly diverse and threatened group of plants because of its massive sampling effort compared to the relatively large spatial and temporal extent, spanning almost three decades. Moreover, the dataset covered c. two-thirds of the orchid species occurring across the European Alps (Aeschimann et al. 2004). At each site, the following variables were also collected: date of sampling, elevation, detailed site description (vegetation, proximity to roads or constructions etc.) and slope. Nomenclature follows Perazza & Lorenz (2013). All the data were stored in the private database of GP and in the GIS-inventory database of the Museo Civico di Rovereto (Rovereto, Trento, Italy).

Resurveys (2018-2019)

To detect local extinction of historically recorded populations, we selected a subset of sites to resurvey orchid populations starting from the database described above. The selection of the sites was performed using a stratified random sampling in a GIS environment (QGIS, version 3.6.1-

Noosa). The strata were the four major habitat types occurring across the elevational gradient: forests, subalpine areas, semi-natural grasslands and wetlands. Further criteria of site selection were: 1) to include the whole elevational distribution of each resurveyed species, 2) to exclude sites with the occurrence of a single individual, 3) to cover most of the geographical area of the historical survey. We revisited 463 sites in all major habitat types, covering the whole elevational range of orchid distributions from the lowlands to high elevation natural areas. Of the final 463 sites, 167 were classified as forests, 53 as subalpine/alpine natural habitats, 198 as semi-natural grasslands and 45 as wetlands. Usually, resurvey studies are constrained by the quality of the baseline data (e.g. relocating the sites), the need to maintain consistent taxonomy, and observer effects (e.g. detecting rare species) (Verheyen et al. 2017). In spring and summer 2018 and 2019, GM and CG revisited the 463 sites following the sampling methodology of the first observer (GP), who constantly helped verifying baseline data, confirming species identification, relocating the sites and assessing habitat alterations. The sites were only visited once either in 2018 or in 2019. The re-survey was performed by actively searching the whole area around the sites surveyed in the historical survey (c. 50 m around the originally referenced point). Orchid species and number of individuals were recorded. Along with the orchid data, the following parameters were recorded: date, elevation, habitat type, and description of any local alteration occurred between the two periods. For the latter, we reported if a local disturbance (e.g. construction sites, touristic activities) or a habitat type change occurred in the second survey by comparing the description of the sites in the initial survey with the current conditions.

Orchid habitat preference

We attributed each orchid species to one of six, non-overlapping categories using the description of habitat preferences according to Perazza & Lorenz (2013) (n = 49 species, Supplementary Table E1). We considered the following categories: 1) specialists of shrubland, broadleaf and conifer forests (forest, n = 12 species), 2) generalist species able to colonize both forests and grasslands (generalist, n = 9 species), 3) species able to colonize grasslands from low elevations to alpine habitats (grassland, n = 6 species), 4) specialists of grasslands below the tree-line including mown meadows, abandoned grasslands, grass margin, extensive perennial crop areas such as vineyards and olive groves (semi-natural grassland, n = 5 species), 5) specialists of subalpine open habitats, i.e. rocky habitats, alpine and subalpine grasslands (subalpine, n = 5 species), and 6) specialists of wetlands, e.g. fens, mires, ponds (wetland). Due to the well-known habitat specialization of Alpine orchids, there was little uncertainty in the category attribution. To provide an ecological characterization of the habitat categories, we derived for each species Landolt's indicator values

(Landolt et al. 2010) (Fig. 2) for light, temperature, and soil moisture. For each orchid species, we also quantified the realized thermal niche breadth using MAT (mean annual temperature) recorded over 1981-2010 from 21 weather stations in the study area. First, we interpolated the missing temperature values on a layer with 25 m^2 resolution with the function regression kriging on SAGA using as auxiliary variable elevation obtained from the DEM (digital elevation model) (EU-DEM Copernicus). Second, we computed coldest and hottest MAT experienced in the study area as 5% and 95% quantiles of the temperature density distribution. Finally, we calculated thermal niche breadth as the difference between these values. The thermal niche breadths characterize the realized thermal niches for orchid populations in the study area while they are not descriptive of the whole range of temperatures enabling their survival and reproduction.

Statistical analyses

Local survival based on resurveys

We analysed orchid probability of survival across 463 sites, where species were observed in the initial surveys. The response variable was binary assuming the value 1 when the second resurvey reconfirmed the occurrence and 0 when the species was absent. We fitted a GLMM with a binomial distribution with species as random factor. We tested as fixed effects time (difference between the year of the initial and second survey, average difference = 20.5 years, SD = 8.4 years), historical population size (number of individuals in the initial survey), habitat alteration (yes or no), the categorical variable of species habitat preference, and elevation. Within each species, elevation was standardized to mean 0 and SD =1 to make the elevational distribution comparable among species and to test whether populations tended to disappear more often at the rear edge than towards the core or upper part of the elevational distribution. This test was valid as the site selection in the re-survey was done to cover the whole elevational distribution of the species included in the analyses. To assess possible collinearity issues between fixed effects, we estimated variance inflation factors (VIFs). VIFs were close to c. 1, indicating very little collinearity among predictors (Akinwande et al. 2015). To match species phenology between the initial and the second survey, we excluded observations with more than 30 day differences between survey dates. The use of smaller or larger thresholds did not qualitatively change the results. Moreover, we excluded species recorded less than 5 times in the initial survey (n = 43 species), and sites revisited after less than 5 years. We present results from the full models. We also performed model simplification by removing with a backward deletion procedure non-significant variables ($p > 0.10$). Model estimates between full and reduced models were stable. Recent advances in Bayesian statistics provide efficient methods to model extinction-colonization dynamics (Kéry et al. 2010). However, these methods rely on the availability of repeated samplings in the same survey period to estimate detectability probabilities. It is important to stress that we had only one visit per period and that our analysis did not focus on estimating real extinction–colonization rates but rather on testing the relative role of different environmental drivers or species traits in explaining population dynamics. Any potential bias in the detectability of the species in the two periods (e.g. different ability between the observers, relocation of the sites) is not expected to be related to any of the tested variables and, therefore, should not influence the conclusions of our analyses.

Temporal trends in population size

To test the effect of time and elevation on orchid population size, we used Generalized Linear Mixed Models (GLMMs). Within each species, we standardized elevation to mean 0 and SD = 1 to make the elevational distribution comparable among species. We ran separate models for each habitat preference category and considered only species with at least 30 records in the first 14 years (1990-2003) and last 14 years (2004-2017) of the historical dataset (n = 44 species). We fitted as fixed effects time (continuous), elevation and their interaction using population size as the response variable. Since population size was a count we used a Poisson distribution. As we expected that population size should be maximum at a thermal or habitat optimum for each species and then decline towards higher and lower elevations, we included the quadratic term of elevation. In all models, we added species as a random intercept and, to correct for overdispersion we used an observation-level random effect (OLRE) crossed with species (Harrison 2014). OLRE models the extra-Poisson variation in the response variable by using a random intercept with a single level for each data point.

Range shifts

Rates of shift in the elevational distribution of species, i.e. changes in optimum, rear (low-elevation) and leading (high-elevation) edge were computed similarly to Rumpf et al. (2018). To quantify the shift between the recent historical (hereafter “historical”) and current range we split the dataset into two periods of 14 years (1990-2003 and 2004-2017). We used time as categorical for two reasons: 1) to minimize the potential bias of botanist sampling effort along the elevation gradient, 2) to obtain solid density distributions to estimate shift of leading and rear edge. Estimating shift at the edge is particularly challenging and therefore pooling 14 years of data allowed to reduce the uncertainty. For each species with more than 30 records per period, we estimated a density distribution of the elevation of occurrence for the first and second period, separately (n = 44 species). The rear and leading edge were calculated as the 5% and 95% quantiles of the density distribution, and the optimum as the highest peak of the density distribution. The shift was measured by subtracting historical (1990-2003) from current (2004-2017) measures of elevational range. We divided the total shift by 14 years to obtain an annual rate.

To test the effect of habitat preference on the observed shift rates, we fitted three general linear models assuming a Gaussian distribution, testing whether species with different habitat preferences exhibited different mean range shift rates at the rear edge, optimum and leading edge separately. In addition, we carried out post hoc pairwise comparisons using the Tukey HSD with the R package multcomp (Hothorn et al. 2007) to show the differences at rear edge, optimum and leading edge between habitat preference categories. For each species, to further understand where and how the elevational distribution changed in the two periods, we compared the distribution in the historical period with that in the current using the function "qcomhd" of the R package WRS2 (Benjamini and Hochberg 1995; Mair and Wilcox 2020). This function compares deciles estimated from two independent density distributions using a percentile bootstrap to calculate confidence intervals and, therefore, it enables a detailed comparison of shifts along the elevational range. For each species, the analysis can quantify the shifts of the single deciles and if these shifts are different from 0 using bootstrapped intervals of confidence. Low, medium and high deciles approximated rear, optimum and leading edge, respectively. In addition, we tested whether the distribution changed between the historical and the current period using the non-parametric Kolmogorov-Smirnov (K–S) test and adjusting the p-values with the Benjamini-Hochberg correction. Species showing a significant or marginally significant shift according to the K-S test were the same that showed a significant difference between deciles.

Potential sampling bias

Since we did not have a fixed network of sites in the two periods, non-random sampling effort across the study region could have biased the estimates of range shift rates (Aikio et al. 2010). To account for these potential problems, we first described the spatio-temporal patterns of sampling effort. There were roughly the same number of sites sampled in the two periods (10,293 vs. 11,308). We also checked the elevational distribution in each period for all sites, and separately for the major habitat types. These analyses did not reveal any strong bias in sampling effort (Supplementary Fig. E2). Our approach of splitting the time series in two periods aimed at comparing two large survey campaigns where sampling was close-to-random in space and time. Second, using the resurvey data from 2018–2019, similarly to Rumpf et al. (2018), we estimated range shift rates for a subset of species (n = 20) for which we had at least 10 records in the first and 10 records in the second survey. This approach estimated the rear and leading edge and the optimum using the density distribution based on a spatially fixed network of sites. We calculated shift rates as the difference between current and historical rear edge/optimum/leading edge divided by the average time elapsed between the two surveys within each species (Supplementary Table E4). Then, we checked the correlation between range shift rates obtained with the two methods. We found a positive and strong correlation between observed shift rates based on the whole dataset and shift rates based on resurveys for the rear shift ($r = 0.71$, $p < 0.01$). For shifts at the leading and optimum the correlation was still positive but weaker ($r = 0.38$, $p = 0.10$; $r = 0.39$, $p = 0.09$, respectively). Based on the analyses of sampling effort and on the comparison between observed shift rates on the whole dataset and shift rates on resurveys, we decided to present the range shifts at rear, leading and optimum positions obtained on the whole dataset.

Software for statistical analyses

All models were run using generalized linear mixed models (GLMMs) or generalized linear models (GLMs) implemented in the package “MASS”(Ripley et al. 2010) and “lme4” (Bates et al. 2015) while model assumptions were visually evaluated using quantile-quantile plots of the residuals and plots depicting residuals vs. predicted values in the packages “DHARMa” and “car” for R 3.5.1(R Core Team 2017).

Results & discussion

Orchid habitat preference

As most orchid species are specialists with clear preferences for a particular habitat type (Wraith and Pickering 2019), we first attributed each species to one of six, non-overlapping categories using a published description of habitat preferences (Perazza et al. 2013) (see Methods for details): 1) specialists of forest (forest), 2) generalists, 3) specialists of grassland habitats with wide thermal niche (grassland), 4) warm-adapted specialists of semi-natural grassland (semi-natural), 5) cold-adapted specialists of subalpine habitats (subalpine), and 6) specialists of wetlands (wetland) (Supplementary Table E1). These habitat preference categories drew together species with a similar ecology and elevational distribution. All orchid species were adapted to open areas and therefore to full light except for forest orchids and generalists (Fig. 2a). Wetland orchids were the only group associated with wet soil conditions (Fig. 2b).

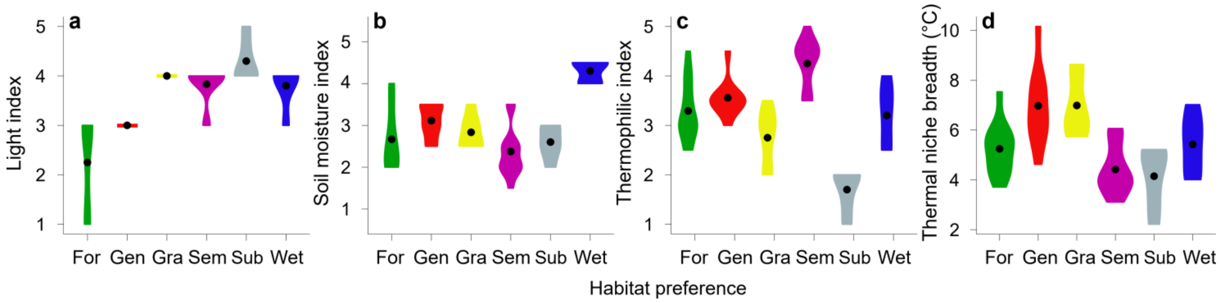

Figure 2: Ecological characterization of habitat preference categories. Landolt ecological indicator values[60] for a) light (from very shady: 1 to very bright: 5); b) soil moisture (from very dry: 1 to flooded: 5); c) temperature (from alpine: 1 to very warm: 5); and d) realized breadth of the thermal niche in the study area based on annual mean temperature. Habitat preference categories: Forest (For), Generalist (Gen), Grassland (Gra), Semi-natural grassland (Sem), Subalpine (Sub), Wetland (Wet). Violin plots were drawn using the geom_violin() function with default settings in the ggplot2 package in R. Points represent medians.

Consistent with their elevational distribution (Fig. 3), subalpine orchids were cold-adapted species, while species occurring in semi-natural grasslands were the most thermophilic across their geographic ranges (Fig. 2c). The remaining four groups preferred intermediate temperatures found at mid-elevations across the study area, with generalists and species living in grasslands being characterized by the widest breadth of thermal niches (Figs. 2c, 2d).

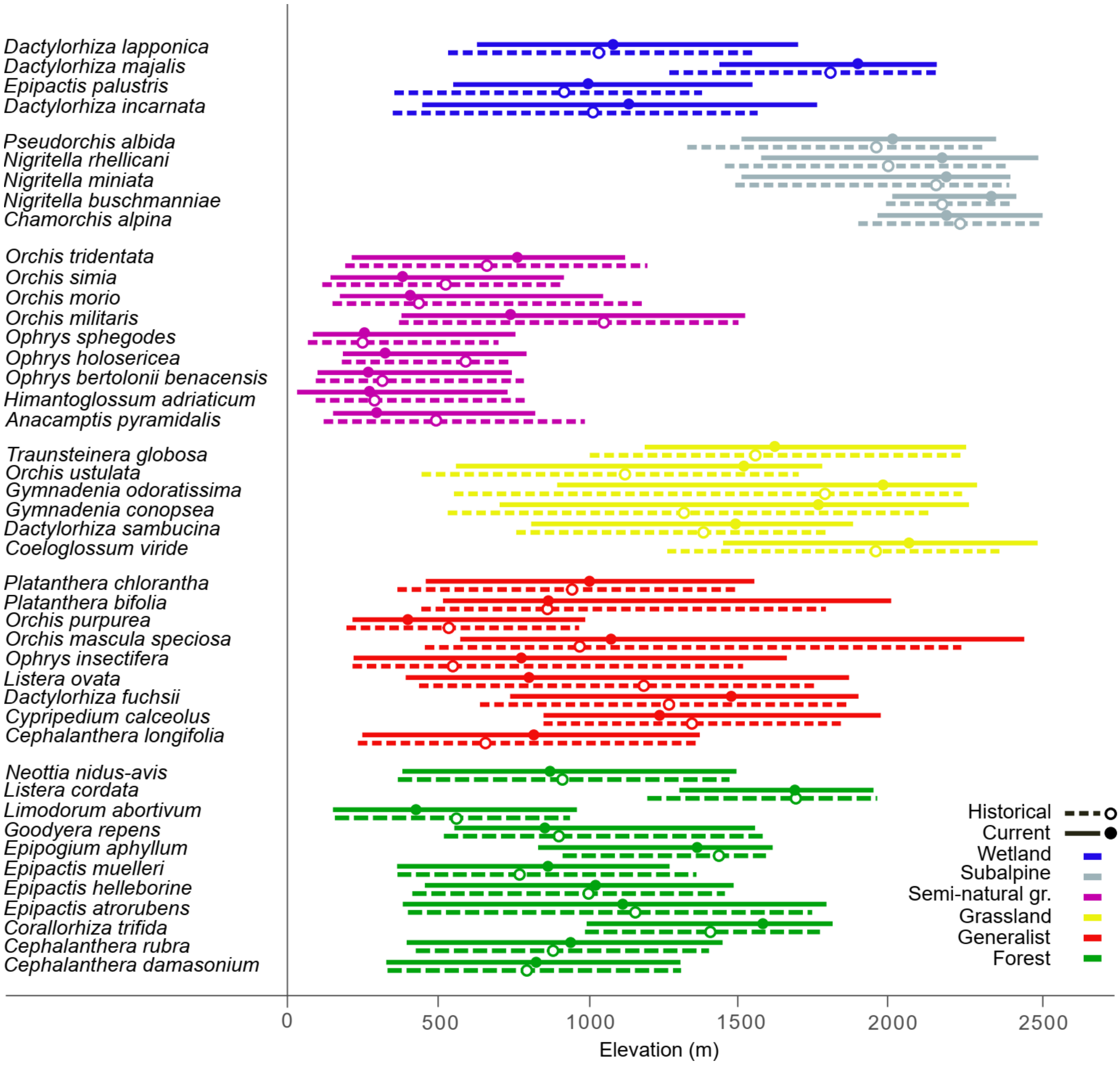

Figure 3: Orchid elevational distribution. Elevational distribution for the orchid species with at least 30 distribution records per period (historical, 1990-2003, and current, 2004-2017) pooled by habitat preference. Dashed bars represent historical (1990-2003) and solid bars current (2004-2017) rear (5%) and leading edges (95%), points represent optima (highest peak) of the density distribution.

