Eco-evolutionary processes in natural populations at the opposing extremes of demographic success: Invasive and declining plant species in the era of anthropogenic global change

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> *"Environmental change will be accompanied by changes in both genetic composition and changes in numerical dynamics. Genetic response is likely to result in compensatory changes in fitness and life-history components. The distinction between 'ecological time' and 'evolutionary time' is artificial and misleading. Changes of both kinds may be on any time scale: in principle, evolutionary and ecological changes are simultaneous"*
>
> Janis Antonovics --- 'The ecological geneticist's creed'

APPENDICES

Appendix 1 - Cáceres Castellianos YK, Schrieber K, **Lachmuth S**, Auge H, Argibay D, Renison D, Hensen I (in revision for *Diversity and Distributions*). Disentangling effects of altitude, land use and microsites on early-life performance of a high mountain tree: insights from an *in situ* sowing experiment

Appendix 2 - Haider S, Palm S, Bruelheide H, de Villemereuil P, Menzel A, **Lachmuth S** (in preperation). Disturbance and indirect effects of climate warming support plant invasions in mountains

Appendix 3 - Lachmuth S, Henrichmann C, Horn J, Pagel J, Schurr FM (2018). An experimental study of pollen limitation and neighborhood effects in the invasive *Senecio inaequidens*. *Journal of Ecology*. 106: 761-773

Appendix 4 - Peng Y, **Lachmuth S**, Gallegos S, Kessler M, Ramsay P, Renison D, Suarez R, Hensen I (2015). Pleistocene climatic oscillations rather than recent human disturbance influence genetic diversity in one of the world`s highest treeline species. *American Journal of Botany* 102: 1676-1684

Appendix 5 - Rosche C, Schrieber K, **Lachmuth S**, Durka W, Hirsch H, Wagner V, Schleuning M, Hensen I (2018). Sex ratio rather than population size affects genetic diversity in *Antennaria dioica*. *Plant Biology* 20: 789-796

Appendix 6 - Rosche C, Durka W, Hensen I, Mráz P, Hartmann M, Müller-Schärer H, **Lachmuth S** (2016). The population genetics of the fundamental cytotype-shift in invasive *Centaurea stoebe* s.l.: genetic diversity, genetic differentiation and small-scale genetic structure differ between cytotypes but not between ranges. *Biological Invasions* 18: 1895-1910

LIST OF PUBLICATIONS AND MANUSCRIPTS RELEVANT FOR THE THESIS

12 papers published in peer-reviewed scientific journals, 3 manuscripts in revision, 1 manuscript in preparation. The contributions are listed and numbered in their order of appearance in chapter 2. Some studies contributed to more than one section. Numbers in squared brackets serve as references for the contributions in chapters 2 and 3. Unpublished manuscripts are listed exclusively here and do not appear in the reference list.

These contributions represent the core of research projects in the evolutionary ecology of invasive and declining plants species that I collaborated in, conducted, coordinated and/or supervised since 2011 (excluding work that originated from my Ph.D. project). Results reported here are based on ideas, study designs and / or data analyses I conceived as part of my work for this habilitation thesis. I was actively involved in the writing processes of all listed manuscripts.

[1] Cáceres Castellianos YK, Schrieber K, **Lachmuth S**, Auge H, Argibay D, Renison D, Hensen I (in revision for *Diversity and Distributions*). Disentangling effects of altitude, land use and microsites on early-life performance of a high mountain tree: insights from an *in situ* sowing experiment

[2] Haider S, Palm S, Bruelheide H, de Villemereuil P, Menzel A, **Lachmuth S** (in preperation). Disturbance and indirect effects of climate warming support plant invasions in mountains

[3] **Lachmuth S**, Henrichmann C, Horn J, Pagel J, Schurr FM (2018). An experimental study of pollen limitation and neighborhood effects in the invasive *Senecio inaequidens*. *Journal of Ecology*. 106: 761-773

[4] Peng Y, **Lachmuth S**, Gallegos S, Kessler M, Ramsay P, Renison D, Suarez R, Hensen I (2015). Pleistocene climatic oscillations rather than recent human disturbance influence genetic diversity in one of the world`s highest treeline species. *American Journal of Botany* 102: 1676-1684

[5] Rosche C, Schrieber K, **Lachmuth S**, Durka W, Hirsch H, Wagner V, Schleuning M, Hensen I (2018). Sex ratio rather than population size affects genetic diversity in *Antennaria dioica*. *Plant Biology* 20: 789-796

[6] Rosche C, Durka W, Hensen I, Mráz P, Hartmann M, Müller-Schärer H, **Lachmuth S** (2016). The population genetics of the fundamental cytotype-shift in invasive *Centaurea stoebe* s.l.: genetic diversity, genetic differentiation and small-scale genetic structure differ between cytotypes but not between ranges. *Biological Invasions* 18: 1895-1910

[7] Rosche C, Hensen I, Mráz P, Durka W, Hartmann M, and **Lachmuth S** (2017). Invasion success in polyploids: the role of inbreeding in the contrasting colonization abilities of diploid *versus* tetraploid populations of *Centaurea stoebe* s.l.. *Journal of Ecology* 105: 425-435

[8] Rosche C, Hensen I, **Lachmuth S** (2018). Local pre-adaptation to disturbance and inbreeding–environment interactions affect colonisation abilities of diploid and tetraploid *Centaurea stoebe*. *Plant Biology* 20: 75-84

[9] Schrieber K & **Lachmuth S** (2017) The Genetic Paradox of Invasions revisited: the potential role of inbreeding x environment-interactions in invasion success. *Biological Reviews* 92: 939-952

[10] Schrieber K, Wolf S, Wypior C, Hoehlig D, Hensen I, Keller SR, **Lachmuth S** (in revision for *Ecology and Evolution*). Enemy release mitigates inbreeding depression in native and invasive *Silene latifolia* populations: experimental insight into the role of inbreeding × environment interactions in invasion success. Preprint available at: https://doi.org/10.1101/401430

[11] van Hengstum T, **Lachmuth S**, Oostermeijer JGB, den Nijs JCM, Meirmans PG, van Tienderen PH (2012). Human-induced hybridization among congeneric endemic plants on Tenerife, Canary Islands. *Plant Systematics and Evolution* 298: 1119-1131

[12] **Lachmuth S**, Molofsky J, Suda J, Milbrath L, Keller SR (in revision for *AoB Plants*). Deconvolution of the invasive meadow knapweed hybrid complex (*Centaurea* ×*moncktonii* C.E. Britton) in eastern North America: associations between genomic ancestry, genome size and capitula morphology

[13] Ley AC, Herzog P, **Lachmuth S**, Abwe AE, Christian MF, Sesink Cleef PR, Abwe EE, Morgan BJ, Gonder MK (2018). Phenotypic variability along a climatic gradient in a perennial afrotropical rainforest understorey herb. *Basic and Applied Ecology* 28: 60-75

[14] Al-Gharaibeh MM, Hamasha HR, Rosche C, **Lachmuth S**, Hensen I (2017). Environmental gradients shape the genetic structure of two medicinal *Salvia* species in Jordan. *Plant Biology* 19: 227-228

[15] Al-Gharaibeh MM, Hamasha HR, **Lachmuth S**, Hensen I (2017). Local adaptation to different phytogeographic regions: habitat-related variations in seed germination in response to temperature and salinity for two medicinal *Salvia* species from Jordan. *Plant Species Biology* 32: 25-35

[16] Schrieber K, Wolf S, Wypior C, Hoehlig D, Hensen I, **Lachmuth S** (2017). Adaptive and non-adaptive evolution of trait means and genetic trait correlations for resistance to natural enemies and performance in an invasive plant. *Oikos* 126: 572-582

1 Introduction

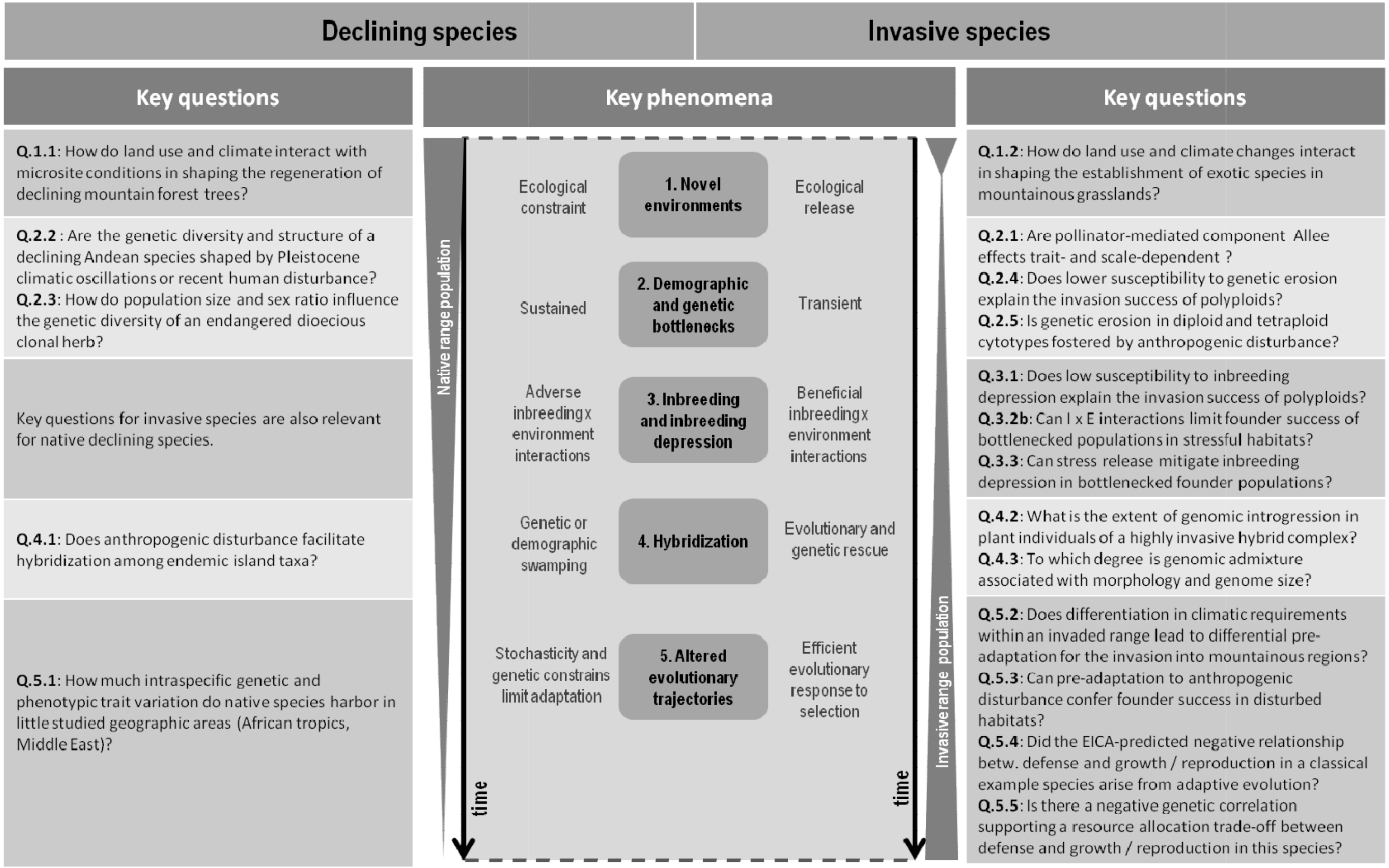
Worldwide, biodiversity is increasingly under pressure from anthropogenic global change (Sala *et al.*, 2000; Pereira *et al.*, 2010; Barnosky *et al.*, 2011) that threatens the persistence of species and ecosystems and thus the services they provide to human societies (Sala *et al.*, 2000; Millennium Ecosystem Assessment (Program), 2005; Maclean and Wilson, 2011; Mantyka-pringle *et al.*, 2012; Urban, 2015). In concert, environmental change and modifications of dispersal pathways continue to induce immense and rapid alterations to species distributions including range retractions, expansions, shifts, and the invasion into new geographic regions (Mack *et al.*, 2000; Parmesan and Yohe, 2003; Root *et al.*, 2003; Dirnböck *et al.*, 2003; Pompe *et al.*, 2008; Pimm *et al.*, 2014). In this context, rare or declining species, which rapidly spiral towards extinction, *versus* invasive species (*sensu* Blackburn *et al.*, 2011), which expand their ranges rapidly, reflect opposite ends of a gradient of ecological and demographic success (Colautti, Alexander, *et al.*, 2017). In the past decades, vast efforts have been put in understanding population and range dynamics and explaining these differential reactions.

One prominent line of research in invasion biology - reaching back to the 1960s when Baker (1965) proposed traits of an “ideal weed”- is based on comparisons of performance-related physiological, developmental and life history traits among invasive and native (van Kleunen *et al.*, 2010), non- or less invasive alien (Grotkopp and Rejmánek, 2007) or endangered species (Jeschke and Strayer, 2008). These approaches often yielded contradictory results (e.g. Daehler, 2003; Pyšek and Richardson, 2007) and for long invasions seemed too idiosyncratic to make any generalizations about their success (Kueffer *et al.*, 2013; van Kleunen *et al.*, 2016). However, increasing progress has been made based on a greater availability and advanced methodological approaches (van Kleunen *et al.*, 2011). Overall, results suggest that successful invaders are typically characterized by high germination and growth rates, short life cycles, high leaf nutrients and specific leaf areas, high investment in reproduction and the production of numerous seeds that are dispersed well (e.g. Grotkopp *et al.*, 2002; Grotkopp and Rejmánek, 2007; van Kleunen *et al.*, 2010; van Kleunen *et al.*, 2015). More recently increasing attention is also being payed to the role of underlying genomic and cytogenetic features, such as ploidy level (Pyšek *et al.*, 2009; Pandit *et al.*, 2011, 2014; te Beest *et al.*, 2012) and genome size (Kubešová *et al.*, 2010; Suda *et al.*, 2014; Pandit *et al.*, 2014; Schmidt *et al.*, 2017). Others propose that different traits are relevant at different stages of the invasion process (van Kleunen *et al.*, 2015) or that trait values have to be considered relative to those of the invaded communities (Divíšek *et al.*, 2018).

Our understanding of range dynamics may furthermore substantially advance by taking into account the ecological and evolutionary context species experience during alterations of their distribution ranges (Gurevitch *et al.*, 2011; Colautti, Alexander, *et al.*, 2017; Schrieber and Lachmuth, 2017 [9]). Range dynamics ultimately arise from the three fundamental demographic processes of birth, death and dispersal, which jointly determine the viability and growth of any given population of organisms (Cohen, 1969; Schurr *et al.*, 2012; Selwood *et al.*, 2015). The demographic processes are shaped by individuals' phenotypic traits, which in turn depend on their genetic make-up in interaction with the environment. Human activities alter population dynamics by affecting demographic processes either directly (e.g. fishery, wild flower harvesting (Cabral *et al.*, 2011), agricultural or ornamental plant cultivation) or through modifying the biotic and abiotic environmental conditions they depend on. Since demographic dynamics induce feedback on the frequencies of cytotypes and alleles (e.g. through drift, selection) as well as genotypes (e.g. through inbreeding) they alter species' evolutionary trajectories often during short time-spans (Colautti, Ågren, *et al.*, 2017). These fast evolutionary changes, in turn, may strongly influence organisms' abilities to cope with anthropogenic influence. Intriguingly - despite their differential demographic success - invasions and extinctions may thus be determined by the same fundamental ecological and genetic processes shaping their demographic rates (Colautti, Alexander, *et al.*, 2017) (see Fig. 1).

Both declining and invasive species experience (1) more or less drastic alterations of their environment in concert with (2) reductions of their population sizes. These demographic bottlenecks frequently induce genetic bottlenecks, enhance genetic among population differentiation and increase levels of inbreeding as well as inbreeding depression (Leimu *et al.*, 2010; Schrieber and Lachmuth, 2017 [9]). Recently, evidence is accumulating that inbreeding depression is environment-dependent (Dudash, 1990) and particularly pronounced under stressful conditions (Armbruster and Reed, 2005; Fox and Reed, 2011). In both declining and invasive species the coincidence of genetic bottlenecks and altered environmental conditions may thus strongly influence fitness via (3) so-called inbreeding x environment interactions. Altered dispersal pathways as a consequence of human activities frequently lead to (4) hybridization between previously isolated taxa, again with considerable fitness consequences. Eventually, all the above-described genetic processes together with novel selective regimes through environmental change may (5) alter the evolutionary trajectories of the species. Still, the outcomes of the relationships between these phenomena and population as well as range dynamics may strongly depend on species traits (Sakai *et al.*, 2001) and may differ for native and alien populations (Blackburn *et al.*, 2015; Colautti, Alexander, *et al.*, 2017).

The projects contributing to the habilitation thesis at hand investigated all five above-described phenomena for declining, invading or both types of plant species. In the following (sections 1.1 - 1.5), I first concisely introduce all five phenomena and their role in species extinctions and invasions based on brief reviews of the current state of research. Where applicable to my work, I also briefly discuss the role of species traits in shaping these processes. At the end of each section, I formulate key questions addressed in this thesis. In chapter 2, I then present results of my and my collaborators' work, again structured according to the five focal phenomena. Here, I will also briefly introduce the study organisms and methods used as far as I consider this information indispensable for interpreting the results. The specific findings are briefly discussed with reference to related literature. Finally, in chapter 3, I synthesize my findings based on the key questions for each of the five phenomena, suggest some directions for further research and recapitulate our work's contribution to our general understanding of range dynamics under global change.



Declining species				Invasive species
Key questions	**Key phenomena**			**Key questions**
Q.1.1: How do land use and climate interact with microsite conditions in shaping the regeneration of declining mountain forest trees?	Ecological constraint	**1. Novel environments**	Ecological release	**Q.1.2**: How do land use and climate changes interact in shaping the establishment of exotic species in mountainous grasslands?
Q.2.2 : Are the genetic diversity and structure of a declining Andean species shaped by Pleistocene climatic oscillations or recent human disturbance? **Q.2.3**: How do population size and sex ratio influence the genetic diversity of an endangered dioecious clonal herb?	Sustained	**2. Demographic and genetic bottlenecks**	Transient	**Q.2.1**: Are pollinator-mediated component Allee effects trait- and scale-dependent ? **Q.2.4**: Does lower susceptibility to genetic erosion explain the invasion success of polyploids? **Q.2.5**: Is genetic erosion in diploid and tetraploid cytotypes fostered by anthropogenic disturbance?
Key questions for invasive species are also relevant for native declining species.	Adverse inbreeding x environment interactions	**3. Inbreeding and inbreeding depression**	Beneficial inbreeding x environment interactions	**Q.3.1**: Does low susceptibility to inbreeding depression explain the invasion success of polyploids? **Q.3.2b**: Can I x E interactions limit founder success of bottlenecked populations in stressful habitats? **Q.3.3**: Can stress release mitigate inbreeding depression in bottlenecked founder populations?
Q.4.1: Does anthropogenic disturbance facilitate hybridization among endemic island taxa?	Genetic or demographic swamping	**4. Hybridization**	Evolutionary and genetic rescue	**Q.4.2**: What is the extent of genomic introgression in plant individuals of a highly invasive hybrid complex? **Q.4.3**: To which degree is genomic admixture associated with morphology and genome size?
Q.5.1: How much intraspecific genetic and phenotypic trait variation do native species harbor in little studied geographic areas (African tropics, Middle East)?	Stochasticity and genetic constrains limit adaptation	**5. Altered evolutionary trajectories**	Efficient evolutionary response to selection	**Q.5.2**: Does differentiation in climatic requirements within an invaded range lead to differential pre-adaptation for the invasion into mountainous regions? **Q.5.3**: Can pre-adaptation to anthropogenic disturbance confer founder success in disturbed habitats? **Q.5.4**: Did the EICA-predicted negative relationship betw. defense and growth / reproduction in a classical example species arise from adaptive evolution? **Q.5.5**: Is there a negative genetic correlation supporting a resource allocation trade-off between defense and growth / reproduction in this species?

Figure 1: The five key phenomena that determine the evolutionary ecology and range dynamics of declining as well as invasive species (adopted from Colautti, Alexander, *et al.*, 2017; Schrieber and Lachmuth, 2017 [9]) and the corresponding key questions addressed in this habilitation thesis.

1.1 Anthropogenic alterations of biotic and abiotic environments

The most relevant human-induced alterations of the environment that affect biodiversity on a global scale comprise changes in land use, atmospheric CO_2 concentration, nitrogen deposition, climate and biotic exchange (Sala *et al.*, 2000; Hof *et al.*, 2011; Pimm *et al.*, 2014). Environmental change is particularly challenging for plants, which are sedentary and can thus not easily escape adverse conditions (Leimu *et al.*, 2010). The quantification of environmental effects and their anthropogenic changes on the performance of native declining and invading plant species is thus an inevitable requirement if we aim to tackle the complex challenges posed by the management of biodiversity.

1.1.1 Climate and land use change and the conservation of native species

Land use activities that either converted natural landscapes for human use or changed traditional management practices on human-dominated land have transformed vast areas of the planet's land surface (Foley *et al.*, 2005) and thus have been in the focus of conservation biology for decades (Fischer and Lindenmayer, 2007; Selwood *et al.*, 2015). These changes have tremendous negative effects on biodiversity by inducing the loss, modification, and fragmentation of habitats, degradation of soil and water as well as through over-exploitation of native species (Sala *et al.*, 2000; Foley *et al.*, 2005; Fischer and Lindenmayer, 2007; Leimu *et al.*, 2010; Selwood *et al.*, 2015). Habitat fragmentation as well as loss and degradation of vegetation cause changes in the physical environments that have been shown to affect plants' vital rates and population viability (Bruna and Oli, 2005; Leimu *et al.*, 2010; Selwood *et al.*, 2015). For example germination and seedling establishment may be affected by altered light and microclimatic conditions (Jacquemyn *et al.*, 2003; Uriarte *et al.*, 2010) as well as wind erosion (Li *et al.*, 2009). Trampling and grazing by livestock may decrease seedling survival (Jansen and Robertson, 2001). Moreover, increased isolation of plant populations within fragmented landscapes will inhibit effective seed and pollen dispersal and thus gene flow among populations and may increase local extinction risk (Hewitt and Kellman, 2002) (see also section 1.2).

Over the past decades changes in climatic conditions have additionally altered the population dynamics of native species and are expected to become an equally or even more important driver of species loss as land use change in the course of the current century (Heller and Zavaleta, 2009; Selwood *et al.*, 2015). Increases in CO^2 levels and temperature as well as altered precipitation and seasonality (IPCC, 2013) can affect the phenology and physiology and consequently growth and fitness of plants both directly and indirectly (Walther, 2003; Körner, 2006; Ge *et al.*, 2015; Estiarte and Peñuelas, 2015; Mora *et al.*, 2015; Colautti, Ågren, *et al.*, 2017; Wadgymar *et al.*, 2018). Increased temperatures as well as heat waves have been shown to reduce germination and early establishment (Chidumayo, 2008; Shevtsova *et al.*, 2009; Al-Hawija *et al.*, 2015) while decreases in rainfall and higher drought frequencies may decrease fruit set (Ågren *et al.*, 2008) and seedling survival (Hallett *et al.*, 2011). Other studies found that all of these climatic anomalies can decrease plant survival (Toräng *et al.*, 2010; Jäkäläniemi, 2011; Andrello *et al.*, 2012). Ultimately these effects on demographic rates can alter interactions between species, their geographic distributions, the structure and composition of communities and ecosystem functioning (Walther *et al.*, 2002, 2009; Walther, 2003; Jump *et al.*, 2009; Michalet *et al.*, 2014; Mora *et al.*, 2015; Selwood *et al.*, 2015; Pecl *et al.*, 2017). Hereby, the negative consequences of climate and land use change interact, for example when habitat fragmentation impedes the migration of species in order to track favorable climatic conditions (Selwood *et al.*, 2015). To sum up, native species are increasingly confronted with novel environmental conditions in their natural habitats that are often both the initial and primary cause of their decline and the ultimate cause of extinction.

