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General Introduction

In 1901, the water hyacinth (*Eichhornia crassipes*) was introduced from South America into China as a good fodder plant. However, one hundred years later this plant has led to serious environmental- and economical problems in China. Because of large coverage of this weed on water, sunlight penetration as well as oxygen content in the water is reduced, which has a severe negative impact on the water ecosystem. For example 60% of the local species living in Dianchi Lake (Yunnan Province) was wiped out by the invasion of the water hyacinth. Furthermore these waters are difficult to cross by ship and many canals have irrigation and drainage problems. In Shanghai more than 10 million USD is spent on this pest species each year (Villamagna and Murphy 2010).

The introduction of species from one area into another is a natural process that has always been a part of evolutionary history. However, the deliberate and undeliberate transport of species by humans, starting circa 10.000 years ago during the Neolithic Revolution added considerably to the frequency of new introductions. As an early example, around 4.000 B.C. domesticated pigs were introduced in Europe from Asia and crossed with wild pigs (Larson et al. 2007). The increase of human migrations and trade in the 19th century was accompanied by the spread of domesticated species like cereals, rice and cattle (Di Castri 1989) and the accidental spread of natural species as contaminants, like the brown rat (Atkinson 1977) and the zebra mussel (Mooney and Cleland 2001). With these activities, species were even able to spread from one continent to the other, crossing almost insurmountable biogeographical barriers (Mooney and Cleland 2001) and maintained themselves in these new environments in many cases.

Invasive plant species are defined as species that manage to cope with the new environment, disperse to other local communities and become extraordinarily prominent in their range (Moutou and Pastoret 2010). Species that adjust to other climate conditions and therefore have a possibility to shift ranges can also be considered as potential invaders (Engelkes et al. 2008). Species can receive a pest status if they have a negative impact on human health, are a pest in agricultural crops, lead to a loss of native biodiversity due to competition or predation, or cause habitat degradation and disruption. Several examples document these negative impacts. The invasive black mustard (*Brassica nigra*) increased the herbivore pressure on a native bunchgrass in the United States (Orrock et al. 2008). Kudzu (*Pueraria lobata*) introduced in the United States for erosion control is now a pest species threatening native ecosystems due to its rapid growth rate (Forseth and Innis 2004). Common ragweed (*Ambrosia artemisiifolia*) originated from North America was introduced undeliberately into Europe and is nowadays presenting a major health problem because of its highly allergenic pollen. Furthermore ragweed is estimated to reduce corn crops yield by 55% (Makra et al. 2005).

Besides the impact on the environment, invasions can have an economic impact in two ways. Firstly invasive species may negatively affect crop and forestry production and grazing capacity. Secondly there are the direct costs of combating invasions like control and quarantine measures (Mack et al. 2000). For the United States the annual cost of all invasive species (plants, animals and microorganisms) is estimated to exceed 138 billion dollar per year (Pimentel et al. 2005).

In this thesis I will focus on the mechanisms that contribute to the invasiveness of a plant species and on finding the source populations of invasive plant species. This is important in light of predicting a potential pest species.

Theories on invasive plant species

To become invasive, a plant has to go through four stages; transport, colonization, establishment and becoming abundant and widespread (Vermeij 1996). Although many species are introduced, only a small number of them can establish and even a smaller proportion can maintain and spread in the new area. Several theories aim to explain the success of invasive plant species (Lodge 1993, Mack et al. 2000, Eppinga et al. 2006, Ren and Zhang 2009, Verhoeven et al. 2010).