Local survival based on resurveys

We analysed local population dynamics of species with different habitat preferences using a resurvey approach (see Methods). In 2018 and 2019, we revisited 463 sites to test for local habitat alteration and population survival since initial surveys (average difference = 20.5 years, SD = 8.4 years). Habitat alteration was observed in 37% of the resurveyed sites and included land-use changes (e.g. abandonment of grasslands and agricultural expansion) or local disturbances related to building infrastructure. Habitat alteration tended to be more likely at lower elevations (GLM binomial, $p = 0.063$). Orchid survival was explained by habitat alteration, elevation and historical population size, irrespective of habitat preference and time elapsed between the two surveys (Table 1, Supplementary Table E2). First, habitat alteration affected survival negatively with a probability reduction of c. 17% (Fig. 4a), supporting previous observations that land-use changes such as afforestation, urbanization and agricultural expansion are key drivers of orchid local extinction (Sletvold et al. 2013; Vogt-Schilb et al. 2016). In particular, the observed loss and degradation of semi-natural grasslands have been related to declines in plant specialists (Auffret et al. 2018). Second, orchid populations were less likely to survive if the population was located at the lower part of the species' elevational range (Fig. 4b). Biogeographical theory suggests that rear edge populations are at higher risk of extinction than populations at the core of the species' range as marginal populations occupy less favourable and deteriorating climates, and are also subjected to constraints including altered biotic interactions and deterioration of genetic diversity (Vilà-Cabrera et al. 2019). As our model controlled for the effects of habitat alteration, the lower probability of survival at the lowest elevations suggests that climate warming could have increased the risk of extinctions at low elevations. However, other factors such as loss of biotic interactions with pollinators and mycorrhizal fungi (themselves potentially related to climate or habitat degradation) could also contribute to the observed patterns. Third, we found a positive effect of historical population size (Fig. 4c), consistent with the predicted negative relationship between population size and extinction in fragmented plant populations (Matthies et al. 2004).

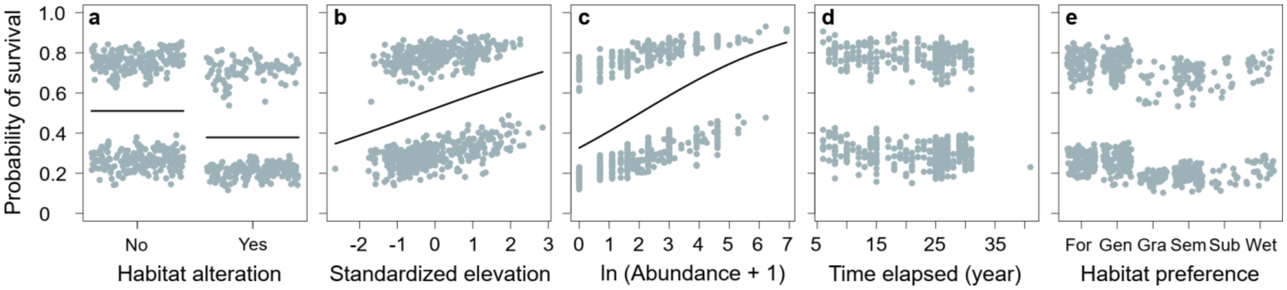

Figure 4: Biotic and abiotic drivers of local population extirpation. Partial residual plots showing the effect of a) habitat alteration; b) elevation; and c) population size on orchid probability of occurrence in resurveyed sites. Also non-significant effects of d) time elapsed between the initial and second survey and e) habitat preference were reported. Elevation was standardized to mean 0 and SD 1 to make elevational ranges comparable among species, i.e. the most negative values corresponded to the rear edge and the largest positive values to the leading edge. Plots were drawn using the visreg() function with default settings in the visreg package in R.

Table 1: Effect of time (difference in years between the two surveys), historical population size, elevation, habitat alteration (yes and no) and habitat preference on the probability that the orchid population survived until the resurvey. We fitted generalized linear mixed models assuming a binomial distribution with species as random factor (random intercept). Elevation was standardized to mean 0 and SD 1 to make elevational ranges comparable among species.

Fixed effects	χ^2	p
Time	1.220	0.269
log (Size)	35.189	<0.001
Elevation	8.906	0.003
Habitat alteration	9.600	0.002
Habitat preference	8.684	0.122

Temporal trends in population size

By testing the effect of time (continuous), elevation and their interaction, we quantified how local population size of orchids with different habitat preferences has changed over the last 28 years across the whole elevational range. To do so we used information from 21,601 orchid sites visited one time between 1990 and 2017. Consistent with the existence of a thermal optimum at mid-elevations, all species exhibited a hump-shaped relationship between elevation and local population size, except for wetland orchids that showed a weaker response (Table 2, Supplementary Table E3). Population size of most species decreased in recent years, but with differences among habitat preference categories, and for some categories at different elevations (Fig. 5). In accordance with an expected negative effect of warming at the rear edge (Vilà-Cabrera et al. 2019), population size at the lower elevational limits of forest (Time x Elevation p = 0.002), grassland (Time x Elevation p = 0.011) and subalpine species (Time x Elevation p = 0.043) declined more strongly than at the upper limits, where population size showed a less pronounced decrease (Figs. 5a, 5c, 5e). Populations of generalist orchids decreased (Fig. 5b), and, even if only with a marginal trend, their decline was also stronger at the rear than at the leading edge (Time x Elevation p = 0.066). This effect on population size is consistent with the higher probability of extinction at the rear edge observed in the re-surveys (Fig. 4b). Population size did not change over time only for two groups with contrasting climate and habitat preferences. Species associated with semi-natural grasslands (Fig. 5d) and species of wetlands did not decline (Fig. 5f). The former are the most thermophilic species

(Fig. 2) and presented a truncated realized thermal niche, i.e. if the lowest elevations in the study area corresponded to their temperature optimum, warmer temperatures may not have caused their decline. As most of the wetlands in the study region are located within protected areas (45% orchid populations occurring in wetlands are protected compared to an average of 25% for the other habitat types), the population size of these species may be maintained by habitat protection and favourable management.

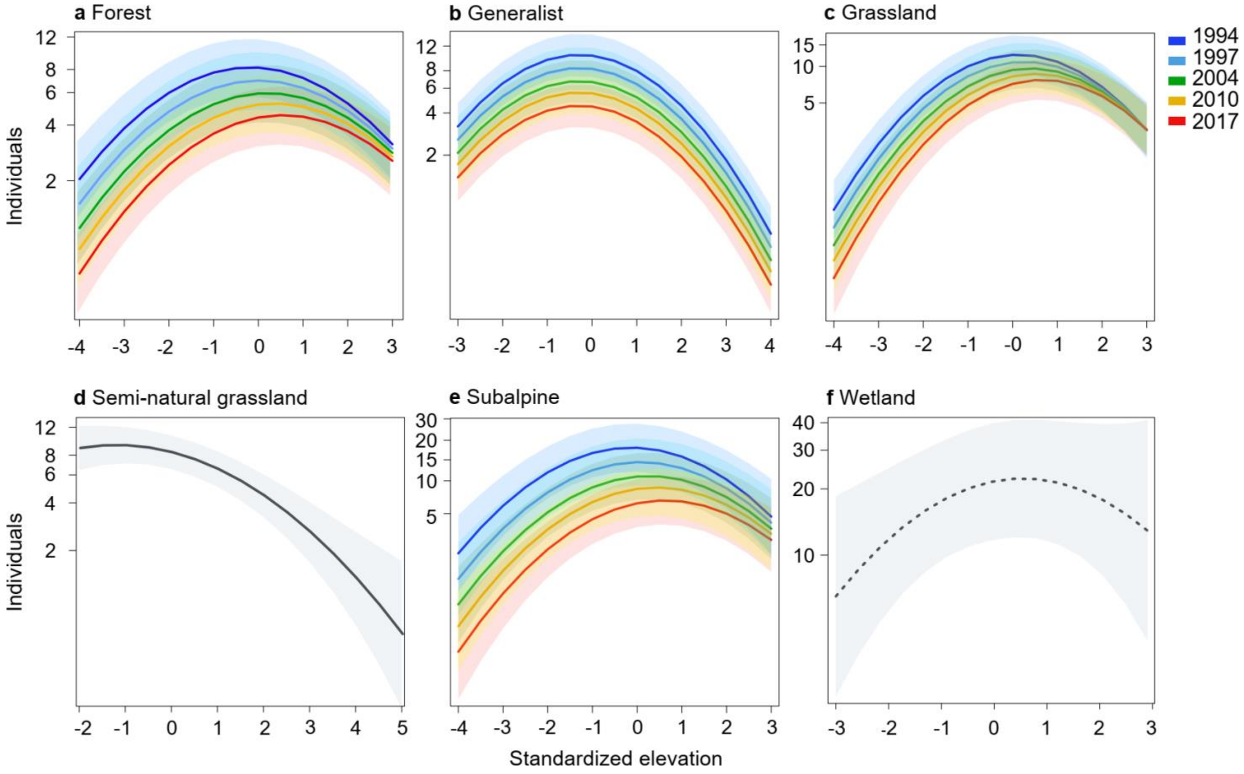

Figure 5: Temporal trends in orchid population size across species elevational range. Plots depicting the effect of time, elevation (linear and quadratic terms) and, if significant, their interaction on population size. Separate models were run for different habitat preference categories. Within each species, elevation was standardized to mean 0 and SD 1 to make elevational ranges comparable among species, i.e. the most negative values corresponded to the rear edge and the largest positive values to the leading edge. The relationship for species showing no effect of time is shown in black. For clarity reasons, colour coding shows only 5 years but orchid population size has been recorded over 28 years (1990-2017). Shading areas shows 95% confidence intervals around model estimates (solid line). For wetland (dashed line), the quadratic effect of elevation was marginal ($p = 0.066$, $n = 534$ observations for 4 species). Plots were drawn using the plotEffect() function in the effects package in R. Partial residuals were not shown due to the large number of data points.

In contrast to previous studies investigating the response of common taxa (Gottfried et al. 2012; Rumpf et al. 2018; Dullinger et al. 2020), no orchid group appeared to be favoured by climate warming, as even the most thermophilic species did not increase their population size in any part of their elevation range. This suggests that other drivers of population dynamics such as the loss of mutualistic interactions (Alexander et al. 2015) or habitat degradation (Vogt-Schilb et al. 2016), as shown in the resurvey, may play an important role in explaining population declines.

Table 2: Effect of time (linear), elevation (linear and quadratic terms) and their interaction on population size for each habitat preference category, separately. To make elevational ranges comparable among species, elevation was standardized to mean 0 and SD 1. We fitted generalized linear mixed models assuming a Poisson distribution with species and an observation-level random factor as crossed random effects (see Methods).

Habitat preference	Fixed effects	χ^2	p
Forest	Time (year)	202.756	<0.001
	Elevation	6.214	0.013
	Elevation^2	111.223	<0.001
	Time (year) x Elevation	9.601	0.002
Generalist	Time (year)	318.201	<0.001
	Elevation	54.868	<0.001
	Elevation^2	284.900	<0.001
	Time (year) x Elevation	3.390	0.066
Grassland	Time (year)	61.820	<0.001
	Elevation	44.409	<0.001
	Elevation^2	141.364	<0.001
	Time (year) x Elevation	6.412	0.011
Semi-natural grassland	Time (year)	0.509	0.476
	Elevation	33.479	<0.001
	Elevation^2	9.794	0.002
	Time (year) x Elevation	0.261	0.609
Subalpine	Time (year)	109.331	<0.001
	Elevation	8.144	0.004
	Elevation^2	46.331	<0.001
	Time (year) x Elevation	4.090	0.043
Wetland	Time (year)	0.031	0.861
	Elevation	2.746	0.097
	Elevation^2	3.373	0.066
	Time (year) x Elevation	1.329	0.249

Range shifts

Both local extinction and demographic changes are expected to result in species range shifts (Kelly and Goulden 2008; Lenoir and Svenning 2013). To understand how orchid distributions changed in the last three decades, we estimated range dynamics of each species at the regional scale (see Methods). To estimate range shift, we split the historical dataset in two periods (1990-2003 and 2004-2017) and evaluated species with at least 30 distribution records in each period. This approach reduced the risks that sampling biases could affect range shift estimation (see Methods). Despite some degree of inter-specific variability within habitat category, we found that orchids shifted their rear edges, optima and leading edges differently according to their habitat preference (Habitat preference for rear edge $p < 0.001$, for optimum $p = 0.001$, for leading edge $p < 0.001$, Fig. 6). The rear edge shifted upwards for species inhabiting grasslands, subalpine habitats and wetlands, while species inhabiting forests, semi-natural grasslands and generalist species showed a stable rear edge (Fig. 6a). We found a similar effect of habitat preference on the optimum shift but with a larger interspecific variability (Fig. 6b). At the optimum, orchids inhabiting semi-natural grasslands exhibited a downslope movement. Finally, the leading edge shifted upwards for wetland, generalist and grassland species, while forest and subalpine orchids did not shift their leading edge (Fig. 6c). Again, semi-natural orchids shifted their leading edge downslope. Considering the average speed of temperature change in the study area (3.8-5.5 m year^{-1}) (Dainese et al. 2017), rear and leading edges of forest species, optimum and leading edge of semi-natural species and optimum of generalist lagged significantly behind climate warming, while only grassland species shifted upwards faster than warming. However, only rear edges and optima of grassland orchids shifted faster than expected probably because of higher local extinctions than expected from climate warming alone.

