Altitudinal distribution of non-native plants:
the effects of climate, habitat and introduction history

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Contents

Summary

1. A major aim of invasion biology is to predict patterns of distribution and particularly the distribution limits of non-native plant species. The distribution pattern in the area of introduction depends on the interaction of traits of the invading species and the environmental conditions. This combination of factors varies in space and time, and a promising way to understand the effect of this variation on species distribution patterns is to study the invasion process along steep environmental gradients. Studying plant invasions along environmental gradients can also help to understand plant responses to environmental variation. Such responses include phenotypic plasticity and adaptive genetic differentiation ("rapid evolution"). Both responses have been observed in non-native species, but their relative importance for invasion success is still poorly understood.

Here, I analysed the role of several factors in shaping the distribution of non-native plant species along elevational gradients. This is an appropriate approach because along steep environmental gradients biotic and abiotic factors and their interaction change over very short distances and thus allow for exclusion of the complicated factor of migration or transportation. I combined different methods (descriptive and experimental), worked at different spatial scales (global, regional and local), and analysed multiple plant species to enable generalizations about the importance of particular factors. Investigations at the regional and local scales were conducted on the island of Tenerife (Canary Islands, Spain). Oceanic islands are generally suitable model systems for studying plant invasions, and Tenerife in particular offers a steep climatic gradient from subtropical conditions at the coast to a subalpine climate at c. 2000 m a.s.l. Most of the non-native species reached their upper distribution limit somewhere along the gradient und it was possible to analyse limiting factors.

2. Almost 1000 non-native plant species were recorded in a global study including 13 mountain regions (data compiled from literature, databases, herbaria and expert knowledge). The comparison of the non-native floras of these regions revealed that the non-native mountain floras had the highest similarity with the respective adjoining lowland flora and not, as one might suspect, with neighbouring mountain regions or with other mountain floras of the same climatic zone. This suggests that in the vast majority of cases the non-native species were introduced at low elevations and spread from there up to higher elevations. Because of that, non-native species in mountains are not mountain specialists that are pre-adapted to a mountain climate, but climatically broad species. Most non-native species in the study regions were herbaceous, originated from Eurasia and were probably introduced unintentionally with pastoralism. However, land use change in mountains can alter the introduction pathways and e.g. with an increase of tourism in mountain regions it is probable that ornamental species which are climatically pre-adapted to a mountain climate will be deliberately introduced more frequently. Because of their pre-adaptation to a mountain climate these species are likely to spread by their own and to become of management concern.

3. A survey of the non-native roadside flora along an elevational gradient on Tenerife also supported the lowland introduction scenario. I compared Mediterranean (climatically well adapted to low elevations on Tenerife) with temperate (climatically maladapted) non-native annual plant species, but the climatic origin of the species did not influence the distribution patterns. Because all non-native species had to establish under lowland climatic conditions first, the climatic origin of a species was mainly important for its establishment, but not for its spread. On the other hand, I found that residence time of the non-native species was important for reaching high elevations, which might be due to the time needed for genetic adaptations to conditions at high elevations. Additionally, there was a strong influence of non-climatic (biotic and edaphic) habitat factors on the species distribution patterns. It is therefore likely that climate change could have indirect effects on non-native species distribution patterns by causing changes of non-climatic habitat factors or the shift of the habitat context.

4. In a climate chamber experiment with multiple herbaceous non-native species from Tenerife, I analysed the relative importance of phenotypic plasticity and genetic adaptation for plant invasions along an elevational gradient. All species showed a plastic response to temperature and reduced their growth under lower temperature sums. A comparison between the lower and the upper part of the elevational gradient revealed that the direction of genetic differentiation between different populations of the same species was consistent in the upper part, but inconsistent in the lower part. In the upper part, except for one species, plants from high elevations always grew lower than plants from mid-elevations, independent of the climate treatment. The different patterns might arise from the different characteristics of the two parts of the elevational gradient: in the lower part, strong anthropogenic influences and high gene flow might hinder genetic adaptation, while in the upper part, reduced gene flow and strong selection pressures exerted by low temperatures could favour genetic differentiation.

5. Research along elevational gradients is a valuable approach to analyse limiting factors of plant invasions. I demonstrated that an integrative approach with different methods and scales and multiple species can help to understand general mechanisms which underlie biological invasions. Elevational gradients are also suitable study systems to analyse the importance of evolutionary processes during plant invasions. However, the study of biological invasions in mountains reveals not only interesting theoretical insights, but is also important for nature conservation. Mountains comprise some of the few remaining natural ecosystems that are not yet heavily affected by biological invasions. Because actions to control or to eliminate undesirable non-native species are promising only in the early stages of an invasion, nature conservation in mountains has the opportunity to act in time. However, since most non-native species in mountains occur only in one or a few mountain regions, it is difficult to predict which species will invade into a particular mountain region. Thus it is important to know which species are invasive or problematic in the adjoining lowlands or in other mountain regions and it is necessary to establish a monitoring system to detect and observe non-native populations.

Zusammenfassung

1. Ein wichtiges Ziel der Invasionsbiologie ist die Vorhersage von Verbreitungsgebieten und besonders der Verbreitungsgrenzen von nicht-einheimischen Pflanzenarten. Das Verbreitungsmuster einer Art im Invasionsgebiet hängt vom Zusammenspiel der Eigenschaften der invadierenden Art und der angetroffenen Umweltbedingungen ab. Die Kombination dieser Faktoren variiert räumlich und zeitlich und ein vielversprechender Ansatz, um die Effekte dieser Variation auf die Artverbreitungsmuster zu verstehen, ist die Untersuchung von Invasionsprozessen entlang von ausgeprägten Umweltgradienten. Die Untersuchung von Pflanzeninvasionen entlang von Umweltgradienten kann auch zu einem besseren Verständnis der Reaktionen von Pflanzen auf Veränderungen der Umweltbedingungen führen. Solche Reaktionen können phänotypische Plastizität oder adaptive genetische Veränderungen sein. Beides wurde bei nicht-einheimischen Pflanzenarten beobachtet, aber ihre relative Bedeutung für den Invasionserfolg ist noch nicht ausreichend bekannt.

In dieser Arbeit habe ich die Bedeutung von ausgewählten Faktoren auf das Verbreitungsmuster von nicht-einheimischen Pflanzenarten entlang von Höhengradienten analysiert. Dies ist eine geeignete Herangehensweise, weil sich biotische und abiotische Faktoren und deren Zusammenspiel entlang von ausgeprägten Umweltgradienten über sehr kurze Distanzen verändern und aufgrund der geringen Distanz das reine Migrations- oder Transportgeschehen ausgeklammert werden kann. Ich habe verschiedene Methoden verwendet (deskriptive und experimentelle), auf verschiedenen räumlichen Ebenen gearbeitet (global, regional und lokal) und eine Reihe von Arten untersucht, um eine Generalisierung der Ergebnisse zur Bedeutung der einzelnen untersuchten Faktoren zu ermöglichen. Die Untersuchungen auf regionaler und lokaler Ebene wurden auf der Insel Teneriffa (Kanarische Inseln, Spanien) durchgeführt. Ozeanische Inseln sind generell geeignete Modellsysteme für die Untersuchung von Pflanzeninvasionen und Teneriffa im Speziellen bietet einen ausgeprägten Klimagradienten, der von subtropischen Bedingungen an der Küste bis zu einem subalpinen Klima auf etwa 2000 m ü. NN. reicht. Die meisten nicht-einheimischen Pflanzenarten erreichen ihre obere Verbreitungsgrenze irgendwo entlang des Höhengradienten und es ist daher möglich, limitierende Faktoren zu analysieren.

2. In einer weltweiten Untersuchung von 13 Gebirgsregionen wurden fast 1000 nicht-einheimische Pflanzenarten registriert (Datengrundlage: Literatur, Datenbanken, Herbarien und Expertenwissen). Der Vergleich der nicht-einheimischen Floren dieser Regionen hat gezeigt, dass die nicht-einheimische Gebirgsflora jeweils die größte Ähnlichkeit zur angrenzenden Tieflandflora hat und nicht, wie man annehmen könnte, zu anderen Gebirgsfloren, die entweder in der gleichen klimatischen Zone oder geographisch nahe liegen. Dies lässt vermuten, dass in der weit überwiegenden Anzahl der Fälle die nicht-einheimischen Arten in den Tieflagen eingeführt wurden und sich von dort aus in höhere Lagen ausbreiteten. Aus diesem Grund sind nicht-einheimische Pflanzenarten in Gebirgen keine Klimaspezialisten, die an ein Hochlagenklima angepasst wären, sondern Klimageneralisten. Die meisten nicht-einheimischen Arten in den untersuchten Gebirgsregionen sind krautig und kommen aus Eurasien. Dies lässt vermuten, dass sie als Weideunkräuter eingeschleppt worden sind. Veränderungen der Landnutzung in Gebirgen

können jedoch die Einfuhrwege verändern und zum Beispiel die Zunahme des Tourismus in Gebirgsregionen kann nach sich ziehen, dass vermehrt Zierpflanzenarten, die an ein Bergklima angepasst sind, absichtlich eingeführt werden. Wegen ihrer klimatischen Vorangepasstheit ist die Wahrscheinlichkeit erhöht, dass sich diese Arten selbständig weiter ausbreiten und deshalb Maßnahmen zu ihrer Kontrolle notwendig werden.

3. Die Kartierung der nicht-einheimischen Flora an Straßenrändern entlang eines Höhengradienten auf Teneriffa bestätigte die Tieflagen-Einführungshypothese. Ich habe bei den nicht-einheimischen annuellen Arten mediterrane (klimatisch besser angepasste) mit temperaten (klimatisch schlechter angepasste) verglichen, aber die klimatische Herkunft der Arten hat das Verbreitungsmuster nicht wesentlich beeinflusst. Da sich alle eingeführten Arten zunächst im Tiefland etablieren mussten, war die klimatische Herkunft einer nicht-einheimischen Art zwar für die Etablierung im neuen Gebiet wichtig, nicht aber für die weitere Ausbreitung. Dagegen konnte ich feststellen, dass die Anwesenheitsdauer einer Art im neuen Gebiet wichtig war, um höhere Lagen zu erreichen, vermutlich weil die Arten Zeit benötigten, um sich genetisch an die Umweltbedingungen der Hochlagen anzupassen. Des Weiteren habe ich einen starken Einfluss der nicht-klimatischen (biotischen und edaphischen) Habitatfaktoren auf die Verbreitungsmuster nicht-einheimischer Arten gefunden. Es ist zu vermuten, dass der Klimawandel auch indirekte Auswirkungen auf die Verbreitung nicht-einheimischer Arten haben wird, indem er zum Beispiel die Veränderung nicht-klimatischer Habitatfaktoren oder die Verschiebung von Habitaten verursacht.

4. In einem Klimakammerexperiment mit nicht-einheimischen, krautigen Arten aus Teneriffa habe ich die relative Bedeutung von phänotypischer Plastizität und genetischer Anpassung für Pflanzeninvasionen entlang eines Höhengradienten untersucht. Alle einbezogenen Arten haben eine plastische Reaktion auf verschiedene Temperatursimulationen gezeigt und reduzierten ihr Wachstum unter niedrigeren Temperatursummen. Ein Vergleich der unteren und der oberen Hälfte des Höhengradienten hat ergeben, dass die Richtung der genetischen Differenzen zwischen verschiedenen Populationen einer Art in der oberen Hälfte konsistent war, nicht aber in der unteren Hälfte. Im oberen Teil des Höhengradienten hatten Pflanzen aus Hochlagen unabhängig von der Klimabehandlung ein geringeres Wachstum als Pflanzen aus mittleren Lagen. Der Unterschied zwischen den Ergebnissen der beiden Hälften des Gradienten kann als Folge der unterschiedlichen Gradienteneigenschaften interpretiert werden: Genetische Anpassungen werden vermutlich durch den starken anthropogenen Einfluss und den damit verbundenen hohen Genfluss (hoher Ausbreitungsdruck und hohe Abundanz von nicht-einheimischen Arten ausgelöst durch das umfangreiche Transportgeschehen) im unteren Bereich des Höhengradienten verhindert, während sie im oberen Bereich des Höhengradienten wahrscheinlich durch einen reduzierten Genfluss und größeren Selektionsdruck gefördert werden.

5. Studien entlang von Höhengradienten sind eine vielversprechende Herangehensweise, um limitierende Faktoren bei Pflanzeninvasionen zu analysieren. Ich habe gezeigt, dass ein integrativer Ansatz mit verschiedenen Methoden und Maßstäben und einer Vielzahl von Arten dabei helfen kann, generelle Mechanismen, die allen biologischen Invasionen unterliegen, zu verstehen. Höhengradienten sind auch dafür geeignet, die Bedeutung von evolutionären Prozessen im Laufe von Invasionen zu analysieren. Die Untersuchung von biologischen Invasionen in Gebirgen ist jedoch nicht nur aus wissenschaftlicher, sondern auch aus Naturschutzsicht interessant. Gebirge enthalten einige der wenigen natürlichen Ökosysteme, die bislang noch nicht oder nur in geringem Ausmaß von biologischen Invasionen betroffen sind. Maßnahmen zur Kontrolle oder Entfernung unerwünschter nicht-einheimischer Arten sind nur dann erfolgversprechend, wenn sie in den frühen Stadien einer Invasion durchgeführt werden. In Gebirgen, wo Invasionen noch nicht weit fortgeschritten sind, haben Naturschützer die seltene Möglichkeit, rechtzeitig zu handeln. Da aber die meisten nicht-einheimischen Arten in Gebirgen nur in einer oder wenigen Gebirgsregionen vorkommen, ist es schwierig vorherzusagen, welche Arten eine bestimmte Gebirgsregion invadieren werden. Daher ist es wichtig zu wissen, welche Arten im angrenzenden Tiefland oder in anderen Gebirgsregionen invasiv oder problematisch sind und es ist notwendig, ein Monitoringsystem einzurichten, um Populationen nicht-einheimischer Arten zu entdecken und zu beobachten.

General Introduction

Research into biological invasions is a well-established field within biology. However, it is still difficult to predict the distribution ranges and particularly the range limits of non-native species. The aim of this thesis is to address these gaps by analysing several factors which might shape non-native plant species distribution patterns and determine their range limits. Therefore, I use elevational gradients in mountains as a model system. I examine non-native plant species distribution patterns at the global, regional and local scales and analyse the role of bioclimatic origin, introduction history and habitat context in shaping it. Additionally, in a climate chamber experiment I focus on the relative importance of phenotypic plasticity and rapid evolution in determining the climatic limit of non-native plant species. Finally, I deduce implications for non-native species management and nature conservation.

Biological invasions

Biological invasions occur when organisms expand their range by overcoming a natural dispersal barrier, usually as a result of human activities, and establish and spread in a region where they did not occur before (Heger & Trepl 2003; Kowarik 2003). Colonization processes which are characterized by a continuous expansion of a species' distribution range are not considered as biological invasions.

Approximately 50 years ago, the interest in and research into biological invasions made a great leap with the publication of Charles Elton's book "*The Ecology of invasions by animals and plants*" (Elton 1958) and thereafter the number of scientific studies and publications increased continuously (Dietz & Steinlein 2003; Drake et al. 1989; Kolar & Lodge 2001; Kueffer & Hirsch Hadorn 2008; Mack & D'Antonio 1998; Richardson & Pyšek 2008; Vitousek et al. 1997). However, knowledge about the role of specific traits (e.g. the advantage of high fecundity) and processes (e.g. the role of propagule pressure) still remain as "snapshots" and a deeper understanding of general principles applying to invasion success is lacking.

Because there is no consistent use of key terms in invasion biology (Colautti & MacIsaac 2004; Davis & Thompson 2000; Hodges 2008; Larson 2005; Richardson et al. 2000; Valéry et al. 2008) I define here how the relevant terms are understood in this thesis. Species which establish in a new area are referred to as "non-native" or "alien". This can be old introductions (archaeophytes) as well as new introductions (neophytes). As a borderline to distinguish between these two groups I use the year 1500, because at this point, after the discovery of America, global trade and transport started abruptly (Trepl & Sukopp 1993) and as a consequence the frequency and the extent of biological invasions increased remarkably (Cassey et al. 2005). "Non-native" or "alien" means here that a species is not native to a region, but it does not imply whether or not a species spreads in the area of introduction or judgements about its possible effects in the new region. A species that spreads in a new region is termed "invasive", independent of the rate of its spread and its impacts ("naturalized" species in the sense of Richardson et al. (2000)). According to the so called "tens rule" (Richardson & Pyšek 2006; Williamson & Fitter 1996; Williamson &

Brown 1986) only 10% of the species that survive in a new region will spread. Of these species 10% have the potential to become "problematic" (e.g. Groves 1991).

A small fraction of the invasive species may have considerable effects on native ecosystems (Millennium Ecosystem Assessment 2003). At the regional and local scales, invasive species can reduce native biodiversity (Fridley et al. 2007; Lake & Leishman 2004) and thus alter significantly ecosystem functions and structure (Cambray 2003; Cassey et al. 2005). At the global scale, non-native and especially invasive species lead to a homogenization of species communities (Lodge 1993; McKinney & La Sorte 2007; Qian & Ricklefs 2006; Sax & Gaines 2003; Winter et al. 2009) and hence are considered as one of the most important threats to global biodiversity (Woods & Moriarty 2001). Invasive species may also lead to economic and other harm (Foster & Motzkin 2003; Henderson et al. 2006; Lagey et al. 1995; Pimentel et al. 2000; Pimentel et al. 2005; Waisel et al. 2008). Actions against problematic non-native species are only promising if applied during the early stages of an invasion (Kowarik 2003).

Key questions in invasion biology have always been, which species traits or ecosystem properties favour biological invasions, i.e. the establishment and spread of non-native species, and what makes a species problematic (Prinzing et al. 2002). For this, numerous hypotheses and theories have been developed which build the backbone of invasion research today. Factors considered as important for a rapid increase of the abundance of non-native species are the availability of empty niches and resources (Davis et al. 2000; Mack 2003), the lack of natural enemies (Bossdorf et al. 2005; Keane & Crawley 2002), high propagule pressure (Lockwood et al. 2005), allelopathic agents of non-native species unknown to native species (Callaway & Aschehoug 2000; Callaway & Ridenour 2004), high genetic variability and hybridization of non-native species with a native congener (Ellstrand & Schierenbeck 2000), high phenotypic plasticity (Baker 1974; Richards et al. 2006; Roy 1990; Scheiner & Goodnight 1984) and positive interactions (mutualisms) between non-native species (Simberloff & Von Holle 1999). Since these theories always focus on a small part of the whole invasion process (Dietz & Edwards 2006; Mack et al. 2000), there is still no general theory about the ecological and evolutionary processes which underlie successful invasions (Daehler 2003; Kolar & Lodge 2001). Therefore, integrative research approaches which account for the complexity of the invasion process are increasingly advocated (Dietz & Edwards 2006; Pyšek 2004; Rejmánek et al. 2004; Richardson 2004; van Kleunen et al. 2010a).

Distribution ranges and distribution limits

A major goal of invasion biology is to predict future distribution ranges of non-native species and to understand factors limiting the invasion process (Elith et al. 2006; Engler & Guisan 2009; Van der Putten et al. 2000). The spatial distribution of a species depends among other things on its habitat requirements, i.e. its ecological niche. Ecological niche modelling aims to predict the new distribution range of a species by determining areas which correspond to the abiotic requirements of the species in its native range (Peterson 2003; Thuiller et al. 2005).

An important issue here is the role of climate matching between the native range and the area of introduction. In fact, in many cases climate matching was considered as important precondition for invasion success (Panetta & Mitchell 1991; Scott & Panetta 1993) and often insufficient climate matching prevents the establishment of non-native species (Pyšek et al. 2003). The

underlying assumption of ecological niche modelling is that the (climatic) niche of a species is conserved in the new region or evolves only very slowly (Holt & Gaines 1992). However, several examples suggested that the climatic niche shifted in the area of introduction and thus the niche-based modelling approach failed to predict the actual distribution range (Beaumont et al. 2009; Gallagher et al. 2010; Maron et al. 2007). For instance, Broennimann et al. (2007) showed that the European species *Centaurea maculosa* established in North America within the climatic niche that it occupies in its native range, but from there extended its climatic niche to invade drier sites.

There are several possible reasons for this. Firstly, the occupied ecological niche in the native range (realized niche) normally does not correspond to the fundamental niche of the species (Pearman et al. 2008). The latter encompasses the range of abiotic conditions which enable the indefinite survival of an organism (Hutchinson 1957). In almost all cases, the fundamental niche is constrained by negative interactions with other organisms (realized niche), e.g. through competition or predation (i.e. natural enemies). Thus, a shift of the realized niche in the invasion range might occur for instance through the absence of enemies in the range of introduction. The realized niche in the native range can also be restricted through geographical reasons, i.e. a species might tolerate a wider range of environmental conditions than it experiences in its native range. An example for this are species that were confined to small islands and might be able to spread outside their realized niche when transported to continental land masses (Alexander & Edwards 2010). Another example is *Senecio inaequidens* of which populations occur in Europe under lower winter temperatures than in the native range (South Africa), where temperature never drops to such low values (Heger 2004; Trepl 2005). A niche shift might also occur as a consequence of evolutionary change, leading to changes in the fundamental niche. Overall, there are examples for niche shift as well as for niche conservatism of non-native species (Broennimann et al. 2007; Gallagher et al. 2010; Godoy et al. 2009). However, it is still unclear, if niche shifts in the course of biological invasions are an exception or the rule (Alexander & Edwards 2010).

Generally, a species' distribution range in the area of introduction depends on the interaction of characteristics both of the species itself and of the invaded ecosystems. This combination of factors is not stable, but changes in space and time. A promising way to understand the effect of this varying interaction is to study the invasion process along environmental gradients. Firstly, biotic and abiotic factors and their interaction change over very short distances if the environmental gradient is sufficiently steep, and, secondly, if a species spreads along an environmental gradient it has to adapt to the changing conditions.

Genetic adaptation and phenotypic plasticity

Understanding plant responses to environmental variation is critical for predicting the spread of non-native species (Richardson & Pyšek 2006; Walther et al. 2009). Such responses include both phenotypic plasticity (i.e. the ability of an organism to adjust its phenotype to different environmental conditions: Crispo 2008; Ghalambor et al. 2007; Richards et al. 2006) and adaptive genetic differentiation (Hairston et al. 2005; Lee 2002; Prentis et al. 2008; Reznick & Ghalambor 2001), which also includes the evolution of increased plasticity (Crispo 2008). However, the relative role of genetic adaptations at ecological timescales (*sensu* Thompson 1998) and high phenotypic plasticity for invasion success is not clear yet (Dietz & Edwards 2006). Environmental gradients are suitable study systems to analyse the relative importance of genetic

and plastic responses, particularly if species reach their distribution limits somewhere along the gradient.

Examples of successfully spreading non-native plant species which showed changes in their genotype in the new area are *Tamarix ramosissima* in North America (Sexton et al. 2002), *Rubus alceifolius* on the island of La Réunion (Baret et al. 2004), *Eschscholzia californica* in Chile (Leger & Rice 2007), *Hypericum perforatum* in North America (Maron et al. 2004) and *Rhododendron ponticum* in Ireland (Erfmeier & Bruelheide 2005). On the other hand, there are numerous examples for non-native species that only have a marginal genetic difference between populations of different habitats (Williamson et al. 1995). The reason for their invasion success might lie in their high phenotypic plasticity (van Kleunen et al. 2010b). For instance, *Verbascum thapsus* showed a plastic response along an elevational gradient in California (Parker et al. 2003).

Whether or not plant species respond plastically or genetically to changing environmental conditions depends both on the environmental conditions and the characteristics of the species itself. Generally, genetic adaptation is favoured, if marginal populations are rather isolated and gene flow between marginal and core populations is low (Crispo 2008; Kawecki & Ebert 2004). Genetic adaptations may also be related to residence time in the new region because changes of the genotype need at least several generations. It is commonly assumed that temporally heterogeneous environmental conditions, i.e. strong and/or short-term and particularly irregular fluctuations, favour phenotypic plasticity (Kawecki & Ebert 2004; van Kleunen & Fischer 2005), while constant environmental conditions may rather lead to genetic adaptations. Genetic adaptations (including the evolution of increased plasticity) probably need sufficient genetic variability to occur (Alexander & Edwards 2010; Colautti et al. 2010; Sakai et al. 2001; van Kleunen & Fischer 2005; Via et al. 1995). The amount of genetic variability in introduced populations strongly depends on the introduction history, e.g. the frequency of introductions and the number of introduced propagules (Wilson et al. 2009). Due to founder effects or genetic bottlenecks, the genetic variability of non-native populations may be reduced (Alexander & Edwards 2010). Further conservation of the genetic variability within the area of introduction strongly depends on life history and reproduction traits of the species. For instance, short-living species (e.g. annuals), species with a high ploidy level (Levin 2003) and out-crossing species (Barrett et al. 2008) are more likely to adapt genetically to changing environmental conditions.