In this thesis I will focus on theories that emphasize the plant's release from herbivores of the native area. The *Enemy Release Hypothesis* (ERH) (Keane and Crawley 2002) states that when plants are introduced into the new area they leave behind their specialist herbivores and therefore experience a reduced herbivore pressure in the invasive area. Building on the ERH, the *Evolution of Increased Competitive Ability* (EICA) hypothesis (Blossey and Notzold 1995) predicts that, under reduced enemy pressure, selection may shift the resource allocation of invasive plant species from defence to growth. This allocation to growth also results in a higher reproduction, giving the invasive plants a competitive advantage over local plants. So in contrast with the ERH, which is based on an ecological change, the EICA hypothesis is also based on an evolutionary change. Although natural selection may decrease defence compounds of plants in the new area, plants are still in need for defences against generalist herbivores in the invasive area. Plants employ different defences against generalist and specialist herbivores. Feeny (1976) and Rhoades & Cates (1976) simultaneously developed the *Apparency theory*, which makes a distinction between "quantitative" and "qualitative" defences (Feeny 1976, Rhoades and Cates 1976). Quantitative defences are digestibility reducers (e.g. tough leaves, thorns) and occur in high concentrations which make them expensive to produce. Quantitative defences act against specialist as well as generalist herbivores. Qualitative defences are toxins (e.g. phenolics, alkaloids) and occur in relatively low quantities, which make them a cheaper defence compared to quantitative defences. They act against generalist herbivores but specialist herbivores are often adapted to these defences and can even use these chemicals as a cue to locate their host plant as a feeding or oviposition stimulant or sequestrate them for their own defence (Bernays et al. 2003, Macel and Vrieling 2003). Digestibility reducers provide protection against both generalist and specialist herbivores but have a high allocation cost (Glawe et al. 2003). On the other hand toxins have a lower allocation cost and defend the plant against generalists but simultaneously makes the plant more vulnerable to adapted specialist herbivores. This dilemma is referred to as the *specialist-generalist dilemma* (van der Meijden 1996). For plants introduced into areas where specialist herbivores are absent, this dilemma does not longer exists. The expectation is that in the invasive area levels of expensive digestibility reducers are decreased at the expense of cheap toxins, through natural selection, yielding an energy surplus that can be diverted to growth and reproduction. This evolutionary shift of quantitative defence to qualitative defence in the invasive area is called the *Shifting Defence Hypothesis* (SDH) (Muller-Scharer et

al. 2004, Joshi and Vrieling 2005). In this thesis I will focus on testing the SDH and particularly I will focus on the predicted decrease in quantitative defences in the invasive area.

Evolution or preadaptation in invasive plant species

The potency of an introduced species to evolve depends on the genetic variation introduced in the new area. About fifty years ago it was already discussed how genetic architecture might impact the possibility of a species to maintain and spread in the new area (Baker and Stebbins 1965). However it lasted another 30 years before proper experimental studies were carried out. These studies of natural populations showed that evolutionary changes can happen rapidly in invasive species (Grant and Grant 1995, Losos et al. 1997, Reznick et al. 1997). Several studies are carried out on trait differences between native and invasive individuals (Siemann and Rogers 2001, Leger and Rice 2003). Apart from some studies (Grant and Grant 1995, Losos et al. 1997) most studies, like the study by Joshi and Vrieling (2005), compared random populations from the native area with those from the invasive area. They assumed that trait differences are based on evolutionary changes without taking preadaptation into account (Bossdorf et al. 2005, Abhilasha and Joshi 2009). Preadaptation assumes the introduction of a (small) subset of genotypes from the native range from one or few populations with by coincidence "preadapted" traits into the invasive range (Dlugosch and Parker 2007). Observed trait differences between native and invasive individuals are in such case not due to adaptation by natural selection acting upon new mutations but by accidental introduction of genotypes which already possessed "adaptive" traits upon introduction. The chance that multiple introductions from different source populations all contain "preadapted" individuals is very small. For this reason preadaptation is only expected to occur when there is one or very few introduction(s).

To establish whether evolution or preadaptation took place in invasive individuals, ecological traits of the source population(s) need to be compared with ecological traits of the introduced population in a common environment (Bossdorf et al. 2005, Abhilasha and Joshi 2009). Evolution has taken place if the introduced and source population differ significantly in the ecological traits of interest. Unfortunately the source population(s) is (are) seldom known.

The room for evolutionary change can be increased if multiple introductions lead to new combinations of genotypes. It has been hypothesized that multiple introductions may lead to especially problematic invaders (Ellstrand and Schierenbeck 2000, Verhoeven et al. 2010). Recent research indicates that multiple introductions are quite common in invasive species (Williams et al. 2005, Chun et al. 2010, Lachmuth et al. 2010). Admixture of genotypes from different sources can lead to novel genotypes in invasive populations compared to native populations which might result in a fast evolutionary response to selection pressure (Hufbauer 2008, Prentis et al. 2008). Furthermore admixture can mask the inbreeding load (Verhoeven et al. 2010). In this thesis I will determine the source populations of an invasive species to determine if this species evolved upon introduction or that preadapted individuals were introduced. As a model system I will use *Jacobaea vulgaris*.