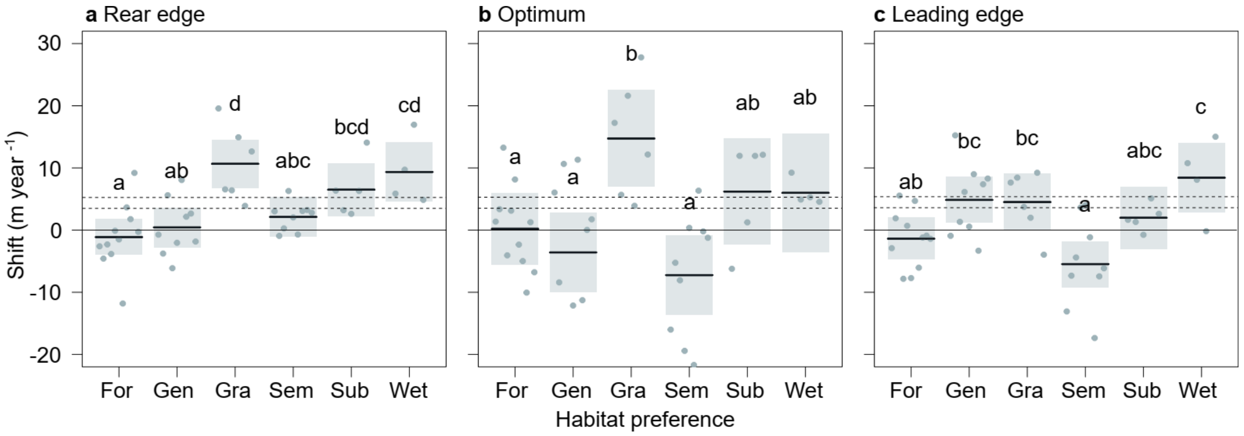

Figure 6: Elevation range shifts of orchids according to habitat preference. The effect of habitat preference on range shift for a) rear edge, b) optimum and c) leading edge. Solid lines indicate model estimates, while shaded grey areas indicate intervals of confidence (95%). Horizontal dashed lines show the expected shift to track climate change based on the current rate of warming in the study area (3.8-5.5 m year^{-1})^{2}. Forest: 11 species; generalist: 9 species; grassland: 6 species; semi-natural grassland: 9 species; subalpine: 5 species; and wetland: 4 species. Superscript letters denote significant differences ($p < 0.05$) in shift rates according to linear regression followed by Tukey's post-hoc test (see Methods). Plots were drawn using the visreg() function with default settings in the visreg package in R.

Given the large interspecific variation observed within each habitat preference group, we also considered the shift rate along the whole elevational distribution for each species, separately. We assessed how and where orchid elevational distributions shifted and whether this shift led to an overall contraction comparing deciles of the two elevation density distributions (Wilcox 2016). We generally observed asymmetric and idiosyncratic range shifts across species, with only a few species showing a symmetric march upwards of both rear and leading edge (e.g. *O. mascula*, *D.*

sambucina, *N. rhellicani*). More than 50% of the species were not able to fully track climate change (Fig. 7). Although most forest species did not change their distribution between the two periods, some species (e.g. *G. repens*, *N. nidus-avis*, *E. muelleri*) showed a downward shift at the leading margin resulting in a range contraction. Only two forest species moved upwards (*C. trifida* and *L. cordata*) but with a slower shift at the leading edge. By contrast, generalists were the only group of orchids that often expanded their range to higher elevations by moving the leading edge faster than the rear edge (e.g. *C. calceolus*, *L. ovata*, *O. mascula*, *P. bifolia*). All grassland orchids moved significantly upwards, however three moved quicker at the rear than at the leading edge, therefore contracting their range (*C. viride*, *G. odoratissima*, *T. globosa*). Semi-natural orchids showed either a stable range (e.g. *H. adriaticuam*) or a downward shift of the leading edge (e.g. *O. morio* and *O. tridentata*), contracting their range. Except for *N. miniata*, subalpine orchids moved upwards with a trend for a slower leading edge shift (e.g. *P. albida*). Finally, two of four species of wetland orchids shifted significantly upwards. It is important to stress that rare species with low numbers of records were over-represented in the wetland and semi-natural group affecting the power of the decile comparison described above (Wilcox 2016) (78 % of the species with less than two-hundreds records belonged to wetland and semi-natural group, Supplementary Table E1).

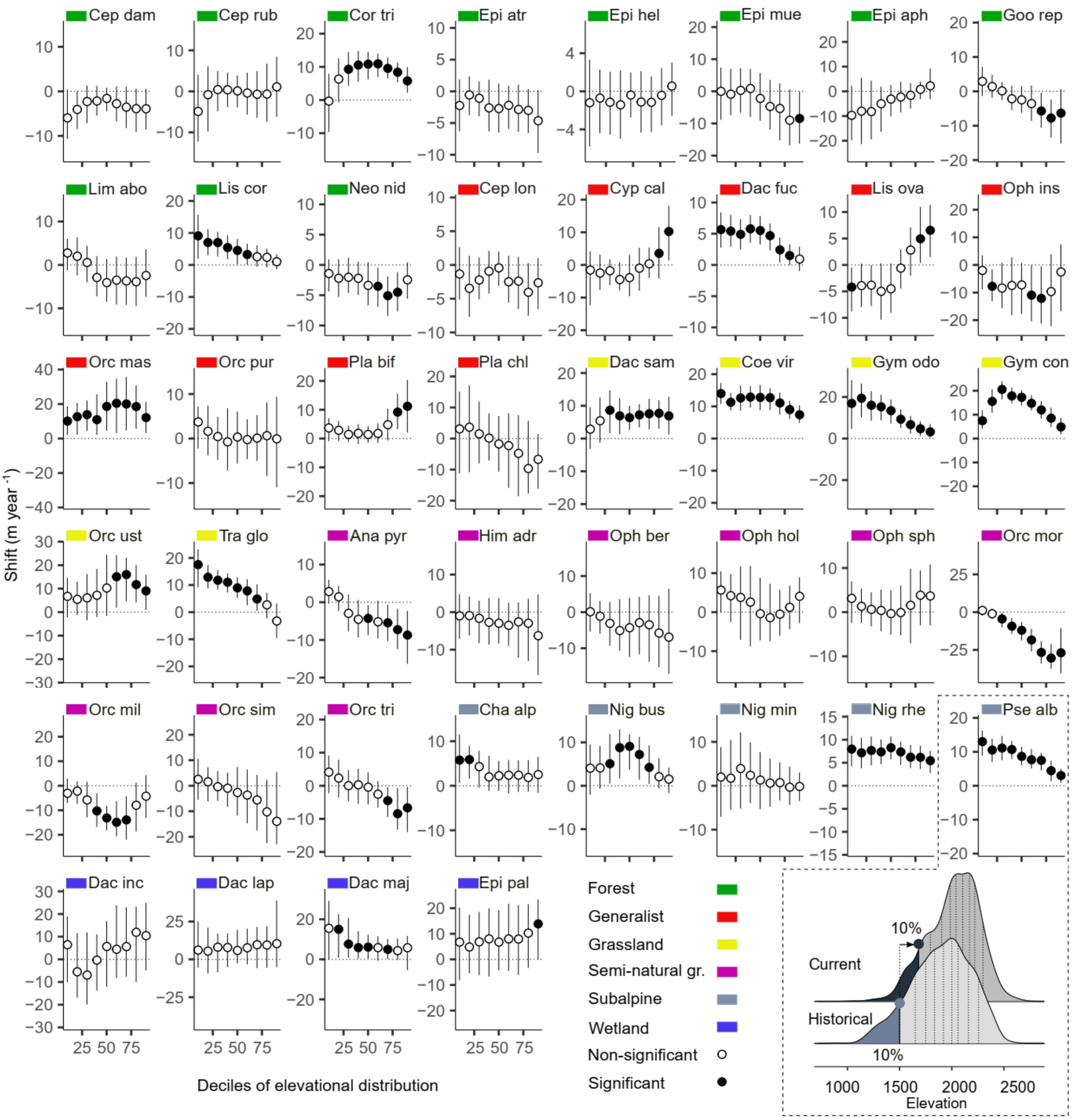

Figure 7: Elevation range shift between 1990-2003 (historical) and 2004-2017 (current) along the whole elevational distribution. For each species with more than 30 records per period, the shift for each decile between historical and current elevation density distribution is plotted (points). Vertical lines indicate 95% bootstrap confidence interval (CI) of each decile difference. Filled points indicate that the shift is different from 0 ($p<0.05$). In the dashed outline, an example of decile comparison between the two density distributions (historical vs. current) for *Pseudorchis albida* (*Pse alb* - Subalpine) is depicted: all deciles' shift upwards (i.e. positive values with 95% CI not crossing the zero line), but less at the leading than at the rear edge. Abbreviations of species names: Ana pyr = *Anacamptis pyramidalis*; Cep dam = *Cephalanthera damasonium*; Cep lon = *Cephalanthera longifolia*; Cep rub = *Cephalanthera rubra*; Cha alp = *Chamorchis alpina*; Coe vir = *Coeloglossum viride*; Cor tri = *Corallorhiza trifida*; Cyp cal = *Cypripedium calceolus*; Dac fuc = *Dactylorhiza fuchsii*; Dac inc = *Dactylorhiza incarnata*; Dac lap = *Dactylorhiza lapponica*; Dac maj = *Dactylorhiza majalis*; Dac sam = *Dactylorhiza sambucina*; Epi atr = *Epipactis atrorubens*; Epi hel = *Epipactis helleborine*; Epi mue = *Epipactis muelleri*; Epi pal = *Epipactis palustris*; Epi aph = *Epipogium aphyllum*; Goo rep = *Goodyera repens*; Gym con = *Gymnadenia conopsea*; Gym odo = *Gymnadenia odoratissima*; Him adr = *Himantoglossum adriaticum*; Lim abo = *Limodorum abortivum*; Lis cor = *Listera cordata*; Lis ova = *Listera ovata*; Neo nid = *Neottia nidus avis*; Nig bus = *Nigritella buschmanniae*; Nig min = *Nigritella miniata*; Nig rhe =

Nigritella rhellicani; Oph ber = *Ophrys bertolonii*; Oph hol = *Ophrys holosericea*; Oph ins = *Ophrys insectifera*; Oph sph = *Ophrys sphegodes*; Orc mas = *Orchis mascula*; Orc mil = *Orchis militaris*; Orc mor = *Orchis morio*; Orc pur = *Orchis purpurea*; Orc sim = *Orchis simia*; Orc tri= *Orchis tridentata*; Orc ust = *Orchis ustulata*; Pla bif = *Platanthera bifolia*; Pla chl = *Platanthera chlorantha*; Pse alb = *Pseudorchis albida*; Tra glo = *Traunsteinera globosa.*

Forest orchids often did not exhibit any shift in their elevational distribution probably because the slow upward movement of forests hindered the range expansion of orchids. Similarly, Lenoir et al. (2008) (Lenoir et al. 2008) reported in the French Alps a non-significant upward shift for four species of forest orchids also included in our analysis. Moreover, previous studies indicate that forest ecosystems may buffer the effects of climate change on plants (De Frenne et al. 2013, 2019; Zellweger et al. 2020), promoting species' persistence and resulting in a delayed response of plant communities (Bertrand et al. 2016). Species that can colonize grasslands from sea level to the highest elevations shifted their rear edge and optimum faster than most other groups and also faster than regional climate warming. These species possess the widest thermal niche that can help them to rapidly take advantage of warming temperature. Several generalists were able to track climate change probably due to their ability to colonize different habitat types over the entire elevational range. Orchids inhabiting semi-natural grasslands below the tree-line shifted their distribution in the direction opposite to climate change, in fact both the leading edge and the optimum shifted downwards. This shift is consistent with the patterns of land-use changes in the study area where open areas were lost due to the natural downward recolonization by forests (Tattoni et al. 2017), leading to increasingly unfavourable conditions towards the upper limit of the range. Previous studies also found that species may shift downslope as a direct consequence of habitat modification following natural or human-induced disturbances or due to other local changes in habitat suitability (Lenoir et al. 2010). Several cold-adapted orchids of subalpine habitats moved their optima and rear edges upwards quickly, while at the leading edge species failed to colonize novel habitats at the same pace. This is consistent with the slow dynamics of subalpine/alpine habitats related to extreme cold temperature and to geometric constraints of mountain tops, i.e. reduced habitat area (Colwell and Lees 2000). Finally, most orchids occurring in wetlands presented a consistent march upwards of rear and leading edge similar to the speed of temperature warming, possibly indicating that the regional network of protected areas is helping the species to track climate change. In conclusion, in accordance with previous studies evaluating shifts at both rear and leading range limits (Freeman et al. 2018; Rumpf et al. 2019b), we observed large interspecific variation that was only partially explained by habitat preference. Idiosyncrasy in range shifts is not consistent with a scenario where temperature is the sole dominant factor driving species range distribution and was previously observed even within-species across regions, highlighting how biotic interactions and local, non-thermal abiotic conditions may often supersede the physiological effects of temperature (Gibson-

Reinemer and Rahel 2015). A full understanding of the response variation among taxa will likely require embracing the complex ways in which species interactions influence range dynamics (Alexander et al. 2015) and the potential role of microscale variation in climate (De Frenne et al. 2019; Zellweger et al. 2020) and habitat quality (Vittoz et al. 2009).

Study limitations

Several limitations of our study should be kept in mind when interpreting our results. First, resurveying historical plots did not allow us to evaluate colonization dynamics, because we did not sample plots beyond the leading edge of historical species distributions. Second, in the resurvey we only monitored orchids during one growing season in both periods. Although a single visit is generally considered as insufficient to count all species at a site (Vogt-Schilb et al. 2013) and among orchid species there is considerable variation in traits that can influence detectability in field observations, our analyses were run at the species level and therefore species detectability should be consistent in the two periods. Third, despite the fine spatial resolution and large sampling effort of our dataset, several species were still too rare to robustly evaluate population and range shift dynamics. Fourth, the mechanisms underpinning the observed population decline and range shifts could not be singled out due to the lack of high resolution, historical data on habitat changes beyond the 463 resurveyed sites.

Conclusions

Except for the most thermophilic species and wetland specialists, we observed population declines, in particular for rear-edge populations. Besides these dramatic demographic trends, different species exhibited idiosyncratic range shifts with more than 50% of the species not able to fully track climate change. Overall, our results show that only a multi-dimensional approach encompassing local extinction dynamics, local population density, and quantification of elevation ranges from rear to leading edges enabled a comprehensive understanding of redistribution dynamics of orchids under global change. At the local scale, in situ management and protection can focus on maintaining habitat quality, while at the regional scale it is crucial to identify and protect habitat patches across elevational ranges to enable species range shifts. Finally, our study highlights the importance of long-term monitoring of rare plant populations and distributions at fine spatial scales (Sletvold et al. 2013; Cotto et al. 2017a; Tye et al. 2018; Wraith et al. 2020), to be able to fully understand and manage the consequences of global change for mountain biodiversity.

Acknowledgments

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Conclusions

Understanding the multi-facet effects of global change on species redistribution is a key challenge to inform ecosystem management and conservation policy (Parmesan 2006; Lenoir and Svenning 2013; Elsen et al. 2020). The main aim of this PhD thesis was to study abiotic and biotic drivers of redistribution dynamics of both native and exotic plant species of the European Alps. Specifically, I focused on the effects of climate change, land-use and biotic interactions, using a combination of different experimental and modelling approaches. In the first three chapters, I report findings from manipulative short-term studies, that focused on the local effect of arthropod herbivores on plant establishment, while in Chapter 4 and 5, I present results from long-term studies that enabled me to explore plant responses to climate change and land use over the last three decades.

In the short term studies, I directly manipulated biotic and abiotic factors in realistic field experiments and observed plant community assembly dynamics. Using exclusion cages and observing different guilds of herbivores, I found that herbivores modulated plant responses to abiotic drivers and likely facilitated exotic plant invasion. I could also appreciate that future responses of grassland herbivores to vegetation changes and temperature warming are highly variable and depend on the feeding strategy and specialisation of the focal herbivore group. Among the abiotic factors investigated in these studies, soil disturbance emerged as a fundamental driver of native and exotic plant establishment. Soil disturbance changed the composition of native plant communities and facilitated exotic plant invasions. Besides human-related disturbance, also natural phenomena such as landslides or small erosion events might be associated with plant invasions due to the high propagule pressure observed across several natural habitats. Therefore, decreasing soil disturbance regime, in particular where propagule pressure is high, represents a top priority to reduce the probability of invasions of exotic plants across temperate mountains. Besides this local management advice, results from the three short-term studies stressed out the critical need of future research to consider herbivores' effect and to adopt a multiple driver approach when assessing global change impacts on plant community dynamics.

