The ecological and evolutionary significance of inbreeding x environment interactions for the success of biological invasions

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Chapter 1

General introduction

Territorial expansion is an obligatory event in the population biology of all species. Colonization episodes at large spatial scales can dislocate founder populations from their ancestral ecological interactions and induce significant evolutionary changes that are often the initial point of speciation. A central question in evolutionary biology is which historical, ecological and demographic processes shape the genetic architecture of colonizing populations and how this, in turn, determines further colonization success and post-colonization evolution (Antonovics 1976; Kirkpatrick & Barton 1997; Holt & Keitt 2005; Parmesan *et al.* 2005; Excoffier *et al.* 2009). These questions have been traditionally investigated from a historical perspective, which could yield only restricted mechanistic insights into the determinants of colonization success (Antonovics 1976; Kirkpatrick & Barton 1997). The increasingly frequent intercontinental transport of species by humans (Loope & Howarth 2002; Perrings *et al.* 2005) provides the opportunity to study these processes at contemporary time scales, especially when focusing on those species that become successfully established outside their native range and expand rapidly from the sites of their initial introduction (i.e. **invasive species**, Mack *et al.* 2000). Following the lead of Baker & Stebbins' (1965) *´The Genetics of Colonizing Species´* researchers began to use invasive species as model systems to study how colonization episodes influence patterns of genetic variation, ecological interactions, and contemporary evolution (reviewed in Barrett 2015)

An idea that has developed right at the start of the field of invasion genetics in 1965 is that invasive species must solve a '**Genetic Paradox of Invasions**' (**GPI**) (Baker & Stebbins 1965; Barrett & Husband 1990; Allendorf & Lundquist 2003; Frankham 2004; Pérez *et al.* 2006; Roman & Darling 2007; Hufbauer 2008; Dlugosch *et al.* 2015). The GPI arises as species succeed in invasion, although it is a common feature of colonizing populations to experience demographic bottlenecks that can reduce genetic diversity and, consequently hamper colonization success due to diminished evolutionary potential, inbreeding depression and the accumulation of drift load (see **Chapter 1.1** for details). The GPI is among the most intensively debated and investigated topics in invasion genetics (Barrett 2015; Dlugosch *et al.* 2015). Its explanation is essential not only for understanding the dynamics of species range limits, but also for understanding and predicting the decline of endangered species, which are just as invaders challenged with reduced genetic diversity in rapidly changing environments. In this thesis, I aim at elaborating and solving open questions with regard to the GPI.

1.1 The Genetic Paradox of Invasions: the genetic constraints of colonization success

Colonization events can be associated with a series of demographic bottlenecks. Demographic bottlenecks can cause genome-wide stochastic shifts in the frequency of alleles within a population (i.e. genetic drift), which often culminates in the successive loss of specific alleles, and consequently in a reduction of standing genetic variation (i.e. genetic depletion) (Barrett & Husband 1990; Austerlitz *et al.* 2000; Arenas *et al.* 2012). These genetic changes can hamper the success of invasions for two reasons:

1.1.1 The loss of adaptive evolutionary potential

Long-distance dispersal exposes colonizing populations to abiotic and biotic selective regimes that can severely differ from those in their native source environments. An adaptive response to environmental change is therefore essential for the establishment and future spread of these populations. Populations can adapt to novel environments either via selection on new arising mutations or via selection on standing genetic variation. Adaptation is markedly faster from standing genetic variation than new mutations, as beneficial alleles i) are immediately available; ii) start at higher frequencies; and iii) have likely been pre-tested by selection in the evolutionary trajectory of a species, which increases the chance for a large scale advantageous effect (reviewed in Barrett & Schluter 2008; Hurst 2009). Genetic depletion is accordingly considered to reduce the potential for adaptive evolution and therefore the fitness, survival, establishment success, and further expansion of colonizing populations (Lee 2002; Willi *et al.* 2006; Prentis *et al.* 2008). Experimental research into these anticipated interrelationships has only recently begun and yielded strong empirical evidence for the positive effect of standing genetic variation on the potential to adapt to novel environments (e.g. Agashe *et al.* 2011; Messina & Durham 2013; Stelkens *et al.* 2014).

1.1.2 Inbreeding depression and drift load

Demographic bottlenecks and genetic depletion can increase the relatedness of individuals within colonizing populations (Keller & Waller 2002; Keller *et al.* 2014). The mating among closely related individuals (i.e. inbreeding) raises genome wide homozygosis in their offspring, which can result in a significant reduction of fitness (i.e. inbreeding depression) (Angeloni *et al.* 2011). Inbreeding depression is based on two mutually non-exclusive genetic mechanisms (reviewed in Charlesworth & Willis 2009). The ‘dominance’ mechanism originates in the increased homozygosity of recessive deleterious alleles that segregate at low frequency in the gene pool (i.e. **segregating load**). The ‘overdominance’ mechanism originates in the increased homozygosity of loci with heterozygote advantage (i.e. heterozygous genotype has higher relative fitness than homozygote dominant and homozygote recessive genotype). The accumulated empirical data make a strong case that dominance is the primary cause for inbreeding depression (Roff 2002; Charlesworth & Willis 2009; Chelo *et al.* 2014; Hedrick *et al.* 2015). This is also supported by the observation that inbreeding depression can be reduced after successive generations of non-random mating as a consequence of the selective removal of segregating load from the gene pool (i.e. **purging**) (reviewed in Crnokrak & Barrett 2002). Recessive deleterious alleles unfold their negative effects not solely via non-random mating. Demographic bottlenecks can result in stochastic increases in the frequency of these alleles, which may culminate in their fixation and again, lead to a severe loss of fitness (i.e. accumulation of **drift load**) (Lynch *et al.* 1995; Mullarkey *et al.* 2013; Willi *et al.* 2013). Inbreeding depression and the accumulation of drift load have strong negative effects on a population’s demographic rate and therefore reduce establishment probability and further expansion of colonizing populations (Hufbauer *et al.* 2013; Szùcs *et al.* 2014).

Finally, it should be noted that the loss of adaptive potential, inbreeding depression, and the accumulation of drift load are not solely constraints to invasion success, but also increase extinction risk in endangered species (Lynch *et al.* 1995; Frankham 2005; Willi *et al.* 2006; Wright *et al.* 2007; Wootton & Pfister 2013). It is merely the trigger for these processes that differs between expanding and declining species. For invasive species it is the colonization process, for threatened species it is anthropogenic habitat change that induces a successive decline of population sizes. In fact, most of the theory on, and investigation into the negative effects of demographic bottlenecks on population fitness was driven by conservation efforts (Frankham 1995; Avise & Hamrick 1996; Hedrick 2001).

1.2 The Genetic Paradox of Invasions revisited: open questions

The relevance of the GPI was highly controversial from the very beginning of research into invasion genetics. Whereas some researchers emphasized that the amount of introduced genetic diversity is a crucial determinant of invasion success, others doubted that reductions of genetic diversity have the potential to limit invasiveness (Baker & Stebbins

1965). Technical advances in molecular genetics provided a growing body of descriptive empirical data on genetic diversity in invasive vs. native populations that could, however, not resolve the dispute on the GPI, as they revealed no consistent results. Genetic diversity was lower, similar high or even higher in invasive range populations of invasive species (reviewed in Roman & Darling 2007; Dlugosch & Parker 2008a; Puillandre *et al.* 2008). Though not overrepresented among this empirical data, increasing emphasis was put on invasions that were associated with increases in genetic diversity as a result of multiple introductions and gene flow among genetically distinct invasion routes (i.e. **genetic admixture**) (Novak & Mack 1995; Frankham 2004; Roman & Darling 2007; Dlugosch & Parker 2008a; Hufbauer 2008; Verhoeven *et al.* 2011). Many contributors to this discussion stated that there is generally no GPI, because invading populations do not experience genetic depletion (e.g. Frankham 2004; Roman & Darling 2007; Hufbauer 2008). Although this point of view was quickly countered by a qualitative review, which revealed that genetic diversity is neither rarely reduced nor frequently increased during invasive range expansion (Uller & Leimu 2011), arguments still linger that reductions in genetic diversity are not strong enough to limit invasion success, or have generally not the potential to do so (Pérez *et al.* 2012; Rius & Darling 2014; Colautti & Lau 2015).

In summary, much of the discussion on the GPI did not focus on explaining the success of invaders in the face of reduced genetic diversity, but on the mere question of whether the GPI exists or not. However, past research on invading species suggests that the GPI must be approached in a more differentiated way. Since attempts to find a consensus on factors promoting successful invasions have largely agreed on their idiosyncrasy (Moles *et al.* 2012), it should not be asked whether there is a GPI, but rather which particular species are challenged with the GPI. As it is generally known that invasions exhibit strong spatial and temporal dynamics (Hastings et al. 2005, Pyšek & Hulme 2005) it should, in addition, be asked if the strength and relevance of genetic depletion differs between populations within species. Indeed, empirical evidence for strong spatial (Lachmuth *et al.* 2010, 2011; Pringle *et al.* 2011; Mullarkey *et al.* 2013; Darling *et al.* 2014) and temporal (Taylor & Keller 2007; Chun *et al.* 2010a; Keller *et al.* 2012; Chapple *et al.* 2013; Schrey *et al.* 2014) variation in genetic diversity between invading populations of one and the same species has accumulated during the past decade. It remains to be discussed which temporal invasion phases and spatial occasions are in particular associated with strong genetic depletion and how important they are to overall invasion success. In this context it must be questioned whether this variation has been captured by the studies that were the basis for the previous evaluation of the GPI. Consequently, the GPI may need a reevaluation with a view to differences in the degree of genetic depletion within and among species for a more realistic assessment of its impact on invasions.

