Analysing plant invasions across multiple scales using *Ageratina adenophora* as a case study

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Summary

Biological invasions across multiple continents can be compared to unplanned large-scale transplant experiments and thus can provide a unique window of opportunity to study many fundamental processes and patterns in ecology. The invasive spread of the Asteraceae *Ageratina adenophora* (Crofton weed) is of global concern, as it has been recognized as a noxious invasive plant species in numerous countries across the globe. Native to Mexico, this apomictic, triploid plant is highly invasive in moist subtropical and sub-temperate montane regions. Using *Ageratina adenophora* as a model species and employing a suite of experimental and macroecological methods at different spatial scales, I have attempted to answer several questions of evolutionary and ecological significance in this thesis. The central research topics of the thesis consist of three parts, in which niche theory can be considered as a central theme.

In the 1st part of the thesis, I focused on local and regional scales (Chapter 2), and addressed the following questions: (i) What is the distribution pattern of *Ageratina adenophora* along an elevational gradient in the Western Himalayas? (ii) Do populations of *Ageratina adenophora* exhibit any evidence of rapid evolutionary changes along a specific elevational gradient in Western Himalayas? (iii) Which life cycle stages are vital in determining the upper and lower range limit of *Ageratina adenophora*? To answer these questions, I carried out distributional surveys, established a reciprocal transplant experiment, and measured different traits related to various life cycle stages such as germination, growth, phenology, survival, and reproduction. *Ageratina adenophora* showed a symmetrical unimodal pattern of distribution along the elevational gradient. I did not find any substantial evidence in favour of rapid evolutionary changes in *Ageratina adenophora*. Furthermore, I found that drought during germination determines the lower limit while frost sensitivity during overwintering limits the upper range limit of *Ageratina adenophora* along the elevational gradient. Few studies have attempted to explain the observed distribution pattern of a species using insights gained from multiple common garden experiments. Specifically, the fact that different lifecycle stages are vulnerable at upper and lower range limits along an elevational gradient has rarely been demonstrated using common garden experiments. Thus, I found that the insights gained from experimental

studies carried at a local scale can help us to understand distribution patterns at larger spatial scales.

In the 2nd part of the thesis (Chapter 3), I asked whether the choice of different data sources of the same type of predictor variables, namely the databases WorldClim 2 and Chelsa 1.2, affects the output of species distribution models (SDMs) in terms of model interpolative performance and transferability. Using the distribution of *Ageratina adenophora* in the Himalayas and predicting for the Indian subcontinent, I found that the performance of SDMs was influenced by the choice of the climatic database. The models developed using Chelsa 1.2 outperformed those developed using WorldClim 2 in terms of internal predictive accuracy. However, in terms of transferability, models based on WorldClim 2 performed substantially better than those based on Chelsa 1.2. This however does not mean that a certain database is always superior.

In the 3rd and final part of the thesis, I asked whether the native climatic niche of *Ageratina adenophora* has shifted in any of the other four invasive ranges across the globe (the USA, the Canary Islands, Asia, and Australia) despite evolutionary limitations due to apomictic (asexual) mode of reproduction. I found that the invasive Asian niche showed the largest amount of niche overlap with the native Mexican niche. On the contrary, the Australian niche of the species had shifted considerably from the native Mexican niche. Furthermore, I found that the climatic niche in the invasive range in Australia was unique due to a high degree of expanded and unfilled niche space. *Ageratina adenophora* also exhibits substantial niche expansion into colder areas of Asia. Since evolutionary studies have indicated the absence of rapid evolutionary changes in the invasive ranges of China and India, the observed niche shift is most likely due to changes in the realized niche space rather than the evolution of fundamental niche space.

Combining different approaches, i.e. common garden experiments, direct observations and statistical modelling based on various data sources and across different scales, I was able to unravel some of the ecological and evolutionary aspects in the invasion process of *Ageratina adenophora*. By conducting a multiple common garden experiment along the entire elevational range of the plant, I primarily focused on the fundamental niche of the plant defined by abiotic factors such as temperature and moisture. The other two studies focused on niche deduced from occurrence data and therefore represented the realized niche of the species rather than the fundamental niche.

Since montane ecosystems are vital from the perspective of biodiversity conservation and ecosystem services, plant invasion can have long-term detrimental effect on native biodiversity and disrupt ecosystem services. By focusing on *Ageratina adenophora*, which is predominantly invasive in mountainous regions across the globe, this thesis underpins the importance of conducting extensive observational as well as experimental studies even in remote mountainous regions such as the Himalayas.

Chapter 1

General Introduction

Plant invasions

Since the dawn of civilization humans have introduced individuals of plant species beyond their native range (Meyerson & Mooney 2007). But this process of introduction has intensified over the last few centuries, especially due to increased transportation and trade facilitated by globalization (Jenkins 1996; Mooney & Cleland 2001; Perrings *et al.* 2005; Seebens *et al.* 2015). Some of these non-native plants that are capable of spreading rapidly from the initial point of introduction within a relatively short period have been termed “invasive plants” (Richardson *et al.* 2000). However, out of a huge pool of non-native species, only a few manage to successfully naturalize and become invasive in the new range by producing self-sustaining populations (Williamson 1993, 1996; Jeschke 2014). Invasive plants are often associated with adverse effects on biodiversity, ecosystem services, human health, and economy ("What are Invasive Alien Species?", CBD 2018). Therefore plant invasion is considered to be one of the challenging problems of today’s world (Hobbs & Humphries 1995; Kolar & Lodge 2001; Pimentel *et al.* 2005; Vilà *et al.* 2010; Simberloff *et al.* 2013).

The process of introduction of non-native organisms into a new biogeographical range and their rapid expansion in the new range have been considered as an interesting framework to understand several fundamental questions related to range expansion and evolutions of organisms (Sakai *et al.* 2001). In fact, it has been considered as an unintended and large-scale field experiment that could be used to answer several fundamental eco-evolutionary questions (Sax *et al.* 2007). Due to the increasing concern to minimize the adverse consequences of biological invasions, there has been a growing effort to better understand the processes leading to invasion success.

Mountains and invasions

Montane ecosystems, in general, are fragile and at the risk of degradation due to various threats posed by increased anthropogenic pressure, climate change and invasive plants (Hofer 2005). From biodiversity and conservation perspective, mountain ecosystems are of paramount importance since many of them overlap with biodiversity hotspots (Grêt-Regamey *et al.* 2012). Furthermore, mountain ecosystems are of direct relevance to human well-being because they are source of valuable services and goods such as freshwater, fertile soil, food and medicinal plants (Grêt-Regamey *et al.* 2012; Haida *et al.* 2016).

Mountains have been relatively resistant to invasions due to their relative remoteness, low traffic and hence low propagule pressure. Spread of non-native plants in mountainous areas is also constrained by physiological limitations imposed by harsh environmental conditions and biotic interactions (Alexander *et al.* 2016). But in recent times the spread of non-native plants in mountainous areas has gained momentum. Studies indicate that increasing number of non-native plants that have scaled new heights along elevational gradients across the globe (Daehler 2005; Khuroo *et al.* 2006; Pauchard *et al.* 2009; McDougall *et al.* 2011a; Alexander *et al.* 2016). The spread of non-native plants in high elevational areas is the consequence directional ecological filtering from their site of introduction in the lowlands to highlands. Moreover, non-native species at high elevations are mostly generalists with broad elevational gradient and not specialists (Alexander *et al.* 2011b, 2016). The spread of non-native plants in high elevational areas is likely to continue due to climate change and direct introduction of preadapted species in high elevations due to globalization (Alexander *et al.* 2016). Invasive plants are relatively more difficult to manage in the mountains compared to lowlands because of inaccessible and rugged terrain and hence might become uncontrollable after they have naturalized (McDougall *et al.* 2011b). Therefore it is necessary to carry out research on the spread of invasive plants in the mountains, especially in regions that have not been studied rigorously (Yu *et al.* 2016). The current thesis focuses on the problem plant invasion in Himalayas.

Rapid evolutionary changes in invasive plants

Invasive plants are capable of undergoing evolutionary changes in the introduced range that allow them to rapidly adapt to wide range of environmental conditions in the introduced range (Parker *et al.* 2003; Prentis *et al.* 2008; Colautti & Lau 2015). Understanding the evolution of invasive plants is useful as it could help us to gauge the invasion potential of the invasive species appropriately. Despite the perceived importance of evolutionary changes in invasive plants, such studies are underrepresented in invasion literature (Parker *et al.* 2003; Prentis *et al.* 2008; Lowry *et al.* 2013).

Microevolution refers to conspecific evolutionary changes that usually occur within different populations of the same species or even within the same population (Hendry & Kinnison 1999). Such evolutionary changes take place over relatively short time scales ranging from few centuries to few decades (Hendry & Kinnison 1999). Invasive species, in general, offer an avenue to investigate micro-evolutionary processes that take place after their introduction into a new biogeographic zone (Vermeij 1996; Maron *et al.* 2004; Colautti & Lau 2015). Interestingly such micro-evolutionary changes can occur in invasive plants within human lifespan and can be detected using specifically designed field experiments and genomic tools (Franks *et al.* 2007; Leimu & Fischer 2008; Colautti & Barrett 2013). Due to the speed of such evolutionary processes, they have also been termed as rapid evolution or contemporary evolution. Such evolutionary changes in invasive plants can be broadly classified into two categories: (i) divergence of invasive plants from native populations (ii) divergence among invasive populations within the introduced range (Colautti & Lau 2015). These changes occur in response to abiotic or biotic selection pressures.

Invasive plants undergo rapid range expansion in the introduced range, often into areas that have markedly different environmental conditions from the area of initial introduction (or even their source range). Rapid evolution may lead to the evolution of locally adapted populations that have higher fitness under local conditions than foreign populations. However, local adaptation is influenced by several factors such as gene flow among populations, temporal variation in selection pressure, and genetic drift (Antonovics 1976; Leimu & Fischer 2008; Colautti & Lau 2015). Two criteria have been used to test local adaptation: (i) “home vs away” criterion (ii) “local vs foreign” criterion (Kawecki & Ebert 2004). The "home vs away" criterion is satisfied when local populations have higher fitness in local habitat conditions than in other habitat conditions (Figure 1.1a). In contrast, the "local vs foreign" criterion is tested across two or more habitats, and the local populations are expected to have higher fitness compared to the foreign populations at each habitat. The "local vs foreign" criterion is considered to be a more rigorous test of local adaptation as it reflects the potential of divergent selection over other evolutionary forces (Kawecki & Ebert 2004) and is recognized by crossing reaction norms (Figure 1.1b). Local adaptation has been detected in several introduced species in relatively short time span (McKay *et al.* 2001; Leimu & Fischer 2008; Colautti & Barrett 2013; Kim & Donohue 2013). A recent meta-analysis showed that local adaptation in invasive plants is as frequent and strong as in native plants (Oduor *et al.* 2016), thus indicating the role of local adaptation towards invasion success.

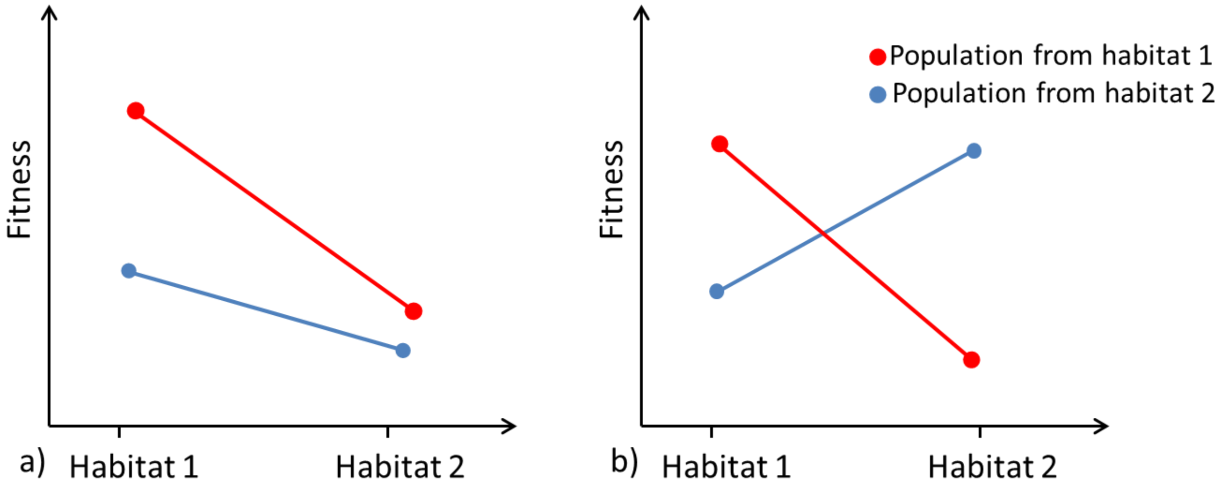

Figure 1.1. Graphical representation of the two criteria commonly used to detect local adaptation. (a) "home vs away" criterion in which population from habitat 1 (red circles) exhibits higher fitness in habitat 1 (i.e., "home") than in habitat 2 (i.e., "away") because of adaptation to local conditions in habitat 1. However, the population from habitat 2 (blue circles) does not fulfil this criterion. (b) "home vs foreign" criterion in which population from each habitat performs better in its respective "home" habitat than "foreign" populations habitat. Fulfilment of "home vs foreign" criterion results in characteristic crossing reaction norm which is considered to be a strong signal for local adaptation as it exhibits divergent selection (adapted from Kawecki & Ebert 2004).

Sometimes range expansion occurring along a continuous environmental gradient may lead to the gradual evolution of clines that show a change in trait values with the environmental gradient (Clausen *et al.* 1941; Endler 1977; Weber & Schmid 1998).

This process of genetic differentiation has been termed as clinal differentiation and may be detected by common garden experiments or using genetic markers (Endler 1977; Keller *et al.* 2009). For example, genetic differentiation in two introduced species of *Solidago* has been detected along a latitudinal gradient in Europe for several traits (Weber & Schmid 1998). Similarly, clinal differentiation has also been reported to occur along elevational gradients in several plant species (Monty & Mahy 2009)

Phenotypic plasticity

Phenotypic plasticity refers the property of a genotype to exhibit variation in phenotypic traits when grown in different environmental conditions (Bradshaw 1965; Sultan 2004; Bossdorf *et al.* 2005)(Figure 1.2). Plasticity of a trait is advantageous only when it is associated with fitness advantage (van Kleunen & Fischer 2005; Davidson *et al.* 2011). In the context of plant invasions, phenotypically plasticity may aid non-native plants to cope up with new environmental conditions without undergoing local adaptation (Baker 1965; Sultan 2004; Davidson *et al.* 2011).

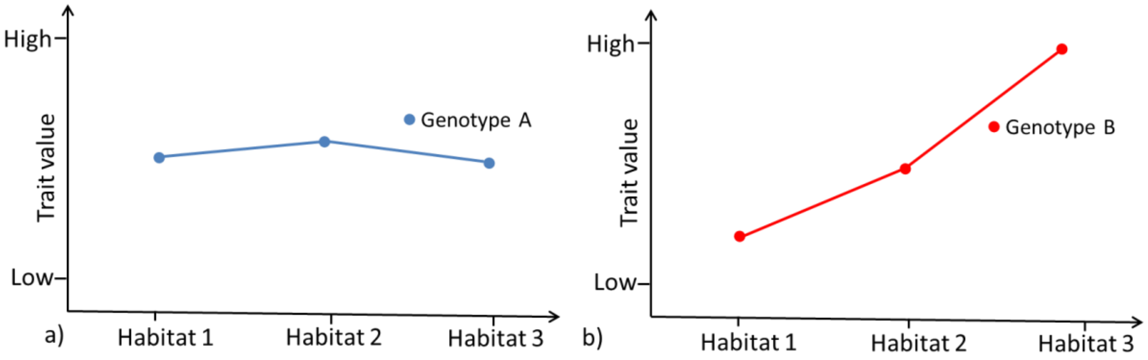

Figure 1.2. Graphical representation of phenotypic plasticity across a range of habitat conditions. (a) Genotype A (blue) exhibits very low variation in trait value across thee habitats. (b) Genotype B (red) shows considerable variation in trait value across the three different habitats and is thus phenotypically more plastic than genotype A.

Therefore, phenotypic plasticity is often proposed as an alternative explanation to local adaptation (Parker *et al.* 2003; Davidson *et al.* 2011). However, local adaptation and phenotypic plasticity are not mutually exclusive processes as locally adapted genotypes would exhibit a certain amount of plasticity in traits across different environmental conditions. Moreover, phenotypic plasticity itself may be subject to evolutionary selection if sufficient genetic diversity for plasticity exists in the population (Callaway *et al.* 2003; Sultan 2004; Ghalambor *et al.* 2007). There are, however, several physiological, developmental, and genetic constraints on the evolution and maintenance of phenotypic plasticity (Dewitt *et al.* 1998). Genotypes with high phenotypic plasticity has also been referred as “general purpose genotypes” due to broad their environmental tolerance (Baker 1965, 1974; Ross *et al.* 2008).

Niche theory

The concept of niche is a central idea in ecology as it strives to explain the relationship between the organisms and its environment. The use of term niche in ecology can be traced back to Grinnell who defined it as the ultimate distributional unit of a species (Grinnell 1924). He associated niche to habitat-related variables that allow a species to occupy its distributional range in geographic space (Grinnell 1917). Elton, however, considered niche as the functional role of the species in the community at a local scale and focused primarily on biotic interactions (Elton 1927). Hutchinson later introduced the concept of the “fundamental niche” defined by n-dimensional hyper-volume (Hutchinson 1957) within which a species can maintain positive growth rate. Furthermore, he coined the term “realized niche,” which refers to a subset of fundamental niche in the presence of biotic interactions (Vandermeer 1972; Chase & Leibold 2003). His concept of n-dimensional hyper-volume allowed the niche concept to be used in applied ecological disciplines such as species distribution modelling. The actual distribution of a species in the geographic space is a result of the intersection three different components: (i) areas with suitable abiotic conditions, (ii) areas with appropriate biotic interactions, and (iii) areas accessible to the species by dispersal (Soberon 2005; Soberon 2007; Soberon and Nakamura 2009).

The concept of niche is particularly relevant in the context of plant invasions as it allows us not only to develop deeper understanding about the spatiotemporal dynamics of invasion but it also enables us to project the future distribution of the invasive species in time and space under changing environmental conditions (Peterson 2006; Soberón & Nakamura 2009; Peterson *et al.* 2011).

About the plant: *Ageratina adenophora*

Ageratina adenophora (Spreng.) R.M.King & H.Rob (commonly called Crofton weed) is a perennial Asteraceae native to Mexico and highly invasive in several sub-tropical and sub-temperate regions across the globe (Parsons & Cuthbertson 2001; Muniappan *et al.* 2009; Tripathi *et al.* 2012; Yu *et al.* 2016). It was introduced in as an ornamental plant to England in the 19th century (Auld & Martin 1975) and was later introduced into different parts of the world (Auld & Martin 1975; Muniappan *et al.* 2009; Tripathi *et al.* 2012). Globally *Ageratina adenophora* has proven to be a highly successful invasive plant as it has crossed biogeographic barriers and successfully invaded several continents (Figure 1.4). Some of the severely infested regions include the sub-tropical and sub-temperate Himalayas (Tripathi *et al.* 2012), mountainous regions of southwestern China (Wang & Wang 2006; Wang *et al.* 2011), mountainous regions of peninsular India, southwestern provinces of Australia (Auld & Martin 1975), and the Hawaiian Islands (Stone *et al.* 1992; Daehler 2005). New reports of naturalization of *Ageratina. adenophora* have accumulated recently from many European countries with Mediterranean climatic conditions such as the south-east coast of France, the Canary Islands of Spain, the Campania region of Italy (Del Guacchio 2013), Maderia and the Azores archipelagos of Portugal, as well as Crete in Greece (http://www.cabi.org/isc/datasheet/23243).

It can easily be recognized in the field from its glandular and purple-tinged stem, strong odour, rhombic leaves with serrated margins and acute tip (Parsons & Cuthbertson 2001) (Figure 1.3 a). In spring and early summer, it bears white flowers (capitula) in dense terminal corymbs (Figure 1.3 a) (Auld & Martin 1975; Yadav *et al.* 1987; Parsons & Cuthbertson 2001). Each capitulum bears 60-70 disc florets (Parsons & Cuthbertson 2001), and a mature plant may produce as many as 2000 heads in the 1st year of growth (Datta *et al.* 2017). The plant keeps growing in the subsequent years by producing numerous branches from the base of the main plant, thus forming a dense, usually monospecific thicket (Parsons & Cuthbertson 2001). The branches produce adventitious roots in moist soil during the rainy season, which further augments the lateral spread and vegetative propagation of the plant (Auld & Martin 1975; Yadav *et al.* 1987). The tiny achenes are equipped with pappus facilitating air and animal dispersal (Wang *et al.* 2011; Del Guacchio 2013). After the reproductive phase (i.e. after spring and early summer), the leaves of the mature plant senesces and many secondary and tertiary branches die off in summer (Parsons & Cuthbertson 2001). Later in the rainy season, the plant grows vigorously, producing plenty of new branches and leaves until autumn, forming a dense thicket. Seeds germinate in moist and humid conditions (Lu *et al.* 2006), generally in the rainy season (July-August). The plant shows luxuriant growth in cool, moist regions along the slopes of hills or mountains, but it is capable of growing in diverse conditions ranging from flat floodplains of lower Himalaya to steep and dry rocky slopes (Datta *et al.* 2017). It invades new regions along road verges and rivers which form a conduit for its dispersal (Lu & Ma 2006)(Figure 1.3 b-d).

Figure 1.3 (a) Young flowering shoot of *Ageratina adenophora*. Luxuriant growth of *Ageratina adenophora* in different habitats such as (b) abandoned fields (c) riversides sand (d) roadsides.

Ageratina adenophora has a rather interesting mode of reproduction. It is a diplosporous apomict (i.e. gametophyte develops directly from the unreduced megaspore mother cell) with a triploid set of chromosomes (n=51) (Baker 1974; Noyes 2007; Bala & Gupta 2014). A high degree of anomaly has been observed during meiosis of the pollen mother cell due to non-synchronized chromosomes, laggard formation and cytomixis (Bala & Gupta 2014). Bagging experiments have also confirmed apomictic nature of the plant (Lu *et al.* 2008). Despite irregularities in the meiotic process, normal seed setting occurs with a large number of viable seeds (Yadav & Tripathi 1982; Lu *et al.* 2008; Datta *et al.* 2017). Rapid evolution in *Ageratina adenophora* is likely to be constrained by apomixes and triploidy (Zhao *et al.* 2012; Datta *et al.* 2017). A study in China indicated that the species is spreading very fast with an average rate of 20km/year, although the rate of dispersal is slower in colder areas in the north (Wang & Wang 2006).

