Investigations on the invasion success of *Ulmus pumila*
- A multi-continental survey -

DISSERTATION

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Halle (Saale), 27. August 2013

Elm Seeds

Scattered, blowing,
drifting,
piled in gutters,
massed against doorsills,
floating in a birdbath
and in a dog's dish —
a confetti-shotgun
approach to life.

- Steve Hight -

CONTENTS

SUMMARY

Due to the ongoing globalization, numerous species have been introduced to regions outside their native ranges. Several of these species have become naturalized, established, and abundant and are now considered invasive. These invasives can have tremendous impacts on ecosystem functions, resilience, biodiversity, the genetic constitution of native species, and human health. Although research intensity on biological invasions increased during the last decades, further research is indispensable for a better understanding of invasion processes and for the prediction and control of invasives.

Besides the negative consequences of invasive non-native species, there are also positives. For example, invasive species are ideal model organisms, because non-native populations are often characterized by increased vigor in contrast to conspecific populations in the native range. Comparative studies between native and non-native populations can therefore help to determine if these differences are based on phenotypic plasticity or rapid evolutionary processes. Furthermore, the supplemental consideration of genetic and environmental information can help to identify the factors which might have induced potentially detected evolutionary shifts. The genetic constitution of non-native populations can thereby be shaped by bottlenecks and founder effects, by genetic admixture due to multiple introductions, or by inter-specific hybridization. In regards to environmental influences, both abiotic (e.g. climatic conditions) and biotic (e.g. decreased enemy pressure) factors can drive evolutionary shifts because they often represent new selection regimes in the new ranges. However, studies on the evolutionary processes triggering the invasiveness of a species are still underrepresented in current research, especially regarding woody non-native species.

Four comparative studies were adopted in this thesis to investigate the invasion success of the non-native tree *Ulmus pumila* L. (Siberian elm) in the Western United States and in central Argentina. The Siberian elm invades natural plant communities as well as disturbed sites and can rapidly establish extended dense stands due to its enormous seed production and fast growth. The management of infested sites proved to be difficult because of the pronounced ability of *U. pumila* to resprout after cutting. Further, no biological control agents are defined so far. Previous studies showed that *U. pumila* can easily hybridize with other co-occurring elm species (i.e. *U. rubra* and *U. minor*) in some regions of its non-native ranges. The genetic admixture between the different species resulted in new genotypes, which seems to be one of the driving factors of the invasiveness in the corresponding regions. However, it remained undetermined if inter-specific hybridization was essential to induce the invasiveness of *U. pumila* even in regions where no other elm species suitable as a hybridization partner naturally occurs (e.g. due to the planting of hybrids).

The first two studies of this thesis were mainly based on classical ecological approaches (i.e. germination and growth experiments under controlled conditions). Non-native populations were characterized by faster germination, enhanced biomass production, and enhanced resource allocation to aboveground biomass. These results point to an evolutionary shift of the early life cycle trait performance in *U. pumila* populations from both non-native ranges which potentially contributed to the invasion success. This assumption was also supported by a significant positive correlation between the genetic diversity, an important precondition for rapid evolutionary responses, and the aboveground biomass production of the tested populations. Further, significant positive correlations between the tested trait performances and climatic conditions (mean annual temperature and annual precipitation) suggested that non-native populations occur under different, less stressful climatic conditions than native populations. Moreover, the outcome of both ecological approaches raised the following question which genetic mechanisms triggered the rapid evolutionary change in non-native species.

This question was answered by conducting two molecular studies using nuclear microsatellite markers and uniparental inherited chloroplast microsatellite markers. The results showed that the occurrence of inter-specific hybrids can be excluded in the investigated non-native populations. In fact, evidence was found for genetic admixture between geographically distinct genetic lineages from the native range due to multiple introductions (intra-specific hybridization). It can be assumed that the resulting high genetic diversity facilitated the rapid evolutionary changes in the tested non-native populations. Additionally, population genetic diversity showed also a significant positive relationship to the considered climatic parameters (annual precipitation and mean annual temperature) across the native and both non-native ranges. This supports the assumption of less stressful climatic conditions in non-native populations and that they most probably facilitated the preservation of genetic diversity created by intra-specific hybridization.

This thesis emphasizes the consequences of uncontrolled multiple introductions of a non-native species from distinct native origins and how abiotic factors in the non-native ranges might have additionally shaped the invasion success. The thesis contributes to a better understanding of evolutionary processes in non-native woody plants and how they can provoke their invasiveness. Moreover, the results of this thesis can help to develop improved management strategies for *U. pumila* infested sites and can be combined with further research to compile predictive scenarios of the ongoing invasion by the Siberian elm.

ZUSAMMENFASSUNG

Im Zuge der immer noch voranschreitenden Globalisierung wurden zahlreiche Arten in Regionen außerhalb ihres natürlichen Areals eingeführt. Viele dieser Arten haben sich so erfolgreich in die neuen Gebiete eingegliedert, dass sie als invasiv bezeichnet werden. Diese invasiven Arten können enorme Auswirkungen auf Ökosystemfunktionen, die Widerstandsfähigkeit von Ökosystemen, die Biodiversität, die genetische Konstitution einheimischer Arten oder auch auf die menschliche Gesundheit haben. Obwohl die Forschung in Hinsicht auf biologische Invasionen in den letzten Jahrzehnten stetig zugenommen hat, sind weitere Forschungsansätze für ein besseres Verständnis von Invasionsprozessen und für die Vorhersage und Kontrolle von biologischen Invasionen unverzichtbar.

Neben den negativen Aspekten von invasiven Arten, stellen diese aber auch ideale Modellorganismen dar. Invasive Populationen zeigen z. B. oft ein verbessertes Wachstum im Vergleich zu nativen Populationen der entsprechenden Art. Vergleichende Studien zwischen nativen und invasiven Populationen können daher helfen, zu verstehen, ob diese Unterschiede auf einer hohen phänotypischen Plastizität oder auf schnellen evolutionären Prozessen beruhen. Zusätzlich berücksichtigte genetische und umweltrelevante Informationen können zudem helfen, die Faktoren, welche die potenziellen evolutionären Veränderungen induziert haben, zu identifizieren. Die genetische Konstitution von invasiven Populationen kann durch sog. Flaschenhalseffekte und Gründereffekte geprägt sein, aber auch durch genetische Vermischung aufgrund mehrerer Einführungsvorgänge oder durch inter-spezifische Hybridisierung. Oftmals stellen auch die Umweltbedingungen in den neuen Arealen einen zusätzlichen Selektionsdruck für die eingeschleppten Arten dar. Daher können evolutionäre Vorgänge sowohl durch abiotische (z. B. klimatische Bedingungen) sowie biotische (z. B. sog. *enemy release*) Faktoren zusätzlich gefördert werden. Jedoch sind Studien, welche die Zusammenhänge zwischen evolutionären Prozesse und des Invasionserfolges von nicht-einheimischen Arten untersuchen, immer noch unterrepräsentiert in der aktuellen Forschung; speziell für invasive Gehölzarten.

Im Rahmen dieser Dissertation wurden vier vergleichende Studien durchgeführt, um den Invasionserfolg der Baumart *Ulmus pumila* L. (Sibirische Ulme) im Westen der Vereinigten Staaten und in Argentinien zu untersuchen. Die Sibirische Ulme dringt in natürliche Pflanzengesellschaften sowie in gestörte Standorte ein, wo sie schnell dichte Bestände aufgrund der Produktion von unzähligen Samen und des schnellen Wachstums etablieren kann. Das Management befallener Standorte ist schwierig, denn *U. pumila* besitzt die Fähigkeit sich sehr schnell mittels Wurzel- oder Stammtriebe zu regenerieren. Bisher sind zudem keine biologischen

Bekämpfungsmittel bekannt. Frühere Studien zeigten, dass *U. pumila* leicht mit anderen Ulmenarten (*U. rubra* und *U. minor*), welche gemeinsam mit der Art in einigen Regionen des Invasionsareals auftreten, hybridisieren kann. Es wird angenommen, dass die genetische Vermischung zwischen den verschiedenen Arten eine der treibenden Kräfte für den Invasionserfolg von *U. pumila* in diesen Gebieten ist. Allerdings ist ungeklärt, ob inter-spezifische Hybridisierung auch in Regionen, in denen keine anderen Ulmenarten natürlich vorkommen, ausschlaggebend für den Invasionserfolg war (z. B. durch Ausbreitung angepflanzter Hybride).

Die ersten beiden Studien dieser Arbeit basierten vorwiegend auf klassischen ökologischen Untersuchungsansätzen (d. h. Keimungs- und Wachstumsexperimente unter kontrollierten Bedingungen). Invasive Populationen zeichneten sich dabei durch schnellere Keimung, höhere Biomasseproduktion und eine stärkere Ressourcenallokation in die oberirdische Biomasse aus. Diese Ergebnisse deuten auf eine evolutionäre Veränderung dieser Merkmale in den untersuchten *U. pumila*-Populationen aus beiden Invasionsarealen hin und dass dies höchstwahrscheinlich eine der Hauptursachen des Invasionserfolges ist. Diese Annahme wurde auch durch eine signifikante positive Korrelation zwischen der genetischen Vielfalt, die wichtig für schnelle evolutionäre Antworten ist, und der oberirdischen Biomasseproduktion der untersuchten Populationen unterstützt. Ferner implizierten signifikante positive Korrelationen zwischen den untersuchten Merkmalen und klimatischen Bedingungen (mittlere Jahrestemperatur und Jahresniederschlag), dass die invasiven Populationen im Vergleich zu nativen Populationen unter reduzierten klimatischen Stress vorkommen. Darüber hinaus warfen die beiden Studien die Frage auf, welche genetischen Mechanismen die schnelle evolutionäre Veränderung in den invasiven *U. pumila*-Populationen ausgelöst haben.

Diese Frage wurde durch zwei molekulare Studien unter Verwendung von nuklearen Mikrosatellitenmarkern und uni-parental vererbten Chloroplasten-Mikrosatellitenmarkern bearbeitet. Die Ergebnisse zeigten, dass inter-spezifische Hybridisierung in den untersuchten invasiven Populationen ausgeschlossen werden kann. Vielmehr konnte gezeigt werden, dass multiple Einführungen in den westlichen Vereinigten Staaten und in Argentinien zu einer Vermischung von ursprünglich geographisch getrennten genetischen Linien aus dem nativen Areal geführt haben (intra-spezifische Hybridisierung). Es kann davon ausgegangen werden, dass die daraus resultierende hohe genetische Diversität die schnellen evolutionären Veränderungen in den untersuchten invasiven Populationen gefördert hat. Außerdem zeigte die genetische Diversität der untersuchten nativen und invasiven Populationen signifikante positive Zusammenhänge mit den berücksichtigten Klimaparametern (mittlere Jahrestemperatur und Jahresniederschlag). Dies bestärkte die Annahme, dass nicht-einheimische Populationen einen reduzierten klimatischen Stress erfahren und dass dies wahrscheinlich den Erhalt der durch intra-spezifische Hybridisierung vermittelten genetischen Vielfalt fördert.