The few attempts that tried to actually explain the GPI predominantly concentrated on the question of how invading species can adapt to novel habitat conditions despite reduced genetic diversity (reviewed in Lee 2002; Pérez *et al.* 2006; Prentis *et al.* 2008; Dlugosch *et al.* 2015). Theory and empirical research into this question has provided multiple solutions as e.g. pre-adaptation (Schlaepfer *et al.* 2010; van Kleunen *et al.* 2011), high phenotypic plasticity (Richards *et al.* 2006; Davidson *et al.* 2011), epigenetic changes (Richards *et al.* 2012), and adaptive mutations (Pérez *et al.* 2006). Significantly less attention has been paid to the question of how founding populations can overcome the negative effects of inbreeding and drift load on population fitness. The few explanations for this aspect of the GPI are based on a variety of mechanisms that avoid inbreeding depression and the accumulation of drift load as e.g. polyploidy (te Beest *et al.* 2012) or asexuality (Hao *et al.* 2011). However, as numerous successful invaders are evidently confronted with inbreeding depression and drift load (e.g. Daehler 1999; Richards 2000; Briskie & Mackintosh 2004; Parisod *et al.* 2004; Facon *et al.* 2011; Lachmuth *et al.* 2011; Mullarkey *et al.* 2013), a mechanism for the tolerance of these events still remains to be identified in order to fully explain the GPI.

There are further open questions with regard to the adaptation aspect of the GPI. This aspect bases on the observation that invaders exhibit rapid evolutionary change in spite of reductions in genetic diversity that lower adaptive evolutionary potential (Bossdorf *et al.* 2005; Dlugosch & Parker 2008b; Dlugosch *et al.* 2015). The paradox consequently arises from two assumptions: i) rapid evolutionary change in invaders is an adaptive response to changes in selective regimes (i.e. **adaptive evolution**); ii) demographic bottlenecks during the invasion are an unconditional constraint to adaptive evolution. Assumption i) neglects that demographic bottlenecks themself can induce strong heritable genetic changes that are no responses to selection (i.e. **non-adaptive evolution**) (reviewed in Keller & Taylor 2008). The processes introduced as constraints to colonization success (genetic drift, genetic depletion, accumulation of drift load) describe non-adaptive evolutionary changes, independently from their detrimental effects on fitness. Recent studies demonstrated that phenotypic divergence in invaders can predominantly arise from such non-adaptive evolutionary processes (Keller *et al.* 2009; Ness *et al.* 2010; Lachmuth *et al.* 2011; Colautti & Lau 2015; Xu *et al.* 2015). Assumption ii) was recently countered by the idea that the invasion process may uncover masked variation in specific phenotypic traits due to changes in the genetic and ecological environment, which may considerably increase adaptive potential (Dlugosch *et al.* 2015). In other words, demographic bottlenecks do not necessarily limit, but may even facilitate rapid adaptive evolution. If demographic disequilibrium initiated by the colonization process itself may foster non-adaptive or even adaptive evolution, it can be asked whether rapid evolution is not rather an obligatory consequence of colonization instead of a paradox. This question remains to be investigated in studies that focus on the role of demographic bottlenecks for evolutionary divergence in invasive species.

Although the past years of research yielded tremendous insights into the eco-evolutionary genetics of invasive species and raised fundamental theories on how to explain invasion success in the face of repeated demographic bottlenecks, there are critical questions concerning the GPI that remain to be answered:

a) Has the Genetic Paradox of Invasions been underestimated as a challenge to invasion success?
b) How can invasive species overcome the negative effects of inbreeding and drift load?
c) Can demographic bottlenecks themself contribute to non-adaptive and adaptive evolutionary change in invasive species?

In this thesis, I addressed these questions with a literature review and synthesis in which I developed a new approach for explaining the GPI, and by testing this approach in a study series using the invasion of *Silene latifolia* Poir. (Caryophyllaceae) in North America as a model system.

1.3 Constituents for a new approach to the Genetic Paradox of Invasions

1.3.1 Inbreeding x environment interactions

Quantitative and qualitative reviews on interactions between inbreeding and stress (i.e. inbreeding x environment (IxE) interactions) demonstrated that inbreeding depression is generally less strong in benign than stressful environments (Armbruster & Reed 2005; Cheptou & Donohue 2011; Fox & Reed 2011; Reed *et al.* 2012). IxE interactions have been observed for numerous abiotic and biotic environmental gradients, such as temperature (Vermeulen *et al.* 2014), water availability (Sedlacek *et al.* 2012), nutrient availability (Hayes *et al.* 2005), exposure to xenobiotics (Swillen *et al.* 2015), pathogen attack (Freitak *et al.*

2014), parasite attack (Hoebe *et al.* 2011), herbivory (Kariyat *et al.* 2013a), and competition (Cheptou *et al.* 2000). The alleviating effects of benign habitats on the magnitude of inbreeding depression arise from two non-exclusive physiological mechanisms (reviewed in Cheptou & Donohue 2011 and Reed *et al.* 2012). Firstly, inbreeding increases the homozygosity of segregating load with deleterious effects for stress responses (stress perception, signal transduction, mechanisms that mediate resistance and tolerance to environmental stressors). The deleterious effects of these alleles, however, only unfold in harsh environments that induce the expression of stress responses (Kariyat *et al.* 2012a, b, 2013c; Vermeulen *et al.* 2014). Secondly, inbreeding depression is manifested in various metabolic dysfunctions and is therefore in itself a stress that induces multiple stress responses (e.g. increased maltose metabolism, increased synthesis of heat shock proteins). This compromises an individual's ability to respond to further external stress (reviewed in Kristensen *et al.* 2010) and conversely, environmental stress may reduce an individual's ability to respond to the stress caused by inbreeding itself. Apart from these two physiological mechanisms it can be assumed that epigenetic factors play an important role for IxE interactions, as they are the genetic basis for large amounts of inbreeding depression and rapid purging (Biémont 2010; Nebert *et al.* 2010; Vergeer *et al.* 2012) and are strongly involved in responses to environmental stress (Chinnusamy *et al.* 2008; Chinnusamy & Zhu 2009; Grativol *et al.* 2012). Independently from their mechanistic basis, IxE interactions have a strong influence on demographic rates and have been shown to be important determinants of population survival (Liao & Reed 2009), colonization success (Hufbauer *et al.* 2013) and evolution (Cheptou & Donohue 2011; Leimu *et al.* 2012; Reed *et al.* 2012).

1.3.2 Enemy release in invaded ecosystems

Many theories on invasion success root in the assumption that introduced populations of invasive species spread under more favorable habitat conditions relative to populations in the native range. During the past decades, this assumption has been addressed in a tremendous number of theoretical approaches, field observations, and experimental studies, which primarily focused on biotic environmental conditions (reviewed in Catford *et al.* 2009). One major focus was on natural enemies, as they are believed to have a strong regulatory influence on their hosts at an ecological as well as an evolutionary level (Leimu *et al.* 2012b). Many field observations demonstrated that successful invasive populations experience less attack by pathogens (Mitchell & Power 2003; Dawson 2015), parasites

(Torchin *et al.* 2003), predators (Lees & Bell 2008; Wallach *et al.* 2010), and herbivores (Keane & Crawley 2002a) compared to populations in the species' native range (i.e. **enemy release**) (but see Maron & Vilà 2001; Parker & Hay 2005; Verhoeven *et al.* 2009; Chun *et al.* 2010b; Heard & Sax 2013). Enemy release is in many cases restricted to enemy species that rely on single hosts or a limited range of phylogenetically related hosts (i.e. **specialists**) (Keane & Crawley 2002; Joshi & Vrieling 2005), but can also involve species with a broad host range (i.e. **generalists**) (e.g. Wolfe 2002). In addition, the release from generalists is often restricted to early invasion phases, but can repeat whenever colonizing populations spread into new habitats at the leading edges of invasion (Dietz & Edwards 2006; Mitchell *et al.* 2006, 2010; Flory & Clay 2013).

Enemy release is one of the most prominent explanations for the success of biological invasions (Richardson & Pyšek 2008), which is largely based on two assumptions. Firstly, a reduction of attack by natural enemies may directly increase the performance of invaders relative to native competitors (Keane & Crawley 2002). Secondly, the relaxation from selection by natural enemies may drive an adaptive resource-reallocation away from costly defense against enemies to competitive ability, growth, reproduction or other traits that increase the inader's performance (i.e. '**Evolution of Increased Competitive Ability' (EICA) hypothesis**) (Blossey & Notzold 1995). Although several case studies provided strong evidence for these assumptions (e.g. Torchin *et al.* 2001; Uesugi & Kessler 2013) meta-analyses yielded only weak general empirical support (Chun *et al.* 2010b; Felker-Quinn *et al.* 2013). In this context it can be asked whether there are other ways in which Enemy release can potentially foster the success of biological invasions.