Mountains as model systems

High mountains are excellent model systems to study non-native species distribution ranges and their response to changing environmental conditions because they offer steep environmental gradients over very short distances and thus allow exclude the complicated factor of migration or transportation. Particularly, elevational gradients are suitable to analyse the role of climate matching and climatic limitation of plant invasions as there is a strong correlation between elevation and temperature (Becker et al. 2005; Daehler 2005; Körner 2007; McDougall et al. 2005).

Unless a species has a broad climatic niche, it needs a large potential for genetic adaptations to colonize the whole elevational gradient. The relative importance of phenotypic plasticity and rapid evolution along elevational gradients is until now rather unclear (Alexander et al. 2009). Some studies presented genetic adaptations of plant growth along elevational gradients

(Montague et al. 2008; Monty & Mahy 2009), but phenotypic effects also seem to be common (Alexander 2010; Bossdorf et al. 2008; Parker et al. 2003).

Extensive climatic gradients can be found on many oceanic islands close to the equator, because there mountains reach from tropical or subtropical conditions at the coast up to subalpine or alpine zones. Oceanic islands are suitable model systems for invasion biology (Denslow et al. 2009; Kueffer et al. 2010) because in most cases they are isolated and species have to overcome a dispersal barrier to establish. Islands are spatially limited and often there is a good documentation of the introduction history of non-native species.

Mountains both on islands and on continents are not heavily invaded yet (Pauchard et al. 2009). However, there is a high diversity of native and endemic species and mountains comprise some of the few remaining natural ecosystems (Körner 2003; Körner & Spehn 2002; Nagy & Grabherr 2009). Therefore, studying biological invasions in mountains is not only interesting from a scientific perspective, but also from the view point of nature conservation.

Here, I investigate the distribution patterns and limits of non-native plant species along an elevational gradient on the island of Tenerife (Canary Islands, Spain). Tenerife was chosen because it offers a steep climatic gradient, ranging from subtropical conditions at the coast to a subalpine climate above 2000 m a.s.l. Non-native plant species are present from low up to high elevations, but most species reach their upper distribution limit at mid-elevations. Beside climate, also the biotic conditions (i.e. edaphic and biotic factors) are changing with altitude.

Outline of the thesis

I combine descriptive (global and regional scale) and experimental (local scale) approaches to analyse the distribution patterns and the distribution limits of non-native plant species in mountains. At the global scale, I analyse and compare the non-native mountain flora of several mountain regions. For the studies at the regional and local scales the island of Tenerife was chosen as study area and I surveyed the non-native vegetation (regional scale) and collected seed material for the experimental part (local scale) of the thesis. Surveys were conducted along roadsides because roads are recognized as major dispersal pathways of non-native species also in mountains. On Tenerife I focused on herbaceous species (herbs and grasses) because this is generally the dominating life form of native plant species in mountains. Additionally, because of the shorter lifecycle of herbaceous and especially of annual species it is very likely that the dispersal is widely advanced or even completed and that these species have already reached their distribution limits. The short generation time also facilitates fast adaptations to environmental conditions and therefore the importance of genetic and plastic adaptation can be better assessed.

In Chapter 1 "*Alien flora of mountains: global comparisons for the development of local preventive measures against plant invasions*" I investigate the taxonomic patterns and non-native species characteristics in 13 mountain regions worldwide. The data set was compiled from literature, databases, herbaria and expert knowledge. In particular, I address the hypothesis that non-native mountain floras are most similar between different regions which are either in the same climatic zone or are geographically close to each other. Further, I investigate whether non-native species in mountains are characterized by specific traits and I compare mountain floras

with adjoining lowland floras regarding life form, origin and utility of the non-native species. This study is the first global analysis of non-native species in mountain regions.

In Chapter 2 "*The role of bioclimatic origin, residence time and habitat context in shaping non-native plant distributions along an altitudinal gradient*" I analyse the distribution of non-native species in roadside habitats along an elevational gradient on Tenerife. I test the hypothesis that the distribution patterns of non-native species depend on their bioclimatic origin, their residence time and the habitat context along the elevational gradient. Particularly, I hypothesized to find a hump-shaped distribution pattern which results from an elevational zonation of non-native species due to bioclimatic origin and from the positive correlation of residence time and occupied elevational range of a species. However, I expect that changes of the habitat context along the elevational gradient modulate the species distribution pattern.

In Chapter 3 "*Genetic differentiation of multiple non-native plants along a steep climatic gradient*" I use a climate chamber experiment with 13 non-native plant species to investigate how species respond to variation in temperature along the elevational gradient on Tenerife. The aim is to assess the relative importance of genetic differentiation and plastic responses to different climatic conditions. Specifically, I ask how frequent phenotypic and genetic growth responses to different temperature treatments are and if the magnitude and direction of phenotypic and genetic responses depend on characteristics of the environmental gradient.

In Chapter 4 "*Pflanzeninvasionen in Gebirgen – Modellsystem für die Forschung, Handlungsbedarf für den Naturschutz*" I argue that mountains are not only suitable model systems for research about biological invasions, but that unique opportunities for nature conservation arise there. I give an overview about the status of current research about plant invasions in mountains and deduce from that how the risk of invasions might change under future conditions (climate and land use change). Finally, I present some management options for nature conservation.

The final discussion summarizes the most important results and draws links between the individual chapters. Particularly, I explain the advantage of linking global, regional and local approaches and descriptive and experimental methods. Additionally, I describe how the factors which were included in the different chapters interact in biological invasions along elevational gradients. In conclusion, I give suggestions for future research and elucidate the importance of the results of this thesis for invasion biology in general.

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Chapter 1

Alien flora of mountains:
global comparisons for the development of local
preventive measures against plant invasions

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Abstract

Aim: We use data from 13 mountain regions and surrounding lowland areas to identify (1) the origins, traits and cultural uses of alien plant species that establish in mountains, (2) the alien species that are most likely to be a threat and (3) how managers might use this information to prevent further invasions.

Location: Australia, Canada, Chile, India, New Zealand, South Africa, Spain, Switzerland, U.S.A.

Methods: Lists of alien species were compiled for mountains and their surrounding or nearby lowlands. Principal co-ordinates analysis was performed on a matrix of similarities created using presence/absence data for alien species. The significance of differences between means for (1) similarity metrics of lowland and mountain groups and (2) species traits of lowland and mountain alien floras was determined using t-tests. In 7 of the 13 mountain regions, lists of alien species undergoing management were compiled. The significance of differences between proportions of traits for species requiring and not requiring management input was determined with chi-square tests.

Results: We found that the proximal lowland alien flora is the main determinant of a mountain region's alien species composition. The highest similarities between mountain floras were in the Americas/Pacific Region. The majority of alien species commonly found in mountains have agricultural origins and are of little concern to land managers. Woody species and those used for ornamental purposes will often pose the greatest threat.

Main conclusions: Given the documented potential threat of alien species invading mountains we advise natural resource managers to take preventive measures against the risk of alien plant invasion in mountains. A strategy for prevention should extend to the surrounding lowland areas and in particular regulate the introduction of species that are already of management concern in other mountains as well as climatically pre-adapted alien mountain plants. These may well become more problematic than the majority of alien plants currently in mountains.

Introduction

Mountains are of great significance to people and biodiversity (Messerli & Ives 1997). The orographic influence of mountains traps rain, providing water that is essential for downstream agriculture and the persistence of major urban and industrial centres (Viviroli et al. 2007). The complexity of mountain habitats typically leads to diverse ecosystems of plants and animals and a high degree of endemism (Körner 2003; Nagy & Grabherr 2009). For these and historic, aesthetic and economic reasons, many mountain systems worldwide have been designated as national parks and reserves for the protection of their biodiversity and natural resources (Spehn et al. 2002).

Mountain biota, however, face increasing pressures, especially from tourism and climate change (Nagy & Grabherr 2009; Price 2006). An expansion of tourism (or a shift from winter- to summer-based activities) will lead to increased disturbance through the provision of new infrastructure (e.g. roads, walking tracks and accommodation) and increased utilization. Climate change may have direct impacts on vegetation by affecting productivity, phenology and competition (e.g. Theurillat & Guisan 2001) but may have a greater indirect impact through changes to hydrology, fire frequency and herbivore abundance (e.g. Beniston et al. 1997; McDougall & Broome 2007; Nagy & Grabherr 2009; Price 2006; Spehn et al. 2006).

High mountains are often considered to be at low risk of plant invasions (Humphries et al. 1991; Millennium Ecosystem Assessment 2003). However, evidence shows that plant invasions do occur and, even though the risk may be lower than in some other ecosystems, it is not insignificant (e.g. Baret et al. 2006; Pauchard et al. 2009; Rouget et al. 2003). The currently observed low number of alien species in mountains may be more related to a time lag effect or less intensive human activities at higher elevations than an inherent resistance of mountain ecosystems to plant invasions (Pauchard et al. 2009; Seabloom et al. 2006). The invasion of new alien plant species may be facilitated by increases in tourism, through anthropogenic disturbance, and climate change, through the creation of favourable environments at higher elevations for species currently limited to low to mid elevations (e.g. Pauchard et al. 2009; Simberloff 2000). Mountains, because of their high levels of endemism, have much to lose from disruptive plant invasions.

It is widely accepted that prevention of invasion is far more cost-effective than eradication or control once an invasion has occurred (e.g. Leung et al. 2002; Lodge et al. 2006; Wittenberg & Cook 2001). Because mountains are generally not as badly affected by alien plant invasions as some other ecosystems, invasive species researchers and managers have the opportunity to respond in time to the threat by preventing invasions. However, effective management will rely on information about the species likely to become problematic. In this paper, we use data from 13 mountain regions and surrounding lowland areas from all continents (except Antarctica) and several oceanic islands to identify (1) the origins, traits and cultural uses of species that typically establish in mountains, (2) the species that are most likely to be a threat and (3) how managers might use this information to prevent further invasions.

Methods

Data

Lists of alien species were compiled for mountains and their surrounding or nearby lowlands in 13 regions: Australia (Alps), Canada (British Columbia), Chile (Mediterranean central zone, temperate south-central zone), India (Kashmir), New Zealand (South Island), South Africa (Drakensberg area), Spain (Canary Islands), Switzerland (Alps), U.S.A. (Alaska, Hawaii, New Mexico, northern Rocky Mountains) (Figure 1).
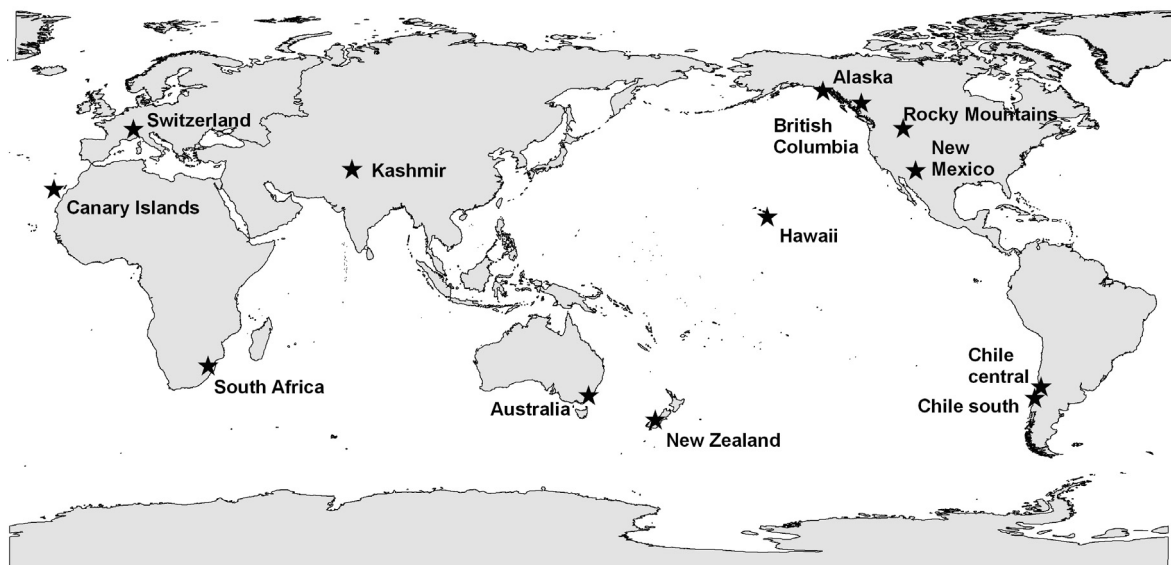

Figure 1: Location of the 13 mountain regions included in the study.

Mountains were defined as areas possessing steep topography that culminates in a treeless alpine or nival zone. Lowlands were below the altitudes of the mountains. Altitudinal limits of mountains and lowlands for each region and source citations are provided in Appendix A1.

In most cases, no distinction was made in the lists between casual, naturalized and invasive species (in the sense of Pyšek et al. 2004), and we refer to all species from these lists as alien. In 7 of the 13 mountain regions (Australia, Canada, New Zealand, U.S.A. (Alaska, Hawaii, New Mexico, northern Rocky Mountains)) we were able to assemble lists of alien species undergoing management from management plans, monitoring reports and personal knowledge (Appendix A1); these species may be considered invasive in a broad sense. In most cases, these species were undergoing management because of their disruptive invasiveness but in a few cases, management was directed at removing new incursions before they became disruptive. The lists cannot be interpreted as comprehensive assessments of invasiveness in a region because they may reflect regional priorities and the resources available for dealing with invasions.

For each alien species, accepted name, origin and utility data were compiled from the Germplasm Resources Information Network (GRIN) online database and species traits were compiled from the USDA Plants database. Synonymy was checked and standardised. Taxa below species level were aggregated. For species not listed in GRIN, other sources were checked (e.g. local floras). Life form and longevity were grouped as annual forb, annual grass, perennial forb, perennial grass, and woody plants (including trees, shrubs, woody vines and succulents). Origin was classified as *Europe* (including northern Africa, the Fertile Crescent of Western Asia and Russia west of the Ural Mountains and the Caspian Sea), *Asia* (south, central, south-east and east), *Australasia/Oceania* (Australia and islands of the south-west Pacific), *southern Africa* (south of the Sahara, including Madagascar), *North America* and *South/Central America* (south of central Mexico) or *unknown*. Where a species occurred in an area near the boundary of two regions, it was attributed to both.

Data analysis

A matrix of similarities between lowland and mountain regional alien floras was created with Primer v.5 (Clarke & Gorley 2001) using the Bray-Curtis metric on presence/absence data. Principal co-ordinates analysis (PCO) was performed on the matrix with R using the vegan package (Oksanen et al. 2009, R Development Team Core Team 2009). The significance of differences between means for (1) Bray-Curtis similarity metrics of lowland and mountain groups and (2) species traits of lowland and mountain alien floras were determined using t-tests. For tests of difference in mean percentage, means were arcsine transformed prior to analysis. Back-transformed means and 95% confidence limits were calculated following analysis. The significance of differences between proportions was determined with Pearson's chi-square tests (Rosner 2006).

Results

Mountain alien flora

In the 13 mountain areas, 972 alien species from 483 genera and 103 families were recorded. The number of alien species recorded per mountain area ranged from 64 for the Canary Islands to 272 for South Africa (mean = 147 ± 19, median = 117). The families Asteraceae and Poaceae accounted for about one-third (31%) of species. More than two-thirds (68%) of species were forbs, almost 40% were annuals and only 13% were woody. The majority of species originated in Europe (64%) and/or Asia (45%). Of species with a documented use, most (57%) were ornamentals.

About 60% of species were recorded from a single mountain area and less than 5% occurred in more than half of the mountain areas. The most frequently-occurring species were *Capsella bursa-pastoris* (11 regions), *Plantago lanceolata* (11), *Plantago major* (10), *Poa annua* (10), *Polygonum aviculare* (10), *Rumex acetosella* (11), *Stellaria media* (12), *Taraxacum officinale* sens. lat. (11) and *Trifolium repens* (11). In their native European range all of these species are

widespread and, in most cases, regarded as ruderals. None is restricted to mountain habitats (Tutin et al. 1968-1980; Tutin et al. 1964).

Comparison of mountain and lowland alien floras

A total of 1993 species was recorded as alien in the 13 regions; 1840 (92%) of these were recorded in lowlands and 972 (49%) were recorded in mountains. The five families with the highest number of species per family were the same in mountain and lowland areas and there was no difference in the mean percentage of species in these families between mountains and lowlands (Table 1). There were a significantly higher mean percentage of perennial grasses and a significantly lower percentage of woody species in mountains compared with lowland areas. Mountain areas had significantly more species from Europe and Asia and fewer species from South and Central America, Australasia/Oceania and southern Africa than lowland areas. The mean percentage of ornamentals was lower in mountains than in lowland areas. About half the species had no documented use in lowlands and mountains.

Similarity among alien floras

The PCO (Figure 2a) shows that mountain and lowland alien floras are generally more similar to each other than to floras of other regions. The first two axes of the PCO explain 27% of the variability in the data. The first axis is negatively correlated with overall similarity ($R^2 = 0.58$, $p < 0.01$). In all but two cases, mountain areas have a lower value on axis 1 than adjoining lowland areas indicating a convergence of the floristic composition of mountain areas (i.e. overall, mountain areas are more similar to each other than lowlands are to other lowlands). Of the mountain areas, those with greatest similarity (lowest values on axis 1) are from the Americas (Alaska, British Columbia, northern Rocky Mountains (U.S.A.), and New Mexico), the Pacific Region (Hawaii, Australia, and New Zealand) and South America (Chile). The mountain floras of Switzerland, Canary Islands and South Africa are highly dissimilar to other mountain floras and to each other. Of the mountain areas with the highest similarity, areas group largely by latitude with most northern hemisphere regions having high values on axis 2, and all southern hemisphere regions having low values on axis 2. An exception is Hawaii, which is most similar to the southern hemisphere regions.

The mean Bray-Curtis similarity between mountain and adjacent lowland alien floras (0.47 ± 0.03) was significantly greater than between nearest mountain alien floras in terms of linear distance (0.31 ± 0.05; $t = 5.6$, d.f. = 12, $p = 0.0001$), latitudinal difference (0.23 ± 0.03; $t = 2.9$, d.f. = 12, $p = 0.01$) and all pairwise similarities among mountain regions (0.21 ± 0.01; $t = 7.7$, d.f. = 89, $p < 0.0001$; Figure 2b).

Table 1: Mean percentage of species in the five most speciose families, and by life form, origin (where known) and utility attributes (where identified) for the 13 mountain (N = 972) and lowland regions (N = 1840), and proportion of species requiring management action (N = 102) or not identified for management action (N = 466) for seven mountain regions. The significance of differences between means was determined by a t-test (d.f. = 12). Percentages were arcsine transformed prior to analysis. Back-transformed means and 95% confidence limits are presented. The significance of differences between proportions was determined with Pearson's chi-square tests (d.f. = 1). Significant differences ($p < 0.05$) are indicated in bold.

|	Mountain regions (mean % of species)	Lowland regions (mean % of species)	t	p	Species requiring management (% of species)	Species not identified for management (% of species)	χ^2	p
Families								
Asteraceae	16.6 ± 1.8	14.4 ± 1.3	2.013	0.067	28.4	12.9	15.325	**< 0.001**
Brassicaceae	6.9 ± 2.1	6.2 ± 1.9	1.064	0.308	3.9	8.8	2.728	0.099
Fabaceae	7.3 ± 2.1	8.3 ± 1.2	1.438	0.176	7.8	4.9	1.371	0.242
Poaceae	18.1 ± 2.7	16.2 ± 2.8	1.546	0.148	12.7	19.5	2.574	0.109
Rosaceae	2.9 ± 2.3	2.9 ± 1.4	0.090	0.930	7.8	4.5	1.923	0.166
Life form								
Annual forb	35.0 ± 1.6	34.0 ± 2.5	0.547	0.594	15.7	35.6	17.322	**< 0.001**
Annual grass	7.2 ± 1.4	7.3 ± 2.2	0.125	0.902	2.0	8.3	4.678	**0.031**
Perennial forb	34.8 ± 2.4	31.8 ± 1.8	1.948	0.075	49.0	33.2	7.897	**0.005**
Perennial grass	12.5 ± 3.0	9.2 ± 3.0	2.729	**0.018**	11.8	14.4	0.406	0.524
Woody	8.7 ± 2.7	14.5 ± 4.3	3.328	**0.006**	21.6	8.5	15.209	**< 0.001**
Origin								
Europe	73.6 ± 6.0	63.6 ± 7.2	3.038	**0.010**	78.4	69.7	3.088	0.079
Asia	51.1 ± 4.6	45.6 ± 4.5	3.000	**0.011**	58.8	48.3	3.719	0.054
North America	14.7 ± 3.8	13.3 ± 3.3	0.980	0.347	13.7	16.1	0.355	0.551
South & Central America	7.5 ± 4.7	12.5 ± 5.1	3.861	**0.002**	2.9	9.4	4.660	**0.031**
Australasia/Oceania	2.3 ± 2.9	3.7 ± 2.5	2.595	**0.023**	2.9	4.9	0.762	0.383
Southern Africa	4.4 ± 2.2	7.6 ± 3.3	2.958	**0.012**	3.9	6.7	1.079	0.299
Utility								
Ornamental	26.1 ± 2.2	31.4 ± 2.4	2.732	**0.018**	40.2	24.0	11.106	**0.001**
Food, timber or tannin	15.6 ± 2.7	14.5 ± 2.2	1.570	0.143	17.7	12.4	6.016	**0.014**
Fodder, pasture or erosion control	11.6 ± 1.8	13.4 ± 2.7	1.048	0.315	14.7	12.4	0.381	0.537
No documented use	54.2 ± 1.4	49.1 ± 2.5	2.146	0.053	43.1	56.7	6.158	**0.013**
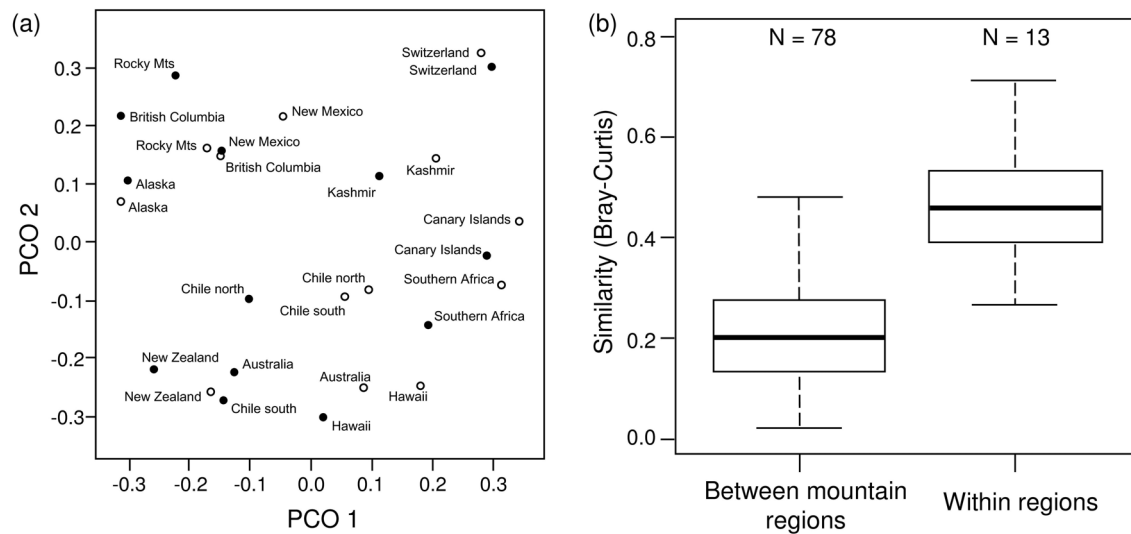
Figure 2: Principal co-ordinates analysis (PCO) (a) of the floristic similarity (Bray-Curtis metric) of the 13 mountain regions (closed points) and adjoining lowland (open points) alien floras. Note that the mountain alien flora of each region tends to cluster close to the corresponding lowland flora. Accordingly the similarity between mountain/lowland datasets within a region (b) is greater than the pairwise similarities among mountain regions.

Alien species requiring management in mountains

Of the 566 alien species occurring in the seven mountain areas for which data were available, 102 species (18%) were deemed to require management in at least one region. There was a significantly greater proportion of Asteraceae, perennial forbs, woody plants and species used as ornamentals, food, tannin or timber, and a significantly smaller proportion of annual forbs and species originating in South and Central America and species with no documented use compared with species that were not identified as requiring management (Table 1). A disproportionately high number of ornamentals were perennial forbs ($\chi^2 = 5.486$; p = 0.019) and woody plants ($\chi^2 = 51.749$; p < 0.001), and a disproportionately high number of food/timber/tannin species were woody ($\chi^2 = 52.111$; p < 0.001). As with the general population of alien species in mountains, the majority of species requiring management originated in Europe and Asia.