Diese Dissertation verdeutlicht die möglichen Folgen von unkontrollierter multipler Einschleppung gebietsfremder Arten und beschreibt, wie abiotische Faktoren in den neuen Gebieten einen zusätzlichen Einfluss auf den Invasionserfolg haben können. Weiterhin trägt diese Arbeit zu einem besseren Verständnis von evolutionären Prozessen und deren Rolle für den Invasionserfolg von gebietsfremden Gehölzarten bei. Darüber hinaus können die Ergebnisse helfen, verbesserte Managementstrategien für Standorte zu entwickeln, welche von invasiven *U. pumila*–Populationen betroffen sind. In Kombination mit zukünftigen Forschungsansätzen können die gewonnenen Erkenntnisse beitragen, effektive Vorhersagemodelle für die weitere Ausbreitung invasiver *U. pumila*-Beständen zu entwickeln.

GENERAL INTRODUCTION

CHAPTER 1

BIOLOGICAL INVASIONS

Biological invasions are one of the most challenging consequences of the globalization (Perrings et al. 2005). Various species were intentionally or unintentionally introduced to regions outside their native ranges in the course of trade, traveling, domestication, pest-control, food-production, or horticultural purposes (Pimentel et al. 2005, Hulme 2009). For example, it is estimated that about 50 000 non-native species became invasive in the United States, costing $120 billion per year due to environmental damages and losses (Pimentel et al. 2005). The ecological impacts of invasive non-native species (herein after referred to as non-native species) causes the alteration of ecosystem functions and resilience (Fischer et al. 2006, Perrings 2011). For instance, the shrub *Tamarix* spp. invaded wide regions of the arid Western United States where it significantly changed the species composition and functioning of riparian ecosystems (Zavaleta et al. 2001). Non-native species can also cause genetic homogenization due to intra- or inter-specific hybridization events (Olden et al. 2004) and some species can even show impacts on human health (Mooney and Hobbs 2000, Juliano and Lounibos 2005). Nevertheless, non-native species can also have neutral or positive impacts as shown by Goodenough (2010). However, although our knowledge about non-native species grew tremendously during the last decades and several hypotheses emerged about their invasion success or failure (Catford et al. 2009, Richardson 2011a), ongoing research is needed in this field to fill still existing knowledge gaps (Richardson 2011b, Lowry et al. 2012). Especially the characterization of possible impacts of non-native species on other species (e.g. hybridization with native species) is important because this will allow more precise management decision-making (Hulme 2006, Shackelford et al. 2013). Consequently, it is crucial to understand the background and mechanisms of factors contributing to the success of the species which become invasive.

EVOLUTIONARY CHANGES IN NON-NATIVE SPECIES

Non-native populations often show increased vigor (e.g. bigger populations, enhanced growth performance) compared to conspecific native populations (Thébaud and Simberloff 2001, Bossdorf et al. 2005, Blumenthal and Hufbauer 2007). Such differences can be based on high phenotypic plasticity or rapid evolutionary shifts (Pyšek and Richardson 2008). The latter can occur during all stages of the invasion process (introduction, establishment, lag phase, and spread) and can be induced by several mechanisms (Prentis et al. 2008). For example, bottlenecks and founder effects can shape the genetic composition of non-native populations as shown by Dlugosch and Parker (2008). Further, intra-specific hybridization due to multiple introductions of individuals from previously distinct native regions as well as interbreeding with closely related species (inter-specific hybridization) in the new range can create new genotypes which might be better adapted or more tolerant to the new conditions (Lavergne and Molofsky 2007, Rieseberg et al. 2007, Schierenbeck and Ellstrand 2009). Additionally, evolutionary responses can also be induced by significant changes in the abiotic or biotic selection regimes due to the novel environmental conditions in the non-native range (Prentis et al. 2008, Pyšek and Richardson 2008). For instance, it was shown that non-native populations can evolve rapid local adaptations to large-scale geographical gradients in the new range (Weber and Schmid 1998, Maron et al. 2004, Chun et al. 2011). In regards to evolutionary shifts induced by biotic factors, it is often assumed that a release of natural enemies in the new range can promote the evolution of enhanced competitive traits because fewer resources have to be dedicated to defense mechanisms (EICA = evolution of increased competitive ability hypothesis; Blossey and Notzold 1995, Joshi and Vrieling 2005). However, among the increasing literature on biological invasions, studies with focus on evolutionary mechanisms which might contribute to the invasiveness are still underrepresented (Lowry et al. 2012). Therefore, further research is necessary to gain a better knowledge about invasion processes as well as fundamental evolutionary mechanisms.

WOODY SPECIES AS INVASIVES AND AS MODEL SPECIES

More than 600 woody species are considered as invasive worldwide and most of them were intentionally introduced to new ranges due to their wide use for horticultural, forestry, or agroforestry purposes (Richardson and Rejmánek 2011). These woody invasives represent less than 1% of the worldwide known woody species, but they have an increasing impact outside their native ranges (Richardson and Rejmánek 2011). For example, the invasion of the non-native tree *Melaleuca quinquenervia* alone causes $3 to $6 million dollar per year for control activities in Florida (Pimentel et al. 2005). In addition, only 35 tree and tall shrub species are native in Britain, but today more than 900 woody species are listed in the British flora due to intensive introduction events (Peterken 2001, Petit et al. 2004).

Despite the increasing influence of non-native woody species, little is known about their invasion ecology (Richardson and Rejmánek 2011). This fact might be partially due to the long generation times of woody species which renders experimental approaches more difficult and time-consuming than for non-woody species (Petit et al. 2004). In contrast, germination and seedling growth, two of the earliest life cycle traits for plants, can be investigated within relatively short time periods even for woody species. These traits can play a crucial role during the colonization of new sites (Donohue et al. 2010), as in the case of range expansion of non-native species. Therefore, shifts of early life cycle trait performance (e.g. faster germination and growth rates) in non-native populations can provide explanations for the invasion success as shown by Erfmeier and Bruelheide (2005) or Siemann and Rogers (2001). Such shifts can be tested now on a genetic level, since the rapid advancement of molecular techniques during the past years allows the consideration of genetic information for the interpretation of results gained by ecological studies about trait performance. For example, Harris et al. (2012) investigated the growth characteristics of native and non-native populations of five woody Fabaceae species in a common garden experiment and combined these results with measurements of genetic diversity. They were able to show that adaptive changes of ecological traits in non-native populations can occur despite reduced genetic diversity. Hence, intensified investigations on characteristics of early life cycle as well as on genetic traits could help to deepen our knowledge about possible mechanisms contributing to the invasiveness of woody species.

STUDY SPECIES – *ULMUS PUMILA* L.

Ulmus L. is a genus of the Ulmaceae that comprises about 40 to 50 species with predominantly north-temperate distributions (Wiegrefe et al. 1994, Mackenthun 2010). *Ulmus* species exhibit hermaphrodite wind-pollinated flowers and have typically a diploid chromosome set of 2n = 28 chromosomes (exceptions: *U. americana* L. and *U. turkestanica* Reg. with 2n = 58 chromosomes; Kubitzki 1993, Hollingsworth et al. 2000). Within the genus, many species can interbreed and produce fertile hybrids (Townsend 1975, Mittempergher 1991). This high crossing compatibility led to the initiation of several breeding programs to develop Dutch elm disease-resistant trees because the disease caused considerable losses of elm populations in Europe and North America (Smalley and Guries 2000, Mittempergher and Santini 2004).

One of the elm species with a pronounced Dutch-elm-disease tolerance is *Ulmus pumila* L. (Siberian elm). This deciduous tree can grow up to 25 m tall and is characterized by a dark gray, deep and irregularly fissured bark (Wu et al. 2003). Leaves are simply or sometimes double serrated, 6-8 cm long, 1.5-3 cm wide, elliptic-ovate to elliptic-lanceolate, and show an oblique to symmetrical base (Fig. 1; Wu et al. 2003, Mackenthun 2010). Flowering and fruiting occur from March to May (depending on such factors as elevation and temperature) and the ripe winged fruits (Samaras) are wind dispersed (Wu et al. 2003).

The native range of *U. pumila* comprises north-west and west China, central Mongolia, and southern Russia (Wesche et al. 2011). In the most parts of this range it is widespread, but in some regions populations are declining or only relict populations remained (Gobi desert, Mongolia and Hunshandak Sandland, China; Shi et al. 2004, Wesche et al. 2011). Typical habitats of the Siberian elm are dunes, slopes, valleys, and plains up to 1 000-2 500 m a.s.l. (Wu et al. 2003, Shi et al. 2004). Its high tolerance of stressful conditions (i.e. long summer droughts, cold winters, alkaline or saline soils, and dust storms; Heybroek 1979) as well as the use in breeding programs led to introductions into several countries outside its native range (Webb 1948, Smalley and Guries 2000). In consequence, *U. pumila* is today considered as naturalized or invasive in the most states of the United States, in Canada (Kartesz 2011, USDA and NRCS 2011), Mexico (Todzia and Panero 1998), Argentina (Mazia et al. 2001, Zalba and Villamil 2002), Spain (Cogolludo-Agustín et al. 2000), Italy (Brunet et al. in press), the European part of Russia, Estonia, Austria (NOBANIS 2012), and Germany (Höcker 2009). Non-native populations occur mainly along roadsides, railroad tracks, stream banks, at pastures, vacant lots, uncultivated land, mesic, dry, and sand prairies (Höcker 2009, USDA and NRCS 2011).

The production of countless seeds per tree and the fast growth can lead to the formation of extensive thickets of Siberian elms saplings (Fig. 4d). This can result in the replacement of native species (especially shade intolerant species) followed by an invasion by other weedy species (USDA Forest Service 2005). Another negative consequence of the invasion of *U. pumila* is genetic pollution of co-occurring elm species due to inter-specific hybridization. For example, *U. pumila* hybridizes extensively with the native *U. minor* in Spain (Cogolludo-Agustín et al. 2000) and Italy (Brunet et al. in press). Further, Zalapa et al. (2009) showed that inter-specific hybridization between *U. pumila* and *U. rubra* is widespread in the eastern and Midwestern parts of the United States.

STUDY REGIONS

This thesis focuses on the success of non-native *U. pumila* populations in western regions of the United States and in Argentina. To gain knowledge about possible evolutionary changes in these non-native populations as well as about their native origin, populations

Fig. 1 Morphological characteristics of *Ulmus pumila* L. (1-3: sterile branches; 4: fruiting branch; 5, 6: fruits). Picture (changed): Flora of China (http://www.efloras.org).

from the Asian native range (i.e. from China, Mongolia, and Russia; Fig. 2) were also considered. Population expansions and sizes of native as well as non-native populations were in some cases very large (i.e. populations ranged over several kilometers along rivers with more than 1000 individuals). Nevertheless, non-native populations tended to be generally denser and were characterized by more distinctive occurrence of seedlings and younger individuals (Fig. 3).

