Rapid evolution or preadaptation in invasive Jacobaea vulgaris

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Summary

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. The increase of human migrations and trade in the 19th century was accompanied by the spread of domesticated species like cereals, rice and cattle and the accidental spread of natural species as transport contaminants, such as weeds and species like the brown rat and the zebra mussel. With these activities, species were even able to spread from one continent to the other, crossing almost insurmountable biogeographical barriers 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 new range. 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. 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 costs of combatting invasions like control and quarantine measures. For the United States the annual cost of all invasive species (plants, animals and microorganisms) is estimated to exceed 138 billion dollar per year.

Out of the thousands of species that are introduced into new area's only a few percent become invasive. It is still relatively poorly understood why some species become invasive and others do not. In this thesis I will focus on the mechanisms that contribute to the invasiveness of the plant species *Jacobaea vulgaris* or common ragwort. This species belongs to the family of Asteraceae and is native in Europe and Asia where this species does not have a pest status. About 130 years ago, it has been introduced to New Zealand, Australia, North America and Canada where it developed into a pest species. This species leads to problems because it can reach high densities and therefore can decreases native biodiversity locally. Besides this, *J. vulgaris* causes problems because it produces defence compounds, pyrrolizidine alkaloids (PAs), which are poisonous to cattle. After consumption of *Jacobaea vulgaris*, the cumulative storage of PAs in the liver leads to a sudden death in apparently healthy cattle. Furthermore PAs can enter the human food chain through milk and honey.

The PAs produced by *J. vulgaris* are defence compounds against herbivores. However, PAs are not equally effective against all types of herbivores. Generalist herbivores, attacking plant species from several plant families, are deterred by PAs in host plants. In contrast, specialist herbivores, attacking

only one or several plant species of one family, are often adapted to PAs and even can be attracted by these compounds. In the invasive area specialist herbivores of *J. vulgaris* like the cinnabar moth (*Tyria jacobaeae*) and the fleabeetle (*Longitarsus jacobaeae*) were initially absent.

A plant introduced in a new area has the direct benefit of leaving behind its specialist herbivores. The EICA (Evolution of Increased Competitive Ability) hypothesis predicts that, under reduced enemy pressure due to the absence of specialist herbivores, 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. This increases the chance of becoming a pest species in the introduced area.

The EICA hypothesis does not take into account the presence of generalist herbivores in the invasive area which can threaten introduced plants. The Shifting Defence Hypothesis (SDH) predicts that invasive plants will adapt their amount of quantitative and qualitative defence compounds to the presence of generalist herbivores and the absence of specialist herbivores.

Quantitative defences act against specialist as well as generalist herbivores. These defence compounds are digestibility reducers (e.g. tough leaves, thorns) and occur in high concentrations which make them expensive to produce. Qualitative defences act against generalist herbivores. These defence compounds are toxins (e.g. phenolics, alkaloids) and occur in relatively low quantities, which make them a cheaper defence compared to quantitative defences. 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 and may sequestrate them for their own defence. So, qualitative defence compounds produced by plants are no longer repellent but often attractive to specialist herbivores. As a consequence, in the native area there is a risk of attracting specialist herbivores when high amounts of such compounds are produced. To be protected against specialist as well as generalist herbivores, selection in the native area will lead to a balance between quantitative and qualitative defences. For invasive areas, where specialist herbivores are absent, the SDH predicts that levels of expensive digestibility reducers are decreased at the expense of cheap toxins, through natural selection. The energy surplus can than can be diverted to growth and reproduction.

In a previous study on the invasiveness of *J. vulgaris* native and invasive individuals were grown in the same environment. Invasive plants produced significantly more PAs and were better protected against generalists, but less defended against specialists. These outcomes are fully explained by the SDH and it suggests that fast evolution has taken place after introduction.