1.4 The study system

For the empirical parts of this thesis, I used native and invasive populations of the weedy plant species *Silene latifolia* Poir. (Caryophyllaceae) and its natural specialist and generalist enemies as a study system. *Silene latifolia* is a short-lived dioecious perennial that primarily inhabits ruderal sites, such as road and field margins, vegetated or open fallows, and hey fields. The species is a prominent study system for research into biotic interactions, epigenetic processes, sex-chromosome evolution, the evolution of sexual dimorphisms, reproductive isolation, and species boundaries (reviewed in Bernasconi *et al.*

2009). In addition, the species is ideally suited for research into the GPI for the following reasons:

1.4.1 An eventful colonization history and a genetic paradox

The population history of *S. latifolia* has been intensively studied by Taylor & Keller (2007) and Keller *et al.* (2009, 2012). The species is native to large parts of Eurasia, where post-glacial expansion from genetically distinct refugia has created strong genetic structure between Eastern and Western geographic regions. In the early 19th century the species expanded to North America with agricultural seed trade and as contaminant of ship ballast. Introduced populations were sampled from a few local sections of the entire native genealogy in Eastern and Western Europe, which resulted in a genetic bottleneck on a continent-wide scale. However, both invasive genetic lineages spread successfully and even without a considerable lag-phase despite reductions in genetic diversity. Later, multiple introductions *locally* admixed the two anciently separated Eastern and Western genetic lineages and collapsed the genetic structure that had built up in the native range. Other studies reported that local genetic admixture had no positive effects on the fitness of invading populations (Wolfe *et al.* 2006; but see Verhoeven *et al.* 2010) and that introduced range populations partially suffer from inbreeding and inbreeding depression (McCAULEY *et al.* 1995; Richards 2000). Given that *S. latifolia* is an obligate outcrossing (dioecious) species, the occurrence of severe inbreeding appears to be unusual. The high degrees of biparental inbreeding in *S. latifolia* can be attributed to restricted pollen transfer among neighboring individuals (McCauley 1997; Wright & Meagher 2004) and to the lack of a dispersal syndrome, which results in the spatial formation of patchy kin-structured groups (McCAULEY *et al.* 1995; Richards 2000; Teixeira *et al.* 2009). In addition, departures from optimal sex ratio during demographic bottlenecks can critically decrease the effective size of already small populations and thereby enhance biparental inbreeding (Öster & Eriksson 2007; Vandepitte *et al.* 2010; Lauterbach *et al.* 2012), which is believed to be one cause for the underrepresentation of dioecious species among successful invaders (Barrett *et al.* 2008). Further studies on the invasion of *S. latifolia* focused on contemporary evolution in introduced populations and revealed strong phenotypic changes in life-history and plant defense traits (Blair & Wolfe 2004; Wolfe *et al.* 2004), which were assumed to arise from adaptation in response to the escape from natural enemies (see Chapter 1.4.2 for details) as proposed by the EICA-hypothesis.

In summary, there is strong evidence that the invasion of *S. latifolia* was accompanied by genetic depletion and inbreeding depression at different spatial and temporal occasions. Nevertheless, the species spread rapidly over large parts of the USA and Canada and exhibits rapid evolutionary changes in introduced range populations. Hence, the successful invasive range expansion of *S. latifolia* from Europe to North America poses a Genetic Paradox.

1.4.2 Enemy release in the invaded habitat

European populations of *S. latifolia* are attacked by a broad range of specialist and generalist enemies. The plants are infested by the specialized holocyclic aphid *Brachycaudus populi* L. (Aphididae), which causes the abort of flowers due to phloem sucking on flowering stems (Wolfe *et al.* 2004). Moreover, flowers of *S. latifolia* can become infected with the specialist fungus *Microbotryum violaceum* Lév (Microbotryaceae), which produces its spores in the anthers of male plants and plants that it has previously transformed from females into males (Ruddat *et al.* 1991; Uchida *et al.* 2003). The fungus is transmitted by pollinators and spreads systemically in its host, which results in a complete sterilization of the infected plant that may persist for several vegetation periods (Ruddat *et al.* 1991). Pollination is mainly performed by the specialist *Hadena bicruris* Hufnagel (Noctuidae), a nocturnal moth, which oviposits on the ovary of female plants whereupon hatched caterpillars feed into the developing capsules in order to predate the seeds of *S. latifolia* (Dötterl *et al.* 2006). This is one of 13 worldwide known pollination mutualisms, where specialist pollinators reproduce at the fitness expense of their host plants (i.e. nursey pollination, Dufaÿ & Anstett 2003). In addition to these reproduction limiting specialists, European populations of *S. latifolia* are attacked by numerous generalist enemies (pers. obs. K. Schrieber). These include gastropods (primarily *Arion vulgaris* Moquin-Tandon (Arionidae)), coleopters, and lepidopters that consume leafs, flowers, and cortical tissues of the shoot. Members of the family Cucurlionidae (weevils) predate the seeds of *S. latifolia* within opened (mature) capsules, especially in the Southern regions of Europe. Moreover, European populations frequently suffer from the extremely high abundance of thysanopters (thrips), which suck on single epidermal cells of leafs, calyx and corolla causing spotty necrosis all over the plants. In addition, populations are occasionally affected by phloem sucking insects, such as Heteroptera, Auchenorrhyncha (cicadas), and Tetranychidae (spider mites), as well as different fungi of the orders Puccinales (rust fungi) and Erysiphales (mildew fungi).

In the invaded range, the specialist aphid *B. populi* is completely absent and the abundance of the specialist fungus *M. violaceum* is restricted to a small region in the state of Virginia with further sporadic occurences in Illinois, Massachusetts, Michigan, and Pennsylvania (Wolfe 2002, Fontaine et al. 2013). Until today, the nursey specialist pollinator *H. bicruris* has not been introduced to North America and its pollination services are substituted by *Hadena ecypa* Morrison (Noctuidea) and other generalist nocturnal moths, which do not predate the seeds of *S. latifolia* (Castillo *et al.* 2014). Tissue consumption by gastropods, coleopters, and lepidopters is outstandingly rare (Wolfe 2002), but the abundance of flower thrips, leaf miners, and rust fungi can be locally very high (pers. observ. K. Schrieber). Hence, invasive *S. latifolia* escaped most of its natural specialist and generalist enemies.

1.5 Objectives and outline of this thesis

In this thesis, I addressed the abovementioned open questions concerning the GPI:

a) Has the Genetic Paradox of Invasions been underestimated as a challenge to invasion success?
b) How can invasive species overcome the negative effects of inbreeding and drift load?
c) Can demographic bottlenecks themself contribute to non-adaptive and adaptive evolutionary change in invasive species?

I addressed these questions in three Chapters (Fig. 1 pp 15). I reviewed existing explanations on the GPI and listed empirical evidence for successful invasions these approaches cannot explain. Based on a comprehensive literature synthesis I developed a new approach that focuses on the advantageous effects of IxE interactions to explain the GPI for the regarding invasive species and outlined a methodological concept to test the mechanisms underlying my new approach empirically. Subsequently, I applied this empirical concept, which included a field study, population genetic analyses, a series of experimental studies, and targeted analytical methods to the invasion of *S. latifolia* to successively test the assumptions underlying the new approach.

CHAPTER 2: “The Genetic Paradox of Invasions revisited: the potential role of inbreeding x environment interactions in invasion success” by Karin Schrieber & Susanne Lachmuth; published online [25.03.2016] in *Biological reviews* (doi: 10.1111/brv.12263)

This chapter presents a review on the discussion about, and the explanations for the GPI, as well as a novel conceptual approach towards the GPI. I argued that the GPI has been underestimated in the past because spatial and temporal variations in genetic diversity with strong degrees of genetic depletion in critical invasion phases (introduction, expansion at leading edges) have been neglected. I discovered that there is a lack of explanation for the GPI for these invasion phases and for invasions that were evidently accompanied by inbreeding depression and drift load in general. Based on a synthesis of literature on invasion genetics and the ecology of invaded habitats (i.e. stress release), I proposed that IxE interactions may explain these aspects of the GPI. I discussed how IxE interactions can foster the persistence and even the spread of genetically depleted inbred populations. Moreover, I argued that IxE interactions can result in rapid non-adaptive evolutionary changes and may even facilitate adaptation in invaders in the absence of high genetic variation, especially in traits related to stress resistance. Finally, I presented an experimental approach to investigate the occurrence of IxE interactions in ongoing invasions, which is based on their evolutionary consequences.

CHAPTER 3: „Empirical evidence for the facilitative role of inbreeding x environment interactions in the success and evolution of invasive species” by Karin Schrieber, Sabrina Wolf, Catherina Wypior, Diana Höhlig, Isabell Hensen, Stephen R. Keller & Susanne Lachmuth; prepared for submission

In this chapter, I applied the empirical test introduced in CHAPTER 2 to investigate whether IxE interactions have the potential to facilitate invasion success using *S. latifolia* and its natural enemies (stressor) as a study system. I specifically asked if advantageous IxE interactions have occurred during the invasive range expansion of my study species, how IxE interactions influence the performance of native and invasive *S. latifolia*, and whether they induced evolutionary divergence in resistance to natural enemies between native and invasive populations (i.e. range-dependent purging). To answer these questions, I conducted a comprehensive field sampling in 18 native and 18 invasive populations and assessed their genetic structure and inbreeding history with ten SSR markers. Based on the results I chose eight native and eight invasive populations for a multiannual series of experiments. I performed two generations of experimental in- and outbreeding within native and invasive populations under controlled conditions. Then I manipulated the strength of attack by natural enemies on the second generation inbred and outbred offspring in a common garden and recorded plant performance and resistance. I determined the interactive effects between range, experimental inbreeding, enemy attack, and inbreeding history in order to investigate the direct and evolutionary effects of IxE interactions on plant performance and resistance.

CHAPTER 4: "Adaptive and non-adaptive evolution of trait means and genetic trait correlations for resistance to natural enemies and performance in an invasive plant" by Karin Schrieber, Sabrina Wolf, Catherina Wypior, Diana Höhlig, Isabell Hensen & Susanne Lachmuth; prepared for submission

In this chapter, I aimed at investigating the drivers of evolutionary divergence between native and invasive *S. latifolia* populations, which I detected in **CHAPTER 3**. Here, I focused on plant resistance and performance traits in experimentally outbred plants in the enemy inclusion / enemy exclusion common garden experiment described in **CHAPTER 3**. First, I aimed at quantifying the amount of variation in performance and resistance explained by non-adaptive vs. adaptive evolution. For this purpose, I i) determined the neutral between- and within population co-ancestry according to an approach of Karhunen & Orvaskainen (2012) based on the ten SSR markers, ii) analyzed the data for performance and resistance in so-called 'animal models' ('pedigreemm' Bates & Vazquez 2009) that account for population co-ancestry, and iii) performed comparisons of variance components between animal models and mixed models that do not account for population co-ancestry. Second, I aimed at investigating whether invasive populations exhibit an adaptive shift of performance and resistance trait values along a genetically based trade-off line as predicted by the EICA-hypothesis. For this purpose, I performed genetic correlation analyses with resistance and performance traits based on outbred families as recommended by Koricheva (2002).