The following species were identified for management in three or more mountain areas: *Carduus nutans*, *Centaurea stoebe*, *Cirsium arvense*, *Cirsium vulgare*, *Cytisus scoparius*, *Hieracium aurantiacum*, *Lepidium draba*, *Leucanthemum vulgare*, *Linaria dalmatica*, *Linaria vulgaris*, *Potentilla recta*, *Verbascum thapsus*. Of these species only *Hieracium aurantiacum* is regarded as a predominantly mountain species in its native range (Tutin et al. 1968-1980; Tutin et al. 1964). At least half of the species of the genera *Pinus*, *Salix*, *Hieracium*, *Carduus*, and *Centaurea* required management (Figure 3).
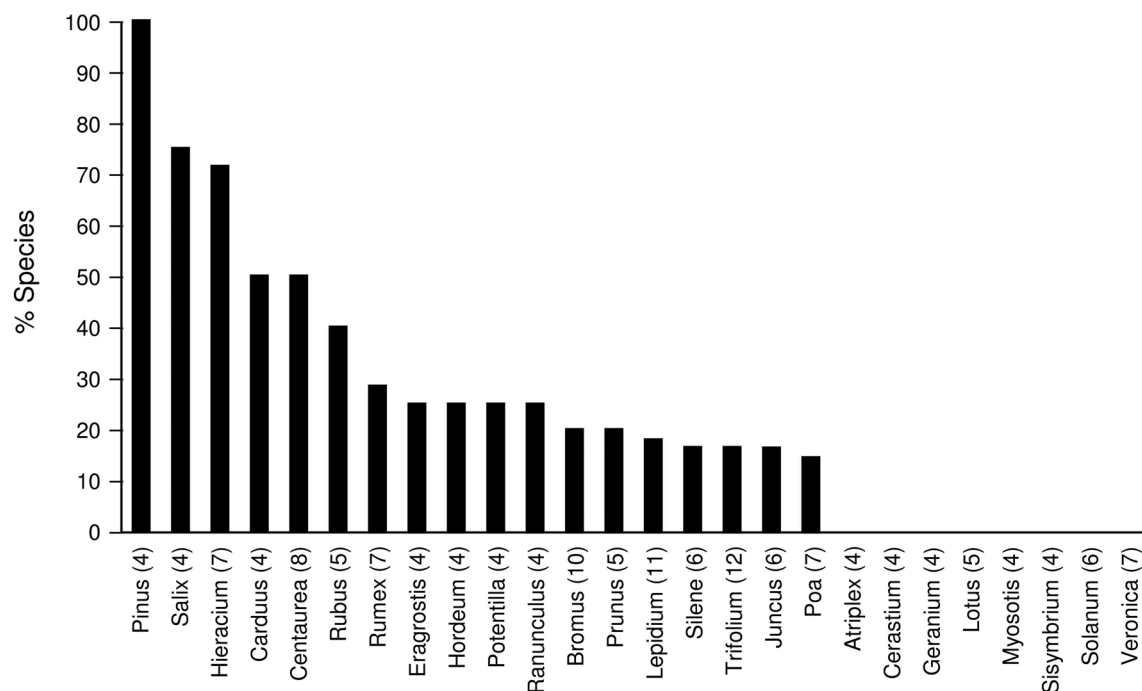
Figure 3: Percentage of species in genera requiring management action. A genus was plotted if it contained four or more species. The number of species in a genus is shown in parentheses.

Discussion

This study represents, to our knowledge, the first global survey of alien plants in mountains. In the mountains of 13 regions from all continents (except Antarctica) and from temperate to tropical climates we found that close to 1000 alien species from over 100 families have naturalized with between 64 and 272 species per region. The fact that about half of species recorded in the adjoining lowlands were also present in mountains indicates that high-elevation ecosystems may not be especially resistant to alien plant invasions. The high proportion of species occurring in only one region suggests that many more alien species are present in other mountain regions not included in this study.

The magnitude of naturalization in mountains globally is currently difficult to determine because comprehensive published data are apparently unavailable for most mountain areas, especially in Africa and Asia. The biased representation of geographic areas is a well-known limitation of invasion biology (Pyšek et al. 2008). For predicting future invasion risks in mountain ecosystems it will be important to include data from other biogeographic and socio-economic contexts (cf. Kueffer 2010). We hope that our study will encourage the publication of comprehensive alien floras from more mountain regions.

Characteristics of mountain alien floras

According to our data, mountain alien floras are characterised by three main features. Firstly, they are typically composed of herbaceous species with an almost equal proportion of annual and perennial species. Although native mountain floras are also dominated by herbaceous species (Körner 2003), these are mostly perennial. Secondly, a majority of species originated in Europe and/or Asia. Thirdly, alien plants in mountains are mainly climatically broad lowland species rather than mountain specialists in their native range (Tutin et al. 1968-1980; Tutin et al. 1964). These climatically broad species also occurred in the lowlands of the 13 regions, leading to a high similarity between lowland and mountain areas within regions. Characteristic mountain genera such as *Primula* or *Gentiana,* which are often cultivated in gardens, were absent from both lowland and mountain alien floras.

The first two observations are in line with characteristics of lowland alien floras. Herbaceous and annual species make up an important proportion of lowland alien weed floras of anthropogenic areas (Daehler 1998; Sutherland 2004), and most observations of alien species in mountains come also from anthropogenic areas such as roadsides or pastures. However, it is important to note that the few alien woody species were disproportionately of more concern to mountain managers. Indeed, in some mountain areas, woody species are the primary focus of management (e.g. the fynbos region of South Africa (Roura-Pascual et al. 2009)). Woody species are also over-represented in lowland floras among natural area invaders in contrast to weeds of anthropogenic areas (Daehler 1998; Kueffer et al. 2010; Sutherland 2004). The predominance of European and Asian species in the mountain and lowland alien floras is also typical of alien floras worldwide (e.g. Goodwin et al. 1999; Prinzing et al. 2002; Rejmánek 1996; Sutherland 2004).

In contrast, the third observation was not expected because pre-adaptation of a species in its native range to the climate of the invaded range (climate matching) is often considered an important predictor of problematic invasive plants (e.g. Kueffer et al. 2010; Parker et al. 2003; Pauchard et al. 2004; Thuiller et al. 2005). One may rather have expected that the harsh climate in mountains would favour species that are pre-adapted to mountain environments in their native range, and consequently that alien species in mountains would be mainly mountain specialists, leading to a convergence of floristic similarity among different mountains, rather than between lowland and mountain floras.

The influence of introduction pathways on mountain alien floras

Recent research in invasion biology has highlighted the importance of introduction pathways and events in shaping plant invasions (Hulme 2009; Kowarik & von der Lippe 2007; Wilson et al. 2009). Past introduction pathways are also likely to have been important in the development of mountain alien floras.

Firstly, the higher frequency of perennial grasses and lower proportion of ornamental plants compared to lowland alien floras, and the predominance of European and Asian species may in our view mainly be explained by the history of land use in mountains. Mack & Lonsdale (2001) describe three phases of invasion by alien plants into the New World which seem to fit well for most of the mountain regions for which we obtained data: the accidental phase (where alien species were inadvertently dispersed as Europeans colonized the New World, e.g. species associated with

pastoralism), the utilitarian phase (where new plants were introduced for direct use by the new colonists, e.g. food species) and the aesthetic phase (where ornamental species were introduced once new colonies became self-reliant). The alien species that were most commonly recorded in mountains are likely to represent invaders of the accidental and utilitarian phases. About three-quarters of the species recorded in mountains had no documented use or may have been used for fodder, pasture, erosion control, food, timber or tannin. However, the high proportion of ornamental species requiring management in mountain areas may represent the growing importance of the aesthetic phase, resulting from the replacement of livestock grazing by tourism in many mountain areas.

Secondly, the predominance of species in mountain areas that also occur in adjoining lowlands may be explained by a lowland introduction pathway. Because there are few direct transport links between mountain regions, the majority of alien species found in mountains are likely to have arrived from adjoining lowland areas along roads and rail links. Such a lowland introduction pathway will also explain why mountain alien plants are mostly climatically broad species rather than mountain specialists, i.e. they need to be able to establish under a lowland climate before they can spread into high elevations (Becker et al. 2005; Haider et al. 2010).

Alien plants of management concern in mountains

At present, alien mountain floras in the regions covered by our analysis are dominated by agrestal and accidentally introduced ruderal alien species that are not specialists of mountain climates. Accidentally introduced ruderal species tend to be less problematic in natural areas than deliberately introduced alien plants (Daehler 1998; Kueffer et al. 2010) and the same seems to be the case for species that are not specifically pre-adapted to a particular climate (e.g. Kueffer et al. 2010; Parker et al. 2003; Pauchard et al. 2004). This may explain why many long-established alien plant species have not posed major problems in mountains. In Australia, for instance, agrestal species that naturalized more than 100 years ago (e.g. *Lolium perenne, Phleum pratense, Trifolium repens*) are infrequent in native vegetation, where they have low cover and never dominate (McDougall & Walsh 2007).

However, more recently, ornamental species have been deliberately introduced to mountain areas, including species from new source areas such as temperate China (Mack 2005; National Academies of Sciences 2002). In Australia, a shift from pastoral use to tourism in mountains has led to the introduction of climatically pre-adapted alien plants for horticulture (McDougall et al. 2005). Our analyses show that species of ornamental use are more likely to be of management concern, so this trend should be of concern to natural resource managers.

Based on our findings, at least 100 alien species recorded in mountains are currently managed for nature conservation purposes. Unless locally native, *Leucanthemum vulgare, Potentilla recta, Verbascum thapsus,* herbaceous plants in the genera *Carduus, Centaurea, Cirsium, Hieracium,* and *Linaria,* and woody plants such as *Acacia* spp., *Cytisus scoparius, Pinus* spp. and *Salix* spp. will often be a threat in mountains.

Impacts from these species and genera in mountains have already been reported. For instance, in 1989, *Hieracium* species (mostly *H. lepidulum* and *H. pilosella*) in montane grasslands in New Zealand were estimated to be costing the pastoral industry between $1.1 and 4.4 million annually in

lost production (Grundy 1989). In the last two decades *H. aurantiacum* and *H. praealtum* have been discovered in mountain protected areas in Australia. Their rapid spread, competitive nature and capacity to invade undisturbed vegetation have alarmed nature conservation managers (e.g. McDougall et al. 2005; Williams & Holland 2007) and necessitated very costly containment and eradication programs. *Centaurea maculosa* is highly invasive in many mountains in western North America. In Montana it threatens the endangered mountain endemic herb *Arabis fecunda* through direct competition (Lesica & Shelly 1996). It is also believed to be having an impact on the reproductive success of chipping sparrows (*Spizella passerina*) in Montana by reducing food availability (Ortega et al. 2006). In Kashmir, invasive *C. iberica* is affecting species composition in montane grasslands and reducing the abundance of palatable species used by the threatened Kashmir Stag (*Cervus elaphus hanglu*) (Reshi et al. 2008). *Pinus* species introduced for forestry operations have escaped in many mountain regions (Pauchard et al. 2009; Peña et al. 2008; Simberloff et al. 2010). As well as direct impacts associated with competition for resources with native species, *Pinus* species may alter mountain fire regimes (Daehler 2005; Richardson & van Wilgen 2004). South African fynbos ecosystems have been heavily invaded by species of the genera *Acacia, Hakea* and *Pinus* (Roura-Pascual et al. 2009), which have greatly reduced water production from watersheds (Le Maitre et al. 2000).

Management implications

Contrary to earlier non-quantitative assessments (Humphries et al. 1991; Millennium Ecosystem Assessment 2003), our study indicates that the potential threat of alien species invading mountains may have been underestimated. It is widely accepted that prevention of invasion is far more cost-effective than eradication or control once invasion has occurred (e.g. Leung et al. 2002; Lodge et al. 2006; Wittenberg & Cook 2001), and our study provides a baseline for preventive measures. Because the proximal lowland alien flora is the main determinant of a mountain region's alien species composition, we suggest that preventive measures for mountain areas must encompass the surrounding lowlands. We also argue that past introduction pathways may have limited the risk of plant invasions in mountain but that this may change, e.g. as a response to a shift from winter to summer tourism and associated increase in the introduction of mountain specialist plants for horticulture (McDougall et al. 2005). A priority preventive measure should thus be to regulate the introduction of climatically pre-adapted alien mountain plants because they may well become more problematic than the majority of alien plants currently in mountains. This measure should commence at national borders through quarantine legislation.

The known invasive behaviour from other regions is one of the best predictors in weed risk assessment systems (e.g. Daehler et al. 2004). We found that several species were invasive and of management concern in multiple regions indicating that such information could be especially important to mountain managers for prioritizing prevention and containment measures. Unfortunately, these data were difficult to obtain and apparently unavailable for most regions so there is an urgent need to gather and publish data on plant invasiveness in mountains. The Mountain Invasion Research Network (MIREN, URL: http://www.miren.ethz.ch) has prepared an online database of alien plants in mountains that should help with the global assessment of plant invasion risks in mountains by centralizing data from published and unpublished sources.

Given the lack of data and the expected change in alien and invasive plant floras in mountains due to novel introduction pathways and climate change, early detection surveys are recommended to identify new incursions of alien plant species when eradication is still possible. The removal of existing alien ornamental plantings in mountain areas is also likely to be a beneficial preventive measure. Future amenity plantings should utilize locally native species.

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Appendix A1

Data sources, spatial limits and number of species in each region.

Country (mountain region); approximate latitude and longitude	Spatial limits		Species (no.)		References		
	Lowland	Mountain	Lowland	Mountain	Lowland	Mountain	Management
Australia (Alps Bioregion); -36°S 148°W	< 800 m	> 1000 m	323	224	Keith et al. 1999; Tindall et al. 2004	McDougall & Walsh 2007; NSW Wildlife Atlas; Victorian Flora information System	Department of Environment and Climate Change 2007; personal knowledge
Canada (British Columbia); 52°N 126°W	< c. 1000 m; Bunchgrass, Coastal Western Hemlock, Coastal Douglas-fir, Ponderosa Pine Zones of Meidinger & Pojar 1991	> c. 1200 m; Alpine Tundra, Engelmann Spruce - Subalpine Fir, Spruce - Willow - Birch Zones of Meidinger & Pojar 1991	325	114	British Columbia Flora, URL: http://www.bcflora.org, accessed 13/02/09	British Columbia Flora, URL: http://www.bcflora.org, accessed 13/02/09	Drinkwater 2005
Chile (central); -33°S 70°W	< 800 m	1500-3600 m	436	96	Herbarium, University of Concepción	L. Cavieres, Instituto de Ecología y Biodiversidad, Chile, unpublished data	
Chile (south); -37°S 71°W	< 800 m	800-1600 m	437	139	Herbarium, University of Concepción	A. Pauchard, unpublished data collected in protected areas	
India (Kashmir); 34°N, 75°E	1600-1900m	> 2300 m	405	235	Khuroo et al. 2007, not including cultivated species	Khuroo et al. 2007, not including cultivated species	
New Zealand (Arthur's Pass National Park); -43°S 172°W	< 400 m	> 450 m	147	117	Wardle 1975; Johnson 1982	Burrows 1986	Department of Conservation 2001, 2007
South Africa (Drakensberg area, KwaZulu Province); -30°S 29°E	< 1800 m	> 2000 m	356	272	Foxcroft et al. 2003; Kobisi 2005	Carbutt & Edwards 2003; Edwards pers. comm.	
Spain (Canary Islands); 28°N 16°W	< 600 m	> 700 m	137	64	Stierstorfer & von Gaisberg 2006	Dickson et al. 1987; Arévalo et al. 2005; personal knowledge	
Switzerland (Alps); 46°N 8°E	< 700 m	> 700 m	345	81	Wittenberg 2005; expert knowledge	Becker et al. 2005	
USA (Alaska); 60°N 143°W	< 100 m	> 330 m	138	95	Alaska Exotic Plant Information Clearinghouse Database, URL: http://akweeds.uaa.alaska.edu, accessed 10/09/2008	Alaska Exotic Plant Information Clearinghouse Database, URL: http://akweeds.uaa.alaska.edu, accessed 10/09/2008	Gilmour & Harper 2008; Weidman & Mahovlic 2008
USA (Hawaii: Islands of Maui and Hawaii); 21°N 156°W	< 1800 m	> 2000 m	258	131	Pratt & Abbott 1996; Medeiros et al. 1998	Daehler 2005	Lloyd Loope (USGS, Haleakala Field Station) pers. comm.
USA (New Mexico: Sandia & Manzano Mountains); 35°N 106°W	All counties 1000-2000 m	> 2000 m	124	103	Southwest Exotic Mapping Program database, URL: http://sbsc.wr.usgs.gov/research/projects/swepic/swemp/swempA.asp, accessed 13/02/09	Sivinski 2007	Berglund (undated)
USA (Northern Rocky Mountains: eastern Oregon, Idaho, Montana, Wyoming); 45°N 111°W	Counties adjoining mountains 600-1500 m	Rocky Mountains alpine and subalpine: > 1600 m	350	245	University of Montana Invaders database, URL: http://invader.dbs.umt.edu/, assessed 13/02/09	Whipple 2001; Parks et al. 2005	National Park Service 2000, 2003

Appendix A1 – References

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Chapter 2

The role of bioclimatic origin, residence time and habitat context in shaping non-native plant distributions along an altitudinal gradient

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Abstract

An important factor influencing whether or not a non-native plant species becomes invasive is the climate in the area of introduction. To become naturalised in the new range, a species must either be climatically pre-adapted (climate matching), have a high phenotypic plasticity, or be able to adapt genetically, which in the latter case may take many generations. Furthermore, patterns of successful establishment across species might vary with habitat context. To address the interaction of these factors on non-native species richness, we recorded the presence of non-native annual plant species along an altitudinal gradient on Tenerife (Canary Islands, Spain). We compared the distributions of species differing in bioclimatic origin (Mediterranean and temperate) and time since introduction (old and recent introductions), and compared richness patterns of these groups in anthropogenic and natural habitats.

Non-native species richness increased strongly from lowlands to mid-altitudes, but dropped sharply at the transition from anthropogenic to natural habitats, and thereafter declined with altitude in the natural habitat. This pattern indicates that the altitude effects reflected changes in both climate and habitat context. Mediterranean and temperate species were distributed similarly along the altitudinal gradient, and we found no effect of bioclimatic origin on species distributions. As almost all species present at the highest sites also occurred in the lowlands, we conclude that most species were introduced to lowland sites and were therefore pre-adapted to those climatic conditions (lowland introduction filter). The altitudinal ranges of species tended to increase with time since introduction, and the species reaching the highest altitudes were mostly old introductions. This effect of time was more pronounced among Mediterranean than temperate species. Thus, while climatic pre-adaptation is important for establishment along this altitudinal gradient, species tend to extend their altitudinal range with time.

Keywords: alien species, climate matching, mountain, lowland introduction filter, plant invasion, roadside vegetation

Introduction

The climatic conditions in the area of introduction have recurrently been shown to influence the outcome of plant invasions (e.g. Kitayama & Mueller-Dombois 1995; Kueffer et al. 2010; Thuiller et al. 2005) and are important for predictions made in weed risk assessment systems (Gordon et al. 2008; Tatem & Hay 2007). Consequently, the invasiveness of a plant species may change considerably with climate change (Dukes & Mooney 1999; Walther et al. 2009).

To establish and spread in a new area, a species must be able to tolerate the prevailing climatic conditions. This is possible if the species originates in a region that is climatically similar; indeed, climate matching has emerged in many studies as a consistent and important predictor of the potentially invaded area of a non-native species (Dawson et al. 2009; Kolar & Lodge 2001). However, although ecological niche modelling based on climate may be useful for predicting whether a species will become invasive (Peterson 2003; Thuiller et al. 2005), the climatic niche of some non-native plants appears to have changed in the introduced range (niche shift; Alexander & Edwards 2010; Beaumont et al. 2009; Broennimann et al. 2007; Maron et al. 2007). For instance, Broennimann et al. (2007) showed that the European herb *Centaurea maculosa* established in the USA within the climatic niche of its native range, but from there it colonized novel niche space. For this reason, the assumption underlying niche modelling – that climatic niches are stable (niche conservatism) – has recently been challenged.

A useful approach for elucidating the role of climate in limiting invasions is to investigate the distribution of non-native species along an altitudinal gradient (e.g. Alexander et al. 2009a; Johnston & Pickering 2001; Marini et al. 2009; Parks et al. 2005; Pauchard et al. 2009; Sullivan et al. 2009). Such studies have consistently shown a strong decrease of non-native species richness with increasing altitude, at least from mid- to high-altitudes (Becker et al. 2005; Daehler 2005; McDougall et al. 2005; Pauchard & Alaback 2004; Pauchard et al. 2009; Wester & Juvik 1983). Studies in other ecosystems have shown that invasibility tends to decline with the severity of environmental conditions (Alpert et al. 2000), and it has therefore been argued that climate is the most important factor limiting the spread of non-native plants to high altitudes (Pauchard et al. 2009), where climate conditions are unfavourable for most species (Körner 2003).

The spread of non-native plants in mountainous regions has usually been studied along roads (Alexander et al. 2009b; Arteaga et al. 2009; Sullivan et al. 2009; Wilson et al. 1992); this is appropriate not only for practical reasons, but because roads are important dispersal corridors (Christen & Matlack 2009; Johnston & Johnston 2004; Lilley & Vellend 2009) and roadsides are usually disturbed habitats (Christen & Matlack 2006; Forman et al. 2003) which favour the establishment of non-native species (Gelbard & Belnap 2003). In addition, with the exception of climate, the most relevant abiotic (e.g. nutrient availability) and biotic conditions (e.g. competition) for non-native species' establishment success are relatively constant along road verges over the whole altitudinal gradient (Ullmann & Heindl 1989; Wilson et al. 1992). Finally, efficient anthropogenic dispersal along roads makes it unlikely that the altitudinal limits of species are dispersal limited but rather are in equilibrium with their climatic limits (e.g. Alexander et al. 2009b).

Although roadsides offer relatively constant site conditions, the distribution of non-native species is also influenced by neighbouring habitats, and previous studies have shown that species richness depends strongly on the habitat context (e.g. Chytrý et al. 2009; Vilà et al. 2007).

We recorded non-native annual plant species along two roads on the island of Tenerife (Canary Islands, Spain). Tenerife was chosen because oceanic islands are convenient model systems for invasion biology (Daehler 2005; Kueffer et al. 2010), and this particular island offers a steep climatic gradient, ranging from subtropical conditions at the coast to a subalpine climate above 2000 m a.s.l. To elucidate whether climatic pre-adaptation matters for non-native plant establishment, we compared the altitudinal distributions of non-native plant species of Mediterranean and temperate origin. Within both groups we also discriminated between old and recent introductions to investigate whether residence time is a factor affecting the altitudinal ranges of non-native plants. Such an effect could reflect either the time that it takes for a species to disperse, or the time needed to adapt to changing conditions along an altitudinal gradient (Becker et al. 2005).

In this paper we address the following hypotheses: (1) there is an altitudinal zonation of non-native species due to bioclimatic origin, with Mediterranean species dominating at low altitude roadside communities and temperate species in high altitude ones; (2) within bioclimatic groups old-established non-native plant species have broader altitudinal ranges than recent introductions. We predict that (3) species richness patterns will show a hump-shaped distribution with altitude due to the overlap of species ranges established under hypotheses (1) and (2). However, we expect that (4) these altitudinal distribution patterns also depend on the habitat context, i.e. the response of species to altitude might be modulated by the zonation of habitat types along the altitudinal gradient.