Using two long-term studies, I explored the effect of abiotic drivers on plant redistribution dynamics over the last three decades (1990 – 2019). In particular, I investigated whether climate change and land use favour exotic plant species and, simultaneously, threaten red-list species. In both studies, I found evidence for the negative effect of warming and habitat alteration on populations of threatened species. Many threatened native plants have experienced a strong erosion of their rear margins, contracting their range, while exotic species have quickly spread upwards, expanding their elevational range. Some threatened orchid species did not shift their range or even moved downwards in the direction opposite to climate change. This variability in range dynamics stressed that climate change is not the only driver of species distribution and biotic interactions and local, non-thermal, abiotic conditions may supersede its effect. In accordance with these results, exploring functional traits related to range expansion or contraction, I found that land use changes such as increased soil disturbance and eutrophication might be at least as important drivers of extinction as temperature warming. In particular, native plant species at low elevations resulted to be those more at risk of extinction due to a combination of climate warming and on-going land use changes. While invasive impact resulted to be lower at mid and high elevations (above c. 1000 m a.s.l.), in the lowlands exotic species might displace threatened plants with low competition ability in the long-term. In the second long term study, I had the chance to have a closer look to the population dynamics of orchid species using a unique long-term dataset of population size. I found that except for the most thermophilic species and wetland specialists, orchid population density decreased over time. Declines were more pronounced for rear-edge populations due to multiple pressures such as climate warming, habitat alteration, and mismatched ecological interactions. These long-term data indicate an urgent need to prioritize the lowlands for conservation measures. However, there are conflicts between biodiversity conservation and economic development, because most income generating activities are confined to low elevation areas. Findings from these two studies highlighted the importance of long-term monitoring of range distributions and population dynamics to be able to fully understand the consequences of global change for biodiversity.

Altogether, findings of my PhD thesis pointed out at three main messages. First, we should adopt a multiple driver approach when assessing global change impacts on species distribution and population dynamics. Most current research focuses on climate change impact, while a scenario where climate change is the only driver is highly unrealistic (Sirami et al. 2017). Future studies should assess interactions between global change drivers, in particular trying to link climate change with land use effects. Second, a better integration of multiple drivers should also incorporate the effects of biotic interactions. In this PhD thesis, I could highlight the important role played by arthropod herbivores, but we could not integrate other key biotic interactions in long-term studies and many questions remain open. Did the loss of mutualistic interactions such as mycorrhizal fungi or pollinators have an effect on plant range dynamics? Do newly established exotic flowering plants attract native insects and which are the cascading effects of these invasions across different trophic levels? What are the implications of novel competitive interactions for species’ ranges dynamics under climate change? Third, we advocate that considering species functional traits should improve predictions of global change responses. The role of functional traits in conservation planning already emerged in several studies (Estrada et al. 2016). We found that both insects and plants responded differently to global change, depending on their specialisation, thermal tolerance, and competition ability. In the context of global change, selecting traits that better predict species responses is a promising strategy. With these five studies, I found answers to few questions, but, more importantly, I identified knowledge gaps and formulated new hypotheses. Answers to these questions await further research to provide insight into the effects of biotic interactions, climate change and land-use change on species distribution, contributing to the establishment of reliable measures for biodiversity conservation under global change.

Appendix

Appendix A (Chapter 1)

Table A S1: Temperatures (°C) and rainfall (mm) over 2008-2018 in the study area (Northeast Italy, Legnaro; 45.8210N; 11.8580E; 6 m a.s.l).

Trial	Season	Mean T	Min T	Max T	Tot rainfall
1 st	Early growing season	20.3	14.9	25.5	155.9
2 nd	Late growing season	23.4	17.7	28.8	125.74

Table A S2: Herbivore community composition over whole duration of the experiment. To study which invertebrate herbivores were excluded using our treatments, we sampled herbivore communities using pitfalls. In the outdoor mesocosm experiment, we placed ten pitfalls in a regular grid and filled them with glycole. Traps were emptied every 2 weeks. We carried out overall 4 rounds, 2 after the first soil disturbance and 2 after the second soil disturbance. Insects were placed in ethanol 70 % for further investigation in the lab.

Main group of collected herbivores	Percentage
Coleoptera	15
Heteroptera	25
Orthoptera	24
Pulmonata Limacidae	27
Pulmonata Elicidae	10

Table A S3: list of plant species occurring in the subplots over the whole duration of the experiment and their relative frequency of occurrence.

Species	Frequency %
Avena fatua L.	0.013
Chenopodium album L.	0.003
Cirsium arvense (L.) Scop.	0.019
Cirsium vulgare (Savi) Ten.	0.034
Convolvulus arvensis L.	0.544
Cornus sanguinea L.	0.006
Crepis biennis L.	0.013
Crepis foetida L.	0.003
Cynodon dactylon (L.) Pers.	0.338
Daucus carota L.	0.063
Epilobium sp.	0.003
Equisetum arvense L.	0.119
Euphorbia helioscopia L.	0.384
Euphorbia prostrata Aiton	0.084
Gallium mollugo L.	0.063
Geranium molle	0.009
Glechoma hederacea L.	0.097
Hedera helix L.	0.006
Helminthotheca echioides (L.) Holub	0.088
Holcus lanatus L.	0.019
Kickxia elatine (L.) Dumort	0.006

Lolium perenne L.	0.034
Lotus corniculatus L.	0.013
Lysimachia arvensis (L.) U. Manns & Anderb	0.003
Oxalis corniculata L.	0.022
Plantago lanceolata L.	0.003
Potentilla reptans L.	0.338
Rubiaceae sp.	0.003
Rubus caesius L.	0.225
Rumex acetosa L.	0.003
Salvia pratensis L.	0.003
Sanguisorba minor Scop.	0.041
Senecio vulgaris L.	0.016
Setaria viridis P. Beauv.	0.066
Silene latifolia Poir.	0.003
Sonchus asper (L.) Hill	0.009
Sonchus oleraceus L.	0.088
Sorghum halepense (L.) Pers.	0.406
Taraxacum officinale sect. Taraxacum F.H.	0.069
Trifolium repens L.	0.050
Verbena officinalis L.	0.013
Vitis sp.	0.003

Table A S4: effects of N, herbivory and the interaction between drought conditions and timing of soil disturbance (early vs. late season) on plant species richness. Coefficients are estimated from final GLMM, assuming Poisson distribution.

Fixed factor	Value	Std.Error	DF	z	p
Timing (late season)	-0.542	0.097	231	-5.591	<0.001
Drought (no)	0.114	0.081	67	1.413	0.158
N (yes)	0.088	0.061	67	1.441	0.150
Herbivory (yes)	0.156	0.062	231	2.543	0.011
Drought (no) × timing (late season)	0.404	0.127	231	3.186	0.001

Table A S5: effects of the interaction between N and timing of soil disturbance (early vs. late season) and between N and herbivory and effect of drought conditions on ln-transformed evenness. Coefficients are estimated from final LMM.

Fixed factor	Value	Std.Error	DF	t	p
Timing (late season)	0.236	0.077	236	3.061	0.003
Drought (no)	-0.163	0.059	68	-2.741	0.008
N (yes)	-0.025	0.097	68	-0.258	0.797
Herbivory (yes)	-0.155	0.077	236	-2.004	0.046
N (yes) × herbivory (yes)	0.245	0.109	236	2.244	0.026
N (yes) × timing (late season)	-0.311	0.109	236	-2.852	0.005

Table A S6: effects of the three and two ways interaction between drought conditions, N, timing of soil disturbance (early vs. late season) and herbivory on root square transformed biomass (g). Coefficients are estimated from final LMM.

Fixed factor	Value	Std.Error	DF	t	p
Timing (late season)	-7.060	1.401	232	-5.040	<0.001
Drought (no)	3.682	1.428	67	2.579	0.012
N (yes)	1.004	1.428	67	0.703	0.485
Herbivory (yes)	0.575	1.253	232	0.459	0.647
Drought (no) × N (yes)	-2.834	1.815	67	-1.562	0.123
Drought (no) × herbivory (yes)	-0.554	1.253	232	-0.442	0.659
N (yes) × herbivory (yes)	-0.765	1.253	232	-0.611	0.542
Drought (no) × timing (late season)	1.594	1.772	232	0.900	0.369
N (yes) × timing (late season)	0.326	1.772	232	0.184	0.854
Herbivory (yes) × timing (late season)	0.374	1.253	232	0.299	0.765
Drought (no) × N (yes) × timing (late season)	6.964	2.505	232	2.779	0.006

Table A S7: effects of drought conditions, N and herbivory on temporal beta replacement. Coefficients are estimated from final LMM.

Response variable	Fixed factor	Value	Std.Error	DF	t	p
Beta replacement[a]	Drought (no)	0.114	0.053	68	2.144	0.036
	N (yes)	0.062	0.053	68	1.178	0.243
	Herbivory (yes)	0.009	0.028	74	0.305	0.762
Beta replacement[b]	Drought (no)	0.119	0.062	68	1.913	0.06
	N (yes)	0.074	0.062	68	1.198	0.235
	Herbivory (yes)	0	0.03	74	-0.009	0.993

[a] Temporal beta replacement was calculated using Jaccard index (see Methods)

[b] Temporal beta replacement was calculated using Sørensen index (see Methods)

Appendix B (Chapter 2)

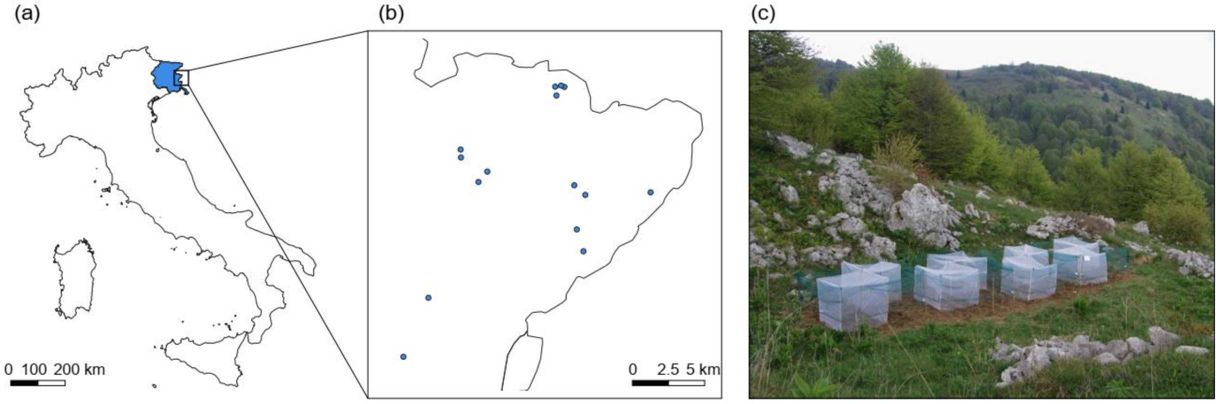


Figure B S1: a) Study area in Northeast Italy; b) the fifteen study sites; and c) example of one experimental site with 4 disturbed plots (2 × 2 m) divided in 4 subplots (1× 1 m) (n= 16 disturbed subplots per site). We installed exclusion cages and added N in half of the disturbed subplots**.** The site was fenced against vertebrate herbivory.

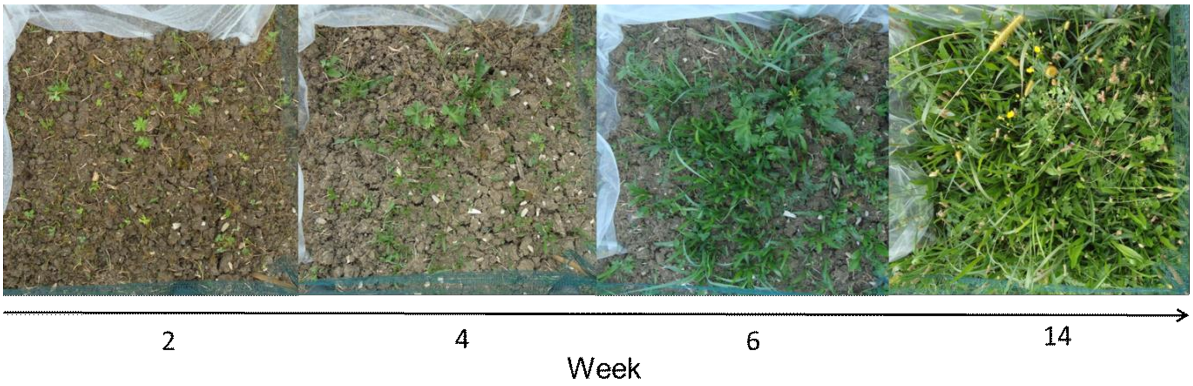


Figure B S2: Development of one subplot over the whole duration of the experiment**.**

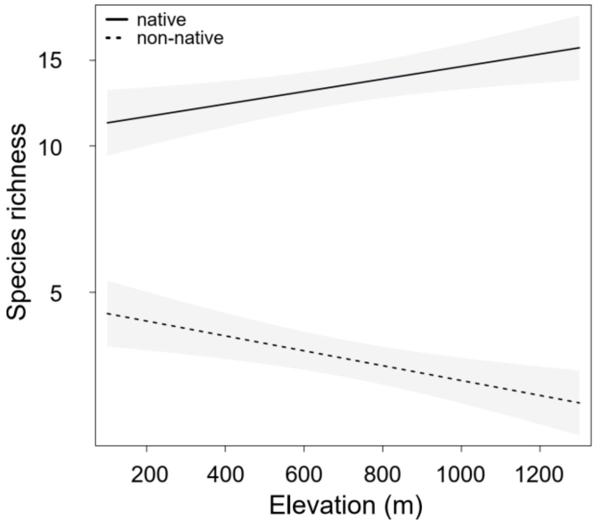


Figure B S3: Effect of the interaction between elevation and status (native and non-native) on plant species richness after soil disturbance.

Table B S1: Non-native species in the disturbed block and in the surrounding vegetation per site. The 15 sites are ordered according to elevation (m a.s.l.).

Site	Elevation	Non-native species richness	
		Disturbed Block	Surrounding Vegetation
OR	100	*A.artemisiifolia*; *A.retroflexus*; *E.annuus*	*E.annuus*
FI	110	*A.altissima*; *A.artemisiifolia*; *A.retroflexus*; *E.annuus*; *P.capillare*	*E.annuus*; *M.sativa*
DO	190	*C.canadensis*; *E.annuus*; *O.fontana*	*E.annuus*
AL	420	*A.retroflexus*; *E.annuus*; *F.esculentum*; *V.persica*	*E.annuus*; *M.sativa*
SA	510	*E.annuus*; *M.sativa*	*E.annuus*; *M.sativa*
CR	520	*C.canadensis*; *E.annuus*; *F.esculentum*; *G.parviflora*; *P.capillare*; *R.pseudoacacia*; *S.halepense*; *V.persica*	*E.annuus*
GN	600	*C.canadensis*; *E.annuus*; *G.parviflora*	-
IA	650	*E.annuus*	-
SP	660	-	-
MC	850	-	-
MC2	920	-	-
M1	1080	*C.canadensis*; *E.annuus*	-
M2	1310	*G.ciliata*	-
M3	1320	-	-
M4	1330	*E.annuus*	-

Table B S2: Dissimilarity between disturbed and undisturbed plant communities, separately for natives and non-natives. We calculated Jaccard and Sørensen similarity indices and their components (replacement and richness; and turnover and nestedness respectively). For sites where no non-native species occurred, beta-diversity could not be assessed. Beta turnover and nestedness components could not be calculated, for those sites with no non-natives in the surrounding vegetation but some non-natives in the disturbed blocks.