Ulmus pumila occurs in almost all mainland states of the United States and in most of these states other elm species occur which might be potential hybridization partners (Kartesz 2011). Zalapa et al. (2009, 2010) showed that hybridization can contribute to the invasion success of *U. pumila* in some parts of the United States. In contrast, this thesis focuses on the invasion success of pure *U. pumila* populations in regions without occurrence of other elm species suitable as hybridization partner. Consequently, the 30 sampled populations in the North American non-native range were located across the states New Mexico, Colorado, Utah, Idaho, Oregon, and Washington (Fig. 2a), states which have no elm species to

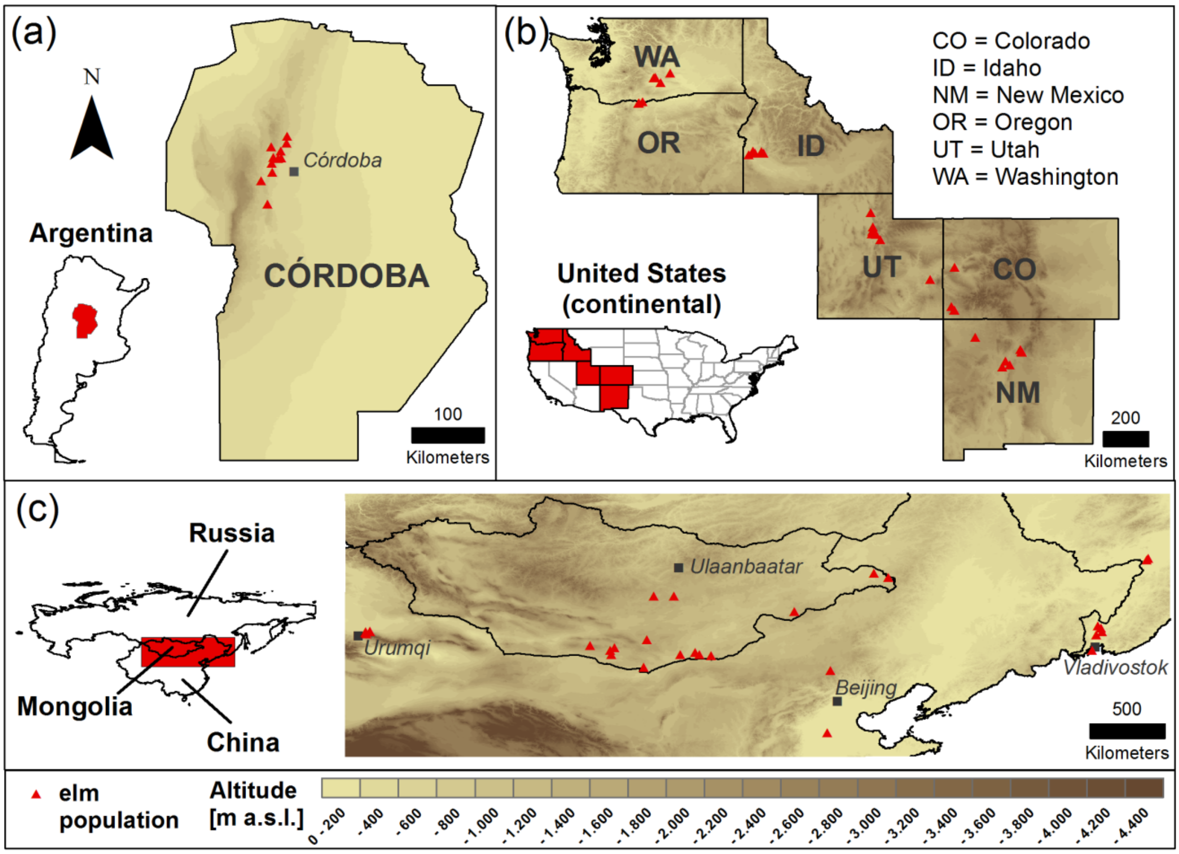

Fig. 2 Populations of *Ulmus pumila* considered in this thesis. The detail maps show the locations of the populations from both non-native ranges (a: Argentina; b: United States) and from the native range (c: Asia). Please note that in the studies of chapter 2, 3 and 4 only a subset of the populations was considered (details are described in the corresponding chapter).

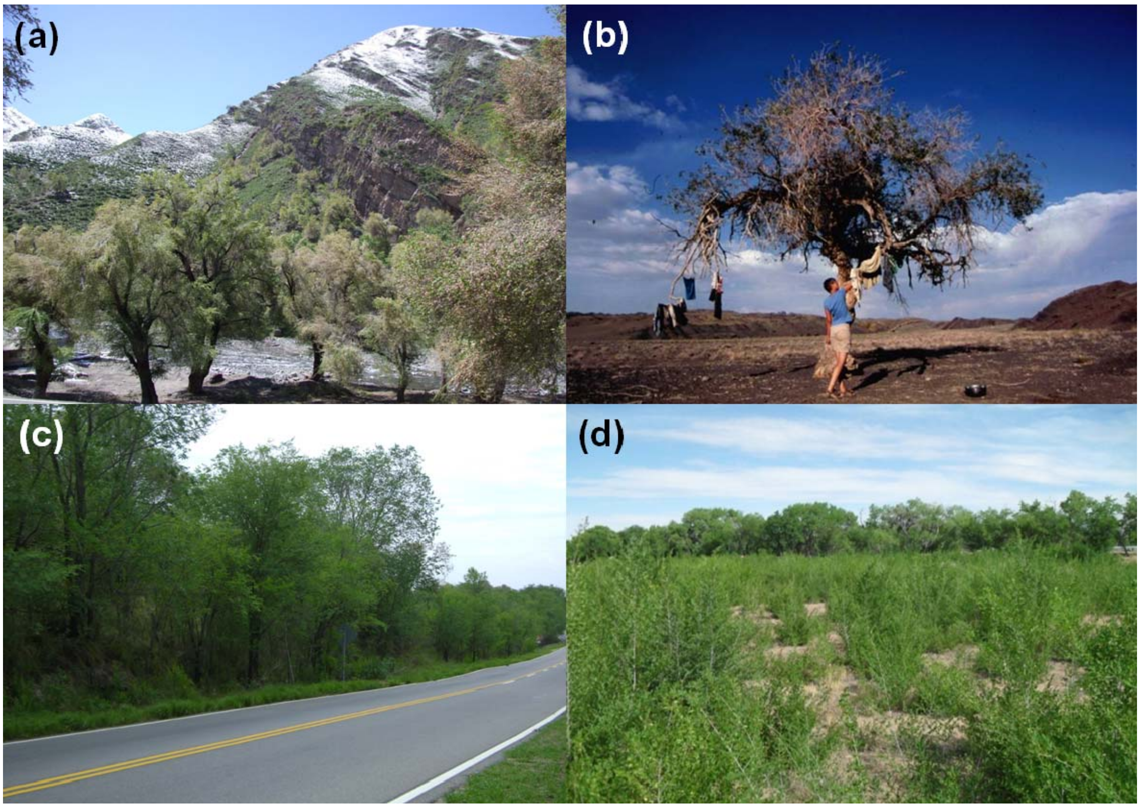

Fig. 3 Examples of *Ulmus pumila* populations in the native range (a: Xinjiang, China, photo by Ximing Zhang; b: Gobi desert, Mongolia, photo by Henrik von Wehrden) and in the non-native ranges (c: Cordóba, Argentina, photo by Ricardo Suarez; d: New Mexico, United States, photo by Heidi Hirsch).

hybridize with *U. pumila*. Overall, the study sites in these states cover arid, warm temperate as well as snow climates according to the climate classification of Kottek et al. (2006). This wide variety is also reflected in the local climate conditions of the considered populations. Annual precipitation ranges between 172 mm and 558 mm and annual mean temperature between 7.1°C and 13.5°C (Hijmans et al. 2005). Minimum temperature during the coldest month varies between -2.3°C and -12.0°C, while maximum temperature during the warmest month varies between 27.2°C and 35.7°C (Hijmans et al. 2005). The study sites were situated along rivers, creeks, roads, at open grasslands or empty lots located at altitudes between 75 m and 2328 m a.s.l. Regarding the initial introduction history, several different accounts exist: It is most frequently assumed that initial introduction of *U. pumila* seeds was in 1905 from regions around of Beijing, China (Webb 1948, Leopold 1980). Other resources indicate that the Siberian elm was introduced in the 1860´s as a landscape tree (USDA 1974). The planting of *U. pumila* was highly promoted by newspapers during the 1930´s (Webb 1948, Klingaman 1999). Multiple introduction events occurred to meet the increasing demand for plantations or for the use in breeding programs (Webb 1948, Smalley and Guries 2000). Consequently, without more detailed genetic information it is impossible to trace the distinct native origin of non-native populations.

In Argentina, where no native elms occur, non-native populations of *U. pumila* can be found in regions around Córdoba (personal observation and communication with D. Renison, R. Suarez, H. von Wehrden, and H. Zimmermann) and in Pampas in the Buenos Aires province (Sarasola and Negro 2006). For this thesis eleven populations were sampled in the Córdoba province which is characterized by a warm temperate climate (Fig. 3b; Kottek et al. 2006). These populations are exposed to annual precipitations ranging between 654 mm and 720 mm and annual mean temperatures ranging between 14.2°C and 16.5°C (Hijmans et al. 2005). Minimum temperature during the coldest month varies between 1.5°C and 3.1°C and maximum temperature during the warmest month varies between 27.1°C and 30.2°C (Hijmans et al. 2005). The study sites were situated along roadsides, at pastures or empty lots located at altitudes between 705 m and 1005 m a.s.l. Regarding the introduction history for the Argentinean non-native range it is only known that *U. pumila* individuals were introduced from the United States in 1928 and that later introductions occurred also from Italy (Moore 1960, Cozzo 1968, Neher and Roic 1972, Cané 2008).

Thirty native populations from northern China (7 populations), Mongolia (16 populations), and southeastern Russia (7 populations) were sampled to cover a wide proportion of the native range (Fig. 2c). Their locations represent regions with arid, warm temperate or snow climate (Kottek et al. 2006). The annual precipitation varies between 74 mm and 725 mm and annual mean temperatures varies between -1.7°C and 13.0°C (Hijmans et al. 2005). Minimum temperature during the coldest month ranges between -8.9°C and -31.0°C and maximum temperature during the warmest month ranges between 24.4°C and 32.4°C (Hijmans et al. 2005). The native study sites were situated along rivers, dry riverbeds of temporary rivers, and slopes at altitudes between 18 m and 1801 m a.s.l.

The complete set of collected samples was not used in each study due to financial and spatial limitations for the setup of the experiments. Further details about the corresponding subset of populations are explained in the appropriate chapters.

OBJECTIVES AND AIM OF THE THESIS

This thesis is focused on the invasion success of non-native tree species using *U. pumila* as the model species. The main objective was particularly focused on early life cycle traits which are important during establishment and colonization processes and for population growth dynamics. Further, the thesis highlights the mechanisms which may facilitate a rapid evolutionary change of these traits. The particular studies of this thesis and the corresponding hypotheses are summarized in Fig. 4.

The first study (**Chapter 2**) contains the comparison of the germination performance between native and non-native populations of *U. pumila*. It was tested if non-native populations are characterized by enhanced germination percentages as well as faster germination which could provide competitive advantages during the colonization of new sites. Further, it was tested if populations located in regions with less stressful climatic conditions are characterized by enhanced germination performance.

The next study (**Chapter 3**) was conducted to investigate post-germination traits of native and non-native populations to see if they show a correlated evolution with the germination performance. The genetic diversity for each of the considered populations was determined with microsatellite markers and climatic information was considered to evaluate factors which can potentially facilitate evolutionary shifts. The hypotheses of this study were as follows: 1) Non-native populations are characterized by a better growth performance. 2) A better growth performance is related to less stressful climatic conditions as well as higher genetic diversity levels.