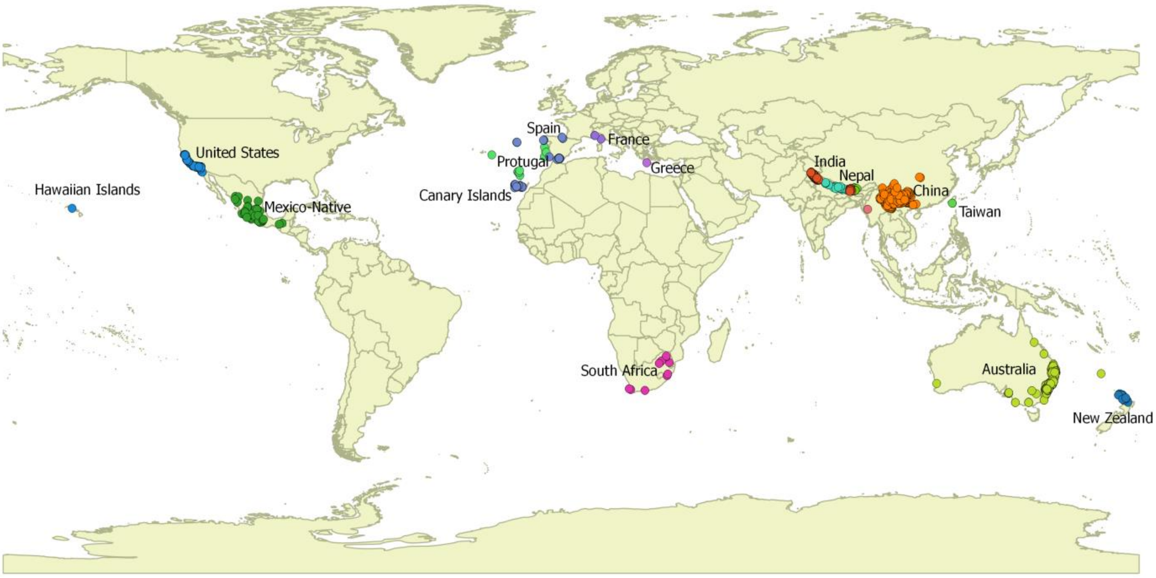

Figure 1.4 Map showing the distribution of *Ageratina adenophora* across the globe. It is native to Mexico and invasive in several countries situated in different biogeographic zones.

Studies carried out in Yunnan province, and Sichuan province in China indicated a significant decline in plant richness in the habitats invaded by *Ageratina adenophora* (Ding *et al.* 2007). The species has been reported to have a severe impact on other plant species primarily due to its allelopathic chemicals. Extract of *Ageratina adenophora* has severe retarding and inhibitory effect on germination rate of several pasture species (Tripathi *et al.* 1981; Zhong *et al.* 2007). The species is also capable of altering the soil microbial composition in a way that promotes its invasion but has negative impacts on native plants (Rajbanshi & Inubushi 1997; Niu *et al.* 2007a). The plant is unpalatable to domesticated animals and has been even known to be poisonous to horses, thereby reducing the economic value of pasture lands (Auld & Martin 1975).

Once it becomes invasive, it is challenging eradicate it from the infested regions and contain its further spread into new areas. This is particularly true because most of the worst infested regions are mountainous where control measures are difficult to implement due to steep and rugged terrains (Stone *et al.* 1992; Wang *et al.* 2011; Datta *et al.* 2017). Biological control using gall-inducing insects and rust causing fungi has been attempted in several infested regions, but the success has been limited

(Muniappan *et al.* 2009; Wan *et al.* 2010; Heystek *et al.* 2011). It is, however, worth mentioning that early control efforts in Australia by mechanical and chemical means have largely been successful (Auld & Martin 1975).

Thus, it is evident that *Ageratina adenophora* has established itself as a highly potent trans-continental invasive plant by in naturalizing in more than 30 countries across different continents over relatively short time period (Figure 1.4). Despite its importance as a noxious invasive plant, it has remained understudied in many severely infested regions such as Himalayas and Nilgiri Hills in South Asia (Yu *et al.* 2016).

Structure of the thesis

This dissertation uses *Ageratina adenophora* as the target species to answer several questions related to its invasion biology. A combination of experimental and macroecological approaches have been used to answer different questions relevant at local, regional, subcontinental, and global scales respectively. In the context of the thesis, local scale refers to the scale of the reciprocal transplant experiment along an elevational gradient spanning approximately 1700m. The regional scale refers to the Western Himalayas; subcontinental scale refers to south Asia. Finally, global scale refers to multiple continents where the species has naturalized.

At the local scale, I attempted to understand the role of rapid evolutionary processes in the spread of *Ageratina adenophora* along a steep elevational gradient in Dhauladhar range (Himachal Pradesh, India) using reciprocal transplant experiment. At the regional scale, I focussed on the distribution pattern of *Ageratina adenophora* in Western Himalaya along the elevational gradient. At subcontinental scale, I evaluated the transferability of distribution model using different climatic datasets. Finally, at the global scale, the degree of climatic niche overlap was analysed between the native Mexican range and different invasive ranges.

Research Questions

Local-scale

- Have invasive populations of *Ageratina adenophora* in western Himalaya undergone rapid evolutionary changes? (Chapter 2, published in *PLoS One*, 12: e0187708. doi: 10.1371/journal.pone.0187708)
- Which life cycle stages are crucial in determining the upper and lower range limit of *Ageratina adenophora*? (Chapter 2, published in *PLoS One*, 12: e0187708. doi: 10.1371/journal.pone.0187708)

Regional-scale

- What is the pattern of distribution of *Ageratina adenophora* along an elevational gradient in Western Himalayas? (Chapter 2, published in *PLoS One*, 12: e0187708. doi: 10.1371/journal.pone.0187708)

Sub-continental scale

- Does the transferability of the models differ if different climatic datasets are used as predictors? (Chapter 3, planned for submission to *Ecological lnformatics*)

Global-scale

- Has the realized climatic niche of *Ageratina adenophora* remained conserved in different invasive ranges across the globe? (Chapter 4, planned for submission to *Ecology and Evolution*).

Chapter 2

Processes affecting altitudinal distribution of invasive *Ageratina adenophora* in Western Himalayas: the role of local adaptation and the importance of different life-cycle stages

Arunava Datta, Ingolf Kühn, Mustaqeem Ahmad, Stefan Michalski, Harald Auge

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Abstract

The spread of invasive plants along elevational gradients is considered a threat to fragile mountain ecosystems but can also provide the opportunity to better understand some of the basic processes driving the success of invasive species. *Ageratina adenophora* (Asteraceae) is an invasive plant species of global importance and has a broad distribution along elevational gradients in the Western Himalayas. Our study aimed at understanding the role of evolutionary processes (e.g., local adaptation and clinal differentiation) and different life history stages in shaping the distribution pattern of the invasive plant along an elevational gradient in the Western Himalaya. We carried out extensive distributional surveys, established a reciprocal transplant experiment with common gardens at three elevational levels, and measured a suite of traits related to germination, growth, reproduction, and phenology. Our results showed a lack of local adaptation, and we did not find any evidence for clinal differentiation in any measured trait except a rather weak signal for plant height. We found that seed germination was the crucial life-cycle transition in determining the lower range limit while winter mortality of plants shaped the upper range limit in our study area, thus explaining the hump-shaped distribution pattern. Differences in trait values between gardens for most traits indicated a high degree of phenotypic plasticity. Possible causes such as apomixes, seed dispersal among sites, and pre-adaptation might have confounded evolutionary processes to act upon. Our results suggest that the success and spread of *Ageratina adenophora* IS dependent on different life history stages at different elevations that are controlled by abiotic conditions.

Introduction

In the process of colonizing new geographic areas, invasive plant species often spread along environmental gradients and become successful in diverse environmental conditions (Theoharides & Dukes 2007). The spread of invasive plants along such environmental gradients offers the opportunity to study the mechanisms underlying successful biological invasions (Monty & Mahy 2009). Exceptionally steep environmental gradients in the mountains across relatively short geographic distances provide a quasi-experimental setup to investigate the fundamental processes that drive the spread of invasive plants. Although mountains have often been considered relatively resistant to plant invasions, recent studies show that invasive plant species have also colonized higher elevations across the globe (Lockwood *et al.* 2005; Pauchard *et al.* 2009; McDougall *et al.* 2011b; Pyšek *et al.* 2011). Invasions in mountain areas are of practical concern since many mountain ecosystems are biodiversity hotspots and source of important ecosystem services (Zhu *et al.* 2007; Li *et al.* 2008). In addition, invasive plants are difficult to manage in the mountains because of inaccessible and rugged terrain and hence might become uncontrollable after successful naturalization (McDougall *et al.* 2011b).

One mechanism behind the successful spread of some invasive plants across a broad elevational range is rapid adaptive evolution. Multiple exotic plant species have undergone adaptive genetic divergence along elevational gradients (Haider *et al.* 2012) and established elevational clines similar to native species (Alexander *et al.* 2009). Environments at the elevational range margins may impose strong selection pressure, leading to adaptive divergence of populations at upper as well as lower range margins (Sexton *et al.* 2011; Halbritter *et al.* 2015).

It has been suggested that rapid evolutionary processes such as local adaptation might play a significant role in the spread of invasive plants in the naturalized range (Parker *et al.* 2003; Colautti & Barrett 2013). If there is a strong selection pressure, sufficient genetic diversity, and isolation of populations (Vellend *et al.* 2007; Hereford 2010), adaptive evolution can occur on very short temporal scales (Bone & Farres 2001; Reznick 2001). Adaptive divergence among plant populations is a rather common phenomenon (Leimu & Fischer 2008) and occurs as frequently among invasive plant species as among native plants (Oduor *et al.* 2016). For instance, it has been repeatedly shown that invasive plant species may rapidly build up latitudinal clines (Weber & Schmid 1998; Kollmann & Bañuelos 2004; Montague *et al.* 2008). Founding populations are often genetically impoverished due to the small population size and hence suffer from genetic bottlenecks (Nei *et al.* 1975). Accordingly, single introduction events may cause severe genetic bottlenecks in invasive species which may hamper local adaptation (Dlugosch & Parker 2008). Although rapid evolutionary changes during invasions have been frequently inferred in spite of genetic bottlenecks, they might be non-adaptive as revealed by simulations models (Colautti & Lau 2015). Apart from local adaptation, the ability of a genotype to exhibit different phenotypes under different environmental conditions (i.e., phenotypic plasticity) has been considered to play a crucial role in plant invasion as phenotypic plasticity allows naturalization along a broad range of environmental conditions (Sultan 2000; Richards *et al.* 2006). In situations when the genetic makeup prevents adaptive evolution, invasion success across environmental gradients may be facilitated by pre-existing phenotypic plasticity (Parker *et al.* 2003).

Although plant demography can be considered crucial to understanding range dynamics (Normand *et al.* 2014), knowledge about demographic processes at range margins is still insufficient (Abeli *et al.* 2014). In general, harsh environments at upper and lower elevational range margins translate into strongly reduced plant fitness, with range-edge populations often acting as demographic sinks (Hargreaves *et al.* 2014; Seipel *et al.* 2016). Most of the exotic species studied so far along elevational gradients show a continuous decrease in frequency of occurrence with increasing elevation ((Alexander *et al.* 2011a; Seipel *et al.* 2016); but see (Becker *et al.* 2005) for exceptions). This pattern is due to unidirectional spread from the lowlands to higher elevations, associated with environmental filtering because only a few invaders succeed under the extreme environmental conditions at high elevations (Alexander *et al.* 2011a). In contrast, many native plant species in montane environments attain maximum frequency at mid-elevation, resulting in a unimodal distribution along elevational gradients (Lenoir *et al.* 2008). Interestingly, such a pattern has been less often documented for exotic species so far but may be expected if abiotic or biotic conditions are sub-optimal both at low and high elevations.

The type of breeding system may have consequences for invasion success because it influences the genetic structure of the invasive population. Invasive plants that reproduce sexually are able to maintain higher genetic diversity due to recombination compared to species that reproduce clonally. On the other hand, clonal plants have the advantage of reproducing independently without any pollen limitation and are able to maintain trait expressions that confer invasiveness. Interestingly, several plant species that reproduce clonally have been very successful invasive plants as well. For example, several members of Asteraceae that reproduce apomictically are known to be aggressive invaders (e.g., *Ageratina adenophora, Eupatorium adenophorum, Ageratina riparia*) across tropical and sub-tropical regions of the world (Noyes 2007; Hao *et al.* 2010). Despite the fact that adaptive evolution in these apomictic plants is limited due to genetic constraints, they are able to colonize huge geographical areas and hence are interesting target species to understand eco-evolutionary processes leading to their success.

To better understand the processes leading to successful invasion, we studied invasive populations of the apomictic plant species *Ageratina adenophora* in western Himalaya. This species is a perennial plant native to Mexico and is invasive in subtropical regions worldwide. We choose this species since it is one of the few invasive plants having a broad elevational distribution. Being a subtropical species, the lower range limit along an elevational gradient might be imposed by hotter and drier climatic conditions while the upper range limit might be determined by low temperature. Reciprocal transplant experiments carried out in China, where *Ageratina adenophora* was introduced ca. 40 years ago, revealed no evidence for local adaptation along an elevational gradient (Zhou *et al.* 2009; Zhao *et al.* 2012). In the Himalayas, however, studies on evolutionary processes behind its successful spread across a broad elevational range are lacking.

Reciprocal transplant experiments enable us to study local adaptation (Ebeling *et al.* 2011; Colautti & Barrett 2013) by rigorously testing whether resident genotypes perform better than those introduced from other sites ('local vs foreign' criterion: (Kawecki & Ebert 2004). Additionally, regressing traits measured in a common garden against environmental conditions (Alexander *et al.* 2012; Konarzewski *et al.* 2012) or geographic coordinates of home sites of populations (Weber & Schmid 1998; Montague *et al.* 2008; Monty & Mahy 2009) allows us to find evidence for clinal differentiation. We combined both approaches, by transplanting offspring of local *Ageratina adenophora* populations from each of three elevational levels (at 570 m, 1330 m and 2100 m a.s.l. on average) into three common gardens, one at each elevation. We studied how germination, growth, survival and reproduction are limited by the particular environments, whether populations perform best at or close to their "home" elevation, and whether there is evidence for clinal variation along the elevational gradient. Combined with extensive field surveys in the Western Himalayaswe used these experiments to answer the following questions:

(1) Is the distribution of invasive *Ageratina adenophora* in the western Himalayas limited by environmental conditions at both, low elevations and high elevations, leading to a unimodal pattern of occurrence?

(2) Which life-cycle stages are most vulnerable at the elevational range margins of this species?

(3) Is there any evidence of rapid evolutionary changes in the western Himalayan populations of *Ageratina adenophora* in form of local adaptation and clinal differentiation?

Methods

Study species

Ageratina adenophora (Spreng.) King & H.Rob. is a herbaceous, perennial, triploid Asteraceae native to Mexico. It has naturalized in more than 30 countries across the globe and is considered to be a noxious invasive plant in south Asia, East Asia, south-east Asia, eastern coast of Australia, and South Africa (Auld & Martin 1975; Wang & Wang 2006; Muniappan *et al.* 2009). Invasive attributes of *Ageratina adenophora* include high reproductive rate due to uniparental reproduction by apomixes (Baker 1974; Hao *et al.* 2010; Bala & Gupta 2014) and vegetative propagation (Wang *et al.* 2011), strong allelopathic effect (Tripathi *et al.* 1981; Zhong *et al.* 2007), and effective wind dispersal of the seeds (Wan *et al.* 2010; Wang *et al.* 2011). The plant shows luxuriant growth in cool moist regions along the slopes of hills or mountains, but it is capable of growing in diverse conditions. The plants invade new regions along road verges and rivers which form a conduit for its dispersal (Lu & Ma 2006).

Distribution survey

The distribution survey was carried out in a region of Western Himalayasbetween 29.96° and 32.55°N and 75.77° and 78.43°E, and elevations between 300 m and 4100 m (for details of survey refer to S2 Appendix) in 2015 and 2016. Previous reconnaissance surveys and existing literature on the distribution of *Ageratina adenophora* in the Himalayas (Tripathi *et al.* 2012; Sekar *et al.* 2015) had indicated that the plant has naturalized in the elevational band between 300 m to 2500 m a.sl (in subtropical and sub-temperate zones) and is completely absent at high elevations beyond 3000 m. We, therefore, conducted our survey primarily in the elevational zone between 300 m and 2500 m but surveyed also some areas beyond the known elevational range of the plant.

The distribution survey was carried out in haphazardly chosen locations between 300 m to 3000 m elevational belt representing diverse landscapes (such as forest land, urban and suburban areas, rural areas, agricultural fields, riversides, floodplains and dams etc.). Although most of the survey was carried out along roadsides, high elevational areas (beyond 2500 m) were surveyed using the trekking routes. A total of 389 locations were surveyed as the presence-absence status was recorded.

Common garden experiments

Seed sampling

Based on the distributional survey, we divided the elevational range of *Ageratina adenophora* into three elevational belts in the southern aspect of Dhauladhar range (Kangra District, Himachal Pradesh, India; see Figure 2.1), i.e. low (400 m-600 m), mid (1100 m-1500 m) and high (1800 m-2200 m) elevations, termed "origins" hereafter (for site-specific climatic conditions see S2 Table). Within each of the three belts, we randomly selected 5 populations, well separated in space and with a minimum population size of ten individuals. Within each population, we collected seeds from five randomly chosen individuals, termed as "seed families" hereafter. Our hierarchical sampling design finally resulted in seeds from 75 seed families representing 15 populations and three elevational origins. Since the plants at low elevational garden flowered earliest, we began sampling at the lowest origin (1st week of April 2014), followed by the mid origin (4th week of April 2014) and finally the highest origin (2nd and 3rd week of May 2014). Floral heads of each maternal plant were stored separately in paper bags and air dried at room temperature. After drying, seeds were separated from other floral parts and stored in vials with dehydrated silica gel at room temperature.

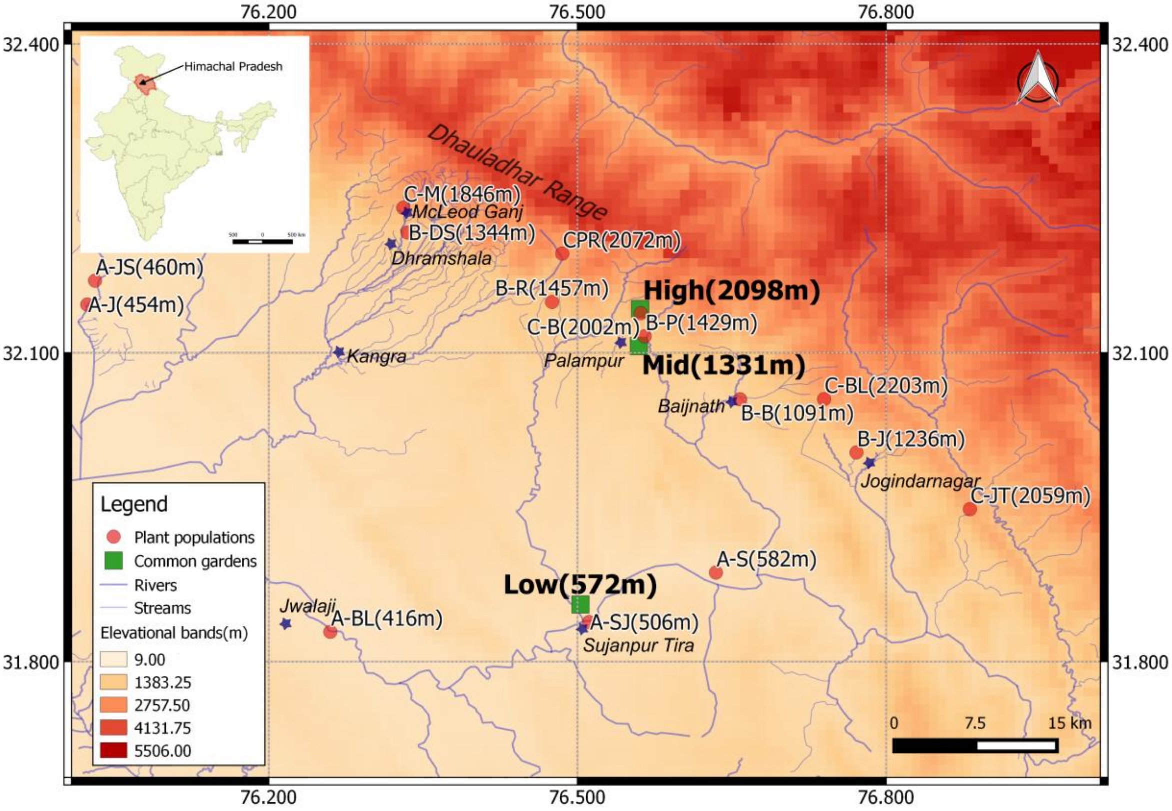

Figure 2.1. Locations of the 15 *Ageratina adenophora* populations and of the three common gardens that are located on the southern aspect of Dhauladhar mountain range in Himachal Pradesh (India). The populations and common gardens are denoted by red circles and green squares respectively. Important places in the vicinity are indicated by blue stars.

Experimental design and measurements

In May-June, 2014, we prepared one common garden at each of the three altitudinal levels in the Dhauladhar range: a low- elevation garden at 570 m, a mid-altitudinal garden at 1330 m, and a high-altitudinal garden at 2100 m. In addition to climatic conditions (Appendix 2.1), the common garden sites differed significantly in soil chemical parameters (Appendix 2.4). Seedlings were grown in nurseries (approximately 4.8 m×1.8 m) adjacent to each common garden. The nurseries were covered with green shading net (which allowed about 50% light transmission) to prevent excessive evaporation. Seeds were germinated in small polythene bags (volume approximately 180 cm^3) filled with a mixture of equal proportions of clay, soil and farmyard manure. Groups of ten polythene bags were assigned to each of the 75 seed families and randomly positioned in the nurseries. Seeds were sown in the 1st week of July 2014 and were watered regularly in order to maintain adequate soil moisture (see Appendix 2.5 for exact dates). After the seeds germinated, 2-3 seedlings were kept in each polythene bag, and any extra seedling was removed at an early stage. The seedlings were maintained for approximately six weeks after sowing (until 3rd - 4th pair of leaves appeared) before transplanting them to the common garden.

Each of the common gardens had a size of 6.4 m × 27 m and was divided into five blocks, arranged along the slope of the gardens. One randomly chosen individual from each of the 75 seed families was randomly assigned to a planting position within each of the blocks (arranged in 25 rows and 3 columns). Distance among seedlings was approximately 0.22 m. This design resulted in 375 (75×5) individual plants arranged randomly in five blocks in each of the three common gardens, and a total of 1125 individual plants (375×3) in the entire experiment. Seedlings were transferred along with their root ball including the potting mixture into small holes made in the soil and were watered regularly for the next two weeks. Seedlings that died within one week after transplantation were replaced with new seedlings from the nursery (see Appendix 2.5 for exact dates of seed sowing and transplantation). No specific permissions were required to conduct our study at any of the locations, and the study did not involve any protected or endangered species.