In **CHAPTER 5**, I summarized and critically discussed the findings obtained from **CHAPTER 2**, **CHAPTER 3**, and **CHAPTER 4**, while highlighting the links between the three studies. Moreover, I outlined their implications and suggested directions for future research.

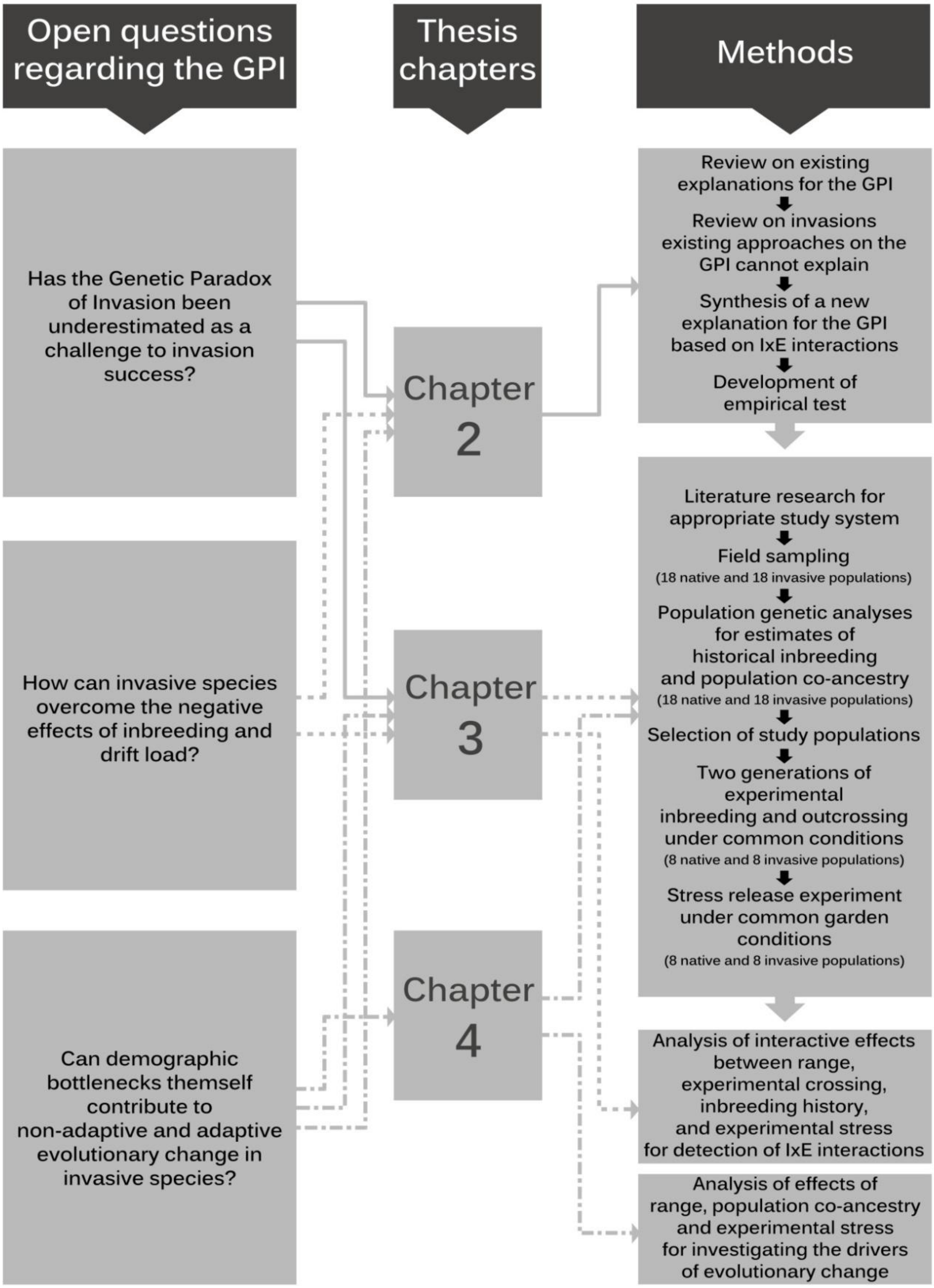

Fig. 1: Schematic thesis outline. The graphic illustrates which open questions concerning the GPI were addressed in the different thesis chapters and which methods were applied in each chapter. It gives an overview of how IxE interactions were elaborated as novel explanation for the GPI and how their role for the invasion of the selected model species *S. latifolia* was investigated emprically in this thesis.

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Chapter 2

The Genetic Paradox of Invasions revisited: the potential role of inbreeding × environment interactions in invasion success

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2.1 Abstract

Invasive species that successfully establish, persist, and expand within an area of introduction, in spite of demographic bottlenecks that reduce their genetic diversity, represent a paradox. Bottlenecks should inhibit population growth and invasive expansion, as a decrease in genetic diversity should result in inbreeding depression, increased fixation of deleterious mutations by genetic drift (drift load), and reduced evolutionary potential to respond to novel selection pressures. Here, we focus on the problems of inbreeding depression and drift load in introduced populations as key components of the 'Genetic Paradox of Invasions' (GPI). We briefly review published explanations for the GPI, which are based on various mechanisms (invasion history events, reproductive traits, genetic characteristics) that mediate the avoidance of inbreeding depression and drift load. We find that there is still a substantial lack of explanation and empirical evidence for explaining the GPI for strongly bottlenecked invasions, or for during critical invasion phases (e.g. initial colonization, leading edges of range expansion) where strong genetic depletion, inbreeding depression and drift load occurs. Accordingly, we suggest that discussion of the GPI should be revived to find additional mechanisms applicable to explaining invasion success for such species and invasion phases. Based on a synthesis of the literature on the population genetics of invaders and the ecology of invaded habitats, we propose that inbreeding × environment (I×E) interactions are one such mechanism that may have strong explanatory power to address the GPI. Specifically, we suggest that a temporary or permanent release from stress in invaded habitats may alleviate the negative effects of genetic depletion on fitness *via* I×E interactions, and present published empirical evidence supporting this hypothesis. We additionally discuss that I×E interactions can result in rapid evolutionary changes, and may even contribute to adaptation of invaders in the absence of high genetic variation. With a view to encouraging further empirical research, we propose an experimental approach to investigate the occurrence of I×E interactions in ongoing invasions. Revived research on the GPI should provide new fundamental insights into eco-evolutionary invasion biology, and more generally into the evolutionary consequences of the interactions between inbreeding and environment.

Key words: biological invasion, contemporary evolution, environmental stress, genetic drift, genetic load, genetic diversity, herbivory, inbreeding depression, purging, stress response.

Chapter 3

Empirical evidence for the facilitative role of inbreeding x environment interactions in the success and evolution of invasive species

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3.1 Summary

1) Inbreeding x environment (IxE)-interactions result in reduced inbreeding depression when the environment is benign. Here, we investigated whether IxE interactions can explain the paradox of successful spread of genetically bottlenecked invaders within introduced ranges where stress is reduced relative to their native range. We hypothesize that, if this is the case, IxE interactions result in weaker purging of segregating load for stress resistance in species within their introduced than native range.
2) We used invasive and native populations of *Silene latifolia* and its natural enemies as study system. We performed experimental in- and outbreeding, a stress release experiment, and population genetic analysis to determine the interactive effects between experimental inbreeding, stress, and inbreeding history on different plant traits.
3) We found that segregating load for stress resistance has been purged in native, but not in invasive populations, whereas segregating load for performance has been purged in both ranges. Moreover, stress release alleviated inbreeding depression for performance in invasive populations.
4) Our results support that IxE interactions occurring during invasions can enhance invasive spread and contribute to evolutionary divergence in stress resistance. This has important implications for predictions on invasion potential and advocates invaders as ideal model systems for investigating the eco-evolutionary consequences of IxE interactions.

Keywords: biological invasion, evolution, genetic paradox, genetic drift, inbreeding depression, inbreeding environment interactions, purging, *Silene latifolia*

Chapter 4

Adaptive and non-adaptive evolution of trait means and genetic trait correlations for herbivory resistance and performance in an invasive plant

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4.1 Abstract:

The EICA-hypothesis predicts that invading plants adapt to their novel environment by evolving increased performance and reduced resistance in response to the release from natural enemies, and assumes a resource allocation trade-off among both trait groups as mechanistic basis of this evolutionary change. Using the plant *Silene latifolia* as a study system, we tested these predictions by investigating whether i) invasive populations evolved lower resistance and higher performance, ii) this evolutionary change is indeed adaptive, and iii) there is a negative genetic correlation among performance and resistance (i.e. a trade-off) in native and introduced individuals. We sampled eight native and eight invasive populations and determined their population co-ancestry based on neutral SSR-markers. We performed controlled crossings to produce five sib-groups per population and exposed them to increased and reduced levels of enemy attack in a full-factorial experiment to estimate performance and resistance. With these data, we performed trait-by-trait comparisons between ranges with 'animal models' that account for population co-ancestry to quantify the amount of variance in traits explained by non-adaptive vs. adaptive evolution. Moreover, we tested for genetic correlations among performance and resistance traits within sib-groups. We found significant reductions in resistance and increases in performance in invasive vs. native populations, which could largely be attributed to adaptive evolution. While we detected a non-significant trend towards negative genetic performance x resistance correlations in native populations, invasive populations exhibited both significant and non-significant positive correlations. In summary, these results do not support a shift of performance and resistance trait values along a trade-off line in response to enemy release, as predicted by EICA. They rather suggest that the independent evolution of both traits is not constrained by a trade-off, and that various selective agents (including resource availability) interact in shaping both traits and in weakening negative genetic correlations in the invaded habitat.