Methods

Study area

The study sites were located in the northern part of Tenerife (Canary Islands, Spain, 28°N, 16°W), which is the largest island (2033 km²) of the volcanic Canarian archipelago and represents the highest mountain of Spain (Pico de Teide, 3718 m a.s.l.). The climate of Tenerife is strongly influenced by north-eastern trade winds, and the northern and southern parts of the island differ greatly in temperature and precipitation. The windward northern part, where our study was located, is characterized by a strong climatic zonation along the altitudinal gradient (Whittaker & Fernández-Palacios 2007). Mean annual temperature declines from 19°C at sea level to 11°C at 2000 m a.s.l. (Figure 1). Low altitudes are characterized by a Mediterranean-type climate with mild, wet winters and warm, dry summers (< 300 mm annual precipitation) (Sperling et al. 2004). A temperature inversion at mid-altitudes causes a relatively persistent cloud layer, typically between 1000 and 1500 m a.s.l., leading to a more humid climate in this altitudinal band (> 700 mm/yr) (Fernández-Palacios 1992). Above the inversion the climate is again dry and cool (< 500 mm/yr). The natural vegetation follows the climatic zonation, with semi-desert scrub below the clouds, *Erica-Myrica* woody heath and humid pine forest (*Pinus*

canariensis) in the cloud layer, and dry pine forest and subalpine scrub above the cloud layer (Fernández-Palacios & de Nicolás 1995). During the growing season, precipitation is mainly very low and differences between altitudes are diminished (Figure 1). In our study area, relatively undisturbed, natural vegetation started at c. 1000 m a.s.l. at the lower boundary of the persistent cloud layer; this was entirely composed of pine forest except for the highest sites at 2000 m a.s.l. where there was a subalpine scrub on loose volcanic gravel. Where the road passes through these vegetation types, referred to as natural habitat (NAT), the herb layer along the roadside is usually sparse (0-16%) due to the dense accumulation of pine needles from the forest. In the study area, the canopy cover in the pine forest ranges from 0 to c. 75%, but varies between the more humid lower part where trees are dense (30-75%) and the drier upper part which is more open (0-20%; S. Haider, personal observation).
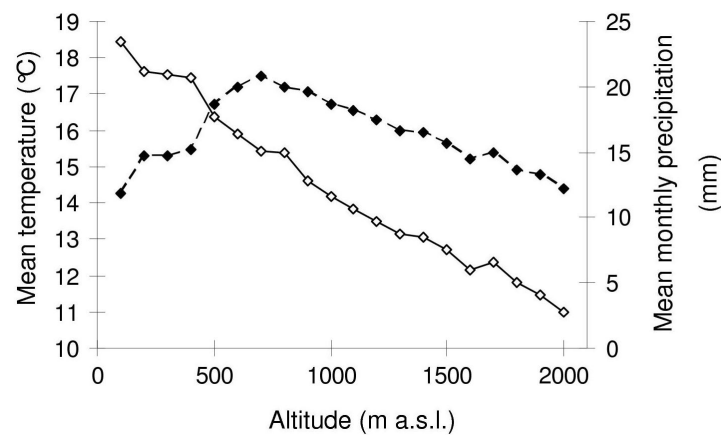
Figure 1: Variation of mean temperature (solid line with open symbols) and mean monthly precipitation (dashed line with filled symbols) with altitude in the study area during the growing season (April to June). Climate data for every site was compiled through Worldclim (URL: http://worldclim.org).

Anthropogenic influences are very high in the zone between the coast and c. 1000 m a.s.l., with agriculture (e.g. bananas, tomatoes) and dense settlements spread over the entire landscape (anthropogenic habitat, ANT). Roadside communities in this habitat consist mainly of open vegetation, which is only rarely shaded by trees (herb layer cover: 4-56% of ground area, canopy cover: 0-9%; S. Haider, unpublished data).

Soil conditions, especially pH values, differ considerably between the lowest sites below 400 m a.s.l. (pH: 7.0-8.0) and higher altitudes (pH: 5.0-6.3; S. Haider, unpublished data). Our roads passed mostly through lava of intermediate age (i.e. in the order of 100 ka), which corresponds to young basaltic bedrock, except for the lowest sites (100 and 200 m a.s.l. at road A and 100 m a.s.l. at road B) that were placed on very old lava (4-5 Ma). No site was situated on an historic lava flow (i.e. within several hundred years old) (Hoernle & Carracedo 2009).

Species

We recorded all non-native annual, flowering plant species that are known to have originated in a region with either a Mediterranean or temperate climate (Dahl 1998; Schultz 2005). We focused on annual plants to avoid confounding the results with different life forms, since it has been shown that lowland and high altitude non-native floras tend to harbour different proportions of annuals and perennials (McDougall et al. 2011). However, we also included species that are not strictly annual (e.g. *Tragopogon porrifolius*, which can also be biennial). Non-native species were further divided into two groups according to their time since introduction. We considered as old introductions all plant species that might have been introduced by the Romans, Spanish or Portuguese before the year 1500, in a period before trade with other continents became common. International trade gained importance from the 16th century, and intensified contacts with the New World and Asia led to the introduction of many new plants, which we regard as recent introductions.

To distinguish between native and non-native species, and to determine the time of introduction and bioclimatic origin of non-native species, we compiled information about species distribution and introduction status in the whole Macaronesian floristic region and classified species based on the literature (Appendix A2), personal communication with other scientists, and our own expertise. Taxonomy was standardized with the Germplasm Resources Information Network (GRIN) online database.

Data collection

Data was collected along two paved roads that were similar with respect to traffic intensity and climatic conditions, and extended from 100 to 2000 m a.s.l. Road A led from Bajamar via La Laguna and La Esperanza to El Portillo where it met road B coming via La Orotava and Aguamansa from El Sauzal (different roads than in Arévalo et al. 2005; Arévalo et al. 2010; Arteaga et al. 2009). Traffic intensity was highest in the vicinity of the cities of La Laguna and La Orotava (c. 20'000 cars/day; Cabildo Tenerife 2007) and declined towards the coast and towards higher altitudes (c. 2'000-12'000 cars/day in coastal areas and mid-altitudes). Above c. 1000 m a.s.l. traffic intensity remained constant with c. 1'000-2'000 cars/day (Cabildo Tenerife 2007).

We recorded the vegetation during two growing seasons – from March to May 2007 and May to June 2008 – to reduce the risk of bias due to extreme conditions in a single year. The sampling period in the second season was shifted to be sure of sampling species with both early and late phenologies. Data from both years were pooled, i.e. a species was identified as present if it was recorded at least in one year. Sampling sites were placed at 100 m altitudinal intervals (hereafter "site"). At each site we recorded the presence of the target species in two 250 m x 2 m transects along both sides of the road and located immediately adjacent to the paved area. Observations for both transects per site were pooled and data analysis was performed with species richness per site.

Within each of the roadside transects we established a subplot of 12.5 m x 2 m (longer side parallel to the road) to record non-native species and total vegetation cover-abundance using the Domin-Scale (1 = very scarce, ≤ 4%, 2 = scarce, ≤ 4%, 3 = scattered, ≤ 4%, 4 = 4-10%, 5 = 10-25%, 6 = 25-33%, 7 = 33-50%, 8 = 50-75%, 9 = 75-95%, 10 = 95-100%; Bannister 1966). Prior to the analysis classification values were transformed according to Currall (1987). Overall we sampled two roads with 20 sites each. At all sites we recorded the habitat type (anthropogenic vs. natural habitat).

Data analysis

To investigate broad patterns of species richness along the altitudinal gradient, and whether these patterns differed between different habitat types (anthropogenic, ANT; natural, NAT), general linear mixed effects models were first fitted using the "lme" function in R (R Foundation for Statistical Computing, version 2.9.1 for Windows; "nlme" package). Four models of total species richness were fitted containing different fixed effects: (1) altitude only, (2) the second-order polynomial of altitude, (3) altitude, habitat type (ANT; NAT) and their interaction and (4) the second-order polynomial of altitude, habitat type (ANT, NAT) and their interaction. All four models included site nested within road as random effects and were fitted using the maximum likelihood method to enable their comparison based on Akaike's Information Criterion (AIC). The model with the lowest AIC score, or the most parsimonious model in the case of a difference in scores of less than 2, was favoured. Additional models with the same random effects were fitted using the REML method to investigate differences in the responses of alternative sub-groups of species (cf. Öckinger et al. 2009). These models contained the fixed effects of altitude, habitat type and either bioclimatic origin (Mediterranean, MED vs. temperate, TEMP) or time since introduction (old introductions, OLD vs. recent introductions, NEW), and all 2- and 3-way interactions. Significant 3-way interactions were further explored by re-fitting these models separately for the ANT and NAT habitats.

We extracted the minimum and maximum altitudes for all species and calculated the altitudinal range for all species that were recorded at least twice. We then used non-parametric Wilcoxon rank-sum tests to compare the altitudinal distributions of species groups with different bioclimatic origins (Mediterranean and temperate species) and different times since introduction (old- and recently-introduced species). We also generated a predicted species richness curve based on the altitudinal species ranges and the assumption that each species occurs in every site within its range.

To test whether the non-native species composition of sites was nested, we calculated the NODF metric of Almeida-Neto et al. (2008) using the R-package vegan (version 1.17-2). We produced two species-site matrices, with sites either maximally packed or ordered by altitude. An additional matrix was constructed assuming species to be present at all sites within their altitudinal range. Tests of nestedness of sites were based on 1000 randomizations of the matrix using a null model that constrained species richness within sites whilst randomizing the occurrence of species within sites (method R1, Wright et al. 1998).

Results

Non-native roadside flora

We recorded a total of 58 non-native annual plant species, of which 79% were of Mediterranean (MED) and 21% of temperate origin (TEMP; Appendix B2). We found more old (OLD) than recent (NEW) introductions (62% and 38% of the species, respectively). Within the TEMP group there were 58% OLD and 42% NEW introductions, while within the MED group 63% were OLD and 37% NEW. A rank-abundance curve showed a rather smooth decline in species' abundance (Figure 2), indicating that the non-native flora is not strongly dominated by a few very abundant species. The most important plant families were Fabaceae (15 species), Asteraceae (11 species), and Brassicaceae (8 species), which comprised together more than half of the sampled species. Altogether the species recorded were from 17 families and 41 genera. Each group contained 11 or 12 families (MED and NEW, and TEMP and OLD, respectively), but the species of the most frequent families were distributed unequally. Almost all Fabaceae, Asteraceae and Brassicaceae species were of MED origin. Whereas Fabaceae and Asteraceae species were more equally distributed between OLD and NEW species, all Brassicaceae species except one belonged to the OLD group.
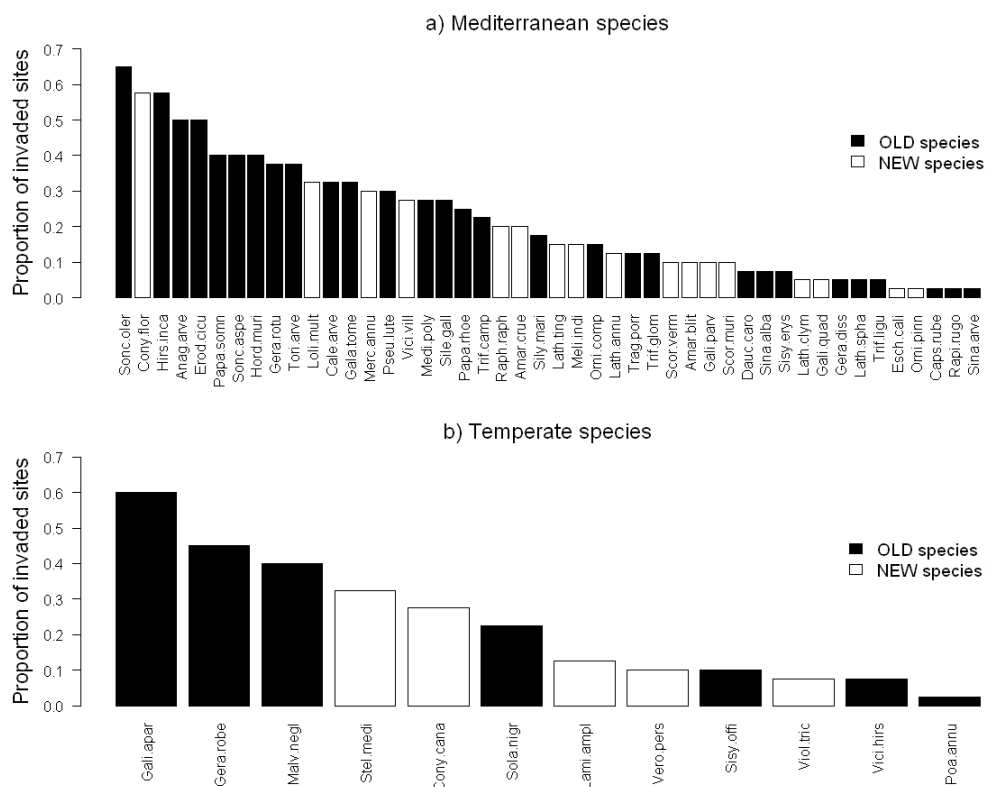
Figure 2: Rank-abundance distribution of the recorded a) Mediterranean (N = 46) and b) temperate (N = 12) non-native species along roadsides. The y-axis indicates the proportion of sites in which each species was present. Black bars represent old-introduced (OLD), white bars recently-introduced (NEW) species. Species abbreviations are always composed by the first four letters of genus and species. Complete species names can be found in Appendix B2.

The cover of individual species was mainly low ($\leq 4\%$ of ground area) and, with few exceptions, constant across sites. Only *Hirschfeldia incana* (MED-OLD) was recorded with cover class 25-33% in one plot at 1000 m a.s.l. and *Sisymbrium erysimoides* (MED-OLD) reached 4-10% in one plot at 100 m a.s.l. There was a positive relationship between non-native species richness and non-native species cover per plot ($R^2 = 0.87$, $p < 0.001$).

Species altitudinal ranges

Eighty-eight percent of the sites contained at least one non-native species. The majority of species were found in plots of the anthropogenic habitat (ANT), and 52% of the species were present only in this habitat (Figure 3). Only three species – *Eschscholzia californica, Tragopogon porrifolius,* and *Trifolium ligusticum* (all MED) – occurred exclusively in the natural habitat (NAT habitat). Fifty-two percent of all MED species and 61% of all OLD species were present in NAT habitat, while these proportions were only 33% and 27% for TEMP and NEW species, respectively (Figure 3). On average, OLD species reached higher altitudes (Wilcoxon rank-sum test, $N = 58$, $W = 557$, $p = 0.009$, two-tailed) and colonized a wider altitudinal range (Wilcoxon rank-sum test, $N = 52$, $W = 449.5$, $p = 0.015$, two-tailed) than NEW species (Figure 4). The groups did not differ in their lower altitudinal limit (Wilcoxon rank-sum test, $N = 58$, $W = 406.5$, $p = 0.869$, two-tailed). For the MED and TEMP groups, there were no significant differences in the lower and upper altitudinal limits of species, nor in their altitudinal ranges (Wilcoxon rank-sum test, lower limit: $N = 58$, $W = 288.5$, $p = 0.813$, two-tailed, upper limit: $N = 58$, $W = 289$, $p = 0.808$, two-tailed, range: $N = 52$, $W = 210.5$, $p = 0.745$, two-tailed).
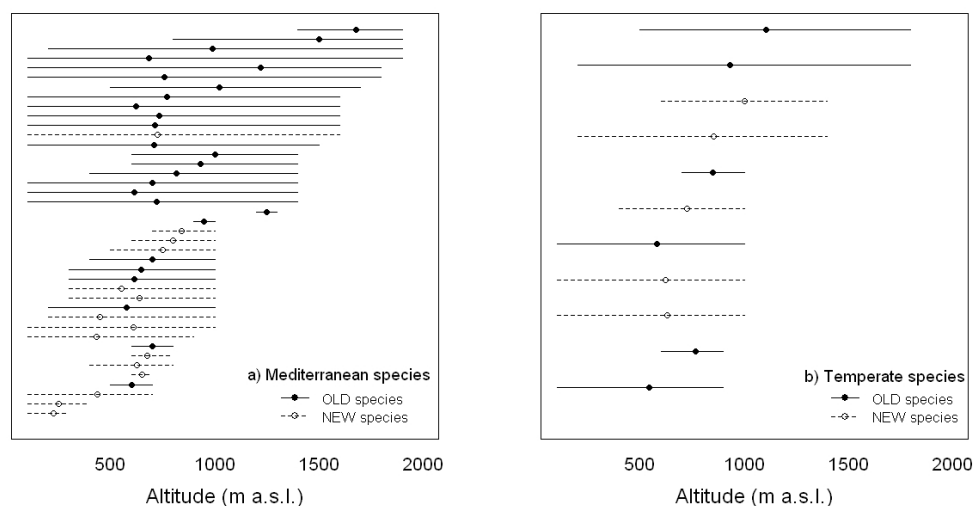
Figure 3: Altitudinal distribution ranges (lines) of non-native a) Mediterranean (N = 41) and b) temperate (N = 11) species that occurred at least twice along the altitudinal gradient. Old-introduced species (OLD) are indicated with solid lines, recently-introduced species (NEW) with dashed lines. The symbols (filled for OLD, open for NEW) are placed at the mean altitude where the species occurred and species are sorted according to their altitude of maximum occurrence. The boarder between anthropogenic and natural habitat is at 1000 m a.s.l.

Although sites were significantly nested using the original presence-absence matrix ($N_{sites} = 40.2$, $z = 2.78$, $p = 0.013$), the species composition of high-altitude sites was not significantly nested in low-altitude sites ($N_{sites} = 24.4$, $z = -0.09$, $p = 0.964$). However, the species composition of sites was significantly nested in relation to altitude under the assumption that species were present at every site within their altitudinal range ($N_{sites} = 53.4$, $z = 9.36$, $p < 0.001$).
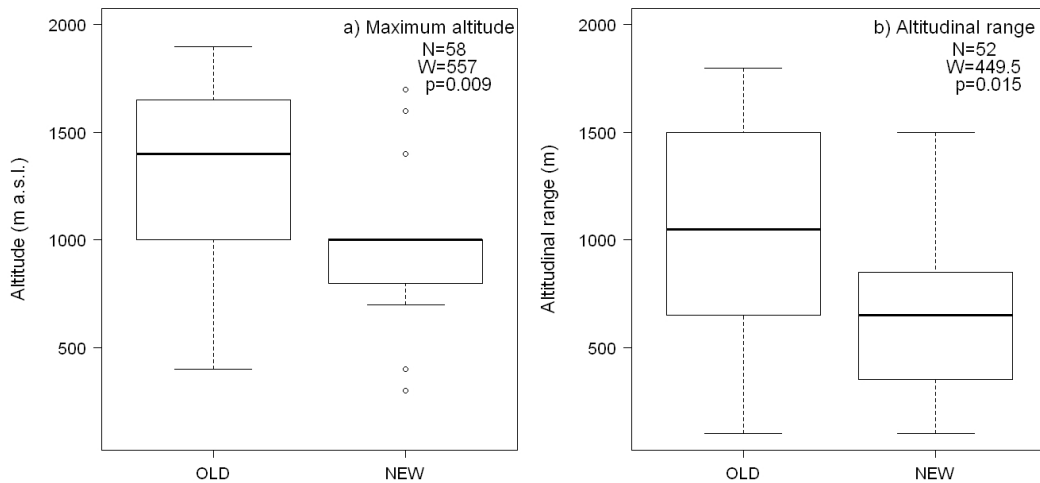
Figure 4: Comparison of a) the maximum altitude and b) the colonized altitudinal gradient of old- (OLD) and recently-introduced (NEW) species. The unusual shape of the box for the maximum altitude of NEW species arises from the fact that almost half of the species have a maximum altitude of 1000 m a.s.l. and above that there are only four outliers (the outlier at 1400 m a.s.l. occurred twice).

Variation in non-native species richness along the altitudinal gradient

Species richness showed a strongly humped relationship with altitude, with richness peaking in the middle of the gradient, between 600 and 1000 m a.s.l. (Figure 5). However, this relationship was not smoothly polynomial (AIC = 283.49; Appendix C2) but rather was best described by a model containing two linear relationships, with a linear increase in richness in the anthropogenic habitat up to c. 1000 m a.s.l., and a much lower and slightly declining richness above this point (significant interaction between altitude and habitat type, AIC = 238.94, $F_{1,35} = 31.64$, $p < 0.001$; Figure 5; Appendix C2).

Along the whole altitudinal gradient (in ANT habitat as well as in NAT habitat) MED species were more numerous than TEMP species, with an average of seven (357%) more MED than TEMP species per site (Table 1). MED species were present in 88%, and TEMP species in 75% of sites. Both bioclimatic groups showed the same response to altitude (Figures 6a and b and Table 2).
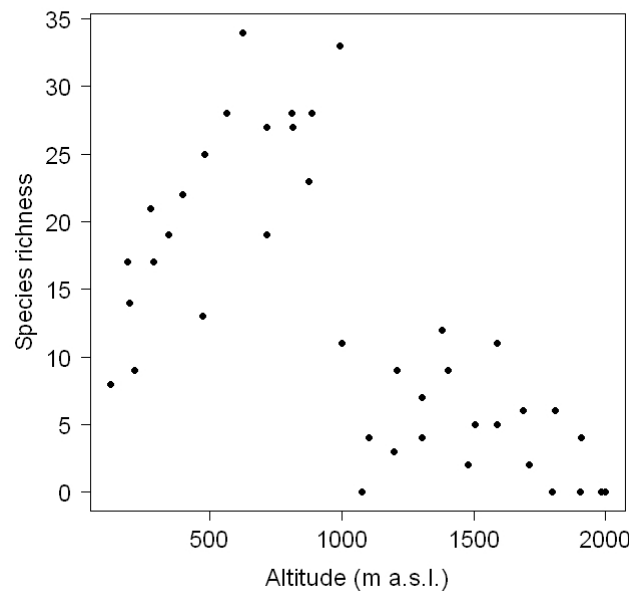
Figure 5: Non-native species richness along the altitudinal gradient.

OLD species were present in 88% of sites, and NEW species in 75%. Across both habitat types the mean number of OLD species per site was significantly higher than the number of NEW species (on average five more OLD species per site; Figures 6c and d). In NAT habitat both groups had a similar decrease in species richness with increasing altitude. However, in ANT habitat the increase of OLD species with increasing altitude was significantly faster than for NEW species (Table 2).

Predicted species richness followed the observed species richness patterns closely with the exception of the lower end of the NAT habitat (Figure 6). Predicted species richness was based on observed species altitudinal ranges (Figure 3) and the assumption that a species occurs in every site that is within its observed altitudinal range.

Table 1: Results of general linear mixed effects models (REML method) of the response of different groups to altitude and habitat type. The fixed effect "group" represents either the two bioclimatic origins (Mediterranean vs. temperate species) or time since introduction (old-introduced vs. recently-introduced species). Both models contained site nested within road as random effects.

Fixed effects	Group: Bioclimatic origin			Group: Time since introduction		
	Resid. d.f.	F	p	Resid. d.f.	F	p
Altitude	35	94.46	< 0.001	35	94.46	< 0.001
Habitat	35	69.68	< 0.001	35	69.68	< 0.001
Group	36	180.35	< 0.001	36	159.11	< 0.001
Altitude x habitat	35	31.64	< 0.001	35	31.64	< 0.001
Altitude x group	36	59.28	< 0.001	36	9.27	0.004
Habitat x group	36	27.62	< 0.001	36	13.04	0.001
Altitude x habitat x group	36	5.55	0.024	36	15.95	0.000

Table 2: Results of general linear mixed effects models (REML method) of the response of different groups (bioclimatic origin (origin) and time since introduction (age), respectively) to altitude in the anthropogenic (ANT) and the natural habitat (NAT). All four models contained site nested within road as random effects.