The objective of the third study (**Chapter 4**) was to test if the patterns of genetic diversity and the relationship to climatic conditions are consistent if a larger set of native and non-native populations is considered. A reference data set with pure *U. pumila*, *U. rubra*, and

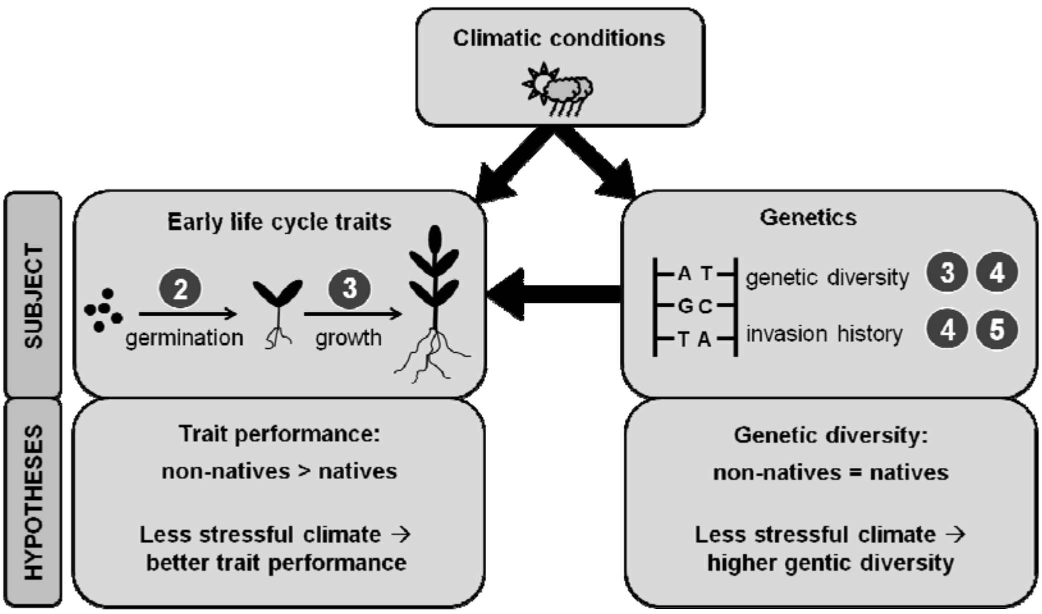

Fig. 4 Summary of the investigated issues in this thesis. The numbers symbolize the chapters with the corresponding studies.

U. minor samples was applied to test for the correctness of the assumption that the investigated non-native populations are not influenced by inter-specific hybridization.

The fourth study (**Chapter 5**) was conducted in addition to the previous study to gain more detailed information about the invasion history and the native origin of the non-native populations using uni-parental inherited microsatellite markers.

This thesis will help to promote a better understanding of the invasion processes of *U. pumila* and of woody species in general. The findings can be utilized in the development of management and control proceedings of non-native *U. pumila* populations.

Germination performance of native and non-native *Ulmus pumila* populations

Chapter 2

Hirsch H, Wypior C, von Wehrden H, Wesche K,
Renison D & Hensen I

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ABSTRACT

Germination is a crucial step for invasive plants to extend their distribution under different environmental conditions in a new range. Therefore, information on germination characteristics of invasive plant species provides invaluable knowledge about the factors which might contribute to the invasion success. Moreover, intra-specific comparisons under controlled conditions will show if different responses between non-native and native populations are caused by evolutionary changes or by phenotypic plasticity towards different environmental influences.

This paper focuses on the germination of native and non-native *Ulmus pumila* populations. We expected that non-native populations would be characterized by their higher final germination percentage and enhanced germination rate, which might indicate an influence due to corresponding climatic conditions.

Germination experiments with a moderate and a warm temperature treatment did not reveal significant differences in final germination percentage. However, seeds from the North American non-native range germinated significantly faster than native seeds ($p < 0.001$). Additionally, mean time to germination in both ranges was significantly negatively correlated with annual precipitation ($p = 0.022$). At the same time, this relationship is stronger in the native range whereas mean time to germination in non-native populations seems to be less influenced by climatic conditions.

Different germination responses of the North American populations could be caused by a fast evolutionary change mediating a higher tolerance to current climatic conditions in the non-native range. However, our findings could also be caused by artificial selection during the introduction process and extensive planting of *U. pumila* in its non-native range. Nevertheless, we assume that the faster germination rate of non-native populations is one potential explanation for the invasion success of *U. pumila* in its new range since it might provide a competitive advantage during colonization of new sites.

KEYWORDS

Climatic influence, survival analysis, biological invasions, *Ulmus pumila*

CHAPTER 3

EVOLUTION OF AN INVASIVE TREE: NON-NATIVE SIBERIAN ELMS OUTPERFORM NATIVE PROVENANCES

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BIOLOGICAL INVASIONS (IN REVIEW)

ABSTRACT

The subject of our study was to investigate post-germination evolutionary processes of non-native woody species using *Ulmus pumila* as the model. In a previous study, we showed that non-native populations are characterized by enhanced germination velocity and we postulated that growth performance of seedlings is correlated. Further, climatic and genetic information was used to gain more information about possible drivers of evolutionary processes.

We conducted a common garden greenhouse experiment over a wide variety of growth conditions to compare the biomass production of *U. pumila* seedlings derived from seven native as well as thirteen populations from two non-native ranges. Further, genetic diversity was determined using microsatellite markers and climatic information for each population was extracted.

Non-native populations are characterized by increased biomass production, enhanced resource allocation to aboveground biomass, and higher genetic diversity. Further, we found significant positive correlations between climatic parameters and biomass production as well as genetic diversity.

We assume that the enhanced growth performance of non-native populations might be one of the contributing factors for the invasion success of *U. pumila*, because this can provide competitive advantages during the colonization of new sites. Moreover, we suggest that our results potentially reflect an evolutionary change that might be mediated by less stressful climatic conditions in the non-native ranges and facilitated by a high genetic diversity resulting from inter- or intra-specific hybridization.

KEYWORDS

Post-germination traits, rapid evolution, genetic diversity, climatic conditions, biomass, greenhouse

CHAPTER 4

IS THE INVASIVE SIBERIAN ELM A HYBRID SUPER VILLAIN? – A MULTI-CONTINENTAL SURVEY

HIRSCH H, ZALAPA JE, BRUNET J, VON WEHRDEN H, HARTMANN M, SCHLAUTMAN BJ, KOSMAN E, WESCHE K, RENISON D & HENSEN I

MOLECULAR ECOLOGY (SUBMITTED)

ABSTRACT

We investigated the genetic diversity of a non-native woody species and how it can be influenced by biotic and abiotic factors during the invasion history. We used *Ulmus pumila* L. as a model species. Previous studies revealed a high proportion of inter-specific hybrids in non-native *U. pumila* populations, resulting in an enhancing effect to the genetic diversity. However, we were interested in the genetic constitution of non-native populations located in regions without suitable hybridization partners. Moreover, we predict that less stressful climatic conditions can facilitate higher genetic variation.

We used microsatellite markers to compare the genetic diversity of 14 native populations from Asia and 30 non-native populations from the Western United States as well as 11 non-native populations from Argentina. To exclude inter-specific hybridization, reference samples of *U. pumila*, *U. rubra* and *U. minor* were included in the analysis. Climatic data was used as a proxy to quantify the relationship between genetic diversity and climatic conditions.

Our results showed that intra-specific, rather than inter-specific hybridization supported the maintenance of high genetic diversity in the investigated non-native populations. Further, we found evidence that less stressful climatic conditions potentially facilitate higher genetic diversity. We discuss our results in regards to the invasiveness, rapid evolutionary changes and possible climate niche shifts of *U. pumila*. This work provides valuable information about invasion processes of woody species and how genetic diversity can be shaped by intra-specific as well as environmental influences.

KEYWORDS

Genetic diversity, native vs. non-native populations, intra- and inter-specific hybridization, climatic conditions

Molecular evidence for multiple introductions of invasive Siberian elms in North and South America

Chapter 5

Hirsch H, Kleindienst C, von Wehrden H, Wesche K, Renison D & Hensen I

(Manuscript)

ABSTRACT

The reconstruction of introduction routes of non-native species provides information on their genetic constitution and may aid the development of efficient control and management strategies. It also allows the comparison of environmental factors (e.g. climatic conditions) between native and non-native populations to quantify their potential impact to the invasiveness of the corresponding species.

Our study focused on the identification of the native origin of non-native *Ulmus pumila* (Ulmaceae) populations in the Western United States and in Argentina. We compared the haplotypes of 41 non-native populations (Argentina: 11 populations; USA: 30 populations) and 30 native populations from Mongolia, Russia and China using chloroplast microsatellite markers. Further, we also considered climatic information of the corresponding regions to assess if non-native populations show shifts in climatic niche.

We found evidence for multiple introductions in both non-native ranges, and identified potential source regions previously unknown from the literature. Our results also indicated possible climatic niche shifts with less extreme climatic conditions in the non-native ranges. Combined with our previous research, we conclude that the multiple introductions facilitated the invasiveness of *U. pumila* resulting in genotypes more vigorous than those of the previously distinct native lineages. We suggest reciprocal climatic niche modeling approaches for further research to test the assumed climatic niche shift in non-native populations and to gain more knowledge on the evolutionary potential of *U. pumila*.

KEYWORDS

Bridgehead effect, chloroplast microsatellites, climatic niche shift, native origin, invasive tree

CHAPTER 6

SYNTHESIS

GENERAL DISCUSSION

The comparison of germination and growth characteristics in this thesis revealed that non-native populations of *U. pumila* seem to have undergone an evolutionary shift leading to an enhanced performance of the tested early life cycle traits (Chapters 2 and 3; Fig. 1). These traits are known to be crucial during the colonization of new sites and to play an important role for the establishment and growth of new populations (Donohue et al. 2010). It can be assumed that the detected faster germination, the increased biomass production as well as the enhanced resource allocation to aboveground biomass are supporting factors for the invasiveness and range expansion of the Siberian elm in the Western United States and in Argentina. It is often argued that an enhanced trait performances in non-native populations of a species might be