1.1.2 Novel biotic and abiotic environments of biological invaders

Non-native species, which are introduced to new ranges beyond natural barriers through human activities, are confronted with a novel environment upon arrival. Climate has been identified as one of the most important filters in early invasion (Rouget *et al.*, 2004; Richardson and Pyšek, 2012). After passing the initial environmental filters during transport, introduction and establishment (Theoharides and Dukes, 2007), as species invade, they are likely to encounter an increasing variety of climatic conditions. This climatic variability is likely to result in large-scale variation of fitness and demographic rates and may cause adaptive genetic differentiation in the invader. Climate change will also affect the population and spread dynamics of invasive species either directly by removing physiological constraints or indirectly by its effects on native species as it may enhance the invasibility of increasingly mal-adapted native communities (Walther *et al.*, 2002, 2009). Moreover, land use change may result in altered levels of disturbance and thus provide opportunities for invasion (Mooney and Hobbs, 2000). Plant invasions are often facilitated by land use practices that disturb natural vegetation (Mooney and Hobbs, 2000). At the same time, abandonment of land use can also facilitate invasions in areas where native communities have adapted over centuries to a particular management regime (e.g. pastures or hay meadows in alpine regions, Tasser and Tappeiner, 2002). Consequently, altered climatic conditions and land use may affect the invaders' demographic rates in all stages of invasion from transport to spread (*sensu* Blackburn *et al.*, 2011) and may allow them to expand into regions where they were previously unable to survive or reproduce (Walther *et al.*, 2009) as for example at high altitudes or latitudes. Ultimately, invaders may pose threat to the native communities synergistically with other components of global change and may thus dramatically increase the overall negative impacts.

In particular in the primary phase of invasion (*sensu* Dietz and Edwards, 2006) - and sometimes beyond - invaders are furthermore likely to benefit from ecological release (Colautti, Alexander, *et al.*, 2017; Schrieber and Lachmuth, 2017 [9]). It has been shown that invasive species frequently experience release from co-evolved pathogens (Mitchell and Power, 2003; Dawson, 2015), parasites (Torchin *et al.*, 2003), predators (Lees and Bell, 2008) and herbivores (Keane and Crawley, 2002) and typically spread in disturbed low competition habitats (Shea and Chesson, 2002; Dietz and Edwards, 2006). These observations stimulated the development of hypotheses and theoretical frameworks that explain invasion success by ecological release, although opposing observations and concepts exist as well (Mitchell *et al.*, 2006; Catford *et al.*, 2009). Enemy release is sometimes restricted to specialists, i.e. enemies that rely on a single or few closely related host species (Keane and Crawley, 2002; Joshi and Vrieling, 2005), but can also involve generalists (Wolfe, 2002). Moreover, there may be spatio-temporal variation in enemy release across the invasion process and invaded range as enemies are most likely to be absent following initial introduction and in new founder populations at the leading edges. In particular generalist enemies are likely to accumulate over time in invading populations (Mitchell *et al.*, 2006, 2010; Dietz and Edwards, 2006; Flory and Clay, 2013). In addition, and as mentioned above, invaders often first spread in disturbed ruderal habitat or also benefit from disturbances in more natural habitats during secondary invasion (*sensu* Dietz and Edwards, 2006). Here, they may benefit from a release from competition and higher resource availability (Davis *et al.*, 2000). At the same time, strong anthropogenic disturbance regimes such as intense trampling or frequent mowing may also pose high stress for an invader and may require specific functional traits or adaptations (Hufbauer *et al.*, 2012). When invading increasingly natural habitats in the secondary phase of invasion non-native species are confronted with by and large novel biotic environments, including potential new enemies, mutualists and competitors (Parker and Gilbert, 2004; Levine *et al.*, 2004; Mitchell *et al.*, 2006).

1.1.3 Key questions

To investigate the effects of altered environmental conditions on native and invasive species in eco-systems particularly vulnerable to anthropogenic global change, we conducted two large field experiments in the Argentinean Andes (**Q.1.1**) (Cáceres *et al.*, in revision) [1] and the German Alps (**Q.1.2**) (Haider *et al.*, in preparation) [2] that addressed the following key questions.

> **Q.1.1**: How do land use and climate interact with microsite conditions in shaping the regeneration of declining mountain forest trees?
> **Q.1.2**: How do land use and climate changes interact in shaping the establishment of exotic species in mountainous grasslands?

Moreover, genetic as well as field surveys and experimental studies addressed how anthropogenic environmental changes affect the genetic diversity of native and invasive populations, how they interact with the effects of inbreeding in shaping fitness, how they facilitate interspecific hybridization and how they alter the evolutionary trajectories of species (sections 1.2 - 1.5).

1.2 Demographic and genetic bottlenecks

Populations of declining native species as well as initially introduced founder populations of non-native species are often smaller and less dense than average populations of the same species in the recent past prior to human impact. Smaller populations are more vulnerable to demographic stochasticity (i.e. the deviance between the observed number of individuals and the number expected based on average vital rates) than larger populations, which, in particular if combined with environmental stochasticity, leaves them prone to a higher risk of extinction (Menges, 1990; Schemske *et al.*, 1994; Mack *et al.*, 2000; Boyce *et al.*, 2006; Fauvergue *et al.*, 2012; Blackburn *et al.*, 2015). The higher degree of isolation in increasingly fragmented landscapes will also prevent demographic rescue through immigration from other populations (Leimu *et al.*, 2010). In addition, small and / or less dense populations often experience disruptions of biotic interactions, such as for example interactions between plants and their pollinators. Pollinators have been shown to respond to sparse and isolated plant populations with reduced visitation rates (Ghazoul, 2005) as well reduced conspecific and out-crossed pollen deposition (Caruso, 2002; Duncan *et al.*, 2004). These reductions of pollen quantity and pollen quality lower the reproductive success of plants (Ashman *et al.*, 2004) following fragmentation and demographic bottlenecks (Aguilar *et al.*, 2006). Such scenarios can cause so-called demographic Allee effects (Allee, 1931; Courchamp *et al.*, 1999, 2008), i.e. a positive population size or density dependence of *per capita* population growth rates at low population density or size (Ågren, 1996; Liebhold and Bascompte, 2003; Drake, 2004; Taylor and Hastings, 2005). If populations fall below a critical threshold of size or density population growth rates may even turn negative and populations are driven towards extinction (Courchamp *et al.*, 1999; Tobin *et al.*, 2011).

Next to the occurrence of ecological Allee effects demographic bottlenecks and limited dispersal frequently lead to a decrease in genetic diversity. These reductions of standing genetic variation are mainly caused by genetic drift, i.e. stochastic shifts in allele frequencies, which often involve a complete loss of rare alleles (Barrett and Husband, 1990; Willi *et al.*, 2007). Theoretical models show that demographic bottlenecks affect allelic richness more strongly and within shorter time than heterozygosity (Fauvergue *et al.*, 2012). Moreover, small population size favors random mating among relatives termed panmictic bi-parental inbreeding. Inbreeding further reduces genetic variation as it increases genome-wide homozygosity - quicker and more drastically than does genetic drift (Ellstrand and Elam, 1993; Keller and Waller, 2002). In consequence, inbreeding depression (see section 1.3 for more detail) and reduced adaptive potential (see section 1.5 for more detail) may lower individual fitness and consequently population growth (Willi *et al.*, 2006). Ultimately, this can put species survival at additional risk (Leimu *et al.*, 2006, 2010; Ralls *et al.*, 2018).

Generally, the susceptibility of species to genetic erosion and inbreeding depends on a variety of species characteristics. Impact is lower in organisms with a perennial life cycle, high dispersal ability, high reproductive rates as well as clonally / asexually reproducing species (Berge *et al.*, 1998; Allendorf and Lundquist, 2003). Furthermore, outcrossing has often been shown to decelerate the loss of genetic diversity as it facilitates high levels of gene flow and reduces inbreeding. In this group, wind pollinated plants are even less affected than animal pollinated plants (Weidema *et al.*, 2000). On the other hand, - as described above - obligate out-crossers may experience mate limitations as population size and / or density decreases whereas species that are able to self-pollinate are less sensitive to such effects. Polyploid species are likely to maintain higher levels of genetic diversity (Soltis and Soltis, 2000; te Beest *et al.*, 2012). In autopolyploids high levels of heterozygosity result from a highly increased portion of heterozygous combinations in polysomic inheritance (Soltis and Soltis, 2000). Many allopolyploids (i.e. polyploids of hybridogeneous origin combining the genomes of two or more parental taxa), due to disomic segregation, exhibit fixed heterozygosity which essentially conserves hybrid vigor over generations (Chen, 2007, 2010).

In bottlenecked populations of self-incompatible species reproductive success may in addition be decreased by a lack of compatible mating partners that do not share alleles at *S*-loci (Brennan *et al.*, 2006; Wagenius *et al.*, 2007; Abbott *et al.*, 2009) since negative frequency-dependent selection that acts to maintain high *S*-allele diversity may be hampered by genetic drift (Pickup and Young, 2008). In species with sporophytic self-incompatibility (SSI), such as two invaders studied for this thesis (*Senecio inaequidens*, *Centaurea stoebe*) SI is controlled by a single *S*-locus. The individual phenotype of a haploid pollen grain is determined by the diploid genotype of the parent when expressed co-dominantly. However, dominance relationships among *S*-alleles may mask recessive alleles and thereby increase mate availability (Brennan *et al.*, 2006). This again seems more likely in genetically depleted populations due to selection. The net-outcomes of these processes are largely unexplored. Among self-incompatible species polyploids are expected to maintain higher *S*-allele diversity during a bottleneck than diploids. At the same time, polyploids have a higher number of *S*-alleles per individual. In particular in SSI, where the pollen phenotype is determined by the polyploid parent genotype, the likelihood of matching *S*-alleles between partners and thus mate limitation can be increased (Fischer *et al.*, 2003; Wagenius *et al.*, 2007; Young and Pickup, 2010). This scenario may have direct negative effects on population growth (Levin *et al.*, 2009) and has thus been termed S-Allee effect (Wagenius *et al.*, 2007). At the same time the restricted mating of relatives may have the positive effects by inbreeding avoidance. Again, the net outcomes of these antagonistic effects on individual fitness and population growth rates have to my knowledge - so far - been entirely unexplored.

1.2.1 The role of demographic and genetic bottlenecks in the decline and extinction of native species

The consequences of small population size and density have first been addressed in context of the conservation of native rare and declining species. Broad empirical evidence shows that small and / or fragmented populations have lower viability or growth rates and are more prone to extinction (Lennartsson, 2002; Henle *et al.*, 2004; Gascoigne and Lipcius, 2004; Willi and Hoffmann, 2009; Kramer *et al.*, 2009; Leimu *et al.*, 2010) and that extreme fragmentation reduces species richness (Benítez-Malvido and Martínez-Ramos, 2003; Cousins, 2009; Matthews *et al.*, 2014; Haddad *et al.*, 2015). Moreover, the total number of individuals introduced, i.e. propagule pressure, is the most relevant determinant of success if species are re-introduced for biological conservation (Fauvergue *et al.*, 2012). Empirical studies have furthermore yielded vast evidence that decreasing population sizes and increasing population isolation as a consequence of habitat loss and fragmentation cause ecological component Allee effects (Forsyth, 2003; Gascoigne and Lipcius, 2004; Aguilar *et al.*, 2006; Cheptou and Avendaño V, 2006). The most often reported component Allee effects are failure to find mates in animals or pollination disruption in plants at low population densities / sizes (Fauvergue *et al.*, 2012). Demographic Allee effects are usually the assumed consequence, but the direct causality is hard to track due to methodological constraints (Ashman *et al.*, 2004; Gascoigne *et al.*, 2009). Rare and declining species further provided evidence that fragmentation and small population sizes reduce genetic diversity and increase genetic differentiation in both neutral and quantitative trait loci (Ellstrand and Elam, 1993; Leimu *et al.*, 2006, 2010; Ralls *et al.*, 2018) including *S*-alleles (Pickup and Young, 2008; Young and Pickup, 2010). Further evidence suggests that mutational load accumulates at the edges of distribution ranges due to past range expansion processes in native species, which leads to reduced individual performance and ultimately contributes to setting range limits (Travis *et al.*, 2007; Peischl *et al.*, 2013; Willi *et al.*, 2018).

1.2.2 The role of demographic bottlenecks in biological invasions

Propagule pressure, which refers to a combination of propagule size (number of individuals in each introduction event) and propagule number (number of different introductions), has by now been widely accepted as a major determinant of invasion success (Lockwood *et al.*, 2005; Fauvergue *et al.*, 2012). Just as in native species, the most important processes likely underlying this finding comprise demographic and environmental stochasticity, ecological Allee effects as well as genetic processes (see section 1.3). Theoretical studies predict that small size or low density of initial founding or leading edge populations can decrease the probability of establishment and cause a slowdown or spatio-temporal variation in spread rates (Veit and Lewis, 1996; Taylor and Hastings, 2005; Tobin *et al.*, 2007; Walter *et al.*, 2017; Sullivan *et al.*, 2017). Both ecological and genetic Allee effects have also been proposed to contribute to the lag-phases frequently observed in invasive species as well as to range pinning at the edges (Sakai *et al.*, 2001; Keitt *et al.*, 2001; Taylor and Hastings, 2005). On the one hand these circumstances may obscure the invasion risks imposed by some species, then again Allee effects provide a potential Achilles' heel that could be exploited to increase the success and lower the costs of invasion management (Liebhold and Bascompte, 2003; Taylor and Hastings, 2005; Johnson *et al.*, 2006; Tobin *et al.*, 2011).

Empirical studies of ecological Allee effects in invasive species provide evidence against (van Kleunen and Johnson, 2005; Monty and Mahy, 2010; Rodger *et al.*, 2013) as well as for (Davis, Taylor, Civille, *et al.*, 2004; Davis, Taylor, Lambrinos, *et al.*, 2004; Elam *et al.*, 2007; Firestone and Jasieniuk, 2012, 2013; Anic *et al.*, 2015) pollination limitation in both wind- and animal-pollinated invasive plants. Likewise, in the intensively studied invasive gypsy moth, *Lymantria dispar* (L.) mate-finding failure evidently causes Allee effects that affect invasion dynamics (Liebhold and Bascompte, 2003; Whitmire and Tobin, 2006; Johnson *et al.*, 2006; Tobin *et al.*, 2007; Contarini *et al.*, 2009). Increase of interspecific-competitive ability for abiotic resources with increasing patch size / density has been documented for an invasive vine (Cappuccino, 2004). Again as for native species, numerous empirical studies document the positive effects of population size, density or propagule pressure on establishment or invasion success (reviewed by Lockwood *et al.*, 2005; Blackburn *et al.*, 2015), which some studies investigated in interaction with genetic and / or environmental effects (Ahlroth *et al.*, 2003; Erfmeier *et al.*, 2013; Szűcs *et al.*, 2014). Still, mechanistic empirical research on component and in particular demographic Allee effects and their role in invasion dynamics seems to lag behind the enormous theoretical progress in this field.

1.2.3 The 'Genetic Paradox of Invasions'

Increasing empirical effort has been attributed to the investigation of genetic erosion and its potential effects on the fitness and adaptive potential of invaders. Theory suggests that a reduction of genetic diversity in invasive species is likely to occur through genetic bottlenecks and drift during initial introduction (Baker, 1955; Dlugosch and Parker, 2008; Dlugosch *et al.*, 2015), but also during subsequent range expansion involving long-distance dispersal events (Austerlitz *et al.*, 2000; Fauvergue *et al.*, 2012). Mutational load may accumulate at the leading edges of range expansion (Edmonds *et al.*, 2004; Travis *et al.*, 2007; Excoffier *et al.*, 2009). Based on the empirical evidence from native species, these processes should severely hamper the success of non-native founder populations through impeding the ecological benefits of genetic diversity (e.g. niche partitioning, sampling effects, Hughes *et al.*, 2008) as well as through inbreeding depression (see section 1.3) and reduced adaptive potential (see section 1.5). The phenomenon that invasive species are successful despite these anticipated limitations has been termed "Genetic Paradox of Invasions" (Allendorf and Lundquist, 2003; Frankham, 2004; Pérez *et al.*, 2006; Roman and Darling, 2007; Hufbauer, 2008; Chapple *et al.*, 2013). Despite the enormous progress on the population genetics and evolutionary ecology of invasive species in the past decades (Bock *et al.*, 2015) the paradox remains an object of vivid debate (Estoup *et al.*, 2016; Schrieber and Lachmuth, 2017 [9]).

To explain the paradox, it has frequently been highlighted that native *versus* introduced comparisons of genetic diversity often do not support a reduction of genetic diversity in the invaded range and that mass or multiple introductions with admixture of previously isolated gene pools may counteract genetic depletion (Allendorf and Lundquist, 2003; Roman and Darling, 2007; Hufbauer, 2008; Verhoeven *et al.*, 2011; Rius and Darling, 2014). Indeed, it has been shown that multiple introductions from different source populations are common (Dlugosch and Parker, 2008), that different introduced gene pools can admix (Lavergne and Molofsky, 2007; Kolbe *et al.*, 2008; Chun *et al.*, 2010) and that admixture may boost genotypic diversity (Kolbe *et al.*, 2008; Bermond *et al.*, 2012), fitness (Keller and Taylor, 2010) and population growth of invaders (Wagner *et al.*, 2017). As a consequence, influx of new genetic material due to repeated introduction or gene flow from other invading populations may lead to sudden population increases in previously inconspicuous species (Keller and Taylor, 2010, but see Chapple *et al.*, 2013).

However, there is also a high number of invasive species that exhibit overall reduced levels of genetic diversity (Puillandre *et al.*, 2007; Dlugosch and Parker, 2008; Uller and Leimu, 2011; Schrieber and Lachmuth, 2017 [9]), among them highly successful plant invaders (Meimberg *et al.*, 2006; Taylor and Keller, 2007; Besnard *et al.*, 2007; Hufbauer and Sforza, 2008). Others found spatial or temporal variation of genetic variation in the invaded range, such as increased drift load (Mullarkey *et al.*, 2013) or reduced genetic variation (Lachmuth *et al.*, 2010, 2015; Short and Petren, 2011) towards the leading or rear (Schrey *et al.*, 2014) edge. The results of the latter study further suggest that genetic diversity was initially low in the center of introduction and increased through admixture at some of the leading edges. Accordingly, lower genetic diversity in early compared to later phases of invasion has been demonstrated by the means of herbarium specimen (Chun *et al.*, 2010), repeated field sampling (Darling *et al.*, 2014) and Approximate Bayesian Computation (Keller *et al.*, 2012). Thus, even if average genetic diversity of invading populations is not reduced in later invasion phases, initial colonization may still have involved severe bottlenecks. Moreover, theoretical models imply that range expansions inevitably involve successive founding of populations with low size, high among population differentiation and low within population genetic diversity (Austerlitz *et al.*, 2000; Excoffier *et al.*, 2009). Also, in some systems one and the same invader spread successfully both with and without admixture along different routes (Chapple *et al.*, 2013; Schrey *et al.*, 2014). In accordance with these scenarios, a study of (Dlugosch and Parker, 2008) based on 80 comparisons of genetic diversity in native *versus* invasive ranges provides evidence that the proportional change in genetic diversity of invaders over time followed a U shape. Allelic richness first decreased up to 80-100 years after first introduction presumably due to drift and selection and then increased again presumably due to gene flow and admixture among different invading populations. This emphasizes that genetic impacts of different demographic events (singular *versus* multiple introduction, bottlenecks *versus* admixture) are not alternative scenarios, but are in fact nonexclusive of each other, even for a single species (Keller *et al.*, 2012; Chapple *et al.*, 2013; Schrey *et al.*, 2014; Yang *et al.*, 2017).

In summary, we have to assume that genetic bottlenecks occur far more frequently at some points during biological invasions than rather simplistic native *versus* introduced comparisons of genetic diversity at a single and usually far advanced temporal stage of invasion may suggest. In addition, such genetic erosion also seems to occur in invasive species that possess one or several biological characteristics such as polyploidy, self-incompatibility, perennial life cycle or high reproductive and dispersal rates that are thought to prevent losses of genetic diversity (Durka *et al.*, 2005; Chun *et al.*, 2010; Lachmuth *et al.*, 2010, 2011, see Schrieber and Lachmuth, 2017 [9] for a more detailed discussion). Moreover, broad evidence suggests that non-native genetically impoverished populations can grow and spread successfully prior to experiencing an opportunity for genetic admixture (Dlugosch and Parker, 2008; Uller and Leimu, 2011; Chapple *et al.*, 2013; Schrey *et al.*, 2014; Jones and Brown, 2014). Thus the 'Genetic Paradox' remains - at least partly- unexplained.

Most conceptual papers that addressed the genetic paradox beyond the potential role of multiple or mass introduction, and proposed alternative mechanisms by which introduced populations could overcome the limitations posed by low genetic diversity, focused on the challenge of adaptation to the novel environments (Lee, 2002; Pérez *et al.*, 2006; Dlugosch and Parker, 2008; Dlugosch *et al.*, 2015; Estoup *et al.*, 2016). Conversely, the potential problems posed by inbreeding depression for establishment and spread of invaders (Blackburn *et al.*, 2015), received far less attention conceptually as well as empirically (but see Frankham, 2004; Szűcs *et al.*, 2014, 2017). This is surprising given the breadth of evidence generated by conservation science illustrating the detrimental effects of inbreeding on fitness and the persistence of small and genetically impoverished populations (Keller and Waller, 2002; Henle *et al.*, 2004; Leimu *et al.*, 2006, 2010; O'Grady *et al.*, 2006; Frankham, 2010; Frankham *et al.*, 2014; Hedrick *et al.*, 2015; Hedrick and Garcia-Dorado, 2016; Ralls *et al.*, 2018, see next section 1.3).

1.2.4 Key questions

In this research field we first developed an experimental-analytical framework that can help investigating component Allee effects in demographically bottlenecked populations. We tested this approach with a field experiment in a founder population of an successful invader (**Q.2.1**) (Lachmuth *et al.*, 2018) [3], but it is also applicable to and of high relevance for native declining species. As low genetic diversity can be an important driver towards extinction as well as a barrier in the early phases of invader establishment and spread, we quantified genetic diversity in native and invasive species and addressed several mechanisms that may counteract or increase genetic erosion (**Q.2.2-5**) (Peng *et al.*, 2015; Rosche *et al.*, 2016; Rosche, Schrieber, *et al.*, 2018) [4-6].

Specifically, we addressed the following key questions:

> **Q.2.1**: Are pollinator-mediated component Allee effects trait- and scale-dependent at the population and community level?
> **Q.2.2**: Are the genetic diversity and structure of a declining Andean tree line species rather shaped by Pleistocene climatic oscillations or recent human disturbance?
> **Q.2.3**: How do population size and sex ratio influence the genetic diversity of an endangered dioecious clonal herb?
> **Q.2.4**: Does a lower susceptibility to genetic erosion add to explaining the invasion success of polyploids?
> **Q.2.5**: Is genetic erosion in diploid and tetraploid cytotypes fostered by anthropogenic disturbance?

In a review and conceptual paper (Schrieber and Lachmuth, 2017) [9] presented in section 2.3 we further developed a novel approach towards the 'Genetic Paradox of Invasions' that focuses on the role of inbreeding depression in invaders and invasion phases that experience or involve genetic depletion.

1.3. Inbreeding depression and inbreeding x environment interactions

1.3.1 Inbreeding depression

Inbreeding – as a consequence of reduced population size and genetic diversity - has been shown to decrease the fitness of plants in offspring of related as compared to unrelated individuals in wild populations (Keller and Waller, 2002; Leimu *et al.*, 2006, 2010; O'Grady *et al.*, 2006; Frankham, 2010; Frankham *et al.*, 2014; Hedrick *et al.*, 2015; Hedrick and Garcia-Dorado, 2016). Such inbreeding depression arises through two non-mutually exclusive mechanisms (Charlesworth and Charlesworth, 1987; Charlesworth and Willis, 2009). Firstly, recessive deleterious alleles that exist at low frequency in the gene pool occur more frequently in a homozygote state in inbred individuals. They thus get expressed and unfold their negative effects on fitness ('dominance' mechanism). Secondly, some loci show heterozygote advantage, i.e. the heterozygote genotype has higher relative fitness than both homozygote genotypes ('overdominance'). According to empirical evidence the dominance mechanism is more relevant in natural populations (Charlesworth and Willis, 2009; Hedrick *et al.*, 2015). The level of (dominance-mediated) inbreeding depression in a bottlenecked population depends on the accumulated segregating mutation load, i.e. the portion of genetic load due to non-fixed deleterious mutations (Haldane, 1937 in Agrawal and Whitlock, 2012), which is in turn influenced by population history (Hedrick and Garcia-Dorado, 2016). This arises as past inbreeding events in concert with strong selection may have purged lethal and deleterious recessive alleles from the gene pool to different degrees in different populations (Agrawal and Whitlock, 2012).