Chapter 5

General discussion

Based on a literature review and synthesis, and a study series that combined field sampling, population genetic analyses, a breeding experiment, and a common garden experiment, this thesis yielded important theoretical and empirical insights into the ecology and evolution of invading species that are challenged with genetic deterioration. In this final chapter, I discuss how my studies contribute to solve the three open questions regarding the Genetic Paradox of Invasions that I raised in the general introduction. Moreover, I suggest potential directions for future research and highlight implications for the management of invasive species, for the conservation of declining and endangered species, and for species that undergo range shifts in response to climate change.

5.1 Solving open questions concerning the Genetic Paradox of Invasions

5.1.1 Has the Genetic Paradox of Invasions been underestimated as a challenge to invasion success?

By reviewing literature on the GPI in **CHAPTER 2** I found that, while not the vast majority of invasions are accompanied by reductions in genetic diversity, still numerous species suffer from substantial genetic depletion during their invasive range expansion. I discovered that genetic depletion prevails in populations during early invasion phases and towards the leading edges of range expansion, which are most critical for invasion success. I suggested that such systematic spatial and temporal variation in the strength of genetic depletion cannot be captured by between-range-comparisons of average genetic diversity in present-day populations with a long history of successful invasion. In addition, I discovered that there is a lack of studies that investigated the direct effects of genetic diversity on the performance of invaders. Nevertheless, for the few species tested I found strong evidence for a negative effect of genetic depletion on performance i.e. for the incidence of inbreeding depression and drift load. Moreover, I illustrated that invading populations can be challenged with substantial genetic depletion, inbreeding depression and drift load, although they exhibit specific traits (e.g. high reproductive rates, polyploidy) or experienced demographic events (e.g. mass introduction, genetic admixture) that were proposed to actually prevent such problems.

The empirical parts of my thesis confirmed these findings for the study species *S. latifolia* with population genetic analyses and a series of experimental studies (**CHAPTER 3** and further studies not implemented in this thesis (Wolf 2014)). SSR-analyses with 18 native and 18 invasive study populations revealed no significant range differences in genetic diversity[1] and evidence for genetic admixture in present day invasive populations[2] (Wolf 2014). However, at the same time the results indicated severe historical genetic bottlenecks[3] (Wolf 2014). These results were consistent with the findings Taylor & Keller (2007) and Keller *et al.* (2012) obtained for other *S. latifolia*-populations. In **CHAPTER 3** I found that measures of performance in eight native and eight invasive experimentally outbred populations of *S. latifolia* were negatively related to an estimate of historical inbreeding. These interrelationships indicated the incidence of inbreeding depression and / or the accumulation of drift load under natural conditions and were generally stronger in invasive than native populations. In summary, these findings illustrate that invasive *S. latifolia* populations are challenged with increased levels of inbreeding depression and drift load, despite the incidence of multiple introductions and genetic admixture, and although there are no significant differences in average genetic diversity between native and invasive populations.

The results obtained from **CHAPTER 2**, **CHAPTER 3** and Wolf (2014) suggested that the studies that were so far in the focus of the discussion on the GPI (i.e. between-range-comparisons of average genetic diversity in present-day populations) have only limited potential to assess whether the GPI is a challenge to the invasion success of a species or not. To answer this question, studies should account for genetic depletion during introduction and establishment by reconstructing the invasion history for the species under consideration (Keller *et al.* 2012; Chapple *et al.* 2013) or by taking repeated measures of genetic diversity over large time-intervals (Pringle *et al.* 2011; Darling *et al.* 2014). In order to assess whether present-day invasive populations are challenged with the GPI, studies should focus on geographic regions that are relevant for the current invasive expansion i.e. on the leading edges of range expansion (Lachmuth *et al.* 2010; Mullarkey *et al.* 2013). Most importantly, purely descriptive estimates of genetic diversity must be related to measures of the invaders' performance (Richards 2000; Briskie & Mackintosh 2004; Hawley *et al.* 2006; Szulkin *et al.* 2010; Lachmuth *et*

[1] No significant differences in observed and expected heterozygosity between 18 native and 18 introduced populations (mean Ho: native 0.68, invasive 0.71; mean He: native 0.36, invasive 0.37).

[2] Structure analyses identified two geographically separated genetic clusters within the native range (cluster I in the North-East of Europe, cluster II in the South-West of Europe) with rare occurrence of genetic admixture between these two clusters (results cluster assignment analysis for 18 native populations: cluster I: 7 populations, cluster II: 10 populations, admixed: 1 population). Both genetic clusters also occurred within the invaded range (without specific geographic structuring) with comparably high occurrence of genetic admixture (results cluster assignment analysis for 18 invasive populations: cluster I: 3 populations, cluster II: 7 populations, admixed: 8 populations).

[3] Significantly higher allelic richness in native than invasive populations (mean Ar: native 9.47, invasive 8.87, $P<0.01$)

al. 2011; Mullarkey *et al.* 2013) or demographic rates (Murren & Dudash 2012; Hufbauer *et al.* 2013) in order to gain a more detailed mechanistic insight into the effects of genetic diversity on invasion success. Moreover, the occurrence of specific traits or demographic events that putatively prevent genetic deterioration, should be evaluated with caution. Although experimental studies provided strong evidence for the positive influence of e.g. polyploidy or genetic admixture on the performance of populations during demographic bottlenecks, these advantages do not necessarily come into effect whenever polyploidy or genetic admixture are associated with an invasion (Soltis & Soltis 2000; Rius & Darling 2014). The positive effects of such traits and events on the performance of genetically depleted populations are context-dependent and should thus not be assumed, but verified in experimental studies for the species under consideration.

In summary, it can be suggested that the GPI should not be put to rest because it is in general no challenge to invasion success (as proposed by e.g. Frankham 2004; Roman & Darling 2007; Hufbauer 2008). The GPI should rather be approached in a more differentiated way by accounting for the idiosyncrasy and the spatial and temporal dynamics of invasions. Past research on mechanisms that avoid the genetic constraints of colonization contributed meaningfully to solve the GPI for many invasions and yielded comprehensive insights into the ecology and evolution of biological invasions. Nevertheless, these approaches cannot fully explain the GPI, since there is unequivocal evidence for the incidence of inbreeding depression and the accumulation of drift load in a significant number of invasions and during crucial invasion phases. The search for mechanisms that mediate the tolerance of these problems once they have occurred is worthwhile, given their implications for the management of invasive species and for the conservation of highly threatened species that face genetic extinction vortexes (Kuussaari *et al.* 2009).

5.1.2 How can invasive species overcome the negative effects of inbreeding and drift load?

In CHAPTER 2 I proposed that IxE interactions present a mechanism to temporally tolerate strong degrees of inbreeding and high amounts of drift load during invasive range expansion. I found that inbreeding and the accumulation of drift load often coincide in space and time (i.e. during early invasion phases and towards the leading edges) with a release from environmental stress (e.g. enemy release) during invasions. I argued that this gives rise to IxE interactions that alleviate the negative effects of inbreeding and drift load on population performance in benign relative to stressful environments. I discussed that advantageous IxE interactions may allow invasive populations to persist despite strong inbreeding and genetic drift. I elaborated that this assumption can be tested when focusing on the evolutionary consequences of IxE interactions. I hypothesized that if advantageous IxE interactions occurred during the invasion of a species this should result in the 'range- and trait-dependent purging' of segregating load: segregating load in stress response will become purged in inbred populations in the harsh native, but not in the benign invasive habitat, whereas segregating load with large scale deleterious effects (i.e. alleles with deleterious effects for house-keeping functions, reproduction, and development) will become purged in both the native and the invaded habitat. Following an approach of Leimu *et al.* (2008) I elaborated an empirical concept to test for range- and trait-dependent purging and, consequently for the incidence of advantageous IxE interactions in invasive populations.

In **CHAPTER 3** and a field study not implemented in this thesis (Wypior 2014) I empirically investigated and largely confirmed the assumptions and hypothesis outlined in **CHAPTER 2** for the invasion of *S. latifolia.* I found that inbreeding depression and the accumulation of drift load (**CHAPTER 3**) coincide with a release from a broad range of natural specialist and generalist enemies (Wypior 2014) in my invasive study populations. The study described in **CHAPTER 3** demonstrated that an experimental release from natural enemies alleviates experimental inbreeding depression in traits related to reproduction (number of flowers and fruits, corolla size) in invasive populations of *S. latifolia*. Moreover, it yielded evidence for range- and trait-dependent purging: segregating load that affected resistance to natural enemies was purged in the native range where natural enemies were present, but not in the invasive range where enemies were absent. In contrast, segregating load that affected traits related to reproduction (number of fruits) was purged in both ranges. The presence of range- and trait-dependent purging in the studied *S. latifolia* populations strongly supported the incidence and the advantageous effects of IxE interactions in invasive populations under natural conditions. In addition, these findings empirically supported that the purging of segregating load with deleterious effects for traits related to reproduction counters inbreeding depression in invasive populations, which has been shown for only few invasive species (Facon *et al.* 2011; Fountain *et al.* 2015).