	Subset ANT			Subset NAT		
Fixed effects	Resid. d.f.	F	p	Resid. d.f.	F	p
Altitude	16	25.96	< 0.001	18	4.52	0.048
Origin	17	158.48	< 0.001	19	24.49	< 0.001
Altitude x origin	17	3.13	0.095	19	2.16	0.158
Altitude	16	25.96	< 0.001	18	4.52	0.048
Age	17	213.74	< 0.001	19	28.39	< 0.001
Altitude x age	17	25.16	< 0.001	19	1.39	0.254
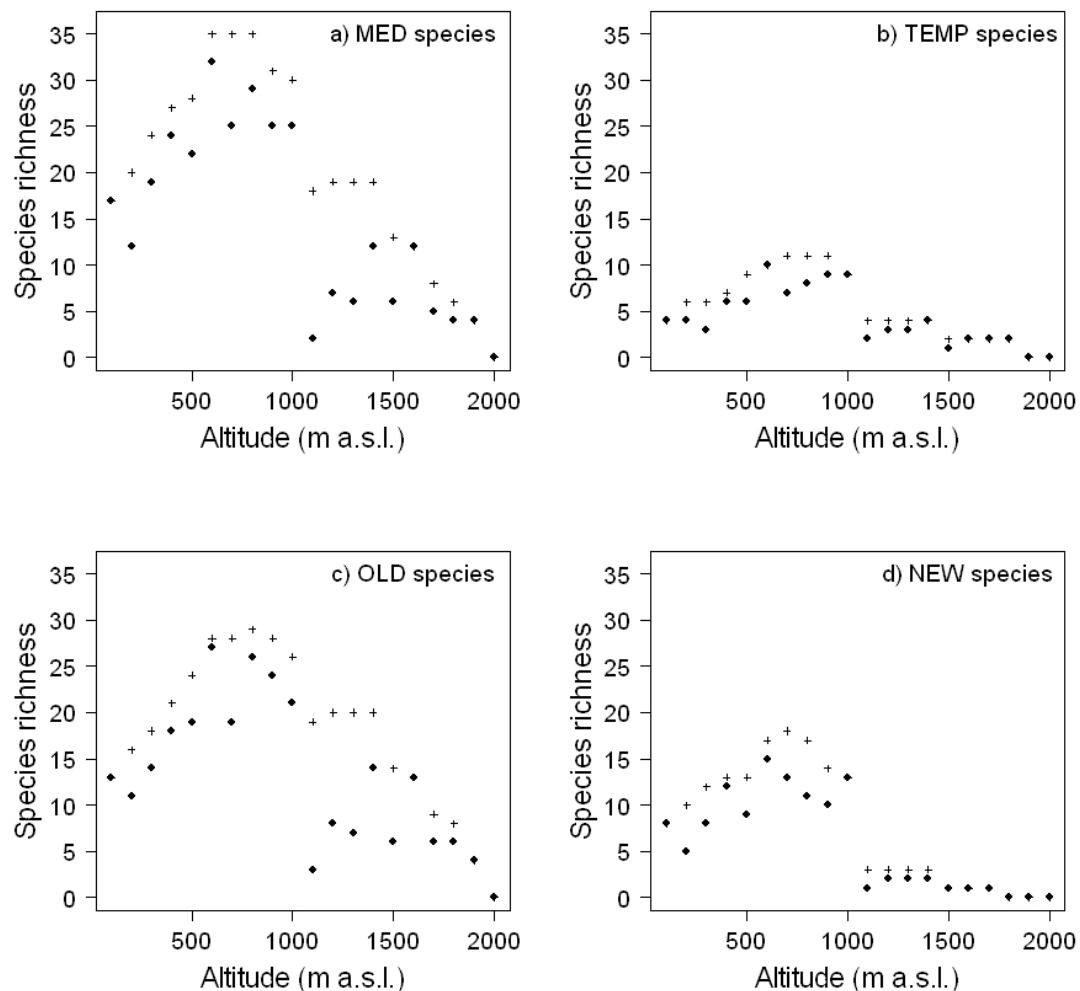
Figure 6: Species richness of a) Mediterranean (MED), b) temperate (TEMP), c) old-introduced (OLD) and d) recently-introduced (NEW) species along the altitudinal gradient. Dots indicate observed species richness. Crosses show species richness predicted from the altitudinal ranges of the species. Predicted species richness was based on the assumption that species occur at all sites within their altitudinal range.

Discussion

Does bioclimatic origin determine species distribution along the altitudinal gradient?

We hypothesised that bioclimatic origin leads to an altitudinal zonation of Mediterranean and temperate non-native annual species. However, Mediterranean and temperate species responded very similarly to altitude, and there was no evidence for any altitudinal separation of the two groups. Indeed, almost all species present at high altitudes also occurred in the lowlands. These patterns may be explained by assuming that most non-native plant species initially establish at low altitudes and thus need to be climatically pre-adapted to lowland conditions (lowland introduction filter; Becker et al. 2005; Pauchard et al. 2009). A lowland introduction filter may also explain why we found overall more Mediterranean than temperate non-native species, since Mediterranean species are pre-adapted to such a lowland climate and may be more likely to establish than temperate species.

Our results are consistent with those from a global survey of non-native floras in mountainous regions compiled by McDougall et al. (2011), which found that high altitude floras tend to be similar to those at low altitudes in the same region, even though the climate may change dramatically along the altitudinal gradient. In contrast, mountain floras in different regions with a similar alpine climate tend to be dissimilar, which the authors interpret as reflecting their differing introduction histories. The distributional patterns in our study differ from those on the oceanic islands of Hawaii, where there is a turnover of species of different bioclimatic origin along the altitudinal gradient (Daehler 2005; Wester and Juvik 1983). A possible explanation is that species introductions in Hawaii took place along a larger altitudinal gradient, including intensely used grasslands at high altitudes (> 2000 m a.s.l.; Daehler 2005); thus many species may have been introduced to higher altitudes rather than dispersing from the lowlands. Further, in accordance with our study, a zonation reflecting bioclimatic origin has been found more commonly for (sub)tropical species than for temperate and Mediterranean species (e.g. Arteaga et al. 2009). Finally, the absence of a zonational pattern could reflect the fact that we only studied annual plants. This was a deliberate choice to avoid confounding of the results by different life forms; and an unequal representation of different life forms in different bioclimatic groups may have confounded results in other studies.

Does time since introduction influence altitudinal ranges of non-native species?

In accordance with our second hypothesis, the altitudinal ranges of old introductions tended to be broader than those of recently-introduced species, and with few exceptions the species in natural habitats at high altitudes were old introductions. Becker et al. (2005) also showed a positive correlation between the highest occurrence of non-native species and their time since introduction in the Swiss Alps. Such a relationship could simply reflect the time it takes for propagules to disperse to higher altitudes (i.e. propagule pressure) (Ross et al. 2008), although other studies suggest that roadside distributions of non-native species are unlikely to be dispersal limited (Alexander et al. 2009b). Another explanation is that it reflects the time needed for populations to adapt genetically to the new conditions (Dietz & Edwards 2006; Roy et al. 2000). In the natural habitat the proportion of old introductions was higher amongst Mediterranean than temperate

species. This could be because Mediterranean species are less likely to be pre-adapted to cold climatic conditions, so that local adaptation would be necessary for them to grow at high altitudes. In contrast, temperate species that establish at low altitudes have to be climatically plastic, which would explain why recently-introduced species have been able to spread to higher altitudes.

Do species ranges explain species richness patterns with altitude?

In line with our third hypothesis, there was a close match between the species richness observed along the gradient and that predicted from the species' range sizes (Figure 6), which led to a hump-shaped richness pattern (Figure 5).

A decrease in species richness at low and high altitudes can therefore be explained by a loss of species with overlapping ranges. A strong decline in the richness of non-native Mediterranean and temperate plant species at low and high altitudes was previously reported for different islands in the Canary Islands (Arévalo et al. 2005; Arteaga et al. 2009). Studies in other mountainous regions have shown either a monotonic decline of non-native plant species richness with altitude or, as in our case, a hump-shaped pattern (Becker et al. 2005; Jakobs et al. 2010; Marini et al. 2009; McDougall et al. 2005; Pauchard et al. 2009). While at temperate latitudes, the limiting climate factor at high altitudes is likely to be low temperatures (Becker et al. 2005; Marini et al. 2009), on subtropical oceanic islands species may be limited at low altitudes by aridity (Arévalo et al. 2005; Hawkins et al. 2003; Jakobs et al. 2010, Figure 1). Thus, the hump-shaped pattern in species richness could reflect either the altitudinal pattern of water availability alone or opposing gradients of climatic harshness – aridity at low altitudes and low temperature at high altitudes (or a combination of both).

It cannot be excluded that a decline in species richness at the extremes of the altitudinal gradient is due to increased habitat resistance to invasion because of competition from established vegetation and/or reduced propagule pressure. However, because we surveyed highly disturbed roadsides where total vegetation cover at the extremes of the gradient was only some 10-60%, we do not think that competitive exclusion played an important role. Propagule pressure is unlikely to decline much towards the lowest altitudes, but it cannot be excluded as a relevant factor at high altitudes; however, the roads in the survey are heavily used by tourists, even at the highest altitudes (1000-2000 cars/day).

Habitat context influences species distribution patterns

The altitudinal distribution pattern of non-native annual species was modulated by the habitat context. About 30% of the species reached a sharp altitudinal distribution limit at the boarder of the anthropogenic and natural habitats, which resulted in a drop in species richness at the transition of the two habitat types (Figures 3 and 5). When comparing the observed and predicted species richness, based on the assumption that a species occurs everywhere within its altitudinal range, it appears that this drop can be explained only partly by an ultimate altitudinal limit of species ranges; indeed, many Mediterranean species reappeared again at higher altitudes, so that the observed and predicted richness of Mediterranean species differ strongly between c. 1000 and 1500 m a.s.l. (Figure 6).

This separation might be explained by the influence of the cloud layer within the natural habitat, which is most pronounced between c. 1000 and 1500 m a.s.l. Moist and shady conditions within the cloud forest at these altitudes might exclude typically light-demanding and drought-adapted Mediterranean ruderal species, which reappear above the cloud layer where the pine forest is more open and light. This habitat effect may also explain contrasting results between this study and previous work in Tenerife. Arévalo et al. (2005), working on the leeward side of Tenerife, where there is no cloud forest, did not find the same mid-altitude drop in numbers of non-native species. Arteaga et al. (2009) found in a narrower altitudinal range between 0 and 650 m a.s.l. a monotonic increase for non-native temperate species richness, consistent with our results for this altitudinal range, but a hump-shaped pattern for non-native Mediterranean species richness. Because of topographic effects, in their study area the transition to cloud forest occurred at c. 600 m a.s.l. (Arévalo et al. 2008; Marzol 2008). This may explain the drop in Mediterranean species richness at a lower altitude.

If, as seems likely, climate change alters the altitudinal distribution of cloud forests on oceanic islands (Loope & Giambelluca 1998), the distribution of non-native plants could indirectly be affected. Indeed, indirect effects of climate change through changes in habitat distribution may prove to be more important than direct climatic effects in shaping non-native species distributions.

Conclusions

Our results suggest that bioclimatic origin does not influence the non-native species richness pattern along an altitudinal gradient. However, climate matching is important for the establishment of non-native species at low altitudes, while plasticity is crucial for species that are not climatically pre-adapted. Niche modelling may thus be useful to predict potential areas of first establishment (cf. Broennimann et al. 2007; Tatem and Hay 2007). Nonetheless, the importance of time since introduction suggests that ongoing adaptation might be important as species extend their ranges upwards along the altitudinal gradient. This could account for the observed time lags between introduction and rapid spread of non-native species (e.g. Richardson & Pyšek 2006). Our results show that the altitudinal distribution of non-native plants is affected both by climatic and habitat conditions. Climate change is therefore likely to affect the occurrence of these species both directly and indirectly, e.g. by altering the distribution of habitats such as cloud forest. So far, this interplay of regional climate and habitat type has not been discussed in studies of non-native species distributions along an altitudinal gradient.

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Appendix A2

Overview of sources used to determine life form, longevity, introduction status, bioclimatic origin and time since introduction for recorded species.

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Appendix B2

Table 3: List of recorded non-native annual plant species with Mediterranean (MED) and temperate (TEMP) bioclimatic origin. Species are grouped in old-introduced (OLD) and recently-introduced (NEW) species.

Species	Family	Bioclimatic origin	Time since introduction
Anagallis arvensis	Primulaceae	MED	OLD
Calendula arvensis	Asteraceae	MED	OLD
Capsella rubella	Brassicaceae	MED	OLD
Daucus carota	Apiaceae	MED	OLD
Erodium cicutarium	Geraniaceae	MED	OLD
Galactites tomentosa	Asteraceae	MED	OLD
Geranium dissectum	Geraniaceae	MED	OLD
Geranium rotundifolium	Geraniaceae	MED	OLD
Hirschfeldia incana	Brassicaceae	MED	OLD
Hordeum murinum	Poaceae	MED	OLD
Lathyrus sphaericus	Fabaceae	MED	OLD
Medicago polymorpha	Fabaceae	MED	OLD
Ornithopus compressus	Fabaceae	MED	OLD
Papaver rhoeas	Papaveraceae	MED	OLD
Papaver somniferum	Papaveraceae	MED	OLD
Pseudognaphalium luteoalbum	Asteraceae	MED	OLD
Rapistrum rugosum	Brassicaceae	MED	OLD
Silene gallica	Caryophyllaceae	MED	OLD
Silybum marianum	Asteraceae	MED	OLD
Sinapis alba	Brassicaceae	MED	OLD
Sinapis arvensis	Brassicaceae	MED	OLD
Sisymbrium erysimoides	Brassicaceae	MED	OLD
Sonchus asper	Asteraceae	MED	OLD
Sonchus oleraceus	Asteraceae	MED	OLD
Torilis arvensis	Apiaceae	MED	OLD
Tragopogon porrifolius	Asteraceae	MED	OLD
Trifolium campestre	Fabaceae	MED	OLD
Trifolium glomeratum	Fabaceae	MED	OLD
Trifolium ligusticum	Fabaceae	MED	OLD
Amaranthus blitum	Amaranthaceae	MED	NEW
Amaranthus cruentus	Amaranthaceae	MED	NEW
Conyza floribunda	Asteraceae	MED	NEW
Eschscholzia californica	Papaveraceae	MED	NEW
Galinsoga parviflora	Asteraceae	MED	NEW
Galinsoga quadriradiata	Asteraceae	MED	NEW
Lathyrus annuus	Fabaceae	MED	NEW
Lathyrus clymenum	Fabaceae	MED	NEW
Lathyrus tingitanus	Fabaceae	MED	NEW
Lolium multiflorum	Poaceae	MED	NEW
Melilotus indicus	Fabaceae	MED	NEW
Mercurialis annua	Euphorbiaceae	MED	NEW
Ornithopus pinnatus	Fabaceae	MED	NEW
Raphanus raphanistrum	Brassicaceae	MED	NEW
Scorpiurus muricatus	Fabeceae	MED	NEW
Scorpiurus vermiculatus	Fabaceae	MED	NEW

Table 3 continued

Species	Family	Bioclimatic origin	Time since introduction
Vicia villosa	Fabaceae	MED	NEW
Galium aparine	Rubiaceae	TEMP	OLD
Geranium robertianum	Geraniaceae	TEMP	OLD
Malva neglecta	Malvaceae	TEMP	OLD
Poa annua	Poaceae	TEMP	OLD
Sisymbrium officinale	Brassicaceae	TEMP	OLD
Solanum nigrum	Solanaceae	TEMP	OLD
Vicia hirsuta	Fabaceae	TEMP	OLD
Conyza canadensis	Asteraceae	TEMP	NEW
Lamium amplexicaule	Lamiaceae	TEMP	NEW
Stellaria media	Caryophyllaceae	TEMP	NEW
Veronica persica	Plantaginaceae	TEMP	NEW
Viola tricolor	Violaceae	TEMP	NEW

Appendix C2

Table 4: Results of the general linear mixed effects models (ML method) to describe the species richness pattern along the altitudinal gradient with respect to the habitat context. The categorical variable "habitat" classified sites (N = 40) according to the anthropogenic and natural habitat type. All models contained site nested within road as random effects. Model 3, which was the best fitting model, described species richness by two linear terms separately for each habitat.

Model	AIC	Fixed effects	Resid. d.f.	F	p
1	288.49	Altitude	37	26.14	< 0.001
2	283.49	Altitude^2	36	18.70	< 0.001
3	238.94	Altitude	35	94.46	< 0.001
		Habitat	35	69.68	< 0.001
		Altitude x habitat	35	31.64	< 0.001
4	238.26	Altitude^2	33	61.92	< 0.001
		Habitat	33	88.02	< 0.001
		Altitude^2 x habitat	33	0.24	0.789

Chapter 3

Genetic differentiation of multiple non-native plants along a steep environmental gradient

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Abstract

The spread of non-native plant species along climatic gradients might be limited by their ability to adapt to changing conditions. Adjustment of the phenotype to different climatic conditions can be realized by phenotypic plasticity and by local adaptation, and both phenomena have been reported from latitudinal gradients. However, the relative importance of these adaptive responses along elevational gradients is less clear and has been analysed only for individual species. We carried out a climate chamber experiment with 13 herbaceous plant species introduced onto Tenerife. As the climate becomes more limiting for plant growth over the upper part of the elevational range than over the lower, we expected greater genetic differentiation between mid- and high elevations than between low and mid-elevations. Along both gradients and for all species, plant growth (biomass production) was reduced under lower temperatures. As expected, we found a consistent genetic differentiation over the upper elevational gradient. Genotypes from high elevations grew more slowly than those from mid-elevations, which might be an adaptive response linked to greater stress tolerance. We suggest that these differences between the lower and upper halves of the elevational range are related both to the contrasting environmental gradients and to the species that grow in them. At lower elevations, genetic differentiation might be hindered by high propagule pressure and gene flow due to strong anthropogenic influences. Furthermore, frequent disturbance produces fluctuating environmental conditions, which probably favours phenotypic flexibility rather than genetic differentiation. In contrast, in the upper part of the elevational range, low temperatures are probably a strong selection pressure that favours a genetic response. Polyploidy is often linked to genetic adaptability of non-native plants, and in line with this, we found larger genetic effects for polyploid species. Our results suggest that genetic differentiation is widespread among non-native plants and an important contributor to invasion success.

Introduction

Understanding plant responses to environmental variation is critical for predicting the spread of invasive species (Richardson & Pyšek 2006; Walther et al. 2009), as well as the ability of native species to adapt to rapid climate change (Atkins & Travis 2010). Such responses can include both phenotypic plasticity (i.e. the ability of an organism to adjust its phenotype to different environmental conditions: Crispo 2008; Ghalambor et al. 2007; Richards et al. 2006) and adaptive genetic differentiation (Lee 2002; Reznick & Ghalambor 2001). Local adaptation to environmental conditions is common among plant species (e.g. Montesinos-Navarro et al. 2011); for example, plants of the same species often become smaller as temperatures decline along latitudinal and elevational gradients (Olsson & Ågren 2002). Such clinal responses have also been observed in populations of non-native species (Alexander et al. 2009; Huey et al. 2000; Kollmann & Bañuelos 2004). Indeed, invasion success has been linked to the ability of a species to adapt rapidly to environmental conditions in the new range (Lee 2002; Roy et al. 2000; Weber & Schmid 1998). Such adaptive responses might also include increases in phenotypic plasticity, another trait that is important for invasion success by allowing populations to rapidly respond to environmental variation (Bossdorf et al. 2008; Crispo 2008; Richards et al. 2006). However, whilst several studies report genetic differentiation in size and growth along latitudinal gradients (e.g. Reinartz 1984; Weber & Schmid 1998), the relative contribution of genetic differentiation or phenotypic plasticity to comparable patterns along elevational gradients is less clear (Alexander et al. 2009). Genetic clines have been reported for some species (Montague et al. 2008; Monty & Mahy 2009; Scott et al. 2010), although responses due to phenotypic plasticity are equally widespread (Alexander 2010; Bossdorf et al. 2008; Parker et al. 2003).

There have been some attempts to identify conditions or species traits that promote rapid evolution in non-native species (Alexander & Edwards 2010; Barrett et al. 2008; Kawecki & Ebert 2004; Schierenbeck & Ellstrand 2009). In particular, adaptive responses depend on the availability of genetic diversity (Gilchrist & Lee 2007; Sakai et al. 2001), and therefore might be stronger in populations with a high ploidy level (Levin 2003). On the other hand, characteristics of the environmental gradients along which non-native species spread are also likely to be important. For example, genetic differentiation might be greater along steep gradients that impose widely varying selection pressures on populations (Lee 2002), but could be constrained if there is too much gene flow amongst these populations (Kawecki 2008). In order to make generalizations about the frequency of genetic or phenotypic responses in non-native species, it is necessary to move from case studies using single-species to comparisons across multiple species and gradients.

Elevational gradients offer excellent model systems to study such questions because environmental conditions change rapidly over short distances (Peterson et al. 1997), so that plant invasions can be investigated in a changing context (Dietz & Edwards 2006). Recent studies have shown that a significant number of non-native plant species are present in mountain areas (McDougall et al. 2011; Pauchard et al. 2009). Since transportation between different high-elevation areas is rather rare, the most important source for the non-native mountain flora is the adjoining lowland (lowland climate filter sensu Becker et al. 2005; McDougall et al. 2011; Alexander et al. in press). Non-native species must therefore first establish under lowland conditions before they can spread upwards to higher elevations. Most non-native species

recorded in mountain areas reach up to mid-elevations, and only a few species are found at the highest elevations. Because of this filtering effect, the species that occur at high elevations are also present at low elevations (Alexander et al. in press; Haider et al. 2010), and are able to tolerate a broad climatic range. For these species, growth under cold conditions at higher elevations might be promoted by genetic differentiation and local adaptation.

Similar patterns in the distribution of non-native plants have been observed on several mountain systems including Tenerife (Canary Islands, Spain). Along the windward side of this island, however, a clear discontinuity is evident at c. 1000 m a.s.l., where two contrasting types of habitat meet (Haider et al. 2010). The lower part of the elevational gradient is strongly influenced by human use, while the upper part consists of more natural habitats, dominated by *Pinus canariensis* forest and subalpine scrub. Many of the non-native species reach their elevational limit at the border between these two zones, probably because they require disturbed and open sites. In contrast, the few non-native species that reach higher elevations are probably limited by climatic factors such as low temperature sums and frost events during the winter (Fernández-Palacios 1992). Thus the conditions for genetic adaptation are likely to differ strongly between the low- and high-elevation parts of the gradient. At the lower end, mixing of populations and gene flow may be frequent due to intense anthropogenic activities, and both climatic and habitat factors affect plant growth. At high elevations, in contrast, propagule pressure and gene flow are much lower, and the range limits are probably set by climatic factors, notably temperature. We therefore hypothesised that genetic differentiation would be greater between populations at mid- and high elevations than between populations at low and mid-elevations.

We tested our hypothesis with a climate chamber experiment with 13 non-native plant species. Specifically, we asked: (1) How widespread is a phenotypic growth response (biomass production) of non-native species to different temperature treatments? (2) How frequent is genetic differentiation of non-native species along a temperature gradient? (3) How do the magnitude of phenotypic and genetic responses differ between the lower and upper elevational ranges?

Methods

Study system

We conducted an experiment with in total 13 herbaceous plant species (Table 1) that were introduced to the island of Tenerife (Canary Islands, Spain, 28° N, 16° W). The first part of the experiment (hereafter "upper range series") compared the growth response to temperature of mid- and high elevational populations of 6 species, while the second part (hereafter "lower range series") compared low and mid-elevational populations of 11 species. We performed two separate series because most non-native species on Tenerife occur either below 1000 m a.s.l. or, in case that they reach up to 2000 m a.s.l., are not present at the lowest elevations (Haider et al. 2010). The few species that were present along the whole elevational gradient and sufficiently abundant were included in both series and served as controls for interpreting differences between the responses of species in the two series.

Table 1: Non-native species included in the experiment, their families, bioclimatic origin and ploidy levels (lower = lower range series; upper = upper range series).

Taxon	Family	Bioclimatic origin	Ploidy level	Series
Bidens pilosa	Asteraceae	Mediterranean	Polyploid	Lower
Centranthus ruber	Valerianaceae	Mediterranean	Polyploid	Lower
Galium aparine	Rubiaceae	Temperate	Polyploid	Lower, upper
Geranium robertianum	Geraniaceae	Temperate	Polyploid	Lower, upper
Geranium rotundifolium	Geraniaceae	Mediterranean	Diploid	Upper
Hirschfeldia incana	Brassicaceae	Mediterranean	Diploid	Lower, upper
Lamium amplexicaule	Lamiaceae	Temperate	Diploid	Lower
Malva parviflora	Malvaceae	Mediterranean	Diploid	Lower
Reseda luteola	Resedaceae	Mediterranean	Polyploid	Upper
Scorpiurus muricatus	Fabaceae	Mediterranean	Polyploid	Lower
Silene vulgaris	Caryophyllaceae	Temperate	Diploid	Lower, upper
Veronica persica	Scrophulariaceae	Temperate	Polyploid	Lower
Vicia villosa	Fabaceae	Mediterranean	Diploid	Lower

Seed of all species were collected from the windward, northern side of Tenerife, which has a Mediterranean climate with warm, dry summers and cool, wet winters (Fernández-Palacios 1992). At lower elevations urban and agricultural land uses dominate and the natural vegetation has largely disappeared. However, more or less natural pine forest remains at higher elevations, followed by subalpine scrub and alpine vegetation (Fernández-Palacios & de Nicolás 1995). For further details see Haider et al. (2010).

For species present over the entire elevational range, we collected seed from low elevational (c. 100 m a.s.l.), mid-elevational (c. 1000 m a.s.l.) and high elevational populations (c. 2000 m a.s.l.; hereafter "seed origins"). For other species, we collected seed at mid-elevations and either low elevations or high elevations, depending on their distribution. Seeds were typically collected from several individuals of several wild populations (lower range series: 1-5 populations per species, mean: 3 populations, c. 1-50 individuals per population; upper range series: 1-4 populations per species, mean: 3 populations, c. 1-20 individuals per population). Populations from different seed origins were bulked for use in the experiment.