During the course of the experiment, we measured various plant functional traits: The onset of flowering was recorded daily from 8th March 2015 until all the plants flowered. A plant was considered to be flowering when at least one floret in the capitulum had opened. The number of days to flower for a plant was calculated as Julian days (i.e., days from 1st of January 2015). To measure specific leaf area (SLA) and leaf dry matter content (LDMC), we sampled five mature and non-senescing leaves from the upper branches of the plant in July 2015 and stored them immediately between moist tissue papers inside a zip-lock bag. Leaves were kept cool in an ice box while transporting them to the laboratory and then stored in a refrigerator at 4 °C. Fresh weight was measured within 24-48 hours, and dry weight was measured after drying the leaves in an oven at 60 °C until constant weight was achieved. Leaf area was determined by scanning the leaves along with a scale in a flatbed scanner at 300 dpi and then analyzing the images using ImageJ software (by converting the images to grayscale and then applying the default thresholding function to delineate the background). SLA was calculated by dividing the one-sided area of the fresh leaf (in cm^2) by the oven-dried biomass (in mg). LDMC obtained by dividing oven leaf dried weight of the leaf (in mg) by water saturated fresh weight of the leaf (in g). The plants were harvested in the 2nd week of August 2015 (S3 Table). The plants were harvested at a height of approximately two centimetres above ground, and the primary branches were counted from the base of the plant. Plant height and fresh weight were measured immediately after the harvest. Biomass (dry weight) could only be measured for a subsample of 150 plants per garden (due to logistic limitations) that were sampled across all blocks and populations. To obtain conversion factors to estimate the biomass of the remaining plants, we first performed an ANCOVA on the biomass of the 150 plants, with garden, block and population as factors and fresh weight as a covariate. Since block and garden had a significant effect on the relationship between biomass and fresh weight, we calculated the conversion factor specifically for each block in each garden. We then used the block-specific conversion factor to estimate the biomass of all remaining plants. Reproductive output of each plant was estimated by counting the number of capitula produced by each plant in April and May 2015. Since the plant reproduces apomictically (Bala & Gupta 2014), pollen limitation does not limit the production of viable seeds and hence count of capitula is a reasonable estimate of reproductive fitness of the plant.

Germination experiment

In addition to the main experiment, we conducted a germination experiment adjacent to the each of the three common gardens from 27th July to 3rd August 2014 in order to compare seed germination among origins, populations and seed families under nearly natural conditions. The germination experiment was performed in paper cups with perforated walls to allow the passage of soil moisture. Each cup was filled with autoclaved potting mixture (see above). The perforated sides of the cups were embedded in the soil to ensure moisture absorption and covered with a transparent nylon net protect to seeds from granivores. The experiment was laid in a randomized block design with three blocks. Each block had 75 paper cups, randomly assigned to the 75 seed families. Twenty seeds from a given seed family were sown in each paper cup. The number of germinated seeds in each cup was counted after one month, and the experiment was terminated thereafter (see Appendix 2.5 for the experimental dates).

Since they are influenced by maternal provisioning (Steinger *et al.* 2000; Easton & Kleindorfer 2009), seed mass or initial seedling size can be considered as a proxy for assessing the influence of maternal effect (see for instance (Wieneke *et al.* 2004; Ebeling *et al.* 2011)). Therefore we included seed mass as a covariate when analysing germination probability, but we found no significant effect of seed mass.

Statistical analysis

In order to evaluate the distribution pattern of *Ageratina adenophora* along the elevational gradient using presence-absence data collected along an elevational gradient, we used a set of seven hierarchical logistic regression models. These models, initially proposed by (Huisman *et al.* 1993), were later implemented as “eHOF” package in R programming environment (R Core Team 2013) by (Jansen & Oksanen 2013). This set of models allows hypothesis testing and is hence considered to be more appropriate than alternatives offered by generalized additive models (Jansen & Oksanen 2013). The first model in the hierarchy is a null model without any trend. The second model is a logistic response curve with increasing or decreasing trend. The third model is similar to the second model, but the maximum is always below the upper limit of the data. The fourth model corresponds to a unimodal and symmetrical hump-shaped response while a skewed unimodal response is modelled by the fifth model. The sixth and seventh models are designed for a bimodal response (Jansen & Oksanen 2013). Amongst all the seven models, the best fitting model was judged based on the lowest AICc value (Appendix 6). The elevation at which the probability of distribution of *Ageratina adenophora* peaks along our elevational gradient was calculated as the maximum of the best fitting function.

Data from the common garden and germination experiments were analysed using generalized linear mixed models (SAS 9.4, proc GLIMMIX) with origin, garden and their interaction as fixed effects, and population within origin, seed family within population and block within garden as well as population × garden and seed family × garden interactions as random effects. Biomass, the number of primary branches, SLA were analysed using a log-normal error distribution. Leaf dry matter content was logit transformed because it represents a proportion. The number of capitula and days to flower were square root transformed to approach normal distribution of residuals, while plant height and leaf area did not require any transformation. For analysing germination data, we applied a model with binomial error distribution and logit link function. To account for possible maternal effects manifested in seed mass, we repeated the analysis with seed weight as a covariate. In all these models, we were particularly interested in the origin × garden interaction with crossing reaction norm to test for local adaptation of populations considering the 'local versus foreign' criterion (Kawecki & Ebert 2004). To test for clinal differentiation of populations along the elevational gradient, we applied an ANCOVA model on the population mean traits with elevation, garden and their interaction term as fixed effects.

Results

Elevational distribution pattern

Ageratina adenophora was present in 49.5% of the surveyed locations (193 out of 389 locations). Hierarchical regression analysis revealed that the distributional pattern of *Ageratina adenophora* along the elevational gradient was best explained by a unimodal and symmetrical model (Model IV, see S5 for details of the models). Elevational band between 1000 m to 1600 m had a high probability of occurrence, and the peak probability of 0.63 was predicted at the elevation of 1319 m (Figure 2.2). The probability of occurrence at the lowest sampled elevation (319 m) was 0.32 while the probability of occurrence above 3000 m was less than 0.1.

Common garden experiments

Germination

In the open germination experiment conducted at the three elevations, all the seeds failed to germinate in the lowermost garden while 10.6 ± 3.4% and 9.8 ± 3.2% of the seeds (least square means ± standard error of the model) germinated respectively in the mid-elevation and high-elevation gardens. The lowermost garden was removed from statistical analysis since germination failed completely. Furthermore, seed weight did not affect the probability of germination ($p = 0.196$); hence we present only results of the model without seed weight as a covariate (Table 1). Analysis of germination data from the mid-elevation and the high-elevation gardens neither revealed a significant difference between the two gardens nor did the origin and the garden × origin interaction affect germination rate (Table 1).

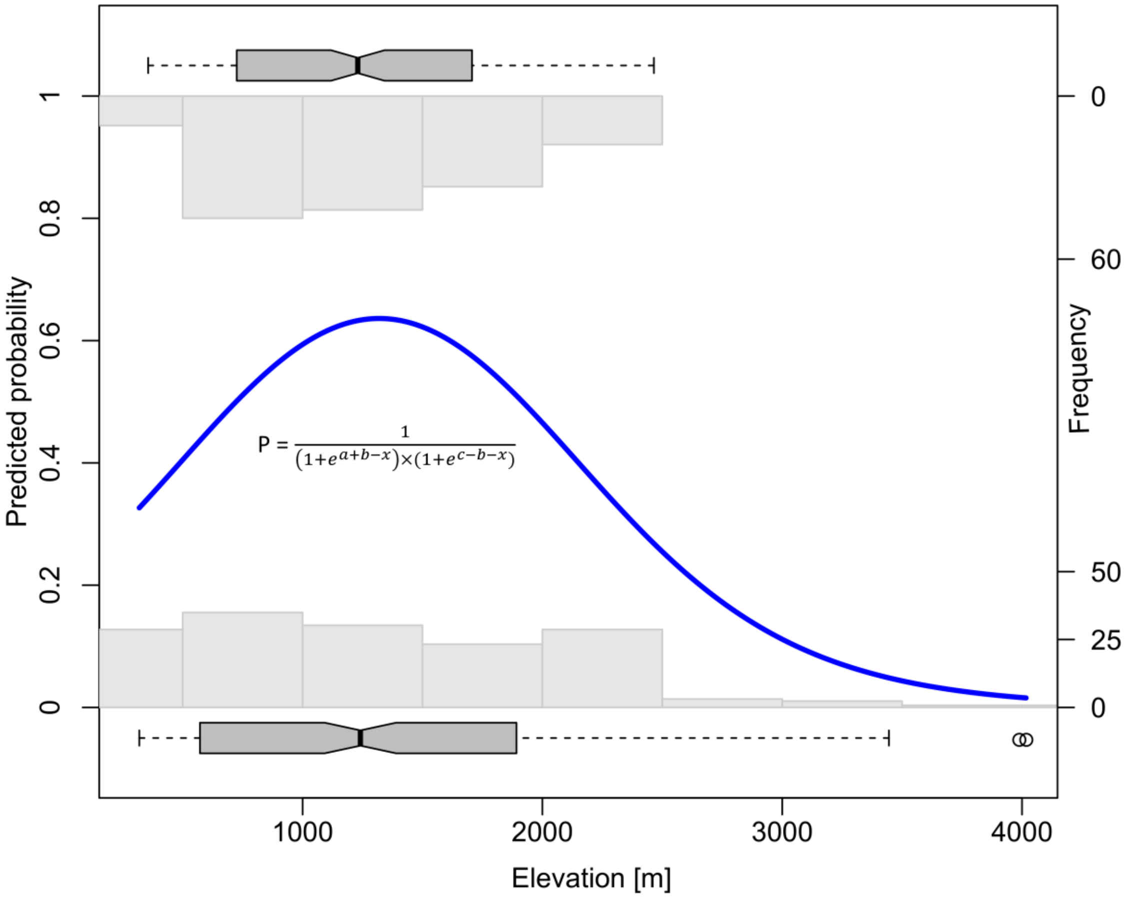

Figure 2.2 The probability of occurrence of invasive *Ageratina adenophora* along an elevational gradient in Western Himalayasshows a unimodal relationship with elevation. The bold blue line represents the predicted probability of occurrence from the model having best fit (according to the AICc values) out of the seven hierarchical models used (Jansen & Oksanen 2013). The equation in the figure shows the function for calculating the probability of occurrence where x is the elevation (predictor), and a, b, c are parameters of the model that are estimated by maximum likelihood procedure. The marginal histograms on the top and bottom of the plot show the frequency of presences and absences respectively, while the marginal boxplots depict the spread of presences and absences along the elevational gradient

Table 2.1 Results of mixed effect models comparing germination, growth- and fitness-related traits as well as leaf functional traits of invasive *Ageratina adenophora* populations between plant origins (low elevation, mid-elevation, high elevation) and between gardens (mid-elevation, low elevation) in the common garden experiment. Population, seed family and experimental block are considered as random effects in the model.

Source of variation	**Fixed effects**	**Origin**	**Garden**	**O × G**	**Random effects**	**Population**	**Seed family**	**P × G**	**S × G**	**Block**
	d.f	2,12	1, 8	2,12						
Germination probability	F	2.27	0.01	1.15	Var	0.19	0.06	0	0	0.32
	p	0.15	0.94	0.35	p	0.03	0.14	-	-	0.096
Number of capitula*	F	0.42	648.05	1.42	Var	0	0	0	0	0.048
	p	0.669	<0.001	0.278	p	-	-	-	-	0.114
Plant biomass*	F	0.49	64.43	1.29	Var	0.0006	0	0	0.0267	0.041
	p	0.62	<0.001	0.31	p	0.43	-	-	0.0038	0.032
Plant height	F	2.24	211.34	0.18	Var	0.278	3.12	0	0	53.34
	p	0.15	<0.001	0.84	p	0.45	0.24	-	-	0.0287
Primary branch number*	F	1	67.13	0.13	Var	0	0.002	0.002	0.005	0.005
	p	0.4	<0.001	0.88	p	-	0.339	0.21	0.189	0.067
Days to flower	F	0.50	732.35	0.30	Var	0.000067	0.00168	0	0	0.0075
	p	0.619	<0.001	0.748	p	0.4404	0.0302	-	-	0.0316
Specific leaf area*	F	0.26	0	1.78	Var	0.000016	0	0	0.0008	0.0065
	p	0.78	0.98	0.21	p	0.46	-	-	0.026	0.026
Leaf dry matter content	F	0.03	0.27	2.18	Var	0	0	0	0.0015	0.009
	p	0.97	0.61	0.16	p	-	-	-	0.0051	0.025
Mean leaf area	F	1.7	25.48	0.69	Var	2.07	0	2.07	3.414	43.69
	p	0.22	0.001	0.52	p	0.25	-	0.25	0.175	0.027

SLA: specific leaf area

LDMC: Leaf dry matter content

F ratios and associated p values are given for fixed effects, variance estimates, and p values of z tests are given for random effects.

The p values are not given for variance estimates set to zero.

*These variables were log transformed, Leaf dry matter content was logit transformed, and Days to flower was square root transformed.

Survival, growth, and reproduction

Survival of plants differed remarkably among the three gardens ($F_{2,12} = 73.78$, $p < 0.0001$). While 99.5 ± 0.4 % and 99.2 ± 0.5 % of the plants survived at low elevation and mid-elevation respectively, nearly all the plants died in the high elevation garden (0.5 ± 0.4 %) most likely due to sub-zero temperatures. Owing to the extremely low numbers of surviving plants in the high elevation garden, we had to remove this factor level from subsequent analyses of traits ($F_{1,8} = 221$, $p < 0.0001$). Growth-related traits (i.e. biomass, plant height and a number of branches) differed significantly between the gardens suggesting large plasticity of these traits (Table 2.1, Figure 2.3). On average, the biomass of plants in the low-elevation garden was almost 3 times as large as the biomass of plants in the mid-altitudinal garden (Figure 3c Table 2.1). Furthermore, plants in the low-altitudinal garden were 1.8 times as tall and had 1.6 times as many branches as the plants from the mid-altitudinal garden. However, neither the origin of plants nor the origin × garden interaction had a significant effect, indicating an absence of population differentiation and local adaptation of these traits (Figure 2.3, Table 2.1). However, the seed family × garden interaction was significant for plant biomass suggesting intra-population genetic variation in the response of this trait to the environment.

We analysed reproductive fitness of individuals in two steps: first, the probability of flowering and second, the number of capitula (as a measure of reproductive output) of those individuals that produced flowers. While all surviving plants flowered in the low-altitudinal garden, only 18% of the surviving individuals flowered in the mid-altitudinal garden. The probability of flowering was low in the mid-elevation garden as merely 16.4 ± 2.0% of the surviving plants produced capitula compared to 97.2 ± 0.9% in the low-elevation garden. There was no significant effect of origin on flowering probability ($F_{2,12} = 1.70$, $p = 0.22$). The number of flower heads produced by those individuals that flowered (as measure of their reproductive output) was almost 50 times larger in the low-elevation garden (754.5 ± 44.6) compared to the mid-elevation garden (15.6 ± 60.7; $F_{2,12} = 96.34$, $p < 0.0001$), but there was neither a difference among the three origins ($F_{2,8} = 0.05$, $p = 0.95$) nor an origin × garden interaction ($F_{2,12} = 0.06$, $p = 0.94$) (Table 1).

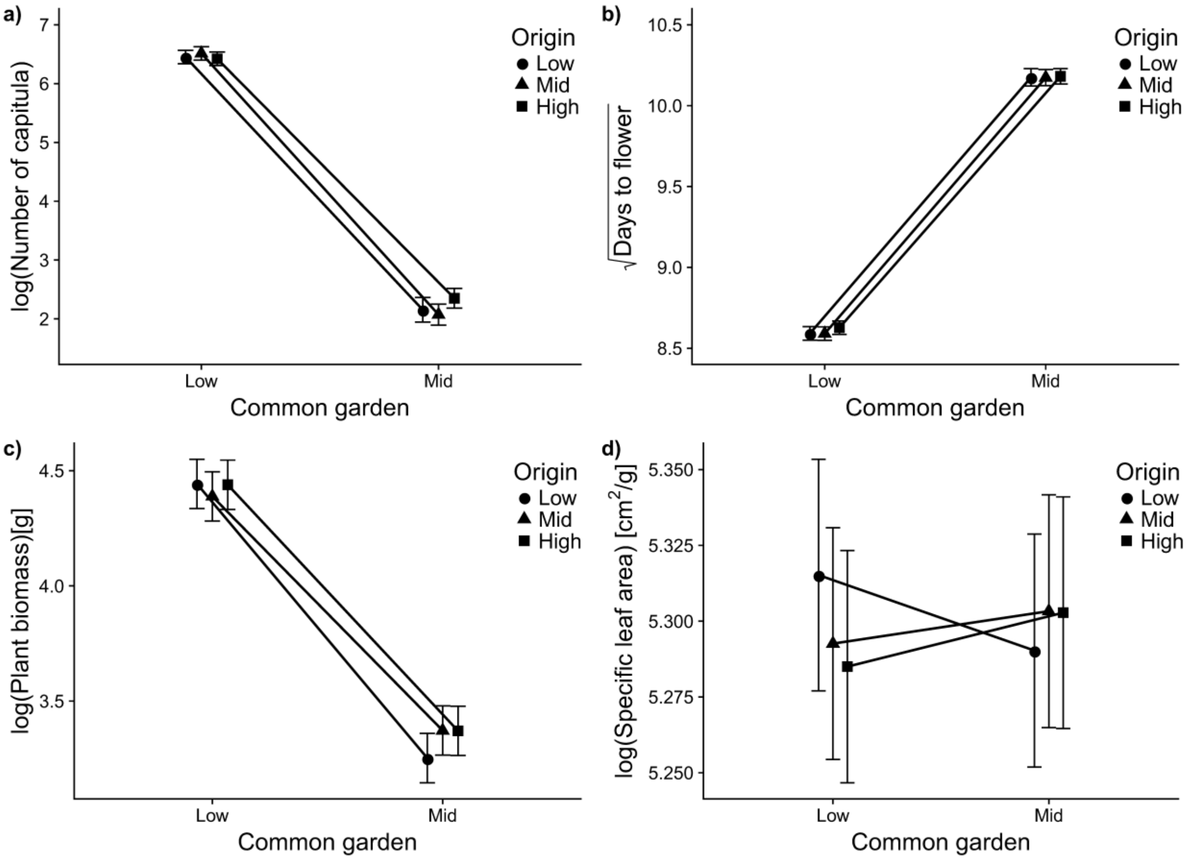

Figure 2.3. Lack of local adaptation in *Ageratina adenophora* populations. Reaction-norms of four important traits (a-d) of invasive *Ageratina adenophora* populations originating from three elevational belts (shown in the legend as Origin) in the western Himalayas to environmental conditions of the low (570m) and the mid-elevation (1330) gardens. Number of capitula, days to flower, and plant biomass differed significantly between gardens. None of them showed a significant origin effect or a significant garden × origin interaction (see Table 1 for results of statistical analyses). Plants belonging to low, mid and high origins are represented by circles, triangles, and squares respectively. The points show least square means and error bars represent standard errors obtained from the mixed effect models.

Among all the nine growth and fitness-related traits measured, only plant height showed a clinal variation along the altitudinal gradient: In both gardens, plant height increased significantly with the elevation from which the populations originated (Figure 4b, Table 2). Furthermore, the probability of flowering in the mid-elevation garden showed a marginally significant increase ($F_{1,12} = 3.20$, $P = 0.097$) with the elevation from which the populations originated (Table 2). We did not find any evidence for clinal variation along elevation in any other measured trait.

Table 2.2. Results of ANCOVAs to test for clinal differentiation among invasive *Ageratina adenophora* populations along the elevational gradient.

Source of variation		**Elevation**		**Garden**		**Elevation × Garden**	
Traits	df	F	p	F	p	F	p
Plant biomass*	1, 26	0.31	0.58	683.99	<0.001	0.4109	0.527
Plant height	1, 26	6.68	0.016	5063.62	<0.001	0.0256	0.874
Primary branch number*	1, 26	0.083	0.775	273.94	<0.001	0.0595	0.809
Specific leaf area*	1, 26	0.24	0.627	0.22	<0.001	1.7186	0.201
Leaf dry matter content	1, 26	0.528	0.82	6.155	<0.0199	3.1689	0.8675
Leaf area	1, 26	0.055	0.817	357.7	<0.001	0.8745	0.358
Days to flower	1, 26	1.776	0.194	5717.07	<0.001	0.0062	0.938
Number of capitula*	1,26	0.153	0.699	846.17	<0.001	0.0527	0.8202
Probability of flowering	1,13	3.2	0.097	-	-	-	-

Elevation of the home site of each population was used as a covariate, and garden as a factor. Please note that probability of flowering could only be tested for the low-elevation garden. *These variables were log transformed, Leaf dry matter content was logit transformed, and Days to flower was square root transformed.

Leaf functional traits

Of the leaf traits measured, only mean leaf area showed a plastic response to the garden environments: in the mid-elevation garden, leaf area was reduced by almost one third compared to the low-elevation garden, but there was no garden × origin interaction (Figure. 2.3, Table 2.1). Specific leaf area and leaf dry matter content did not show any significant effect of either garden, origin or their interaction. While we did not detect an origin × garden interaction for any of the leaf functional traits, we did find a significant seed family × garden interaction in the case of SLA and LDMC. Additionally, we found no evidence for clinal differentiation along the elevational gradient for any of the leaf functional traits (Table 2.2, Figure 2.4).