In summary, **CHAPTER 2** and **CHAPTER 3** theoretically and empirically documented that advantageous IxE interactions can help invading populations to overcome the negative effects of inbreeding and drift load on performance. Hence, IxE interactions can contribute to further solve the puzzle posed by the GPI. It is important to note that the advantageous effects of IxE interactions are not mutually exclusive with other explanations that were proposed to explain the GPI. Apart from the fact, that different mechanisms can explain the GPI for different invaders, multiple mechanisms can contribute to overcoming the genetic constraints to colonization success in one and the same invasion, either at distinct spatial or temporal occasions or in direct coincidence. This will rather be the norm than the exception, since the advantageous effects of IxE interactions are restricted to the duration of stress release, which often ceases in later invasion phases (Dietz & Edwards 2006; Mitchell *et al.* 2006, 2010). Moreover, the alleviation of inbreeding depression and drift load via IxE interactions alone does certainly not make a successful invader. Although it has been observed in some case studies that inbred individuals suffer no performance decrements at all under stress release (reviewed in Fox & Reed 2011; Murren & Dudash 2012; Campbell *et al.* 2013), advantageous IxE interactions are unlikely to result in the rapid proliferation of strongly inbred invasive populations. They rather help such populations to persist until other beneficial mechanisms come into action. Advantageous IxE interactions may for example prolong the persistence of inbred founder populations during initial introduction, which increases the chance for genetic rescue due to multiple introductions and genetic admixture (Rius & Darling 2014; Whiteley *et al.* 2015). Likewise, advantageous IxE interactions may temporarily ensure the survival of inbred founder populations at the leading edges of range expansion, which enhances the probability for migration events from populations that have already become successfully established behind the leading edge. In most cases, advantageous IxE interactions will coincide with the purging of large scale deleterious recessive alleles from the gene pool (i.e. deleterious alleles that affect house-keeping functions, reproduction and development) (Cheptou & Donohue 2011; Reed *et al.* 2012). Purging can result in a full recovery of population fitness after successive generations of inbreeding as long as selective death or reproductive failure of the homozygous recessives does not result in population extinction (Crnokrak & Barrett 2002). Advantageous IxE interactions can reduce the risk of population extinction by alleviating the effects of negative selection on individuals, which carry conditionally deleterious recessive alleles for stress response that have no disadvantage in the benign invasive environment. This may simultaneously increase purging success for large scale deleterious recessive alleles. Finally, favorable species traits like for example high asexual and sexual reproductive rates can considerably enhance the positive effects of IxE interactions under stress release, thereby even allowing moderate positive population growth in inbred populations (Murren & Dudash 2012; Hufbauer *et al.* 2013). *Silene latifolia* is an excellent example for the coincidence of multiple traits and events in countering the negative effects of inbreeding and drift load during invasions: the species exhibits high reproductive rates and introduced populations have evidently experienced advantageous IxE interactions in response to enemy release (**CHAPTER**

3, Wypior 2014), purging of segregating load with large scale deleterious effects (**CHAPTER 3**), and heterosis due to multiple introductions and genetic admixture (Verhoeven *et al.* 2011 but see Wolfe *et al.* 2006).

In summary, it is highly likely that the negative effects of inbreeding and drift load are countered by a combination of different traits and events in most successful invasions. Nevertheless, it can be suggested that advantageous IxE interactions are important key drivers for invasion success, as they provide first aid for genetically deteriorated populations during most critical invasion phases. On the other hand, increased stress in newly colonized habitats can strongly magnify inbreeding depression (Liao & Reed 2009; Murren & Dudash 2012; Hufbauer *et al.* 2013) and thus be a strong constraint to invasion success, which additionally emphasizes the importance of IxE interactions for biological invasions.

5.1.3 Can demographic bottlenecks themself contribute to non-adaptive and adaptive evolutionary change in invasive species?

In **CHAPTER 2** I proposed that IxE interactions can not only explain how founding invaders overcome the negative effects of inbreeding and drift load on fitness, but also why invaders exhibit strong evolutionary divergence in spite of strong demographic disequilibrium. I discussed that inbreeding itself induces significant changes in genetic architecture by increasing genome wide homozygosis, which exposes recessive *conditionally* deleterious alleles to selection. As illustrated by the almost ubiquitous incidence of IxE interactions (Armbruster & Reed 2005; Kristensen *et al.* 2010; Cheptou & Donohue 2011; Fox & Reed 2011; Reed *et al.* 2012) the expression effects of these alleles depend on the magnitude of environmental stress, which in turn determines their selective values. I discussed that this applies in particular to recessive alleles with deleterious effects on stress response. These alleles may have negative selection values in stressful habitats (i.e. in the native range) and neutral selection values in stress poor habitats (i.e. in the invaded range). If the depletion of stress responses allows for an improvement of fitness (e.g. via a resource-mediated trade-off), the frequency of these alleles may rapidly increase as soon as inbreeding exposes them to selection in the recessive homozygote. If so, IxE interactions can be considered to foster adaptation to stress poor environmental conditions. In summary, I hypothesized that IxE interactions may induce non-adaptive or even adaptive evolutionary divergence in stress responses in invaders via range- dependent purging.

In **CHAPTER 3** I empirically tested and partially confirmed this hypothesis for *S. latifolia*. Segregating load that reduced resistance to natural enemies has been purged in native populations but not in invasive populations when it was exposed to selection by inbreeding. Moreover, invasive populations accumulated higher amounts of drift load in stress resistance than native populations as indicated by a stronger negative relation between stress resistance and historical inbreeding in experimentally outbred individuals. Jointly both results indicate that conditionally deleterious recessive alleles affecting resistance to natural enemies experience markedly less negative selection in the enemy free invaded range than in the native range where enemies are present. Hence, it can be assumed that IxE interactions have indeed the potential to induce evolutionary divergence in stress responses of invaders as hypothesized in CHAPTER 2. Nevertheless, it remained open whether segregating load has accumulated as a consequence of genetic drift or adaptation. The latter scenario was supported by the observation that invasive individuals simultaneously exhibited reduced resistance and increased performance relative to native plants. This indicated an adaptive shift of resistance and performance trait values along a resource-mediated trade-off line in introduced populations as predicted by the EICA-hypothesis (Blossey & Notzold 1995). However, as long as these evolutionary changes were not investigated in an empirical framework that accounts for non-adaptive evolution, and as long as the genetic basis of the performance-resistance trade-off could not be confirmed, it remained unclear whether IxE interactions have indeed contributed to adaptation in *S. latifolia*.

In CHAPTER 4 I investigated evolutionary divergence in resistance and performance of *S. latifolia* whilst accounting for, and quantifying the effects of non-adaptive evolution. Lower resistance and increased reproductive performance in invasive populations were nearly unaffected by genetic drift. Hence, the findings of CHAPTER 4 indicate that the accumulation of segregating load and drift load in resistance observed in CHAPTER 3 can at least partially be attributed to adaption as hypothesized in CHAPTER 2. However, I hypothesized that IxE interactions can only contribute to adaptation in the enemy free invaded habitat if the degradation of resistance to natural enemies simultaneously allows for an increase in performance via a resource mediated trade-off. The results obtained in CHAPTER 4 yet showed that the negative genetic correlation between performance and resistance that would confirm a genetically based trade-off was not present in native and invasive populations. Instead, the results indicated that the genetically based trade-off dissolved during invasive range expansion and turned towards a positive genetic correlation. I suggested two mutually non-exclusive potential explanations for these findings, the validation of which, however, requires further research: i) the genetically based trade-off between performance and resistance dissolved due to increased resource supply in the invaded habitat; ii) the genetically based trade-off between performance and resistance exists, but could not be detected in the specific trait combinations addressed in CHAPTER 4; and iii) enemy release itself weakend the negative genetic correlations. As these explanations are mutually non-exclusive, the findings generally not refute the existence of a resource-mediated performance-resistance trade-off as potential mechanism for an adaptive reduction of stress response via IxE interactions. In summary, CHAPTER 4 indicated that IxE interactions have contributed to adaptive evolution in invasive populations of *S. latifolia*, but the drivers of this adaptive change could not be certainly identified without further research.

Demographic disequilibrium is major driver of rapid evolution in invasive species. Apart from the fact that it often induces strong non-adaptive changes that do not implicitly contribute to invasion success (Keller & Taylor 2008; Lachmuth *et al.* 2011; Colautti & Lau 2015, but see CHAPTER 4) it can considerably foster adaptive divergence. While some demographic non-equilibrium situations (i.e. genetic admixture, inter specific hybridization) are generally viewed as drivers of post-invasion adaptation (Roman & Darling 2007; Schierenbeck & Ellstrand 2009; Verhoeven *et al.* 2011; Rius & Darling 2014), others are assumed to inevitably hamper evolutionary responses to selection (i.e. demographic bottlenecks, inbreeding) (Keller & Waller 2002; Kuussaari *et al.* 2009). The latter assumption was at least partially opposed by the results obtained from this thesis. Inbreeding may potentially foster specific adaptive changes if it coincides with a shift in the selective regime for stress from stressful to stress poor habitats, which is a requirement often met during invasive range expansions. This is consistent with an idea proposed by Dlugosch *et al.* (2015), who hypothesized that invasions reveal so-called ‘cryptic genetic variation’ that is variation based on alterations of the phenotypic effects (and consequently selective values) of specific genetic variants depending on environmental conditions (i.e. Genotype x Environment (GxE) interactions). The authors suggested that such hidden sources of variation may be particularly important for rapid adaptation and, consequently invasion success. This thesis yielded first empirical support for adaptation via cryptic genetic variants in invaders, since IxE interactions are eventually types of GxE interactions. As IxE interactions are most likely to occur during early invasion phases and towards the leading edges (CHAPTER 2) where adaptive responses to the environment are most urgently required for establishment and further expansion (Kirkpatrick & Barton 1997; Lee 2002; Lee & Gelembiuk 2008; Prentis *et al.* 2008), adaptation via IxE interactions may indeed increase invasion success. If so, the resulting evolutionary change may act like a range-wide selective sweep and may therefore not be restricted to populations, in which IxE interactions occur, but also affect populations that have overcome the phases of genetic deterioration long ago. Nevertheless, it must be noted that adaptation via advantageous IxE interactions in invaders has limitations. Inbreeding does not solely increase the phenotypic expression of conditionally deleterious recessive alleles that have advantageous effects in stress poor environments, but also the expression of unconditionally deleterious alleles that reduce fitness in each environment. The negative expression effects of the latter can only be partially reduced, but not completely neutralized by benign environmental conditions (mechanism described in **CHAPTER 2**, Fig 1B p. 36; Kristensen *et al.* 2010). This is consistent with the observation that inbreeding depression is often weakened, but not completely absent in benign environments (Armbruster & Reed 2005; Fox & Reed 2011). Adaptive responses to selection are therefore likely slowed by the negative effects of inbreeding on demographic rates, even in benign habitats. However, this constraint to adaptation via IxE interactions could be countered effectively by the purging of unconditionally deleterious recessive alleles, which likely accompanies advantageous IxE interactions (**CHAPER 3**; Cheptou & Donohue 2011; Facon *et al.* 2011; Reed *et al.* 2012). Comprehensive future research is needed to evaluate the facilitative effects of IxE interactions in benign environments against the general negative effects of inbreeding for adaptation, and to certainly identify the selective drivers and causal mechanisms underlying adaptive change via IxE interactions.