In addition, the strength of inbreeding depression as well as resultant purging may vary for different fitness components such as survival, mating or reproduction and inbreeding may affect phenotypic traits correlated with fitness, such as growth or metabolic traits, as well (Angeloni *et al.*, 2011; Hedrick and Garcia-Dorado, 2016). Both also depend on life history and other species characteristics. Species traits that favour or enforce outbreeding such as sequential hermaphrodism, self-incompatibility or dioecy help avoiding inbreeding and thus inbreeding depression. Moreover, long-lived organisms have a lower number of generations per unit time, therefore the level of inbreeding may increase at a lower rate per year than in short-lived organisms (Angeloni *et al.*, 2011). On the other hand, in populations that traditionally had low rates of inbreeding mutational load should have accumulated, as there was no opportunity for purging. In such cases inbreeding depression will be stronger when (biparental) inbreeding is enforced, e.g. by sudden population bottlenecks. This may explain why rare or endemic species often show lower inbreeding depression than wide-spread species (Angeloni *et al.*, 2011).

Polyploidy, just as fostering the maintenance of genetic diversity during demographic bottlenecks (see section 1.2) may also help avoiding inbreeding depression in case genetic erosion occurs nonetheless. Empirical studies support increased heterozygosity in allozyme and neutral markers in polyploids (Brown and Young, 2000; Hardy and Vekemans, 2001). Low population size during early polyploid establishment may in addition purge genetic load (Lande and Schemske, 1985). However, on the long term deleterious alleles may accumulate and genetic load may even exceed that of diploids when populations approximate mutation-selection equilibrium (Ronfort, 1999). Furthermore, the polyploid organism may experience genomic downsizing (Leitch and Leitch, 2008) leading to diploidization (Soltis and Soltis, 2000). Experimental studies are still scarce, but indicate low inbreeding depression in polyploids (Galloway *et al.*, 2003) or a reduction in comparison to conspecific diploid populations (Husband and Schemske, 1997).

1.3.1.a The significance of inbreeding depression for the decline of native species

Inbreeding depression was first investigated in the context of the evolution of breeding systems (Darwin, 1868, 1876; Lande and Schemske, 1985; Charlesworth and Charlesworth, 1987), dispersal (Ronce, 2007) and behaviour (Pusey and Wolf, 1996) as well as animal breeding or domestication (Ralls *et al.*, 1988). However, in the past decades population and conservation biologists became increasingly aware of the issue and showed that loss of genetic diversity reduces individual fitness (Leimu *et al.*, 2006, 2010; Elam *et al.*, 2007; Ralls *et al.*, 2018) as well as population viability and growth rates (Henle *et al.*, 2004; Honnay *et al.*, 2005; Ralls *et al.*, 2018). Numerous experimental studies with native species (reviewed in Lienert, 2004; Angeloni *et al.*, 2011) in combination with reliable estimates of inbreeding depression (Jimenez *et al.*, 1994; Crnokrak and Roff, 1999; Briskie and Mackintosh, 2004) and estimates of demographic rates in the wild (Oostermeijer *et al.*, 2003) have lead to the now widely accepted view that inbreeding depression has high significance for the population viability, persistence and consequently conservation of rare and declining species in their natural fragmented habitats (Lande, 1995; Keller and Waller, 2002; Leimu *et al.*, 2010; Ralls *et al.*, 2018).

1.3.1.b The little investigated role of inbreeding depression in biological invasions

Possibly due to the prevailing assumption that invaders rarely encounter severe losses of genetic diversity (see section 1.2.3), research into inbreeding depression in invaders is scarce. An early study on smooth cord grass (*Spartina alterniflora* Loisel., Poaceae) invading San Francisco Bay documented severe genetic depletion and inbreeding depression in particular through reduced juvenile growth and survival (Daehler, 1999) as well as reduced herbivore resistance (Daehler and Strong, 1997; Daehler, 1999). For the exceptionally rapid invader *Senecio inaequidens* DC. (1838) (South African ragwort, Asteraceae) - a self-incompatible, polyploid species that was mass-introduced multiple times to Europe - Lachmuth *et al*. not only found a decrease of genetic diversity towards the invasion front (2010), but also that such loss of diversity decreases fitness (2011). A comprehensive review of studies on reproductive success of 15 bird species introduced to New Zealand demonstrated that severe bottlenecks (<150 individuals) substantially and persistently increased hatching failure most likely due to inbreeding depression (Briskie and Mackintosh, 2004). Facon *et al*. (2011) showed that inbreeding depression occurred and lead to purging of genetic load in invasive harlequin ladybirds (*Harmonia axyridis* (Pallas, 1773), Coccinellidae). Similarly, (Parisod *et al.*, 2005) found no inbreeding depression in a highly inbred exotic founder population of the mainly outcrossing pitcher plant *Sarracenia purpurea* L. (Sarraceniaceae). The authors concluded that genetic load had not only apparently been purged, but that some form of selection for inbreeding had occurred due to co-adaptation between loci since outbreeding depression was evident in the respective population. Further experimental evidence of the potential role of inbreeding depression in invasions came from studies that addressed inbreeding x environment interactions in non-native species (see section 1.3.2b).

1.3.2 Inbreeding x environment interactions

Evidence is accumulating that inbreeding depression is environment-dependent (Dudash, 1990; Jimenez *et al.*, 1994) and particularly pronounced under stressful conditions (Darwin, 1876; Armbruster and Reed, 2005; Liao and Reed, 2009; Fox and Reed, 2011; Cheptou and Donohue, 2011; Reed *et al.*, 2012). Such inbreeding x environment (I x E) interactions have first been observed when researchers compared the severity of inbreeding depression between *ex situ* / captive and natural environments (Dudash, 1990; Jimenez *et al.*, 1994; Crnokrak and Roff, 1999; García-Fernández *et al.*, 2012). In the meanwhile, studies have documented I x E interactions for a variety of specific environmental factors in both plants and animals including temperature (Vermeulen *et al.*, 2014), water availability (Cheptou, Berger, *et al.*, 2000; Sedlacek *et al.*, 2012; Prill *et al.*, 2014; Schou *et al.*, 2015), nutrient availability (Hayes *et al.*, 2005), pathogen and parasite attack (Freitak *et al.*, 2014), herbivory (Ivey *et al.*, 2004; Hayes *et al.*, 2004; Campbell *et al.*, 2013; Kariyat, Balogh, *et al.*, 2013; Kalske *et al.*, 2014) and intra- (Schmitt and Ehrhardt, 1990; Cheptou *et al.*, 2001; Yun and Agrawal, 2014) as well as interspecific competition (Cheptou, Imbert, *et al.*, 2000). However, whereas all these studies found that stress and inbreeding synergistically negatively influenced fitness-related traits, others reported lower or equal inbreeding depression under natural or stressful *versus* benign conditions (e.g. Henry *et al.*, 2003; Leimu *et al.*, 2008; Waller *et al.*, 2008; Sandner and Matthies, 2016, 2017).

In principle, I x E interactions can be caused by two different mechanisms (see Fig. 1 in Schrieber and Lachmuth, 2017 [9] for a detailed description). First, increased homozygosity may unmask recessive deleterious alleles at loci involved in stress responses (Kariyat, Mena-Ali, *et al.*, 2012; Kariyat, Mauck, *et al.*, 2013; Kariyat, Balogh, *et al.*, 2013). Second, inbreeding depression is a stress in itself as it causes various metabolic dysfunctions that induce stress responses (Kristensen *et al.*, 2010). As such inbreeding depression may compromise an individual's capacity to respond to additional environmental stresses and *vice versa*. Alternatively, the 'phenotypic variation hypothesis' (Waller *et al.*, 2008) predicts that enhanced phenotypic variation in a certain environment leads to increased inbreeding depression instead of direct effects of stress intensity.

On the theoretical site, (Liao and Reed, 2009) demonstrated *in silico* that I x E interactions can influence demographic rates and increase the extinction risk of species. Surprisingly I x E interactions where suggested to be most relevant for populations of intermediate size that were previously considered relatively safe from environmental and genetic stresses acting independently. Several authors also discussed how I x E interactions may influence (eco-) evolutionary dynamics (Cheptou and Donohue, 2011; Reed *et al.*, 2012; Leimu *et al.*, 2012). Here, the most relevant aspect for this thesis is the assumption that, as consequence of I x E interactions, also the degree of purging will likely differ among environments depending on the selective pressure they exert (i.e. environment-dependent purging) (Cheptou and Donohue, 2011; Hedrick *et al.*, 2015; Sandner and Matthies, 2016). Moreover, at certain loci some alleles may only be deleterious in specific environments as for example under a particular stressor. Such alleles are termed conditionally deleterious (Kariyat, Mauck, *et al.*, 2012; Kariyat, Mena-Ali, *et al.*, 2012; Vermeulen *et al.*, 2014), and may get purged in the stressful environment, but accumulate in other environments even if severe inbreeding occurs (Cheptou, Berger, *et al.*, 2000).

1.3.2.a Inbreeding x environment interactions in native declining species

Most empirical studies on I x E interactions were conducted with native populations of applicable study organisms. However, only the following were specifically related to habitat fragmentation, population declines or more generally range dynamics. (Sedlacek *et al.*, 2012) found for the rare plant *Echium wildpretii* subsp. *wildpretii* [H. Pearson ex Hook.f.] (Boraginaceae) - endemic to the arid subalpine zone of the island of Tenerife - that inbreeding depression in seedling performance is higher under drought stress, which is predicted to increase at the Canary Islands under climate change. An empirical study on native populations of *Silene ciliata* Pourr. (Caryophyllaceae) at its southernmost distribution limit along an environmental (altitude/aridity) gradient suggested that inbreeding depression plays an important role in the fitness of early life stages of the species. Only for two of the tested fitness components (seed mass, seedling survival) the results supported the hypothesis that specifically summer drought enhances the severity of inbreeding depression (García-Fernández *et al.*, 2012). However, for most fitness components inbreeding depression was higher under field than laboratory conditions. By contrast, Sandner and Matthies (2017) did not find an increase in inbreeding depression under stress by poor host quality in the rapidly declining root hemiparasite *Rhinanthus alectorolophus* (Scop.) Poll. (Orobanchaceae).

1.3.2.b Inbreeding x environment interactions and purging in invasive species

Studies on I x E interactions in invasive species are still relatively scarce. For exotic founder populations, the potential emergence of I x E interactions implies that an ecological release (e.g. of co-evolved enemies and competitors) in the novel range may buffer against inbreeding depression in populations during initial colonization, in the primary phase of invasion (*sensu* Dietz and Edwards, 2006) or towards the leading edges of expansion. The growth rates of these populations are particularly influential on invasion dynamics and speed of expansion (Keitt *et al.*, 2001; Tobin *et al.*, 2007; Fauvergue *et al.*, 2012). As described in detail in section 1.1, such ecological release is common and forms the basis of various theories that aim at explaining invasion success (Mitchell *et al.*, 2006; Catford *et al.*, 2009). Conversely, genetically depleted founding populations in more natural habitats may be hampered not only by a lack of adaptive potential to their novel antagonists, but also by an amplification of inbreeding depression in these more stressful environments (Hufbauer *et al.*, 2013; Szűcs *et al.*, 2014, 2017).

First empirical hints that I x E interactions may also play a role for invasive species came from the above-cited finding of inbreeding depression in the herbivore resistance (Daehler and Strong, 1997; Daehler, 1999) of invasive *Spartina alterniflora*. Moreover, (Daehler, 1999) found that inbreeding depression in seedling and juvenile performance in this species was environment-dependent. Another striking example is the invasion of house finch (*Carpodactus mexicanus*, Fringillidae) in the eastern USA, which was extremely successful despite a severe founder effect during initial introduction (a few dozens of individuals) before a disease epidemic caused by the bacterium *Mycoplasma gallisepticum* (Mycoplasmataceae) hit the genetically depleted invading populations (Hawley et al., 2006). An experimental study supported the suspicion that a drastic loss of heterozygosity may have mediated the high susceptibility to *M. gallisepticum*, a pathogen that previously did not even infect species of the genus *Carpodactus* or other wild passerines but has now also spread to native house finch populations (Hawley *et al.*, 2005).

Hufbauer and colleagues (Hufbauer *et al.*, 2013) investigated the role I x E interactions in the colonization of a novel host species by *Bemisia* white flies (Aleyrodidae), whereby the novel host was considered as more challenging environment and indeed increased inbreeding depression experienced by the flies as compared to a natal host. This effect, however, did not impact the net reproductive rate. This study was particularly interesting as it also aimed at disentangling demographic and genetic effects. In fact, both high propagule pressure and an outbred genetic background facilitated the establishment of larger populations, whereby only the genetic background consistently affected net reproductive rate. Larger propagules resulted in more established individuals, but did not change reproductive rates. In a similar experiment with *Tribolium* beetles (Tenbrionidae) (Szűcs *et al.*, 2014) inbreeding only negatively affected the growth of small, but not large populations and genetic diversity positively affected dispersal distances and increased dispersal rates in particular in low quality novel-host environments.

Inbreeding x environment interactions are likely to act as an evolutionary force during invasions as they may influence the degree of purging that acts in different invasion phases and invaded habitats. Generally, the occurrence of inbreeding depression in early stages of invasion as well as at the leading edges is likely to purge deleterious alleles and decrease inbreeding depression during subsequent founder events and population bottlenecks. However, due to the environment-dependence of purging (Cheptou, Berger, *et al.*, 2000), while bottlenecks may purge parts of the genetic load, deleterious alleles involved in stress reactions or competitive ability may or may not be maintained depending on the stress release or increase experienced in the invaded habitat. Environment-dependent purging may thus leave a genetic signature of the evolutionary and ecological history of the invading populations that may be used by researchers to reconstruct and understand this history (Schrieber and Lachmuth, 2017 [9]). In summary, I x E interactions may be another field of eco-evolutionary research for which biological invasions may serve as 'big unplanned experiments' (Sax *et al.*,

2007) yielding insights of relevance not only for the management of exotic, but also of rare and declining species (Colautti, Alexander, *et al.*, 2017).

1.3.3 Key questions

In this research field the studies contributing to this thesis worked exclusively with invasive plants with the overall aim to help explaining the 'Genetic Paradox of Invasions'. Nevertheless, - as indicated above - the results will have important transferable implications for rare or declining species, which often face a combination of inbreeding and environmental change as well. Moreover, all experiments also included native populations of the investigated species. Specifically, we combined artificial breeding with common garden experiments that simulated stressful *versus* benign environments with two invasive plant species to address the following key questions:

> **Q.3.1**: Does a low susceptibility to inbreeding depression add to explaining the invasion success of polyploids? (Rosche *et al.*, 2017) [7]
> **Q.3.2**: Can inbreeding x environment interactions limit the founder success of genetically bottlenecked populations in stressful disturbed habitats? (Rosche, Hensen, *et al.*, 2018) [8]
> **Q.3.3**: Can stress release mitigate the inbreeding depression in genetically bottlenecked founder populations and thereby contribute to their success? (Schrieber and Lachmuth, 2017; Schrieber *et al*., in revision)[9,10]

1.4. Interspecific hybridization

Anthropogenic alterations to habitats as well as dispersal pathways have increased the occurrence of hybridization between previously distinct taxa. For declining as well as invasive species hybridization can have diverse evolutionary outcomes and whether those are regarded positive or negative is ultimately a question of the respective conservation goals. As summarized by Todesco *et al*. (2016), hybridization can either increase or decrease diversity. A diversity increase may result from the establishment of stable hybrid zones and the formation of novel hybrid taxa, reinforcement of reproductive isolation as well as origin or transfer of adaptations and the evolutionary rescue of inbred populations. The opposite outcome of decreased diversity can occur if reproductive barriers break down, previously separate evolutionary lineages merge and or parental populations go extinct.

From a demographic perspective, positive effects of hybridization on population growth may result from several non-mutually exclusive mechanisms (Hovick and Whitney, 2014): 1) Hybridization can create novel phenotypes relative to the parental taxa, including novel combinations of parental phenotypic traits and transgressive phenotypes with trait values exceeding the ranges of the parental taxa, which may be more successful particularly in novel habitats. 2) Hybridization may increase standing genetic and phenotypic variation on which selection can act and thus the evolutionary potential and capacity to cope with environmental or demographic stochasticity. However, the benefits of genomic admixture decrease with the degree of local adaptation (Verhoeven *et al.*, 2011; Rius and Darling, 2014; Colautti, Alexander, *et al.*, 2017). 3) Particularly F1 hybrids may experience heterosis, i.e. an increase in fitness due to increased heterozygosity. In combination with mechanisms that fix heterosis over generations or longer time spans (e.g. polyploidy, vegetative reproduction, agamospermy) hybrids may exhibit greater vigor compared to the parental taxa.

1.4.1 The threat of interspecific hybridization for native species

For rare or declining species hybridization with more common taxa may lead to species extinction via either demographic or genetic swamping (*sensu* Wolf *et al.*, 2001) . In the first case, hybrids exhibit a lower fitness than the parent(s) (outbreeding depression) and thus get removed by selection. Here, low population sizes and low effective recombination limit the ability of selection to decouple maladaptive from adaptive introgressed alleles (Colautti, Alexander, *et al.*, 2017). Moreover, declining species are more often locally adapted than invasive species and thus novel alleles are likely maladaptive. If hybridization occurs frequently under such circumstances, reproductive effort can be wasted to an extent that leads to negative population growth rates. By contrast, in the case of genetic swamping, hybrids are more fit than the parental taxa (heterosis, hybrid vigour) and thus outperform and replace one or both of them. In a quantitative review of studies investigating the role of hybridization in extinction (Todesco *et al.*, 2016) found that extinction risk is higher in the absence of reproductive barriers and if introgression occurs into the direction of the rare parental taxon. Moreover, genetic swamping seems to be more common than demographic swamping. The authors emphasize that more research is needed to understand how the role of hybridization in extinction is influenced by components of global change such as climate change.

1.4.2 The benefits of hybridization for biological invasions

Among the genetic and evolutionary processes that may promote invasiveness hybridization has long been considered (Stebbins, 1985; Abbott, 1992; Lambrinos, 2004). Ellstrand and Schierenbeck (2000) presented a first list of 28 taxa in which hybridization preceded invasion, which they later on expanded to 35 taxa (Schierenbeck and Ellstrand, 2009, see also Hovick & Whitney 2014 for an extension to 72 taxa). The main reasons are the above-listed increases of genetic variation and heterozygosity, which are expected to be mainly beneficial in invaders due to a lack of local adaptation to the novel environments. Hovick and Whitney (2014) pointed that several factors may complicate empirical investigations into these causal relationships between hybridization and invasiveness. For example, the effects of hybridization on performance may vary tremendously across generations (due to heterosis and later hybrid breakdown), but also within hybrid classes (due to differing parental backgrounds). The authors conducted a meta-analysis on experiments that thoroughly tested the relative differences in performance between hybrids and parental taxa. The results confirmed strong inter- and intra- hybrid class variation, but also that wild hybrids were on average significantly larger, more fecund and, in the case of plants, also had higher survival than their parental taxa. Moreover, hybridization is often associated with polyploidy, which also confers invasion success (te Beest *et al.*, 2012).

Hybridization in polyploid invasive species may in addition be advantageous as it induces genomic rearrangements and genomic downsizing. Whereas te Beest *et al.* (2012) argued that the greater genome size of polyploids may increase their life span, size, competitive ability, and thus invasiveness, a growing body of literature (Bennett *et al.*, 1998; Grotkopp *et al.*, 2004; Kubešová *et al.*, 2010; Lavergne *et al.*, 2010; Suda *et al.*, 2014; Pandit *et al.*, 2014; Schmidt *et al.*, 2017) rather supports a previous hypothesis of Rejmánek (1996) according to which small genome size promotes invasion. It is assumed that species with small genomes comprise a wider range of trait values (Knight *et al.*, 2005). Moreover, whereas holoploid genome size positively affects cell size, small monoploid genome size leads to high cell division rates associated with traits such as short generation times, small seeds or high relative growth rates (Suda *et al.*, 2014). Several authors (Chen *et al.*, 2010; Pandit *et al.*, 2014; Schmidt *et al.*, 2017) thus argue that polyploidy may not confer invasion success due to its positive effects on holploid genome size, but rather by reducing monoploid genome size during subsequent genome downsizing (Leitch and Bennett, 2004), which has also strongly been supported by within-species studies (Lavergne *et al.*, 2010; Pyšek *et al.*, 2018).

The fact that species are transported globally with increasing frequency will lead to continued introduction of invasive hybrids to new regions as well as to the formation of novel hybrid taxa. Therefore, the hypothesized connection between hybridization and invasion success is likely to remain a critical issue for conservation of native species (Todesco *et al.*, 2016) as well as fundamental invasion and eco-evolutionary research (Hovick and Whitney, 2014).

1.4.3 Key questions

In this research field, we combined surveys of neutral genomic markers with studies of morphometric variation (**Q.4.1-2)** as well as genome size (**Q.4.3)** in order to assess the extent of interspecific hybridization among three endemic island taxa (van Hengstum *et al.*, 2012) [11] as well as an invasive hybrid complex (Lachmuth *et al*., in revision) [12].

Specifically, we addressed the following key questions:

Q.4.1: Does anthropogenic disturbance facilitate hybridization among endemic island taxa?
Q.4.2: What is the extent of genomic introgression in plant individuals of a highly invasive hybrid complex?
Q.4.3: To which degree is genomic admixture in invasive hybrid individuals associated with morphology and genome size?

1.5. Altered evolutionary trajectories

The novel environments that plants experience either as a consequence of human-induced changes to their native habitats or when they are translocated to new geographic areas, not only have ecological consequences as described in section 1.1, but also alter the selective pressures species experience and thus their evolutionary trajectories (Franks *et al*., 2014; Valladares *et al*., 2014; Colautti, Ågren, *et al*., 2017). The demographic success of species will depend on their ability to migrate, their phenotypic plasticity and their ability to respond to selection and to adapt to novel environments. Starting with the classical example of peppered moth (*Biston betularia* L., Geometridae), which evolved melanism in response to industrial pollution (Kettlewell, 1972), there is mounting evidence that natural populations can successfully and rapidly adapt to environmental changes based on the standing genetic variation available at the onset of change (Hoffmann and Sgrò, 2011).

The rate at which a species evolves should be strongly influenced by generation time. Moreover, the amount of heritable genetic variation - in interaction with the strength of selection - determines the adaptive potential of populations. In the course of environmental change, individuals in a population will become increasingly mal-adapted and selection will first lead to a decrease in fitness as adaptation lags behind. The probability that a population can persist through this time lag between the onset of change and adaptation to the new phenotypic optimum depends upon the spread of genetic variation in the population, the degree of phenotypic plasticity and individual growth rate (Rice and Emery, 2003).

Next to a lack of heritable genetic variation, genetic correlations among traits may constrain adaptive differentiation even if genetic variation for the respective traits exists. Such genetic correlations represent a lack of genetic variation for particular trait combinations and lead to a fitness trade-off as selection cannot improve both traits simultaneously (Lande, 1979; Colautti *et al.*, 2010). A very common-case are resource allocation trade-offs where a particular genetic pathway contributes to both traits under consideration and resources can only be invested in one trait at the expense of the other (Koricheva, 2002). Thus costs and benefits may cancel each other out, yielding no net change in fitness (Rice and Emery, 2003). However, optimizing one trait at the expense of the other may still be beneficial depending on the environment.

Differentiation among populations may not only arise from adaptive evolution, but also from the non-adaptive evolutionary processes of mutation, drift and genetic admixture. These processes may cause random geno- and phenotypic divergence among invading populations, which falsely suggests or masks adaptive evolution. Statistical tests for adaptive evolution thus have to control for non-adaptive differentiation arising from variation in the co-ancestry of populations (Keller and Taylor, 2008; Keller *et al.*, 2009; Lachmuth *et al.*, 2011; Karhunen *et al.*, 2013; Agrawal *et al.*, 2015). Moreover, non-adaptive differentiation in life history traits may itself cause variation in population growth rates. Since stochastic processes generally play an important role during phases of range retractions, shifts or expansions (Keller and Taylor, 2008; Excoffier *et al.*, 2009), population dynamics under global change are likely to fluctuate in response to bottlenecks, genetic drift and admixture of previously isolated genetic material.