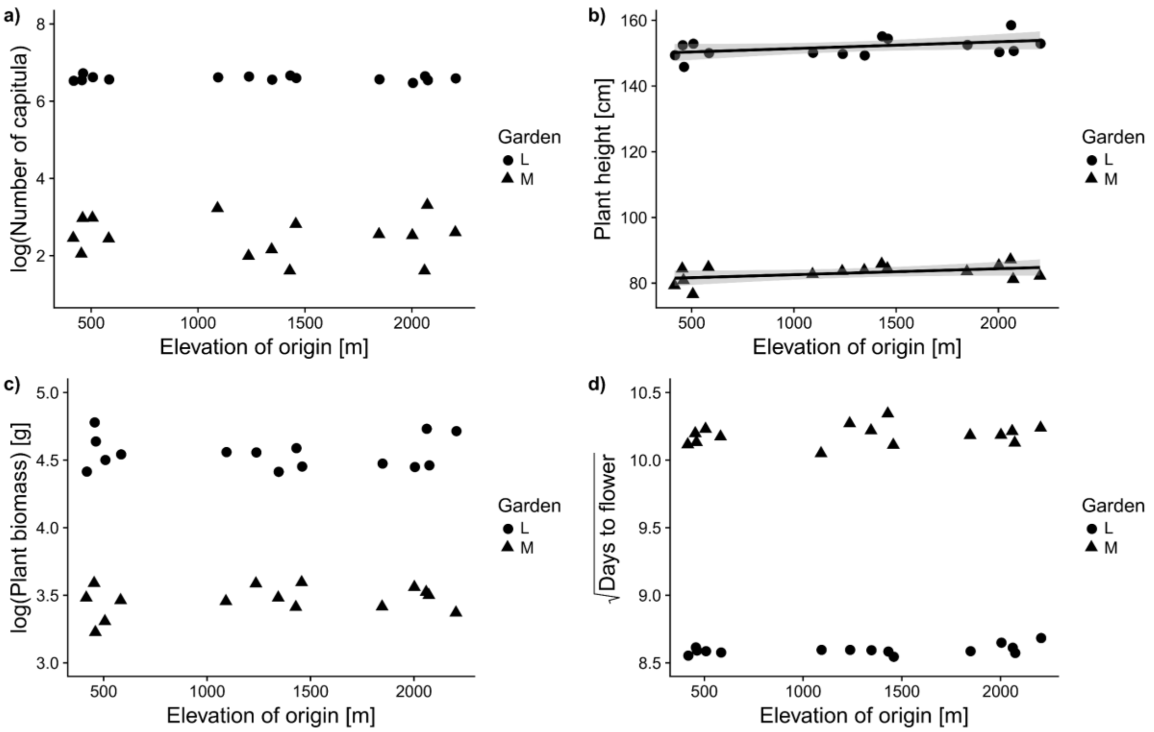

Figure 2.4. Absence of clinal differentiation of 15 invasive populations of *Ageratina.adenophora* along the elevational gradient for four important traits except for plant height (b) which shows significant but weak positive relationship. The scatter plots show the relationship between elevation at the home site of the 15 invasive *Ageratina adenophora* populations and their trait means measured in two common gardens (mid-elevation and low-elevation). Regression lines have been plotted for the only significant relationship, i.e. of plant height with elevation ($F_{1,26} = 6.68$, $p = 0.0157$, see Table 2 for details of ANCOVA results). Solid circles and triangles represent low and mid-elevation garden respectively.

Discussion

Distribution pattern and life history stages

Our field survey revealed clear evidence for a unimodal distribution of invasive *Ageratina adenophora* populations along the elevational gradient in the western Himalaya: The probability of occurrence peaks at 1320 m a.s.l., and steeply declines at both ends of the elevational gradient. Although we did not observe a complete absence of *Ageratina adenophora* from lower elevations in our study area, the species has a distinct lower range limit and is not reported from the plains (Tripathi *et al.* 2012). Physiological tolerance of a species to abiotic conditions plays a crucial role in determining the pattern of distribution along latitudinal or elevational gradients

(Osmond *et al.* 1987). This should be particularly true for the upper range margin at high elevations (Normand *et al.* 2009). Indeed, our common garden experiment suggests that the upper range limit is determined by low temperature (sub-zero) in winter, as plants failed to survive the winter at the uppermost site. Interestingly, during our field surveys, we observed that *Ageratina adenophora* populations were confined mostly to habitats that are likely to provide shelter during winter such as steep rocky slopes and to forest sites.

In contrast to the upper range limit, the lower range margin is thought to be primarily shaped by biotic interactions (Normand *et al.* 2009). However, our results suggest that even the lower range margin of a species may be predominantly determined by abiotic condition conditions if the environmental gradient is large enough as in the Himalayas. The distributional range of *Ageratina adenophora* in western Himalaya spans a thermal gradient of roughly 11°C, which is much larger than most studies conducted in temperate regions. It has been proposed that a symmetrical and steep response is to be expected if abiotic stress controls the abundance pattern of the species while the response is likely to be skewed if biotic interactions play a crucial role (Normand *et al.* 2009). The distributional pattern we observed is, however, largely symmetrical and steep, suggesting a crucial role of abiotic conditions also towards the lower end of the elevational gradient. Habitats of the lowermost populations in our study area are characterized by high summer temperature (around 37°C in the low-elevation garden, see Appendix 2.2) coupled with dry spells. Under these conditions, seeds completely failed to germinate in our experiment. The optimal temperature for seed germination of *Ageratina adenophora* is 25 °C, and temperatures above 35 °C are detrimental for germination (Lu *et al.* 2008). High temperature coupled with desiccation may, therefore, have inhibited seeds from germinating in our experiment. Accordingly, our field survey indicated that *Ageratina adenophora* populations in the lower elevational limit were specifically confined to ravines and water channels suggesting the requirement of higher soil moisture at the time of germination in summer.

Hence, our common garden experiment revealed that different life-history transitions are particularly vulnerable at the lower and the higher end of the elevational gradient, respectively: while winter survival appeared to be the most important determinant of the upper range limit, seed germination was crucial at the lower range margin. We, therefore, conclude that, although plants growing in the lowermost garden had the highest biomass and reproductive fitness, environmental conditions at mid-elevation are most favourable as they allow *Ageratina adenophora* populations to successfully complete crucial life-stages, i.e. to germinate, survive, and reproduce.

Absence of rapid evolutionary changes

To detect population differentiation and local adaptation of *Ageratina adenophora* populations along the elevational gradient, we applied two approaches: First, we combined the common garden approach with reciprocal transplantation, and second, we searched for a relationship between various phenotypic traits measured in the common garden and the elevation from which the populations originated. However, our experiments revealed neither evidence for local adaptation nor any evidence for clinal variation among *Ageratina adenophora* populations. Our result is in contrast to other case studies showing that adaptive divergence among populations may facilitate the range expansion of invasive plant species along environmental gradients. For instance, *Lythrum salicaria* (Colautti & Barrett 2013) has been found to be locally adapted along a latitudinal gradient in North America, and *Solidago altissima* (Konarzewski *et al.* 2012), as well as *Senecio inaequidens* (Monty and Mahy 2009), have shown clear-cut patterns of clinal differentiation along an environmental gradient in the invasive range. However, several studies have also reported the absence of genetic differentiation between invasive plant populations. For example, *Buddleja davidii,* (Ebeling *et al.* 2011) and *Mahonia aquifolium* (Ross *et al.* 2008) have spread across different habitats without showing evidence of local adaptation. In such cases, preadaptation to conditions in the invasive range (Bossdorf *et al.* 2008) and high phenotypic plasticity (Annapurna & Singh 2003; Geng *et al.* 2006) have been attributed to the success of invasive populations. For example in invasive *Acer negundo*, high amount of pre-adapted phenotypic plasticity plays a crucial role (Lamarque *et al.* 2013). We included seed weight as a covariate to test any evidence of maternal effect manifested due to the provisioning of nutrition. However, there are several other mechanisms by which maternal environments can influence offspring (e.g. epigenetic changes). Although we cannot rule out that some of them might have influenced our experimental results, our data (as many other data from common garden experiments) do not allow estimating the magnitude of these effects. Nevertheless, we found almost no evidence for local adaptation in phenotypic traits despite huge differences among maternal environments.

In our study, there was an overall lack of strong evidence for clinal differentiation along an elevational gradient in most traits that we recorded. Several processes might have inhibited adaptive differentiation after the invasion western Himalaya. First, the plant has been reported to be a triploid with 51 chromosomes (Khonglam & Singh 1980). Triploid plants are not capable of undergoing the normal process of meiosis, and hence they do not produce seeds by the sexual process (Bala & Gupta 2014). Developmental studies of this species have further indicated that the embryo development may initiate even before meiosis and fertilization, which implies that the plant is capable of producing seeds apomictically (Baker 1974; Noyes 2007; Lu *et al.* 2008; Bala & Gupta 2014). Lack of sexual reproduction thus locks the existing genetic variation in the population by preventing recombination, and may, therefore, reduce its potential for adaptive evolution. Second, it is rather likely that genotypes are "swapped" among populations and elevational belts due to seed dispersal by the wind, water or animals. We admit that the lack of gene flow by pollen among populations may then facilitate a pattern of population differentiation according to random drift or isolation by distance, in addition to any local adaptation that may have taken place. Third, herbarium records indicate that *A. adenophora* was introduced in 1927 to Western Himalayas an ornamental plant in the experimental garden of the Forest Research Institute, Dehradun. If the current populations in Western Himalaya have originated from the initial introduction event, it is likely that the plant suffered from a genetic bottleneck. A period of 90 years since introduction may not be sufficient for the plant to accumulate enough genetic variation to undergo local adaptation, especially because of its apomictic nature. Although there is evidence (unpublished result: voucher number CNH-225216, Calcutta) of separate introduction in events in the hills of peninsular India (botanical garden of Ootacamund, Tamil Naidu) prior to the introduction in Western Himalaya, chances that these geographically isolated populations have intermingled are rather scarce. Finally, the existence of a high degree of phenotypic plasticity of *Ageratina adenophora* (Feng *et al.* 2007) suggests that plasticity may have contributed to invasive spread across a broad environmental gradient without undergoing adaptive evolution. Indeed, the large differences in trait values between our common gardens on the origin, population, and seed family levels suggest a high degree of phenotypic plasticity in this species.

Genotype × environment interactions signify differential response of genotypes to different environmental conditions. From an evolutionary perspective, genotype × environment interactions provide the basis of adaptive divergence in response to different environmental conditions. In our experiment, we detected significant seed family × garden interaction term for biomass, SLA and LDMC. This interaction indicates the existence of intra-population genetic variation in response to the environment for various traits, which in turn may provide the opportunity for adaptive evolution in future. In addition, accumulation of mutations can further increase the genetic diversity of *Ageratina adenophora* populations in the long run (Colautti & Lau 2015). However, our results together with findings of other studies strongly suggest that recent invasive spread of *Ageratina adenophora* is mostly due to its high phenotypic plasticity. Plastic responses across a broad range of environmental conditions may be crucial to the success of a triploid and apomictic species that lacks sexual recombination (Baker 1965). According to our results, further spread of *Ageratina adenophora* to higher elevations is currently constrained by its sensitivity to low temperature.

Acknowledgements

The work was a result of collaborative effort between Helmholtz Centre for Environmental Research – UFZ (Germany) and CSIR-IHBT (India). We express our deep gratitude to Dr Rakesh Devsran Singh (deceased), Dr Paramvir Singh Ahuja (deceased) and Dr Sanjay Kumar who had played a pivotal role in hosting the research work at CSIR-Institute of Himalayan Bioresource Technology (IHBT). We are deeply grateful to Dr Pravir Kumar Paul, Dr Surendra Kumar Vats, Dr Brij Lal, Dr Amit Chawla, Dr Sanjay Kumar Uniyal, Dr Walter Durka, Mr Dinesh Thakur and for their insightful suggestions and scientific discussions. We want to acknowledge the logistic support provided by Dr Gopichand, Dr Manoj Kumar and Mr Ramji Lal Meena. Furthermore, we acknowledge Mr Monu Kumar and Mr Ashok Kumar for their assistance in carrying out the field work. Finally, we express our gratitude to Mr Santosh Kapoor and Mrs Swarna Devi for granting permission to allow us to conduct our experiment in their private land.

Appendix 2 (for Chapter 2)

Appendix 2.1 Survey map

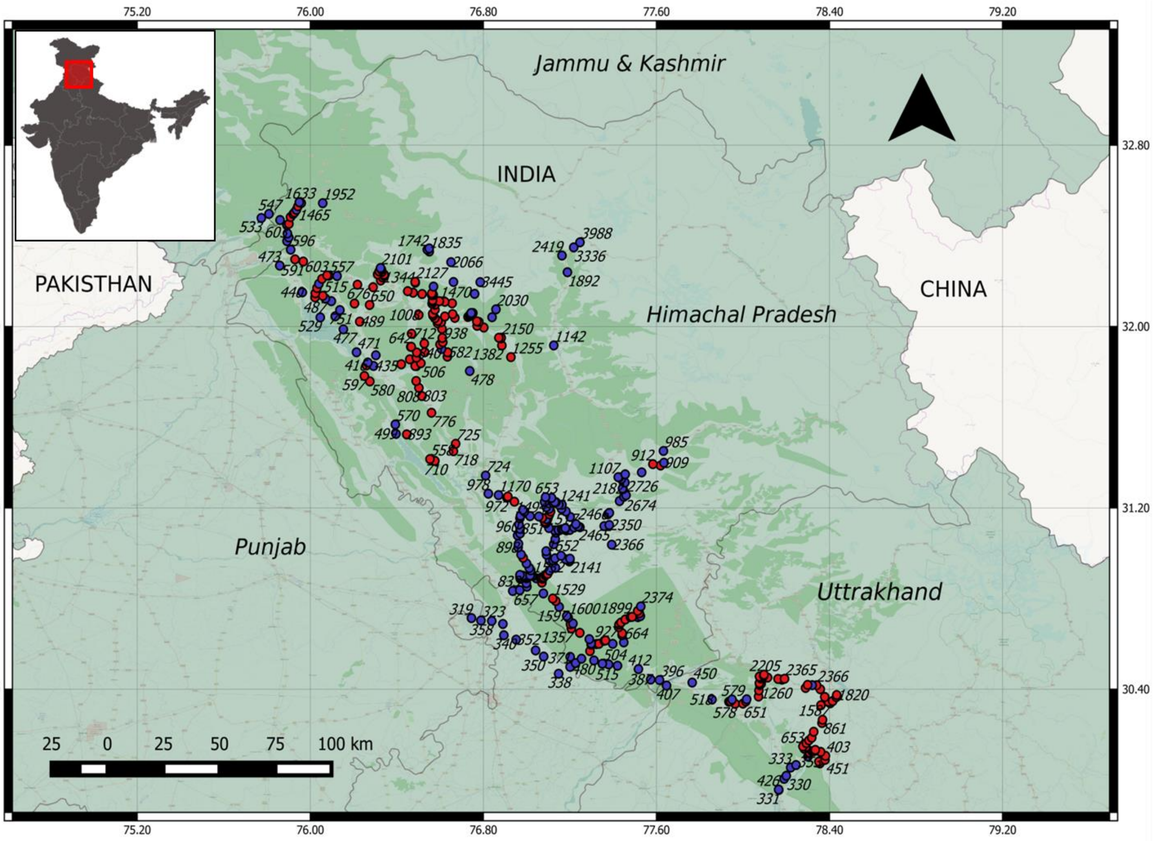

Figure 2.5 Map showing the survey locations (n = 389) of Ageratina adenophora located in the western part of Himalayas. The presences (n = 193) and absences (n = 196) are depicted using red and blue coloured circles respectively. The elevation of the surveyed location in meters is indicated in by the number next to the circle.

Appendix 2.2 Climatic conditions of natural at the sites from wherepopulations of *Ageratina adenophora* were sampled

Table 2.3 Geographic coordinates, elevation and major climatic variables[1]of home sites of the 15 *Ageratina adenophora* populations used for the common garden and germination experiments. All the populations are located in Western Himalaya (Himachal Pradesh, India).

Location	**Latitude [°N]**	**Longitude [°E]**	**Elevation a.s.l. [m]**	**Mean annual temp [°C]**	**Mean annual prec[mm]**	**Max temp of Coldest Month [°C]**	**Min temp of Warmest Month [°**
Balaru (Dehra)	31.8288	76.2597	416	23.2	1523	38.7	6.7
Jwali Bridge	32.1468	76.0234	454	22.9	1854	38.9	6.4
Jwali Stone Grinder	32.17	76.031	460	22.7	1956	38.4	6.4
Sandhol	31.8864	76.6345	582	22.4	2155	37.1	6.9
Sujanpur	31.8383	76.5111	506	22.9	1986	38	6.9
Baijnath	32.0548	76.658	1091	20.2	2182	33.6	6.3
Dhramshala	32.2168	76.3347	1344	17.9	2612	30.4	4.7
Jogindernagar	32.0031	76.7711	1236	19.4	1920	32.3	5.7
Palampur	32.116	76.5653	1429	18.6	2422	31.2	5.4
Rakh	32.1493	76.4752	1457	18.3	2544	30.8	5.2
Lower Birni	32.1384	76.5614	2002	15.8	2254	27.9	2.7
Billing	32.0549	76.7396	2203	14.4	2057	26.3	1.2
Jhitingiri	31.948	76.8814	2059	15.5	1987	27.5	2.6
Macleodganj	32.2408	76.3306	1846	16.9	2475	29.2	3.7
Jia Power Project	32.1963	76.4852	2072	15.6	2274	27.7	2.4

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[1] Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. Very high resolution interpolated climate surfaces for global land areas. Int J Climatol. Wiley Online Library; 2005;25: 1965–1978.

Appendix 2.3 Climatic conditions at the common garden sites

Table 2.4 Geographic coordinates, elevation, and major climatic variablesof sites used for common garden and germination experiments in Western Himalaya (Himachal Pradesh, India).

Common garden	Latitude [°N]	Longitude [°E]	Elevation a.s.l. [m]	Mean annual temp[°C]	Mean annual prec [mm]	Mean max temp[°C]	Mean min tempe[°C]
High-elevation garden	32.1424	76.5608	2098	14.7	2151	26.7	1.5
Mid-elevation garden	32.1065	76.5596	1331	18.9	2428	31.5	5.5
Low-elevation garden	31.8554	76.5028	572	22.5	2025	37.4	6.8

Appendix 2.4 Nutrient concentration at common garden sites

Table 1 Concentration (mean±sd) of important nutrients at the three experimental gardens (High, Mid, Low).

Soil parameters	High(n=12)	Mid(n= 13)	Low(n=14)
Ca in mg/Kg	1715.83±91.40	2060.71±698.78	1578.46±81.63
K in mg/Kg	2365.83±141.39	2330.71±205.97	4930.77±255.33
Mg in mg/Kg	1911.67±262.78	2860.71±377.90	7996.92±344.01
P in mg/Kg	684.17±46.41	400.00±38.23	244.62±9.67
N (%)	0.26±0.04	0.07±0.01	0.09±0.01
C (%)	2.89±0.44	0.78±0.10	1.10±0.08

Appendix 2.5 Experimental dates

Table 2 Table showing key experimental dates of reciprocal transplant experiment. Please note that due to mortality of the plants at high elevation (>99%) biomass could not be harvested. Similarly seeds did not germinate in the germination experiment at the lowermost garden.

Site	**Sowing of seeds for main experiment**	**Transplantation of seedlings for main experiment**	**Sowing of seeds for germination experiment**	**Counting of germinated seeds**	**Date of Biomass Harvest**
High-elevation garden	3-7-2014	23-8-2014	27-7-2014	31-8-2014	_
Mid-elevation garden	6-7-2014	16-8-2014 to 18-8-2014	23-8-2014	5-9-2014	15-8-2015 and 16-8-2015
Low-elevation garden	8-7-2014	18-8-2014	1-8-2014	_	22-8-2015 and 23-8-2015

Appendix 2.6 Result of hierarchical regression models using eHOF package in R

Table 3 Result of hierarchical regression models using eHOF package in R (Huisman *et al.* 1993; Jansen & Oksanen 2013). The probability of occurrence along elevational gradient was predicted using presence- absence data of Ageratina adenophora. Seven models with increasing level of complexity were fit using maximum likelihood procedure. Model IV had the lowest AIC value indicating unimodal and symmetric pattern of distribution of *Ageratina adenophora* along elevational gradient.

Model	**Shape of the response curve**	**Deviance**	**logLikelihood**	**AICc**	**ΔAIC**
I	Straight line-Null model	539.2042	269.602	541.2146	22.6169
II	Logistic - increasing trend	538.4934	269.247	542.5245	23.9269
III	Logistic - increasing trend but below the upper bound	521.2176	260.609	527.28	8.6823
IV	*Unimodal symmetric pattern*	*512.5353*	*256.268*	*518.598*	*0*
V	Unimodal skewed pattern	512.5350	256.268	520.6392	2.0416
VI	Bimodal pattern	512.5353	256.268	520.6395	2.0418
VII	Bimodal pattern	512.5353	256.268	522.692	4.0943

Chapter 3

Quality of climatic data can determine the transferability of species distribution models: a case study with *Ageratina adenophora*

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Planned for submission to *Ecological Informatics*

Abstract

The effect of the source of predictor variables on the predictive performance of species distribution models (SDMs) has remained relatively underexplored. Past research on species distribution modelling has focused mainly on methodological issues pertaining to the choice of appropriate modelling algorithm. Bioclimatic variables are commonly used as predictors in correlative species distribution models. Currently, several online sources offer the same set of bioclimatic variables. In this paper, we asked if the internal predictive performance and transferability of SDMs is affected by the choice of two different bioclimatic databases viz. WorldClim 2 and Chelsa 1.2. We used invasive *Ageratina adenophora* as our study species to investigate the effect of WorldClim 2 and Chelsa 1.2 predictor databases on the performance of SDMs. Presence-absence data from Western Himalaya was used to train a generalized linear model with a binomial distribution. Multi-model inference approach was used to average model coefficients across several competitive models. A set of independently collected presence-only dataset from central and Western Himalaya was used to evaluate the transferability of the SDMs beyond the training range based on Boyce Index. Our results showed that performance of SDMs could be affected by the choice of the climatic dataset. We found that models based on Chelsa 1.2 outperformed WorldClim 2 in terms of internal evaluation. However, when the model was transferred beyond the training and calibration range to central and eastern Himalaya, models based on WorldClim 2 performed substantially better than Chelsa 1.2. We recommend that the choice of predictor data set should not be based on subjective decision whenever several options are available. Instead, such decisions should be based robust evaluation of most appropriate dataset for a given geographic region and

species being modelled. Moreover, decisions could also depend on the objective of the study, i.e., within range or beyond range projection. Therefore, evaluation of predictor dataset from different competitive sources should be routinely performed as an integral part of modelling procedure.

Introduction

Correlative species distribution models are used to estimate the potential geographic distribution of species by using the relationship between known occurrences of a species with its environmental conditions (Guisan & Zimmermann 2000; Pearson & Dawson 2003; Heikkinen *et al.* 2006; Elith & Leathwick 2009). These models directly relate species occurrence to its realized multi-dimensional niche (Hutchinson 1957; Pearson & Dawson 2003) in the environmental space (Soberón & Nakamura 2009; Peterson *et al*. 2011). Climatic conditions are crucial in determining the large-scale distribution patterns of organisms (Woodward & Williams 1987; Woodward *et al.* 2004) and are hence widely used for modelling species distributions (Pearson & Dawson 2003).

Species distribution models (SDMs) have emerged as powerful tools due to their versatile applicability in ecology, conservation biology, evolutionary biology, agriculture and epidemiology (Peterson et al. 2011). Climatic niche modelling of invasive species is frequently used to predict climatically suitable regions and identify key the predictors that determines their current and potential future distribution (Thuiller *et al.* 2005; Ervin & Holly 2011; Jaryan *et al.* 2013). Results from such models can help in preventing future invasions in regions that have not yet been invaded by developing early detection systems (Zhu *et al.* 2007; Peterson *et al.* 2011; Adhikari *et al.* 2015). Moreover, it can help to strategically manage the control efforts by mapping the areas potentially vulnerable to invasions (Thuiller *et al.* 2005; Peterson *et al.* 2011).