5.2 Future research into IxE interactions in the context of plant invasions

My thesis corroborated that IxE interactions can play an important role for the ecology and the evolution of invasive plant species, which should be further explored in the future. Comprehensive information on the effects of multiple stressors on invasions success (Catford *et al.* 2009) and their general effects on the expression of inbreeding depression (Fox & Reed 2011) can serve to identify appropriate study systems for investigating different types of IxE interactions. Each of these study systems can be used to address both the facilitative and the inhibitory effects of specific environmental factors on inbred invasive populations. Competition is a promising biotic stressor for such investigations, since it combines several resource deficiency stresses (light-, water-, nutrient deficiency) with the direct detrimental effects of interference (e.g. via allelochemicals) in itself. As, competition is known to have strong effects on the expression of inbreeding depression (Cheptou *et al.* 2000; Yun & Agrawal 2014) its deterministic effects on invasions success (Levine *et al.* 2004; Gross *et al.* 2005; Mitchell *et al.* 2006) likely involve IxE interactions. Promising study systems for research into the effects of abiotic stressors may be found in invasions of mountain ecosystems, which have gained increasing attention during the past decade (Pauchard *et al.* 2009; McDougall *et al.* 2011a, b;

Pyšek *et al.* 2011; Seipel *et al.* 2012). High altitudes are associated with a variety of abiotic stresses such as high radiation, low temperature, drought and nutrient deficiency due to specific substrate conditions, or high mechanical disturbance due to wind or snow load (Körner 2003). It has been established that a partial reduction of these stresses due to global change (nutrient input, climate change) has increased the invasibility of mountain ecosystems during the past century (Pauchard *et al.* 2009; Pyšek *et al.* 2011). This process likely involves effects of IxE interactions, which should be investigated in future studies.

Once the invasive study system is identified, IxE interactions may be addressed in different empirical frameworks (for detail see Murren & Dudash 2012; Hufbauer *et al.* 2013; Szùcs *et al.* 2014, this study) that can basically be categorized into two alternative approaches involving i) a breeding treatment and an exposal to stressful vs. stress poor controlled experimental conditions, or ii) a breeding treatment and a transplantation to natural native vs. natural invaded habitats. Approach i) can address a single stressor, as well as the interactive effects of multiple stressors (stress treatment for two stressors a and b involves: stress a, stress b, stress a+b, control) and thereby allows disentangling the effects of the stresses under consideration. This approach is particularly suited for investigations into the evolutionary consequences of IxE interactions for specific stress responses with the inclusion of population genetic data. The second approach complicates statements on the ecological and evolutionary effects of specific stressors, because native and invaded habitats generally differ in several environmental attributes, the effects of which cannot be disentangled in transplant experiments. Nevertheless, approach ii) captures the interactive effects of different stressors under natural conditions in both ranges, which gives a more realistic insight into the ecological effects of IxE interactions. In summary, both approaches hold advantages and disadvantages and must be chosen depending on whether the evolutionary or ecological effects of IxE interactions are in the focus of interest.

Independently from the experimental approach applied, it is reasonable to acquire a broad range of data on performance and stress response. For performance data, studies should ideally capture the entire life-history of the species from germination to seed release and additionally collect demographic data (see e.g. Hufbauer *et al.* 2013). These data can be implemented in matrix population models (Caswell 2001) or integral projection models (Metcalf *et al.* 2013), which provide estimates for population growth that hold high informative value in the context of colonization ability. Data on stress response should combine measures of stress injury and morphological resistance (Mittler 2006) with global or targeted metabolomics that qualify and quantify the secondary compounds involved in responses to specific stressors (Edreva *et al.* 2008; Campbell *et al.* 2013; Kariyat *et al.* 2013b). The latter should address the effects of inbreeding on both constitutive and induced levels of secondary metabolites, as it has been shown that both stress response strategies can respond distinctly to inbreeding (Campbell *et al.* 2013) and selection in the invaded habitat (Cipollini *et al.* 2005; Zas *et al.* 2011). Further insight into the general genetic and physiological basis of IxE interactions and their effects on evolution could be obtained with other 'omic' techniques. Transcriptomic studies can reveal changes in gene expression for responses to environmental stress resulting from inbreeding (Kristensen *et al.* 2005; Thompson & Goggin 2006; Padmalatha *et al.* 2011), while targeted proteomics can address the stress responses trended towards inbreeding itself by quantifying the synthesis of ubiquitous protein control systems (e.g. heat shock proteins, proteasoms; Kristensen *et al.* 2010). Functional genomic studies such as Quantitative Trait Loci (QTL) analysis have been used to identify loci under selection in invasive species (McKay & Latta 2002; Weinig *et al.* 2006) and loci governing inbreeding depression (Vermeulen *et al.* 2008a, b). Accordingly, it would be feasible to test whether loci that govern inbreeding depression in stress resistance of native and invasive populations are also involved in adaptive reductions in stress resistance in introduced populations, which would further support that IxE interactions can contribute to adaptive evolution. However, most of the 'omic' techniques described require broad prior knowledge on the organism under consideration, which is usually restricted to commercially used species or prominent model organisms such as Drosophila. However, a study of Kariyat *et al.* (2012b) demonstrated that the information available from such study systems can be reliably transferred to closely related taxa. The authors applied commercially available transcriptomic micro array chips for tomato to *Solanum carolinense* L. This species is ideally suited for investigations into IxE interactions in the context of invasions because it i) expanded rapidly from its native range in South America to North America, Europe, Asia, and Australia where it is considered as serious weed (Follak & Strauss 2010); ii) exhibits a mixed mating system and high degrees of natural inbreeding (Kariyat *et al.* 2012b); and iii) partially escaped its natural enemies in the invaded range (Imura 2003). By transferring prior knowledge for 'omic' techniques from model organisms to phylogenetically closely related invasive taxa, native vs. invasive population comparisons for responses to inbreeding and stress can give comprehensive and novel insights into IxE interactions under natural conditions. Studies of this kind hold important implications that extend far beyond invasive species.

5.3 Implications

The results obtained from this thesis and from the suggested future research hold some important implications for applied invasion biology. Data on the effects of IxE interactions on the performance and demography of invaders could be implemented in models that predict invasions dynamics or the efficiency of control measures, which can increase the precision of these approaches (Simberloff 2003; Lennox *et al.* 2015). In order to optimize the cost-benefit ratio for the active control of invaders, it has been proposed to reduce propagule pressure, population size, and gene flow among populations instead of completely eradicating them (Hulme 2006; Bogich & Shea 2008; Yokomizo *et al.* 2009). These measures aim at inducing ecological 'Allee effects' (Courchamp *et al.* 2009) and genetic deterioration in the target populations, which ideally result in population extinction. However, my results indicate that the advantageous effects of IxE interactions in benign invaded habitats may prevent population extinction and foster purging thereby making the target populations resistant to such measures. Hence, programs of this kind should be complemented with measures that cease stress release for introduced populations (Hulme 2006; Buckley *et al.* 2007). My results for *S. latifolia* hint at the possibility that biological control may be an appropriate measure to attain this objective. However, it may be more reasonable to further reduce anthropogenic disturbance that translates into stress release for invaders (Blumenthal 2005; Gross *et al.* 2005; Hulme 2006) instead of additionally disturbing the invaded ecosystem with the application of biological control agents that hold generally limited prospects of success (Babendreier 2008).

Research into IxE interactions in the context of invasions has implications that go far beyond the applied model species. IxE interactions are not solely linked to invasive range expansions, but to all directions of a species' range dynamic. They are assumed to set the limits of a species' native range by magnifying inbreeding depression in range edge habitats with unsuitable environmental conditions (Ronce *et al.* 2009; Sun & Cheptou 2012). Consequently, IxE interactions are expected to play an important role for range shifts in response to climate change where they may foster colonization at the leading edges while accelerating population declines at the trailing edges (Leimu *et al.* 2010; Levin 2012). However, there is a lack of direct empirical evidence for this assumption. The native vs. invaded range comparisons for responses to inbreeding and stress addressed in this thesis can easily be transferred to leading edge vs. trailing edge comparisons. Data obtained from such studies can again be implemented in models predicting the range dynamics in response to climate change in order improve their precision (Fordham *et al.* 2012).