	Site	Beta diversity jaccard index	Beta replacement	Beta richness	Beta diversity sørensen index	Beta turnover	Beta nestedness
Native	AL	0.705	0.682	0.023	0.544	0.536	0.008
	CR	0.717	0.528	0.189	0.559	0.483	0.076
	DO	0.824	0.627	0.196	0.700	0.640	0.060
	FI	0.804	0.391	0.413	0.673	0.500	0.173
	GN	0.756	0.667	0.089	0.607	0.577	0.030
	IA	0.720	0.640	0.080	0.563	0.533	0.029
	M1	0.796	0.531	0.265	0.661	0.565	0.096
	M2	0.635	0.577	0.058	0.465	0.441	0.024
	M3	0.719	0.702	0.018	0.562	0.556	0.006
	M4	0.720	0.720	0.000	0.563	0.563	0.000
	MC	0.768	0.580	0.188	0.624	0.556	0.068
	MC2	0.759	0.483	0.276	0.611	0.500	0.111
	OR	0.833	0.424	0.409	0.714	0.560	0.154
	SA	0.714	0.600	0.114	0.556	0.512	0.043
	SP	0.690	0.483	0.207	0.526	0.438	0.089
Non-native	AL	0.800	0.400	0.400	0.667	0.500	0.167
	CR	0.875	0.000	0.875	0.778	0.000	0.778
	DO	0.667	0.000	0.667	0.500	0.000	0.500
	FI	0.833	0.333	0.500	0.714	0.500	0.214
	GN	1.000	0.000	1.000	1.000	NA	NA
	IA	1.000	0.000	1.000	1.000	NA	NA
	M1	1.000	0.000	1.000	1.000	NA	NA
	M2	1.000	0.000	1.000	1.000	NA	NA
	M3	NA	NA	NA	NA	NA	NA
	M4	1.000	0.000	1.000	1.000	NA	NA
	MC	NA	NA	NA	NA	NA	NA
	MC2	NA	NA	NA	NA	NA	NA
	OR	0.667	0.000	0.667	0.500	0.000	0.500
	SA	0.000	0.000	0.000	0.000	0.000	0.000
	SP	NA	NA	NA	NA	NA	NA

Table B S3: Plausible candidate models (ΔAICc < 2) explaining species richness, separately for native and non-native plants. Models are ranked according to their second order Akaike's information criterion (AICc). Parameter estimates, degrees of freedom (df), difference in AICc values compared to the best fitting model (ΔAICc) and model weight (w_i) are reported. Variables names are abbreviated: Int = intercept; dst = disturbance; and elv = elevation.

+ indicates that the variable was included in the model.

	Ranking	Int	dst	elv	dst x elv	df	ΔAICc	w_i
a) Natives								
	1st	2.815	+	0.148		7	0.00	0.493
	2nd	2.815	+			6	0.67	0.353
b) Non-natives								
	1st	-2.169	+	-1.438		6	0.00	0.636

Table B S4: Plausible candidate models (ΔAICc < 2) explaining biomass. Models are ranked according to their second order Akaike's information criterion (AICc). Parameter estimates, degrees of freedom (df), difference in AICc values compared to the best fitting model (ΔAICc) and model weight (w_i) are reported. Variables names are abbreviated: Int = intercept; hrb = herbivory; N= N addition and elv = elevation.

+ indicates that the variable was included in the model.

Ranking	Int	hrb	N	elv	hrb x N	hrb x elv	N x elv	hrb x N x elv	df	ΔAICc	w_i
1st	5.205	+							5	0.00	0.392
2nd	5.218	+	+						6	1.98	0.146

Table B S5: Plausible candidate models (ΔAICc < 2) explaining species richness in disturbed blocks. Models are ranked according to their second order Akaike's information criterion (AICc). Parameter estimates, degrees of freedom (df), difference in AICc values compared to the best fitting model (ΔAICc) and model weight (w_i) are reported. Variables names are abbreviated: Int = intercept; hrb = herbivory; N= N addition; elv = elevation and stt = status (native or non-native).

+ indicates that the variable was included in the model.

Ranking	Int	hrb	N	elv	stt	hrb x N	hrb x elv	hrb x stt	N x elv	N x stt	elv x stt	hrb x N x elv	hrb x N x stt	hrb x elv x stt	N x elv x stt	hrb x N x elv x stt	df	ΔAICc	w_i
1st	2.591			0.121	+						+						8	0.00	0.265
2nd	2.597	+		0.121	+						+						9	1.54	0.123
3rd	2.594		+	0.121	+						+						9	1.97	0.099

Table B S6: Plausible candidate models (ΔAICc < 2) explaining bare ground cover %. Models are ranked according to their second order Akaike's information criterion (AICc). Parameter estimates, degrees of freedom (df), difference in AICc values compared to the best fitting model (ΔAICc) and model weight (w_i) are reported. Variables names are abbreviated: Int = intercept; hrb = herbivory; wk= week, N= N addition and elv = elevation.

+ indicates that the variable was included in the model.

Ranking	Int	hrb	wk	N	elv	hrb x wk	hrb x N	hrb x elv	wk x N	wk x elv	N x elv	hrb x wk x N	hrb x wk x elv	hrb x N xelv	wk x N x elv	hrb x wk x N x elv	df	ΔAICc	w_i
1st	128.9	+	-38.32		-0.420	+				2.561							9	0.00	0.171
2nd	129.9	+	-38.32	+	-0.437	+				2.560							10	0.32	0.146
3rd	128.8	+	-37.62	+	-0.428	+			+	2.555							11	1.56	0.079
4th	128.8	+	-38.29		-0.232	+		+		2.559							10	1.91	0.066

Table B S7: Plausible candidate models (ΔAICc < 2) explaining plant cover. Models are ranked according to their second order Akaike's information criterion (AICc). Parameter estimates, degrees of freedom (df), difference in AICc values compared to the best fitting model (ΔAICc) and model weight (w_i) are reported. Variables names are abbreviated: Int = intercept; hrb = herbivory; wk= week, N= N addition, elv = elevation and stt= status. The full model did not test for interactions with N addition, because the model structure including five fixed factors and their interactions was too complex.

+ indicates that the variable was included in the model.

Ranking	int	hrb	wk	N	elv	stt	hrb x wk	hrb x elv	hrb x stt	wk x elv	wk x stt	elv x stt	hrb x wk x elv	hrb x wk x stt	hrb x elv x stt	wkxelv x stt	hrb x wk x elv x stt	df	ΔAICc	w_i
1st	-1.238	+	3.621		-0.201	+	+		+	0.147	+	+				+		14	0.00	0.131
2nd	-1.319	+	3.621	+	-0.200	+	+		+	0.147	+	+				+		15	0.05	0.128
3rd	-1.084	+	3.526		-0.201	+			+	0.147	+	+				+		13	1.38	0.066
4th	-1.164	+	3.526	+	-0.200	+			+	0.147	+	+				+		14	1.43	0.064
5th	-1.279	+	3.646		-0.201	+	+		+	0.147	+	+		+		+		15	1.54	0.061
6th	-1.360	+	3.646	+	-0.200	+	+		+	0.147	+	+		+		+		16	1.59	0.059

Table B S8: Frequency (%) of the species recorded in disturbed subplots (N= 240), control subplots (N= 30) and in the surrounding vegetation (N= 15). Non-native species are shown in bold*.

Species	Disturbed subplot	Control subplot	Surrounding vegetation
Acer campestre L.	0.01		
Acer pseudoplatanus L.		0.03	
Achillea millefolium aggr.	0.37	0.43	0.53
Aegopodium podagraria L.	0.09	0.10	0.27
Aethusa cynapium L.	0.01		
Agrostis capillaris L.	0.15	0.37	
***Ailanthus altissima* (Miller) Swingle**	0.02		
Ajuga genevensis L.	0.01		
Ajuga reptans L.			0.33
Alchemilla vulgaris aggr.	0.05	0.07	0.20
Allium carinatum L. subsp. *pulchellum* Bonnier & Layens		0.17	
***Amaranthus retroflexus* L.**	0.03		
***Ambrosia artemisiifolia* L.**	0.08		
Anagallis arvensis L.	0.04		
Anemone nemorosa L.			0.13
Anisantha sterilis (L.) Nevski			0.13
Anthericum ramosum L.	0.02	0.13	
Anthoxanthum odoratum L. subsp. *odoratum*	0.01	0.13	0.47
Anthyllis vulneraria L.	0.02	0.07	0.13
Arenaria serpyllifolia L.			0.07
Aristolochia rotunda L.	0.03		0.13

Arnica montana L.			0.07
Arrhenatherum elatius (L.) Presl	0.10	0.10	0.60
Asperula cynanchica L.		0.03	0.07
Astragalus glycyphyllos L.	0.01	0.03	
Avena barbata Pott. ex Link.	0.004		
Betonica alopecuros L.			0.13
Betonica officinalis L.	0.08	0.27	0.20
Betula pendula Roth	0.02		0.07
Biscutella laevigata L.		0.03	0.07
Brachypodium rupestre (Host) Roem. & Schult.	0.11	0.43	0.53
Briza media L.	0.05	0.30	0.07
Bromopsis erecta (Huds.) Fourr.	0.17	0.73	0.73
Buphthalmum salicifolium L.	0.12	0.17	0.40
Calluna vulgaris (L.) Hull			0.13
Calystegia sepium (L.) R. Br.	0.15	0.07	
Campanula scheuchzeri Vill.	0.03	0.10	
Capsella bursa-pastoris (L.) Medicus			0.07
Carex capillaris L.	0.03		
Carex caryophyllea La Tourr.			0.33
Carex flacca Schreb.	0.17	0.07	0.27
Carex hirta L.			0.07
Carex montana L.	0.10	0.13	0.33
Carex ornithopoda Willd.			0.07
Carex pallescens L.			0.13

Carex pilulifera L.		0.03	0.07
Carex sylvatica Huds.	0.04		0.07
Carum carvi L.	0.05	0.13	0.27
Centaurea jacea aggr.	0.36	0.60	0.53
Centaurea nigrescens aggr.	0.08		0.33
Centaurea scabiosa L.	0.04		0.20
Cerastium brachypetalum Desp. ex Pers.			0.07
Cerastium fontanum Baumg.	0.03		0.13
Cerastium pumilum Curtis		0.03	
Chamaecytisus hirsutus (L.) Link		0.07	0.07
Chenopodium album L.	0.08		
Chenopodium polyspermum L.	0.05		
Chrysopogon gryllus (L.) Trin.	0.01	0.10	0.07
Cirsium arvense (L.) Scop.	0.05		
Cirsium pannonicum (L.fil.) Link	0.04	0.10	0.27
Clematis vitalba L.	0.05		
Clinopodium vulgare L.		0.07	
Coeloglossum viride (L.) Hartm.			0.07
Colchicum autumnale L.		0.13	0.13
Convallaria majalis L.	0.01	0.13	0.13
***_Conyza canadensis_ (L.) Cronq.**	0.03		
Corylus avellana L.			0.07
Crepis capillaris (L.) Wallr.	0.004		
Crepis vesicaria subsp. *taraxacifolia* (Thuill.) Thell.			0.13

Crocus vernus (L.) Hill			0.13
Cruciata glabra (L.) Ehrend.	0.04	0.10	0.13
Dactylis glomerata L.	0.15	0.47	0.60
Daucus carota L.	0.08	0.03	0.13
Dianthus carthusianorum L. subsp. *sanguineus* (Vis.) Williams			0.07
Digitaria sanguinalis (L.) Scop.	0.06		
Echinochloa crus-galli (L.) P.P.Beauv.	0.004		
Echium vulgare L.	0.004		
*Elytrigia repens (*L.) Desv. ex Nevski	0.10		
Equisetum telmateja Ehrh.	0.05	0.03	
****Erigeron annuus* (L.) Pers.**	0.41	0.23	0.40
Eupatorium cannabinum L.	0.03		
Euphorbia cyparissias L.	0.10	0.10	0.20
Euphorbia dulcis L.	0.01		
Euphorbia verrucosa L.	0.06	0.23	0.20
****Fagopyrum esculentum* Moench**	0.01		
Ferulago galbanifera (Mill.) W.D.J. Koch			0.13
Festuca arundinacea Schreb			0.13
Festuca filiformis Pourr.			0.20
Festuca rubra L.	0.08	0.53	0.53
Festuca rupicola Heuffel			0.07
Filipendula vulgaris Moench	0.13	0.23	0.33
Fragaria vesca L.	0.02	0.07	0.27
Fraxinus ornus L.	0.03		

Galeopsis speciosa Miller	0.02		
***Galinsoga ciliata* (Rafin.) Blake**	0.004		
***Galinsoga parviflora* Cav.**	0.02		
Galium anisophyllum Vill.	0.04	0.17	0.20
Galium lucidum All.	0.004		0.13
Galium mollugo L.	0.23	0.03	0.67
Galium verum L.	0.19	0.33	0.53
Genista germanica L.	0.01		0.07
Genista tinctoria L.	0.01	0.03	0.13
Gentiana cruciata L.	0.01		
Gentiana pneumonanthe L.		0.03	
Geranium columbinum L.	0.04		
Geranium dissectum L.			0.07
Geranium molle L. subsp. *molle*	0.004		0.07
Geranium sylvaticum L.	0.004		
Geum urbanum L.			0.07
Gladiolus palustris Gaudin		0.13	0.07
Glechoma hederacea L.	0.03		
Gymnadenia conopsea (L.) R. Br.		0.07	0.20
Helianthemum nummularium (L.) Mill. subsp. *obscurum* (Celak.) Holub		0.07	0.07
Helictotrichon pubescens (Huds.) Pilg.			0.13
Helleborus odorus Waldst. & Kit. ex Willd		0.03	0.13
Heracleum sphondylium L.	0.01	0.03	0.33

Hieracium umbellatum L.	0.03	0.03	
Hippocrepis comosa L.			0.07
Holcus lanatus L.	0.03	0.30	0.20
Hypericum maculatum Crantz	0.02		0.33
Hypericum perforatum L.	0.11	0.13	
Hypochaeris maculata L.	0.02		0.13
Inula hirta L.	0.02		0.07
Iris graminea (L.) Medik.			0.07
Knautia drymeia Heuffel	0.01	0.17	0.07
Knautia illyrica Beck	0.06	0.27	0.80
Koeleria pyramidata (Lam.) Domin	0.01	0.23	0.07
Lathyrus pratensis L.	0.18	0.23	0.33
Lathyrus vernus (L.) Bernh.			0.07
Leontodon hispidus L.	0.35	0.33	0.53
Leucanthemum ircutianum (Turcz.) DC.	0.25	0.13	0.33
Lilium bulbiferum L.			0.07
Lilium martagon L.		0.03	0.07
Linum bienne Miller	0.05		0.07
Lolium perenne L.	0.01		
Lotus corniculatus L.	0.33	0.37	0.53
Luzula campestris L. (inc. *Luzula multiflora* (Ehrh.) Lej.)			0.33
Lysimachia vulgaris L.	0.13	0.07	
Medicago falcata L.	0.01		
Medicago lupulina L.	0.15		

*Medicago sativa L.	0.03	0.03	0.20
Medicago x *varia* Martyn		0.03	
Molinia coerulea (L.) Moench *subsp. arundinacea* (Schrank) H.K.G.Paul	0.28	0.10	0.20
Narcissus radiiflorus L.			0.20
Nardus stricta L.		0.03	
Onobrychis arenaria (Kit.) DC.		0.03	
Ononis spinosa L.	0.01	0.03	
Orchis mascula (L.) L.			0.13
Orlaya grandiflora (L.) Hoffm.		0.03	0.13
Ornithogalum umbellatum L.			0.07
Orobanche caryophyllacea Sm.			0.07
Orobanche gracilis Sm.			0.07
Ostrya carpinifolia Scop.	0.004		
*Oxalis fontana Bunge	0.07	0.07	
*Panicum capillare L.	0.03		
Papaver rhoeas L.			0.07
Pastinaca sativa L.	0.01		
Persicaria maculosa Gray	0.01		
Petrorhagia saxifraga (L.) Link	0.01	0.03	
Peucedanum cervaria (L.) Lapeyr.			0.07
Peucedanum oreoselinum (L.) Moench	0.37	0.53	0.53
Phyteuma zahlbruckneri Vest	0.01	0.20	0.20
Picris hieracioides L.	0.004		