1.5.1 The role of evolution in the fate of native declining species under global change

The conservation of rare and declining species may be complicated if small, bottlenecked and genetically isolated populations experience decreases in adaptive potential due to a lack of genetic variation (Willi *et al.*, 2006). Nevertheless, microevolution may be an important way of escaping extinction in the face of global change. And indeed adaptive evolutionary changes have been documented for a broad range of traits and mostly in response to anthropogenic pressures (Rice and Emery, 2003). Still, intraspecific trait variation has long received little attention in comparison to interspecific trait variation.

Across their native range populations may have locally adapted to differential environmental conditions. Some of these local adaptations may provide pre-adaptations for future conditions at other sites and thus species exhibiting greater intraspecific variation may have a greater chance of coping with global change (Thuiller et al., 2004). Nevertheless, such scenario requires sufficient genetic exchange across the landscape. However, high gene flow among populations in the past may have counter-acted local adaptation and may also swamp new developing local adaptations, since ultimately local adaptation arises from a function of the relative strength of selection and gene flow (Kawecki and Ebert, 2004). Thus, local adaption poses challenges to restoration efforts that involve the introduction of new genetic material, which may be maladapted to the current or future conditions at a particular site. A further critical question is how much genetic variation should be maintained or introduced to allow for adaptation to future conditions, since not all evolution is adaptive (McKay et al., 2005). Moreover, although local adaptation is common in plants, it is not ubiquitous and can differ in its magnitude due to differences in past gene flow selection balance (Leimu and Fischer, 2008).

1.5.2 Adaptive and non-adaptive evolution in the course of plant invasions

The influence of evolutionary process on invasions starts already prior to introduction with the evolutionary history of the native populations. In this context, climatic pre-adaptation has long been considered and received most attention due to the prominent role of climate as abiotic filter for successful establishment (Erfmeier, 2013; Gallien *et al.*, 2015). Relatively novel theory, moreover, suggests that human-mediated disturbance regimes in native habitats, such as frequent mowing, trampling or traffic as well as resultant fluxes in resource availability (Davis *et al.*, 2000) may pre-adapt species for primary invasion in similarly disturbed or ruderal habitats in the new range (Anthropogenically Induced Adaptation to Invade (AIAI) hypothesis, Hufbauer *et al.*, 2012). Similarly, climatic or other local adaptations acquired within the invaded range may serve as pre-adaptations for continued range expansion.

In the past two decades, rapid post-introduction micro-evolutionary change has increasingly been recognized as a mechanism that may foster biological invasions. This development is reflected in an increasing number of conceptual frameworks for explaining invasion success (Blossey and Nötzold, 1995; Sakai *et al.*, 2001; Müller-Schärer and Steinger, 2004; Facon *et al.*, 2006; Dietz and Edwards, 2006; Hufbauer and Torchin, 2007; Prentis *et al.*, 2008; Catford *et al.*, 2009, 2018; Phillips *et al.*, 2010; Zenni *et al.*, 2017) and reviews documenting the role of evolutionary change during invasions (Lambrinos, 2004; Bossdorf *et al.*, 2005; Sax *et al.*, 2007;

Whitney and Gabler, 2008; Vanderhoeven *et al.*, 2010; Felker-Quinn *et al.*, 2013; Colautti and Lau, 2015; van Kleunen *et al.*, 2018). Empirical research on evolution during invasions was noticeably stimulated by the publication of the EICA (Evolution of Increased Competitive Ability) hypothesis (Blossey and Nötzold, 1995), which postulated that invading plants should evolutionarily adapt to enemy release in their novel range (see section 1.1.2) by shifting resource allocation from defense to (vegetative and/or reproductive) performance.

Later on, it has been proposed that allocation may rather shift from defense against specialist co-evolved herbivores to defense against generalists (shifting defense hypothesis, Müller-Schärer *et al.*, 2004), which also received empirical support (Joshi and Vrieling, 2005; Felker-Quinn *et al.*, 2013). Further empirical research focused for example on changes of physiological tolerances and adaptation to new habitat types (Parker *et al.*, 2003; Maron *et al.*, 2004; Meimberg *et al.*, 2010; Dyer *et al.*, 2010). Moreover, changes in resource allocation to competitive *versus* reproductive and dispersal ability among different regions of the invaded range such as rear *versus* leading edge (Travis and Dytham, 2002; Urban *et al.*, 2008; Pizzatto *et al.*, 2017), different invasion phases (Dietz and Edwards, 2006) or in response to local adaptive regimes (Lachmuth *et al.*, 2011) were addressed.

Moreover, researchers investigated processes that may either facilitate or constrain adaptive evolution during invasions. High attention was paid to the facilitating role of intraspecific admixture following multiple or mass introductions (Kolbe *et al.*, 2008; Verhoeven *et al.*, 2011; Rius and Darling, 2014; Estoup *et al.*, 2016) as well as interspecific hybridization (Ellstrand and Schierenbeck, 2000; Lambrinos, 2004; Hovick and Whitney, 2014), which both increase genetic variation on which evolution can act. Constraints may arise from resource allocation trade-offs (e.g. EICA, shifting defense) or more generally genetic correlations as described above (Colautti *et al.*, 2010; Hornoy *et al.*, 2011).

One major challenge remains to prove that the observed genetic differentiation among invading populations or between invasive and native populations is actually adaptive (Felker-Quinn *et al.*, 2013; Colautti and Lau, 2015; van Kleunen *et al.*, 2018). Although the issue has been raised in a highly cited publication from 2008 (Keller and Taylor, 2008) and in macro-evolutionary research accounting for phylogenetic relatedness has long become standard (Housworth *et al.*, 2004), only few empirical studies published in the past decade on genetically based trait differentiation in invaders accounted for the influences of stochastic processes such as drift (but see Chun *et al.*, 2009; Keller *et al.*, 2009; Meimberg *et al.*, 2010; Xu *et al.*, 2010; Lachmuth *et al.*, 2011; Agrawal *et al.*, 2015). Also attempts to demonstrate the fitness gains of evolved invasive populations through reciprocal transplant experiments have only rarely been undertaken (van Kleunen *et al.*, 2018), possibly due to ethical or legal restrictions concerning the (re-)introduction of invasive genotypes into native natural habitats.

Still, there is reason to believe that invasive species may show a more rapid evolutionary response to novel environments than native species (Colautti, Alexander, *et al.*, 2017) and that adaptive evolution may significantly alter the performance, impact and range dynamics of invasive species. Adaptive changes may enhance the speed of invasions (Phillips *et al.*, 2006), inflate their potential range limits and habitat types invaded as well as their impact on native communities (van Kleunen *et al.*, 2018).

1.5.3 Key questions

In this research field, we firstly quantified genetic (Al-Gharaibeh, Hamasha, Rosche, *et al.*, 2017) [14] and phenotypic variation (Al-Gharaibeh, Hamasha, Lachmuth, *et al.*, 2017; Ley *et al.*, 2018) [15,13] of native species to assess their evolutionary potential under climate change (**Q.5.1**). Secondly, we used a field common garden experiment (**Q.5.2**) (Haider *et al*., in preparation) [2] and a common garden clipping experiment (**Q.5.3**) (Rosche, Hensen, *et al.*, 2018) [8] to explore the role of pre-adaptation in establishment success of invaders. Finally, we utilized data from the common garden enemy release experiment of Schrieber *et al.* (in revision) [10] to investigate whether evolutionary changes in successful invader that follow the predictions of EICA are actually adaptive (**Q.5.4**) and based on a genetic correlation between defense and performance related traits (**Q.5.5**).

Specifically, we addressed the following key questions:

> **Q.5.1**: How much intraspecific genetic and phenotypic trait variation do native species harbor in little studied geographic areas (African tropics, Middle East)?
> **Q.5.2**: Does genetic differentiation in climatic requirements within an invaded range lead to differential pre-adaptation for the invasion into mountainous regions?
> **Q.5.3**: Can pre-adaptation to anthropogenic disturbance mitigate confer founder success in disturbed habitats?
> **Q.5.4**: Did the EICA-predicted negative relationship between defense and performance in a classical example species arise from adaptive evolution?
> **Q.5.5**: Is there a negative genetic correlation supporting a resource allocation trade-off between defense and growth / reproduction in this species?

2 Own research contributions to the evolutionary ecology of native declining and invasive species

2.1 Research contributions: Anthropogenic alterations of biotic and abiotic environments

Relevant publications (see appendices 1-2)

[1] Cáceres Castellianos YK, Schrieber K, **Lachmuth S,** Auge H, Argibay D, Renison D**,** Hensen I (in revision for *Diversity and Distributions*). Disentangling effects of altitude, land use and microsites on early-life performance of a high mountain tree: insights from an *in situ* sowing experiment

[2] Haider S, Palm S, Bruelheide H, de Villemereuil P, Menzel A, **Lachmuth S** (in preparation). Disturbance and indirect effects of climate warming support plant invasions in mountains

2.1.1 Interactions of landuse and climate alter facilitative and competitive native species interactions

High mountain forests represent global biodiversity hotspots making up one third of all natural forest cover world-wide and are drastically under threat through anthropogenic global change (Beniston, 2003; Bonan, 2008). Mountain tree species provide habitat and resources to numerous often endemic or threatened species associated with them (Gareca *et al.*, 2010; Price *et al.*, 2011). Both intensified land use practices leading to habitat degeneration, fragmentation and loss as well as changes in precipitation and temperature regimes pose considerable threats to these foundation tree species (Walther, 2003; Parmesan, 2006). South American *Polylepis* mountain forests are widely distributed along the Andes and adjacent mountain ranges, with individual trees reaching altitudes of up to 5000 m. They are, however, severely threatened by human activities such as logging, fire clearance and over-grazing as well as climate change (Zimmermann *et al.*, 2009; Gareca *et al.*, 2010; IUCN, 2014). Understanding the regeneration niche requirements of endangered mountain tree species such as *Polylepis* taxa is therefore imperative for assessing future range dynamics and planning mountain forest restoration, but often limited by methodological constraints and high seedling mortality under field conditions.

In the study of Cáceres *et al*. (in revision) [1] we present results of an exceptionally massive *in situ* sowing approach that aimed at disentangling the effects of natural and anthropogenic small- and large-scale variation in biotic and abiotic conditions on early-life performance of the foundation tree line species *Polylepis australis*. Early-life performance reacts highly sensitively to environmental conditions and is regarded a primary determinant of species ranges and local extinction processes (Kitajima and Fenner, 2000; Young *et al.*, 2005). Theory suggests that range limits mainly depend on abiotic constraints in harsh environments (for example at high altitudes) and primarily on biotic interactions in abiotically benign environments (Louthan *et* *al.*, 2015). At the same time, positive interactions between species are assumed to prevail under abiotically harsh conditions, whereas competition is assumed to be more pronounced in benign environments (Callaway *et al.*, 2002). The role of microsite conditions and vegetative or micro-topographic facilitation in successful germination and early establishment has only recently received increasing attention (Gómez-Aparicio *et al.*, 2004; Arredondo-Núñez *et al.*, 2009; Smith *et al.*, 2009).

The field experiment of Cáceres *et al*. (in revision) [1] was conducted in the Andean Sierras de Córdoba ('Los Gigantes' region) in central Argentina and involved a total of 432000 sawn seeds of *P. australis*. The approach was based on a comprehensive split-plot design that integrated spatial scales ranging from 0.4 m2 microsite subplots via livestock ex- and enclosure plots of several hectares in size to an altitudinal gradient of more 1000m. Each two experimental sites were established at altitudes of 1300 m, 1800 m and 2300 m. Along this gradient mean annual as well as soil temperature decrease, whereas annual precipitation and soil moisture increase. At each site we maintained one livestock inclosure and one fenced ex-closure plot. Livestock density was constant throughout time and across altitudinal levels (0.2-0.4 cattle equivalents per hectare). Within each plot, 120 microsite subplots nested within 30 blocks were marked, which were associated with or directly adjacent to vegetative and micro-topographic structures namely rocks, grass tussocks, pasture lawns or bare soil. In early April 2016, 300 *P. australis* seeds were added to each sub-plot and germination as well as seedling establishment and performance were documented over a period of one year.

Harsher climatic conditions at higher altitudes and - to a lesser extent - livestock presence both negatively affected early-life performance. However, these effects were mostly additive. Only the proportion seedling showing signs of stress (reddened leaves) was disproportionally increased at highest altitude under livestock presence. We therefore have only week indication of trade-offs among various stress responses at least for actual components of fitness such as seedling emergence or survival. Furthermore, we show that microsite characteristics play a fundamental role in *P. australis* establishment. These effects, however, are modulated by complex interactions with climate, land use for livestock or both. First of all, the relevance of microsite effects decreased with increasing altitude owing to the fact that at the highest altitude environmental conditions limited performance and survival to a degree that other factors could no longer take effect. At the lowest altitude any accompanying structure (e.g. tussocks or rocks) provided shelter from harsh environmental conditions and facilitated *P. australis* early-life performance. By contrast, at mid altitudes, a release from competition in bare soil or pastures was beneficial.

By analyzing multiple components of early-life performance we also identified remarkable seed-seedling conflicts concerning the net-outcome of competitive *versus* facilitative interactions complicating regeneration niche assessment. For example, positive effects of moderate cattle stocking on seedling emergence through e.g. increases in light availability and soil temperature (see also Darabant *et al.*, 2007; Zimmermann *et al.*, 2009) turned negative in later life stages presumably due to highly detrimental consequences of browsing, trampling and soil degeneration (see also Renison *et al.*, 2004; Pollice *et al.*, 2013; Granger *et al.*, 2017).

Our results support that imminent negative effects of climate change and land use intensification include alterations of species interactions as well as micros-site conditions that ultimately diminish opportunities for natural forest regeneration (Hansen *et al.*, 2001). More generally, our findings highlight the necessity of ample experimental effort in order to disentangle the combined effects of global change components on native vegetation and are highly relevant for fundamental ecological theory as well as management of mountain biodiversity.

2.1.2 Positive disturbance effects on invader establishment in the Alps are diminished by climate warming

Also in the context of biological invasions, the investigation of geographic areas at extreme altitudes is of particular interest as it allows investigating the physiological constraints and environmental limits of invading species. For a long time, regions at high altitudes have been assumed to be less susceptible to invasions and thus received low attention in invasion research. Mechanisms that may limit invasions at high altitudes comprise: a) extreme environmental conditions, b) low levels of anthropogenic disturbance, c) biotic resistance of the native communities, d) low propagule pressure (Pauchard *et al.*, 2009). However, over one thousand alien species have become established in natural areas at high elevations worldwide (Pauchard *et al.*, 2009). Although many of these are not (yet) invasive (Alexander *et al.*, 2011), some may pose a considerable threat to native mountain ecosystems that harbor high numbers of endemic species, have high conservation value and provide important ecosystem services (Pauchard *et al.*, 2009). A better understanding of the mechanisms that impose limitations to invasive spread in high altitudes is needed to protect the vulnerable ecosystems in mountainous regions (Pauchard *et al.*, 2009). Moreover, climate change may decrease the climatic differences between high-elevation sites and the lowlands conditions to which invaders have locally adapted during the past decades. At the same time, biotic resistance to invasion might be reduced in high-elevation plant communities under climate warming and increasing land use intensity.

In the experimental study of Haider *et al*. (in preparation) [2], we for the first time investigated the effect of these two components of global change in mountains together and additionally addressed the role of intraspecific differentiation of the invading species. We transplanted plant community turfs between a low-elevation (Grainau village; 758 m.a.s.l.) and a high-elevation (Hochalm; 1737 m.a.s.l.) common garden site in the German Alps in order to decouple climate change from community origin effects. At each site, 112 turfs with a size of 25 cm x 25 cm were cut at a depth of 15 cm. Half of the turfs were transplanted to the other site and half were transplanted within their home-site. From each origin, half of the turfs were placed upside down into the holes to simulate a one-time disturbance event that removes the resident vegetation*,* which is a common consequence of land use intensification. We then investigated how community origin, climate change and disturbance interact in shaping community invasibility as well as the invasiveness of a potential future plant invader of the European Alps. Here, we planted -into the transplanted turfs- juvenile individuals of 16 western and central European populations of the South African ragwort *Senecio inaequidens*, which we anticipated to be differentially pre-adapted to a wide range of climatic conditions.

The species is a perennial chamaephytic herb native to the Drakensberg and Maloti Mountains in Lesotho and South Africa. In the native region the geographical range of the investigated tetraploid cytotype reaches elevations up to 3100 m.a.s.l. (Lachmuth *et al.*, 2010). Here, it inhabits a wide range of naturally or anthropogenically disturbed habitats such as riverbanks, rocky slopes, heavily grazed or recently burned grasslands, and road verges (Hilliard, 1977). In the end of the 19th and beginning of 20th century *S. inaequidens* has been accidentally introduced to several locations in Europe with wool transports (Ernst, 1998; Jeanmonod, 2002; Heger and Böhmer, 2005). Since then populations established across large parts of western and central Europe, covering a wide climatic gradient (Lachmuth *et al.*, 2010). Its expansion has been documented very well in the floristic literature. So far, the species has mainly spread along traffic routes and mostly invaded ruderal habitats. Accordingly, *Senecio inaequidens* has been described as a weak competitor (Heger and Böhmer, 2005; Lachmuth *et al.*, 2011), which benefits from disturbance and thus release from competition (Ernst, 1998; Scherber *et al.*, 2003; Garcia-Serrano *et al.*, 2004; Caño *et al.*, 2007). Nevertheless, it also increasingly colonizes (grazed) grasslands e.g. in Southern Europe (Garcia-Serrano *et al.*, 2004). Most likely, the spread of *S. inaequidens* is not completed yet (Heger and Böhmer, 2005) and a recent modeling study suggests that the lack of populations at higher elevations is rather caused by dispersal limitation than by physiological limits of the species itself (Vacchiano *et al.*, 2013). The plants produce high amounts of seeds, which mostly germinate right away and across a wide temperature range (López-García and Maillet, 2005). They are well dispersed by wind and traffic or other human activities that may increasingly transport the species into mountains in the future. Experimental studies further demonstrated genetically based clinal variation in vegetative growth along elevatinal gradients in Europe suggesting high adaptive potential (Monty and Mahy, 2009; Monty *et al.*, 2009).

The results of our transplant experiment attest a strong and consistent role of disturbance, which directly increased community invasibility, and indirectly promoted the invasiveness of the non-native species through the creation of low-competition habitat. We found positive effects of our disturbance treatment on growth, flowering probability and survival of *S. inaequidens* target individuals. These results are in accordance with the previously observed low competitive ability of *S. inaequidens*. Furthermore, disturbance is considered to be one of the most important factors that support invasion success in general (Alpert *et al.*, 2000; Catford *et al.*, 2009; Moles *et al.*, 2012) as well as in mountain ecosystems (Seipel *et al.*, 2012; Lembrechts *et al.*, 2016; Haider *et al.*, 2018). We had furthermore expected a more pronounced positive effect of disturbance in more productive communities with stronger competition (i.e. at in lowland communities / at the low-elevation site). This hypothesis was on the one hand confirmed as disturbance caused a stronger increase in biomass and survival probability in *S. inaequidens* in lowland compared to highland turfs. However, at the low-elevation site, biomass increase was less strong compared to the high-elevation site. We attributed this finding to the fact that we only applied a one-time disturbance treatment, and that re-growth of the surrounding plant community evidently occurred much faster at the warmer low-elevation site compared to the high-elevation site. Thus, contrary to our original assumption, the positive effect of disturbance for non-native species establishment may eventually be stronger and longer-lasting at high-elevations as the local native species re-establish and re-grow more slowly under the harsh abiotic conditions (Moloney and Levin, 1996).

Positive effects of climate warming on the growth of highland plant communities also seem to be the explanation for our second unexpected finding of a decrease in their invisibility in the low-elevation common garden. Here, vegetation cover was even higher and survival of *S. inaequidens* was even lower compared to the lowland communities. A possible explanation for these unexpected results is that temperature warming may increase soil microbial activity, net nitrogen mineralization as well as nutrient availability (Rustad *et al.*, 2001; Wang *et al.*, 2016) and consequently growth rates as well as interspecific competition in the plant community (Rustad *et al.*, 2001). These processes, however, may only be a short-term effect during our 1.5 years of observation. With continued warming, particularly in combination with aboveground biomass removal (e.g. through mowing or grazing), the stock of organic material in shallow high-elevation soils should decrease (Eze *et al.*, 2018) and consequently competition should decrease again. In addition, climate warming may disrupt established biotic interactions and alter community composition, and thereby eventually weaken biotic resistance (Alexander *et al.*, 2015). Thus, we urgently require studies of the long-term effects of climate warming and disturbance on high-elevation plant communities to gain a better understanding of how these complex interactions may shape mountain invasions in the future.

2.2 Research contributions: Demographic and genetic bottlenecks

Relevant publications (see appendices 3-6)

[3] **Lachmuth S**, Henrichmann C, Horn J, Pagel J, Schurr FM (2018). An experimental study of pollen limitation and neighbourhood effects in the invasive *Senecio inaequidens*. *Journal of Ecology* 106: 761-773

[4] Peng Y, **Lachmuth S**, Gallegos S, Kessler M, Ramsay P, Renison D, Suarez R, Hensen I (2015). Pleistocene climatic oscillations rather than recent human disturbance influence genetic diversity in one of the world`s highest treeline species. *American Journal of Botany* 102 (10): 1676-1684

[5] Rosche C, Schrieber K, **Lachmuth S**, Durka W, Hirsch H, Wagner V, Schleuning M, Hensen I (2018). Sex ratio rather than population size affects genetic diversity in *Antennaria dioica*. *Plant Biology* 20: 789-796

[6] Rosche C, Durka W, Hensen I, Mráz P, Hartmann M, Müller-Schärer H, **Lachmuth S** (2016). The population genetics of the fundamental cytotype-shift in invasive *Centaurea stoebe* s.l.: genetic diversity, genetic differentiation and small-scale genetic structure differ between cytotypes but not between ranges. *Biological Invasions* 18 (7): 1895-1910

2.2.1 Pollination-mediated component Allee effects are trait- and scale-dependent

The fitness of plant populations strongly depends on competitive and facilitative interactions with con- and heterospecific neighbor plants. In small or sparse populations, conspecific density-dependence is often positive and causes Allee effects (Allee, 1931; Courchamp *et al.*, 1999). In the paper of Lachmuth *et al*. (2018) [3] we developed an experimental and analytical framework for the investigation of pollination-mediated component Allee effects in plants. We applied the approach to a typical founder population of the invasive South African ragwort *Senecio inaequidens* (see section 2.1.2 for details on the species) in order to explore the degree and underlying causes of pollen limitation. However, the framework is applicable to and relevant for both native and introduced species. Our approach targets the problem that observational studies in natural plant communities cannot distinguish whether reproduction is limited by pollination-mediated interactions plant-plant interactions or by other neighborhood effects such as the competition for abiotic resources. Furthermore, even experimental pollen supply cannot distinguish whether variation in reproduction is caused by direct effects of density or by plant traits that correlate with density. Finally, the spatial scale over which pollination-mediated interactions occur remains largely unknown. To circumvent these problems we simultaneously (1) manipulated pollen availability and quality by hand pollination and pollinator exclusion, (2) manipulated neighborhoods by transplanting target plants, and (3) used spatially explicit trait-based neighborhood models to analyze the effects of con- and heterospecific neighborhoods on *S. inaequidens* reproduction.

Although *S. inaequidens* is self-incompatible and insect-pollinated - a condition that is expected to induce strong pollination-mediated demographic Allee effects towards the invasion front (Tobin *et al.*, 2011) - it is known as one of Europe's fastest plant invaders (Werner *et al.*, 1991). However, our results showed that seed set, as a component of overall fitness, was indeed strongly pollen limited and increased with conspecific density. As such, we detected a component Allee effect (Stephens *et al.*, 1999), but the degree to which it translates to a demographic Allee effect remains to be clarified. *S. inaequidens* typically forms dense stands along traffic routes such as railways and highways, which were already previously shown to mediate high gene flow among populations of the species (Lachmuth *et al.*, 2010). Here, the species may additionally benefit of pollination mediated Allee effects. In this wind-dispersed species, strongly isolated individuals and initially very scarce populations are still very likely to occur following long-distance dispersal and may suffer from pollen limitation hampering initial population growth. Combined with negative fitness effects of low genetic diversity (Lachmuth *et al.*, 2011) and further limitation of mate availably due to reduced *S*-allele diversity (as observed for *Centaurea stoebe* as part of this thesis (Rosche *et al.*, 2017) [7], see section 2.3), pollination-mediated neighbor effects may even have contributed to the long lag-phase observed after initial introduction of the species (Ernst, 1998).