Common ragwort

Common ragwort, or *Jacobaea vulgaris*, formerly known as *Senecio jacobaea* (Pelser et al. 2004), belongs to the Asteraceae. It is a native Eurasian plant species whose native range extends from southern Norway into northern Spain and from Great Britain to the Ural mountains (Harper and Wood 1957). It has been introduced to New Zealand, Australia, North America and Canada where it is a pest species

(Harper and Wood 1957). This perennial monocarpic species has four distinct life history stages: seeds, seedlings, rosettes and flowering plants. Rosettes must achieve a minimum size before they can be vernalized (Wesselingh and Klinkhamer 1996), but under ideal conditions plants behave as strict biennials (van der Meijden and van der Waals-Kooi 1979). Common ragwort produces a large number of seeds which can survive for several years in the soil (van der Meijden and van der Waals-Kooi 1979) and are dispersed by wind. It is self-incompatible (Kirk et al. 2005) and pollinated by insects, mainly bees, wasps (hymenopteran) and flies (dipteran) (Harper and Wood 1957).

In Great Britain *J. vulgaris* is attacked by more than 70 specialist as well as generalist herbivores (Harper and Wood 1957). Especially the presence of specialist herbivores like the cinnabar moth (*Tyria jacobaeae*), the fleabeetle (*Longitarsus jacobaeae*) and the ragwort seed fly (*Botanophila seneciella*) can have a negative impact on the fitness of *J. vulgaris* (McEvoy and Coombs 1999). As a defence against attackers *J. vulgaris* produces pyrrolizidine alkaloids (PAs). PAs are deterrent against generalist herbivores whereas specialist herbivores are attracted to it and it can even function as oviposition and feeding stimulants (van Dam and Vrieling 1994, Macel and Vrieling 2003). It is reported for several specialist herbivores that they sequester PAs and use these as a defence against their predators (Eisner and Eisner 1991). PAs can be lethal to many vertebrates like cattle and horses, who can not distinguish toxic ragwort from non-toxic herbs in hay (Harper and Wood 1957). The cumulative storage of PAs in the liver leads to a sudden death in apparently healthy cows and horses. These PAs can even pose a threat to humans as it can be found in milk and honey (Hoogenboom et al. 2011), (Deinzer et al. 1977). They can reduce butterfat of cow's milk and can make honey bitter and off-color (Stegelmeyer et al. 1999). Besides defence, another strategy of *J. vulgaris* to cope with defoliation of herbivores is the ability of fast re-growth after defoliation. After complete defoliation of above ground parts, individuals of *J. vulgaris* still have resources stored in their roots that can be used for fast re-growth (van der Meijden et al. 1988).

Ragwort has become invasive in North America, Australia and New Zealand. Around 1850 *J. vulgaris* was first spotted outside its native range on the east coast of Canada (Harris et al. 1971), followed by New Zealand (Thomson 1922) and Australia (Schmidl 1972) around 1874, and it was noted for the first time on the west coast of the USA (Gilkey 1957) in 1901.

Ragwort is most troublesome in pastures, waste areas and along roadsides because seed survival is related to the amount of vegetative cover (Poole 1940). For example, grazed pastures on Prince Edward Island in Canada had about eight times more *J. vulgaris* plants than ungrazed pastures. Infestations can result in significant livestock losses, decreased pasture yields till 50% and increased management costs (Jacobs 2009). The annual costs of common ragwort to Australia has been estimated at four million dollar, including production losses to the dairy and beef industries and the costs of control (McLaren 1997). Because of the big negative impact in the introduced areas, biocontrol agents like the cinnabar moth (*Tyria jacobaeae*), fleabeetle (*Longitarsus jacobaeae*), a plume moth (*Platptilia isodactylis*) and the ragwort seed fly (*Botanophila seneciella*) were introduced, however with mixed results (Julien et al. 1984, McEvoy et al. 1993).

In a common garden experiment on the invasiveness of *J. vulgaris*, Joshi and Vrieling (2005) (Joshi and Vrieling 2005) examined life history traits in relation to the EICA hypothesis and the SDH. Invasive individuals had a higher growth rate and reproduction compared to native individuals. Furthermore they were better protected against generalists, but less defended against specialists, had a lower ability for

re-growth and produced more pyrrolizidine alkaloids. These outcomes are fully explained by the SDH and partly in line with the EICA hypothesis. It seems that within 200 years *J. vulgaris* has adapted to the invaded area by the evolution of some fitness related life history traits. These trait differences are beneficial under the novel selection conditions and therefore evolution could have occurred (Bossdorf et al. 2005). However, as indicated before, a hypothesis alternative to these assumed evolutionary changes in life history traits, is that invading individuals were preadapted and are a selection of the genotypes present in the native range. To make a distinction between evolution and preadaptation it is crucial to determine the source population(s).