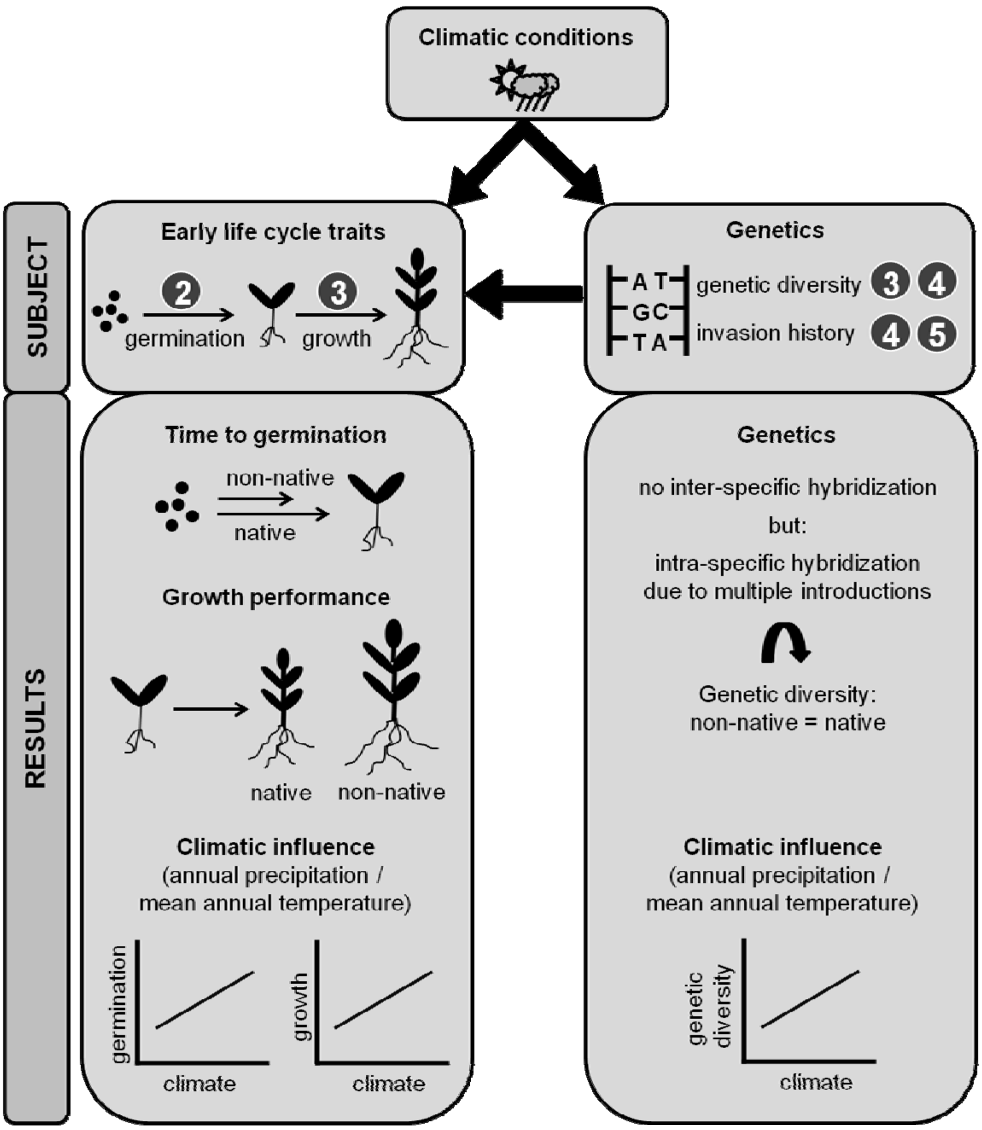

Fig. 1 Summary of the investigated issues and the main results of this thesis. The numbers symbolize the chapters with the corresponding studies.

mediated by the evolution of increased competitive ability (EICA) due to an escape from enemies (Blossey and Notzold 1995, Zou et al. 2007, Henery et al. 2010). However, it has to be noted that both classic ecological experiments were conducted in the absence of inter- or intra-specific competition. Thus, the observed patterns do not imperatively suggest that non-native *U. pumila* populations are characterized by more competitive ability in any circumstance. It could also be possible that they are only be more advantageous in habitats with reduced competition as it was shown for other species by Blumenthal and Hufbauer (2007) and Leger and Rice (2003). Comparative competition experiments would therefore be useful to clarify if the enhanced performance of early life cycle traits is also relevant in habitats with competition by other co-occurring woody species and to predict areas vulnerable to the invasion of *U. pumila* more precisely. Additionally, comparative surveys on the impact of specialist and generalist enemies (e.g. herbivores, pathogens) in native and non-native populations would be needed to test the EICA hypothesis. However, frequently observations during the sample collection in non-native populations (i.e. infestation of *U. pumila* individuals by the elm leaf beetle *Xanthogaleruca luteola* and the European elm scale *Gossyparia spuria*; browsing by deer; Wetwood disease caused by bacteria) render the EICA hypothesis for the tested non-native populations rather unlikely. This is also supported by the other findings of this thesis suggesting that different processes were facilitating the evolutionary shift (see below).

The results of both genetic approaches suggest that the evolutionary shift was most likely supported by a genetic admixture between primarily separated native lineages due to multiple introductions (intra-specific hybridization) rather than by inter-specific hybridization (Chapters 4 and 5; Fig. 1). The genetic admixture contributed to the pronounced genetic diversity in non-native populations which is in turn an important qualification for rapid evolutionary responses (Hughes et al. 2008). First, this highlights the potential consequences of uncontrolled introductions and commercial distributions of non-native plant species. Second and in comparison with previous studies by Zalapa et al. (2010) or Brunet et al. (in press), it shows that different genetic mechanisms can trigger the invasiveness within a single non-native species (i.e. inter-specific hybridization in *U. pumila* populations from the Midwestern States or from Italy vs. intra-specific hybridization in the Western United States and in Argentina).

The consideration of climatic information in this thesis provided valuable information about possible additional impacts of abiotic conditions to the detected germination, growth, and genetic patterns. The revealed positive relation between the investigated early life cycle trait performances as well as the genetic diversity and the considered climatic parameters lead to the assumption that climatic conditions in the non-native ranges are less stressful for *U. pumila*. Similar relationships along abiotic gradients were otherwise mainly shown in reference to evolutionary processes over much longer term periods, so far (e.g. Volis et al. 2002, Harder and Johnson 2009). Nevertheless, several studies have demonstrated the generally high potential of rapid evolutionary changes in non-native plants (Maron et al. 2004, Whitney and Gabler 2008, Whitney et al. 2010) and that these are indeed possible along abiotic gradients (Leger and Rice 2007). This reinforces the assumption that climatic conditions might have additionally influenced the observed patterns between native and non-native *U. pumila* populations. However, further research of climatic information is needed to determine if there is a real climatic niche shift between native and non-native Siberian elm populations.

In conclusion, the findings of this thesis contribute significantly to a better understanding of the invasion process of *U. pumila*. The results can also provide valuable information in regards to the ongoing spread of the Siberian elm in other non-native ranges. It is known that *U. pumila* has become established in several regions of Europe (NOBANIS 2012). The revealed knowledge about the invasion success could aid in predicting possible consequences of an unobstructed spread of *U. pumila* in these other regions and in developing guidelines for appropriate management. Further, the thesis results are supportive for the understanding of evolutionary processes in woody invasives in general. They highlight that trait evolution in woody species is possible over relatively short periods (< 110 years) and that distinct genetic mechanisms can trigger the invasiveness of a single woody invasive species. Finally, this thesis indicates further research approaches needed for a better prediction and control of areas threatened by the non-native Siberian elm.

IMPLICATION FOR MANAGEMENT

As the results of this thesis show, non-native *U. pumila* populations are characterized by enhanced early life cycle traits (germination and sapling growth) compared to native populations. It is therefore advisable to inhibit the further spread of seeds to prevent the rapid establishment of new populations. This could be done by cutting or girdling of older trees and applying chemicals to prevent resprouting. For the next step, younger trees, saplings, and seedlings should be removed and the corresponding areas should be reseeded or replanted with native species. A detailed overview of these and other methods for controlling already established populations, as well as for follow-up treatment and monitoring is given in the booklet of the USDA Forest Service (2012).

Although several control methods already exist, it is essential to fund further research with focus on the enhancement of existing control methods or the invention of new methods. For instance, no appropriate biological control agent is currently available for the non-native Siberian elm, but anecdotal reports indicate that a well-regulated grazing by goats could decrease *U. pumila* infestations in certain areas (USDA Forest Service 2012).

In general, more intensive public education regarding non-native species is required. For example, in the case of *U. pumila* it would be helpful to make landowners or land manager aware of the potential consequences of the planting of this tree (e.g. high seed production and establishment of dense sapling stands). Additionally, the still ongoing commercially distribution of *U. pumila* by tree nurseries (e.g. http://www.greenwoodnursery.com/page.cfm/283) should be curtailed and native trees should be proposed as alternative plantations.

The focus of attention should also be on the early detection and prediction of further areas suitable for non-native populations of the Siberian elm. Such an approach is planned for further research and is therefore described in more detail in the following paragraph.

OUTLOOK

For an effective management of non-native species, the prediction and the early detection of potentially areas of threat are of high importance (Evangelista et al. 2012). This can be realized by applying model approaches which allow the prediction of the potential habitat distribution of a species by combining occurrence and environmental information (predictive habitat modeling; Hoffman et al. 2008). In this context, maximum entropy (MaxEnt) models based on presence-only occurrence data are well suited for non-native species models (Phillips et al. 2006, Holcombe et al. 2010, Evangelista et al. 2012). Therefore, it is my intention to combine the results of this thesis with such models for future research on the Siberian elm. First, I plan to model the potential distribution range of *U. pumila* by considering occurrence data of native as well as non-native populations. The results of the reciprocal model approach will facilitate the identification of further areas suitable as potential habitat and can provide valuable information on the environmental factors important for the presence of *U. pumila*. Additionally, the results could show if the hybridization (intra- or inter-specific) in the non-native ranges might be responsible for potential shifts in the fundamental climate niche. A second approach will consider additional elm species suitable as hybridization partner for the Siberian elm. With these comparative predictive habitat models it will be possible to forecast prospective hybridization hotspots and to develop appropriate recommendations for risk assessment and management frameworks.

REFERENCES

REFERENCES

Blossey B , Notzold R (1995) Evolution of Increased Competitive Ability in Invasive Nonindigenous Plants - a Hypothesis. *Journal of Ecology* 83: 887-889.

Blumenthal DM , Hufbauer RA (2007) Increased plant size in exotic populations: a common-garden test with 14 invasive species. *Ecology* 88: 2758-2765.

Bossdorf O, Auge H, Lafuma L, et al. (2005) Phenotypic and genetic differentiation between native and introduced plant populations. *Oecologia* 144: 1-11.

Brunet J, Zalapa JE, Peccori F, Santini A (in press) Hybridization and introgression between the exotic Siberian elm, *Ulmus pumila*, and the native Field elm, *U. minor*, in Italy. *Biological Invasions*.

Cané L (2008) *Árboles que se cultivan en la Argentina*. Revista Jardín, Buenos Aires.

Catford JA, Jansson R, Nilsson C (2009) Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Diversity and Distributions* 15: 22-40.

Chun Y, Le Corre V, Bretagnolle F (2011) Adaptive divergence for a fitness-related trait among invasive *Ambrosia artemisiifolia* populations in France. *Molecular Ecology* 20: 1378-1388.

Cogolludo-Agustín MÁ, Agúndez D, Gil L (2000) Identification of native and hybrid elms in Spain using isozyme gene markers. *Heredity* 85: 157-166.

Cozzo D (1968) Concepto forestal de la naturalización de especies exóticas y su ocurrencia en Argentina. *Revista Forestal Argentina* 12: 118-124.

Dlugosch KM , Parker IM (2008) Invading populations of an ornamental shrub show rapid life history evolution despite genetic bottlenecks. *Ecology Letters* 11: 701-709.

Donohue K, Rubio de Casas R, Burghardt L, Kovach K, Willis CG (2010) Germination, postgermination adaptation and species ecological ranges. *Annual Review of Ecology and Systematics* 41: 293-319.