In our experiment reproduction was not only affected positively by the density of conspecifics, but also by heterospecific neighbor density, a process previously referred to as community-level Allee effect (Nottebrock et al., 2013, 2016). Moreover, the strength and direction of neighborhood effects depended on neighbor traits and thus changed with the trait composition of the neighborhood. Theoretically, positive interaction with heterospecific neighbors may mitigate pollen limitation and enhance reproduction of *S. inaequidens* in mixed stands. Two circumstances likely limit this positive outcome: 1) due to its low competitive ability (Scherber *et al.*, 2003; Lachmuth *et al.*, 2011) South-African ragwort mostly spreads into sparse ruderal vegetation were it may not benefit from community-level Allee effects; 2) in vegetation denser than that investigated on our early succession study site, *S. inaequidens* may actually suffer from competition for pollination from multiple species with attractive floral display. In addition to pollinator-mediated facilitation pollination-independent interactions, such as amelioration of abiotic conditions through neighbors, contributed - to a lesser extent - to the positive neighbor effects. These pollination - independent interactions were restricted to smaller spatial scale (< 2m) than pollination - mediated interactions (< 4m), which underlines the necessity of multiple scale neighborhood analyses.

In summary, the experimental and analytical framework developed for this study, may advance research into the complex interactions underlying Allee effects not only for declining and invading species considered in this thesis, but range shifting species in general. Considering that variation in the strength of demographic Allee effects increases the unpredictability of range dynamics, gaining a deeper understanding of the extent as well as scale-and trait dependence of pollination-mediated plant–plant interactions and their ultimate effects on population, community and range dynamics are imperative to managing biodiversity under global change.

2.2.2 Other factors than population size affect genetic diversity of native species in fragmented landscapes

In the study of (Peng *et al.*, 2015) [4], we aimed at disentangling the effects of Pleistocene climatic oscillations *versus* recent anthropogenic habitat fragmentation on genetic diversity in *Polylepis tarapacana*, one of the world's highest tree line species endemic to the Central Andes. Climate oscillations during the Pleistocene influenced the geographical distribution of species worldwide inducing (Hewitt, 2000). These glacial- interglacial cycles of range contraction and expansion had significant genetic consequences as they influenced spatial variation in genetic diversity as well as diversification in complex and species-specific ways (Avise, 2000, 2004; Hickerson *et al.*, 2010). Some high-elevation species probably expanded to lower elevations during cooler periods while being restricted to high mountain ranges during warmer periods. Since interglacial periods of population isolation were relatively short (15 000 years) as compared to glacial periods involving downwards expansion (100 000 years) such species exhibit relatively low population divergence and weak phylogeographic structure (Stewart *et al.*, 2009). In other cases genetic diversity apparently has been preserved in long-term refugia either at the benign edges of the species distribution areas or in multiple glacial refugia in mountain areas with heterogeneous topographies (Premoli *et al.*, 2000). In such cases, where species supposedly survived *in situ,* they show pronounced genetic differentiation among populations (Opgenoorth *et al.*, 2010).

Forest trees are useful models to study the effects of such historical events as they preserved the resultant genetic imprints due to their large population sizes, long generation times, and survival through periods of drastic environmental change (Hamrick, 2004; Petit and Hampe, 2006). The genus *Polylepis* (Rosaceae) comprises 30 wind-pollinated tree and shrub species, all endemic to the Andean mountain chain from Argentina and Chile to Venezuela (Kessler and Schmidt-Lebuhn, 2006). Studies on various species of the genus showed that both Pleistocene glacial-interglacial cycles and recent anthropogenic fragmentation affected genetic diversity. However, it is mainly human impact that rendered *Polylepis* forests one of the most endangered ecosystems world-wide (IUCN, 2014). Most devastating human activities comprise timber extraction as well as cattle grazing and associated grassland burning (Zimmermann *et al.*, 2009; Gareca *et al.*, 2010). In particular re-current, often anthropogenic fires hindered the re-colonization of high-elevation sites after the last Glacial Maximum. That such drastic habitat fragmentation and population bottlenecks may have decreased genetic diversity and increased genetic among population differentiation is easily conceivable.

In our study, we analyzed Amplified Fragment Length Polymorphism (AFLP, Vos *et al.*, 1995) fingerprints of each 384 seedlings and adults of *P*. *tarapacana* from 32 sites within 18 forest remnants. The sampling covered a 600 km latitudinal gradient and most of the species' elevational distribution (4100 m to ~5000 m). We did not detect a decreased genetic diversity in seedlings compared to adult individuals and thus have no indication of negative impacts of recent human disturbances on the genetic diversity of the sampled populations. Instead, we found a generally very low genetic diversity and high among population differentiation, which is in contrast to results of other studies on the genus *Polylepis* (Hensen *et al.*, 2011). These results indicate that the species was historically more widespread at low elevations and retracted to refugia during warmer periods. The analyses further documented a decrease of genetic diversity toward the equator, which may be related to decreasing aridity and identified potential refugia in the southern part of the species' current range in the Argentinean Andes. In summary, the findings highlight that Pleistocene climate oscillations rather than recent human impact have influenced genetic diversity in this particular tree line species.

As outlined in section 1.2 the sensitivity of plant species to genetic erosion also strongly depends on life history characteristics. Outcrossing has often been shown to decelerate the loss of genetic diversity as it facilitates high levels of gene flow and reduces inbreeding (Hamrick and Godt, 1996). On the other hand, obligate out-crossers may experience mate limitations as population size and / or density decreases whereas species that are able to self-pollinate are less sensitive to such effects. In dioecious species male and female flowers occur on separate individuals enforcing obligate out-crossing, which has long been assumed to prevent genetic erosion in these species. However, the few empirical studies that addressed this issue in fragmented populations of dioecious plants did not support this assumption (Vandepitte *et al.*, 2010; Lauterbach *et al.*, 2012). The fact that biased sex ratios may lead to mate limitation and thus further decrease effective population sizes (Frankham, 1995) of fragmented populations has long been ignored.

In another co-authored study (Rosche, Schrieber, *et al.*, 2018) [5] we therefore addressed the effects of recent anthropogenic habitat fragmentation on the genetic diversity of the endangered (Korneck *et al.*, 1996) dioceous and clonal herb *Antennaria dioica* (L.) J. Gaertn.. The life span of the clones is unknown. The species is diploid and is effectively pollinated by dipterans, colepoterans, lepidopterans and hymenopterans. Seeds are wind-dispersed. The species mainly occurs in subalpine and mountainous zones with a geographic distribution stretching from Western Europe to Eastern Russia. In Central Europe it can occasionally be found in lowland habitats as for example in dry grasslands, which are all characterized by shallow soils and nutrient deficiency. As a consequence of land use change, i.e. the abandonment of traditional practices such as extensive livestock grazing, these once wide-spread habitat types have drastically declined during the past decades.

The first and second author originally sampled 32 populations in central, northern and eastern Germany as well as in western Czech Republic (see also Rosche *et al.*, 2014), covering a vast majority of all stands reported from these regions. After excluding very small and unisexual populations we eventually worked with 14 populations. We first assessed their genetic diversity based on AFLP markers. Our analyses then aimed at disentangling the effects of population size and sex ratio (proportion of females) on genetic diversity, whereby we expected a uni-modal relationship for the latter with highest genetic diversity at a balanced sex ratio of each 50% male and female individuals. Overall, we found moderate levels of genetic diversity and only weak population differentiation although isolation by distance had occurred. Given the strong population fragmentation these findings are surprising and indicate that *A. dioica* once formed larger populations and was more wide-spread and more continuously distributed across Central European lowlands. Moreover, functional connectivity through seed dispersal *via* traditional land use practices such as livestock grazing may have enhanced gene flow in the past (Rico *et al.*, 2014). We also did not find any significant effect of current population size on genetic diversity, which is contrary to a large body of literature (see the review of Leimu *et al.*, 2006). Since fragmentation of its habitats occurred in the more recent past, the current small population sizes have obviously not (yet) lead to genetic erosion at least within the range of population size covered by our study. Sex ratio was slightly female biased across all analyzed populations (61.5 %) and independent of population size, which ranged between six and 176 patches. Whereas unaffected by population size, genetic diversity did increase significantly with the proportion of females in the populations. Our study is among the first to reveal a significant effect of sex ratio on genetic diversity in dioceous plants. We did, however, not find the expected uni-modal relationship between the two variables. Apparently, a loss of female individuals has severe consequences and more immediate effects on genetic diversity than population size due to a population-level decrease of sexual reproductive output. Under such circumstances, a female-bias may be advantageous not only compared with male-bias but also with balanced sex ratios, which may explain the prevalence female biased populations in this species as also reported by other authors (Eriksson, 1997; Varga and Kytöviita, 2011).

In view of the objectives of this habilitation thesis, although we did not find the expected effects of fragmentation on genetic diversity, this study illustrates the demographic challenges faced by declining dioecious species. Demographic bottlenecks are likely to induce stochastic fluctuations in sex ratios counteracting the selection towards the optimal sex ratio, which may further limit population growth. Moreover, the erosion of genetic diversity is possibly just delayed (genetic extinction debt, Honnay *et al.*, 2006) and may hit if the current generations of clones demise without having generated sufficient sexually produced offspring.

2.2.3 Low susceptibility of polyploids to genetic erosion may mediate invasion success

In the Ph.D. project of Dr. Christoph Rosche (Rosche, 2016), we explored mechanisms that may counteract the loss of genetic diversity and the occurrence of inbreeding depression (see section 2.3) during biological invasions, with a focus on the role of polyploidy. As a model system we used *Centaurea stoebe* s.l. L. (syn. *C. maculosa* Lam., spotted knapweed, Asteraceae), one of the most noxious invasive weeds in North American grasslands. The polyploid complex comprises a diploid predominantly monocarpic cytotype (*C. stoebe* L. subsp. *stoebe,* 2n = 2x =18) and a polycarpic tetraploid cytotype (*C. stoebe* L. subsp. *micranthos* (Gugler)*,* 2n = 4x =36). Recently, Mráz *et al.* (2012) reported evidence for allopolyploidization although the second parental species remains unknown. However, Mráz (personal communication) found clear evidence of tetrasomic inheritance when screening four microsatellite loci in controlled crosses. Triploid hybrids between the two cytotypes are infertile (Mráz *et al.*, 2012). Both cytotypes are strictly self-incompatible, insect pollinated with a similar pollinator spectrum (Mráz *et al.*, 2012) and their seeds are dispersed by barochory.

In the native European range, diploids are the majority cytotype (Broennimann *et al.*, 2014) with a geographic distribution covering western, central and northern Europe, whereas tetraploids prevail in South Eastern Europe and Asia minor (Španiel *et al.*, 2008). Recently, however, tetraploids have been expanding to Central Europe, causing the ranges of both cytotypes to overlap (Korneck, 2006; Welss *et al.*, 2008; Otisková *et al.*, 2014). In North-America, the species was first introduced in the late 19th century (Hahn, Buckley, *et al.*, 2012). It is commonly assumed that initially both cytotypes were introduced (Treier *et al.*, 2009), but to date only tetraploids have been documented (Mráz *et al.*, 2011). Since the taxonomic status of members of the complex remains unresolved, we considered the species *C. stoebe* s. l. as taxonomic entity for all our studies on this polyploid complex.

Despite high control efforts in the United States the tetraploid cytotype expanded continuously and is now widespread in grasslands of nearly all states (Jacobs, 2012). Due to its low nutritious value and high catechin content, it is avoided by cattle and thus causes costs of $150*10^6$ US$ per year (Story, 2002). Molecular analyses suggest that *C. stoebe* was introduced repeatedly and at multiple locations (Hufbauer and Sforza, 2008; Marrs *et al.*, 2008) and spread along at least two separate invasion routes: one expanding from the east coast near Westford, MA, U.S. and one from the west coast near Victoria, BC, Canada (Broennimann *et al.*, 2012). Our studies focuses on the invasion of the North-West where spotted knapweed is one of the most successful and destructive plant invaders (Ridenour and Callaway, 2001; Ortega and Pearson, 2011).

In Rosche *et al*. (2016) [6], as a first step towards clarifying the role of polyploidy in overcoming demographic and genetic challenges of founder populations, we explored the population genetics of the existent three geo-cyptotypes. Firstly, we compared the genetic diversity of the three cytotypes in order to clarify whether tetraploids harbor higher levels of genetic diversity than diploids in the native range and if they were able to preserve this high level of genetic diversity in the invaded range. Accordingly, we assumed that diploid individuals would be more closely related than tetraploid individuals on small spatial scales within populations. Secondly, we tested the hypothesis that genetic among population differentiation is stronger in native diploid than in native tetraploid populations and even less pronounced in invasive tetraploid populations. Thirdly, we aimed at discovering the effects of population size and habitat type on genetic diversity within each of the cytotypes. Here, we hypothesized that larger populations and populations occurring in natural habitats exhibit higher genetic diversity.

We used neutral genetic markers, namely eight microsatellite loci, to address these topics. The sampling included 18 to 20 populations of varying size and habitat type for each geo-cytotype (as confirmed by flowcytometry). We sampled 19 to 31 individuals per population and estimated population sizes based on flowering individuals. The distinction of habitats followed the European classification system of habitat types (EUNIS, 2008) following the protocol of (Broennimann *et al.*, 2014). As (semi-) natural habitats we considered semi-natural grasslands, natural rocky outcrops and diluvial sediments, whereas ruderal habitats comprised agricultural as well as artificial and industrial habitats.

We indeed found higher genetic diversity, lower genetic among-populations differentiation and lower levels of inbreeding at small spatial scales in native tetraploid as compared to diploid populations. Moreover, high levels of genetic diversity and low levels of differentiation among populations were maintained in invasive tetraploids with no significant deviation from the native tetraploids. Since high genetic variation is generally assumed to be beneficial for invasion success (Frankham, 2004; Hufbauer, 2008), these results suggest that the ability of the tetraploid cytotype to preserve high levels of genetic diversity contributed to the remarkable shift in cytotype frequencies between the two distribution ranges (Treier *et al.*, 2009). Our additional finding that in tetraploid populations –both native and invasive- genetic diversity did not decrease with decreasing population size or in ruderal as compared to semi-natural habitats, whereas smaller as well as ruderal diploid populations had significantly reduced genetic diversity, underlines that polyploidy may have substantially contributed to founder and colonization success. Invasive populations also showed higher degrees of genetic admixture between genetic clusters than native tetraploids most probably as consequence of multiple introduction and subsequent merging of the introduced gene pools. In congruence with our results also previous cluster analyses suggested multiple introductions from different parts of the native range and subsequent admixture (Marrs *et al.*, 2008). However, before genetic admixture can occur, the involved genetic lineages not only have to persist, but often spread widely and rapidly, despite having suffered severe demographic bottlenecks (Henry *et al.*, 2009; Chun *et al.*, 2010; Keller *et al.*, 2012; Schrieber and Lachmuth, 2017 [9]). Mechanisms that prevent severe genetic erosion, such as polyploidy, may help founding and colonizing populations to successfully pass through these early erratic phases of invasion until demographic or genetic rescue occurs. In case of the *C. stoebe* diploid-polyploid complex, besides polyploidy the longevity of the tetraploid cytotype likely contributes to this effect (Nybom, 2004; Mráz *et al.*, 2011). After all, this is one of the first studies to address polyploidy in the context of the 'Genetic Paradox of Invasions'. More research is necessary to reach more general conclusions about its role in founder success.

2.3 Research contributions: Inbreeding depression and inbreeding x environment interactions

Relevant manuscripts and publications (see appendices 7-10):

[7] Rosche C, Hensen I, Mráz P, Durka W, Hartmann M, and **Lachmuth S** (2017). Invasion success in polyploids: the role of inbreeding in the contrasting colonization abilities of diploid *versus* tetraploid populations of *Centaurea stoebe* s.l.. *Journal of Ecology* 105: 425-435

[8] Rosche C, Hensen I, **Lachmuth S** (2018). Local pre-adaptation to disturbance and inbreeding–environment interactions affect colonisation abilities of diploid and tetraploid *Centaurea stoebe*. *Plant Biology* 20: 75-84

[9] Schrieber K & **Lachmuth S** (2017). The Genetic Paradox of Invasions revisited: the potential role of inbreeding x environment-interactions in invasion success. *Biological Reviews* 92: 939-952

[10] Schrieber K, Wolf S, Wypior C, Hoehlig D, Hensen I, Keller SR, **Lachmuth S** (in revision for *Ecology and Evolution*). Enemy release mitigates inbreeding depression in native and invasive *Silene latifolia* populations: experimental insight into the role of inbreeding × environment interactions in invasion success. Preprint available at: https://doi.org/10.1101/401430

In the studies of Rosche *et al.* (2017) [7] and Rosche, Hensen, *et al.* (2018) [8], we again used the three geo-cytotypes of *Centaurea stoebe* (see section 2.2.3 for an introduction of the study system) to investigate three different mechanisms by which inbreeding can hamper founder success as well as the role of polyploidy in overcoming these barriers for invasion. First, in self-incompatible plants closely related individuals are likely to share identical *S*-alleles, which may reduce cross-compatibility (Willi *et al.*, 2005; Levin *et al.*, 2009). Here, polyploidy may even amplify the negative effects as related polyploid partners might have a higher probability of sharing *S*-alleles (but see Pickup and Young, 2008). Second, inbred offspring may show inbreeding depression, i.e. reduced fitness as compared to outbred offspring (Charlesworth and Willis, 2009). Polyploidy is assumed to counter-act inbreeding depression through higher heterozygosity and higher probability of masking deleterious alleles (Otto and Whitton, 2000). Third, recently, evidence is accumulating that inbreeding depression is environment-dependent due to inbreeding x environment (I x E) interactions (Dudash, 1990; Liao and Reed, 2009) and particularly pronounced under stressful conditions (Fox and Reed, 2011; Cheptou and Donohue, 2011; Reed *et al.*, 2012). In case of *C. stoebe*, primary invasion in North America takes place in ruderal habitats that are characterized by frequent anthropogenic disturbance (Emery and Rudgers, 2012). On the one hand, such habitat conditions likely facilitate invasion as they can for example generate short-term increases in resource availability that can readily be exploited by invaders (Sher and Hyatt, 1999; Davis *et al.*, 2000; Theoharides and Dukes, 2007, but see Liu *et al.*, 2018) and a release from interspecific competition (Crawley *et al.*, 1999; Hood and Naiman, 2000; Catford *et al.*, 2009). On the other hand, disturbances such as mowing, trampling or traffic also cause physical damage to the invading plants, which may decrease their performance and even eradicate small founder populations (Kallimanis *et al.*, 2005). Inbreeding depression may increase the vulnerability to such disturbance effects and *vice versa* (see section 1.3.2). Here, tetraploid *C. stoebe* subsp. *micranthos* may have an advantage if they do in fact generally experience lower inbreeding depression than diploids and / or are better adapted to disturbed habitats. The latter is suggested by the fact that native tetraploids recently expanded their range in Central Europe mostly by colonizing ruderal habitats (Broennimann *et al.*, 2014). Also, due to their polycarpic lifecycle, tetraploids may better buffer physical disturbance as they can re-sprout and reproduce in the next year (Mráz *et al.*, 2012).

We worked with a high number of populations of each geo-cytotype, a circumstance that allowed us to shed light on the influence of population history on the outcomes of these processes. We assumed that populations with a higher average degree of relatedness among individuals would show lower cross-compatibility, but also lower inbreeding depression due to purging of genetic load in past generations. Moreover, we expected lower inbreeding depression in invasive as compared to native populations as a result of repeated bottlenecks and purging during the invasion process. With respect to I x E interactions, local pre-adaptation to disturbed conditions may leave some populations less sensitive to I x E interactions than others depending on the habitat type of origin.

For (Rosche *et al.*, 2017) [7], we conducted a breeding experiment (sib-mating *versus* outcrossing) with 14 native diploid, 13 native tetraploid and 15 invasive tetraploid populations. We recorded cross-compatibility and calculated a cumulative index of F1 offspring fitness. The latter was based on measurements of germination success, survival, flowering probability and capitula produced. Average within population relatedness of individuals was estimated based on the eight micro-satellite loci analyzed in (Rosche *et al.*, 2016) [6] (see also section 2.2.3). To explore the role of I x E interactions (Rosche, Hensen, *et al.*, 2018) [8] we moved greenhouse raised F1 offspring of the same inbred and outbred lines into a low competition sun exposed common garden environment. Here, we subjected individuals of all geo-cytotype x breeding treatment combinations to a clipping experiment simulating disturbance-mediated stress through physical damage in ruderal habitats (frequencies: zero, once or two times of clipping aboveground biomass 2 cm above the root collar in the growing season). Aboveground biomass by the end of the growing season and re-sprouting success in the following year served as fitness proxies.

Our results (Rosche *et al.*, 2017) [7] did not confirm an expected disadvantage of tetraploids regarding cross-compatibility. Both sib-mating as well as outcrossing in populations with higher average relatedness negatively affected pollination success. These results support that close relatives are likely to share *S*-alleles, which may severely limit mate availability and thus population growth in bottlenecked or founder populations (Wagenius *et al.*, 2007; Levin *et al.*, 2009). However, these effects did not differ between cytotypes. The only previous study that compared cross- compatibility in diploid *versus* polyploid cytotypes of *Rutidosis leptorrhynchoides* F.Muell. (Asteraceae) yielded the same outcome (Pickup and Young, 2008).

The authors attributed their result to high *S*-allele diversity and reduced drift in bottlenecked polyploid populations.

Inbreeding significantly reduced cumulative fitness in the diploid cytotype whereas tetraploid offspring did show a similar trend, but no significant inbreeding depression (Rosche *et al.*, 2017) [7]. Among the investigated fitness components survival contributed most to these differences in cumulative inbreeding depression. Reduced inbreeding in polyploids likely results from effective masking of genetic load through genome duplication (Otto and Whitton, 2000), which should be particularly effective in tetraploids with tetrasomic inheritance (Bever and Felber, 1992; Galloway and Etterson, 2007) and of neopoloploid origin (Ronfort *et al.*, 1998; Galloway and Etterson, 2007) such as *C. stoebe* subsp. *micranthos* (Mráz *et al.*, 2011; Rosche *et al.*, 2016 [6]). This should confer tetraploid founders a clear advantage over diploids as severe inbreeding depression is considered a critical obstacle to establishment and invasion success (Hufbauer *et al.*, 2013; Szűcs *et al.*, 2014; Schrieber and Lachmuth, 2017 [9]). Our conclusion that introduced tetraploid *C. stoebe* did not suffer inbreeding depression is further supported by the fact that we did not find strong indication of purging during past generations in populations of this cytoytpe since the strength of inbreeding depression did not differ between invasive and native tetraploids except for germination success (see e.g. Facon *et al.*, 2011 for an example of purging in the invaded range). Alternative explanations for this latter finding may be that purging seems generally not very effective in *C. stoebe.* Note in this context that we also did not find any significant relationships between within-population relatedness and inbred fitness across geo-cytotypes. Moreover, our previous population genetic study (Rosche *et al.*, 2016) [6] as well as the study of Marrs *et al.* (2008) suggested a lack of genetic bottlenecks in invasive tetraploids -likely due to polyploidy - as well as multiple introductions to North America and subsequent genetic admixture. Additionally, evidence indicates that native tetraploids recently expanded their range in Central Europe along ruderal habitats possibly leading to comparable population and colonization histories in both tetraploid geo-cytotypes (Broennimann *et al.*, 2014) - a conclusion that was also supported by our finding of weak genetic differentiation in this geo-cytotype (Rosche *et al.*, 2016) [6].