The ability of a SDM to predict accurately beyond its training and calibration range is termed as transferability (Elith & Leathwick 2009). The model transfer may often involve extrapolation if the range of values of the predictors is beyond the training range. Model transferability is a particularly challenging issue in species distribution modelling (Araújo & Guisan 2006; Elith & Leathwick 2009; Soberón & Townsend Peterson 2011; Wenger & Olden 2012). The success of distribution modelling in applied ecological purposes such as predicting the potential range of an invasive plant is highly contingent on model transferability to other regions. Therefore evaluation of model transferability using an independent data set collected from a different region has been considered to be crucial (Heikkinen *et al.* 2012; Fernández & Hamilton 2015). Much of past research has focused on the development of modelling algorithms to increase the predictive performance of SDMs (Guisan & Zimmermann 2000; Elith & Leathwick 2009). SDMs have seen steady development in the last two decades due to the advent of more sophisticated modelling techniques and increase in processing power of computers (Guisan & Zimmermann 2000; Elith & Leathwick 2009). Advances in SDMs have also considerably benefitted from the availability of freely available climatic predictors at very high resolutions in the form of GIS layers from different sources (Soberón & Nakamura 2009; Peterson *et al.* 2011). Although ample of studies are available on the effect of choosing different modelling algorithms on transferability (Randin *et al.* 2006; Heikkinen *et al.* 2012; Wenger & Olden 2012), studies focusing exclusively on the consequence of choosing different predictor datasets (such as climatic variables) has been relatively scarce. Consequently, researchers often rely on subjective decisions for the choice of the predictor dataset, if several are available, for modelling species distributions, although the inappropriate choice of predictor datasets could lead to potentially unreliable predictions (Bobrowski & Udo 2017; Karger *et al.* 2017). Although different climatic databases offer the same set of variables, they could differ in terms of predictive performance because they rely on different source data and use different interpolation algorithms (Bobrowski & Udo 2017; Karger *et al.* 2017).

Bioclimatic variables are set of 19 climatic variables that include not only annual trends but also the extreme limiting climatic conditions which are relevant to the physiology of biological organisms. These variables are generated from mean, minimum, maximum temperature, and monthly precipitation data gathered from global records and averaged across several decades. For instance, bioclimatic dataset includes variables like the minimum temperature of the coldest month (bio 6) and precipitation of driest quarter (bio 17) that are derived from the primary temperature and precipitation variables (minimum, maximum and mean) and represent limiting conditions. Currently, several databases offer free access to these bioclimatic variables in the form of spatial raster. WorldClim1.4 is one of the most popularly used high resolution (30 arc seconds) global bioclimatic dataset which was made available by Hijmans et al. in 2005. This dataset was interpolated from ground weather stations across the globe by thin plate interpolation using latitude, longitude, and elevation as independent variables (Hijmans *et al.* 2005). However, in the recent version of WorldClim (Version 2, Fick & Hijmans 2017), satellite-derived covariates such as land surface temperature and cloud cover has been used in the interpolation process to improve the data quality in areas where ground observations are scarce. Chelsa (Version 1.2, Karger *et al*. 2017, hereafter referred as Chelsa 1.2), is a newly released climatic database that offers the same set of bioclimatic variables at very high resolutions (30 arc seconds). Chelsa1.2 is fundamentally different from WorldClim 2 database because unlike WorldClim 2 it accounts for orographic patterns of precipitation in mountainous terrains (i.e., it accounts for factors such as aspect and valley exposition by including wind effects, see Karger *et al.* 2017). CliMond (Kriticos *et al.* 2014) is yet another database that offers interpolated climate data, but its application is restricted due to its relatively coarse resolution (10 arc minutes). Many high elevational areas of the world such as the Himalayas suffer from a low density of weather stations due to remoteness, and therefore these corrections are likely to improve the quality of the dataset.

Understanding the effect of source of predictor variables on the performance of a SDM is crucial. In this paper, we asked, if models calibrated on Chelsa1.2 and WorldClim 2 data, respectively, differ in terms of within range and out of range predictive performance. To this end, we used the invasion of *Ageratina adenophora* (Spreng.) R.M.King & H.Rob. in the Himalayas as our study system. Using presence-absence data of *Ageratina adenophora* from the Western Himalayas as the response, we calibrated generalized linear models on Chelsa1.2 and WorldClim2 data. Transferability of models calibrated on these two datasets were evaluated using an independent set of presence-only data from central and eastern parts of Himalaya

Methods

Target species

Ageratina adenophora (Crofton weed, Asteraceae) is a plant native to Mexico and invasive (or even noxious) in more than 30 countries in subtropical regions across the globe (Auld & Martin 1975; Qiang 1998; Tian *et al.* 2007; Muniappan *et al.* 2009). It is a multi-stemmed, perennial herb or undershrub that grows up to 2 meters and flowers profusely in spring (Tripathi *et al.* 2012). It was introduced as an ornamental plant to England in the 19th century (Auld & Martin 1975) and was later introduced in different parts of the world (Muniappan *et al.* 2009). It was introduced to India as an ornamental plant in the early 20th century (Datta *et al.* 2017). Within a century it has established itself as a troublesome invasive plant in subtropical and sub-temperate mountainous regions throughout South Asia (Muniappan *et al.* 2009; Heystek *et al.* 2011). *Ageratina. adenophora* affects the native biodiversity (Ding *et al.* 2007), livestock (Tian *et al.* 2007), agriculture (Yadav & Tripathi 1982), and local economy of the infested regions (Wan *et al.* 2010). Once established, it is difficult to manage this species since it grows nearly as monospecific strands (Lu *et al.* 2006) in the rugged and inaccessible mountainous terrains. In south Asia, it is distributed almost throughout the subtropical and sub-temperate belt of the Himalayas, ranging from Arunachal Pradesh in the east to Himachal Pradesh in the west (Raizada 1976; Tripathi *et al.* 2012) and in mountains of peninsular India (e.g., Western Ghats).

Study area and survey

Our study was carried out in a region of the Western Himalayas (Singh & Singh 1987) between 29.96°N and 32.55°N latitudes and 75.77 °E and 78.43°E. Broadly, our study area covered five provinces in northwestern India and stretched from Dhauladhar range (Himachal Pradesh province) in the west to the mountains of Gharwal region (Uttrakhand province) in the east. We also covered a considerable part of low-lying foothills of Himalayas (Siwalik range) situated in Himachal Pradesh, Punjab, and Uttrakhand provinces of India.

We haphazardly surveyed 389 locations and recorded the presence or absence data of *Ageratina adenophora* in the subtropical and temperate zones of Western Himalaya between 300m to 3000m elevation (Figure 3.1). We targeted this elevational belt based on prior knowledge about the distribution of the plant from previous reconnaissance surveys and existing literature on the distribution of the plant (Datta *et al.* 2017). The surveys were conducted in the vegetation periods of 2014 and 2015. Most of the surveys were carried out along road and riversides as these are conduits for dispersal of propagules and are also initial establishment sites of *Ageratina* *adenophora* (Lu & Ma 2006; Wang *et al.* 2011). However, many high elevational areas beyond 2500m were not accessible by road, and hence we used trekking trails for surveying such remote locations. To check the performance of the model beyond the study area, we used an independent set of presence-only records (n=85) that were collected by experts from central and eastern Himalaya (Figure 3.1).

Climatic data and variable selection

We used the latest bioclimatic dataset available from WorldClim 2 (Fick & Hijmans 2017) and Chelsa 1.2 (Karger *et al.* 2017) at the resolution of 30 arc seconds. The values for all corresponding survey locations were extracted in R (version 3.4.1, R Core Team 2017) using the "raster package" (Hijmans 2015).

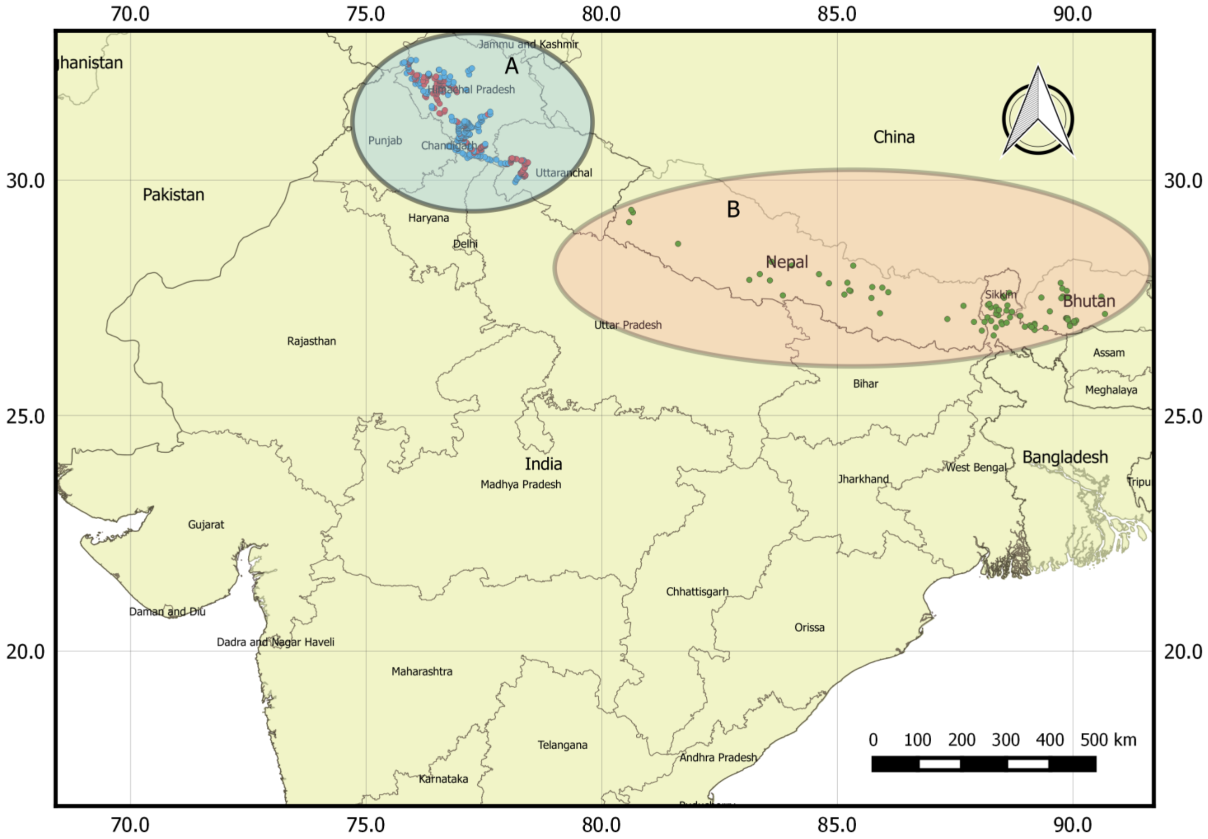

Figure 3.1 Map showing the survey location of *Ageratina adenophora*. The region marked by an ellipse (A) shows the survey area in Western Himalaya from where 192 presences (red) and 197 absences (blue) were used to train the model. The region marked by an ellipse (B) shows central and eastern Himalaya from where an

additional set of 85 presence only locations (green) were obtained for evaluating the transferability of the models trained in Western Himalaya.

Due to high collinearity among the bioclimatic variables, we used cluster analysis for variable selection (Dormann *et al.* 2013). A dendrogram was constructed based on Spearman's rank correlation matrix and UPGMA (unweighted pair-group method with arithmetic averages) agglomeration. A threshold value of 0.7 (Dormann *et al.* 2013) was used to prune the dendrogram and select variables that were not highly collinear. From the set of selected variables in the previous step, we checked for collinearity of a variable with its quadratic term. In most cases, we found that the variables were highly collinear with its quadratic term, except Bio6 of Chelsa 1.2 dataset. The final set of bioclimatic variables selected for each dataset is shown in Table 3.1.

Table 3.1 Variable selection table for Chelsa 1.2 and WorldClim 2 databases using cluster analysis to reduce collinearity among the variables. Highly correlated variables were removed from each dataset (using threshold of Spearman's rho = 0.7, see text for details). The selected variables from Chesla 1.2 and WorldClim 2 are represented by tick mark (✓) against the respective variable.

Abbreviation	Climatic variable	Chelsa1.2	WorldClim2
BIO1	Annual Mean Temperature		
BIO2	Mean Diurnal Range	✓	
BIO3	Isothermality	✓	✓
BIO4	Temperature Seasonality	✓	
BIO5	Max Temperature of Warmest Month		
BIO6	Min Temperature of Coldest Month	✓	✓
BIO7	Temperature Annual Range		
BIO8	Mean Temperature of Wettest Quarter		
BIO9	Mean Temperature of Driest Quarter		
BIO10	Mean Temperature of Warmest Quarter		
BIO11	Mean Temperature of Coldest Quarter		
BIO12	Annual Precipitation	✓	✓
BIO13	Precipitation of Wettest Month		
BIO14	Precipitation of Driest Month		✓
BIO15	Precipitation Seasonality	✓	✓
BIO16	Precipitation of Wettest Quarter		
BIO17	Precipitation of Driest Quarter		
BIO18	Precipitation of Warmest Quarter		
BIO19	Precipitation of Coldest Quarter		

Note: Bio6^2 was selected for Chelsa1.1 in addition to the variables indicated (for details see text).

Modelling procedure

We used a multi-model inference approach to arrive at the final model to be used for prediction (Grueber *et al.* 2011; Symonds & Moussalli 2011; Burnham 2015). The following steps were carried out: (1) We fitted generalized linear model with binomial error distribution to the presence or absence data of *Ageratina adenophora* using previously selected climatic variables (Table 3.1). All the predictor variables were scaled to zero mean and unit standard deviation. (2) We then obtained all possible models with different variable combinations using the “dredge” function in “MuMIn” package (Barton 2015). (3) A subset of best models that had AIC values within 2 AIC units of the topmost model was considered for the model averaging process (hereafter referred as “best subset”) (Grueber *et al.* 2011; Liu *et al.* 2016). (4) We then averaged model coefficients weighted by the Akaike weights across all the models in the best subset. We used the default “full average” method for calculating the averaged coefficients (if a variable is absent from one of the component models, a parameter estimate of “zero” is substituted in the averaging process (Symonds & Moussalli 2011)). This method results in shrinkage of parameter estimates for those variables which are less important (Grueber *et al.* 2011). This method has been suggested when prediction from the averaged model is intended (Symonds & Moussalli 2011).

The variable selection process using cluster analysis on Chelsa 1.2 and WorldClim 2 data yielded slightly different sets of variables. We ran four models, two models with variables selected specifically for WorldClim 2 and Chelsa 1.2 databases respectively (hereafter these models are referred to as “WorldClim -WorldClim” and “Chelsa - Chelsa”). In the other two models, we used WorldClim and Chelsa data but the selected set of variables were crossed in order to make the SDMs comparable (hereafter referred to as WorldClim - Chelsa and Chelsa -WorldClim.

Model evaluation

In order to classify the continuous probability values into binary predictions, a suitable threshold needs to be defined (Fielding & Bell 1997; Tsoar *et al.* 2007). We calculated the optimal threshold by maximizing the true skill statistic (TSS), which accounts for both omission and commission errors (Allouche *et al.* 2006). Moreover, TSS is known to be independent of prevalence. Hence TSS is a better metric compared to Cohen's

Kappa (Allouche *et al.* 2006). The value of TSS ranges from -1 to +1. A value close to +1 indicates good agreement while a value close to or less than 0 indicates that the model does not perform better than a random model (Allouche *et al.* 2006). AUC is a commonly used metric for evaluating the performance of SDMs; however, its efficiency has recently been questioned (Jiménez-Valverde *et al.* 2008; Lobo *et al.* 2008), and therefore we do not report AUC values.

To assess the transferability (i.e., predictive performance of the model beyond our study area in the Western Himalaya where it was trained and calibrated), we used an independent set of presence-only data from of central and eastern Himalaya (Nepal, Sikkim, Darjeeling, and Bhutan, see acknowledgement for contributors). Since we did not have true absence data from these regions, we could not use traditional model evaluation metrics such as TSS. Therefore, we used Boyce's index for assessing transferability (Boyce *et al.* 2002; Hirzel *et al.* 2006). Boyce index compares the ratio of predicted frequency and expected frequency of evaluation points across the prediction gradient using a moving window approach (Hirzel *et al.* 2006; Petitpierre *et al.* 2012b). It is a threshold independent metric ranging between -1 and +1. Positive values close to 1 indicate very good agreement of observed presences with the model prediction while values very close to zero indicate that the predictions are not better than random. Negative values of Boyce's index shows that the model is worse than a random model and makes predictions in areas that are not suitable for the species (Hirzel *et al.* 2006). It was calculated using the "ecospat.boyce" function implemented in the "ecospat" package (Cola *et al.* 2017) implemented in R. Moreover, Boyce index was also calculated for internal evaluation (i.e., training range) to facilitate direct comparison.

The models were projected on a much larger geographic area (entire south Asia) compared to the training area to make general qualitative (visual) assessment based on prior knowledge about its distribution from existing literature.

Results

Internal evaluation based on TSS and AUC of the models using presence and absence data showed that Chelsa 1.2 performed marginally better than WorldClim 2 (Table 2). The "Chelsa - Chelsa" model had the highest value of TSS among all the models. Internal evaluation using Boyce's index (based on presence-only data) also revealed that models based on Chelsa performed better than WorldClim in the internal evaluation. “Chelsa data -WorldClim variables” had the highest Boyce index for internal evaluation.

In general, models based on WorldClim 2 had higher transferability compared to models based on Chelsa 1.2 data. “WorldClim - WorldClim” model performed the best in terms of transferability. A reliable estimate of Boyce’s Index could not be calculated for “Chelsa data - Chelsa variables” model because the occurrence probability was very high for all the grid cells (close to 1) of evaluation region (i.e., central and eastern Himalayas). However, visual inspection of the prediction maps showed that “Chelsa data - Chelsa variables” model produced very unrealistic over predictions (Figure 2c). For instance, the model showed most parts of South Asia to be potentially suitable for *Ageratina adenophora* including warm tropical regions of peninsular India. However, in reality, the species is known to be restricted to moist subtropical and temperate regions only. To be sure if this overprediction was simply due to the selection of variables made for Chelsa, we looked at the performance of “Chelsa data - WorldClim variables” model (Figure 2d). This improved the situation slightly, although many potentially unsuitable areas in central and southern India were still being predicted to be climatically suitable for the spread of *Ageratina adenophora.*

Table 3.1 Model evaluation metrics for different models using Chelsa 1.2 and WorldClim 2 datasets. Database refers to the climatic database used for modelling. Variable selection refers to the specific set of variables selected using cluster analysis for Chelsa 1.2 and WorldClim 2 datasets (see Table 1 and method section for further details). Sensitivity is the rate of true positives while specificity is the rate of true negatives. Boyce internal refers Boyce index calculated for the area where the model was trained, and Boyce external refers to Boyce index calculated for central and eastern Himalaya where the model was transferred. Chelsa 1.2 and WorldClim 2 are written as Chelsa and WorldClim in the table

Database	**Variable selection**	**Thr**	**PCC**	**Sen**	**Spe**	**TSS**	**MSE**	**Boyce internal**	**Boyce external**
WorldClim	WorldClim	0.69	0.76	0.6	0.92	0.52	0.24	0.59	0.62
Chelsa	Chelsa	0.4	0.81	0.82	0.8	0.62	0.19	0.61	NA
WorldClim	Chelsa	0.47	0.79	0.74	0.84	0.58	0.21	0.45	0.53
Chelsa	WorldClim	0.54	0.75	0.73	0.77	0.51	0.25	0.91	0.36

Thr: Threshold
Sen: Sensitivity
Spe: Specificity
PCC: Percent correctly classified
TSS: True skill statistic
MSE: Mean square error

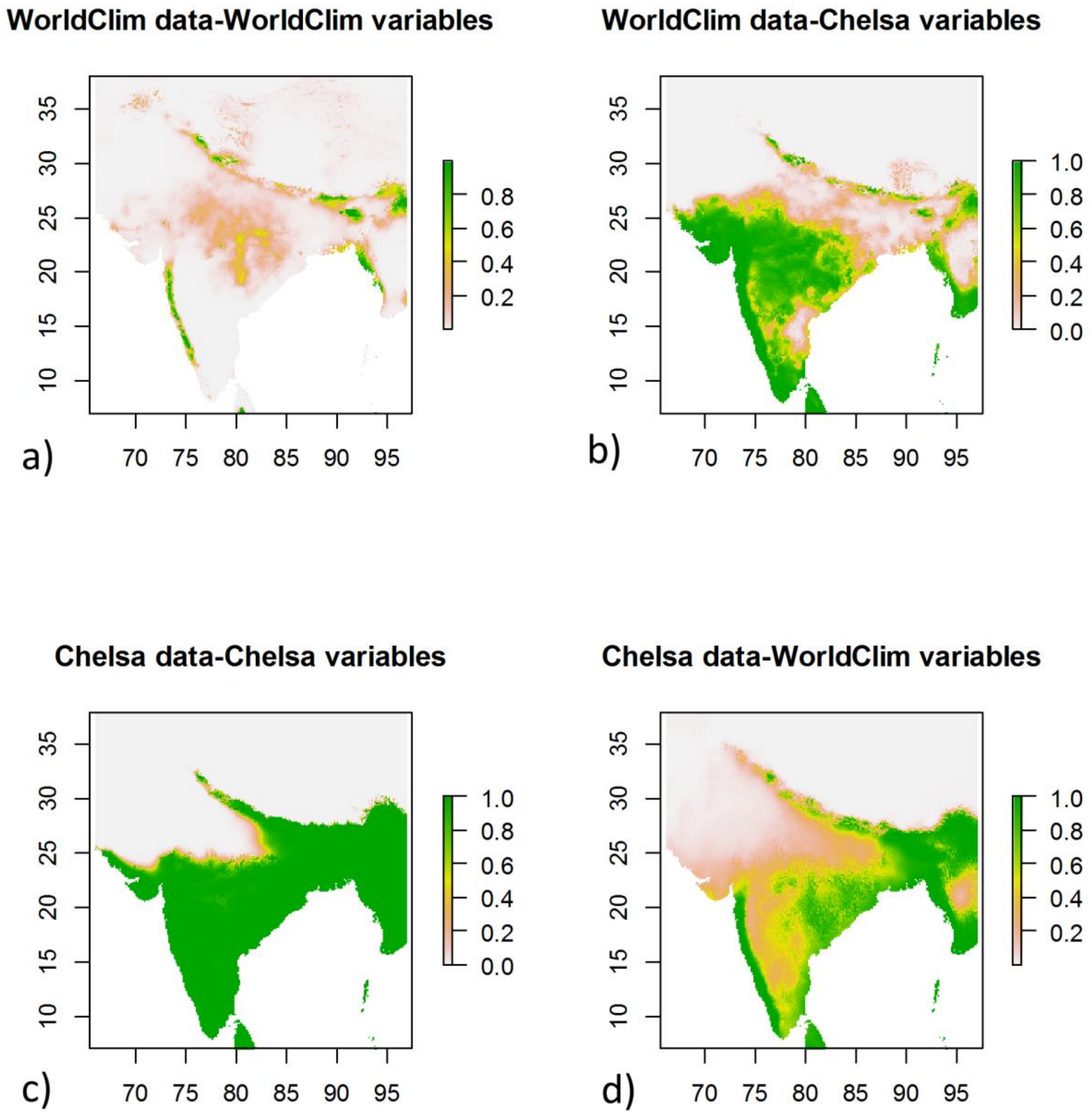

Figure 3.2 Maps showing the prediction of the distribution models of *Ageratina adenophora* in South Asia. Map (a) shows prediction using WorldClim data and variables selected for WorldClim; map (b) shows prediction using WorldClim data but variables selected for Chelsa; map (c) shows prediction using Chelsa data and variables selected for Chelsa while map (d) shows predictions using Chelsa data but variables selected for WorldClim.