While many species indeed respond with range-shifts to climate change, others exhibit considerable range retractions, because the rapid speed of recent climate change and other components of global change impede range migration or species persistence in situ (Davis & Shaw 2001; Parmesan 2006). IxE interactions also have vital implications for such organisms of conservation interest (Reed *et al.* 2012). Global change fosters the fragmentation, isolation and decline of populations in these species leading to strong genetic deterioration under increased stress levels (Vitousek 1994; Frankham 2005; Wright *et al.* 2007; Courchamp *et al.* 2009; Kuussaari *et al.* 2009). There is ample evidence that the resulting IxE interactions accelerate population declines and extinction (Pray *et al.* 1994; Bijlsma *et al.* 2000; Reed *et al.* 2002; Liao & Reed 2009; Leimu *et al.* 2010). My results indirectly support this observation and therefore emphasize the need for specific conservation practices and the need to stick to specific rules when applying them. Propagation programs for species threatened with extinction should absolutely avoid inbreeding under captive / artificial (stress poor) conditions, although this is may be associated with substantial costs and organizational effort (Kleiman 1989). Otherwise, the neutral or adaptive accumulation of segregating load in stress response via IxE interactions may have devastating effects on the fitness of individuals under natural (stressful) conditions, which is a constraint to the success of release efforts. IxE interactions can considerably contribute to so-called ‘adaptation to captive conditions’, which resulted in the failure of several captive breeding programs in the past (Snyder *et al.* 1996; Frankham 2008). For the conservation of declining populations in the wild, my thesis theoretically underlines the effectiveness of management strategies focusing on the reduction of anthropogenic disturbance as overarching stressor (Hofer & East 1998; Daehler 2003; Chape *et al.* 2005). Such strategies have a two-fold positive effect. They partially cure the direct cause for population declines and the incidence of inbreeding, and partially reduce the negative effects of interactions between inbreeding and novel anthropogenic stresses thereby increasing the persistence times of declining populations (Liao & Reed 2009). Nevertheless, given that genetic deterioration will relax only slowly in response to such conservation efforts (Frankham 2005) and that many endangered species inhabit physiologically challenging habitats (e.g. plant species that inhabit semi-natural dry grasslands in Central Europe), populations may still suffer from the interactions between inbreeding and naturally occurring stress. These species may have a genetic predisposition for the negative effects of IxE interactions: the higher the specialization to stressful habitat conditions, the more genes are involved in stress response and the higher the magnifying effect of either (natural or anthropogenic) stress on the expression of inbreeding depression via both physiological mechanisms governing IxE interactions. Hence, the negative effects of IxE interactions may be expected to be particularly strong in the regarding species compared to species that generally inhabit physiologically less challenging habitats. Therefore, the artificial introduction of new alleles for heterosis effects (i.e.

genetic rescue; Tallmon *et al.* 2004; Whiteley *et al.* 2015) may be an additional measure absolutely necessary to prevent extinction in such populations.

5.4 Conclusions

This dissertation provided answers to three important open questions concerning the GPI, which centered around IxE interactions. The studies yielded a comprehensive theoretical basis and strong empirical evidence that the GPI is indeed a challenge to the invasion success of many species and that advantageous IxE interactions can explain the GPI for the regarding invaders. The results support that advantageous IxE interactions have the potential to explain both aspects of the GPI. Firstly, they may allow invasive populations to persist and even to slowly expand despite the incidence of inbreeding and drift load. Secondly, they may induce significant neutral or even adaptive evolutionary changes in the absence of high genetic diversity. My empirical studies exclusively incorporated natural enemies as trigger for IxE interactions in invaders, but the theory can be transferred to other stressors such as competition and harsh abiotic conditions. Although the primary focus of my thesis was on the role of IxE interactions in promoting plant invasions in benign environments, it is consistent to assume that they may also be a strong selective barrier for invasion success in harsh habitats. My studies on IxE interactions in invaders can therefore be well integrated into numerous hypothesis on the facilitative effects of benign ecological conditions (Enemy Release, Enemy Reduction, Novel Weapons, Increased Resource Availability, Resource-Enemy Release, Disturbance, Empty Niches) and the inhibitory effects of harsh ecological conditions (Biotic Resistance, Increased Susceptibility, Habitat Filtering) for invasion success (hypothesis designated according to Catford *et al.* 2009). IxE interactions add a new population genetic component to these theoretically and empirically well established hypotheses. To date, evidence for the effects of IxE interactions on the performance and evolution of populations came exclusively from experiments that incorporated varying stress regimes under controlled artificial conditions. The methodological approach applied in this thesis provides an effective tool to test for the direct and evolutionary effects of IxE interactions in natural systems via environment (range)- and trait-dependent purging. Incorporated in this empirical concept, invasive species can serve as excellent model systems helping us gain fundamental mechanistic insights into I×E interactions. Studies of this kind hold important implications for the prediction and management of invaders, but also for species that undergo range-shifts and -retractions in the context of global change.

5.5 References

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Summary

Colonization events often involve successive demographic bottlenecks that can result in a loss of genetic diversity. Such genetic depletion can compromise the fitness of individuals in colonizing populations, as it may be associated with inbreeding depression and reduced evolutionary potential. With a view to biological invasions, this has raised the question of how introduced species can successfully establish, persist and further expand outside their native range – a question referred to as the 'Genetic Paradox of Invasions' (GPI). Most of the discussion on the GPI concentrated on invasions, in which a loss of genetic diversity was prevented by specific invasion history events (e.g. mass introductions, genetic admixture) or favorable species traits (e.g. high reproductive rates, polyploidy). Fewer attempts were made to identify invasive species that spread successfully although they were challenged with strong genetic depletion, and to explain how these species could overcome the negative effects of inbreeding or how they were able to respond to novel selection pressures in the face of strong demographic bottlenecks. In this thesis, I addressed these largely unexplored aspects of the GPI.

I reviewed existing explanations on the GPI that focus on the avoidance of genetic depletion and listed empirical evidence for successful invasions these approaches cannot explain. Based on a synthesis of literature on invasion genetics, the ecology of invaded habitats (i.e. stress release), and interactions among inbreeding and environmental stress, I theoretically elaborated a new approach to explain the GPI for the regarding species. Moreover, I outlined a methodological concept to test the assumptions underlying this approach empirically. Subsequently, I applied this empirical concept, which combined field sampling, population genetic analyses, a multiannual breeding experiment, a common garden (stress release) experiment, and targeted analytical methods. As a study system I used native European and invasive North-American populations of the weedy plant species *Silene latifolia* (Poir.) and its natural enemies (stressor) as a study system.

In the literature, I found broad evidence for strong genetic depletion and its negative effects on the performance of invaders, even for species that experienced demographic events or exhibited traits (e.g. genetic admixture, polyploidy) that were actually assumed to prevent genetic deterioration. Genetic depletion and inbreeding were in particular evident during early invasion phases and towards the leading edges of range expansion, which are most crucial for invasion success. Based on the observation that i) these particular invasion phases are often accompanied by a release from environmental stress (e.g. enemy release); and that ii) inbreeding depression is substantially alleviated in benign compared to stressful

environments, I elaborated a new approach to explain the GPI for the regarding species. I proposed that stress release in invaded habitats can reduce the negative effects of inbreeding on performance and allow inbred populations to persist and to slowly expand (i.e. advantageous inbreeding x environment (IxE) interactions). I hypothesized that if advantageous IxE interactions occur in an invader, this should result in 'range- and trait-dependent purging': segregating load that directly affects stress response (e.g. herbivory resistance) will become purged in inbred populations in the harsh native, but not in the benign invasive habitat, whereas segregating load that directly affects performance (e.g. growth, reproduction) will become purged in both the native and the invaded habitat. I elaborated that the incidence of range- and trait-dependent purging may not only confirm the past occurrence of advantageous IxE interactions in invasive populations under natural conditions, but that it also confirms the contribution of advantageous IxE interactions to evolutionary divergence in traits related to stress response. I hypothesiszed that if the increased phenotypic expression of recessive alleles with deleterious effects for stress responses following inbreeding allows for a resource-reallocation away from costly stress response to other traits that increase performance, IxE interactions may even contribute to adaptation to stress poor habitat conditions in invaders. My study series with *S. latifolia* largely confirmed the findings obtained from the literature review and synthesis empirically. Increased levels of inbreeding coincided with a release from natural enemies in invasive field populations of the species. Moreover, enemy release alleviated inbreeding depression under experimental conditions. In addition, the study series revealed evidence for range- and trait dependent purging: segregating load in performance has been purged in both ranges, whereas segregating load in resistance to natural enemies has been purged in the native, but not in the invasive range. These results supported that advantageous IxE interactions have occurred in invasive *S. latifolia* populations under natural conditions. Moreover, Range-dependent purging clearly contributed to an evolutionary degradation of resistance to natural enemies in invasive populations, which primarily arose from adaptive responses to selection as empirically demonstrated by the study series. However, it was challenging to identify the causal mechanisms underlying this adaptive change. Genetic correlation analyses for investigating performance-resistance trade-offs yielded mixed results that could neither refute nor confirm the hypothesis that IxE contribute to adaptation via resource re-allocation from resistance to performance without further research.

My thesis confirmed that the GPI is indeed a challenge to the invasion success of many species, since there is broad evidence for strong genetic deterioration during most critical invasion phases in the literature, which emphasiszes the need for further explanation. My studies yielded a comprehensive theoretical basis and strong empirical evidence that

advantageous IxE interactions can explain the GPI for the regarding species. Firstly, IxE interactions can foster the persistance of inbred invasive populations in habitats associated with a release from environmental stress. Secondly, IxE interactions in stress poor invaded habitats can contribute to an adaptive degradation of stress responses in the absence of high genetic diversity. At the same time, IxE interactions can pose strong constraints to invasion success in habitats that are associated with equally high or higher stress levels relative to a species' native range. My thesis emphasized that invading species can be excellent model systems for research into the ecological and evolutionary effects of IxE interactions under natural conditions. Studies of this kind hold important implications for the management and prediction of invading species, but also for species that undergo range-shifts and -retractions in response to global change.

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Eigenständigkeitserklärung

Hiermit erkläre ich an Eides statt, dass ich die Arbeit mit dem Titel „The ecological and evolutionary significance of inbreeding x environment interactions for the success of biological invasions“ selbständig und ohne fremde Hilfe verfasst habe. Des Weiteren erkläre ich, dass ich keine anderen als die von mir angegebenen Quellen und Hilfsmittel benutzt habe und die den benutzten Werken wörtlich oder inhaltlich entnommenen Stellen als solche kenntlich gemacht habe. Zudem versichere ich, dass ich keine vergeblichen Promotionsversuche unternommen habe und diese Dissertation in der gegenwärtigen Fassung weder bei der Martin-Luther-Universität Halle-Wittenberg noch bei einer anderen wissenschaftlichen Einrichtung zum Zweck der Promotion vorgelegt habe.

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