Climate chamber experiment

The experiment was conducted in climate chambers located at the Technische Universität München in Freising-Weihenstephan. In Mediterranean ecosystems, spring represents the main growth period, and most species complete flowering before the onset of summer aridity (Mitrakos 1980). Therefore, we used the monthly mean values of April in our climate treatments, which were chosen to simulate temperature and humidity conditions during the growing season at low (c. 100 m a.s.l.), mid- (c. 1000 m a.s.l.) and high elevations (c. 2000 m a.s.l.) on Tenerife; these are referred to here as the low-climate, mid-climate and high-climate treatments. The daily temperature sum was 414.8 K (15.0-20.5°C daily temperature range; 65-75% rel. humidity) for the low-climate treatment, 250.3 K (7.5-15.5 °C; 65-85% rel. humidity) for the mid-climate treatment and 176 K (6.0-13.5°C; 50% rel. humidity) for the high-climate treatment (values from Centro Meteorológico Territorial en Canarias Occidental, Ministerio de Medio Ambiente). The

day length in all climate treatments was 12.5 hours. Plants were watered daily as needed. Within the climate chambers we arranged plants according to a randomized block design with each block containing one plant per seed origin per species. We changed the arrangement of plants within each block during the experiment to reduce differences in growth resulting from different locations in the climate chamber or neighbouring plants.

In order to maximise our ability to generalise our findings, replication was focused at the species level, rather than at the individual level (N = 6 per species, climate treatment, and seed origin in the lower range series, and N = 5 in the upper range series). However, this does not preclude significant within-species analyses. Overall, the upper range series included 6 species x 2 seed origins x 2 climate treatments x 5 replicates = 120 plants, and the lower range series included 11 species x 2 seed origins x 2 climate treatments x 6 replicates = 264 plants, giving a total of 384 individuals.

Seed were germinated in August (lower range series) and December 2007 (upper range series) on fine compost in a greenhouse, maintained at a constant 22°C. For some species germination was facilitated by scarifying the seeds or treating them with a bleaching agent. Eighteen days after sowing, the seedlings were separately transplanted into 14 cm pots containing 2 L of nutrient-poor garden soil and 2 mm sand (1:1 mixture by volume). Nitrogen (N), phosphate (P) and potassium (K) were balanced and constantly kept on a moderate level during the experiment. The plants were kept for a further two weeks in the greenhouse (without supplementary light), by which time they had developed their first true leaves. After moving the pots into the climate chambers, conditions were maintained as in the greenhouse for the first week to enable plants to acclimatize to the new environment. With the beginning of the climate simulation (in the upper range series five days later) the initial size of each plant was estimated by counting the number of leaves. Because we did not have enough seedlings, we could not harvest plants at this moment to destructively measure the initial biomass. However, final leaf number was correlated with the biomass of the plants at harvest (upper range series: $R^2 = 0.16$, $p < 0.001$, lower range series: $R^2 = 0.21$, $p < 0.001$).

The plants were harvested either at the onset of flowering or, for those that did not flower, after three months. The duration of the growth period therefore varied among species, ranging from 45 to 96 days in the upper range series and from 30 to 85 days in the lower range series. All plants of a given species under the same climate treatment were harvested at the same time and their aboveground biomass determined after drying at 70°C for 48 hours. These data were then converted to biomass production per day.

Statistical analyses

All statistical analyses were performed with R (version 2.10.1 for Windows, The R Foundation for Statistical Computing). To evaluate the effects of climate treatment and seed origin on biomass production per day we ran linear mixed effects models (lmer() in the R-package lme4) separately for each species, including climate treatment, seed origin and their interaction as fixed effects and block as a random effect. The initial leaf number was included as a covariate to account for differences in plant size before the beginning of the climate treatment (cf. Rose et al. 2009). Model checking plots were inspected to ensure that model assumptions were met, but no further transformations were necessary. The response variable was standardized

(z-transformation) to allow direct comparisons of coefficients between species. The coefficients for the climate treatment and seed origin effects represent the magnitude and direction of a species' phenotypic and genetic responses to the climate treatment, respectively (hereafter "species responses"). For example, positive coefficients indicate that plants grown under a lower elevation climate treatment, or collected from lower elevations, grew larger. The coefficients were extracted from mixed models for each species fitted without the interaction term, because the interaction was significant only for one species.

Results

All plants survived throughout the experiment. However, those in the upper range series developed rather slowly, and only 8.5% had produced flowers before harvesting, with two species (*Reseda luteola* and *Silene vulgaris*) producing no flowers. In the lower range series, all species except *Centranthus ruber* were flowering at the time of harvest (overall 46% of plant individuals). For most species, flowering was slightly more frequent among plants under the low-climate treatment. However, there were also two species (*Galium aparine* and *Veronica persica*) that flowered only under the mid-climate treatment.

Climate treatment effect

In both series and for all species, plant growth (biomass production per day) was reduced under lower temperatures (significant climate treatment effect for all species except *G. aparine* and *Geranium robertianum* in the upper range series and *Scorpiurus muricatus* and *Vicia villosa* in the lower range series; Figures 1 and 2 and Table 2).
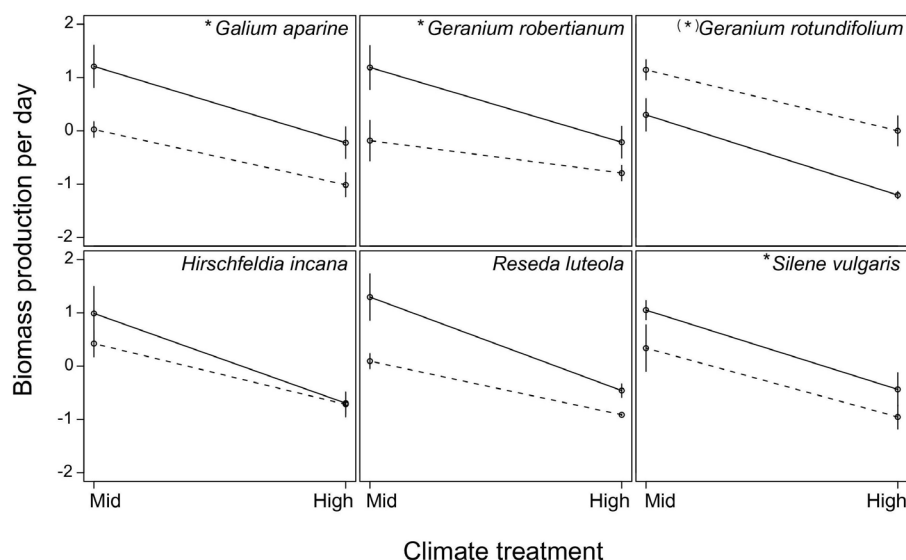
Figure 1: Biomass production (z-standardized) of species in the upper range series under mid-and high-climate treatment, separately shown for middle (solid line) and high seed origin (dashed line). Species with a significant seed origin effect (p < 0.05) are indicated with an asterisk, marginally significant species (p < 0.1) are indicated with a bracketed asterisk (see Table 2).

This trend was the same for both seed origins except in the case of *S. muricatus* in the lower range series, in which plants of low seed origin were slightly larger under the mid-climate treatment (however, no significant interaction of climate treatment and seed origin, $F = 1.2$, d.f. = 1, $p = 0.3$). Among the four species used in both series, there was a consistently significant climate treatment effect for *Hirschfeldia incana* and *S. vulgaris* and biomass production per day declined continuously with increasing elevation.
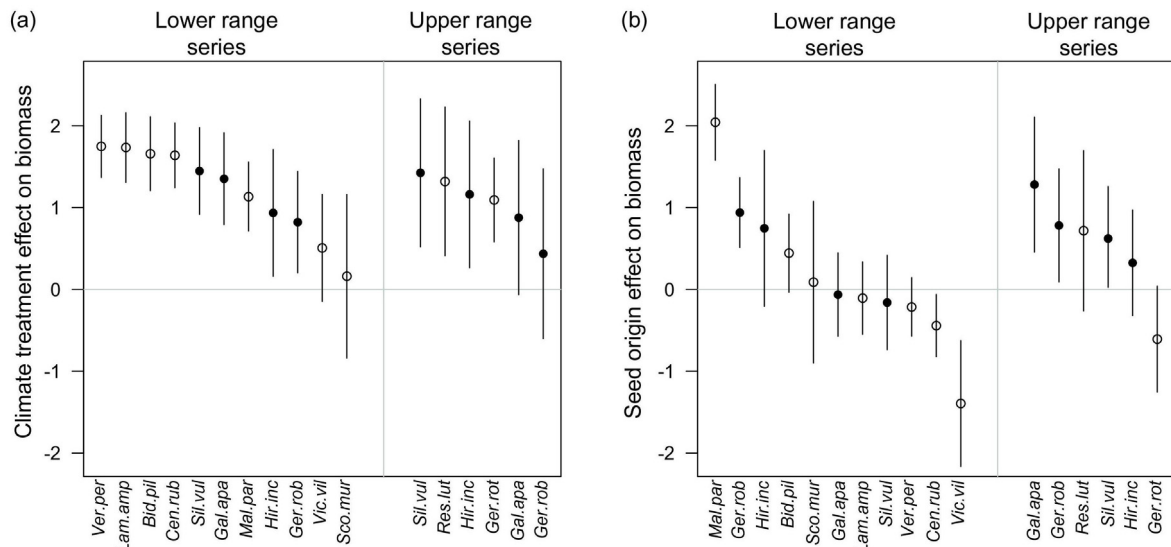
Figure 2: Effect sizes of each species for (a) climate treatment effect and (b) seed origin effect in biomass production. The effect is significant if the error bar (95% confidence intervals) does not cross zero (horizontal grey line). Species that were included in both series are indicated with filled dots.

Seed origin effect

In the upper range series, plants of high seed origin were smaller and grew more slowly than those of middle seed origin (except for *G. rotundifolium*), although this effect was not significant for all species (significant seed origin effect for *G. aparine*, *G. robertianum* and *S. vulgaris*, marginally significant for *G. rotundifolium*; Figure 1 and Table 2). The steepness of decline in biomass production per day was similar for both seed origins (no significant interactions between climate treatment and seed origin).

In the lower range series, we found no consistent difference in biomass production per day between plants of different seed origins. For *C. ruber* and *V. villosa*, plants of low seed origin were bigger and grew faster than plants of middle seed origin (significant seed origin effects). In contrast, for *G. robertianum* and *Malva parviflora*, plants of middle seed origin were larger under both climate treatments (significant seed origin effects). Among the species included in both series, *G. robertianum* was the only one to show a significant seed origin effect in both series (Figure 2), with plants of lower seed origin having a higher rate of biomass production.

To test whether the differences in aboveground biomass between plants of middle and high seed origin were due to changes in biomass allocation between below- and aboveground parts, we measured the root:shoot ratios of plants (data not shown). Biomass allocation to roots was lower under the high-climate than under the mid-climate treatment, except in the case of *R. luteola*. And for all species except *G. rotundifolium*, root allocation under the high-climate treatment was slightly lower in plants of high than of middle seed origin. These results indicate that aboveground biomass reduction cannot be explained by changes in biomass allocation patterns, but that it is a direct growth response of the species to reduced temperature (highly significant correlation between aboveground and total biomass, $R^2 = 0.95$, $p < 0.001$).

In both series, the climate treatments had a larger effect upon biomass production than did seed origin (i.e. comparing the means of the absolute values of the effect sizes; Figure 2). However, the differences between the climate treatment and seed origin effects were much smaller in the upper range series (1.05 vs. 0.72) than in the lower range series (1.19 vs. 0.60, respectively).

Table 2: Results of the mixed effects models with climate treatment and seed origin as main effects, block as random effect and initial number of leaves as covariate to control for differences in growth before the climate treatments. Positive effects indicate a bigger response value under the lower-climate treatment (for climate treatment effect) and for plants of the lower seed origin (for seed origin effect), respectively. N = 24 for all species in the upper range series and N = 20 in the lower range series. Significant effects are highlighted in bold.

| | Biomass production per day | | | | | |
| | Climate treatment effect | | | Seed origin effect | | |
Upper range series	Effect	p	F	Effect	p	F
Galium aparine	0.88	0.056	20.877	**1.28**	**0.005**	10.344
Geranium robertianum	0.44	0.328	0.173	**0.78**	**0.031**	5.564
Geranium rotundifolium	**1.09**	**< 0.001**	15.678	-0.61	0.058	4.135
Hirschfeldia incana	**1.16**	**0.016**	7.720	0.32	0.229	1.563
Reseda luteola	**1.32**	**0.006**	7.934	0.72	0.133	2.527
Silene vulgaris	**1.43**	**0.004**	8.634	**0.62**	**0.017**	7.055
Lower range series						
Bidens pilosa	**1.66**	**< 0.001**	56.354	0.44	0.065	3.803
Centranthus ruber	**1.64**	**< 0.001**	82.156	**-0.44**	**0.028**	5.651
Galium aparine	**1.35**	**< 0.001**	18.151	-0.06	0.802	0.065
Geranium robertianum	**0.82**	**0.011**	7.850	**0.94**	**< 0.001**	21.262
Hirschfeldia incana	**0.93**	**0.037**	4.510	0.75	0.055	4.173
Lamium amplexicaule	**1.74**	**< 0.001**	59.762	-0.11	0.485	0.506
Malva parviflora	**1.13**	**< 0.001**	0.290	**2.04**	**< 0.001**	86.477
Scorpiurus muricatus	0.16	0.719	0.166	0.09	0.857	0.033
Silene vulgaris	**1.45**	**< 0.001**	35.508	-0.16	0.590	0.300
Veronica persica	**1.75**	**< 0.001**	87.045	-0.21	0.209	1.6852
Vicia villosa	0.51	0.126	2.2728	**-1.39**	**0.001**	14.402

Discussion

We investigated the genetic and phenotypic responses of non-native plant species to temperature conditions associated with different elevations on Tenerife. For both the upper and lower elevational ranges, growth was consistently reduced at lower temperatures. However, consistent effects due to the seed origin of the plant material were only found in the upper range series, with high seed origin plants showing generally slower growth than plants of middle seed origin.

Phenotypic response to temperature

The consistently lower growth of plants under increasingly high climate treatments indicates that temperature is an important factor influencing plant growth in both parts of the elevational range. From our data we cannot distinguish whether reduced plant growth under lower temperatures is an adaptively plastic response or a non-adaptive reaction to environmental stress, which constrains growth. However, the direction of this response was consistent with the observed genetic response, at least in the upper range series, suggesting that it could be partly adaptive. Similar phenotypic responses to temperature have been observed in other studies. For example, in a common garden experiment in Switzerland, Trtikova et al. (2010) showed that reduced growth of *Erigeron annuus* at high elevations was a phenotypic response, with no differentiation of populations along elevational gradients. Interestingly, the magnitude of the phenotypic responses to temperature that we observed were similar along both gradients and not larger at high elevations. This indicates that reduced growth is due to growing season temperature (growing degree days or daily temperature sum) rather than minimum temperatures (Fernández-Palacios & de Nicolás 1995); in our experiment, the daily temperature sum was reduced by approximately two-thirds for each elevational step, while the minimum temperatures in the high- and mid-climate treatments were almost the same.

Genetic differentiation among seed origins

Although not significant for all species, our data suggest that genetic differentiation along elevational gradients is widespread among non-native species. Similar results have also been reported for instance by Monty and Mahy (2009) for non-native *Senecio inaequidens* populations, and also along latitudinal gradients (e.g. Kollmann & Bañuelos 2004; Sexton et al. 2002), but not previously for a large set of species from a single experiment. This genetic response was very consistent among the species reaching the highest elevations on Tenerife, suggesting that these differences might arise from local adaptation to climatic conditions at high elevations. For example, slower growth has been shown to be a genetic adaptation to cold temperature and shorter growing seasons for other species along elevational as well as latitudinal gradients (e.g. Bastlová et al. 2006; Jia et al. 2010; Li et al. 1998; Olsson & Ågren 2002). A reduced growth has also been associated with enhanced stress tolerance (Grime 2001; Stanton et al. 2000). Slow-growing plants are less likely to exhaust the available resources and more likely to survive periods when no growth is possible (Grime & Hunt 1975). An alternative explanation, that pre-adapted ecotypes have been directly introduced to high elevations on Tenerife, is unlikely for all species, especially given that most species spread upwards from the lowlands (Becker et al. 2005; Haider et al. 2010; Pauchard et al. 2009).

G. rotundifolium was the only species for which plants of high seed origin grew bigger under both climate treatments. This is perhaps explained by the fact that this is the only species that occurs at high elevations in its native range (Klotz et al. 2004).

Genetic differences among seed origins were also found in the lower range series. However, these were inconsistent, with plants of low seed origin growing larger than those of middle seed origin for some species but not others. Furthermore, whilst the magnitudes of phenotypic and genetic responses were similar in the upper range series, genetic responses were comparatively small in the lower range series. This difference between the elevational gradients may be related both to the characteristics of the gradient and the species that occur along them. Firstly, while lower elevations on Tenerife are characterized by a high anthropogenic influence, higher elevations comprise more natural habitats (see Haider et al. 2010 for details). Because of the high anthropogenic influence, propagule pressure and gene flow are probably greater at low elevations, which could hinder genetic differentiation (Kawecki 2008; Kawecki & Ebert 2004). Secondly, although the temperature gradient at low to mid-elevations probably does not impose a strong selection pressure, a number of other abiotic factors such as drought at low elevations might lead to genetic differentiation (Fernández-Palacios & de Nicolás 1995; Haider et al. 2010), with different effects on different species. Thus, the genetic differentiation detected in the lower range series might be explained as responses to selection pressures other than temperature. In contrast, the consistent responses at high elevations might arise from the stronger selection pressure imposed by lower temperatures (Lee 2002). Thirdly, the higher anthropogenic disturbance and multiple stress gradients leading to fluctuating environmental conditions characteristic of low elevations might favour phenotypic flexibility rather than genetic differentiation (Lee & Gelembiuk 2008). Consistent with this hypothesis, the phenotypic response to the climate treatments was relatively much greater than the genetic response in the lower range series. On the other hand, longer, predictable fluctuations or environmental stress, as in the upper part of the elevational gradient, might favour local adaptation (Lee & Gelembiuk 2008; Meyers et al. 2005). This might explain the relatively larger and more consistent genetic effects in the upper range series, and is in line with the assumption that environmental stress acts as a driver of adaptation during biological invasions (Gilchrist & Lee 2007).

Finally, the likelihood of genetic differentiation might depend on the species in question. Most species are lowland species introduced at low elevations (Haider et al. 2010; Pauchard et al. 2009). It could therefore be that whilst phenotypic plasticity is sufficient for species to reach mid-elevations, genetic differentiation is required to reach high elevations. This might also select for those species that have the ability for rapid genetic responses. The capacity of non-native species to respond to selection depends on the level of genetic variation within populations (Gilchrist & Lee 2007; Sakai et al. 2001), which in turn is affected by traits such as life-history or ploidy level. For instance, polyploid species might be better or faster able to adapt to local conditions because they have a greater pool of alleles to respond to selection (Hegarty & Hiscock 2007). In support of this idea, we found in the upper range series a tendency for a greater difference in growth between seed origins for polyploid than diploid species, i.e. polyploid species had a larger seed origin effect ($F_{1,4} = 3.9$, p = 0.1). Additionally, using data from a field survey along the same elevational gradient (Haider et al. 2010) we found a higher proportion of polyploids among the species that reached higher elevations than those that reached only mid-elevations (chi-squared = 3.3, d.f. = 1, p = 0.07).

We consistently detected genetic differentiation in populations collected from along a strong climatic gradient. This suggests that despite potentially low genetic variability in introduced populations (e.g. due to founder effects, Sakai et al. 2001), populations are capable of rapid genetic responses to changing environmental conditions. To assess the relative role of genetic adaptations might be important for predicting future distribution ranges of non-native as well as native species. Numerous modelling approaches are based on the assumption that introduced species conserve their climatic niche in the new range. However, as a consequence of genetic responses to selection pressures in the new range (Alexander & Edwards 2010), species niches might shift and model predictions may be misleading.

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Chapter 4

Pflanzeninvasionen in Gebirgen – Modellsystem für die Forschung, Handlungsbedarf für den Naturschutz

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Plant invasions in mountains.
A model system for research, a priority for conservation action

Summary

Mountain biodiversity and ecosystems have not yet been heavily affected by biological invasions. However, recent studies indicate that there are already at least some 1,500 non-native plant species present in mountain regions worldwide. Most of these non-native species were recorded only in one or a few mountain regions, and it can be assumed that many more non-native plant species are present in mountain regions not yet studied. Conservation managers consider at least 100 of these species as problematic. Non-native plant species richness consistently declines towards the highest altitudes in mountain regions from all continents and temperate to tropical climate zones. Climate change, increased land use intensity and increased transportation will most probably significantly increase the risk of plant invasions into mountains in the near future. Due to warmer temperatures lowland invasive plants will spread into mountain ecosystems. An intensification of land use at high elevations may lead to increased introduction rates of non-native plants (propagule pressure) and anthropogenic habitat disturbances and thereby further enhance future invasion risks.

The limited presence of non-native species in mountains gives researchers and managers the unique opportunity to respond in time to this emerging threat. Preventive measures may include the regulation of new plant introductions, especially of mountain specialist plants, the establishment and maintenance of a comprehensive monitoring system, and awareness building and networking with stakeholders (e.g. the horticultural and tourism industries and the general public).

Einführung

Das Forschungs- und Naturschutzinteresse an biologischen Invasionen konzentriert sich derzeit auf das Flachland. Aber auch in Gebirgen sind entgegen der weit verbreiteten Meinung zahlreiche gebietsfremde Pflanzenarten zu finden. Gebirge eignen sich als Modellsysteme für die Forschung, um zu verstehen, wie Klimafaktoren die Ausbreitung von gebietsfremden Arten begrenzen. Zudem hat der Naturschutz in Gebirgen die einmalige Möglichkeit, Neueinwanderungen, die z. B. die natürliche Biodiversität verringern könnten, vorbeugend zu verhindern.

Gebirge sind in weiten Teilen vom Menschen nur wenig beeinflusst und beherbergen zahlreiche natürliche Ökosysteme. Charakteristisch ist der hohe Anteil an Arten, die natürlicherweise ausschließlich in einem eingeschränkten Areal vorkommen (Endemiten). Um diese besondere Biodiversität sowie ihre natürlichen Ressourcen zu erhalten, aber auch aufgrund ihrer ästhetischen, gesellschaftlichen und ökonomischen Bedeutung wurden zahlreiche Gebirgsregionen unter Schutz gestellt.

Forschung zu biologischen Invasionen ist in Gebirgen aus zwei Gründen wichtig: Einerseits sind Höhengradienten interessante Modellsysteme für die Forschung zu Pflanzeninvasionen; insbesondere, um zu verstehen, wie sich gebietsfremde Arten an ausgeprägte Klimagradienten anpassen und welche Klimafaktoren ihre Ausbreitung begrenzen. Andererseits stellen biologische Invasionen in Gebirgen besondere Herausforderungen an den Naturschutz, weil es dort noch möglich ist, vorbeugende Maßnahmen gegen gebietsfremde Arten zu ergreifen, die sich großflächig ausbreiten könnten. Ein solches präventives Vorgehen gilt als besonders effektive Managementstrategie, um zukünftige ökologische und ökonomische Schäden (z. B. erhöhte Erosion) durch problematische Arten zu minimieren.

Gebietsfremde Floren in Gebirgen

Daten zur Verbreitung von gebietsfremden Pflanzen sind bisher nur aus relativ wenigen Gebirgsregionen erhältlich (Abbildung 1), dennoch wurden weltweit bereits etwa 1500 verschiedene gebietsfremde Pflanzenarten in Gebirgen entdeckt (McDougall et al. 2009). Weil nur wenige dieser Arten zugleich in mehreren Gebirgsregionen vorkommen, kann man davon ausgehen, dass in neuen Untersuchungsgebieten viele weitere Arten gefunden würden. Trotz der begrenzten Datenmenge zeigen sich bereits Muster, die für Gebirge in allen Klimazonen und auf allen Kontinenten ähnlich sind. Insbesondere nimmt die Anzahl gebietsfremder Pflanzenarten weltweit in Gebirgen mit zunehmender Höhe stark ab (Pauchard et al. 2009). Im Tiefland hingegen unterscheiden sich die Diversitätsgradienten je nach Klimazone (Abbildung 2a). Während in der temperaten (gemäßigten) Klimazone die Zahl gebietsfremder Arten auch bis zu den tiefsten Lagen kontinuierlich zunimmt (z. B. Alexander et al. 2009; Becker et al. 2005; Abbildung 2b), findet man in der mediterranen und subtropischen Klimazone häufig eine Abnahme der Artenzahlen sowohl in den tiefsten als auch höchsten Lagen (z. B. Arévalo et al. 2005; Jakobs et al. 2010; Abbildung 2c). Eine mögliche Erklärung für die Abnahme der gebietsfremden Artenvielfalt in

Tieflagen in diesen Gebieten könnte Trockenheitsstress sein, und tatsächlich findet man eine Abnahme nur für Arten aus einem temperaten Heimatgebiet nicht aber für mediterrane, an Trockenheitsstress angepasste Arten (Abbildung 2c).