*Pimpinella major (*L.) Huds.	0.07	0.10	0.27
Pimpinella saxifraga L.	0.01	0.07	
Plantago argentea L.		0.03	0.07
Plantago lanceolata L.	0.53	0.40	0.73
Plantago major L.	0.04	0.03	
Plantago media L.	0.08	0.10	0.27
Poa pratensis L.			0.27
Poa trivialis L.		0.03	0.07
Polygala comosa Schkuhr.			0.13
Polygala vulgaris L.		0.03	0.07
Polygonatum verticillatum (L.) All			0.07
Portulaca oleracea L.	0.004		
Potentilla alba L.	0.01	0.07	0.07
Potentilla erecta (L.) Räuschel	0.24	0.30	0.13
Potentilla pusilla L.		0.03	
Potentilla reptans L.	0.01		
Primula vulgaris Huds.		0.03	0.13
Prunella grandiflora (L.) Scholler	0.17	0.23	0.20
Prunella vulgaris L.	0.15	0.07	
Prunus avium L.	0.004		
Pseudorchis albida (L.) Á. Löve & D. Löve			0.07
Pteridium aquilinum (L.) Kuhn		0.03	0.07
Pulmonaria officinalis L.	0.004		
Ranunculus aconitifolius L.			0.07

Ranunculus acris L.	0.13	0.03	0.53
Ranunculus bulbosus L.	0.01		0.13
Ranunculus lanuginosus L.		0.03	
Ranunculus montanus Willd			0.13
Ranunculus polyanthemophyllus Koch & Hess	0.25	0.20	0.27
Ranunculus repens L.	0.02		
Rhinanthus freynii (A.Kern. ex Sterneck) Fiori	0.004		0.33
Rhinanthus glacialis Personnat		0.20	0.20
*Robinia pseudoacacia L.	0.02		
Rubus caesius L.	0.01		0.07
Rubus idaeus L.	0.12	0.03	0.20
Rubus ulmifolius Schott.			0.07
Rumex acetosa L.	0.03	0.10	0.47
Rumex alpestris Jacq.	0.004		0.13
Salix appendiculata Vill.	0.004		
Salix caprea L.	0.02		
Salvia glutinosa L.			0.07
Salvia pratensis L.	0.13	0.20	0.47
Sanguisorba minor Scop.	0.04	0.07	0.07
Scabiosa triandra L.	0.05	0.03	0.07
Scorzonera humilis L.	0.05	0.07	0.13
Scorzonera villosa Scop.		0.03	0.07
Securigera varia (L.) Lassen		0.03	0.07
Senecio jacobaea L.			0.07

Serratula tinctoria L.	0.03	0.07	0.13
Sesleria caerulea (L.) Ard			0.13
Setaria pumila (Poir.) Roem. & Schult.	0.14		
Setaria viridis (L.) P.Beauv. subsp. *pycnocoma* (Steud.) Tzvelev	0.18		
Setaria viridis (L.) P.Beauv. subsp. *viridis*	0.06		
Sherardia arvensis L.			0.13
Silene nutans L.			0.13
Silene vulgaris (Moench) Garcke subsp. *vulgaris*	0.05		0.13
Solanum nigrum L.	0.14		
Solidago virgaurea L.	0.01		
Sonchus oleraceus L.	0.08		0.07
***Sorghum halepense* (L.)Pers.**	0.004		
Stachys recta L.	0.01		
Stellaria graminea L.		0.07	
Stellaria holostea L.			0.07
Stellaria media (L.) Vill.	0.004		
Succisa pratensis Moench			0.07
Symphytum tuberosum L.			0.07
Taraxacum sect. *Taraxacum* F.H. Wigg	0.20	0.03	0.47
Teucrium chamaedrys L.	0.01		
Thalictrum aquilegifolium L.		0.03	0.13
Thesium bavarum Schrank			0.07
Thymus pulegioides L.	0.07	0.27	0.20

Tilia cordata Miller	0.004		0.07
Tragopogon pratensis L.	0.004		0.33
Traunsteinera globosa (L.) Rchb.			0.07
Trifolium campestre Schreb.	0.01		0.13
Trifolium incarnatum L.			0.13
Trifolium montanum L.	0.07	0.20	0.20
Trifolium pratense L.	0.37	0.37	0.67
Trifolium repens L.	0.14	0.07	
Trifolium rubens L.		0.07	0.13
Trisetum flavescens (L.) P. Beauv		0.03	0.13
Trollius europaeus L.	0.01	0.10	0.20
Tussilago farfara L.	0.03		0.07
Ulmus minor Miller	0.01		
Urtica dioica L.	0.01		0.07
Valeriana officinalis L.		0.03	
Valeriana tripteris L.	0.01		
Veratrum lobelianum Bernh.			0.07
Verbascum chaixii Vill.	0.08	0.17	
Verbascum nigrum L.			0.07
Verbascum phoeniceum L.			0.07
Veronica chamaedrys L.	0.04		0.33
*Veronica persica Poir.	0.02		
Vicia cracca L.	0.08	0.07	0.13
Vicia hirsuta (L.) S.F.Gray		0.03	

Vicia sativa L.			0.07
Vicia sepium L.	0.01	0.10	0.20
Vincetoxicum hirundinaria Medik.		0.03	0.07
Viola canina L.		0.03	
Viola hirta L.	0.03	0.03	0.07
Viola reichenbachiana Boreau		0.03	
Viola riviniana Rchb.		0.03	

Invertebrate herbivores

Supplementary methods

To study which invertebrate herbivores were excluded using our treatments, we sampled herbivore communities using two sampling methods: sweep-net and pitfalls. We carried out overall 6 rounds of both methods. To collect ground-dwelling insects, we placed three pitfalls in each block and filled them with glycole. Traps were emptied every 2 weeks. We sampled herbivore insects using a sweep net along a 50 m long transect in each selected site. Insects were placed in ethanol 70 % for further investigation in the lab. We pooled all 6 rounds and counted orthopteran (Orthoptera: Caelifera) and leafhopper (Auchenorrhyncha) individuals sampled by sweep net, and, at a broader taxonomical level, all orthopteran and gastropod individuals captured by pitfall. We did not find any response of herbivore abundance to elevation (Table S8).

Table B S9: Pearson's correlation tests for each taxon. Correlation tests revealed no significant relationship between logarithmic transformed abundance and elevation.

Sampling	Taxon	*r*	p
sweepnet	leafhoppers	-0.46	0.09
	orthopterans	-0.27	0.32
pitfalls	gastropods	-0.41	0.13
	orthopterans	-0.36	0.18

Appendix C (Chapter 3)

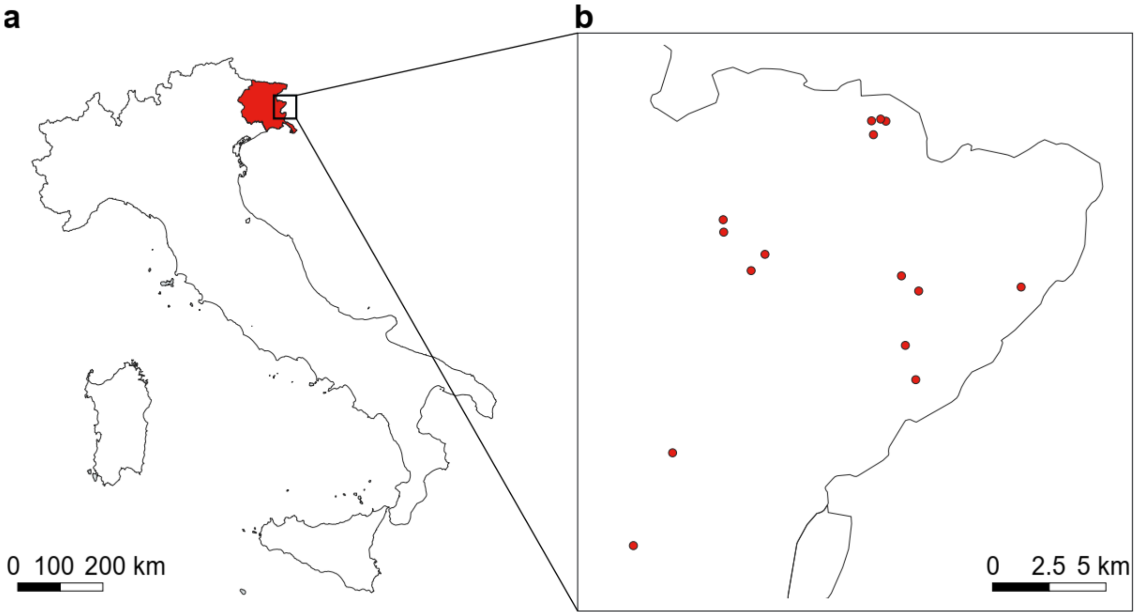


Figure C S1: study area in North Eastern Italy (a) and site location (b).

Table C S1: geographic coordinates and elevation of the 15 selected sites.

Site	Long	Lat	Elevation
1	13.5463055	46.1134	420
2	13.555669	46.13448	520
3	13.5464704	46.14088	190
4	13.4102486	46.07602	110
5	13.6142242	46.13372	600
6	13.550968	46.09943	650
7	13.5349292	46.19735	1080
8	13.539894	46.20277	1310
9	13.539549	46.20335	1320
10	13.539421	46.20355	1330
11	13.446384	46.16219	850
12	13.446485	46.16712	920
13	13.3846645	46.04031	100
14	13.4692074	46.1525	510
15	13.4611034	46.14618	660

Table C S2: list of the plant species recorded in the 15 semi-natural dry grasslands. Nomenclature follows Poldini et al. (2001).

Species
Achillea millefolium aggr.
Aegopodium podagraria L.
Ajuga reptans L.
Alchemilla vulgaris aggr.
Anemone nemorosa L.
Anisantha sterilis (L.) Nevski
Anthoxanthum odoratum L. subsp. *odoratum*
Anthyllis vulneraria L.
Arenaria serpyllifolia L.
Aristolochia rotunda L. subsp. *rotunda*
Arnica montana L.
Arrhenatherum elatius (L.) Presl subsp. *elatius*
Asperula cynanchica L.
Betonica alopecuros L.
Betonica officinalis L.
Betula pendula Roth
Biscutella laevigata L.
Brachypodium rupestre (Host) Roem. & Schult.
Briza media L.
Bromopsis erecta (Huds.) Fourr.
Buphthalmum salicifolium L.
Leontodon hispidus L.
Leucanthemum ircutianum (Turcz.) DC.
Lilium bulbiferum L.
Lilium martagon L.
Linum bienne Miller
Lotus corniculatus L. s.s.
Luzula campestris L.
Medicago sativa L.
Molinia coerulea (L.) Moench
Narcissus radiiflorus L.
Orchis mascula (L.) L.
Orlaya grandiflora (L.) Hoffm.
Ornithogalum umbellatum L.
Orobanche caryophyllacea Sm.
Orobanche gracilis Sm.
Papaver rhoeas L.
Peucedanum cervaria (L.) Lapeyr.
Peucedanum oreoselinum (L.) Moench
Phyteuma zahlbruckneri Vest
Pimpinella major (L.) Huds.
Plantago argentea L.

Calluna vulgaris (L.) Hull
Capsella bursa-pastoris (L.) Medicus
Carex caryophyllea La Tourr.
Carex flacca Schreb.
Carex hirta L.
Carex montana L.
Carex ornithopoda Willd.
Carex pallescens L.
Carex pilulifera L.
Carex sylvatica Huds.
Carum carvi L.
Centaurea jacea aggr.
Centaurea nigrescens Willd.
Centaurea scabiosa L.
Cerastium brachypetalum Desp. ex Pers.
Cerastium fontanum Baumg.
Chaerophyllum hirsutum L.
Chamaecytisus hirsutus (L.) Link
Chrysopogon gryllus (L.) Trin.
Cirsium pannonicum (L.fil.) Link
Coeloglossum viride (L.) Hartm.
Colchicum autumnale L.
Conyza canadensis (L.) Cronq.
Securigera varia L.
Plantago lanceolata L.
Plantago media L.
Poa pratensis L.
Poa trivialis L.
Polygala comosa Schkuhr.
Polygala vulgaris L.
Polygonatum verticillatum (L.) All
Potentilla alba L.
Potentilla erecta (L.) Räuschel
Primula vulgaris Huds.
Prunella vulgaris L.
Pseudorchis albida (L.) Á. Löve & D. Löve
Pteridium aquilinum (L.) Kuhn
Ranunculus aconitifolius L.
Ranunculus acris L.
Ranunculus bulbosus L.
Ranunculus montanus Willd
Ranunculus polyanthemophyllus Koch & Hess
Rhinanthus freynii (A.Kern. ex Sterneck) Fiori
Rhinanthus glacialis Personnat
Rubus caesius L.
Rubus idaeus L.
Rubus ulmifolius Schott.
Rumex acetosa L.

Corylus avellana L.

Crepis vesicaria subsp. *taraxacifolia* (Thuill.) Thell.

Crocus vernus (L.) Hill

Cruciata glabra (L.) Ehrend.

Dactylis glomerata L.

Daucus carota L.

Dianthus carthusianorum L. subsp. *sanguineus* (Vis.) Williams

Erigeron annuus (L.) Pers.

Euphorbia cyparissias L.

Euphorbia verrucosa L.

Ferulago galbanifera (Mill.) W.D.J. Koch

Festuca arundinacea Schreb

Festuca filiformis Pourr.

Festuca rubra L.

Festuca rupicola Heuffel

Filipendula vulgaris Moench

Fragaria vesca L.

Galium anisophyllum Vill.

Galium lucidum All.

Galium mollugo L.

Galium verum L.

Genista germanica L.

Genista tinctoria L

Rumex alpestris Jacq.

Salvia glutinosa L.

Salvia pratensis L.

Sanguisorba minor Scop.

Scabiosa triandra L.

Scorzonera humilis L.

Scorzonera villosa Scop.

Senecio jacobaea L.

Serratula tinctoria L.

Sesleria caerulea (L.) Ard

Sherardia arvensis L

Silene nutans L.

Silene vulgaris (Moench) Garcke

Solidago canadensis L.

Sonchus oleraceus L.

Stellaria holostea L.

Succisa pratensis Moench

Symphytum tuberosum L.

Taraxacum sect. *Taraxacum* F.H. Wigg

Thalictrum aquilegifolium L.

Thesium bavarum Schrank

Thymus pulegioides L.

Tilia cordata Miller

Geranium dissectum L.

Geranium molle L. subsp. *molle*

Geum urbanum L.

Gladiolus palustris Gaudin

Gymnadenia conopsea (L.) R. Br.

Helianthemum nummularium (L.) Mill. subsp. *obscurum* (Celak.) Holub

Helictotrichon pubescens (Huds.) Pilg.

Helleborus odorus Waldst. & Kit. ex Willd

Heracleum sphondylium L.

Hippocrepis comosa L.

Holcus lanatus L.

Hypericum maculatum Crantz

Hypochaeris maculata L.

Inula hirta L.

Iris graminea (L.) Medik.

Knautia drymeia Heuffel

Knautia illyrica Beck

Koeleria pyramidata (Lam.) Domin

Lathyrus pratensis L.

Lathyrus vernus (L.) Bernh.

Tragopogon pratensis L.

Trifolium campestre Schreb.

Trifolium incarnatum L.

Trifolium montanum L.

Trifolium pratense L.

Trifolium rubens L.

Trisetum flavescens (L.) P. Beauv

Trollius europaeus L.

Tussilago farfara L.

Urtica dioica L.

Valeriana montana L.

Verbascum nigrum L.

Verbascum phoeniceum L.

Veronica chamaedrys L.

Vicia cracca L.

Vicia sativa L.

Vicia sepium L.

Vincetoxicum hirundinaria Medik.

Viola hirta L.

Table C S3: List of orthopteran species reporting percentage of occurrence, total abundance, mobility and rarity (see Methods). Total abundances indicate the number of individuals per identified species, when modeling overall abundance per site we considered also individuals identified to the genus level. Interm = intermediate Nomenclature follows Fontana et al. (2002).