Discussion

We found that the choice of the climatic dataset had a substantial effect on model transferability of species distribution models in the Himalayas. Although Chelsa 1.2 climatic data performed better than WorlClim 2 internally within the training region, model transfer accuracy was much better for WorldClim 2.

Most of the methodological studies on species distribution models have compared the effect of choosing different modelling algorithms on the predictive performance of SDMs (Randin *et al.* 2006; Heikkinen *et al.* 2012; Wenger & Olden 2012). Although the choice of predictor dataset can be consequential in terms of predictive performance of the models, it has not widely been discussed literature. By using two openly available bioclimatic datasets, we showed that the source of the predictor data could have a determining effect on the final output of SDMs.

Chelsea 1.2 climatic dataset is intended to perform well in mountainous areas because it corrects for orographic patterns of precipitation. Earlier studies based in the Himalayas and the Swiss Alps showed that the performance of Chelsa was superior to WorldClim. For example, Bobrowski & Udo 2017 found that Chelsa 1 dataset outperformed WorldClim 1.4 in predicting the distribution of tree line forming Himalayan birch in the Himalayas. Karger *et al.* (2017) also found marginally superior performance of Chelsa 1 dataset over WorldClim 1.4 in predicting the distribution of 67 species from Switzerland using 10-fold cross-validation technique.

However, our study yielded contradictory results, especially in terms of model transfer efficiency onto other regions. This difference could be due to the following reasons: 1) Earlier studies used older version of the two climatic databases. WorldClim has considerably updated their data in the latest version (WorldClim 2) by incorporating remotely sensed variables such as land surface temperature and cloud cover. This update might have significantly improved the quality of the data in contrast to previous versions. 2) Since Chelsa 1.2 data makes several corrections to account for orographic patterns, especially for precipitation data (Karger *et al.* 2017), these corrections might have changed the correlation structure among the variables at a local scale (Mesgaran *et al.* 2014). Therefore, when the models are projected onto a new region having different correlation structure among the variables, the transferability of the model might be compromised.

It is worth noting that the values of TSS were not very high for any of the models, indicating the possibility that climatic variables alone are not sufficient in explaining the distribution pattern of *Ageratina adenophora*. For example, empirical studies have shown that the species has a narrow pH range from slightly acidic to neutral (pH 5 to 7) and cannot tolerate highly saline condition (Lu *et al.* 2006). Moreover, biotic interactions and dispersal limitations are also crucial in determining plant distribution (Soberón & Nakamura 2009; Peterson *et al.* 2011). Therefore, the inclusion of such variables could help in improving the transferability of SDMs.

Although in this study, we found Chelsa 1.2 to perform better in terms of model transferability, it is premature to give generalized recommendations for preferring one dataset over the other. The species being studied, and the geographic area of the study may be equally important. We would instead recommend that the evaluation of climatic dataset should be performed routinely as an integral part of modelling exercise and the database with better predictive performance should be chosen.

Acknowledgement

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Chapter 4

Niche expansion of invasive *Ageratina adenophora* despite evolutionary constraints

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Abstract

Studies on niche dynamics of rapidly range expanding transcontinental invasive plants provide valuable insights into some of the fundamental ecological and evolutionary processes driving invasion. They further help us to assess the invasion potential of alien plants under current and future climatic conditions. Moreover, analysing the niche dynamics of an invasive species across multiple ranges allows us to explicitly test the hypothesis of niche conservatism. We used the invasive plant *Ageratina adenophora* (Asteraceae) as a model organism and performed a global niche overlap analysis between its native range (Mexico) and its different invasive ranges (Asia, USA, Canary Islands, and Australia), respectively. Being apomictic, its potential for rapid evolutionary changes is largely limited due to lack of sexual recombination. Therefore, we hypothesized that the occupied climatic niche of *Ageratina adenophora* should have remained largely conserved after invading new ranges. To this end, we carried out a Principal component analysis and quantified the pairwise niche overlap between native and invasive ranges. Additionally, we also estimated the amount of unfilled and expanded niche for all the pairwise comparisons between native and invasive ranges. Niche equivalency tests showed that niches in all invasive ranges differed from the native range. However, the degree of niche overlap differed considerably between different areas ranging from notably high overlap between Mexico and Asia to considerable niche shifts between Mexico and Australia. The occupied climatic niche in the invasive range in Australia was unique due to both its high amount of expanded and unfilled niches. The species also showed considerable niche expansion into colder areas of Asia. Drawing evidence from other empirical studies on *Ageratina adenophora*, we discuss that the observed changes in niche space are not due to evolutionary changes in the fundamental niche but due to changes in the occupied niche likely driven by biotic interactions, dispersal limitations and control efforts.

Introduction

Studying dynamics of rapidly expanding invasive species at a global scale can help to better understand fundamental eco-evolutionary processes (Broennimann *et al.* 2007; Warren *et al.* 2008) and further provide deeper insight about the invasion potential of alien species and their responses to climate change (Early & Sax 2014). For such assessments, the ecological niche is a fundamental concept. For instance, climatic conditions experienced by plants directly affect their physiology and therefore play a key role in determining their large-scale distributional patterns (Woodward & Williams 1987; Woodward *et al.* 2004). The multivariate space defined by multiple climatic variables, within which a species can occur according to its physiological tolerance corresponds closely to Hutchinson's concept of "fundamental niche" within which a species maintains positive growth rate (Hutchinson 1957; Soberón & Nakamura 2009; Peterson *et al.* 2011). As a consequence, species that can easily shift their niches are also likely to adjust better to new climatic conditions in contrast to those species with higher levels of niche conservatism. Niche dynamics can further be categorized into niche stability, niche expansion and niche unfilling. Niche stability refers to the proportion of exotic niche that intersects with the native niche. Niche expansion refers to the proportion the exotic niche that has not been occupied in the native range. Niche unfilling refers to the proportion of native niche that has not yet been occupied in the exotic range (Petitpierre *et al.* 2012a; Guisan *et al.* 2014).

Comparisons of the niche space of the native range with those of the invasive ranges are often used to assess the levels of niche conservatism in invasive species (Thuiller *et al.* 2005; Broennimann *et al.* 2007; Gallagher *et al.* 2010). The climatic niche of a species is said to be conserved if the climatic niches overlap highly between invasive and native ranges (Martinez *et al.* 2004; Wiens & Graham 2005; Broennimann *et al.* 2007; Petitpierre *et al.* 2012b). This assumption of niche conservatism is also one of the bases of transferring distribution modelling results of invasive species to new ranges. (Whitney & Gabler 2008; Mandle *et al.* 2010; Guisan *et al.* 2014). However, the validity of this crucial assumption of niche conservatism is not always scrutinized in a rigorous way prior to modelling the distribution (Goncalves *et al.* 2014; Guisan *et al.* 2014). Recent studies have indicated that the niche of the species in its exotic range may exhibit a shift from its native range (Broennimann *et al.* 2007; Early & Sax 2014).

Such niche shifts may be due to rapid evolutionary changes in response to the new environmental conditions of the exotic range (Broennimann *et al.* 2007; Alexander 2013).

However, such assessments are usually based on the niche estimated from distributional data which can be constrained by other factors such as biotic interactions or dispersal limitations. Therefore, this niche estimation is rather a realized subset of the fundamental niche (Pulliam 2000; Soberón 2007; Soberón & Nakamura 2009; Peterson *et al.* 2011). Thus, niche shifts could also be detected due to non-equilibrium situations, i.e., if the species has a large fundamental niche and occupies different subsets of this fundamental niche in its native and exotic ranges, respectively (Soberón & Townsend Peterson 2005, 2011). Additionally, changes in biotic interaction (Tingley *et al.* 2014) and dispersal limitations in the exotic range could also influence the realized niche space (Barve *et al.* 2011; Soberón & Townsend Peterson 2011). Consequently, the different reasons for observed niche shifts, evolutionary adaptation or utilizing different realizations of the larger fundamental niche, are usually hard to disentangle.

To overcome this shortcoming, we focused on *Ageratina adenophora* (Crofton weed), a trans-continental invasive plant with limited evolutionary potential. The evolutionary potential of *Ageratina adenophora* is largely limited due to the apomictic mode of reproduction and triploid genome (Baker 1965, 1974; Hao *et al.* 2010; Bala & Gupta 2014). Any change in the occupied climatic niche space could be attributed to reasons other than the evolution of the fundamental niche, such as epigenetic changes, biotic interactions, dispersal limitation etc. Using occurrence data from its native range (i.e., Mexico) and four invasive ranges (*viz*. Asia, Australia, USA, and Canary Islands), we ask whether the climatic niche of *Ageratina adenophora* has remained conserved? Or whether potential niche shifts have occurred after the invasion in different ranges?

Methods

About the species

The spread of invasive *Ageratina adenophora* (Crofton weed) is considered a severe problem in more than 30 countries in Asia, Africa, Oceania, Europe and North America (Qiang 1998; Parsons & Cuthbertson 2001; Muniappan *et al.* 2009; Heystek *et al.* 2011;

Del Guacchio 2013; Yu *et al.* 2016). It adversely affects native biodiversity (Ding *et al.* 2007), livestock (Parsons & Cuthbertson 2001; Tian *et al.* 2007), and agricultural productivity (Yadav & Tripathi 1982; Parsons & Cuthbertson 2001). Native to Mexico, this apomictic (Hao *et al.* 2010; Bala & Gupta 2014), triploid Asteraceae (Baker 1965; Bala & Gupta 2014) grows gregariously as subshrub in moist tropical and subtropical mountainous regions across the globe (Stone *et al.* 1992; Wang & Wang 2006; Wan *et al.* 2010; Yu *et al.* 2016). It was initially introduced as an ornamental plant in the 19th and 20th centuries in several countries such as Australia (Auld 1969), India (Bhatt et al. 2012) and South Africa (Kluge 1991) where it had naturalized and had spread rapidly to neighboring countries. Due to prolific production of wind-dispersed seeds (Auld 1970; Yadav & Tripathi 1982; Wang *et al.* 2011), vegetative reproduction (Parsons & Cuthbertson 2001) and strong allelopathic potential (Tripathi *et al.* 1981; Evans *et al.* 2011), *Ageratina adenophora* often dominates as dense monospecific strands (Lu *et al.* 2006) in the forest understory (Kunwar 2003; Niu *et al.* 2007b) and along steep mountain slopes (Kunwar 2003; Heystek *et al.* 2011).

Species occurrences and study areas:

The initial step in our analysis was to build a robust global database of occurrence dataset for *Ageratina adenophora*. For this purpose, we not only used well known global databases of species occurrence data but also used data collected from the field, contributed by regional field experts, and published in occurrence map. This was essential to overcome potential geographic bias in the global databases (Meyer *et al.* 2016). For example, we found that occurrence Australia and USA was well represented in Global Biodiversity Information Facility (GBIF), but countries such as China, Mexico, India were poorly represented. We used occurrence records from the species' native range in Mexico (Figure 4.1) well as the invasive ranges in Asia, Australia, USA and the Canary Islands. The "Asian range" comprised of the Himalayan range and southern China (since it forms a nearly contagious corridor of invasion). Occurrences from Western Himalaya were obtained from extensive field surveys carried out in the Indian provinces of Himachal Pradesh, and Uttarakhand (see Datta et al. 2017 for details on the methods). Occurrence data from central Himalaya (Nepal) and Eastern Himalaya were contributed by experts in the field of invasion biology (see acknowledgement section for the name of the experts). Occurrence data from the invasive range in China were georeferenced and retrieved from a published map with occurrence points by Wang and Wang (2006). Occurrence data for the alien ranges of Australia and the USA were retrieved from the Global Biodiversity Information Facility (GBIF) database (http://www.gbif.org, accessed on 9/11/2015). GBIF had only a few locations from native range (Mexico). Therefore we collected additional data from the World Biodiversity Information Network (REMIB) REMIB had occurrence data from only from native Mexican range. The REMIB database was accessed from http://www.conabio.gob.mx/remib/doctos/remib_esp.html, on 12/1/2016.

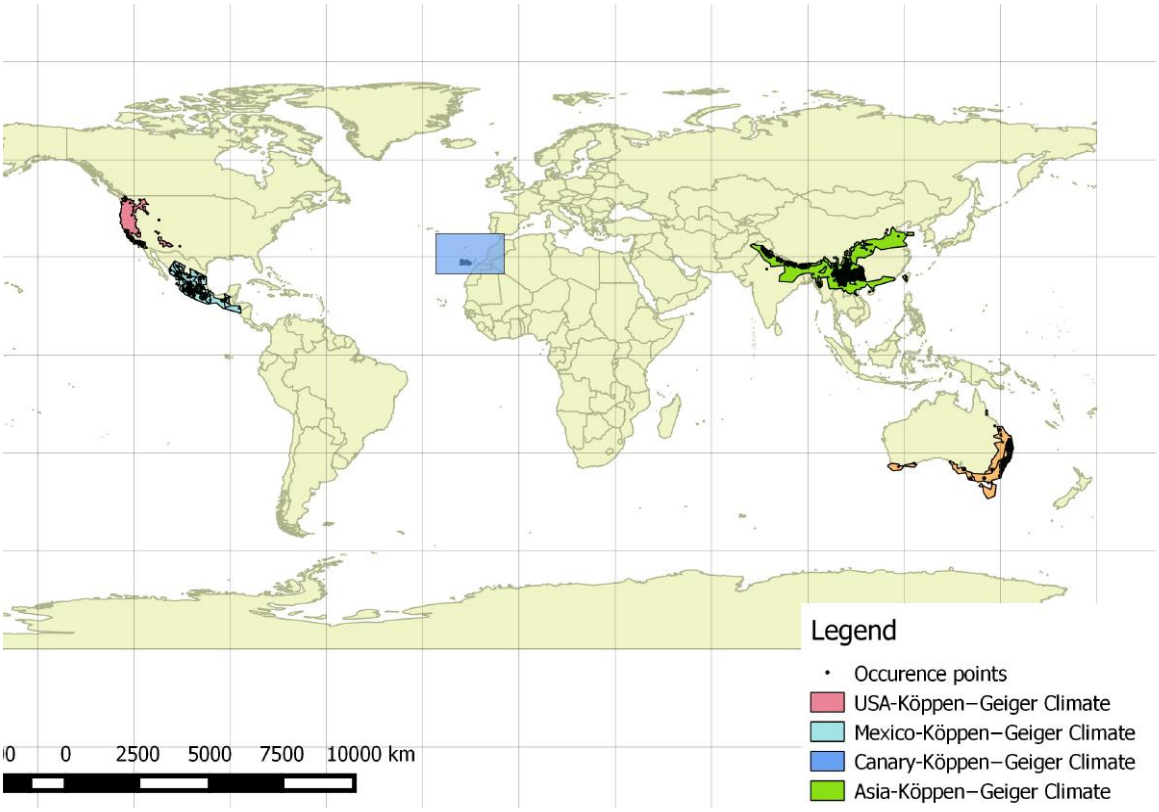

Figure 4.1. Map showing the location of occurrence data of *Ageratina adenophora* (black points) and in coloured polygons the climatic regions in native and invasive ranges that were considered to be potentially available (i.e., background climate) using Köppen-Geiger climate classification system. The blue rectangle shows the Canary islands.

We aggregated occurrence records to the resolution of the climatic raster (i.e., 2.5 arc minutes) to avoid pseudo-replication. Finally, we had the following number of occurrence points from each range: Mexico: 62; Asia: 313; Australia: 419, Canary Islands: 33 and USA: 53. All the occurrence records for the analysis can be found in the supplementary material.

Climatic data:

Bioclimatic variables derived from primary climatic data represent the relevant seasonal trends and physiological limits of the species (Nix 1986; O'Donnell & Ignizio 2012) and hence are useful in understanding and predicting species distributions (Lobo *et al.* 2010; Hodgins & Rieseberg 2011; Goncalves *et al.* 2014; Ramírez-Albores *et al.* 2016). We used all 19 bioclimatic variables (see Table 4.1) from WorldClim, version 1.4 (Hijmans *et al.* 2005) layers at 2.5 arc minutes resolution. n

Table 4.1 List of 19 bioclimatic variables from the WorldClim database (Hijmans *et al.* 2005) that were used for constructing the multivariate niche space.

Abbreviation	**Variable**
BIO1	Annual Mean Temperature
BIO2	Mean Diurnal Range
BIO3	Isothermality (BIO2/BIO7) (* 100)
BIO4	Temperature Seasonality
BIO5	Max Temperature of Warmest Month
BIO6	Min Temperature of Coldest Month
BIO7	Temperature Annual Range (BIO5-BIO6)
BIO8	Mean Temperature of Wettest Quarter
BIO9	Mean Temperature of Driest Quarter
BIO10	Mean Temperature of Warmest Quarter
BIO11	Mean Temperature of Coldest Quarter
BIO12	Annual Precipitation
BIO13	Precipitation of Wettest Month
BIO14	Precipitation of Driest Month
BIO15	Precipitation Seasonality
BIO16	Precipitation of Wettest Quarter
BIO17	Precipitation of Driest Quarter
BIO18	Precipitation of Warmest Quarter
BIO19	Precipitation of Coldest Quarter

Analytic framework:

Traditionally niche overlap metrics (such as "Schoener's *D*") have been used in ecological literature to measure resource partitioning at microhabitat scale between two related species (Schoener 2016). Warren et al. (2008) suggested that these metrics could also be used to measure niche overlap at macroecological scales using the output of niche models (i.e., the probability of occurrence). Later Broennimann et al. (2012) made significant methodological improvements by using smoothed occurrence density in gridded environmental space. They compared different niche modelling and ordination techniques and found that principal component analysis calibrated on the entire environmental space (referred as "PCA-env") of the two ranges was capable of estimating the simulated niche overlap most accurately. Defining the extent of the study area to be considered as available for the species within each range is crucial since the PCA-env is calibrated on the climatic data corresponding to the study area. Ideally, the extent should include the complete geographic distribution of the species in the given range (Guisan *et al.* 2014). It should not, however, be as large as an entire continent or the subcontinent of since climatic conditions could drastically change over very large spatial extents. In the absence of information about the complete distribution of the species, the extent of study area should be chosen objectively based on ecological relevance such as biome classification schemes or climate classification schemes (Guisan *et al.* 2014). Since climate is one of the most dominating factors shaping the distribution of terrestrial plants (Woodward & Williams 1987; Woodward *et al.* 2004), we used the Köppen-Geiger climatic classification scheme (Kottek *et al.* 2006) for sub-setting the available or background environment. For a given range, all those Köppen-Geiger climatic zones where the species was found were considered to be potentially suitable for the species (see Figure 4.1.). Bioclimatic variables corresponding to the Köppen-Geiger climatic zones were used for the subsequent analysis. We used QGIS (QGIS 2015) and 'raster'(Hijmans 2015) package in R (R Core Team 2017) for extracting values from raster layers. The following step describes the details of our analysis:

(i) PCA-env was performed by calibrating a PCA on the pooled available climatic conditions (19 bioclimatic variables, described in Table 1) of all the ranges. In order to account for the bias due to the geographic difference in range sizes, an additional weight (w) was used for each range in the PCA analysis (w = 1- fraction of pooled range). This ensured that large ranges were weighed down and did not have a disproportionately large effect on the analysis. Weighted PCA was performed using "ade4"(Dray *et al.* 2007) in R.

(ii) Predicted scores from the 1st and 2nd axis of PCA-env were used to set two-dimensional "global PCA space." The global PCA space was then gridded by dividing it into 100×100 cells of equal size wherein each cell represented a unique set of climatic conditions defined by the combination of the 19 bioclimatic variables (Broennimann *et al.* 2012).

(iii) The density of occurrence, as well as the density of environmental pixels for each cell in the global PCA space, was subjected to a nonparametric smoothing procedure using Gaussian Kernel density function with Silverman's bandwidth as the smoothing parameter (Silverman 1986). Smoothing was performed because occurrence data obtained from databases such as GBIF are sometimes incomplete (Beck *et al.* 2014; Meyer *et al.* 2016) , resulting in potential gaps in occurrence density in the PCA space which in turn leads to underestimation or bias in niche overlap (Broennimann *et al.* 2012; Guisan *et al.* 2014). The occurrence densities were standardized for comparison across different ranges so that they ranged between 0 and 1 (i.e. rescaled by dividing it by the maximum value).

(iv) The extent of niche overlap was calculated using Schoener'*D* (Schoener 1968; Warren *et al.* 2008):

$$\mathrm{D} = 1 - \frac{1}{2}\left(\sum |\, z_{1ij} - z_{2ij} \,|\right)$$

where, z_{1ij} and z_{2ij} are the occurrence densities (0 to 1) of *Ageratina adenophora* in the *i*th and *j*th bin of the two-dimensional gridded global PCA space in range 1 and 2, respectively. The value of *D* ranges between 1 and 0, indicating complete overlap and no overlap, respectively. Summing the differences in occurrence density between two ranges, i.e. $\sum |\, z_{1ij} - z_{2ij} \,|$) allows us to make a direct (cell to cell) assessment of niche overlap between both ranges. This index is much more sensitive in detecting finer changes in occurrence density within the niche space compared with estimating niche overlap from centroid shift or overlap from minimum convex hulls (Broennimann *et al.* 2012; Guisan *et al.* 2014). It is worth mentioning that Broennimann et al. (2012) corrected the occurrence density of the species for the relative availability of environmental conditions in the global PCA space by dividing the occurrence density in a cell by density of available environment in that cell. However, in our case, we found that this correction led to unreliable changes in the observed pattern of occurrence density, hence we did not apply this correction (see Appendix 1 for further details).