Die Abnahme der Artenvielfalt in Hochlagen zeigt sich insbesondere über der Waldgrenze. Auch treten dort bisher nur sehr wenige gebietsfremde Arten in ungestörten, natürlichen Habitaten auf und die Anzahl problematischer Arten ist bisher gering (Kueffer 2010a; McDougall et al. 2011). Aus diesen Beobachtungen sollte man jedoch nicht schließen, dass Gebirgsökosysteme generell resistent gegen Pflanzeninvasionen sind. Immerhin findet man im Durchschnitt etwa die Hälfte der gebietsfremden Arten, die im Tiefland einer Gebirgsregion registriert wurden, auch in den angrenzenden Hochlagen, und mindestens 100 verschiedene gebietsfremde Arten werden weltweit in Gebirgen von Naturschutzfachleuten bereits als problematisch eingestuft (McDougall et al. 2011), weil sie sich dominant ausbreiten und die natürliche Biodiversität oder andere Ökosystemdienstleistungen negativ beeinflussen. Eine dieser problematischen Arten ist die Kleinblütige Königskerze (*Verbascum thapsus*), welche sich auf Hawaii bis auf 3500 m ü. NN ausbreiten konnte und vor allem zwischen ca. 2000 und 2500 m ü. NN dichte Bestände bildet (Daehler 2005; Foto 1).
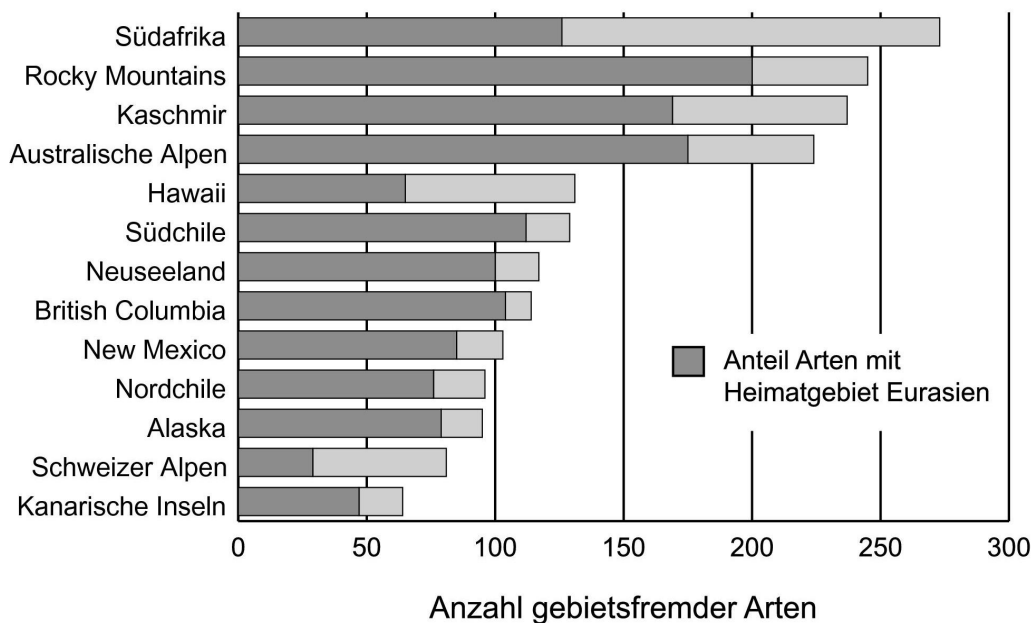
Abbildung 1: Anzahl gebietsfremder Arten in verschieden Gebirgsregionen der Erde und der jeweilige Anteil von Arten mit Heimatgebiet in Eurasien. (Datenquelle: McDougall et al. 2011)
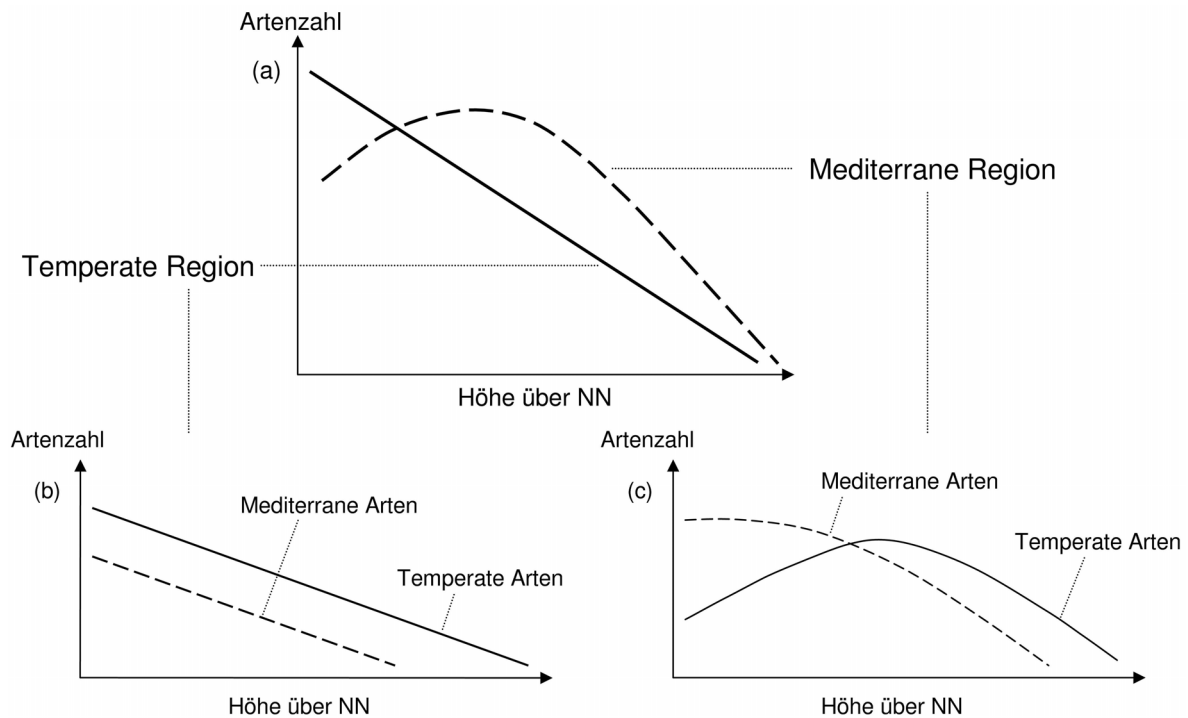
Abbildung 2: Gebietsfremder Artenreichtum entlang des Höhengradienten in Gebieten der mediterranen und temperaten Klimazone (a). Innerhalb jedes Klimagebietes wird unterschieden zwischen Pflanzenarten mit mediterranem und temperatem Heimatgebiet (b und c).

Ein zweites Muster betrifft die Herkunft und ökologische Spezialisierung der gebietsfremden Pflanzenarten in Gebirgen weltweit. Die weiteste Verbreitung haben Arten, die in Eurasien heimisch sind (Abbildung 1). Es handelt sich dabei in der Regel um krautige, d. h. nicht am Stängel verholzende, relativ kurzlebige Pflanzenarten (z. B. Gewöhnliches Knäuelgras (*Dactylis glomerata*), Kleiner Sauerampfer (*Rumex acetosella*) und Weiß-Klee (*Trifolium repens*)). Fast die Hälfte dieser gebietsfremden Krautpflanzen sind einjährige Arten, obwohl diese ökologische Gruppe in einheimischen Gebirgsfloren wenig vertreten ist. Interessanterweise sind gebietsfremde Arten in Gebirgen fast ausschließlich Generalisten in Bezug auf klimatische Wachstumsbedingungen und es wurden bisher kaum Arten entdeckt, die in ihrem Heimatgebiet Bergspezialisten sind.

Foto 1: Die Kleinblütige Königskerze (*Verbascum thapsus*) konnte sich auf dem Vulkan Mauna Kea auf Hawaii bis auf 3500 m ü. NN ausbreiten. (Foto: Christoph Küffer)

Im Gegensatz zu diesen generellen Trends der Vielfalt gebietsfremder Pflanzen und der ökologischen und biogeographischen Zusammensetzung von gebietsfremden Gebirgsfloren, sind kaum generalisierbare taxonomische Muster zu erkennen. Typischerweise sind nur etwa 10% bis ein Drittel der gebietsfremden Floren von zwei Gebirgsregionen identisch (McDougall et al. 2011; Abbildung 3). Die taxonomische Ähnlichkeit zwischen verschiedenen Gebieten lässt sich auch nur zum Teil durch die klassischen Faktoren der Biogeographie – die geographische Nähe und Vernetzung und die großräumigen klimatischen Zonierungen – erklären (Abbildung 3). Nahe Gebiete haben zum Teil eine ähnliche Artenzusammensetzung der gebietsfremden Floren – z. B. Nord- und Südchile –, aber das gilt auch für weit auseinander liegende Gebiete – z. B. Südchile und Australien. Die Globalisierung hat zu einer neuen globalen Verteilung von Pflanzenarten geführt und diese globale Durchmischung von Floren wird in Zukunft weiter zunehmen (sogenannte biotische Homogenisierung). Interessant ist die Frage, ob in dieser global durchmischten Gebirgsflora klimatische Zonierungen sichtbar bleiben werden. Es gibt Anzeichen, dass die Gebirgsfloren von Südafrika, Australien, Südchile und Hawaii, also von Gebieten mit einem zum Teil sehr trockenen mediterranen oder subtropischen Flachlandklima, eine erhöhte taxonomische Ähnlichkeit zueinander aufweisen. Wie wir diskutieren werden, spielt das Tieflandklima eine wichtige Rolle für die Zusammensetzung von gebietsfremden Gebirgsfloren.

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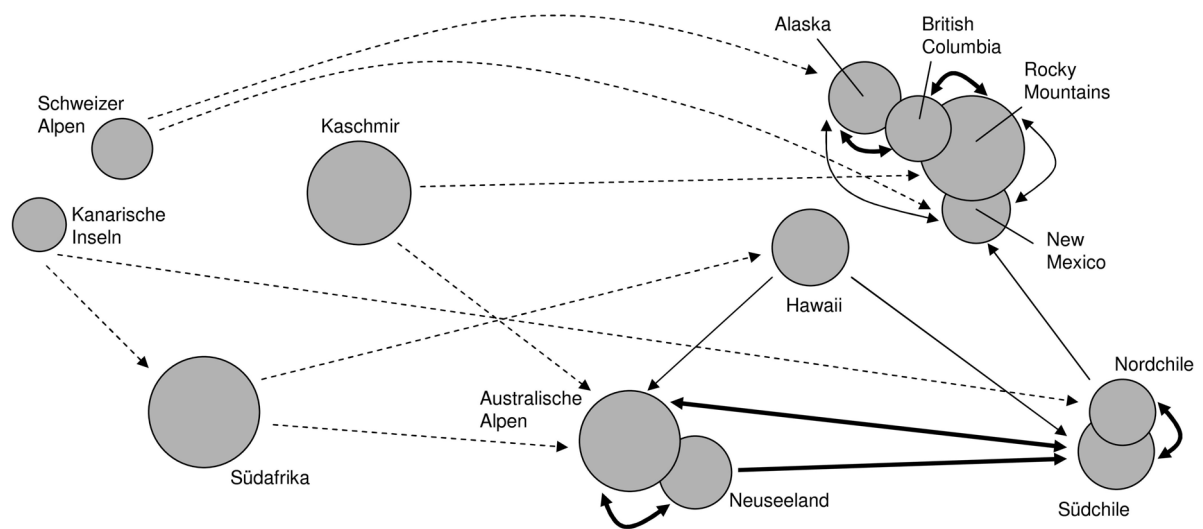
Abbildung 3: Taxonomische Ähnlichkeit von verschiedenen gebietsfremden Gebirgsfloren. Die Pfeile zeigen an, zu welchen beiden anderen gebietsfremden Gebirgsfloren die Flora einer Gebirgsregion die größte Ähnlichkeit besitzt. Die Pfeilspitzen geben die Richtung, die Linienstärke den Grad der Ähnlichkeit an. Die Größe der Kreise entspricht der Anzahl gebietsfremder Arten. (Datenquelle: McDougall et al. 2011)

Welche Faktoren beeinflussen Pflanzeninvasionen in Gebirgen?

Durch Studien von biologischen Invasionen im Flachland konnte in den letzten Jahrzehnten ein umfassendes Verständnis der verschiedenen relevanten biologischen und anthropogenen Prozesse, welche eine Invasion ermöglichen, entwickelt werden (Kueffer & Hirsch Hadorn 2008). Diese Theorie der Invasionsbiologie kann als Ausgangspunkt dienen, um Invasionen in Gebirgen zu verstehen (Pauchard et al. 2009; Abbildung 4a). Ein wichtiger Faktor, den es zu verstehen gilt, ist der Einfluss des Klimas auf die Höhenverteilung gebietsfremder Arten (Haider et al. 2010; Jakobs et al. 2010). Man vermutet, dass in der temperaten (gemäßigten) Klimazone vor allem tiefe Temperaturen im Winter, Frost oder eine kurze Vegetationsperiode im Sommer das Vorkommen gebietsfremder Pflanzen in Hochlagen begrenzen. In mediterranen und subtropischen Gebieten kann dagegen auch Trockenheit ein begrenzender Faktor sein.

Ein zweiter wichtiger Faktor sind die direkten Einflüsse von menschlichen Aktivitäten. Indikatoren wie das Bruttosozialprodukt oder die Bevölkerungsdichte korrelieren oft mit der Anzahl gebietsfremder Arten in verschiedenen geographischen Regionen – z. B. in Europa (Pyšek et al. 2010) oder auf ozeanischen Inseln (Kueffer et al. 2010). Dieser enge Zusammenhang von menschlichen Aktivitäten und dem Auftreten von gebietsfremden Arten kann durch zwei Prozesse erklärt werden; diese Arten profitieren erstens von anthropogenen Habitatstörungen und zweitens hängt die Anzahl der in ein Gebiet eingeführten Samen, Sporen, Pflanzenteile oder ganzen Individuen gebietsfremder Arten (Ausbreitungsdruck; engl.: *propagule pressure*) vom Transportgeschehen ab. Mit zunehmender Höhe in Gebirgen nehmen anthropogene Störungen und Ausbreitungsdruck in der Regel ab. Die Abnahme von menschlichen Aktivitäten entlang des Höhen-

gradienten ist also neben dem Klimagradienten eine mögliche Erklärung für die relativ niedrigen Artenzahlen und Vorkommensdichten gebietsfremder Arten in Hochlagen (Abbildung 4a).

Eine dritte spannende Forschungsfrage der Invasionsbiologie betrifft den lokalen Zusammenhang zwischen einheimischer und gebietsfremder Artenvielfalt. Im Tiefland wurde beobachtet, dass eine hohe einheimische Artenvielfalt das Risiko von Invasionen reduzieren kann. Es wird vermutet, dass in artenreicher Vegetation eine größere Konkurrenz um Ressourcen wie Licht oder Nährstoffe herrscht, welche neuen Arten die Etablierung erschwert. Dieser Diversitätseffekt könnte sich aber mit zunehmender Höhe ändern. Unter harschen abiotischen Bedingungen wird oft beobachtet, dass positive, einseitig nützliche oder sich gegenseitig fördernde Interaktionen zwischen verschiedenen Pflanzen (z. B. Schutz vor Wind) wichtiger werden als Konkurrenz. Eine solche zunehmende Bedeutung positiver Interaktionen mit zunehmender Höhe konnte in einem weltweiten Vergleich von Pflanzeninteraktionen in Gebirgen experimentell bestätigt werden (Callaway et al. 2002). Das heißt, dass in Gebirgen eine ungestörte und artenreiche Vegetationsdecke zum Teil Invasionen fördern statt verhindern kann, und dies wurde tatsächlich für die Invasion von Löwenzahn (*Taraxacum officinale*) in den Chilenischen Anden gezeigt (Cavieres et al. 2005). Wahrscheinlich spielen alle genannten Faktoren – Klimagradient, anthropogene Habitatstörungen, Ausbreitungsdruck und biotische Interaktionen (Abbildung 4a) – eine wichtige Rolle bei Pflanzeninvasionen in Gebirgen. Im Detail ist die relative Bedeutung der unterschiedlichen Faktoren noch nicht geklärt, aber es ist wahrscheinlich, dass sie in komplexer Weise interagieren.
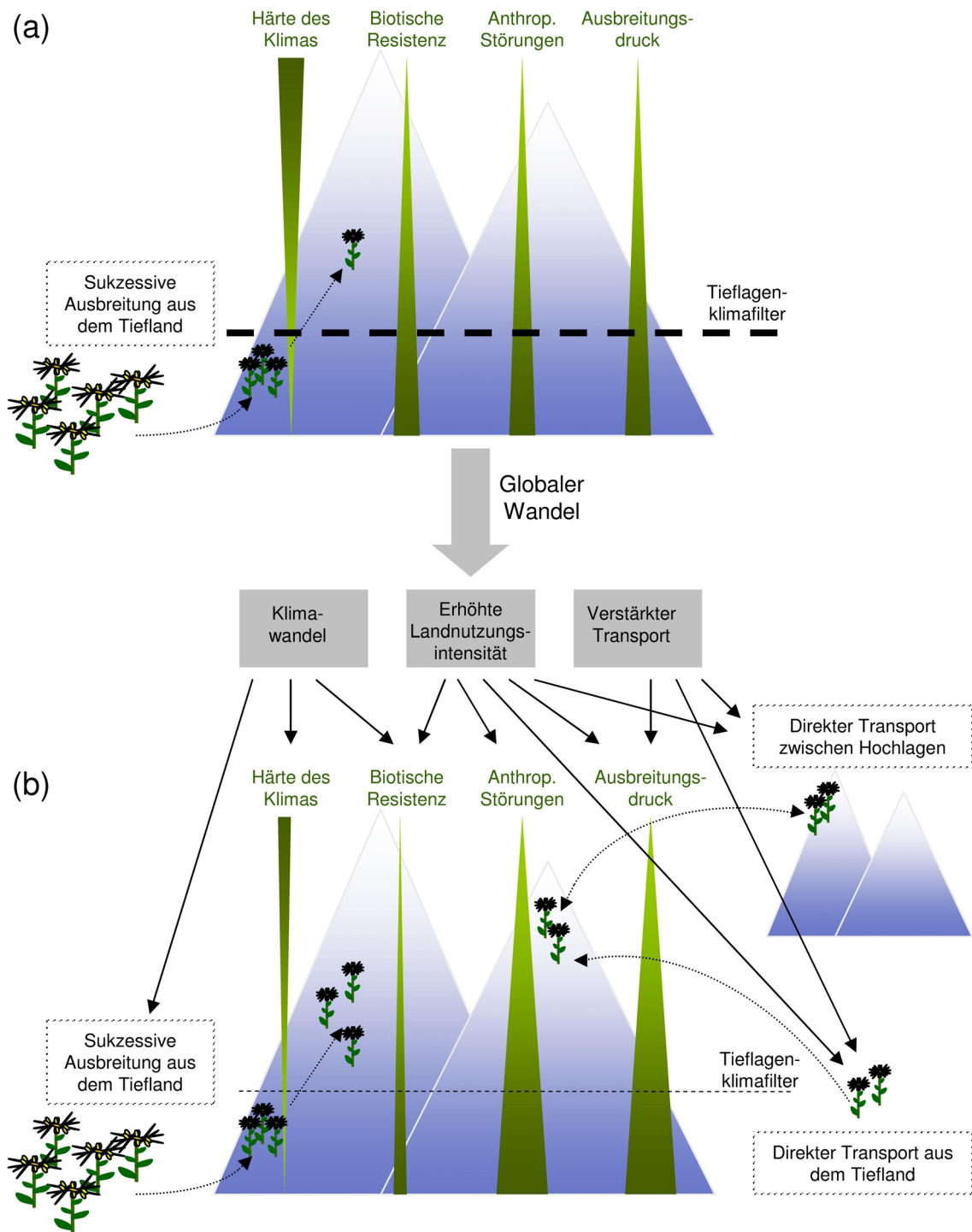
Abbildung 4: (a) Faktoren, welche die Ausbreitung von gebietsfremden Pflanzenarten in Gebirgen beein-flussen (grüne Dreiecke; dunkle Schattierung und breite Basis = größere Relevanz) und (b) wie sich diese im Zuge des globalen Wandels verändern könnten. Auswirkungen des globalen Wandels (graue Rechtecke) wirken sich sowohl auf diese Faktoren als auch auf die Einfuhrwege aus (schwarze Pfeile stehen für die Auswirkungen; punktierte Pfeile verdeutlichen die Einfuhrwege). Als Folge davon reduziert sich die Bedeu-tung des Tieflagenklimafilters (gestrichelte Linie). (Abgeändert nach Pauchard et al. 2009. Nachdruck mit Bewilligung von Frontiers in Ecology and the Environment und der Bayerischen Akademie für Naturschutz und Landschaftspflege.)

Europäische Siedler, Tieflagenklimafilter und Klimageneralisten

Aufgrund des momentanen Wissensstandes lässt sich die Ausbreitung von gebietsfremden Arten in Gebirgen durch eine Kombination von historischen menschlichen Aktivitäten in Gebirgen und biologischen Prozessen erklären. Europäische Siedler haben seit etwa 1500 sukzessive die meisten Gebirgsregionen der Welt von Nordamerika bis Australien oder abgelegene Inseln wie Hawaii besiedelt. In einer ersten Phase dürften Siedler viele der in Gebirgen heute häufigen gebietsfremden Ruderal- und Wiesenpflanzen unabsichtlich, z. B. als Verunreinigung von Samenmischungen, oder gezielt für die Weidewirtschaft aus Europa eingeführt haben. Dies dürfte die Häufigkeit von eurasischen Arten in gebietsfremden Gebirgsfloren weltweit erklären (Abbildung 1). Später wurden dann gebietsfremde Gehölze gezielt zur Bodenverbesserung oder für die Forstwirtschaft eingeführt (z. B. Besenginster (*Cytisus scoparius*), Stechginster (*Ulex europaeus*), Akazien (*Acacia* spec.), Weiden (*Salix* spec.) oder Kiefern (*Pinus* spec.)). Sich stark ausbreitende Gehölze sind zwar in Gebirgen noch relativ selten (McDougall et al. 2011), aber das könnte damit zu tun haben, dass Invasionen oft erst nach einer Zeitverzögerung erfolgen – insbesondere im Fall von langlebigen Gehölzen. Zudem werden schon heute im Gegensatz zu den häufigeren gebietsfremden Krautpflanzen gebietsfremde Gehölze als besonders problematisch für den Naturschutz in Gebirgen angesehen (McDougall et al. 2011). Die historische Landnutzung dürfte also eine wichtige Rolle für die Zusammensetzung der heutigen gebietsfremden Gebirgsfloren gespielt haben. Die Landnutzung in Gebirgen ändert sich weiterhin und damit werden sich in Zukunft wohl auch die gebietsfremden Gebirgsfloren weiterentwickeln. Insbesondere hat sich der Tourismus intensiviert, wodurch das Anpflanzen von Zierpflanzen zugenommen hat. Beispiele für problematische Arten, die aus Zierpflanzungen verwildern konnten, sind Flockenblumen (*Centaurea* spec.), Habichtskraut- (*Hieracium* spec.) oder Leinkrautarten (*Linaria* spec.).
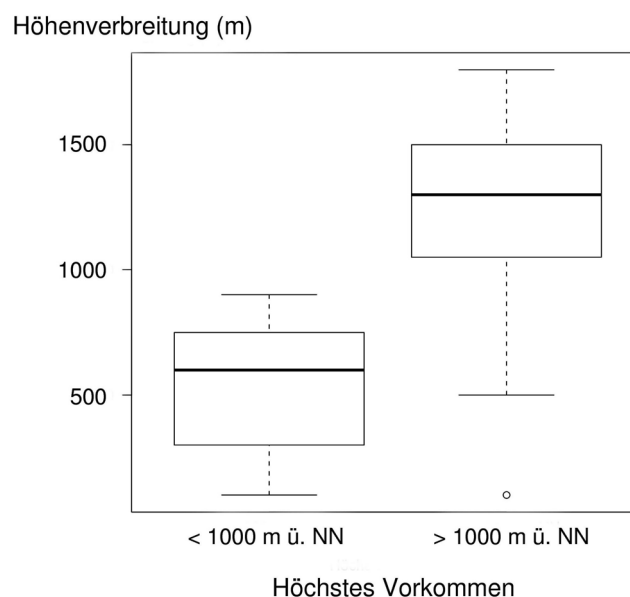
Abbildung 5: Daten aus Teneriffa zeigen, dass gebietsfremde, einjährige Pflanzenarten, die über 1000 m ü. NN vorkommen, eine größere vertikale Verbreitungsamplitude haben (Mittelwert: 1254 m) als Arten, die nur maximale Höhen von 1000 m ü. NN erreichen (Mittelwert: 526 m). (Datenquelle: Haider et al. 2010)

Die gebietsfremden Gebirgsfloren wurden aber nicht nur durch die historische Landnutzung, sondern auch durch die damit verbundenen Einfuhrwege von gebietsfremden Pflanzen geprägt. Weil die Landnutzung vor allem in tieferen Lagen stattfand, wurden die meisten Arten ins Tiefland eingeführt. Die meisten in Gebirgen vorgefundenen gebietsfremden Arten dürften also aus dem Tiefland sukzessive eingewandert sein, anstatt sich direkt in Hochlagen etabliert zu haben. Dieser Umweg über das Tiefland wird als „Tieflagenklimafilter" bezeichnet (Becker et al. 2005) und bedeutet, dass sich nur Arten in Gebirgen etablieren können, welche sowohl in einem Tieflagen- als auch Hochlagenklima wachsen können. Dieses Szenario erklärt, weshalb in Gebirgen fast ausschließlich Klimageneralisten anstatt Bergspezialisten vorkommen und weshalb fast alle diese gebietsfremden Pflanzen einen sehr ausgedehnten Höhengradienten von typischerweise über 1000 m Höhendifferenz besiedeln (Abbildung 5). Arten, welchen eine breite klimatische Toleranz fehlt, werden durch den Tieflagenklimafilter an einer Etablierung in Gebirgen gehindert. Obwohl sie möglicherweise gut an ein Hochlagenklima angepasst wären, gelingt ihnen die Etablierung im Tiefland nicht. Eine breite klimatische Toleranz erreicht eine Pflanzenart z. B. durch phänotypische Plastizität oder die Fähigkeit zur schnellen genetischen Anpassung an neue Umweltbedingungen. Unter phänotypischer Plastizität versteht man die Fähigkeit einer Art sich ohne genetische Veränderungen an unterschiedliche Umweltbedingungen anzupassen, indem z. B. die Wachstumsrate oder die Anzahl und Größe von Samen variiert wird (Foto 2).