The potency of an introduced species to adapt depends on the genetic variation introduced in the new area. With high levels of genetic variation, selection can take place without the necessity of new mutations. Such selective processes can lead to genetic differences between individuals in native and invasive areas. These genetic differences can also occur when multiple native populations are introduced into the invasive area and admixture takes place. In this case invasive populations can have higher genetic variation compared to the native populations. An alternative explanation for differences between native and invasive individuals is that by coincidence introduced individuals already contained the traits that were beneficial to maintain themselves in the new area, this is called preadaptation. To establish whether the invasive success of *J. vulgaris* is caused by evolution or preadaptation, it is necessary to trace the source population(s) in the native area. Evolution has taken place if the introduced and source population differ significantly in the ecological traits of interest. If multiple introductions have taken place that lead to invasiveness, there is very little chance that all introduced individuals from different populations already obtaines the preadapted traits before introduction. Therefore the assumption is that preadaptation only can take place with one or few introductions.

My thesis is divided into two parts. In the first part (chapter 2 and 3) I will focus on the mechanisms related to herbivore pressure that can have contributed to the invasiveness of *J. vulgaris*. The second part (chapter 4,5 and 6) is based on tracing the (native) source population(s) of introduced *J. vulgaris* individuals. Detecting the source population is important to investigate if trait differences between native and invasive individuals are driven by evolution or preadaptation. In my thesis the following research questions are posed.

1. Has invasion led to a reduction in costly quantitative defence products and if so, what are the consequences for other fitness related traits?
2. Is the shifting defence a general phenomenon in invasive plant species?
3. What are the source population(s) of invasive individuals of *J. vulgaris*?
4. Is the genetic diversity 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?

In chapter 2 research was carried out on differences in anatomical, physiological- and growth parameters between native and invasive plants of *J. vulgaris*. Due to a decreased herbivore pressure in the invasive area, I hypothesized that selection would lead to a lower production of quantitative defence compounds like thicker cell walls and tougher leaves that are more difficult to digest. Cell walls do contain a substantially amount of nitrogen. The surplus of nitrogen, due to the reduced cell wall thickness can be used for photosynthesis, resulting in more competitive individuals. Results of chapter 2 showed that total photosynthesis is equal or higher in invasive *J. vulgaris* individuals compared to individuals from the native area. However, when photosynthesis was measured per surface unit, no difference was found between native and invasive individuals. Furthermore no differences were found between native and invasive individuals of *J. vulgaris* concerning traits related to quantitative defence, like the amount of cell wall material and leaf dry weight per area, thickness of cell walls and leaf toughness. However a difference in allocation of native individuals of *J. vulgaris* to cope with herbivore pressure of specialists was found. The root-shoot ratio was higher for native *J. vulgaris* plants. A bigger investment in root mass is detrimental to photosynthetic capacity and results in a smaller plant. So, investment in root mass is costly. However, a bigger investment in roots is positively correlated with the capacity of shoot regrowth after defoliation. Native individuals of *J. vulgaris* are often completely defoliated by the larvae of the cinnabar moth (*T. jacobaeae)*. In the native area *J. vulgaris* individuals will be selected for investment in roots, because these plants can regrow fast after defoliation. In the invasive area where *Tyria jacobaeae* is absent, selection favours plants with less investment in roots, yielding a faster growth.

In chapter three I investigated two predictions of the SDH based on a literature study. I have used a biogeographical approach, using only results of studies that compared native and invasive individuals under the same circumstances. My research question was if invasive plants indeed contained a higher level of qualitative defence compounds (toxins) and reduced levels of quantitative defence compounds (digestibility reducers). As expected invasive plants produced a higher concentration of toxins compared to native plants. However, in contrast to our expectation, no difference was found in the amount of quantitative defence compounds between native and invasive individuals. Our results do not completely support the SDH.