(v) To statistically test our hypothesis of niche conservatism in *Ageratina adenophora*, we carried out a niche equivalency test. It explicitly tests whether the observed niche overlap is better than at random. This test is based on randomization with 100 permutations. For each permutation, the species occurrences from both the ranges are pooled together and then randomly reallocated into two halves and the overlap index

(D) is calculated for each iteration. This results in a distribution of simulated overlap values which is then used to test any evidence of niche shift (introduced by Warren et al. 2008, and later implemented by Broennimann et al. 2012). If the observed value of niche shift is significantly lower than the random simulated distribution, it indicates that the niches are not equivalent. We also calculated 95% confidence intervals for the overlap index (D) using a resampling procedure with 100 iterations. Ten percent of the occurrence points were randomly dropped, and the niche overlap was recalculated in each iteration.

(vi) Furthermore, a set of three niche dynamic indices *viz*. "niche stability," "niche expansion," and "niche unfilling" (Petitpierre *et al.* 2012a; Guisan *et al.* 2014) were calculated to obtain a holistic picture of the niche dynamics beyond the overlapping regions. Calculations were performed using 'ecospat' package (Cola *et al.* 2017). It has been suggested that for meaningful interpretation of niche dynamics, the analysis should be based on the shared climatic envelope (i.e. analogue climate) between the two ranges being considered (Fitzpatrick & Hargrove 2009; Guisan *et al.* 2014). Therefore, we primarily focused on the analogous climatic space. However, we also calculated the metrics for non-analogous parts in order to check if the species has expanded into non-analogous climatic space.

Results

The 1st and 2nd axis of the PCA of the 19 bioclimatic variables explained 37.8% and 20.4% of the variance, respectively (Figure 4.2). The 1st axis of the PCA can be interpreted as the thermal axis as it has high loadings of variables such as mean annual temperature (bio1), mean temperature of the coldest quarter (bio11), and minimum temperature of the coldest month (bio 6). The 2nd axis is explained by precipitation-related variables such as precipitation of driest quarter (bio17), precipitation of driest month (bio14) and annual precipitation (bio12).

Schoener's D revealed very low to moderate levels of overlap between native and invasive ranges (Table 2, Fig 4.2). We, however, did not find evidence for a completely dislocated niche (i.e., D = 0) in any of the pairwise comparisons. Schoener's D value was highest between Mexico and Asia followed by Mexico and the Canary Islands (Table 2).

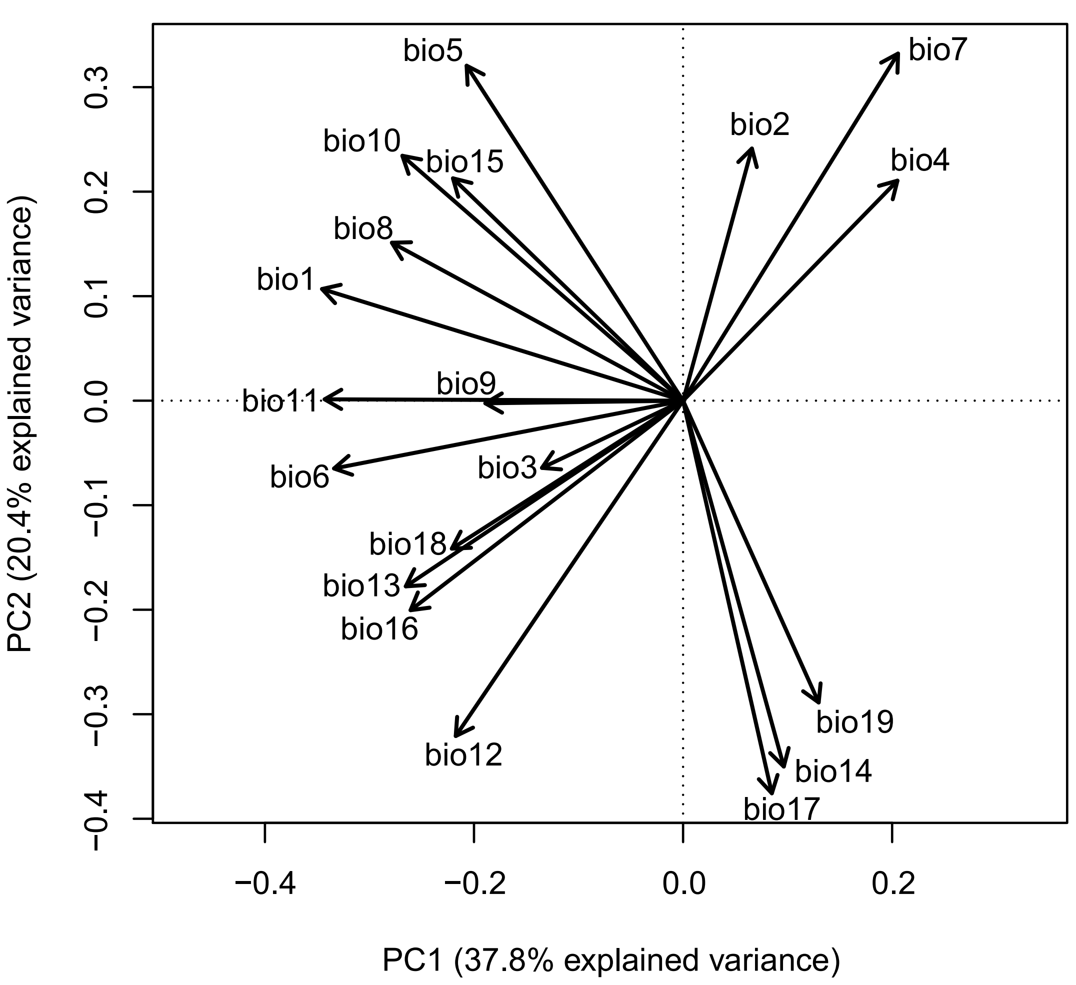

Figure 4.2. PCA plot of 19 bioclimatic variables used to determine niche overlap and dynamics of *Ageratina adenophora*. The 1st axis is mainly represented by temperature-related variables while the 2nd axis is represented by precipitation-related variables.

On the contrary, the Australian niche showed a very low degree of overlap with the native Mexican range and with most other invasive ranges. 95% confidence intervals for Schoener's *D* were very narrow for all the pairwise comparisons (Table 2). Results of the one-tailed niche equivalency test showed that the observed value of niche overlap was always significantly lower than the random niche overlap ($p<0.001$), indicating lack of niche equivalency (Table 4.2).

Niche dynamic indices indicated a moderate degree of niche expansion in the Asian range although considerable niche stability was detected (Figure 4.3b, Table 4.3a). Furthermore, in Asia, the species occupies the largest area in the PCA space (Figure

4.3b) which signifies the wide range of climatic conditions experienced by the species in Asia. In its invasive range of USA, we also found large degree of stability and a moderate degree of niche overlap and unfilling (Figure 4.3c, Table 4.3a). The niche of the Canary Island is almost a subset of the native Mexican niche. The Australian niche (Figure 4.3e) is unique because of a high degree of unstable niches (i.e., both expanded and unfilled niches, Table 3) and is concurrent with a very low value of Schoener's *D* (Table 4.3). The separation of the Australian niche from the Mexican niche is largely on the 2nd axis of the PCA, which is predominantly driven by precipitation related variables. Including non-analogous climatic space in the analysis affected the values of unfilled niches in the USA and the Canary Islands only, but the values of niche expansion were hardly affected (Table 4.3b).

Table 4.2 Pairwise niche overlap indices (Schoner's D) of *Ageratina.adenophora* between native and invasive ranges. 95% CI were generated by bootstrapping. p-values for niche equivalency tests are based on 100 permutations

Pair wise ranges	**Overlap index (D)**	**95% CI**		**p**
Mexico-Asia	0.4285	0.4251	0.432	<0.001
Mexico-USA	0.2367	0.2337	0.2396	<0.001
Mexico-Australia	0.0883	0.0859	0.0908	<0.001
Mexico-Canary Islands	0.3407	0.3367	0.3448	<0.001

Finally, we also pooled the global niche of *Ageratina adenophora* and compared it with the native Mexican niche to obtain a global picture of the invasion dynamics. Interestingly the native niche is almost entirely a subset of the global invasive niche (Figure 4.3f). But large amounts of niche expansion within the analogous climate indicates that *Ageratina adenophora* has not occupied all suitable climatic regions in the native range (Figure 4.3f) while lack of unfilled niches shows that the native niche space has been entirely occupied in the invasive ranges.

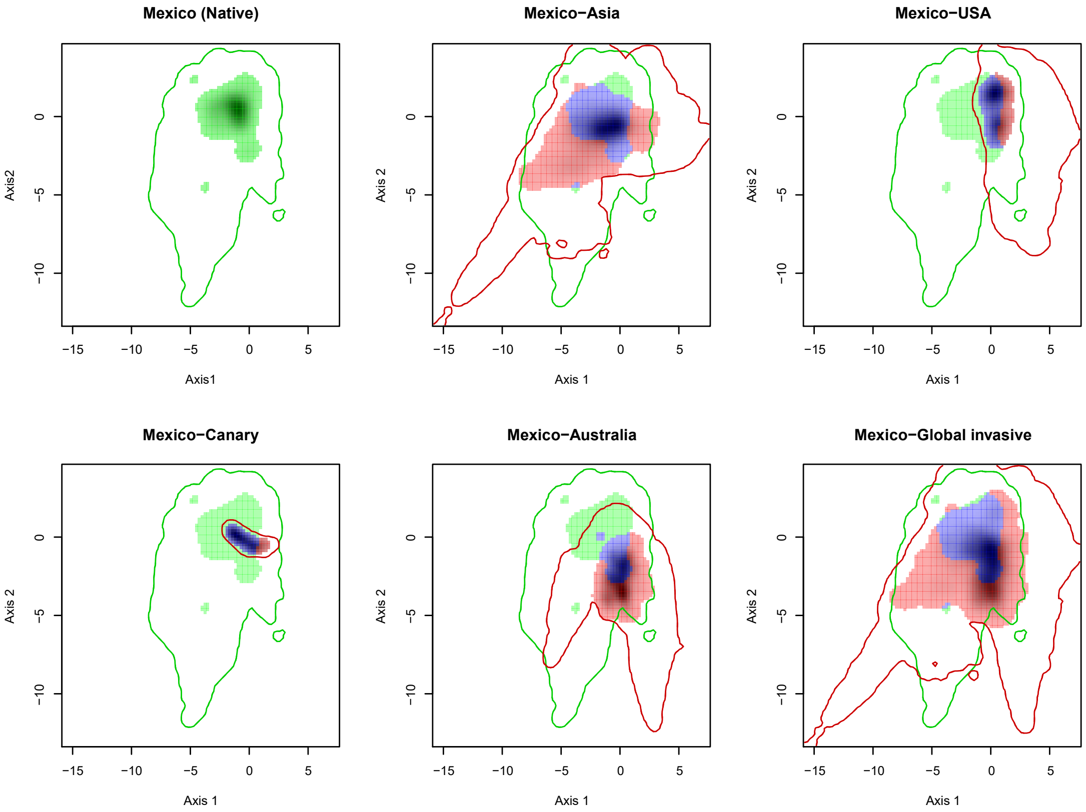

Figure 4.3. Visualization of native niche space in Mexico (a) and niche dynamics in the invasive ranges of Asia (b), the USA (c), the Canary Islands (d), Australia and the pooled global invasive range (f) of *Ageratina adenophora* in PCA space. The 1st axis of the PCA represents temperature-related variables while the 2nd axis is largely explained by precipitation-related variables. Unfilled, stable and expanded niches are represented by green, blue and red shades, respectively. The grey shading shows the smoothed occurrence density in the native range in figure (a) and invasive range in rest of the panel plots (b-f). The bold line marks the available environment in each range (green native, red invasive). Values of niche overlap indices were calculated separately for the analogous climatic conditions and entire environmental conditions in both the ranges (Table 3a and Table 3b).

Discussion

Our analysis revealed that the native occupied climatic niche of *Ageratina adenophora* has not remained entirely conserved in the invasive ranges of Asia, USA, and Australia. Niche unstability was most pronounced in Australia with large degree of expansion and unfilling.

Several studies have already documented niche shifts after invasion (Broennimann *et al.* 2007; Gallagher *et al.* 2010), however very few have attempted to explain the difference between real niche shift caused by the evolution of the fundamental niche and niche shift detected due to other factors such as biotic interactions and dispersal limitations (Tingley *et al.* 2014). In our study, we can neglect evolutionary aspects because reproductive attributes of our study species. Due to lack of sexual reproduction and the triploid genome of *Ageratina adenophora* (Baker 1974; Lu *et al.* 2008; Bala & Gupta 2014), it is less likely that the observed differences in the climatic niches of *Ageratina adenophora* in the different regions across the globe are consequences of evolutionary changes in the fundamental niche. Experimental studies on *Ageratina adenophora* have indicated the absence of local adaptation in China (Zhao *et al.* 2012). Although some genetic diversity exists in different lineages (Gui *et al.* 2008), it has apparently not lead to the selection of locally adapted genotypes (Zhao *et al.* 2012; Datta *et al.* 2017). In principle, accumulation of mutations can also lead to genetic diversity and adaptive evolution, but it is unlikely to occur within a relatively short time span since introduction in 19th and 20th century (Kunwar 2003; Feng *et al.* 2011; Bhatt *et al.* 2012).

Table 4.3 Niche dynamic indices calculated of *Ageratina adenophora*, using global distributions between (a) the analogous climates of invasive and native niche and (b) entire available environment, i.e. by including non-analogous climate as well.

(a) **Analogous climate**	**Expanded niche**	**Stable niche**	**Unfilled niche**
Mexico-Asia	0.322	0.678	0.059
Mexico-USA	0.299	0.701	0.383
Mexico-Canary Islands	0.141	0.859	0.257
Mexico-Australia	0.587	0.413	0.735
Mexico-Global invasive	0.465	0.534	0.01

(b) **Entire climate**	**Expanded niche**	**Stable niche**	**Unfilled niche**
Mexico-Asia	0.325	0.675	0.059
Mexico-USA	0.299	0.701	0.668
Mexico-Canary Islands	0.141	0.859	0.655
Mexico-Australia	0.592	0.408	0.771
Mexico-Global invasive	0.46	0.539	0.01

The niche of *Ageratina adenophora* is restricted to relatively arid conditions (towards upper direction along 2nd PCA axis, see Figure 4.3f.) in the native as well as the invasive ranges, indicating that moisture requirement is crucial for the plant. Germination experiments in China have clearly indicated susceptibility of seed germination to drought stress (Lu *et al.* 2006).

Despite the limitations on the evolutionary potential of *Ageratina adenophora*, we found a considerable amount of niche expansion as well as niche unfilling in the invasive ranges of Australia and Asia indicating the presence of suitable climatic areas that have not been occupied in both the native and invasive ranges. We thus think that the observed changes in the niche space are due to non-equilibrium situations in native as well as invasive ranges. Comparison of native Mexican vs global invasive revealed a considerable amount of unoccupied niche in native Mexican range. High amount of unoccupied niche in the native range may be explained by the presence of natural enemies such as insect herbivores and pathogen (see natural enemy hypothesis: Maron and Vilà 2001). For example, a gall-inducing fly (*Procecidochares utilis*) occurring in native Mexican range causes shoot gall in *Ageratina adenophora* (Muniappan *et al.* 2009; Heystek *et al.* 2011). Similarly, pathogenic fungi such as leaf spot fungus (*Cercospora eupatorii*) and rust causing fungi (*Baeodromus eupatorii*) have been found in Mexico (Dodd 1961; Heystek *et al.* 2011). On the contrary, the absence of natural enemies in the invasive ranges might have facilitated the observed niche expansion and in turn the spread of *Ageratina adenophora.* Moreover, germination of *Ageratina adenophora* is sensitive to pH and salinity (Lu *et al.* 2006). Hence climatically suitable regions having inappropriate edaphic conditions may not allow the growth and spread of *Ageratina adenophora* (Lu *et al.* 2006). The existence of large unfilled niches in Australia despite the availability of suitable climatic conditions (Fig 3e) may be explained by dispersal limitation or effective control measures on the spread of *Ageratina adenophora* at an early stage by biological, mechanical, and chemical measures (Dodd 1961; Auld 1972; Auld & Martin 1975).

The plant has also invaded much colder niches in Asia (towards left along the 1st axis of PCA, see Fig 2.). This can be related to a study carried out in China (Xie *et al.* 2015) that has clearly demonstrated the importance of epigenetic control in regulating cold tolerance in different populations of *Ageratina adenophora*. Xie et al. (2015) found a significant correlation between freezing tolerance and number of methylated sites that controlled the expression of downstream genes conferring cold tolerance in *Ageratina adenophora*. Furthermore, they also found populations from colder regions (northern populations) to be more cold tolerant than populations from warmer regions of China (southern populations) due to epigenetic changes. Therefore, despite the constraints on evolution in *Ageratina adenophora*, epigenetic mechanisms might play a key role in rapid adaptation to new environmental conditions.

Our study also highlights a potential pitfall in inferring the distribution of an invasive species using its native range alone, since the fundamental niche of the species is much larger than the realized niche in the native range. For instance, Papes & Peterson 2003, predicted the distribution of *Ageratina adenophora* in China using a model trained on occurrence data from native Mexican range. Our analysis, however, shows that *Ageratina adenophora* has expanded its realized niche in Asia beyond its native niche and therefore the earlier predictions might not be realistic. Therefore, it is advisable to use the pooled occurrence data from native as well as all the invasive ranges in order to get closer to the fundamental niche for species with reduced evolutionary potential. Similarly, while conducting risk assessment studies under future climatic scenarios, caution should be taken to interpret the results by extrapolating the niche models to regions having analogous climate only.

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Appendix 4 (for Chapter 4)

Justification for not using occupancy

It has been suggested by Broennimann et al. (2012) that the niche overlap analysis should be performed on the corrected occurrence density, i.e. “occupancy” of the species in relation to the available background environment. Occupancy was calculated by dividing the occurrence density by density of available background environment and then rescaling it.

We visually compared the plots after the correction was performed and found that this correction may at times lead to inversion of true occurrence patterns. One extreme form of this was observed in the Asian range (Figure 4.3). Therefore, in order to avoid any potential bias or errors in the estimation of niche overlap (i.e. Schoener’s *D*), we used the uncorrected occurrence density rather than corrected occurrence density.

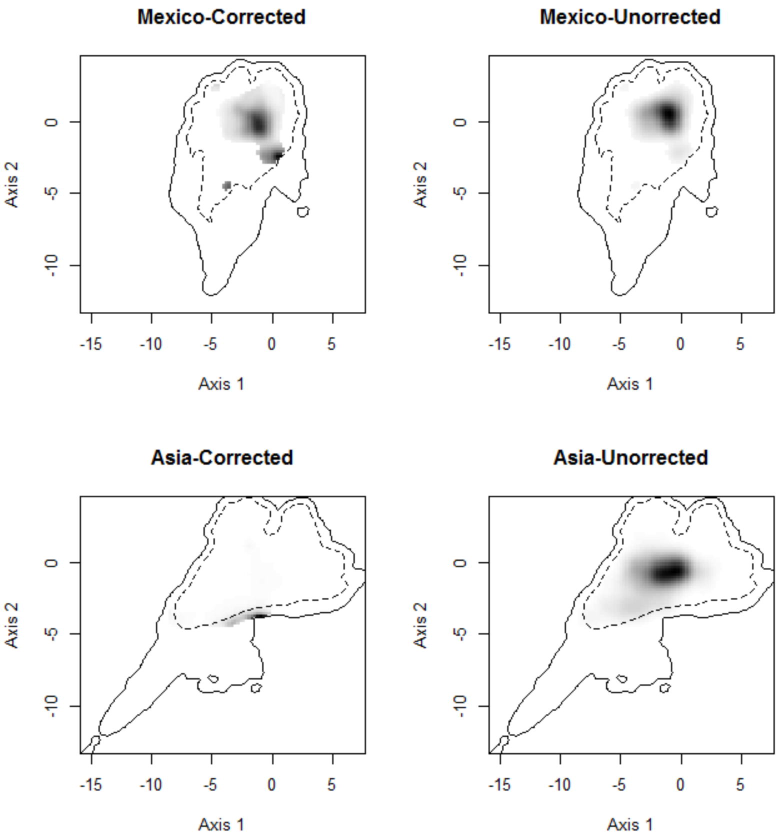

Figure 4.4 Plots visualizing the effect of correcting occurrence density by environmental availability for *Ageratina adenophora* in native range of Mexico and invasive range in Asia.

Chapter 5

General discussion

Key findings

Experimental and macroecological studies can complement each other to improve the overall understanding of a given study system, especially when different spatial scales are considered. The main theme of the thesis revolves around different processes and patterns associated with the niche of invasive *Ageratina adenophora* across spatial scales using both experimental as well macroecological approaches. Some of the main findings of the thesis are as follows:

At the local scale, I studied the role of evolutionary processes with an emphasis on different lifecycle stages along an elevational gradient in Western Himalaya (Chapter 2, Datta *et al.* 2017). I found no evidence for rapid evolutionary changes in the form of local adaptation or clinal differentiation. However, I found a strong plastic response in most of the traits analysed. Additionally, I found that germination was crucial at the lower elevations while overwintering response was decisive in upper elevations.

At the regional scale, I analysed the distribution pattern of *Ageratina adenophora* along a broad elevational gradient in the entire Western Himalaya using presence-absence data. I found a unimodal pattern of distribution along elevation with optimal elevation at ca.1300m (Chapter 2, Datta *et al.* 2017).

At subcontinental scale (Chapter 3), I investigated the effect of the source of input dataset of the same topical variables (bioclimatic variables) provided by Chelsa 1.2 and WorldClim 2, respectively, on the performance of distribution models of *Ageratina adenophora* with focus on model transferability in the Himalayas. While it was previously known that modelling algorithm affects interpolation accuracy and transferability (Heikkinen *et al.* 2012), I found that also the choice of the dataset affected the transferability of the SDMs. In this study, SDMs developed using Chelsa 1.2 data as predictors performed better in terms of interpolation accuracy, but SDMs that used WorldClim 2 data outperformed those of Chelsa 1.2 in terms of model transferability.

In the 4th chapter of the thesis, I explored the global niche dynamics of *Ageratina adenophora*. The results indicate that the native Mexican niche of *Ageratina* *adenophora* has not remained conserved in the invasive ranges of Australia, USA, and Asia. Niche shift was most pronounced in Australia with a large degree of expansion. In the following sections, I discuss the relevance of my work in the light of other studies and outline future research prospects.

Relevance

In order to develop a deeper understanding of eco-evolutionary patterns and processes driving the success of invasive plants, manipulative field experiments are often necessary. Reciprocal transplant experiments are effective techniques in the toolbox of ecologists and evolutionary biologists seeking to understand genetic adaptation and range limits of organisms along environmental gradients. My experimental gardens were distributed across a broad elevational gradient (ca. 1500m). This allowed me to the test hypothesis of rapid evolutionary changes in response to strong selection pressures.