Erfmeier A , Bruelheide H (2005) Invasive and native *Rhododendron ponticum* populations: is there evidence for genotypic differences in germination and growth? *Ecography* 28: 417-428.

Evangelista P, Young N, Carter L, et al. (2012) Mapping habitat and potential distributions of invasive plant species on USFWS national wildlife refuges. *Colorado State University and Fort Collins Science Center;* http://ibis-live.nrel.colostate.edu/WebContent/WS/ColoradoView/images/Colorado%20Data%20Page/USFWS_Refuge_Report_Evangelista_et_al.pdf [accessed: 03.04.2013]

Fischer J, Lindenmayer DB, Manning AD (2006) Biodiversity, ecosystem function, and resilience: ten guiding principles for commodity production landscapes. *Frontiers in Ecology and the Environment* 4: 80-86.

Goodenough AE (2010) Are the ecological impacts of alien species misrepresented? A review of the "native good, alien bad" philosophy. *Community Ecology* 11: 13-21.

Harder LD , Johnson SD (2009) Darwin's beautiful contrivances: evolutionary and functional evidence for floral adaptation. *New Phytologist* 183: 530-545.

Harris CJ, Dormontt EE, Le Roux JJ, Lowe A, Leishman MR (2012) No consistent association between changes in genetic diversity and adaptive responses of Australian acacias in novel ranges. *Evolutionary Ecology* 26: 1345-1360.

Henery ML, Bowman G, Mráz P, et al. (2010) Evidence for a combination of

pre-adapted traits and rapid adaptive change in the invasive plant *Centaurea stoebe*. *Journal of Ecology* 98: 800-813.
Heybroek H (1979) Mini-monograph of elms in agroforestry, technical consultation on fast-growing broadleaved trees for Mediterranean and temperate zones. FAO, FO: FGB-79-78/77: 423–441.
Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25: 1965-1978.
Höcker R (2009) Ulmus pumila L. - neu im Großraum Nürnberg / Fürth. *RegnitzFlora - Mitteilungen des Vereins zur Erforschung der Flora des Regnitzgebietes* 3: 44-49.
Hoffman JD, Narumalani S, Mishra DR, Merani P, Wilson RG (2008) Predicting potential occurrence and spread of invasive plant species along the North Platte river, Nebraska. *Invasive Plant Science and Management* 1: 359-367.
Holcombe TR, Stohlgren TJ, Jarnevich CS (2010) From points to forecasts: Predicting invasive species habitat suitability in the near term. *Diversity* 2: 738-767.
Hollingsworth PM, Hollingsworth ML, Coleman M (2000) The european elms: Molecular markers, populations genetics, and biosystematics. *in* Dunn CP, editor. *The elms - Breeding, conservation, and disease management*. Kluwer Academic Publishers, Norwell, Massachusetts, USA.
Hughes AR, Inouye BD, Johnson MTJ, Underwood N, Vellend M (2008) Ecological consequences of genetic diversity. *Ecology Letters* 11: 609-623.
Hulme PE (2006) Beyond control: wider implications for the management of biological invasions. *Journal of Applied Ecology* 43: 835-847.
Hulme PE (2009) Trade, transport and trouble: managing invasive species pathways in an era of globalization. *Journal of Applied Ecology* 46: 10-18.
Joshi J , Vrieling K (2005) The enemy release and EICA hypothesis revisited: incorporating the fundamental difference between specialist and generalist herbivores. *Ecology Letters* 8: 704-714.
Juliano SA , Lounibos LP (2005) Ecology of invasive mosquitoes: effects on resisdent species and on human health. *Ecology Letters* 8: 558-574.
Kartesz JT (2011) North American Plant Atlas. http://www.bonap.org/MapSwitchboard.html [accessed 11.10.2011].
Klingaman G. (1999) Plant of the week - Siberian elm. http://www.arhomeandgarden.org/plantoftheweek/articles/Siberian_Elm.htm [accessed 13.04.2010].
Kottek M, Grieser J, Beck C, Rudolf B, Rubel F (2006) World map of the Köppen-Geiger climate classification updated. *Meteorologische Zeitschrift* 15: 259-263.
Kubitzki K (1993) *The families and genera of vascular plants*. Springer, Berlin, Heidelberg.
Lavergne S , Molofsky J (2007) Increased genetic variation and evolutionary potential drive the success of an invasive grass. *Proceedings of the National Academy of Sciences* 104: 3883-3888.
Leger EA , Rice KJ (2003) Invasive California poppies (*Eschscholzia californica* Cham.) grow larger than native individuals under reduced competition. *Ecology Letters* 6: 257-264.
Leger EA , Rice KJ (2007) Assessing the speed and predictability of local adaptation in invasive California poppies (*Eschscholzia californica*). *Journal of Evolutionary Biology* 20: 1090-1103.
Leopold DJ (1980) Chinese and Siberian elms. *Journal of Arboriculture* 6: 175-179.
Lowry E, Rollinson EJ, Laybourn AJ, et al. (2012) Biological invasions: a field

synopsis, systematic review, and database of the literature. *Ecology and Evolution* 3: 182-196.

Mackenthun G (2010) Handbuch der Ulmengewächse. www.ulmen-handbuch.de [accessed 19.10.2010].

Maron JL, Vilá M, Bommarco R, Elmendorf S, Beardsley P (2004) Rapid evolution of an invasive plant. *Ecological Monographs* 74: 261-280.

Mazia CN, Chaneton EJ, Ghersa CM, Leon RJC (2001) Limits to tree species invasion in pampean grassland and forest plant communities. *Oecologia* 128: 594-602.

Mittempergher L (1991) Hybridization studies in the Eurasian species of elm (*Ulmus* spp.). *Silvae Genetica* 40: 237-243.

Mittempergher L , Santini A (2004) The history of elm breeding. *Investigación agraria-Sistemas y recursos forestales* 13: 161-177.

Mooney HA , Hobbs RJ (2000) *Invasive species in a changing world*. Island Press, Washington, D.C.

Moore G (1960) El cultivo de *Ulmus pumila* ofrece buenas perspectivas en la Argentina. *Revista Forestal Argentina* 4: 77-81.

Neher EF , Roic LD (1972) Nota sobre la naturalización de especies arbóreas en las Sierras de Córdoba. *Revista Forestal Argentina* 16: 123-125.

NOBANIS (2012) European Network on Invasive Alien Species. www.nobanis.org [accessed 10.07.2012].

Olden JD, Poff NL, Douglas MR, Douglas ME, Fausch KD (2004) Ecological and evolutionary consequences of biotic homogenization. *Trends in Ecology & Evolution* 19: 18-24.

Perrings C (2011) Elton and the economics of biological invasions.*in* Richardson D, editor. *Fifty years of invasions ecology. The legacy of Charles Elton*. Wiley-Blackwell, Oxford.

Perrings C, Dehnen-Schmutz K, Touza J, Williamson M (2005) How to manage biological invaisons under globalizations. *Ecology & Evolution* 20: 212-215.

Peterken GF (2001) Ecological effects of introduced tree species in Britain. *Forest Ecology and Management* 141: 31-42.

Petit RJ, Bialozyt R, Garnier-Géré P, Hampe A (2004) Ecology and genetics of tree invasions: from recent introductions to Quaternary migrations. *Forest Ecology and Management* 197: 117-137.

Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190: 231-259.

Pimentel D, Zuniga R, Morrison D (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. *ecological Economics* 52: 273-288.

Prentis PJ, Wilson JRU, Dormontt EE, Richardson D, Lowe AJ (2008) Adaptive evolution in invasive species. *Trends in Plant Science* 13: 288-294.

Pyšek P , Richardson D (2008) Invasive plants. Pages 2011-2020 *in* Jørgensen S, editor. *Encyclopedia of ecology*. Elsevier, Amsterdam.

Richardson D (2011a) *Fifty years of invasion ecology. The legacy of Charles Elton*. Wiley-Blackwell, Oxford.

Richardson D (2011b) Invasion science: The roads travelled and the roads ahead. *in* Richardson D, editor. *Fifty years of invasion ecology. The legacy of Charles Elton*. Wiley-Blackwell, Oxford.

Richardson D , Rejmánek M (2011) Trees and shrubs as invasive alien species - a global review. *Diversity and Distributions* 17: 788-809.

Rieseberg lH, Kim S-C, Randell RA, et al. (2007) Hybridization and the colonization of novel habitats by annual sunflowers. *Genetica* 129: 149-165.

Sarasola JH , Negro JJ (2006) Role of exotic tree stands on the current distribution and social behaviour of Swainson's hawk, Buteo swainsoni in the Argentine Pampas. *Journal of Biogeography* 33: 1096-1101.

Schierenbeck KA , Ellstrand NC (2009) Hybridization and the evolution of invasiveness in plants and other organisms. *Biological Invasions* 11: 1093-1105.

Shackelford N, Hobbs RJ, Heller NE, Hallett LM, Seastedt TR (2013) Finding a middle-ground: The native/non-native debate. *Biological Conservation* 158: 55-62.

Shi L, Zhang Z, Zhang C, Zhang J (2004) Effects of sand burial on survival, growth, gas exchange and biomass allocation of Ulmus pumila seedlings in the Hunshandak Sandland, China. *Annals of Botany* 94: 553-560.

Siemann E , Rogers WE (2001) Genetic differences in growth of an invasive tree species. *Ecology Letters* 4: 514-518.

Smalley EB , Guries RP (2000) Asian elms: sources of disease and insect resistance. Pages 215-230 *in* Dunn CP, editor. *The elms - breeding, conservation, and disease management*. Kluwer Academic Publishers, Boston.

Thébaud C , Simberloff D (2001) Are plants really larger in their indroduced ranges? *The American Naturalist* 157: 231-236.

Todzia CA , Panero JL (1998) A new species of *Ulmus* (Ulmaceae) from southern Mexico and a synopsis of the species in Mexico. *Brittonia* 50: 343-347.

Townsend A (1975) Crossability patterns and morphological variation among elm species and hybrids. *Silvae Genetica* 24: 18-23.

USDA (1974) *Seeds of woody plants in the United States*. USDA Forest Service.

USDA , NRCS (2011) The PLANTS Database. National Plant Data Team, Greensboro, NC 27401-4901 USA. http://plants.usda.gov [accessed 05.10.2011].

USDA Forest Service (2005) Weed of the week - Siberian elm (*Ulmus pumila* L.). http://www.na.fs.fed.us/fhp/invasive_plants/weeds/siberian-elm.pdf [accessed 13.02.2013].

USDA Forest Service (2012) Field guide for managing Siberian elm in the Southwest. http://www.fs.usda.gov/Internet/FSE_DOCUMENTS/stelprdb5410128.pdf [accessed 20.04.2013].

Volis S, Mendlinger S, Ward D (2002) Differentiation in populations of *Hordeum spontaneum* along a gradient of environmental productivity and predictability: life history and local adaptation. *Biological Journal of the Linnean Society* 77: 479-490.

Webb WE (1948) A report on *Ulmus pumila* in the Great Plains region of the United States *Journal of Forestry* 46: 274-278.

Weber E , Schmid B (1998) Latitudinal population differentialtion in two species of *Solidago* (Asteraceae) introduced into Europe. *American Journal of Botany* 85: 1110-1121.