Species	Occurrence %	Total abundance	Mobility	Rarity
Aiolopus strepens (Latreille, 1804)	20	4	macropterous	interm.
Anisoptera fusca (Fabricius, 1793)	40	38	macropterous	common
*Bicolorana bicolor (*Philippi, 1830)	20	7	brachypterous	interm.
Calliptamus italicus (Linnaeus, 1758)	13	4	macropterous	rare
Chorthippus dorsatus (Zetterstedt, 1821)	53	47	brachypterous	common
*Chorthippus parallelu*s (Zetterstedt, 1821)	73	126	brachypterous	common
Euchorthippus declivus (Brisout, 1848)	20	14	brachypterous	interm.
Euthystira brachyptera (Ocskay, 1826)	27	25	brachypterous	interm.
Glyptobothrus brunneus (Thunberg, 1815)	7	1	macropterous	rare
Glyptobothrus mollis (Charpentier, 1825)	27	22	macropterous	interm.
Gomphocerippus rufus (Linnaeus, 1758)	40	25	macropterous	common
Mecostethus parapleurus (Hagenbach, 1822)	13	15	macropterous	rare
Metrioptera brachyptera (Linnaeus, 1761)	7	1	brachypterous	rare
Micropodisma salamandra (Fischer, 1853)	53	400	apterous	common
Omocestus haemorroidalis (Charpentier, 1825)	7	1	macropterous	rare
Omocestus rufipes (Zetterstedt, 1821)	53	50	macropterous	common
Omocestus viridulus (Linnaeus, 1758)	13	2	macropterous	rare
Pachytrachis gracilis (Brunner v. W., 1861)	67	44	brachypterous	common
Pachytrachis striolatus (Fieber, 1853)	13	2	brachypterous	rare

Pezotettix giornae (Rossi, 1794)	20	8	squamipterous	interm.
Pholidoptera littoralis (Fieber, 1853)	13	2	brachypterous	rare
Poecilimon elegans (Brunner von Wattenwyl, 1878)	7	1	brachypterous	rare
Poecilimon ornatus (Schmidt, 1849)	13	2	brachypterous	rare
Polysarcus denticauda (Charpentier, 1825)	7	1	brachypterous	rare
Roeseliana roeselii (Hagenbach, 1822)	20	6	brachypterous	interm.
Ruspolia nitidula (Scopoli, 1786)	60	32	macropterous	common
Stauroderus scalaris (Fischer v. W., 1846)	7	1	macropterous	rare
Stenobothrus lineatus (Panzer, 1796)	7	1	macropterous	rare
Tetrix bipunctata (Linnaeus, 1758)	47	33	squamipterous	common
Tetrix subulata (Linnaeus, 1758)	7	1	squamipterous	rare
Tetrix tenuicornis (Sahlberg, 1893)	13	2	squamipterous	rare

Table C S4: List of leafhopper species reporting percentage of occurrence, total abundance, mobility and rarity (see Methods). Total abundances indicate the number of individuals per identified species, when modelling overall abundance per site we considered also identified to the genus level. Interm = intermediate. Nomenclature follows Biedermann, & Niedringhaus (2009).

Species	Occurrence %	Total abundance	Mobility	Rarity
Acanalonia conica (Say, 1830)	13	2	macropterous	rare
Acanthodelphax spinosa (Fieber, 1866)	33	8	brachypterous	common
Adarrus multinotatus (Boheman, 1847)	80	153	macropterous	common
Allygidius abbreviatus (Lethierry, 1878)	27	10	macropterous	interm.
Allygidius commutatus (Fieber, 1872)	7	1	macropterous	rare
Anaceratagallia laevis (Ribaut, 1935)	7	1	macropterous	rare
Anaceratagallia ribauti (Ossiannilsson, 1938)	27	17	macropterous	interm.
Anakelisia perspicillata (Boheman, 1845)	13	14	brachypterous	rare
Aphrodes bicincta (Schrank, 1776)	7	1	macropterous	rare
Aphrodes makarovi Zachvatkin, 1948	60	42	macropterous	common
Aphrophora alni (Fallén, 1805)	73	46	macropterous	common
Arboridia parvula (Boheman, 1845)	7	1	macropterous	rare
Arthaldeus striifrons (Kirschbaum, 1868)	33	14	macropterous	common
Asiraca clavicornis (Fabricius, 1794)	7	3	brachypterous	rare
Balclutha punctata (Fabricius, 1775)	7	1	macropterous	rare
Balclutha saltuella (Kirschbaum, 1868)	53	14	macropterous	common
Chlorita sp.	20	21	macropterous	interm.
Cicadella viridis (Linnaeus, 1758)	40	82	macropterous	common
Cicadula persimilis (Edwards, 1920)	33	16	macropterous	common

Cixius sp.	7	1	macropterous	rare
Deltocephalus pulicaris (Fallén, 1806)	20	10	macropterous	interm.
Dicranotropis divergens Kirschbaum, 1868	53	25	brachypterous	common
Dicranotropis hamata (Boheman, 1847)	47	82	brachypterous	common
Dictyophara europaea (Linnaeus, 1767)	40	45	macropterous	common
Ditropis flavipes (Signoret, 1865)	13	7	brachypterous	rare
Doratura impudica Horváth, 1897	40	65	brachypterous	common
Elymana sulphurella (Zetterstedt 1828)	20	18	macropterous	interm.
Emelyanoviana mollicula (Boheman, 1845)	40	29	macropterous	common
Empoasca pteridis (Dahlbom ,1850)	20	9	macropterous	interm.
Eupelix cuspidata (Fabricius, 1775)	7	1	macropterous	rare
Eupteryx atropunctata (Goeze 1778)	13	6	macropterous	rare
Eupteryx austriaca (Metcalf, 1968)	7	2	macropterous	rare
Eupteryx notata Curtis, 1837	47	27	macropterous	common
Eupteryx tenella (Fallén 1806)	13	14	macropterous	rare
Euscelis incisus (Kirschbaum, 1858)	87	171	macropterous	common
Evacanthus interruptus (Linnaeus, 1758)	20	14	macropterous	interm.
Forcipata citrinella (Zetterstedt, 1828)	33	42	macropterous	common
Forcipata flava Vidano, 1965	20	13	macropterous	interm.
Goniagnathus brevis (Herrich-Schäffer, 1835)	7	2	macropterous	rare
Graphocraeus ventralis (Fallen, 1806)	40	17	macropterous	common
Hesium domino (Reuter, 1880)	13	10	macropterous	rare
Horvathianella palliceps (Horvath, 1897)	20	22	brachypterous	interm.
Hyalesthes scotti Ferrari, 1882	7	4	macropterous	rare

Issus muscaeformis (Schrank, 1781)	7	1	macropterous	rare
Jassargus flori (Fieber, 1869)	27	198	macropterous	interm.
Jassargus obtusivalvis (Kirschbaum 1868)	67	458	macropterous	common
Laodelphax striatella (Fallen, 1826)	20	8	brachypterous	interm.
Lepyronia coleoptrata (Linnaeus, 1758)	47	38	macropterous	common
Macropsis fuscula (Zetterstedt, 1953)	7	1	macropterous	rare
Macrosteles cristatus (Ribaut, 1927)	20	6	macropterous	interm.
Megadelphax sordidulus (Stal, 1853)	7	7	brachypterous	rare
Megophthalmus sp.	7	1	macropterous	rare
Metcalfa pruinosa (Say, 1830)	13	2	macropterous	rare
Mocydia crocea (Herrich-Schäffer, 1837)	40	57	macropterous	common
Muellerianella extrusa (Scott, 1871)	27	10	brachypterous	interm.
Muirodelphax aubei (Perris, 1857)	20	7	brachypterous	interm.
Neophilaenus campestris (Fallén, 1805)	20	5	macropterous	interm.
Neophilaenus infumatus (Haupt, 1917)	7	1	macropterous	rare
Ophiola sp.	7	1	macropterous	rare
Orientus ishidae (Matsumura, 1902)	20	4	macropterous	interm.
Philaenus spumarius (Linnaeus, 1758)	80	223	macropterous	common
Planaphrodes sp.	7	1	macropterous	rare
Psammotettix alienus (Dahlbom ,1850)	27	44	macropterous	interm.
Psammotettix cephalotes (Herrich-Schäffer, 1834)	20	4	macropterous	interm.
Psammotettix confinis (Dahlbom, 1850)	27	15	macropterous	interm.
Psammotettix nardeti Remane, 1965	13	3	macropterous	rare
Psammotettix striatus (Linnaeus, 1758)	7	1	macropterous	rare

Recilia coronifer (Marshall, 1866)	13	2	macropterous	rare
Reptalus cuspidatus (Fieber, 1876)	20	15	macropterous	interm.
Rhopalopyx elongata Wagner, 1952	7	5	macropterous	rare
Ribautiana sp.	7	1	macropterous	rare
Ribautodelphax pungens (Ribaut, 1953)	53	139	brachypterous	common
Stenocranus minutus (Fabricius, 1787)	27	15	macropterous	interm.
Stictocephala bisonia Kopp e Yonke, 1977	13	8	macropterous	rare
Tetartostylus illyricus (Kirschbaum, 1868)	7	1	macropterous	rare
Tettigometra sp.	7	1	macropterous	rare
Thamnotettix sp.	7	1	macropterous	rare
Toya propinqua (Fieber, 1866)	7	1	brachypterous	rare
Turrutus socialis (Flor, 1861)	20	32	macropterous	interm.
Utecha trivia (Germar, 1821)	7	2	macropterous	rare
Zygina sp.	13	2	macropterous	rare
Zyginidia pullula (Boheman 1845)	7	1	macropterous	rare

Table C S5: Effects of temperature and plant species richness (plant spr) on the species richness (spr) and abundance (abu) of common, intermediate, and rare species of orthopterans and leafhoppers, separately.

Response variable	Mobility	Fixed factor	χ^2	df	F	p
Orthopteran spr	Common	temperature	0.225	1	2.472	0.142
		plant spr	0.049	1	0.539	0.477
	Intermediate	temperature	0.001	1	0.007	0.936
		plant spr	0.741	1	3.331	0.093
	Rare	temperature	0.122	1	0.477	0.503
		plant spr	0.008	1	0.033	0.860
Orthopteran abu	Common	temperature	0.071	1	0.104	0.752
		plant spr	0.570	1	0.840	0.377
	Intermediate	temperature	0.446	1	0.389	0.545
		plant spr	0.822	1	0.717	0.414
	Rare	temperature	1.250	1	2.515	0.139
		plant spr	0.399	1	0.804	0.388
Leafhopper spr	Common	temperature	0.029	1	0.206	0.658
		plant spr	0.060	1	0.417	0.531
	Intermediate	temperature	0.009	1	0.041	0.844
		plant spr	0.009	1	0.044	0.837
	Rare	temperature	1.191	1	2.518	0.139
		plant spr	0.582	1	1.230	0.289
Leafhopper abu	Common	temperature	1.672	1	1.627	0.226
		plant spr	0.501	1	0.488	0.498
	Intermediate	temperature	0.764	1	0.716	0.414

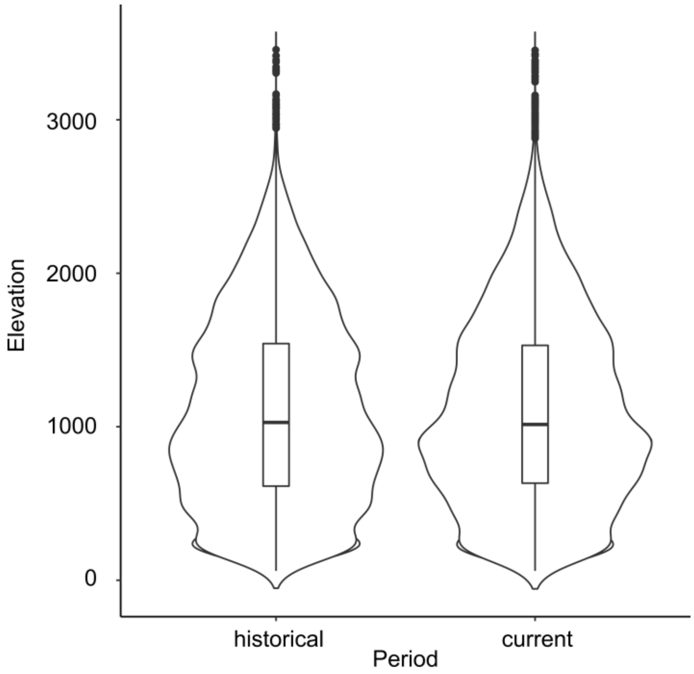
	plant spr	0.070	1	0.066	0.802
Rare	temperature	3.143	1	3.298	0.094
	plant spr	1.282	1	1.346	0.269

Table C S6: Effects of temperature and plant species richness (plant spr) on the species richness (spr) and abundance (abu) of macropterous and non-macropterous orthopteran and leafhoppers, separately.

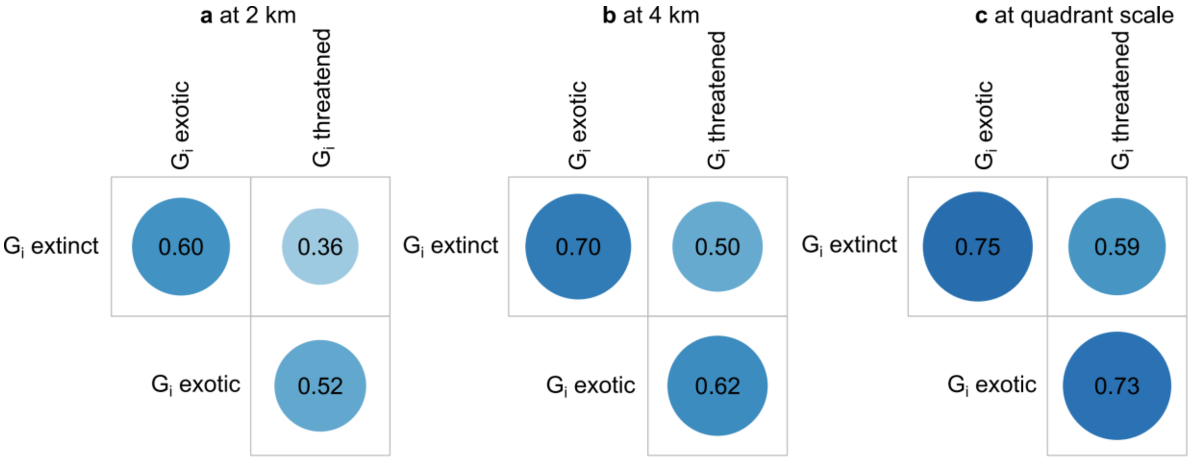
Response variable	Mobility	Fixed factor	χ^2	df	F	p
Orthopteran spr	Macropterous	temperature	0.050	1	3.629	0.081
		plant spr	0.029	1	2.065	0.176
	Non-macropterous	temperature	0.063	1	0.569	0.465
		plant spr	0.093	1	0.844	0.376
Orthopteran abu	Macropterous	temperature	5.261	1	7.801	0.016
		plant spr	0.870	1	1.290	0.278
	Non-macropterous	temperature	0.091	1	0.103	0.754
		plant spr	0.151	1	0.170	0.687
Leafhopper spr	Macropterous	temperature	0.088	1	0.436	0.521
		plant spr	0.023	1	0.116	0.739
	Non-macropterous	temperature	0.215	1	0.860	0.372
		plant spr	0.557	1	2.224	0.162
Leafhopper abu	Macropterous	temperature	2.203	1	2.347	0.152
		plant spr	0.663	1	0.707	0.417
	Non-macropterous	temperature	0.912	1	0.783	0.394
		plant spr	1.985	1	1.704	0.216

Appendix D (Chapter 4)