The findings of Rosche, Hensen, *et al.* (2018) [8] clearly document negative fitness effects of physical damage through clipping as well as inbreeding depression under such stressful conditions, whereas inbreeding depression was not apparent under benign control conditions. These I x E interactions were comparably pronounced in all three geo-cytotypes, thus plants of the tetraploid cytotype do not seem to have a pre-adaptive advantage in counteracting negative effects of I x E interactions. However, we did find differentiation in the overall tolerance of physical damage among populations from different habitat types, presumably due to local adaptation to disturbance regimes (see section 2.5.2 for a more detailed discussion). Also, irrespective of breeding and clipping treatments our data revealed higher re-sprouting success in tetraploids most likely due to their polycarpic life cycle (Mráz *et al.*, 2011). This capability should substantially contribute to the success of tetraploids at disturbed sites and in both the native and invaded range.

In summary, the net outcome of demographic bottlenecks, inbreeding and life history effects in diploid *versus* tetraploid cytotypes should be positive for tetraploids. Across our studies

(Rosche *et al.*, 2016, 2017; Rosche, Hensen, *et al.*, 2018) [6-8] tetraploids showed greater ability to counter losses of genetic diversity and lower inbreeding depression in case bi-parental inbreeding should still occur as a consequence of genetic erosion in extremely bottlenecked founder populations. Moreover, their polycarpic life cycle likely plays a substantial role in lasting through phases of mate limitation or physical damage in disturbed habitats (Mráz *et al.*, 2012). These explanations for the invasion success of tetraploid *C. stoebe* subsp. *micranthos* are not mutually exclusive with previous findings of other authors, which regard climatic as well as ecological pre-adaptation as the main explanation for the tetraploids' invasion success (Treier *et al.*, 2009; Henery *et al.*, 2010). Furthermore, increased competitiveness may result from pre-adaption in tetraploids compared to diploids (Thébault *et al.*, 2011) and subsequent post-introduction selection among tetraploids (Henery *et al.*, 2010; Hahn, Buckley, *et al.*, 2012). Native tetraploids also exhibited greater plasticity (Hahn, van Kleunen, *et al.*, 2012), higher soil seed bank survival (Hahn *et al.*, 2013) and higher life-time fecundity than native diploids (Broz *et al.*, 2009). Only few studies addressed inbreeding depression in plants under different competitive regimes and none in the context of plant invasions. Moreover, variation in I x E interactions among plants of different ploidy levels has never been investigated before. This project thus made novel contributions to fundamental eco-evolutionary and invasion research.

Inbreeding x environment interactions further played a central role in the Ph.D. project of Dr. Karin Schrieber (Schrieber, 2016) with which we aimed at reviving the discussion of the 'Genetic Paradox of Invasions'. In a first conceptual paper (Schrieber and Lachmuth, 2017) [9], we briefly review the published explanations for the paradox that are mainly based on the avoidance of genetic diversity loss and inbreeding or focus on the problem of adaptive potential (see section 1.3.1.b for more detail). The review brings to light a substantial lack of explanation and empirical evidence for explaining the genetic paradox for strongly bottlenecked invasions or critical invasion phases, such as initial colonization or leading edges of range expansions, where strong genetic depletion, inbreeding depression and drift load occur. We propose that I x E interactions may be a mechanism with strong explanatory power for invasion success of the species and in the invasion phases concerned. More specifically, we suggest -based on empirical evidence- that a temporary or permanent release from stress in invaded habitats may alleviate the negative effects genetic depletion on fitness. We further discuss evolutionary consequences of such I x E interactions through environment-dependent purging of conditionally deleterious alleles and how these evolutionary imprints my serve to retrospectively trace the occurrence if I x E interactions in the history of an invasion.

To test our theory we then conducted a study that investigated the combined effects of inbreeding and infestation by natural enemies on the performance of the White Campion *Silene latifolia* Poir. (Caryophyllaceae, syn. *S. alba* (Mill.)) (Schrieber *et al*., in revision) [10]. The species is a short-lived dioecious perennial that primarily occurs at ruderal sites such as road or field margins, fallows and hey fields. The native region comprises large parts of Eurasia, from where the species was introduced to North America in the early 19th century as a contaminant of agricultural seed supplies and ship ballast (McNeill, 1977). Several aspects of its demographic and ecological invasion history render *S. latifolia* an ideal study system to investigate potential facilitating effects of I x E interactions during invasions. First, its introduction to North America involved a continental-scale genetic bottleneck since the introduced populations were sampled from a few restricted regions of the native range, where glaciation history shaped strong genetic structure. However, the two introduced genetic lineages spread successfully and without a considerable time lag despite their low genetic diversity, before the later on locally admixed (Keller *et al.*, 2009, 2012). Second, inbreeding and inbreeding depression were reported to occur in introduced populations (McCauley *et al.*, 1995; Richards, 2000). Third, the species evidently experienced a release from its native generalist as well as specialist enemies (Wolfe, 2002; Wolfe *et al.*, 2004; Schrieber, 2016) including the specialized phloem sucking aphid *Brachycaudus populi* L. (Aphididae), the moth *Hadena bicruris* Hufnagel (Noctuidae), with which *S. latifolia* maintains a nursery pollination syndrome (Dufaÿ and Anstett, 2003), and the sterilizing anther-smut fungus *Microbotryum violaceum* Lév (Microbotryaceae) (Ruddat *et al.*, 1991). This extensive enemy release has previously been used as an explanation for observed increased susceptibility to enemies as well as higher reproductive ability of the species in the novel range (Wolfe *et al.*, 2004).

With plants from eight native and eight invasive populations, we performed two generations of experimental inbreeding and outcrossing in the greenhouse and then exposed the offspring to low and high levels of natural enemy attack in a common garden, and measured traits related to growth, reproduction and infestation damage. The results support the occurrence of strong inbreeding depression in vegetative and reproductive performance as well as herbivore resistance in plants from both ranges. However, for inbreeding effects on fruit damage we found opposing trends for the two ranges. Whereas inbreeding slightly increased fruit damage in native plants, fruit infestation by *H. bicruris* was considerably lower on inbreds than outbreds in invasive plants. The latter might result from higher inbreeding depression in inbred invasive than native plants in volatile production, which has previously been shown to determine *H. bicruris* oviposition (Dötterl *et al.*, 2009). At the same time, invasive populations experienced higher overall fruit infestation and have previously been shown to emit higher amounts of volatiles than native plants. Generally, we found significant increases in both infestation damage and performance in invasive compared to native populations, presumably due to adaptive evolution. Moreover, performance reduction through herbivore infestation was more pronounced in invasive than native populations. Most importantly, significant I x E interactions mitigated inbreeding depression in fruit production under herbivore exclusion, which emphasizes the relevance of enemy release for the invasion success of inbred founder populations. In summary, enemy release in the invaded range may help increasing the persistence of founder populations not only by directly increasing performance (this study) or by allowing a shift in resource allocation towards reproductive or competitive ability (Wolfe *et al.*, 2004, but see Schrieber *et al.*, 2017 [16], section 2.5.2), but also by mitigating the effects of inbreeding depression. The latter may occur through purely additive negative effects of enemy infestation and inbreeding on performance or - as in the case of fruit production - through a reduction of inbreeding depression in performance under enemy release. Furthermore, our results emphasize that genetic differentiation among native and invasive populations, e.g. through range dependent purging (Schrieber and Lachmuth, 2017) [9], might shape the magnitude or even direction of inbreeding effects. The findings thus have important implications for understanding invasion dynamics in particular in early phases and towards the leading edges.

Still, our empirical work so far lacks a proof of the actual occurrence of I x E interactions in the *S. latifolia* invasion *via* their potential evolutionary consequences as proposed by Schrieber and Lachmuth (2017) [9]. According to our concept the relaxation of selection by natural enemies should have lead to the accumulation of deleterious recessive mutations in defense related traits and thus higher enemy-induced inbreeding depression in invasive than native plants following experimental inbreeding. However, inbreeding effects on damage and I×E interaction effects on fitness were not more strongly pronounced in invasive than native populations. There are two possible explanations for this finding. First, invasive populations may -contrary to the available data- still have experienced considerable selective pressure by generalist enemies in invaded North America, which countered the accumulation of deleterious recessive mutations in defense traits. Second, it is not only the strength of selection, but also the degree of naturally occurring inbreeding in population history that influence the amount of accumulated genetic load. Our finding could thus result from a scenario in which native populations did not experience sufficient inbreeding to purge their load in resistance- related traits, whereas invasive populations might not have purged due to a lack of selection. However, for the time being these explanations remain speculative. A major challenge in this context remains the requirement of an adequate metric that well represents the level of historical inbreeding in populations with complex demographic histories such as invasive populations (but see Druet and Gautier, 2017 for a novel model-based approach, which might be useful for future studies).

2.4. Research contributions: Interspecific hybridization

Relevant publications and manuscripts (see appendices 11-12)

[11] van Hengstum T, **Lachmuth S**, Oostermeijer JGB, den Nijs JCM, Meirmans PG, van Tienderen PH (2012). Human-induced hybridization among congeneric endemic plants on Tenerife, Canary Islands. *Plant Systematics and Evolution* 298: 1119-1131

[12] **Lachmuth S**, Molofsky J, Suda J, Milbrath L, Keller SR (in revision for *AoB Plants*). Deconvolution of the invasive meadow knapweed hybrid complex (*Centaurea* ×*moncktonii* C.E. Britton) in eastern North America: associations between genomic ancestry, genome size and capitula morphology

Two studies relevant for this habilitation thesis addressed the topic of hybridization, one for three endemic taxa of the genus *Pericallis* (Asteraceae) at the Macaronesian island of Tenerife and the second for invasive taxa of the *Centaurea jacea* / *C. nigra* complex in the North eastern United States. Both studies provide a snapshot of transient stages in still ongoing formations of hybrid swarms as a consequence of recent anthropogenic changes in species distributions and can be regarded exemplary for the effects of hybridization on species at the opposing extremes of demographic success.

2.4.1 Anthropogenic disturbance facilitates hybridization among endemic island taxa

Oceanic islands are characterized by geographic isolation and limited interchange with mainland and other island biota. As a consequence and in tight linkage to the archipelagos' geological history, processes such as adaptive radiation, multiple colonization events, diversification following vicariant events (e.g. lava flows) and genetic drift have lead to high degrees of endemism in faunas and floras (Emerson, 2002; Kier *et al.*, 2009; Harter *et al.*, 2015). Endemic island taxa frequently exhibit extremely narrow geographic distributions, small population sizes, high specialization, but only weak reproductive isolation from their congeners (Francisco-Ortega *et al.*, 2000; Emerson, 2002) rendering them vulnerable to extinction (Whittaker and Fernandez-Palacios, 2007). Increased human activities on islands such as habitat destruction through deforestation or the development of infrastructure may not only threaten island biota directly, but also enhance opportunities for hybridization among previously isolated endemic taxa by eliminating ecological and geographical barriers and providing novel disturbed habitats potentially suitable for the emerging hybrid taxa. Although such hybridization events may at first increase island biodiversity, consequent demographic or genetic swamping of the parental taxa may ultimately lead to the extinction of island endemics of high conservation value (Todesco *et al.*, 2016).

In the study of van Hengstum *et al*. (2012) [11], we combined a population genetic survey and morphometric analyses to assess where and to what extent hybridization between the three Canary island endemics *Pericallis echinata*, *P. cruenta* and *P. tussilaginis* has occurred as a consequence of human activities on the island of Tenerife. The genus *Pericallis* comprises 14 species (Nordenstam, 1978), whereby solely the three investigated species occur on Tenerife. *Pericallis echinata* is endemic to Tenerife, whereas *P. cruenta* is also found on La Gomera, Gran Canaria as well as El Hierro and *P. tussilaginis* has been reported from Gran Canaria. On Tenerife, the core distributions of *P. echinata* and *P. tussilaginis* are located in Teno and Anaga, respectively, which represent two of the three previously separated oldest parts of the island that were only connected when Teide volcano first arose about 0.2 Mya years ago. By contrast, *P. cruenta* has its core distribution in areas of much younger volcanic depositions that connected the Teide volcano with Anaga around 0.8 Mya years ago (Ancochea *et al.*, 1990). Nowadays, the three species have limited, partly overlapping distributions.

We sampled a total of 53 populations comprising morphologically uniform populations of all three taxa as well as morphologically diverse mixed populations. The sampling covered most of the known ranges of the species. It included typical habitats of the parental species (laural forest and its margins for *P. echinata* and *P. tussilaginis*, pine forest for *P. cruenta*) mainly at the Northern site of the island from east to west as well as road margins connecting the forest belts. For all 256 sampled individuals we measured 17 morphological traits including eight floral and nine vegetative characters and conducted population genetic AFLP analyses using 53 polymorphic markers.

Our results of both the morphometric and genetic analyses confirmed the hypothesis that there is ongoing hybridization between all three species. Whereas the three parental taxa formed clearly separate morphological and genetic units in ordination and cluster analyses, populations previously classified as mixed contained pure as well as morphologically and genetically intermediate plants, and were distributed within and between the clusters of the putative parental species in ordination spaces. Hybrids comprised individuals of approximately equal ancestry from each two parental taxa as well as putative back-crosses to either parent. Moreover, even some individuals with admixture between all three parental species were observed. Such complex admixture patterns are usually regarded as evidence of several generations of hybridization (Lepais *et al.*, 2009; Thompson *et al.*, 2010).

Our evaluation of the geographic distribution and habitat preferences of the different taxa further revealed that hybrid populations occurred more often in road verges than uniform populations of the parental taxa. However, habitat separation was not absolute, as hybrid populations were also found in other types of disturbed habitats adjacent to road verges and uniform populations, especially of *P. tussilaginis*, also occurred in road verges. Broadly speaking, in the three core areas of the parental species' original distributions mainly pure populations occurred not only in the original habitats, but also in road verges. Road verges that connect these core areas mainly harbored mixed populations. Taken together, these findings strongly suggest secondary contact between parental populations previously restricted to the three core areas as a consequence of infrastructural development. If the emergence of this hybrid swarm resulted in a complete merging of the three *Pericallis* species, this would further erode the biodiversity of the Canary Islands (Francisco-Ortega *et al.*, 2000).

2.4.2 High degree of genomic introgression and genome size variation in a highly invasive hybrid complex

The genus *Centaurea* (Asteraceae) is the most abundant noxious weed in the western United States based on county and state lists. Representatives of the genus have invaded and persistently dominate millions of hectares of North American grasslands ecosystems (Lejeune and Seastedt, 2002). In the second half of the 20th century taxa of *Centaurea* subg. *jacea* (Mill.) Hayek, sometimes referred to as the *C. jacea / nigra* complex (Gardou, 1972), introduced from Eurasia in the late 1800s, have first become increasingly wide-spread in the Pacific Northwest (Roché and Roché, 1991a) and over the last decades have rapidly expanded their range. As part of the complex, meadow knapweed (*C. ×moncktonii* C.E. Britton) is a fertile hybrid between *C. jacea* L. and *C. nigra* L. with either brown or black knapweed as the female parent and freely backcrosses with the parental species (Roché and Coombs, 2003). Meadow knapweed (and its parental taxa) have been reported from approximately 25 of the United States and four Canadian provinces, ranging from the Atlantic to the Pacific and South to North Carolina (Miller and Lucero, 2014) and are common in parts of New York State and New England (Eckel, 2012). However, pure parental forms do not appear to permanently persist at least in Western North American hybrid zones (Roché and Roché, 1991b).

Despite their relevance as noxious weeds in the United States (Roché and Coombs, 2003), members of the complex have only been studied in Europe where it is native and not in North America (Garcia-Jacas *et al.*, 2000, 2006; Vanderhoeven *et al.*, 2002), and no genetic studies have resolved the ancestry of parental and hybrid types within this complex. Furthermore, it is not clear whether Eastern North American populations represent a hybrid complex of knapweed species or whether only *C. ×moncktonii* persists as advanced generation hybrids following initial introduction. Consequently, potential effects of genomic recombination and genome size variation on invasive spread remained entirely unexplored.

In the study of Lachmuth *et al*. (in revision) [12], we took advantage of the fact that recently formed invasive hybrid swarms such as North American *C. ×moncktonii* are ideal study systems to gain insight into the genomics of invasiveness. We combined a genomic survey of single nucleotide polymorphisms (SNPs) with analyses of reproductive morphology and assessments of genome size for *Centaurea ×moncktonii* samples collected from 20 locations in the states of New York and Vermont. We for the first time evaluated the ploidy level, taxonomic identity and genomic ancestry for individuals from eastern North American populations of the *C. jacea / nigra* complex. We assessed the occurrence of various hybrid classes and quantified the degree of interspecific recombination as well as its effect on genome size variation. In the light of literature reports on the introduction history of the species, we explored potential demographic scenarios that may have shaped the present-day genomic structure.

As previously reported for the Western coastal states (Roché and Roché, 1991b), our results confirmed that also Eastern invasive *C.* x *moncktonii* populations are tetraploid. Our evaluation of the taxonomic and genomic composition of northeastern American populations of the species complex revealed clearly defined genetic clusters of genotypes suggestive of the parental taxa, but also many hybrid individuals displaying a continuous gradation of hybrid ancestry. Assignment of hybrids to genotype classes showed many advanced generation backcrosses, consistent with a high level of introgression and lack of strong reproductive barriers between parental taxa. Just as for *Pericallis*, these various degrees of admixture suggest that hybridization has been ongoing for several generations (Lepais *et al.*, 2009; Thompson *et al.*, 2010). However, although *C.* ×*moncktonii* hybrids were widespread in our study region, relatively pure populations of the parental taxa persisted and we found a strong signal of among-population geographic structure. Regardless, northeastern American populations likely represent a transient stage in this invasion, with ongoing dispersal and gene flow likely to result in introgression and eventual replacement of parental populations by hybrids. Despite overall strong associations among genomic ancestry, genome size, and morphology, hybrid genotypes expressed greater variation in capitula traits and genome size, indicating transgressive segregation. Advanced generation hybrids often had comparably small genome size relative to additive expectations, possibly due to genomic rearrangements and genomic downsizing, which has been hypothesized to confer invasiveness (Pandit *et al.*, 2014).

The results provide a foundation for further exploration of the genomic consequences of hybridization as well as the genomic basis of adaptive evolution of invasiveness in the *C. jacea* / *nigra* species complex. Our findings advocate to focus management measures on eradicating highly admixed *C.* ×*moncktonii* populations, in particular in New York State, and on preventing continued hybridization among the parental taxa as well as back-crossing of hybrids to the parental taxa. Moreover, genome size should be considered as additional taxonomic characteristic for distinguishing the parental taxa also in Europe. Since species are transported globally with increasing frequency leading to continued introduction of invasive hybrids to new regions as well as to the formation of novel hybrid taxa, the hypothesized connection between genomic admixture and invasion success is likely to remain a critical issue for conservation of native species as well as fundamental invasion and eco-evolutionary research.

2.5 Research contributions: Altered evolutionary trajectories

Relevant publications and manuscripts (see appendices 13-15, 2, 8, 10, 16)

[13] Ley AC, Herzog P, **Lachmuth S**, Abwe AE, Christian MF, Sesink Cleef PR, Abwe EE, Morgan BJ, Gonder MK (2018). Phenotypic variability along a climatic gradient in a perennial afrotropical rainforest understorey herb. *Basic and Applied Ecology* 28: 60-75

[14] Al-Gharaibeh MM, Hamasha HR, Rosche C, **Lachmuth S**, Hensen I (2017). Environmental gradients shape the genetic structure of two medicinal *Salvia* species in Jordan. *Plant Biology* 19-227-228

[15] Al-Gharaibeh MM, Hamasha HR, **Lachmuth S**, Hensen I (2017). Local adaptation to different phytogeographic regions: habitat-related variations in seed germination in response to temperature and salinity for two medicinal *Salvia* species from Jordan. *Plant Species Biology* 32: 25-35

[2] Haider S, Palm S, Bruelheide H, de Villemereuil P, Menzel A, **Lachmuth S** (in preperation). Disturbance and indirect effects of climate warming support plant invasions in mountains

[8] Rosche C, Hensen I, **Lachmuth S** (2018). Local pre-adaptation to disturbance and inbreeding–environment interactions affect colonisation abilities of diploid and tetraploid *Centaurea stoebe*. *Plant Biology* 20: 75-84

[10] Schrieber K, Wolf S, Wypior C, Hoehlig D, Hensen I, Keller SR, **Lachmuth S** (in revision for *Ecology and Evolution*). Enemy release mitigates inbreeding depression in native and invasive *Silene latifolia* populations: experimental insight into the role of inbreeding × environment interactions in invasion success. Preprint available at: https://doi.org/10.1101/401430

[16] Schrieber K, Wolf S, Wypior C, Hoehlig D, Hensen I, **Lachmuth S** (2017). Adaptive and non-adaptive evolution of trait means and genetic trait correlations for resistance to natural enemies and performance in an invasive plant. *Oikos* 126: 572-582

2.5.1 Native species show genetic and phenotypic trait variation along environmental gradients

The studies conducted on native species in this research field centered on quantifying intraspecific genetic variation and its distribution along climatic gradients since the standing genetic variation potentially arising from local adaption forms the basis adaptive evolution can act on under climate change. Whereas in temperate regions the necessity of quantifying intraspecific trait variability has been increasingly recognized in recent years, very little progress has been made on this topic in the tropics. At the same time, it is often assumed that tropical species may exhibit lower trait variation as they encounter less variable environmental conditions than species in temperate regions (Cunningham and Read, 2003). In the study of Ley *et al*., (2018) [13], we took a step towards closing this knowledge gap by estimating the phenotypic variability in *Sarcophrynium prionogonium* (Marantaceae), a still widespread perennial under-storey herb from the tropical African rain forests. The first and several of the co-authors conducted 18 months of field surveys on 14 key functional traits in eight populations that largely covered the climatic range of the species with the overall aim of assessing how it may react to the predicted increase of dryness under climate change in its native habitats. We found considerable intraspecific variability within and across populations. Plant vegetative growth decreased with dryness and also seasonal patterns of flower and fruit development were strongly associated with seasonal rainfall. Productivity was positively related to a combination of high temperatures and precipitation. In particular in habitats with favorable climatic conditions productivity further increased with light availability. These findings suggest that the species may experience fitness losses and range retractions under climate change, but also harbors substantial variation evolution may act upon. Since traits were exclusively studied in the field it remained to be clarified how much of this variation is genetically determined and adaptive, a corresponding publication is currently in review.

Two co-authored studies that formed part of the Ph.D. project of Dr. Mohammad M. Al-Gharaibeh (Al-Gharaibeh, 2017) addressed neutral and quantitative trait differentiation in two medicinal herbs of the genus *Salvia* in Jordan. The country offers an ideal opportunity to study genetic differentiation as four phytogeographic regions (Mediterranean, Irano-Turanian, Saharo-Arabian, Sudanian) meet on its territory, which reflects the high environmental heterogeneity species face over very short distances in the region. Our studies focused on a steep precipitation gradient spanning from the arid Irano-Turanian and Saharo-Arabian regions with highly variable and unpredictable rainfall to the moister Mediterranean region with less variable and more predictable rainfall. The first author sampled populations of *Salvia syriaca* and *S. spinosa* across all three regions in order to investigate the neutral genetic differentiation (Al-Gharaibeh, Hamasha, Rosche, *et al.*, 2017) [14] by the means of AFLP markers. For the vast majority of these populations we then also analyzed differentiation in responses of germination behavior to variation in salinity and temperature along the precipitation gradient (Al-Gharaibeh, Hamasha, Lachmuth, *et al.*, 2017) [15]. Both species are diploid, short-lived perennial herbs, that are pollinated by insects and their diaspores are dispersed by blown tumbling of the panicles.

In both species genetic distance was independent of geographic distance, but significantly correlated with environmental distance. This strong environmentally shaped genetic structure was also supported by the formation of two phytogeographical clusters of populations in the in Irano-Turanian and Saharo-Arabian region and the Mediterranean region in both species. Since neutral markers are presumably not subjected to selection, this finding points to a restriction of gene flow among the regions possibly due to evident divergence in flowering phenology. Moreover, genetic diversity increased with temperature in both species and was thus higher in the Irano-Turanian / Saharo-Arabian than the Mediterranean region. In *S. syriaca* diversity also increased with drought, but was unaffected by population size, whereas smaller populations of *S. spinosa* had a lower genetic diversity. The finding of higher genetic diversity at the more stressful end of the temperature / aridity gradient has also been observed for other species in the region and may be related to the fact that temperature and aridity decline towards higher altitudes were species distributions get more fragmented. Our laboratory experiments additionally suggested that the germination of both species is adapted to high temperatures and moderate salinity. *Salvia spinosa*, the distribution of which reaches more deeply into the Saharo-Arabian region, was - contrary to *S. syriaca* - also able to germinate at very low temperatures (8/4°C, day/night). This germination behavior may allow the species to exploit favorable moisture conditions in late autumn or winter in these regions. Accordingly, germination at 8/4°C was most pronounced for *S. spinosa* populations sampled in the Saharo-Arabian region indicating local adaptation. Moreover, both species showed differentiation in germination response to salinity among phytogeographic regions, which may be mediated by both local adaptation and maternal effects. In summary, these findings suggest that both species on a range-wide level harbor genetic variation on which selection can act under climate change provided that sufficient gene flow occurs. Further research is needed to separate genetic differentiation from maternal effects, to test whether the trait differentiation is actually adaptive under natural conditions and to analyze a wider range of life history traits.