The experiment showed that the success of different lifecycle stages is crucial in different environmental conditions and plays a pivotal role in shaping the overall pattern of distribution along an environmental gradient. Although this seems to be all too obvious, very few experiments have explicitly tested it. In my study, I did not only measure reproductive output, which is a common measure of a plant's fitness but also emphasized on the success of different stages in the life cycle of the plant and assessed their respective roles in imparting fitness advantage (Chapter 2: Datta *et al.* 2017). I focused on a suite of different life cycle stages that covered germination success, phenology, vegetative growth, reproductive output, and overwintering success of plants grown in different common gardens along the elevational gradient.

Instances of reciprocal transplant experiments from very remote areas such as the Himalayas are rather rare in literature. For example, Klimeš & Doležal, 2010 conducted a transplant experiment on native Himalayan plants in very high elevations to determine the upper elevational range limit of vascular plants. However, their experiment did not use a completely crossed reciprocal transplant design. Therefore, by carrying out completely crossed reciprocal transplant experiment (Chapter 2: Datta *et al.* 2017) this study has set a precedent in the Himalayas in particular, especially in the context of invasive plants.

The observed humped shaped distribution pattern of *Ageratina adenophora* (Chapter 2: Datta *et al.* 2017) can be explained by the insights gained from its life cycle pattern at different experimental gardens. The optimal elevation for *Ageratina adenophora* (ca.1300m) is perhaps jointly determined by the suitability of temperature as well as moisture requirements (Lu *et al.* 2006) that allow the plant species to maintain high positive growth rate (see Figure 1). Conditions at low elevations are too warm and dry so that germinating seeds desiccate (Lu *et al.* 2006; Datta *et al.* 2017) while winter temperatures at elevations beyond 2300m are too harsh for the plant to overwinter and maintain viable population size (Chapter 2: Datta *et al.* 2017).

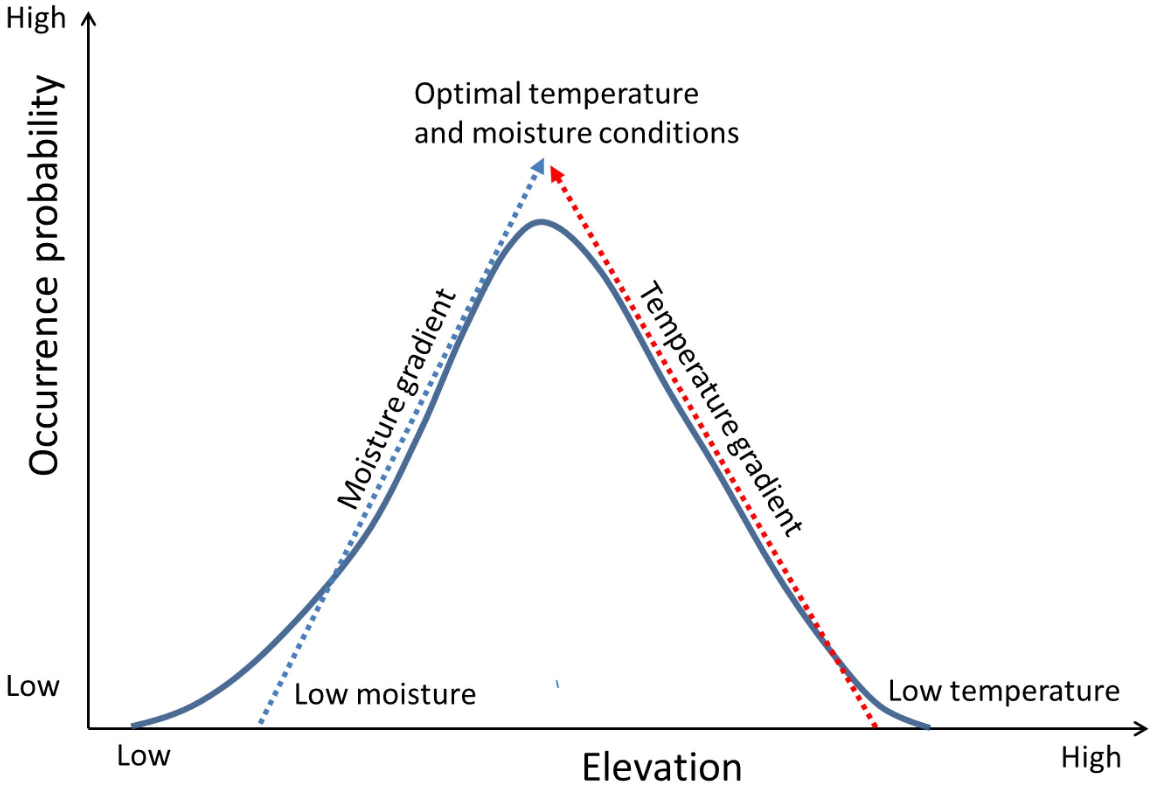

Figure 5.1 Graphical representation showing the importance of moisture and temperature gradient in shaping the distribution pattern of *Ageratina adenophora* along the elevational gradient based on the insights from the multiple common garden experiments.

The absence of local adaptation in *Ageratina adenophora* is in agreement with another similar study carried out in Yunan province of China (Zhao *et al.* 2012). Previous studies have demonstrated that populations of *Ageratina adenophora* exhibit a high degree of phenotypic plasticity (Zhou *et al.* 2009; Zhao *et al.* 2012). Similarly, in my study, I found most of the traits to be phenotypically plastic. Therefore, phenotypic plasticity appears to play a crucial role in ensuring broad environmental tolerance despite lack of any evolutionary adaptation. Moreover, preadaptation to a broad range of environmental conditions in the native Mexican range might explain its broad environmental tolerance along the elevational gradient (van Kleunen *et al.* 2011).

A study in China has indicated that different populations of *Ageratina adenophora* differ in the degree of cold tolerance. This finding has been supported by another study from China that has found evidence for epigenetic changes that confer cold tolerance to *Ageratina adenophora* populations growing in colder regions (Xie *et al.* 2015). Such epigenetic changes may not be stable from an evolutionary perspective but might play an important role in explaining broad environmental tolerance and rapid range expansion of *Ageratina adenophora* in colder regions (Xie *et al.* 2015).

Transient population dynamics might play an important role in maintaining fringe populations at the extremes of the climatic gradient (Seipel *et al.* 2016) rather than local adaptation. The mid elevational populations might act as source populations, and the fringe populations might be sink populations with small population size and high population turnover. Hence, the fringe populations at the extremes of the range possibly experience local extinctions and colonization events facilitated by dispersal pathways like animals, roadways, and river (Seipel *et al.* 2016). Specific microhabitat conditions and source-sink dynamics might help to explain the existence of small fringe populations of *Ageratina adenophora* in the uppermost and lowermost end of the distribution although common garden experiments found that these sites were not suitable for completing the crucial lifecycle stages (Figure 1).

Results from all chapters in this thesis can be interpreted in the light of niche theory (Peterson *et al.* 2011). The outcome of the experimental study can be directly related to the fundamental climatic niche of *Ageratina adenophora* along elevational gradient, which is determined by the physiological tolerance range within which *Ageratina adenophora* can maintain positive growth rate. The 3rd and 4th chapter of the thesis deal with estimating the climatic niche based on plant occurrence data. This type of niche, however, does not correspond to the fundamental niche but rather to the realized niche due to the presence of biotic interactions and dispersal limitations (Peterson *et al.* 2011). Thus, niche theory emerges as a cross-cutting theme across all the studies included in this thesis.

Most of the evolutionary studies on invasive plants have focused on plant species reproducing sexually (example: Maron *et al.* 2004; Colautti & Barrett 2013; Kim & Donohue 2013). Therefore, the knowledge about rapid evolutionary changes in apomictic or vegetatively reproducing species is rather limited. This is particularly interesting because obligate apomicts do not undergo sexual recombination and therefore the genetic diversity of such apomictic populations remains relatively constant. Therefore, it can be expected that the possibilities of natural selection and other evolutionary changes are greatly reduced. However, enough genetic diversity might already exist in different apomictic lineages which in turn might undergo selection. In fact, studies have indicated the presence of genetic diversity within the Chinese populations of *Ageratina adenophora* (Gui *et al.* 2008, 2009). By choosing a species that does not reproduce asexually, I investigated the scarce possibility of evolutionary changes that might occur due to reasons such as accumulation of mutations and accidental sexual reproduction.

Species distribution models are usually evaluated internally (i.e., using training and calibration range of the input data). However, in order to be able to predict invasion in space or time, evaluating the transferability of the model beyond the training range is crucial. Independent sets of data from a different region are rarely used to check model transferability. In order to address this issue, I used an independently collected set of presence only from central and eastern Himalaya to evaluate the model trained in Western Himalayas. In the past, emphasis has been laid on the choice of the most appropriate modelling algorithm on the output of species distribution models. However, the potential effect of climatic datasets has been rarely assessed (Marmion *et al.* 2009; Heikkinen *et al.* 2012). The 3rd chapter of the thesis explicitly focuses on the effect of climatic databases (WorldClim 2 and Chelsa 1.2) on the predictive performance of SDMs at a subcontinental scale. The results indicate that the choice of the climatic database should not be based on subjective decisions but should rather be based on sound evaluation of different options available for a given region and species. In Chapter 4, I calibrated a global niche space based on the pooled climatic data from all the five ranges. This allowed me to make simultaneous pairwise comparisons between several ranges in the same global PCA environmental space and gain insights about the direction of shift in each range. This is in contrast to previous studies where different PCA were performed for each pairwise comparison (Goncalves *et al.* 2014).

As discussed previously, obligate apomicts are less likely to undergo rapid evolutionary changes in the fundamental niche space. Therefore, by focusing on an apomictic species in the niche overlap analysis, I could at least partly control the possible role of rapid evolutionary changes in niche dynamics.

Caveats and future directions

Common gardens should ideally mimic the conditions of the natural habitat from where the populations are sampled. In order to mimic most of the abiotic and biotic conditions, the common gardens should be located in the natural habitats or in close vicinity to the natural habitats so that the microclimatic conditions are also accounted for (Kawecki & Ebert 2004). However, this is often impossible due to practical reasons. For example, some of the populations in my study were sampled from relatively inaccessible locations such as riversides, forest understory, and rocky slopes. Hence, it was not possible to establish large common garden experiments in such locations and replicate the exact microclimatic conditions. Therefore, we were not able to test the effect of site-specific microclimatic conditions and biotic factors on the rapid evolution of *Ageratina adenophora*. However, the main focus was to establish the common gardens in matching elevational zone so that the macroclimatic conditions are similar to that of the natural populations. This approach allowed us to test for the effect of environmental factors that change with elevation but not small-scale microclimatic differences in the habitat.

Our experimental study focused only on populations originating from a small region in the Western Himalayas. However, the plant has a much broader distribution not only across the Himalayas but also in mountains of south India. In fact, herbarium specimens have indicated the possibility of separate introduction event in Nilgiri hills of south India (unpublished work based on oldest herbarium specimens at Central national herbarium of Botanical survey of India). It would, therefore, be interesting to investigate any possibility of evolutionary and genetic changes at subcontinental scale. The 3rd and 4th chapters of the thesis focus on regional and large-scale distribution of *Ageratina adenophora* using coarse interpolated bioclimatic rasters. These databases (namely BioClim 2 and Chelsa 1.2) are commonly used in macroecology due to the paucity of high-density weather stations across the globe. However, the quality of data from such interpolated databases is dependent on the quality of ground data available from weather stations, the method used for interpolation, and resolution of the raster layers. Also, the quality of biotic data is crucial. In the 4th chapter, I relied partly on occurrence data available from secondary sources such as Global Biodiversity Information Facility (GBIF) for the global niche shift analysis. Although such databases have been widely used in for macroecological analysis, species occurrences may not cover the complete and current distribution of the species. This is especially true for rapidly range expanding invasive species like *Ageratina adenophora* (Wang & Wang 2006). Therefore, it may be necessary to repeat such studies when better quality occurrence and climatic dataset become available.

Methodologically, the issue of modelling the distribution of species that are constantly expanding its range is a particularly challenging problem as it may violate the assumption of equilibrium of the species with its environment (Elith *et al.* 2010; Hattab *et al.* 2017). SDMs generally rely on presence and absence data to estimate the probability of occurrence of a species. But the absence of a species from a location does not only imply unsuitable environmental conditions but could also be due to dispersal limitations. Thus, the inability to distinguish these two types of absences in the modelling procedure may lead to difficulties in interpreting the output of SDMs for applied purposes. Recently a method has been developed to specifically address this issue by distinguishing these two types of absences using an index for calculating the probability of real absences due to unsuitable environmental conditions (Hattab *et al.* 2017). This index relies on the assumption that absences that are far away from observed presences in geographical space but very close in environmental space are likely due to dispersal limitation rather than environmental conditions (Hattab *et al.* 2017). The use of a similar modelling strategy for rapidly expanding *Ageratina adenophora* populations (Wang & Wang 2006) could help us to identify those areas that have not been invaded due to dispersal limitations at present but could be potentially invaded in future due to the availability of suitable climatic conditions.

The statistical tools available for evaluating niche overlap are rapidly developing, and the choice of the most appropriate method is not very straightforward. The global niche overlap analysis (Chapter 4) was carried out according to the method introduced by Broennimann *et al.* (2012) in the reduced two dimensional PCA ordination space using kernel density smoothing ("ecospat" package in R, Broennimann *et al.* 2016). By using the 1st and the 2nd axis of PCA for niche overlap analysis, 58% of the variance in the entire climatic data was represented in the analysis. Blonder *et al.* (2014) introduced another method (implemented in R package "hypervolume") that could directly analyse the niche overlap in high dimensional space using multivariate kernel density estimation approach. However, this method suffers from problems due to the high dimensionality of data (Qiao *et al.* 2016) and the requirement for multivariate normality. Recently, yet another related method called "dynamic range boxes"(Junker *et al.* 2016) has been developed to overcome many of the previous problems. It is a non-parametric technique that measures niche overlap in the n-dimensional hypervolume (Hutchinson 1957) but is free from the assumption of multivariate normality (implemented in R package "dynRB," Junker *et al.* 2016). However, I could not implement these newer methods as the manuscript was already in final stage for submission.

Understanding the causes of niche dynamics can be enhanced by incorporating knowledge about population genetics. Specifically, such studies can help us to disentangle niche shift due to evolutionary changes from niche shifts due to changes in the realized niche space. Recently a study used genetically informed niche shift analysis of seaweed (*Gracilaria vermiculophylla*) and found that native Asian populations occur in colder and seasonal habitats while warmer and less-seasonal habitats are occupied in the non-native range (Sotka *et al.* 2018). Moreover, they detected parallel evolution of heat tolerant clines in both native (Asian) as well as invasive range (North America). Using a similar approach on *Ageratina adenophora* can help to understand whether evolutionary changes in different ranges has indeed been constrained due to its asexual mode of reproduction.

In contrast to correlative models, mechanistic niche models directly reflect the physiological tolerance levels and are therefore capable of closely approximating the fundamental niche of a species (Peterson *et al.* 2015). For example, Tingley *et al.* (2014) used the prior knowledge from a mechanistic model to estimate fundamental niche of the cane toad (*Rhinella marina*) and analyzed its niche dynamics. They concluded that the observed niche shift was due to shifts in the species' realized niche. Therefore, the development of a mechanistic model for *Ageratina adenophora* could be specifically useful to gauge its fundamental climatic niche thereby improving our understanding of its global niche dynamics and its potential invasive ranges.

Conclusions

A recent systematic review of published literature on *Ageratina adenophora* detected the presence of geographical and thematic bias in past research effort (Yu *et al.* 2016). Most of the published studies were carried out in China (92%), while a handful of the studies were available from Himalayas (7%). Similarly, they also found a paucity of research effort on fundamental ecological and evolutionary aspects of *Ageratina adenophora* invasion. By addressing some questions of eco-evolutionary importance, this study has attempted to partly fill up the knowledge gap about the invasion of *Ageratina adenophora* in the Himalayas.

Ageratina adenophora is a rapidly range expanding invasive species, especially in mountainous regions of the world that are also home to many of the biodiversity hotspots. Regular monitoring and management of fresh infestations of *Ageratina adenophora* in mountainous regions that are climatically suitable is necessary. In the Western Himalayas, an elevational belt between 700m – 1800m is highly infested; therefore special care must be taken to contain the invasion in this belt.

The renowned weed biologist Baker had enumerated several attributes of an “ideal weed” (Baker 1974). The current thesis affirms that indeed *Ageratina adenophora* possesses many of the attributes that make it an ideal weed. Some of these characters are its ability for uniparental reproduction (apomictic), high seed production, a high degree of phenotypic plasticity, vigorous vegetative growth, effective dispersal of seeds and allelopathic potential. He had also introduced the concept of “general purpose genotype” (Baker 1965; Parker *et al.* 2003; Ross *et al.* 2008) for genotypes of a species having high phenotypic plasticity. He had explicitly referred to *Ageratina adenophora* for its broad environmental tolerance. In our common garden experiments, we indeed found the genotypes of *Ageratina adenophora* to be highly plastic for most of the traits. Although apomixis imposes severe evolutionary constraints on an invasive species, it can still be of advantage as it helps to preserve and perpetuate the versatile “general purpose genotypes,” thus enabling rapid range expansion in diverse conditions (Baker 1965).

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Supplements

Curriculum Vitae

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Education

2005-2008	St Xavier's College Ranchi, Ranchi University, India Bachelor of Science in Botany (Hons.), June 2008
2008-2010	Banaras Hindu University, India Master of Science in Botany, June 2010

Academic positions

2013-	PhD Student Helmholtz Centre for Environmental Research
2011-2013	Junior research Fellow CSIR-Institute of Himalayan Bioresource Technology, Palampur, India

Research Interests

- Invasive plants: Niche dynamics and distribution modelling
- Microevolution and local adaptation: Using transplant experiments

Research Experience

- Completed M.Sc dissertation on the topic: *"Do abandoned urban plots act as breeding place for invasive species?"*
- Studied plant community at alpine tree line in Western Himalaya.
- Species distribution modelling of invasive plants and endangered plants in Western Himalaya
- Conducted common garden experiments to study local adaptation of an invasive plant.

Technical skills

- Statistical programming in R
- Basic geoprocessing in QGIS
- Designing, establishing and management of field experiments
- Plant functional trait analysis
- Soil physicochemical analysis

Research grants and academic achievements

2017	Post-doctoral bursary from South African National Biodiversity Institute
2013	Scholarship from DAAD to do PhD at Helmholtz centre for environmental research
2010	Qualified CSIR NET*- Junior research fellow (All India rank: 48) held in June 2010
2010	Qualified as Junior research fellow at Botanical Survey of India. (Position declined)
2009	Qualified CSIR UGC NET-LS** (rank: 58) held in December 2009
2009	Qualified GATE***2009

*National eligibility test conducted by Council for Scientific and Industrial Research and University Grants Commission, India

**LS: Eligibility for lectureship (from University Grants Commission, India)

***Graduate Aptitude Test for Engineers conducted jointly by the Indian Institute of Science and seven Indian Institutes of Technology

Publications

2017 Datta, A., Kühn, I., Ahmad, M., Michalski, S. & Auge, H. (2017). Processes affecting altitudinal distribution of invasive *Ageratina adenophora* in western Himalaya: The role of local adaptation and the importance of different life-cycle stages. PLoS One, 12, e0187708

2016 Jaryan, V., Uniyal, S.K., Datta, A., Gupta, R.C., 2016. Late fruiting in *Sapium sebiferum*: an effective dispersal strategy. Trop. Ecol. 57, 375–379.

2014 Lal, B., Datta, A., Parkash, O., Deosharan, R., 2014. Rediscovery of *Jasminum parkeri* Dunn, an endemic and endangered taxon from the western Himalaya, India. Biodivers. Res. Conserv. 34, 11–16.

2013 Jaryan, V., Datta, A., Uniyal, S.K., Kumar, A., Gupta, R.C., 2013. Modelling potential distribution of *Sapium sebiferum* – an invasive tree species in western Himalaya. Curr. Sci. 105, 1282–1288.

2012 Kumari, A., Datta, A. & Uniyal, S.K.,2012. *Cryptogramma stelleri* (gmel.) prantl.- A new fern record for Himachal Pradesh. J. Indian For.35, 393–395.

Conference participation

2017 Poster presentation at PopBio, Halle, Germany

2017 Oral presentation at Macroecology conference, University of Vienna

2016 Poster presentation at Neobiota conference, Vienden, Luxembourg

2010 Oral presentation at YETI, IISc Banglore, India

Extracurricular achievements

2010 Represented India in International Youth Conference on Biodiversity, 2010 held in Aichi, Japan

2009 Represented India in Asia Youth Biodiversity Conference 2009 held in Nagoya, Japan

2008 3rd Prize in Photography, St Xavier's College Ranchi

2004 1st Prize in Science Exhibition in Class 10, Denobili School, CFRI

Eigenständigkeitserklärung

Hiermit erkläre ich, dass die Arbeit mit dem Titel „Analyzing plant invasions across multiple scales using *Ageratina adenophora* as a case study " bisher weder bei der Naturwissenschaftlichen Fakultät I Biowissenschaften der Martin-Luther-Universität Halle-Wittenberg noch einer anderen wissenschaftlichen Einrichtung zum Zweck der Promotion vorgelegt wurde.

Darüber hinaus erkläre ich, dass ich die vorliegende Arbeit eigenständig und ohne fremde Hilfe verfasst sowie keine anderen als die im Text angegebenen Quellen und Hilfsmittel verwendet habe. Textstellen, welche aus verwendeten Werken wörtlich oder inhaltlich übernommen wurden, wurden von mir als solche kenntlich gemacht.

Ich erkläre weiterhin, dass ich mich bisher noch nie um einen Doktorgrad beworben habe.

Halle (Saale), 26.03.2018

Arunava Datta

(Arunava Datta)
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Erklärung über den persönlichen Anteil an den Publikationen

Chapter 2

Datta, A., Kühn, I., Ahmad, M., Michalski, S. & Auge, H. (2017). Processes affecting altitudinal distribution of invasive *Ageratina adenophora* in western Himalaya: The role of local adaptation and the importance of different life-cycle stages. PLoS One, 12, e0187708

Field work:	Datta, A (90%) Ahmad, M (5%) Kühn, I (5%)
Data analysis:	Datta, A (70%) Auge, H (20%) Kühn, I (5%) Michalski, S (5%)
Manuscript writing:	Datta, A (70%) Auge, H (20%) Kühn, I (5%) Michalski, S (5%)

Chapter 3

Datta, A., Schweiger,O., Kühn, I. (2017). Niche expansion of invasive *Ageratina adenophora* despite evolutionary constraints. (Under review in Journal of Biogeography)

Field work:	Datta, A (90%) Kühn, I (10%)
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Chapter 4

Datta, A., Schweiger,O., Kühn, I Quality of climatic data can determine the transferability of species distribution models: a case study with *Ageratina adenophora.* (Under preparation for submission)

Field work:	Datta, A (90%) Kühn, I (10%)
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