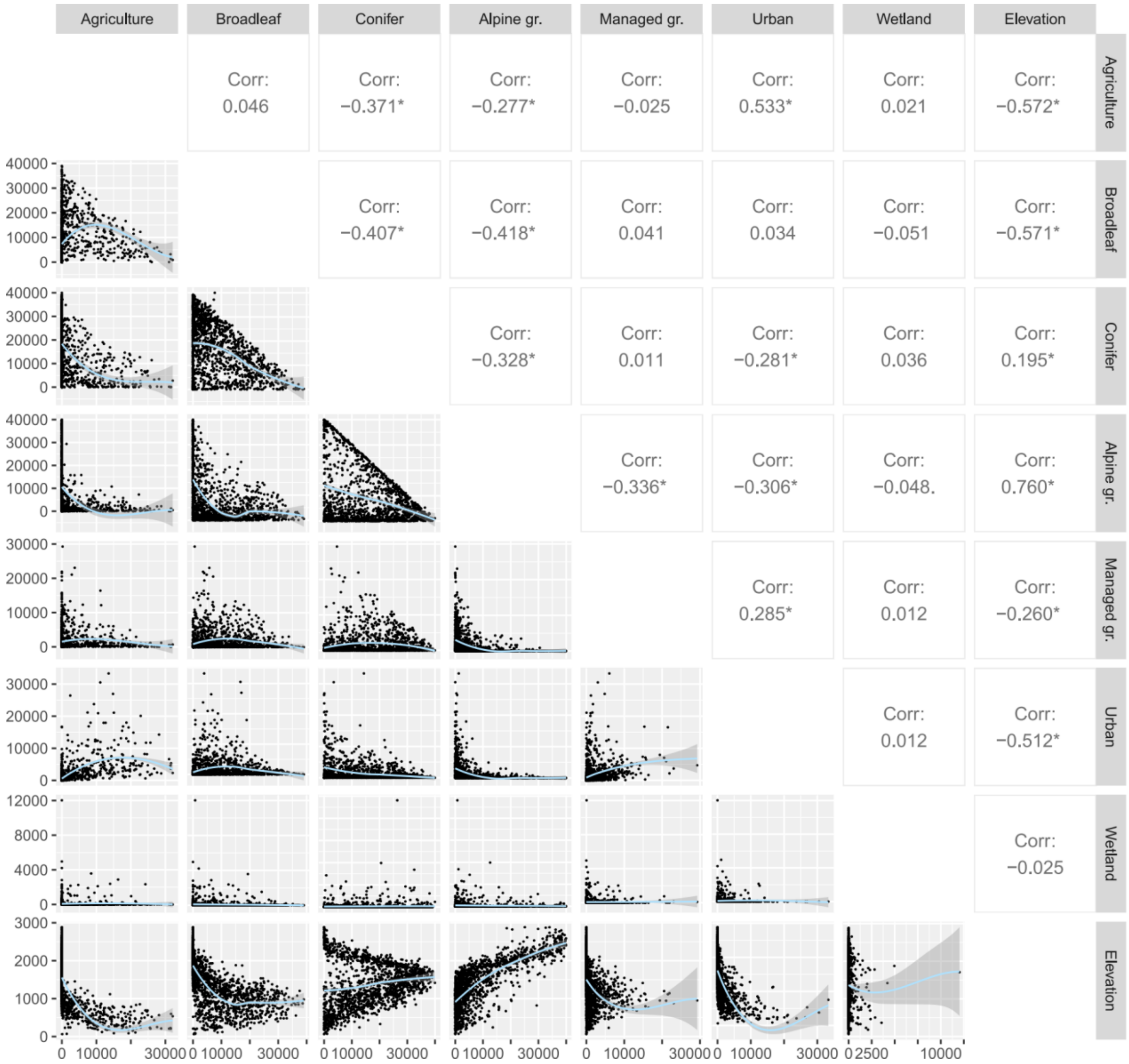
Supplementary Figure D1: Study area in the Trento Province, NE Italy, 6’207 km^2, elevation range 66–3’769 m a.s.l.



Supplementary Figure D2: Number of records along the elevational gradient in the historical and current period (1990-2004; 2005-2019). In the two periods, there were roughly the same number of records (640’851 vs. 512’310).



Supplementary Figure D3: Pearson correlations between ln-transformed G_i statistics at a) 2 × 2 km^2 , b) 4 × 4 km^2 , c) quadrant level.

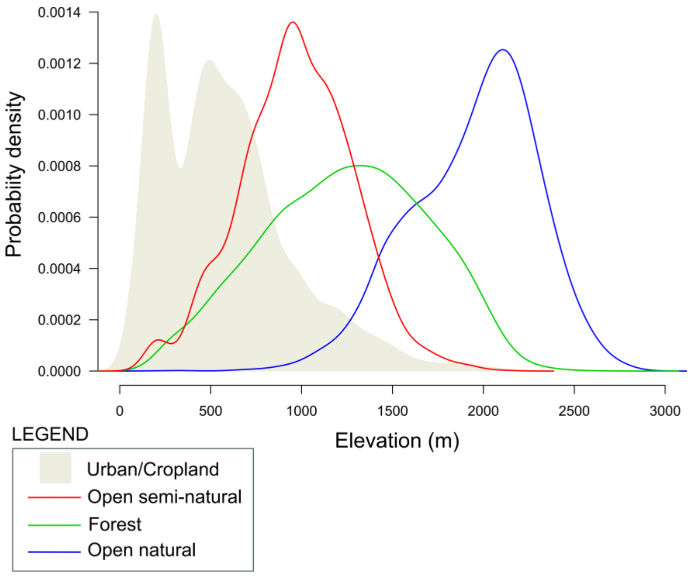


Supplementary Figure D4: correlation between landscape variables measured in each grid cell (2 × 2 km^2): agriculture, broadleaf forest, conifer forest, alpine grassland, managed grassland, urban, wetland and mean elevation. Light blue lines indicate smooth local regression. Corr indicates Pearson correlation coefficients.

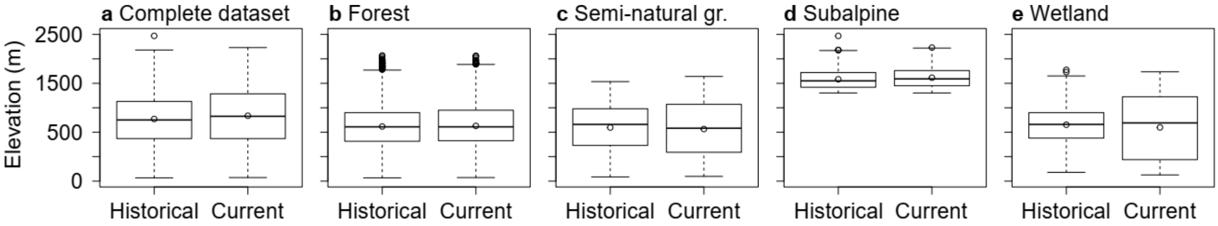
Supplementary Table D1: effect of the interaction between plant status and edge type on range shift. Shift values were transformed to achieve normality of the residuals (see Methods). Coefficients are estimated from LMM. N = 1491 species.

Fixed effect	Value	Std.Error	df	t	p
Edge (Rear)	-0.892	0.236	1387	-3.775	< 0.001
Status (Common)	-0.470	0.189	1499	-2.485	0.013
Status (Threatened)	-1.053	0.227	1499	-4.650	< 0.001
Edge (Rear) : Status (Common)	1.109	0.241	1387	4.606	< 0.001
Edge (Rear) : Status (Threatened)	2.003	0.287	1387	6.979	< 0.001

Appendix E (Chapter 5)



Supplementary Figure E1: Density function of habitat availability at the regional scale over the elevational gradient. Data come from regional land-use maps. Wetlands did not present a clear elevational pattern, i.e. areas were more or less equally distributed across different elevations.



Supplementary Figure E2: Sampling effort over the elevational gradient in both the historical (1990-2003) and current (2004-2017) periods for the complete dataset and for each habitat type. Complete dataset: n = 10,293 historical sites, n = 11,308 current sites. Boxplots display minimum, maximum, median, first quartile, and third quartile and were drawn using the default settings in the boxplot() function in R.

Supplementary Table E1: List of the orchid species with the number of records in the historical (1990-2003) and current (2004-2017) time periods, habitat preferences, min and max elevation reported in the dataset, and threat category as indicated in the Italian Red List of Threatened Species[*]. Red List categories as follows, in increasing level of threat: NE – Not Evaluated; LC – Least Concern; NT – Near Threatened; VU – Vulnerable; EN – Endangered. We followed Perazza & Lorenz (2013) for the nomenclature of the species. In the last column, we indicated if the species was included in the population dynamics and range shift analyses (Hist) and/or resurvey analysis (Res).

Species	Count historical	Count current	Habitat preference	Elevation (m)		Red list	Analysis
				Min	Max		
Anacamptis pyramidalis	285	282	Semi-natural	85	1620	NT	Hist, Res
Cephalanthera damasonium	556	547	Forest	140	1650	NE	Hist, Res
Cephalanthera longifolia	1215	1100	Generalist	95	2040	NE	Hist, Res
Cephalanthera rubra	428	228	Forest	125	1700	NE	Hist, Res
Chamorchis alpina	224	163	Subalpine	1580	2660	NE	Hist
Coeloglossum viride	1285	1257	Grassland	570	2970	NE	Hist, Res
Corallorhiza trifida	468	187	Forest	615	2150	NE	Hist, Res
Cypripedium calceolus	556	259	Generalist	380	2295	LC	Hist, Res
Dactylorhiza fuchsii	2840	3759	Generalist	230	2450	NE	Hist, Res
Dactylorhiza incarnata	141	51	Wetland	179	1820	VU	Hist, Res
Dactylorhiza lapponica	94	35	Wetland	400	2145	VU	Hist, Res
Dactylorhiza majalis	66	73	Wetland	1156	2276	NT	Hist, Res
Dactylorhiza sambucina	521	310	Grassland	250	2220	NE	Hist
Epipactis atrorubens	1580	1389	Forest	160	2400	NE	Hist, Res
Epipactis bugacensis	0	82	Wetland	126	212	NE	Res
Epipactis helleborine	1020	1083	Forest	140	1890	NE	Hist, Res
Epipactis muelleri	158	138	Forest	184	1490	NE	Hist, Res

Epipactis palustris	132	48	Wetland	194	1610	NT	Hist, Res
Epipogium aphyllum	120	78	Forest	695	1850	VU	Hist
Goodyera repens	848	359	Forest	250	1960	NE	Hist, Res
Gymnadenia conopsea	2286	1747	Grassland	165	2620	NE	Hist, Res
Gymnadenia odoratissima	827	622	Grassland	100	2500	NE	Hist, Res
Himantoglossum adriaticum	44	203	Semi-natural	270	1030	VU	Hist, Res
Limodorum abortivum	338	267	Forest	66	1180	NE	Hist, Res
Liparis loeselii	16	13	Wetland	437	1018	EN	Res
Listera cordata	383	252	Forest	900	2130	NE	Hist, Res
Listera ovata	1472	950	Generalist	100	2235	NE	Hist, Res
Neottia nidus avis	1392	1440	Forest	140	1820	NE	Hist, Res
Nigritella buschmanniae	51	93	Subalpine	1880	2545	NE	Hist
Nigritella miniata	195	284	Subalpine	1280	2690	NT	Hist
Nigritella rhellicani	1179	1301	Subalpine	1155	2720	NE	Hist, Res
Ophrys apifera	22	70	Semi-natural	98	890	NT	Res
Ophrys bertolonii	70	55	Semi-natural	100	820	EN	Hist, Res
Ophrys holosericea	57	106	Semi-natural	145	1020	VU	Hist, Res
Ophrys insectifera	280	173	Generalist	200	2100	NE	Hist, Res
Ophrys sphegodes	175	134	Semi-natural	85	950	NT	Hist, Res
Orchis coriophora	29	6	Semi-natural	540	1330	NE	Res
Orchis mascula	408	223	Generalist	240	2570	NE	Hist, Res
Orchis militaris	389	174	Semi-natural	100	2140	NT	Hist, Res
Orchis morio	276	188	Semi-natural	90	1470	NT	Hist, Res
Orchis purpurea	121	196	Generalist	140	1500	NT	Hist, Res

Orchis simia	76	63	Semi-natural	90	1040	NT	Hist, Res
Orchis tridentata	429	224	Semi-natural	98	1540	NE	Hist, Res
Orchis ustulata	328	115	Grassland	215	2050	NE	Hist, Res
Platanthera bifolia	1313	1048	Generalist	180	2480	NE	Hist, Res
Platanthera chlorantha	200	67	Generalist	250	1700	NE	Hist, Res
Pseudorchis albida	977	1210	Subalpine	900	2705	NE	Hist, Res
Spiranthes spiralis	14	32	Semi-natural	90	790	NE	Res
Traunsteinera globosa	578	441	Grassland	375	2560	NE	Hist

[*] IUCN & Società Botanica Italiana. Lista rossa della flora Italiana. 58 (2013).

Supplementary Table E2: Effect of time (difference in years between the two surveys), historical population size, habitat preference, elevation, and habitat alteration (yes and no) on the probability that the orchid population survived until the resurvey. We fitted generalized linear mixed models assuming a binomial distribution with species as random factor (see Methods). Elevation was standardized to mean 0 and SD 1 to make elevational ranges comparable among species.

	Estimate	SE	t	p
Time	-0.094	0.086	-1.104	0.269
log (Size)	0.521	0.088	5.932	<0.001
Generalist	0.140	0.254	0.551	0.582
Grassland	-0.758	0.386	-1.962	0.050
Semi-natural grassland	-0.413	0.258	-1.602	0.109
Subalpine	-0.386	0.496	-0.778	0.437
Wetland	-0.148	0.388	-0.380	0.704
Elevation	0.274	0.092	2.984	0.003
Habitat alteration	-0.539	0.174	-3.098	0.002

Supplementary Table E3: Effect of time (year 1990-2017), elevation and their interaction on population size within each habitat preference category. Elevation was standardized to mean 0 and SD 1 to make elevational ranges comparable among species. We fitted generalized linear mixed models assuming a Poisson distribution with species and OLRE as random effects (see Methods). All variables were scaled.

	Fixed factor	Estimate	SE	t	p
Forest	Elevation^2	-0.123	0.012	-10.546	<0.001
	Elevation	0.028	0.012	2.418	0.016
	Time	-0.163	0.012	-14.074	<0.001
	Elevation x Time	0.036	0.012	3.098	0.002
Generalist	Elevation^2	-0.212	0.013	-16.879	<0.001
	Elevation	-0.093	0.012	-7.479	<0.001
	Time	-0.222	0.013	-17.610	<0.001
	Elevation x Time	0.023	0.013	1.841	0.066
Grassland	Elevation^2	-0.236	0.020	-11.890	<0.001
	Elevation	0.123	0.019	6.403	<0.001
	Time	-0.140	0.019	-7.515	<0.001
	Elevation x Time	0.048	0.019	2.532	0.011
Semi-natural grassland	Elevation^2	-0.095	0.030	-3.129	0.002
	Elevation	-0.172	0.030	-5.763	<0.001
	Time	0.023	0.030	0.749	0.454
	Elevation x Time	0.016	0.031	0.511	0.609
Subalpine	Elevation^2	-0.175	0.026	-6.807	<0.001
	Elevation	0.066	0.025	2.690	0.007
	Time	-0.253	0.025	-10.266	<0.001
	Elevation x Time	0.049	0.024	2.022	0.043
Wetland	Elevation^2	-0.136	0.074	-1.836	0.066
	Elevation	0.106	0.073	1.451	0.147
	Time	0.015	0.074	0.204	0.839
	Elevation x Time	0.086	0.075	1.153	0.249

Supplementary Table E4: Range shifts (m year^{-1}) calculated on resurveyed species with at least 10 records per survey.

Species	Rear edge	Optimum	Leading edge	Count Initial survey	Count Second survey
Anacamptis pyramidalis	2.307	3.402	-4.566	52	38
Cephalanthera damasonium	1.19	1.826	-4.583	28	30
Cephalanthera longifolia	-0.758	10.343	-9.273	74	46
Cephalanthera rubra	8.284	6.285	2.334	24	18
Coeloglossum viride	25.528	29.605	4.376	27	12
Dactylorhiza fuchsii	2.958	-1.234	-3.614	96	76
Dactylorhiza incarnata	2.915	2.334	8.177	40	19
Epipactis atrorubens	3.403	3.666	6.354	56	36
Epipactis helleborine	-0.597	26.613	-4.22	56	45
Gymnadenia conopsea	15.101	42.903	-2.055	80	45
Himantoglossum adriaticum	-7.841	-4.428	1.398	26	13
Limodorum abortivum	1.093	0.201	-13.158	37	26
Listera ovata	-1.932	0.529	8.231	50	43
Neottia nidus avis	6.049	23.805	0.643	60	38
Nigritella rhellicani	2.878	2.748	7.459	25	16
Orchis morio	-2.582	-3.048	-7.309	54	22
Orchis purpurea	9.324	7.405	-8.974	14	10
Orchis tridentata	-2.068	12.285	-1.235	47	25
Platanthera bifolia	5.761	1.688	-8.362	64	24
Pseudorchis albida	14.562	-1.699	2.381	29	14

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