Foto 2: Ausbreitung der phänotypisch plastischen Art *Eschscholzia californica* entlang von Straßen in die Hochlagen von Teneriffa. (Foto: Sylvia Haider)

Im Gegensatz zu phänotypischer Plastizität erfolgt eine Anpassung durch Evolution erst durch genetische Differenzierung über mehrere Generationen. Es wurde ein Zusammenhang zwischen der Anwesenheitsdauer einer Art in einem neuen Gebiet und der maximal erreichten Höhe im Gebirge beobachtet (z. B. Becker et al. 2005). Eine mögliche Erklärung dafür ist, dass die Arten Zeit für eine evolutive Anpassung an ein Gebirgsklima brauchen. In diesem Sinne lassen sich die Ergebnisse einer Studie auf Teneriffa (Kanarische Inseln) interpretieren. Hier wurde dieser Zusammenhang bei mediterranen Arten, welche schlecht an kalte Temperaturen angepasst und daher auf evolutive Anpassung angewiesen sind, nicht aber bei temperaten und bereits gut an ein Gebirgsklima angepasste Arten beobachtet (Haider et al. 2010).

Handlungsbedarf für den Naturschutz

Klimaänderung, erhöhte Landnutzungsintensität und zunehmende Mobilität dürften dazu beitragen, dass sich in Zukunft das Risiko von biologischen Invasionen in Gebirgen erhöht (Abbildung 4b). Arten, die im Tiefland häufig sind, werden sich aller Voraussicht nach durch die Klimaerwärmung auch in höhere Lagen ausbreiten können (Kueffer 2010a, Petitpierre et al. unveröffentlichte Daten). Auch können Klimaerwärmung und andere anthropogene Faktoren die Vegetation in Gebirgen empfindlich stören und dadurch Invasionen vereinfachen.

Von besonderer Bedeutung dürfte zudem insbesondere eine Zunahme der Einfuhr von gebietsfremden Pflanzenarten direkt in Hochlagen ohne den Umweg via das Tiefland sein (Kueffer 2010b; Pauchard et al. 2009). Im Gegensatz zu früher, als eine Art eine große klimatische Anpassungsfähigkeit besitzen musste, um sich zunächst im Tiefland etablieren und dann weiter in die Hochlagen ausbreiten zu können, werden sich in Zukunft deshalb möglicherweise vermehrt Arten in Gebirgen etablieren, die bereits in ihrem einheimischen Ursprungsgebiet speziell an ein harsches Hochlagenklima angepasst sind. Von diesen z. B. durch den Tourismus als Zierpflanzen eingeführten Bergspezialisten geht ein deutlich größeres Invasionsrisiko aus als von Klimageneralisten.

Nur in der Anfangsphase einer biologischen Invasion können als problematisch bewertete Arten kostengünstig und vor allem effektiv bekämpft werden (z. B. Kueffer & Hirsch Hadorn 2008). Da Gebirge noch nicht stark von problematischen Arten betroffen sind, hat der Naturschutz hier die einmalige Möglichkeit, nicht „zu spät" zu sein. Dem Vorsorgeprinzip, das auch im gesetzlichen Naturschutz verankert ist, kommt daher die größte Bedeutung zu. Der erste Schritt für das Management von gebietsfremden Arten in Gebirgen sollte deshalb sein, potentiell problematische Arten frühzeitig zu identifizieren (McDougall et al. 2011; Foto 3).

Foto 3: *Lupinus polyphyllus*, heimisch in Nordamerika, wurde von Einwanderern als Zierpflanze nach Australien gebracht. (Foto: Sylvia Haider)

In einer von MIREN (Mountain Invasion Research Network; vgl. Textbox) erstellten, online verfügbaren, globalen Datenbank sind derzeit etwa 1500 Pflanzenarten erfasst (McDougall et al. 2009). Die Datenbank kann als wichtige Informationsquelle für Naturschutzverantwortliche dienen, um im Sinne des Vorsorgeprinzips die Einfuhr von gebietsfremden Arten, welche in anderen Regionen bereits ein problematisches Verhalten zeigen, zu reglementieren. Zur Prävention gehört weiter, dass ein umfassendes Monitoring-System aufgebaut und unterhalten wird, um neu einwandernde Arten frühzeitig zu erkennen und zu kontrollieren. Generell sind Maßnahmen zur Verhinderung von biologischen Invasionen nur erfolgreich, wenn das Bewusstsein der Bevölkerung für dieses Thema sensibilisiert wird und eine Zusammenarbeit zwischen dem Naturschutz und relevanten Interessensgruppen, wie z. B. der Fremdenverkehrsbranche und dem Pflanzenhandel, angestrebt wird. Der Naturschutz hat in Gebirgen im Gegensatz zum Flachland die einmalige Chance, frühzeitig auf die Gefahr von Invasionen zu reagieren und präventiv zu handeln. Diese Chance sollte genutzt werden, um ungewollte ökologische und ökonomische Folgen zu minimieren.

Textbox:

Das Mountain Invasion Research Network (MIREN)

Seit dem Jahr 2005 dokumentiert und erforscht das Mountain Invasion Research Network (MIREN, www.miren.ethz.ch) Pflanzeninvasionen in Gebirgen auf globaler Ebene. Das Netzwerk verfolgt einen integrativen Ansatz, der Vegetationsuntersuchungen im Gelände, experimentelle Forschung im Freiland und unter kontrollierten Bedingungen sowie die fachliche Unterstützung von Naturschutzmaßnahmen umfasst (Dietz et al. 2006). Diese Aktivitäten werden parallel in zehn beteiligten Forschungsregionen durchgeführt: in den Schweizer Alpen, dem Wallowa-Gebirge (Oregon) und dem Yellowstone-Nationalpark im Nordwesten der USA, den mittleren und südlichen chilenischen Anden, den Australischen Alpen, auf Hawaii, auf den Kanarischen Inseln, im indischen Teil des Himalaya-Gebirges (Kaschmir) sowie in Südafrika. Die Forschungsgebiete umfassen temperate bis tropische Klimazonen auf allen Kontinenten und mehreren ozeanischen Inseln.

Schlussfolgerungen

Pflanzeninvasionen in Gebirgen sind ein ausgezeichnetes Beispiel für die komplexen Zusammenhänge, welche biologische Invasionen prägen. Sehr unterschiedliche räumliche und zeitliche Skalen spielen eine Rolle. Diese reichen von evolutiven Anpassungsprozessen entlang von Höhengradienten auf wenigen Kilometern bis zu globaler menschlicher Migration. Die Rückkopplung von gesellschaftlichen Veränderungen, z. B. Veränderungen der Landnutzung, auf biologische Prozesse macht Vorhersagen von Pflanzeninvasionen und ihren Folgen in Gebirgen wie auch in anderen Ökosystemen mit globalem Wandel besonders schwierig (Kueffer 2010b).

Wir haben in diesem Artikel biologische Invasionen von Pflanzen in Gebirgen diskutiert und aufgezeigt, welche Faktoren für die Ausbreitung von gebietsfremden Arten eine Rolle spielen. Man muss davon ausgehen, dass ähnliche Risiken auch bei anderen Gruppen von Organismen, z. B. gebietsfremden Tieren oder Krankheiten von Menschen, Tieren und Pflanzen, zunehmen werden. Leider fehlen bisher dazu die Datengrundlagen und es besteht dringender Forschungs- und Handlungsbedarf.

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General Discussion

Linking global, regional and local studies and descriptive and experimental approaches

Biological invasions are a complex phenomenon and this is one of the major reasons why attempts to describe general mechanisms which underlie biological invasions have been limited (cf. e.g. Lodge 1993; Richardson & Pyšek 2006). To an extent this is because it is difficult to draw generalizations from studies which focus on different spatial and temporal stages of invasions (cf. Dietz & Edwards 2006; Heger 2004; Pauchard & Shea 2006). Furthermore, the majority of studies concentrate on *one* scale (Pauchard & Shea 2006; Sagarin & Pauchard 2010) and use *one* method for their analyses. Each scale and each method has advantages and disadvantages. However, to account for the complexity of biological invasions, it is advisable to integrate different scales and methods in a single study (Pauchard & Shea 2006; Theoharides & Dukes 2007). In this way, the strengths of the different approaches may be aggregated and weak points may be compensated (Poll 2007). The use of a single scale might lead to wrong conclusions because patterns and processes are determined by different factors at different scales and thus might be even contradictory at different scales (Levin 1992). For instance, Sax & Gaines (2003) showed that habitat destruction and biological invasions as main parts of global change lead globally to a decrease of species richness (McKinney & Lockwood 1999; Morris & Heidinga 1997), while at the regional and local scales an increase in species richness was frequently observed (Sax et al. 2002). Large-scale studies (i.e. at a regional or larger level) are mostly descriptive and often correlate distribution patterns of non-native species with abiotic factors (Theoharides & Dukes 2007). This traditional approach may not be seen as out-of-date. Rather, it should be increasingly considered as an adequate method for ecological research in the light of ubiquitous and extensive anthropogenic changes of ecosystems (Sagarin & Pauchard 2010). For instance, large-scale studies enable the analysis of causes of the distribution limits of non-native plant species or the role of different introduction histories. Contrarily, small-scale studies, i.e. analyses at the community level, often deal with biotic factors and may also use an experimental approach, because at that scale it is easier to isolate and manipulate singular factors which might influence the invasion success. Many of the core hypotheses of invasion biology (e.g. biotic resistance hypothesis (Tilman 1997), resource-enrichment hypothesis (Davis et al. 2000), EICA hypothesis (Blossey & Nötzold 1995), enemy release hypothesis (Keane & Crawley 2002), novel weapons hypothesis (Callaway & Ridenour 2004), invasional meltdown hypothesis (Simberloff & Von Holle 1999)) were developed at the community level (Poll 2007).

In this thesis I combined descriptive investigations at the global, regional and local scales, and at the regional and local scales I combined descriptive and experimental approaches (cf. Hewitt et al. 2007). By doing this, I could show that the processes underlying the distribution patterns were the same at the regional (Chapter 2) and global scales (Chapter 3). This is one reason why non-native species richness generally decreases towards high elevations. At the global scale it is difficult to isolate single factors and thereby identify the role of each factor in shaping the distribution pattern because of the specific way in which the factors interact in each region. However, this is possible at the regional and local scales. In a first step I searched for correlations between the non-native species distribution pattern and traits both of the species and the invaded sites (Chapter 2). I hypothesized that residence time of a non-native species is positively

correlated with the occupied elevational range in the new region. This was confirmed and old-introduced species reached higher elevations than recent introductions, suggesting that time since introduction is important for adaptive processes. In a second step I analysed in a climate chamber experiment (Chapter 3) if the indication of genetic differentiation between populations (Chapter 2) can be confirmed.

Biological invasions along elevational gradients

I analysed the process of plant invasions along steep elevational gradients in mountains (cf. Poll & Alexander 2009) with the aim of investigating which factors determine the distribution patterns and particularly the distribution limits of non-native plant species. The distribution pattern of non-native species on Tenerife suggested that most species were introduced at low elevations from where they spread towards higher elevations (Chapter 2). This interpretation was based on the finding that most species that occurred at high elevations were also present at low elevations and that there were almost no species which exclusively occurred at high elevations. This pattern did not apply only to Tenerife, but was also found in the global study of 13 non-native mountain floras (Chapter 1). In all recorded mountain regions the non-native mountain flora had the highest similarity to the adjoining non-native lowland flora and not, as one might presume, to mountain floras which are geographically close to each other or are situated in the same climatic zone. This pattern is basically the same for the native flora, but there is a major difference: native mountain and lowland floras might share the same genera, but not the same species, or the lowland and mountain individuals of the same species are genetically very distinct, so that the latter *can* be mountain specialists. This differentiation in the native flora arose from evolution over very long time. However, the same dispersal pathway of native and non-native species (i.e. spread from low to high elevations) and the observed ability of non-native species to evolve in ecological times, suggest that the differentiation between the lowland and the mountain non-native flora will increase and that non-native mountain specialists will evolve.

On Tenerife I compared the distribution of non-native species that were climatically pre-adapted to the lowland conditions in a strict sense (Mediterranean species) with species that were climatically maladapted (temperate species) (Chapter 2). The so called lowland climate filter (*sensu* Becker et al. 2005) hindered the establishment of maladapted temperate species and is thus most probably the reason why I found predominantly Mediterranean non-native species on Tenerife and why currently temperate non-native species do not have a peak of species richness in mid- and high elevations what would match with the climatic requirements of their native range. This contradicted my original hypothesis that due to "climate matching", i.e. when the climatic conditions in the native range of a species match with the new conditions, Mediterranean species would dominate at low and temperate non-native species at high elevations. Instead, both bioclimatic species groups (Mediterranean and temperate species) had the same distribution pattern along the elevational gradient, with an increase of non-native species richness from low to mid-elevations, followed by a decrease of the species richness from mid- to high elevations. I concluded that climate matching is particularly important for the *establishment* of non-native plant species (cf. Broennimann et al. 2007), but not for further spread to higher elevations.

Although the distribution pattern of the two bioclimatic species groups was very similar, there was a clear difference with regard to the species' residence time on Tenerife. Species occurring at high elevations were mostly old introductions, and this especially applied to Mediterranean

species. Because the vegetation data was collected along roadsides where propagule pressure is generally high (Christen & Matlack 2009), this is unlikely to be a time-lag in the dispersal of the species to higher elevations. Rather, time appears to have been important for the adaptation of marginal populations to the local conditions. For native as well as non-native plant species it has been shown that tolerance of different environmental conditions may result from a high phenotypic plasticity (Crispo 2008; Richards et al. 2006) or from genetic adaptation (Lee 2002; Prentis et al. 2008). Time is only important for the latter because adaptations of the genotype need at least several generations. In a climate chamber experiment I tested for genetic differences between populations of 13 plant species from different elevations (Chapter 3). To my knowledge, this is the first study which analyses plastic and genetic responses to different temperature treatments for multiple non-native species. This enables better generalizations of the results than would be possible in case studies of individual species.

In the experiment all species showed plastic responses of the phenotype to temperature and all species strongly reduced their growth (biomass production) under lower daily temperature sums. This might be non-adaptive plasticity insofar as low temperatures do not allow for a stronger growth. However, reduced growth might also be interpreted as a genetic adaptation to low temperatures or other correlating environmental factors (Grime 2001). The experiment included two different series that allowed distinguishing the adaptive processes along different gradients (lower vs. upper part of the elevational gradient). I could show that the direction of genetic differentiation in the upper part of the gradient (under probably more constant environmental conditions and a higher selection pressure caused by environmental stress) was more consistent than in the lower part of the gradient (i.e. under more fluctuating environmental conditions) (cf. Gilchrist & Lee 2007; Lee & Gelembiuk 2008). In the upper part of the gradient, plants of high elevation seed origin had with only one exception a lower growth than plants of mid-elevation seed origin, under both high and mid-elevation climate treatments.

I followed from these contrasting results of the lower and the upper part of the gradient that the respective adaptive processes are determined by the interaction of species traits and characteristics of the gradient. At lower elevations genetic differentiations were impeded perhaps due to a high gene flow between the populations (cf. Kawecki 2008; Kawecki & Ebert 2004). At high elevations gene flow is potentially reduced because of the generally lower abundance of non-native species and the lower traffic intensity. Among the species traits, those that preserve a high genetic variability are especially relevant (Colautti et al. 2010; Sakai et al. 2001). This applies for instance to polyploid species (Levin 2003). In fact, I found on Tenerife a higher proportion of polyploid species among the species which reached higher elevations than among the species which were restricted to lower elevations (Chapter 2). In line with this, polyploid species had a larger genetic differentiation between mid- and high elevation populations than diploid species (Chapter 3).

Although adaptation to climate might be important in determining distribution limits, habitat boundaries might have a stronger influence on species distributions. On Tenerife, there is a sharp transition between two strongly contrasting types of habitat at approximately 1000 m a.s.l. Below 1000 m a.s.l. there is a strong anthropogenic influence with a high settlement density and many intensely used (especially agricultural) areas. Above this zone there is more or less natural pine forest (Fernández-Palacios & de Nicolás 1995). The number of non-native species drops abruptly at the point where the two habitat types meet each other. This cannot be ascribed only to climatic

conditions because these do not change abruptly or have extreme values at this elevation. Rather, the lack of shade tolerance which is essential for entering the pine forest hinders the spread of many species. Thus, the elevational gradient on Tenerife is an example for the case that a species cannot occupy all sites that would match with its climatic niche because in a certain type of habitat another factor (here light availability) acts as limiting factor.

Implications for invasion biology and nature conservation

Early research into biological invasions focused mainly on species traits (Baker 1965; Pyšek et al. 1995; Rejmánek & Richardson 1996; Roy 1990) or ecosystems characteristics which increased the probability of a successful invasion (Davis et al. 2000; Elton 1958; Lonsdale 1999; Pyšek & Prach 1993). A series of hypotheses arose from these studies, but it did not lead to an explanation of why some species become invasive or problematic and others do not. As a consequence, it was attempted to combine species traits and ecosystem properties in a common approach. However, studies which really include both aspects are still rare. Beside that, the differentiation of the invasion process was increasingly considered and it became apparent that the relevance of certain species traits or habitat characteristics changes in different stages of invasions (Dietz & Edwards 2006; Heger 2004; Theoharides & Dukes 2007).

I consider studies which include several scales as indispensable to analyse the complicated and changing interactions of different factors. (1) This might be studies which use different methods. In this thesis the combination of descriptive vegetation surveys and the experimental manipulation of selected factors in the climate chamber has proved of value. Other possibilities for an experimental approach could be common garden studies or transplant experiments (e.g. Alexander 2010; Poll et al. 2009), but it depends always on the spatial scale which method is suitable. (2) To allow for an adequate analysis of the factors involved, I see the inclusion of different spatial scales as important. This might be a comparison of global, continental, regional and local studies. Because detailed studies at a large scale are rather time-consuming and expensive, studies along pronounced environmental gradients (e.g. elevational gradients) offer a suitable alternative. (3) To identify the relative importance of individual factors during the invasion process, the distinction of different invasion stages (cf. Heger & Trepl 2003) is recommendable and only studies that focus on the same stage should be compared. Here, I have compared the distribution patterns of old and recent introductions (Chapter 2). Only by this simple differentiation, I could show that there are differences with regard to the species' adaptation to local environmental conditions and that genetic adaptation seems to be more important for old introductions. A more detailed differentiation of the species (e.g. in casual alien, naturalized and invasive species *sensu* Richardson et al. (2000)) might provide further insights into the relevance of individual factors (cf. van Kleunen et al. 2010). It would be also interesting, however difficult to conduct, to compare species which established in a new region and species that failed to establish. (4) Independent of the chosen method and the spatial and temporal scale, it makes sense for the generalization of the results not only to carry out studies about individual species, but also to conduct multi-species studies. This has been done mostly in descriptive studies which for instance describe the correlation of species richness and environmental factors, but is not common yet in experimental approaches (exceptions are e.g. Blumenthal & Hufbauer 2007; Schlaepfer et al. 2010). The course of biological invasions is highly idiosyncratic and strongly depends on the combination of the traits of the invading species and the characteristics of the invaded ecosystems. Therefore, it is not surprising that studies about

individual species partly lead to contradicting conclusions. Through the inclusion of several species in one study, as it was done here in the climate chamber experiment (Chapter 3), trends about the importance of single factors can be revealed. This approach can help to develop general rules about the mechanisms underlying invasions despite the fact that there will probably always remain exceptions, as it is typical for complex phenomena.

An important result of the thesis is that the distribution pattern of non-native plant species is determined only to some extent by climatic factors and that for instance habitat context (i.e. the non-climatic habitat factors) plays an important role (Chapter 2). However, often only the climatic requirements of a species are used to model the potential invasion range of a species (e.g. in Thuiller et al. 2005). Hence, it is not surprising that the predicted distribution does not always correspond to the actual distribution of a species. Including for instance habitat types and thus also biotic interactions may improve the prediction accuracy considerably (Pearson & Dawson 2003). Additionally, it should be considered that the suitability of climate matching to predict the whole invasion range of a species is generally limited, but rather that it can help to predict the area where a new species might establish first (Broennimann et al. 2007). Because of that it is important to consider introduction pathways (Wilson et al. 2009) since they might limit the areas to which a species can be introduced.

A second important result of the thesis is that genetic differentiation between populations of non-native species occurs more frequently than so far expected and that it depends on the combination of species traits and gradient characteristics. For better predictions about possible genetic alterations of a species, and thus about changes of its ecological niche, more comparative studies are necessary and possibly relevant factors must be analysed separately for a multitude of species.

Invasion biology is able to predict the minimum invasion range of a species, but it is difficult to estimate to which adjoining habitats a species might adapt. Another uncertainty is the transport of the species and one can hardly predict when a species will be transported to a certain area. In mountain ecosystems predictions become even more difficult, as indicated by the finding that most of the non-native plant species worldwide occur only in one mountain region (Chapter 1). Therefore, there is certainly a large number of non-native species in mountain regions which were not recorded in this study. For nature conservation there are two main information resources for identifying potential invasive or problematic species. The first is knowledge about the non-native and invasive flora of the lowlands (as most important source for species reaching high elevations) and the second is knowledge about invasive or problematic species in other mountain regions. Because of the lowland climate filter non-native plant species in mountains are commonly not specialists that are pre-adapted to a mountain climate, but climatically broad species. This means that if there is no change of the main introduction pathway, species adapted to a mountain climate are not *per se* the most probable species to invade other mountain areas because they might not be able to tolerate the lowland climatic conditions what is necessary for the establishment in a new region. Generally, species with a broad climatic tolerance are more likely to become successful mountain invaders.

Mountains comprise many natural ecosystems that are not or only in a few cases affected by biological invasions. To avoid future invasions it is essential to establish a monitoring program to observe present populations of non-native species and to detect new populations of potentially

invasive or problematic species in time (Chapter 4). Actions against invasive and problematic species are only effective and promising if conducted during the first stage of the invasion process (Kowarik 2003). In most ecosystems the spread of invasive species has advanced so far that actions would be very costly and, nevertheless, would be unlikely to be successful in eradicating or controlling the invasive species. However, in mountain ecosystems biological invasions are still at an early stage and therefore nature conservation has the opportunity to limit the spread of invasive species.

In summary, the results of the thesis showed that research along elevational gradients is a valuable approach to analyse limiting factors of plant invasions. The varying conditions along the gradient allowed an interpretation of the relative importance of single factors. Additionally, the thesis demonstrated that integrative approaches and studies combining different scales are necessary to gather more insights into the mechanisms that underlie biological invasions. For future research, I suggest to move from case studies about single-species to comparisons across multiple species and gradients. Generalizations gained from such studies can help to improve modelling techniques by adding other relevant factors than climate. By doing this, predictions about non-native species distributions should become more precise and hence also more valuable for an applied use.

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