Wesche K, Walther D, von Wehrden H, Hensen I (2011) Trees in the desert: Reproduction and genetic structure of fragmented *Ulmus pumila* forests in Mongolian drylands. *Flora - Morphology, Distribution, Functional Ecology of Plants* 206: 91-99.

Whitney KD , Gabler CA (2008) Rapid evolution in introduced species, ‘invasive traits’ and recipient communities: challenges for predicting invasive potential. *Diversity and Distributions* 14: 569-580.

Whitney KD, Randell RA, Rieseberg lH (2010) Adaptive introgression of abiotic tolerance traits in the sunflower *Helianthus annuus*. *New Phytologist* 187: 230-239.

Wiegrefe SJ, Sytsma KJ, Guries RP (1994) Phylogeny of elms (Ulmus, Ulmaceae): Molecular evidence for a sectional classification. *Systematic Botany* 4: 590-612.

Wu ZY, Raven PH, Hong DY, editors. (2003) Flora of China. Vol. 5 (Ulmaceae through Basellaceae).

Science Press, Beijing, and Missouri Botanical Garden Press, St. Louis. http://www.efloras.org [accessed 20.11.2010].

Zalapa JE, Brunet J, Guries RP (2009) Patterns of hybridization and introgression between invasive *Ulmus pumila* (Ulmaceae) and native *U. rubra*. *American Journal of Botany* 96: 1116-1128.

Zalapa JE, Brunet J, Guries RP (2010) The extent of hybridization and its impact on the genetic diversity and population structure of an invasive tree, *Ulmus pumila* (Ulmaceae). *Evolutionary Applications* 3: 157-168.

Zalba SM , Villamil CB (2002) Woody plant invasion in relictual grasslands. *Biological Invasions* 4: 55-72.

Zavaleta ES, Hobbs RJ, Mooney H (2001) Viewing invasive species removal in a whole-ecosystem context. *Ecology & Evolution* 16: 454-459.

Zou J, Rogers WE, Siemann E (2007) Differences in morphological and physiological traits between native and invasive populations of *Sapium sebiferum*. *Functional Ecology* 21: 721-730.

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I thank Heike Zimmermann and Henrik von Wehrden for their suggestion to investigate the invasion success of *Ulmus pumila*. Furthermore, my thanks go to Karsten Wesche and Daniel Renison. Both provided valuable help for the thesis design and during the publication processes. I also thank Matthias Schleunig for his support during the planning of this thesis.

This thesis would not have been possible without the many people assisting in the sample collection. Therefore I would like to thank Ricardo Suarez for the sampling in Argentina. I thank Ximing Zhang, Zhenying Huang, Lidia Yakovchenko, Batlai Oyuntsetseg, and Alexander Suchorukow for sending samples from Asia. I am grateful to Denny Walter and Karsten Wesche who dedicated samples from former research to me. In regards to my field trip and sample collection in the United States I wish to thank Al and Betty Schneider, Steve and Patti Hegji, Dick and Jennie Bosch, Roger and Marie Peterson, Bob Sivinski, Tim Lowrey, Tony Frates, James Smith, and Bill King for leading me to *U. pumila* populations and/or providing hospitality and for making this trip an unforgettable experience. I am also thankful to the members of the native plant societies of New Mexico, Colorado, Utah, Idaho, Oregon, and Washington State who contributed to the detection of elm populations or to the obtaining of interesting facts about the invasion process of the Siberian elm.

I am thankful to the students who willingly consented to serve as guinea pigs to test my supervising skills. Matthias Hartmann and Catherina Wypior, my first two bachelor students, did a great job during all phases of their work. I am also really thankful for their additional assistance, patience and good spirit. I would like to thank Carolin Kleindienst who completed a great bachelor thesis and who was a great help in the lab. I am thankful to Jenny Klatt for doing a great job during the research group internship.

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In regards to my research visit at the University of Wisconsin I would like to thank Johanne Brunet, Juan Zalapa, and their working group members. They made me feel truly welcome and provided invaluable help during my work there. I am indepted to Brandon Schlautman for his help in respect to the genotyping issues. I also thank Matthias Hartmann for his companionship and work during this visit. I really enjoyed the time.

I thank Heike Zimmermann, Henrik, Linus, and Alwin von Wehrden for the kind hospitality during my research visits in Lueneburg. I am also thankful to Jannes Münchow for his company during several of these stays and for the nice discussions with him. Furthermore I thank Fabienne Gralla and Patric Brandt who admitted me very quickly to the Lueneburg working group.

I would like to thank all co-authors. They provided invaluable help and I have learned a lot from their experience. My thanks also go out to everyone who helped on various questions and practical issues: Kathleen Prinz, Christiane Ritz, Evsey Kosman, Heike Hecklau, Grit Winterfeld, Nicole Fuentes, Tim Scharbel, Elke Seeber, Viktoria Wagner, Erik Welk, Walter Durka, Sabine Both, Alexandra Erfmeier, Susanne Lachmuth, and Helge Bruelheide.

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Christoph Rosche and Lotte Korell gave me diverse support for my thesis as well as in my private life. Thanks for being who you are!

I am thankful for financial support by the graduate scholarship from the government of the state of Saxony-Anhalt and by travel grants from the German Academic Exchange Service (DAAD). I thank Christoph Rosche, Lotte Korell, and Matthias Hartmann for having a final look over the thesis text, and I thank Al Schneider for polishing my written English.

Last but not least I will share the credit for my work with my family and friends for their support, appreciation and patience during the whole time.

APPENDIX 1

PUBLICATIONS OF THE DISSERTATION

Hirsch H, Wypior C, von Wehrden H, Wesche K, Renison D, Hensen I (2012) Germination performance of native and non-native *Ulmus pumila* populations. *NeoBiota* 15: 53-68.

Hirsch H, von Wehrden H, Wesche K, Renison D, Wypior C, Hartmann M, Hensen I (in review) Evolution of an invasive tree: invasive Siberian elms outperforme native individuals. *Biological Invasions*.

Hirsch H, Zalapa JE, Brunet J, von Wehrden H, Hartmann M, Schlautman BJ, Kosman E, Wesche K, Renison D, Hensen I (submitted) Is the invasive Siberian elm a hybrid super villain? - A multi-continental survey. *Molecular Ecology*.

Hirsch H, Kleindienst C, von Wehrden H, Wesche K, Renison D, Hensen I (manuscript) Molecular evidence for multiple introductions of invasive Siberian elms in North and South America.

OTHER PUBLICATIONS BY THE AUTHOR

In preparation / submitted:

Hartmann M, Hirsch H, von Wehrden H, Brunet J, Zalapa JE, Schlautman BJ, Hensen I (in prep.) A comparative study on morphological leaf traits of native and non-native *Ulmus pumila* populations.

Hensen I, Hamasha H, Hirsch H, Wesche K (in prep.) Genetic structure of the rare *Poa badensis* (Poaceae) in Europe.

Hirsch H, Hartmann M, Herzog P, Wagner V, Wesche K, Hensen I, von Wehrden H (submitted) A critical comparison of GENALEX and R regarding explained variance in PCoA. *Molecular Ecology Resources*.

Lett I, Hensen I, Hirsch H, Rension D (submitted) No differences in genetic diversity between native and invasive of *Cotoneaster franchetii* shrubs between native and non-native ranges.

Schlautman BJ, Zalapa JE, Cooper KJ, Thomasson JR, Hirsch H, Hartmann M, Guries RP, Brunet J (in prep.) Using genotypic profiles to identify morphological traits distinguishing *Ulmus pumila*, *U. rubra*, and their hybrids.

Stein K, Hirsch H, Kindermann A, Köhler J, Rosche C, Hensen I (in review) The influence of fragmentation on clonal diversity and genetic structure of *Heliconia angusta*, an endemic understorey herb of the Brazilian Atlantic Rainforest. *Journal of Tropical Ecology*.

Wagner V, Hirsch H, Seifert M, Danihelka J, Ruprecht E, Hensen I (in prep.) Genetic evidence for the central-marginal hypothesis in *Adonis vernalis*.

Wypior C, Hirsch H, Seeber E, Hensen I (in prep.) Does population size influence genetic diversity and germination in *Salvia pratensis*?

2011:

Hensen I, Teich I, Hirsch H, von Wehrden H, Renison D (2011) Range-wide genetic structure and diversity of the endemic treeline species *Polylepis australis* (Rosaceae) in Argentina. *American Journal of Botany* 98: 1825-1833.

Hensen I, Cierjacks A, Hirsch H, Kessler M, Romoleroux K, Renison D, Wesche K (2011) Historical fragmentation has highly affected one of the world highest tropical mountain forests. *Global Ecology and Biogeography* 21: 455-464.

Hirsch H, Zimmermann H, Ritz CM, Wissemann V, von Wehrden H, Renison D, Wesche K, Welk E, Hensen I (2011) Tracking the Origin of Invasive *Rosa rubiginosa* Populations in Argentina. *International Journal of Plant Sciences* 172: 521-529.

2010:

Schmidt-Lebuhn AN, Fuchs J, Hertel D, Hirsch H, Toivonen J, Kessler M (2010) An Andean radiation: Polyploidy in the tree genus *Polylepis* (Rosaceae, Sanguisorbeae). *Plant Biology* 12: 917-926.

Zimmermann H, Ritz CM, Hirsch H, Renison D, Wesche K, Hensen I (2010) Highly reduced genetic diversity of *Rosa rubiginosa* L. populations in the invasive range. *International Journal of Plant Sciences* 171: 435–446.

CONFERENCE CONTRIBUTIONS AND INVITED TALKS

2012:

Hirsch H: Investigations on the invasion success of *Ulmus pumila*. Leuphana University Lueneburg, 05.12.2012. Invited talk.

Hirsch H, von Wehrden H, Wesche K, Renison D, Hensen I: The adaptive evolution of an invasive tree. 42nd Annual Meeting of the Ecological Society of Germany, Austria and Switzerland (GfÖ), 10.-14.09.2012, Lüneburg. Talk.

Hirsch H: The adaptive evolution of an invasive tree in North America and Argentina. Leuphana University Lueneburg, 06.06.2012. Invited talk.

Hirsch H, Kleindienst C, von Wehrden H, Wesche K, Renison D, Hensen I: Studies on the introduction history and climatic adaptation of invasive *Ulmus pumila* populations in North America and Argentina using cpSSR markers. 45th Population Genetics Group Meeting, 04.-07.01.2012, Nottingham, UK. Talk.

2011:

Hirsch H: Invasion success of *Ulmus pumila* L. (Ulmaceae) in North America and Argentina: adaptation or environment?, Department of chemical ecology, Universtity Bielefeld, 17.11.2011. Invited talk.

Rosche C, Hirsch H, Schrieber K, Lachmuth S, Hensen I: Zur Populationsökologie von *Antennaria dioica*. Versammlung des Ziel 3 / Cíl 3-Programms zur Förderung der grenzübergreifenden Zusammenarbeit 2007 - 2013 zwischen dem Freistaat Sachsen und der Tschechischen Republik, 05.11.2011, Ústí nad Labem. Talk by C. Rosche.