2.5.2 Pre-adaptation as well as rapid post-introduction adaptive evolution contribute to invasion success

May recent local adaptation to a wide range of climatic conditions have pre-adapted plants from some invasive populations of *Senecio inaequidens* for a potential invasion into high-elevation areas of the European Alps? This was an additional question we asked in the study of Haider *et al*. (in preparation) [2] next to the role of land use and climate change (see section 2.1.2 for more detail on the experiment). To this end, we estimated climatic distances between our low-elevation and high-elevation common-garden sites and the 16 source populations of planted *S. inaequidens* seedlings and analyzed the effect of these distances on sapling performance. We ruled out potential effects of non-adaptive (i.e. stochastic) differentiation by using so-called 'animal models' that accounted for population co-ancestry (Lachmuth *et al*., 2011) as estimated based on neutral genetic markers (Lachmuth *et al.*, 2010). Climatic distance significantly affected aboveground biomass production as well as survival and flowering probability. This result points to an adaptation of *S. inaequidens* populations to local climatic conditions during the species' spread across Europe. First-year (i.e. including winter) survival probability increased with decreasing climatic distance to the source population. The existence of such genetically determined variation in combination with the raise of human infrastructural development and tourism in mountainous regions increases the probability that genotypes get introduced that are able to survive the harsh winters. Such climatically pre-adapted plants also produced more aboveground biomass, however, just in the low-elevation garden. This difference is surprising at first, but may be explained by our finding that the low site apparently posed more adverse conditions, possibly due to higher competition in particular in disturbed plots (see 2.1.2). Flowering probability increased with increasing climatic distance. Although unexpected, this result might also point to local adaptation to climatic conditions at population origins as the climatically most distant Mediterranean populations may experience selection towards early reproduction in order to escape summer drought conditions (Chaves *et al.*, 2003). Under slowed development in the cooler Alpine regions, such differentiation may determine whether or not plants flower at all in the first year. The long-term demographic consequences of these divergent strategies remain to be investigated. However, as *S. inaequidens* individuals can have a life span of up to 10 years (Monty and Mahy, 2010), it seems highly likely that winter survivors may have a higher lifetime fecundity than plants that flower in the first year at the cost of winter survival. Our study also indicates that climate warming might favor the establishment of non-native species in mountain communities by reducing the distance between the climatic optimum of invaders and the climatic conditions at higher elevations. However, the degree to which an introduced genotype can benefit from these changes may not only depend on its specific climatic pre-adaptation, but also depend on the ecological context, specifically on competitive and/or disturbance regimes in the invaded habitats.

In Rosche, Hensen, *et al.* (2018) [8] (see section 2.3 for more detail) - next to the study of I x E interactions - we addressed adaptive differentiation in the tolerance of physical aboveground damage, which is likely to occur as a result of anthropogenic disturbance in ruderal sites. There were reasons to believe that such differentiation may have occurred a) between native diploid *versus* tetraploid cytotypes, as tetraploids prevail over diploids at disturbed sites in the native range (Otisková *et al.*, 2014; Broennimann *et al.*, 2014); b) between native *versus* invasive tetraploids as a result of post-introduction adaptation to primary invasion in disturbed habitats (Dietz and Edwards, 2006; Rey *et al.*, 2012) as previously shown for competitive ability (Ridenour *et al.*, 2008) and seed mass (Hahn *et al.*, 2013) in this study system; c) between populations originating from natural *versus* ruderal habitats as a result of local adaptation. As such native populations occurring in habitats prone to anthropogenic disturbance may have been pre-adapted to invade (AIAI hypothesis) (Hufbauer *et al.*, 2012). Whereas we had to reject hypotheses a and b due to a lack of significance in geo-cytotype x clipping treatment interactions, our results did yield support for the third hypothesis (c). Populations from disturbed sites showed higher clipping tolerance than populations from (semi-) natural sites across all geo-cytotypes. Since tolerance did not differ between native and invasive tetraploids, we interpreted this finding as a result of local adaptation within geo-cytotypes independent of range, which seems to be more relevant than differentiation between geo-cytotypes. According to the AIAI hypothesis (Hufbauer *et al.*, 2012), primary invasion in habitats prone to anthropogenic disturbance may be fostered by comparable anthropogenic influence in the native range - pre-adapting the respective populations for invasion. Furthermore, our results add to the growing body of literature that shows that adaptive differentiation along environmental gradients in the native ranges can be re-established in invaded areas (Huey *et al.*, 2000; Maron *et al.*, 2004; Colautti *et al.*, 2009, 2010; Alexander *et al.*, 2009; Colautti and Barrett, 2013; Colautti, Ågren, *et al.*, 2017). Finally, the findings correspond well with new results on the *C. stoebe* diploid-polyploid complex suggesting that drought tolerance did not differ between geo-cytotypes (as previously suggested e.g. by Treier *et al.*, 2009; Henery *et al.*, 2010, see section 2.3) but rather along latitudinal gradients within cytotypes due to local adaptation to precipitation (Mráz *et al.*, 2014). This result highlights that within geo-cytotype differentiation matters and should be accounted for when investigating evolutionary change during the invasion process.

In the study of Schrieber *et al*. (2017) [16], we combined the data acquired for the out-crossed progeny from the herbivory experiment with native and invasive populations of *Silene latifolia* (Schrieber *et al*., in revision) [10] with estimates of population co-ancestry as obtained from microsatellite analyses. With this combination we investigated whether: 1) invasive populations evolved lower resistance and higher performance, 2) this evolutionary change can in fact be attributed to adaptive processes, 3) there are negative genetic correlations that would support a trade-off between resistance and vegetative and / or reproductive performance in native and invasive individuals. We performed trait-by-trait comparisons between ranges by the means of 'animal models' that weigh the population random effect by co-ancestry in order to account for non-adaptive evolutionary differentiation (Lachmuth *et al*., 2011). In addition, we tested for genetic correlations among plant resistance and performance within sib-groups (i.e. family mean correlations, Astles *et al*., 2006) based on enemy infestation data recorded in enemy inclusion plots and performance traits quantified in enemy exclusion plots. Our findings revealed a significant increase in infestation damage and significant increases in performance in invasive compared to native populations, which was largely attributed to adaptive evolutionary processes. However, none of the investigated performance traits exhibited a significant negative correlation with any of the tested resistance traits. The results thus do not support a shift of performance and resistance trait values along a trade-off line in response to enemy release (Koricheva, 2002), as predicted by EICA. Moreover, we did not observe consistent trends across traits or in native *versus* invasive range populations. Whereas we detected non-significant negative trends for native populations, invasive populations showed both significant and non-significant positive correlations. This shift towards positive correlations may have evolved as a response to higher resource availability in invaded habitats (Davis *et al.*, 2000; van Kleunen *et al.*, 2018), allowing for increased resource allocation into a wide range of different traits as costs for resource acquisition are released (Reznick *et al.*, 2000). Such shift has previously been documented for invasive *Ulex europaeus* (Hornoy *et al.*, 2011). Moreover, climate may strongly influence differentiation in resource allocation among and within ranges (Colautti and Barrett, 2013; Boheemen *et al.*, 2018). In summary, our findings rather suggest that the independent evolution of both types of traits is not actually constrained by a trade-off, and that multiple selective agents may interact in shaping trait variation and in weakening negative genetic correlations in the invaded range.

Synopsis

This habilitation thesis assembles the results of empirical studies that investigated five phenomena in the eco-evolutionary dynamics of declining and invasive plant species, namely 1) novel biotic and abiotic environments, 2) demographic and genetic bottlenecks, 3) inbreeding depression and inbreeding x environment interactions, 4) interspecific hybridization, and 5) altered evolutionary trajectories. The five preceding sections of chapter 2 paint a differentiated picture of the ecological and evolutionary processes that shape demographic success.

Broadly speaking the results of the two field experiments presented in section 2.1 support the assumption that disturbance favors the establishment of non-native species through a release from competition (Lembrechts *et al.*, 2016) and limits the seedling emergence and thus regeneration of declining native species (Hansen *et al.*, 2001). Taken together the findings would give a bleak prospect for native mountainous ecosystems under increasingly intensified land use. Nevertheless, both studies also showed that the effects of disturbance are context-dependent as they interact with climatic clines as well as with conditions at a particular microsite or within a particular plant community. Also the spatial extent and duration of disturbance as well as the timing with respect to the plants' life stages happen to play a role.

Our experiment with the invasive *Senecio inaequidens* in the German Alps (Haider *et al*., in preparation) [2] emphasized that the degree to which an invader can benefit from a singular small-scale disturbance event strongly depends on how fast the surrounding native vegetation re-grows. Here, climate came into play and - contrary to our expectation - climate warming did not amplify the beneficial effect of disturbance for invader establishment, but rather fueled a quick re-growth of the native highland community. Irrespective of climate, however, the invader's benefit of disturbance in terms of biomass increase was stronger in the more productive low-elevation turfs. The results of Cáceres *et al*. (in revision) [1] further revealed climatic limits to native tree regeneration mostly at high, but also at low compared to mid elevation. Under climate warming, the findings of both studies thus suggest an increase in growth of native species at higher elevations, which is also supported by upward range shifts observed globally since the 20th century (Parmesan and Yohe, 2003). Non-competitive invaders such as *S. inaequidens* will require a competitive release through substantial disturbance in order to expand to higher elevations under such conditions. The long-term effects of climate warming for the native communities will nevertheless also depend on changes in the nutrient availability in the shallow highland soils (Eze *et al.*, 2018) and on potential changes in species composition (Alexander *et al.*, 2015), which could both not (yet) be assessed in our experiments.

The results of Cáceres *et al*. (in revision) [1] further revealed seed – seedling conflicts in the reaction to disturbance. Whereas we observed a prevalence of slightly positive effects of moderate cattle stocking on seedling emergence, possibly due to increases in light and soil temperature, later life stages suffered from the effects of trampling and browsing. As shown by the study of Rosche, Hensen, *et al.* (2018) [8] (section 2.3), also invaders experience severe losses in fitness if a removal of biomass through disturbance occurs in later life stages and not prior to seedling emergence. This seems to apply in particular, if the invaders are not previously pre-adapted to such disturbance or are inbred as a consequence of founder effects. However, here, we did not take into account the reactions of the native invaded community to the disturbance although invasion success will certainly depend on the fitness loss of the invader relative to its neighbor plants.

Both studies emphasized the necessity of large-scale as well as long-term experimental efforts if we aim at disentangling the complex interplay of climate, disturbance and alterations in species ranges in order to conserve mountain ecosystems under global change. Coming back to the key questions posed in section 1.1 (**Q1.1, Q1.2**), our experiments corroborate that the complexity of climate and land use effects on the seedling establishment of native and exotic species mainly arises from the manifold and sometimes unexpected modulation of competitive and facilitative species interactions through the abiotic environmental changes.

Pollination-mediated plant-plant interactions strongly depend on populations size and / or intra- as well as interspecific density. As one central contribution to research field (2) we thus developed an experimental-analytical framework to disentangle neighborhood effects on plant reproduction (**Q.2.1**) (Lachmuth *et al.*, 2018) [3]. Applying this framework to a typical founder population of *S. inaequidens* we observed that reproduction was increased through pollinator-mediated facilitation by both con- and heterospecific neighbors, which may lead to (community-level) Allee effects. Pollination-independent facilitative interactions occurred, but were weaker and acted at smaller spatial scales. The strength and direction of neighborhood effects depended on target and neighbor traits and thus changed with the trait composition of the neighborhood. Our approach helps to comprehensively analyze density dependence of plant reproduction in a spatially explicit way. It enhances our ability to understand the dynamics of sparse populations following demographic bottlenecks or founding events.

Another level of complexity arises if we take into account intraspecific genetic variation as well as the ways in which it may be altered during species declines or invasions, and in which it may, in turn, affect the reactions of the species to environmental change. Relating to the former, we expected negative effects of recent fragmentation and small population sizes on genetic diversity. Again, our findings were more multifaceted as we found that - rather than recent fragmentation - the consequences of Pleistocene climatic oscillations still shape the genetic diversity of the declining Andean tree line species *Polylepis tarapacana* (**Q.2.2**) (Peng *et al.*, 2015) [4]. Also the genetic diversity of endangered dioecious *Antennaria dioica* in fragmented European grasslands was independent of population size, but increased with the proportion of females in a population (**Q.2.3**) (Rosche, Schrieber, *et al.*, 2018) [5]. Such dependence of genetic diversity on sex ratio has rarely been shown or addressed, neither in native nor invasive species (but see Vandepitte *et al.*, 2010; Lauterbach *et al.*, 2012 for native species). Still, the result has also important implications for invading dioecious species, which may not just suffer reduced reproduction due to mate limitation and thus demographic Allee effects (see also **Q.2.1**, section 2.2.1) in populations with sub-optimal sex ratios, but also further genetic erosion. For native diploid populations of *Centaurea stoebe* (Asteraceae) we did, however, find evidence of genetic erosion in small populations and ruderal habitats, whereas the tetraploid cytotype on average harbored higher genetic diversity across native and invasive populations and without significant decrease in small populations or in ruderal habitats (**Q.2.4, Q.2.5**) (Rosche *et al.*, 2016) [6]. Moreover, following artificial inbreeding, tetraploids showed lower inbreeding depression than diploid *C. stoebe* (**Q.3.1**) (Rosche *et al.*, 2017) [7]. These findings support polyploidy as a species property that serves to prevent losses of genetic diversity as well as inbreeding depression and may thus foster invasion success (te Beest *et al.*, 2012).

Whereas species such as polyploid *C. stoebe* do ultimately not pose a genetic paradox (Estoup *et al.*, 2016), other invasive species are indeed confronted with genetic erosion and thus increased levels of inbreeding in their novel ranges (Schrieber and Lachmuth, 2017) [9]. Here, the question arises how inbreeding depression may influence the founder and invasion success in different environments (**Q.3.2, Q.3.3**). Inbreeding x environment interactions in the context of the 'Genetic Paradox of Invasions' were a core area of my group's research in the past years. An experimental study with *C. stoebe* revealed that clipping of aboveground biomass, which simulated the effects of trampling or mowing in anthropogenically disturbed habitats, actually induced inbreeding depression. Such inbreeding x stress interactions may thus additionally hamper performance in disturbed habitats (**Q.3.2**) in this polyploid invader - in case inbreeding should occur following extreme demographic bottlenecks despite the tetraploids' low susceptibility to genetic erosion (**Q.2.4**). Inbreeding x stress interactions may be even more relevant for other invasive or declining species with a higher risk of inbreeding and inbreeding depression.

In the conceptual paper of Schrieber and Lachmuth (2017) [9] we elaborated the converse hypothesis that ecological release, e.g. a release of biotic interactions with co-evolved antagonists (see section 1.1), may allow alien species to persist and even expand despite the occurrence of inbreeding through ameliorating effects of I x E interactions. The subsequent test of this theory by Schrieber *et al*. (in revision) [10] indeed confirmed that enemy release mitigates inbreeding depression in *Silene latifolia* and may thus have fostered the invasion success of the species under evident release from specialist and generalist herbivores in North America (**Q.3.3**). This mitigation may result from purely additive negative effects of enemy infestation and inbreeding on some performance traits or through a reduction of inbreeding depression under enemy release as found here for fruit production.

Since the role of I x E interactions in both extinctions and invasions is still largely unexplored more experimental work on other species with different ecological preferences, functional traits and evolutionary histories is urgently required. Of particular interest I would consider species that are declining in their native range but invasive in other regions. The inclusion of a broader set of studied species should go hand in hand with integrating interactions of inbreeding effects with additional biotic (e.g. specialist herbivores, competition) and abiotic (e.g. drought, UV radiation) stressors depending on the ecological challenges of the species under consideration. For native declining species that are increasingly mal-adapted to their changing local habitats, inbreeding may certainly amplify the negative fitness consequences (Colautti, Alexander, *et al.*, 2017). In the context of invasions and with respect to the results of section 2.1.2 it would be very interesting to explore to which degree negative effects of inbreeding x stress interactions may hamper invasive spread into more extreme environments such as alpine, arctic or dessert regions. Moreover, the evolutionary consequences of I x E interactions such as the potential increase or even fixation of conditionally deleterious alleles at stress response loci under stress release should be considered (Cheptou and Donohue, 2011; Schrieber and Lachmuth, 2017 [9]). Here, genomic methods may serve not only to estimate genetic diversity and relatedness, but also to identify functional loci involved in inbreeding depression (Kristensen *et al.*, 2010).

With the subject of interspecific hybridization our work addressed another phenomenon that may differentially affect native declining and invasive species. Whereas invaders with little local adaptation to their novel habitats may highly benefit from an increase in genetic variation in hybrid populations, which may boost fitness and allow for faster adaptation (Verhoeven *et al.*, 2011; Rius and Darling, 2014), rare native species may additionally be threatened by genetic or demographic swamping through the hybrid taxa (Todesco *et al.*, 2016). We used neutral genetic markers and morphological traits to confirm the occurrence of extensive interspecific hybridization between three endemic *Pericallis* species on Tenerife (van Hengstum *et al.*, 2012) [11]. So far, the hybrids mainly occurred in the verges of roads that rather recently connected the previously isolated natural distribution areas of the parental taxa. This on the one hand suggests that the increasing establishment of human infrastructure initiated hybridization (**Q.4.1**). On the other hand, it shows that the original habitats still serve as refugia for the parental endemic taxa. Continued monitoring is necessary to find out whether hybrids stay mostly associated with disturbed areas or if they may eventually replace the parental taxa in their natural habitats. Similarly, for invasive *Centaurea ×moncktonii* in the northeastern United States we identified numerous hybrid populations, but also populations of the putative parental taxa continue to persist in the study region (Lachmuth *et al.*, in revision) [12]. Just as for *Pericallis*, we found various degrees of introgression, but mostly higher generation hybrids or backcrosses (**Q.4.2**), suggesting that hybridization has been going on for several generations (Lepais *et al.*, 2009; Thompson *et al.*, 2010). Strong associations existed among genomic ancestry, genome size and morphology across the parental and hybrid taxa. Hybrid populations expressed great variation in capitula traits in particular in advanced generation hybrids and back-crosses indicating transgressive trait segregation. Moreover, advanced generation hybrids often had comparably small genome size possibly due to genomic rearrangements and genomic downsizing (**Q.4.3**). Further analyses are in progress to clarify how the degree of genomic admixture and genome size affect traits conferring invasiveness in the hybrid complex. Our findings advocate for eradicating highly admixed *C. ×moncktonii* populations and for preventing continued hybridization among the parental taxa as well as back-crossing of hybrids. Genome size should be considered as additional taxonomic characteristic for distinguishing the parental taxa also in Europe.

These two case studies strikingly exemplify how the challenge of hybridization may lead to opposing demographic outcomes for rare *versus* invading species, although both are cases of demographic success from the perspective of the hybrid taxon and of threat from the perspective of the parental taxa. Whereas the parental taxa of an exotic invading hybrid may be save from harm in their native distribution area, the ultimate consequence of both cases may be the decline or even extinction of sympatric native species, be it the native parental taxa in case of a native hybrid taxon or the native co-occurring biota in the case of an invading hybrid taxon. From a conservation perspective that aims at preserving native species, both processes are deemed detrimental (Todesco *et al.*, 2016).

The evolutionary adaptation of declining and invasive species to changing environments under global environmental change depends on the available intraspecific genetic variation either within populations or resulting from local adaptation within distribution ranges (Rice and Emery, 2003). We quantified genetic and / or phenotypic trait variation of native species in understudied geographic regions that may be strongly affected by climate change. For the two studied medicinal *Salvia* species in Jordan (Al-Gharaibeh, Hamasha, Lachmuth, *et al.*, 2017; Al-Gharaibeh, Hamasha, Rosche, *et al.*, 2017) [14, 15] as well as the tropical African rainforest understory herb *Sarcophrynium prionogonium* (Ley *et al.*, 2018) [13] we indeed found considerable variation along the investigated gradients. Since the latter was so far studied exclusively in field populations we cannot rule out a substantial involvement of phenotypic plasticity. Still, our results suggest that all three species harbor considerable genetic variation on a range-wide level on which selection can act under climate change, provided that sufficient gene flow among populations occurs (**Q.5.1**).

Also for invasive species the role of evolutionary adaptation in their demographic success starts already prior to their introduction to a novel environment. Whereas it has long been known that climatic pre-adaptations are necessary for successful establishment (Gallien *et al.*, 2015), our results of the clipping experiment with *C. stoebe* (Rosche, Hensen, *et al.*, 2018) [8] support a more recent theory on pre-adaptation, the AIAI (Anthropogenically Induced Adaptation to Invade) hypothesis of (Hufbauer *et al.*, 2012) (**Q.5.3**). Across all geo-cytotypes (native diploids native and invasive tetraploids) we found that populations sampled from ruderal habitats that frequently experience anthropogenic disturbance showed a higher clipping tolerance. This may have pre-adapted genotypes from native ruderal sites for primary invasion in anthropogenically disturbed habitats. At the same time the results show that among-habitat differentiation along environmental present in the native range, may re-establish in invaded regions (Colautti, Ågren, *et al.*, 2017). The consequences of among-population differentiation in the invaded range was in the focus of the study of Haider *et al*. (in preparation) [2]. This time, we focused on climate and found that invasive European populations of *S. inaequidens* may be differentially pre-adapted to further spread into climatically harsh mountainous regions (**Q.5.2**). The fact that populations with a lower climatic distance to our common garden sites in the German Alps showed a higher probability of surviving the harsh winters further implies that climate change may indirectly facilitate establishment of *S. inaequidens* at high elevations by reducing the climatic distance to the lowland conditions to which the species has locally adapted over the past decades. However, as outlined above, establishment may only be successful at highly disturbed mountain sites **(Q.1.2)**.

In Schrieber *et al.* (2017) [16], we addressed one of the most prominent evolutionary hypotheses in plant invasion biology, which postulates the Evolution of Increased Competitive Ability (EICA, Blossey and Nötzold, 1995) arising from a genetically based trade-off with defense against natural enemies - under enemy release in novel ranges. Despite the vast research effort this hypothesis has mobilized (Felker-Quinn *et al.*, 2013), our study is the first that directly quantifies genetic trait correlations to actually assess if such evolutionary changes rest upon a genetically determined performance-defense trade-off. Although our findings for the invasive *Silene latifolia* confirmed the EICA-predicted decreases in enemy defense and increases in vegetative and reproductive performance, our family mean correlations could not support an underlying shift along a resource allocation trade-off line, since there were only weak insignificant negative correlations in native populations which turned neutral or even positive in the invaded range (**Q.5.5**). The altered phenotypes may instead have evolved in response to a relaxation of resource constraints in the novel habitats and strikingly exemplify the shifts in evolutionary trajectories species may experience under anthropogenic environmental change.

Since evolutionary among-population divergence cannot only arise in response to selection (i.e. adaptive evolution), but also as a consequence of stochastic processes such as genetic drift, analyses of adaptive evolution have to test against a null-model of neutral differentiation. In the EICA-related study of Schrieber *et al.* (2017) [16] we used a novel statistical approach which extended mixed 'animal-models' to account for population co-ancestry and provides conservative tests for adaptive evolution. In contrast to a former study on *S. inaequidens* (Lachmuth *et al.*, 2011), our analyses for *S. latifolia* showed a lower influence of non-adaptive evolution and rather confirmed that the observed decreases in enemy defense and increases in performance resulted from selection (**Q.5.4**). These non-adaptive evolutionary processes are likely to occur during demographic non-equilibrium situations such as range shifts or biological invasions. We thus hope that they receive more attention from empiricists in the future, which would allow for a broader assessment of their role across different species and demographic scenarios.