In chapter 4 I have used nuclear AFLP ("Amplified Fragment Length Polymorphisms") markers to trace the source population of *J. vulgaris* and to unravel the route of introduction. Neutral markers like AFLPs are useful for this research because no selection takes place on these markers. In total 38 native individuals spread over 15 populations and 44 invasive individuals spread over 16 invasive populations were analysed. Only ten percent of the total genetic variation in AFLP markers was explained by the difference between individuals coming from the native and invasive area. Within the native area populations of *J. vulgaris* differed significantly from each other in genetic variation, in contrast with invasive populations. Despite the big geographical distance, populations from the different invasive regions (Australia, New Zealand and North America) did not differ from each other in the amount of genetic variation. Besides, no decrease was found in the number of polymorphic AFLP markers although the allele frequencies did differ of individuals from the invasive area compared with individuals from the native area. This suggests that there have been multiple source populations. Moreover the lack of differentiation between invasive regions suggests that either introductions may have occurred from the native sources in all invasive regions or subsequent introductions took place from one into another invasive region and the same mix of genotypes was subsequently introduced into all invasive regions. With an assignment test, populations from Ireland, The Netherlands and the United Kingdom most resembled the invasive populations and were the most likely source populations of invasive *J. vulgaris* individuals of all populations tested.

To get more insight about the route of introduction and the source population(s) of *J. vulgaris* there was a need to develop markers with higher resolving power than AFLP markers. The chloroplast genome behaves as one locus, does not recombine and is only passed on through the maternal line (seeds). Because of the limited seed dispersal and the absence of recombination, it is easier to trace the source of populations. In chapter 5 I describe how I made use of a next generation DNA sequencing technique to sequence the DNA of seventeen chloroplast genomes. Twelve chloroplast genomes derived from native individuals and five genomes derived from invasive individuals. By comparing these genomes with a length of circa 150.000 basepairs, I found 32 SNPS ("Single Nucleotide Polymorphisms") and over 34 microsatellite locations. To find as much polymorphic markers as possible, selected individuals were geographically wide spread. These markers can be used to trace the source population(s) of *J. vulgaris*.

Eight SNPs and 9 microsatellite markers were selected to genotype native and invasive individuals. In chapter 6 in total 90 native and 87 invasive individuals were genotyped, spread over respectively 11 and 29 populations. The genetic variation was significantly higher in the native area. This outcome was also expressed in the number of allele combinations that was found, the so called haplotypes. In the native area 63 haplotypes were found compared with 26 in the invasive area. In agreement with the AFLP study low genetic variation was found between individuals coming from the invasive regions Australia, New Zealand, Canada and North America. Four haplotypes from Europe were identical to the invasive haplotypes, these were two individuals originated from Ireland, one individual from Norway and the fourth individual was coming from Sweden. Possibly these populations contained individuals that were introduced into the invasive area. This finding is partly in agreement with the AFLP study where the most likely source populations also originated from Northwest- Europe. In the invasive regions individuals with identical haplotypes did often occur in multiple or even all invasive regions. This result in combination with the low genetic variation between regions suggests once more multiple source populations originated from Europe and introduced into the new areas.

Conclusions

Native and invasive individuals of *Jacobaea vulgaris* differ from each other in a number of traits related to defence and growth. Despite the more vigorous growth of invasive individuals, defence related products were not lower for invasive individuals compared to native individuals as predicted by the EICA hypothesis. Furthermore a shift to a bigger investment in quantitative defence products of native individuals compared to invasive individuals, as predicted by the SDH, was also not found. Two separate studies with different genetic markers and partly also with different individuals both reveal that the most likely scenario of invasive *J. vulgaris* individuals is that they originated from multiple source populations. The chance of preadaptation is very little because it is very unlikely that all these different source populations contained individuals that were already adapted to the new environment. An alternative explanation for the differences in defence and growth between native and invasive individuals is that after introduction fast evolution has taken place. The introduction of different source populations and the admixture of individuals from different populations have likely contributed to the fast evolution of *J. vulgaris*. Admixture increased the genetic variation and has also lead to recombination of native individuals that were isolated from each other in the native area. The occurrence of new genetic combinations increased the potency of natural selection in the invasive areas.

The invasive character of *Jacobaea vulgaris* is especially expressed by the lower root- shoot ratio. With this change the competition with local species is increased. Bigger shoots leads to a higher photosynthetic capacity and more growth. Besides, within *J. vulgaris* plant size is positively correlated with the amount of seeds produced. As a result of this, spread and abundance of *J. vulgaris* easily increases.