Cierjacks A, Hensen I, Hirsch H, Kessler M, Romoleroux K, Renison D, Wesche K: Fragmentation affects genetic diversity of a high-altitude *Polylepis* forest. 41st Annual Meeting of the Ecological Society of Germany, Austria and Switzerland (GfÖ), 05.-08.09.2011, Oldenburg. Talk by A. Chierjacks.

Hirsch H, Zalapa JE, Brunet J, Kosman E, von Wehrden H, Wesche K, Renison D, Hensen I: Genetic diversity and extent of hybridization of invasive *Ulmus pumila*. 41st Annual Meeting of the Ecological Society of Germany, Austria and Switzerland (GfÖ), 05.-08.09.2011, Oldenburg. Talk.

Hirsch H, Wypior C, von Wehrden H, Wesche K, Renison D, Hensen I: Are invasives better? - A comparison of hydrochoric spread and germination performance between native and invasive *Ulmus pumila* populations. 24th Annual conference of the Plant Population Biology Section of the Ecological Society of Germany, Switzerland and Austria (GfÖ), 02.-04.06.2011, Oxford, UK. Talk.

2010:

Hirsch H, von Wehrden H, Wesche K, Renison D, Hensen I: Invasion success of *Ulmus pumila* in North America and Argentina: environment or adaptation? 6th NOEOBIOTA conference, 14.-17.09.2010, Copenhagen. Poster.

Zimmermann H, von Wehrden H, Hirsch H, Damascos M, Bran D, Welk E, Wesche K, Ritz C, Wissemann V, Renison D, Hensen I: The invasion success of *Rosa rubiginosa* across diverse ecosystems and climates despite its highly reduced genetic diversity. 6th NEOBIOTA conference, 14.-17.09.2010, Copenhagen. Talk by H. Zimmermann.

2009:

Teich I, Hirsch H, Renison D, von Wehrden H, Hensen I: Genetic structure of endemic *Polylepis australis* Bitt. tree populations in Argentina. 39th Annual conference of the Ecological Society of Germany, Switzerland and Austria (GfÖ), 14.-18.09.2009, Bayreuth. Poster.

Hirsch H, Zimmermann H, von Wehrden H, Renison D, Ritz CM, Wissemann V, Wesche K, Welk E, Hensen I: *Rosa rubiginosa* L. (Rosaceae) invasion in Argentina: European origin and potential progression. 39th Annual conference of the Ecological Society of Germany, Switzerland and Austria (GfÖ), 14.-18.09.2009, Bayreuth. Talk.

Hirsch H, Zimmermann H, von Wehrden H, Renison D, Ritz CM, Hensen I: Where is the European origin of the *Rosa rubiginosa* L. (Rosaceae) invasion in Argentina? 22nd Annual conference of the Plant Population Biology Section of the Ecological Society of Germany, Switzerland and Austria (GfÖ), 21.-24.05.2009, Bern. Poster.

CURRICULUM VITAE

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University education

October 2003 – November 2008	Studies in biology, Martin-Luther-University (MLU) Halle-Wittenberg	
	Major subject:	Geobotany
	Minor subjects:	Zoology, soil science, nature conservation
	Diploma thesis:	„European origin of the invasive *Rosa rubiginosa* L. (Rosaceae) in Argentina - an analysis with microsatellite markers“
	Thesis advisor:	Prof. Dr. Isabell Hensen
	Final mark: 1.0 (excellent)	
January 2010 – present	PhD student at the MLU Halle-Wittenberg, Institute of Biology / Geobotany and Botanical garden	
	Reseach topic:	“Investigations on the invasion success of *Ulmus pumila* – A multi-continental survey”
	Funding:	Scholarship of the federal state Sachsen-Anhalt; German Academic Exchange Service (DAAD)
	Thesis advisors:	Prof. Dr. Isabell Hensen and Prof. Dr. Henrik von Wehrden

Practical and occupational experience

July 2006 – August 2006	Internship at the lower nature conservation authority of the city Zwickau, Germany (4 weeks)
April 2007 August 2007 September – November 2007 August 2008 October – December 2008	Student research assistant at the MLU Halle-Wittenberg, Institute of Biology, Geobotany and Botanical Garden
January 2009 – December 2009	Scientific assistant at the MLU Halle-Wittenberg, Institute of Biology, Geobotany and Botanical Garden (annual deputyship parental leave)

Research experience abroad

February – March 2007	5 weeks fieldwork in Argentina (vegetation assessments within the DFG project "Explanation and prediction of the invasion processes of *Rosa rubiginosa* L. and *Cotoneaster franchetii* Bois (Rosaceae) in Argentina")
May – August 2010	3 months fieldwork in the United States (New Mexico, Colorado, Utah, Idaho, Oregon, and Washington) for my PhD project
February – April 2012	2 months post graduate research at the University of Wisconsin, Madison for my PhD project (collaboration with Prof. Dr. Juan E. Zalapa and Prof. Dr. Johanne Brunet)

Teaching

February – March 2009	Seminar "Introduction to R" at the MLU Halle-Wittenberg (together with H. von Wehrden, J. Hanspach, H. Zimmermann, H. Bruelheide, S. Ebeling and J. Wehnert)
April 2009, May 2010 and April 2011	Excursion for students (Vegetation of riparian forests) at the MLU Halle-Wittenberg
June 2009	Lecture "Introduction to the R language" at the MLU Halle-Wittenberg
November 2009	Seminar “Statistics for ornithologists” for members of the ornithological societies Saxony and Saxony-Anhalt (together with M. Beckmann)
January – February 2011	R introduction for statistics (together with H. Bruelheide, S. Lachmuth and D. Eichenberg) at the MLU Halle-Wittenberg

May, July 2011 and 2012	Basic practicum in ecology at the MLU Halle-Wittenberg (teaching assignments)
October / November 2012	Seminar “Introduction to statistics in R” at the Georg-August-University Goettingen (teaching assignment)

Supervision of theses and research group internships

2010 / 2011	Matthias Hartmann. Bachelor thesis: “Comparison of genetic diversity and structure between native and invasive populations of *Ulmus pumila* L.”. Obtained excellent grade.
2010 / 2011	Catherina Wypior. Bachelor thesis: “Hydochory and germination performance in native and invasive *Ulmus pumila* populations”. Obtained excellent grade.
2011	Carolin Kleindienst. Bachelor thesis: “Native origin of invasive *Ulmus pumila* populations in North America and Argentina. Obtained excellent grade.
2011	Jenny Klatt. Research group internship: Analysis of soil parameters in *Ulmus pumila* populations.
2011 / 2012	Matthias Hartmann. Research group internship: Comparison of the leaf morphology in native and invasive *Ulmus pumila* populations.
2011 / 2012	Catherina Wypior. Research group internship: Genetic diversity of *Salvia pratensis* in connection with population size.

Miscellaneous

2009 / 2010	Mentee within the mentoring program for junior female scientists in MINT subjects (MLU Halle-Wittenberg and Otto-von-Guericke-University Magdeburg); mentor: Prof. Dr. Caroline Müller (University Bielefeld)
July 2011	Final editing of the accreditation for the faculty of natural sciences, MLU Halle-Wittenberg

Language skills

German (native speaker)

English (fluency in both written and spoken)

Spanish (basic knowledge)

APPENDIX 2

ERKLÄRUNG ÜBER DEN PERSÖNLICHEN ANTEIL AN DEN PUBLIKATIONEN

1. Study (Chapter 2):

Hirsch H, Wypior C, von Wehrden H, Wesche K, Renison D, Hensen I (2012) Germination performance of native and non-native *Ulmus pumila* populations. *NeoBiota* 15: 53-68.

Field work:	**Heidi Hirsch** (50 %); Zhenying Huang and Ximing Zhang (together 50 %)
Laboratory work:	Catherina Wypior (85 %); **Heidi Hirsch** (15 %)
Analysis:	**Heidi Hirsch** (70 %); Henrik von Wehrden and Catherina Wypior (together 30 %)
Writing:	**Heidi Hirsch** (80 %; corrections by Isabell Hensen, Daniel Renison, Henrik von Wehrden, Karsten Wesche and Catherina Wypior)

2. Study (Chapter 3):

Hirsch H, von Wehrden H, Wesche K, Renison D, Wypior C, Hartmann M, Hensen I (in review) Evolution of an invasive tree: invasive Siberian elms outperforme native individuals. *Biological Invasions*.

Field work:	**Heidi Hirsch** (40 %); Zhenying Huang, Ricardo Suarez and Ximing Zhang (together 60 %)
Laboratory work:	**Heidi Hirsch** (80 %); Matthias Hartmann and Catherina Wypior (together 20 %)
Analysis:	**Heidi Hirsch** (90 %); Henrik von Wehrden (10 %)
Writing:	**Heidi Hirsch** (80 %; corrections by Matthias Hartmann, Isabell Hensen, Daniel Renison, Henrik von Wehrden, Karsten Wesche and Catherina Wypior)

3. Study (Chapter 4):

Hirsch H, Zalapa J, Brunet J, von Wehrden H, Hartmann M, Schlautman B, Kosman E, Wesche K, Renison D, Hensen I (submitted) Is the invasive Siberian elm a hybrid super villain? - A multi-continental survey. *Molecular Ecology*.

Field work:	**Heidi Hirsch** (50 %); Zhenying Huang, Ricardo Suarez, Juan Zalapa and Ximing Zhang (together 50 %)
Laboratory work:	**Heidi Hirsch** (80 %), Matthias Hartmann and Brandon Schlautman (together 20 %)
Analysis:	**Heidi Hirsch** (80 %), Johanne Brunet, Matthias Hartmann, Evsey Kosman, Bandon Schlautman and Juan Zalapa (together 20 %)
Writing:	**Heidi Hirsch** (80 %; corrections by Johanne Brunet, Matthias Hartmann, Isabell Hensen, Evsey Kosman, Daniel Renison, Brandon Schlautman, Henrik von Wehrden, Karsten Wesche and Juan Zalapa)

4. Study (Chapter 5):

Hirsch H, Kleindienst C, von Wehrden H, Wesche K, Renison D, Hensen I (manuscript) Molecular evidence for multiple introductions of invasive Siberian elms in North and South America.

Field work:	**Heidi Hirsch** (50 %); Zhenying Huang, Batlai Oyuntsetseg, Ricardo Suarez, Alexander Suchorukow and Ximing Zhang (together 50 %)
Laboratory work:	Carolin Kleindienst (70 %), **Heidi Hirsch** (30 %)
Analysis:	**Heidi Hirsch** (60 %), Carolin Kleindienst and Henrik von Wehrden (together 40 %)
Writing:	**Heidi Hirsch** (90 %; corrections by Isabell Hensen, Carolin Kleindienst, Daniel Renison, Henrik von Wehrden and Karsten Wesche)

EIGENSTÄNDIGKEITSERKLÄRUNG

Hiermit erkläre ich, dass diese Arbeit nicht bereits zu einem früheren Zeitpunkt der Naturwissenschaftlichen Fakultät I – Biowissenschaften der Martin-Luther-Universität Halle-Wittenberg oder einer anderen wissenschaftlichen Einrichtung zur 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. Im Übrigen erkläre ich, dass ich mich bisher noch nie um einen Doktorgrad beworben habe.

Halle (Saale), den 23.05.2013

Unterschrift: ________________________________

(Heidi Hirsch)