Determining source populations

Reconstructing invasion histories to find source populations is generally a difficult task, as introduction events can occur over large temporal and spatial scales. However, genetic markers can help to identify source populations and can also give insight in the level of admixture by comparing the genetic diversity of introduced and native populations (Bossdorf et al. 2005, Lavergne and Molofsky 2007, Hufbauer and Sforza 2008). Often genetic markers from neutrally evolving areas of the genome are used because these will not be affected by natural selection (Marrs et al. 2008). In several studies polymorphic markers are used to trace source populations with different outcomes. In a study of Lachmuth 2010 et al (Lachmuth et al. 2010) the genetic structure and the source population of the invader *Senecio inaequidens* was investigated. They used nuclear microsatellites and they showed that invasive populations from *S. inaequidens* originated from multiple introductions. Furthermore with the help of historical data, different invasion routes of *S. inaequidens* were clarified. In another study, which also used nuclear microsatellites, the source population of the aggressive weed *Ambrosia artemisiifolia* was traced. It turned out that French invasive populations originated also from a mixture of sources (Chun et al. 2010). Research on the introduction history of the Brazilian peppertree (*Schinus terebinthifolius*), using nuclear microsatellites and chloroplast DNA (cpDNA), identified at least two independent introductions into Florida (Williams et al. 2005). In contrast, research on the invasive plant species *Macfadyena unguis-cati*, using chloroplast microsatellites showed that this invader most probably originated from one single introduction out of the native area (Prentis et al. 2009). I will use AFLP markers and cpDNA markers to determine the source populations of *J. vulgaris*.

Research questions

In this thesis I will test the prediction of a decrease in costly quantitative defence products of invasive *J. vulgaris* individuals as expected by the SDH. In light of possible trade offs, I will investigate if this decrease has consequences for other life history traits. To get more insight about the generality of the SDH I conducted a literature study on several invasive plant species and investigated if the outcomes are supported by the SDH.

To investigate if trait differences between native and invasive individuals of *J. vulgaris* are driven by evolution or preadaptation I searched for the source population(s) of *J. vulgaris*. To get an indication if admixture played a role in the invasive character of this species I have unravelled the genetic structure of native and invasive populations. I have focussed on the following questions.

- 1) Has invasion led to a reduction in costly quantitative defence products and if so, what are the consequences of other fitness related traits?
- 2) Is the shifting defence hypothesis a general phenomenon in invasive plant species?

- 3) Which is/ are the source population(s) of invasive individuals of *J. vulgaris*?
- 4) Is the genetic diversity and differentiation rate of *J. vulgaris* lower in invasive populations compared to native populations and did admixture occur?
- 5) Are trait differences between native and invasive individuals of *J. vulgaris* driven by evolution or preadaptation?

Outline of this thesis

To answer the first question, morphological and physiological traits of native and invasive individuals are measured to investigate if a resource allocation of invasive individuals takes place from expensive quantitative defence as a response to the absence of specialists into life history traits that are beneficial in the new environment (**chapter 2**). In addition in **chapter 3** the second question is answered based on a literature study. A biogeographical approach is used to compare the amount of defence products in native and invasive individuals of the same species. The remaining three questions are answered in chapter 4, 5, and 6. In **chapter 4** an AFLP study is carried out to test for genetic bottlenecks in the invasive populations and to investigate the invasion pathways of *J. vulgaris* from Europe to New Zealand, Australia and North America. In the following chapter (**chapter 5**) polymorphic markers, microsatellites and single nucleotide polymorphisms (SNPs), on the chloroplast genome are developed by sequencing the complete chloroplast genomes of several native and invasive individuals of *J. vulgaris*. The microsatellites and SNPs of the chloroplast are used in **chapter 6** to trace the source population(s) and study the genetic structure of the native and invasive populations of *J. vulgaris*. **Chapter 7** summarizes the findings presented in this thesis and presents general conclusions.

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