In summary, the research gathered in this thesis contributes to a more general understanding of the important role of eco-evolutionary processes in the demographic success and thus management implications of declining and invasive species. I join with (Colautti, Alexander, *et al.*, 2017) in advocating for a stronger communication between conservation and invasion science as an exchange of knowledge may serve progress at both sites. Moreover, the thesis emphasizes the relevance of several understudied topics, such as I x E interactions or non-adaptive evolutionary changes that may have implications for a wider range of ecological and evolutionary research areas. Most importantly, range dynamics seem to be driven by a complex interplay of multiple ecological and evolutionary mechanisms the exploration of which requires integrative trans-disciplinary research concepts.

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Summary

Worldwide, biodiversity is increasingly under pressure from anthropogenic climate and land use change. In concert, environmental change and modifications of dispersal pathways induce immense and rapid alterations to the geographic distributions of species including range retractions, expansions, shifts, and the invasion into novel regions. Rare or declining species, which spiral towards extinction, *versus* invasive species, which expand their ranges rapidly, represent the opposite ends of a gradient of demographic success. Intriguingly - despite their differential demographic success - invasions and extinctions may be determined by the same fundamental ecological and genetic processes. This habilitation thesis assembles conceptual and empirical research in five research fields corresponding to five phenomena that likely determine the eco-evolutionary dynamics of natural plant populations under global change:

Both declining and invasive species experience (1) alterations of their environment in concert with (2) reductions of their population sizes. Frequently these demographic bottlenecks induce genetic bottlenecks (i.e. reductions in genetic diversity) and increase levels of inbreeding as well as inbreeding depression. Inbreeding depression can be environment-dependent and is often more pronounced under stress. Thus, the coincidence of genetic bottlenecks and altered environmental conditions may strongly influence fitness *via* (3) so-called inbreeding x environment (I x E) interactions. Altered dispersal pathways frequently also lead to (4) hybridization between previously isolated taxa. Eventually, all the above-described genetic processes together with novel selective regimes in altered environments (5) change the evolutionary trajectories of species. The exact mechanisms underlying the relationship between these phenomena and population as well as range dynamics may strongly depend on species traits and may differ for native and alien populations.

In the first research field (1) the results of two large-scale field experiments in mountainous regions corroborated that the complexity of climate and land use effects on demographic rates mainly arises as abiotic environmental changes modulate competitive and facilitative species interactions. Pollination-mediated plant-plant interactions strongly depend on populations size and / or intra- as well as interspecific density. As one central contribution to research field (2) we thus developed an experimental-analytical framework to disentangle neighborhood effects on plant reproduction. Applying this framework to a typical founder population of *Senecio inaequidens* (Asteraceae) we observed that reproduction was increased through pollinator-mediated facilitation by both con- and heterospecific neighbors. The strength and direction of neighborhood effects depended on target and neighbor traits. Our approach helps to comprehensively analyze density dependence of plant reproduction in a spatially explicit way and enhances our ability to understand the dynamics of sparse populations.

Another level of complexity arises if we take into account intraspecific genetic variation, how it may be altered by demographic disequilibrium and in which ways it may, in turn, affect the species' reactions to environmental change. Concerning genetic bottlenecks our results again were multifaceted as we found that not current population sizes of native declining species, but rather historical range shifts or current sex ratios, shaped neutral genetic diversity. For the *Centaurea stoebe* polyploid complex (Asteraceae) our research established that polyploidy buffers against genetic erosion in small populations and ruderal habitats as well as against inbreeding depression and may thus explain the invasion success of the tetraploid cytotype and polyploids in general.

Further experimental studies (research field 3) with invasive species exemplified how inbreeding x stress interactions may hamper founder success, whereas ecological release, e.g. a release of biotic interactions with co-evolved antagonists, may allow alien species to thrive despite the occurrence of inbreeding through ameliorating effects of I x E interactions. We did not investigate I x E interactions in the context of extinctions, but if species are increasingly mal-adapted to their changing local habitats, inbreeding may certainly amplify the negative fitness consequences. Since the role of I x E interactions in both extinctions and invasions is still largely unexplored more experimental work on other species with different ecological preferences, functional traits and evolutionary histories is urgently required.

With the subject of interspecific hybridization (4) our work addressed another phenomenon that may differentially affect declining and invasive species. Whereas invaders with little local adaptation may benefit from an increase in genetic variation in hybrid populations, rare native species may additionally be threatened by genetic or demographic swamping through hybrid taxa. We studied hybridization among three endemic oceanic island taxa and the degree of genomic admixture in an invasive hybrid complex. In both cases, we found various degrees of introgression and strong associations among genomic ancestry, morphology and genome size.

Fast evolutionary adaptation is seen as one of the most relevant mechanisms by which species may cope with rapidly changing environments. We studied (5) three native species in understudied geographic regions that may be strongly affected by climate change and found considerable genetic and / or phenotypic trait variation on a range-wide level on which selection could act under changing climates, if sufficient gene flow occurred. At the side of invasive species our findings suggest that genetic differentiation between ruderal and natural habitats in the native range may serve as pre-adaption for invasion into different habitat types, and further that local adaptation within the invaded range may pre-adapt invaders for spread into more extreme environments. Further experimental research addressed the Evolution of Increased Competitive Ability (EICA) rooted in a genetically based trade-off between performance and defense against natural enemies from which invaders are often released. Although we could confirm that such evolutionary change resulted from adaptation rather than drift in one of the classical example species for this hypothesis (*Silene latifolia*, Caryophyllaceae), we could not detect an underlying negative genetic correlation. The altered phenotypes possibly evolved through a relaxation of resource constraints in the novel habitats and strikingly exemplify shifts in evolutionary trajectories under environmental change.

In summary, the research assembled in this thesis contributes to a more general understanding of the important role of eco-evolutionary processes for the demographic success and thus management implications of declining and invasive species. It emphasizes the relevance of several understudied topics, such as I x E interactions or non-adaptive evolution that may have implications for a wider range of ecological and evolutionary research areas.

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Erklärung zur vorgelegten schriftlichen Leistung

Hiermit erkläre ich an Eides statt, dass diese Habilitationsschrift selbständig und ohne fremde Hilfe verfasst wurde. Andere als die angegebenen Quellen und Hilfsmittel wurden nicht benutzt und die den benutzten Werken wörtlich oder inhaltlich entnommenen Stellen wurden als solche kenntlich gemacht.

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Rosche C, Schrieber K, **Lachmuth S**, Durka W, Hirsch H, Wagner V, Schleuning M, Hensen I (2018) Sex ratio rather than population size affects genetic diversity in *Antennaria dioica*. *Plant Biology* 20: 789-796

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Ley AC, **Lachmuth S**, Abwe AE, Christian MF, Abwe EE, Morgan BJ, Gonder MK (submitted) Adaptability to climate change in tropical plants – evidence from reciprocal transplant and common garden experiments in Cameroon

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Halle (Saale), den 04.12.2018 Dr. Susanne Lachmuth

Appendix

Appendix 1

Disentangling effects of altitude, land use and microsites on early-life performance of a high mountain tree: insights from an *in situ* sowing experiment

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Abstract

Aim. Understanding the forces that drive range shifts in forest landscapes is imperative for predicting species distributions under anthropogenic climate and land use change. However, empirical studies exploring how these components jointly influence critical early-life stages of mountain tree species across environmental gradients are scarce. We used the high mountain tree *Polylepis australis* as model species to investigate the relative importance of altitude and associated climatic conditions, land use for livestock and microsite characteristics on early-life performance
Location. Córdoba Sierras, central Argentina.
Methods. We set up an extensive in situ sowing experiment with a robust split-plot design that integrated spatial scales ranging from 0.4 m2 microsite subplots (associated to vegetative and micro-topographic structures) via livestock ex- and enclosure plots of several hectares, to an altitudinal gradient of 1000 m. Components of early-life performance were monitored across two subsequent growing seasons.
Results. Altitude and livestock presence negatively affected early-life performance, but effects were purely additive disproving trade-offs among responses to various stresses. Microsite characteristics played a fundamental role in *P. australis* establishment, whereby multiple shifts in microsite effects with altitude and land use suggested alternate operating mechanisms: facilitation (reducing desiccation) dominated at low altitude while at high altitude abiotic stress (frost and radiation) overruled any microsite effects. At mid altitude benefits of competition release prevailed over facilitation and microsite effects gained importance under livestock presence. Uncoupled responses of seedling 28 emergence and performance illustrated that net outcomes of facilitative vs. negative interactions shift throughout early-life: a favorable location for seeds may abruptly turn adverse for seedlings.
Main conclusions. We unravel how changes in environmental constraints, anthropogenic disturbances and microsite characteristics jointly modulate facilitative and negative interactions across stages of early establishment. Such information is fundamental when categorizing specific

microhabitats as “safe sites” for tree regeneration in high-mountain environments with high spatio-temporal heterogeneity.

Keywords: Abiotic factors, competition, facilitation, livestock, microsites, *Polylepis australis*, recruitment, seedlings, safe sites, seed regeneration

Appendix 2

Disturbance and indirect effects of climate warming support plant invasions in mountains

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Abstract

Climate warming, changes in land use and biological invasions are key components of global change, which may severely threaten high-elevation ecosystems. Thereby, warming of temperature as well as increased disturbance as a common consequence of land use changes are expected to support the establishment of non-native species at high-elevations by increasing both the invasibility of native communities and the invasiveness of non-native species. However, we are the first to address this interplay in a single study.

We transplanted grassland turfs between a low- and a high-elevation common-garden site in the European Alps in order to decouple climate change from community origin effects. We then investigated how both of these factors interacted with disturbance in shaping community invasibility as well as the invasiveness of differentially climatically pre-adapted populations of a potential future plant invader. Our results attest a strong and consistent effect of disturbance, which directly increased community invasibility, and indirectly promoted the invasiveness of non-native species through the creation of habitat which perfectly suits typical characteristics of non-native species. Contrary to our expectation, experimentally induced climate warming did not increase community invasibility. However, we did find mostly positive effects of pre-adaptation to conditions climatically similar to our common-gardens. Climate change may thus, in combination with disturbance, indirectly promote the invasiveness and the survival of a newly established non-native species by reducing the climatic distance between non-native source populations and mountainous regions.

Appendix 3

Neighbourhood effects on plant reproduction: An experimental–analytical framework and its application to the invasive *Senecio inaequidens*

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Abstract

1. Density dependence is of fundamental importance for population and range dynamics. Density-dependent reproduction of plants arises from competitive and facilitative plant–plant interactions that can be pollination independent or pollination mediated. In small and sparse populations, conspecific density dependence often turns from negative to positive and causes Allee effects. Reproduction may also increase with heterospecific density (community-level Allee effect), but the underlying mechanisms are poorly understood and the consequences for community dynamics can be complex. Allee effects have crucial consequences for the conservation of declining species, but also the dynamics of range edge populations. In invasive species, Allee effects may slow or stop range expansion.

2. Observational studies in natural plant communities cannot distinguish whether reproduction is limited by pollination-mediated interactions among plants or by other neighbourhood effects (e.g. competition for abiotic resources). Even experimental pollen supply cannot distinguish whether variation in reproduction is caused by direct density effects or by plant traits correlated with density. Finally, it is unknown over which spatial scales pollination-mediated interactions occur.

3. To circumvent these problems, we introduce a comprehensive experimental and analytical framework which simultaneously (1) manipulates pollen availability and quality by hand pollination and pollinator exclusion, (2) manipulates neighbourhoods by transplanting target plants, and (3) analyses the effects of con- and heterospecific neighbourhoods on reproduction with spatially explicit trait-based neighbourhood models.

4. Applying this framework to *Senecio inaequidens*, one of Europe's fastest plant invaders, we found that the seed set was strongly pollen limited. Reproduction had increased by pollinator-mediated facilitation by both con- and heterospecific neighbours which may lead to (community-level) Allee effects. Pollination-independent interactions, such as amelioration of abiotic conditions through neighbours, contributed to additional positive neighbour effects. However, these pollination-independent interactions were weaker than the pollination-mediated interactions and they occurred over smaller spatial scales. Finally, the strength and direction of neighbourhood effects depended on neighbour traits and thus changed with the trait composition of the neighbourhood.

5. Synthesis. By manipulating both pollen availability and target plant locations within neighbourhoods, we can comprehensively analyse spatially explicit density dependence of plant reproduction. This experimental approach enhances our ability to understand the dynamics of sparse populations and of species geographical ranges.

Keywords: Allee effect, biological invasion, competition, density dependence, facilitation, plant–plant interactions, pollination, reproductive success, spatially explicit model, trait-based neighbourhood model

Appendix 4

Pleistocene climatic oscillations rather than recent human disturbance infl uence genetic diversity in one of the world's highest treeline species

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Abstract

PREMISE OF THE STUDY: Biological responses to climatic change usually leave imprints on the genetic diversity and structure of plants. Information on the current genetic diversity and structure of dominant tree species has facilitated our general understanding of phylogeographical patterns.
METHODS: Using amplified fragment length polymorphism (AFLPs), we compared genetic diversity and structure of 384 adults of *P. tarapacana* with those of 384 seedlings across 32 forest sites spanning a latitudinal gradient of 600 km occurring between 4100 m and 5000 m a.s.l. in *Polylepis tarapacana* (Rosaceae), one of the world's highest treeline species endemic to the central Andes.
KEY RESULTS: Moderate to high levels of genetic diversity and low genetic differentiation were detected in both adults and seedlings, with levels of genetic diversity and differentiation being almost identical. Four slightly genetically divergent clusters were identified that accorded to differing geographical regions. Genetic diversity decreased from south to north and with increasing precipitation for adults and seedlings, but there was no relationship to elevation.
CONCLUSIONS: Our study shows that, unlike the case for other Andean treeline species, recent human activities have not affected the genetic structure of *P. tarapacana* , possibly because its inhospitable habitat is unsuitable for agriculture. The current genetic pattern of *P. tarapacana* points to a historically more widespread distribution at lower altitudes, which allowed considerable gene flow possibly during the glacial periods of the Pleistocene epoch, and also suggests that the northern Argentinean Andes may have served as a refugium for historical populations.

Keywords: AFLP, central Andes, elevational gradient, latitudinal gradient, phylogeography, *Polylepis tarapacana*, post-glacial migration

Appendix 5

Sex ratio rather than population size affects genetic diversity in *Antennaria dioica*

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Abstract

Habitat fragmentation and small population size can lead to genetic erosion in threatened plant populations. Classical theory implies that dioecy can counteract genetic erosion as it decreases the magnitude of inbreeding and genetic drift due to obligate outcrossing. However, in small populations, sex ratios may be strongly male- or female-biased, leading to substantial reductions in effective population size. This may theoretically result in a unimodal relationship between sex ratios and genetic diversity; yet, empirical studies on this relationship are scarce.

Using AFLP markers, we studied genetic diversity, structure and differentiation in 14 highly fragmented *Antennaria dioica* populations from the Central European lowlands. Our analyses focused on the relationship between sex ratio, population size and genetic diversity.

Although most populations were small (mean: 35.5 patches), genetic diversity was moderately high. We found evidence for isolation-by-distance, but overall differentiation of the populations was rather weak. Females dominated 11 populations, which overall resulted in a slightly female-biased sex ratio (61.5%). There was no significant relationship between population size and genetic diversity. The proportion of females was not unimodally but positively linearly related to genetic diversity.

The high genetic diversity and low genetic differentiation suggest that *A. dioica* has been widely distributed in the Central European lowlands in the past, while fragmentation occurred only in the last decades. Sex ratio has more immediate consequences on genetic diversity than population size. An increasing proportion of females can increase genetic diversity in dioecious plants, probably due to a higher amount of sexual reproduction.

Keywords: AFLP, biased sex ratio, dioecy, fragmentation, genetic differentiation, genetic diversity, genetic erosion, small population size

Appendix 6

The population genetics of the fundamental cytotype-shift in invasive *Centaurea stoebe* s.l.: genetic diversity, genetic differentiation and small-scale genetic structure differ between cytotypes but not between ranges

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Abstract

Polyploids are overrepresented in invasive species. Yet, the role of genetic diversity and drift in colonization success of polyploids remains unclear. Here, we investigate genetic diversity, genetic differentiation and small-scale genetic structure in our model system, the three geo-cytotypes of *Centaurea stoebe*: monocarpic diploids and polycarpic (allo)tetraploids coexist in the native range (Eurasia), but only tetraploids are reported from the invasive range (North America). For each geo-cytotype, we investigated 18–20 populations varying in size and habitat type (natural vs. ruderal). Population genetic analyses were conducted at eight microsatellite loci. Compared to diploids, tetraploids revealed higher genetic diversity and lower genetic differentiation, whereas both were comparable in tetraploids between both ranges. Within spatial distances of a few meters, diploid individuals were more strongly related to one another than tetraploids. In addition, expected heterozygosity in diploids increased with population size and was higher in natural than in ruderal habitats. However, neither relationship was found for tetraploids. The higher genetic diversity of tetraploid *C. stoebe* may have enhanced its colonization abilities, if genetic diversity is correlated with fitness and adaptive capabilities. Furthermore, the inheritance of a duplicated chromosome set as well as longevity and frequent gene flow reduces drift in tetraploids. This counteracts genetic depletion during initial introductions and in subsequent phases of small or fluctuating population sizes in ruderal habitats. Our findings advocate the importance of studying colonization genetic processes to gain a more mechanistic understanding of the role of polyploidy in invasion dynamics.

Keywords: Biological invasion, *Centaurea stoebe*, Colonization, Genetic diversity, Geo-cytotype, Polyploidy

Appendix 7

Invasion success in polyploids: the role of inbreeding in the contrasting colonization abilities of diploid versus tetraploid populations of *Centaurea stoebe* s.l.

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Abstract

1. As a consequence of founder effects, inbreeding can hamper colonization success: First, in species with self-incompatibility controlled by an S-locus, inbreeding may decrease cross-compatibility, mainly due to the sharing of identical S-alleles between closely related mating partners. Secondly, inbreeding can reduce fitness of inbred relative to outbred offspring (i.e. inbreeding depression). Polyploids often show reduced inbreeding depression compared to diploids, which may contribute to the overrepresentation of polyploids among invasive species. This is thefirst study that tests how the effects of inbreeding differ between geocytotypes (i.e. ploidy levels within a given range).

2. Our model organism, *Centaurea stoebe*, is strictly self-incompatible and comprises three geocytotypes: diploids are more frequent than tetraploids in the native range, while only tetraploids occur in the invasive range. We conducted a breeding experiment (sib-mating vs. outcrossing) with 14 native diploid, 13 native tetraploid and 15 invasive tetraploid populations. We recorded cross-compatibility and estimated a cumulative index for offspring fitness. Since frequent inbreeding can result in purging of genetic load responsible for inbreeding depression, our analyses included a metric for within-population relatedness, based on eight microsatellite markers, to assess the effect of purging.

3. Inbreeding was found to reduce cross-compatibility, which was similarly pronounced in diploids and tetraploids. It also caused inbreeding depression in cumulative fitness, which was significant indiploids but not in tetraploids. No evidence of purging was observed as inbred fitness was not affected by within-population relatedness.

4. Synthesis. Our results provide new insights into the contrasting invasion success of the cytotypes of *C. stoebe*. As the effects of cross-compatibility and purging were comparable between cytotypes, both processes can be ruled out to affect the colonization success of diploids versus tetraploids. Ourfindings are consistent with the hypothesis that polyploidy increases the masking of recessive mutations, which maintains high fitness in inbred tetraploids and may thus facilitate colonization of new ranges. We highlight that reduced inbreeding depression may add to previously acknowledged

advantages of polyploids in range expansions, a mechanism that may hitherto have been underestimated due to a lack of data on variation in inbreeding depression across geocytotypes.

Keywords: coefficient of relationship, founder effects, genetic bottleneck, geocytotype, inbreeding depression, invasion ecology, purging, S-alleles, sporophytic self-incompatibility, spotted knapweed

Appendix 8

Local pre-adaptation to disturbance and inbreeding – environment interactions affect colonisation abilities of diploid and tetraploid *Centaurea stoebe*

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Abstract

Primary colonisation in invasive ranges most commonly occurs in disturbed habitats, where anthropogenic disturbance may cause physical damage to plants. The tolerance to such damage may differ between cytotypes and among populations as a result of differing population histories (adaptive differentiation between ruderal verus natural habitats). Moreover, founder populations often experience inbreeding depression, the effects of which may increase through physical damage due to inbreeding–environment interactions. We aimed to understand how such colonisation processes differ between diploid and tetraploid *Centaurea stoebe* populations, with a view to understanding why only tetraploids are invasive. We conducted a clipping experiment (frequency: zero, once or twice in the growing season) on inbred versus outbred offspring originating from 37 *C. stoebe* populations of varying cytotype, range and habitat type (natural versus ruderal). Aboveground biomass was harvested at the end of the vegetation period, while re-sprouting success was recorded in the following spring. Clipping reduced re-sprouting success and biomass, which was significantly more pronounced in natural than in ruderal populations. Inbreeding depression was not detected under benign conditions, but became increasingly apparent in biomass when plants were clipped. The effects of clipping and inbreeding did not differ between cytotypes. Adaptive differentiation in disturbance tolerance was higher among populations than between cytotypes, which highlights the potential of pre-adaptation in ruderal populations during early colonisation on anthropogenically disturbed sites. While the consequences of inbreeding increased through clipping-mediated stress, they were comparable between cytotypes, and consequently do not contribute to understanding the cytotype shift in the invasive range.

Keywords: AIAI hypothesis; biological invasion; clipping; geo-cytotype; polyploidy; rapid evolution; spotted knapweed

Appendix 9

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

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***Biological Reviews*, 2017, 92: 939-952, doi: 10.1111/brv.12263** **review article**

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.

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

Appendix 10

Enemy release mitigates inbreeding depression in native and invasive *Silene latifolia* populations: experimental insight into the role of inbreeding × environment interactions in invasion success

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Abstract

Inbreeding and enemy infestation are common in plants and can synergistically reduce their performance. This inbreeding × environment (I×E) interaction may be of particular importance for the success of plant invasions if introduced populations experience a release from attack by natural enemies relative to their native conspecifics. Using native and invasive plant populations, we investigate whether inbreeding affects infestation damage, whether inbreeding depression in performance is mitigated by enemy release and whether genetic differentiation among native and invasive plants modifies these I×E interactions. We used the plant invader *Silene latifolia* and its natural enemies as a study system. We performed two generations of experimental out- and inbreeding within eight native (European) and eight invasive (North American) *S. latifolia* populations under controlled conditions using field- collected seeds. Subsequently, we exposed the offspring to an enemy exclusion and inclusion treatment in a common garden in the species' native range to assess the interactive effects of population origin (range), breeding treatment and enemy treatment on infestation damage as well as plant performance. Inbreeding increased flower and leaf infestation damage in plants from both ranges, but had opposing effects on fruit damage in native *versus* invasive plants. Both inbreeding and enemy infestation had negative effects on plant performance, whereby inbreeding depression in fruit number was higher in enemy inclusions than exclusions in plants from both ranges. Moreover, the magnitude of inbreeding depression in fruit number was lower in invasive than native populations. Our results support that inbreeding increases enemy susceptibility of *S. latifolia*, which magnifies inbreeding depression in the presence of enemies. Enemy release in the invaded habitat may thus increase the persistence of inbred founder populations and thereby contribute to successful invasion. Moreover, our findings emphasize that genetic differentiation among native and invasive plants can shape the magnitude and even the direction of inbreeding effects.

Keywords: biological invasion, genetic differentiation, genetic paradox, herbivory, purging, white campion

Appendix 11

Human-induced hybridization among congeneric endemic plants on Tenerife, Canary Islands

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Abstract

Endemic genera on oceanic islands often evolved striking morphological and ecological differences among species, withweak postzygotic reproductive isolation.Human activities can lead to increased connectivity and can thereby promote secondary contact and hybridization between previously isolated species.Westudied this phenomenon in three species of the genus Pericallis (Asteraceae) on Tenerife, Canary Islands. A total of 53 populations was sampled, including morphologically uniform as well as mixed populations containing morphologically diverse individuals. All plants were analyzed both genetically using AFLP markers and morphometrically. As expected, morphological analysis clearly separated the plants from the uniform populations in three clusters, with distinguishing characters corresponding to those used in species identification. The three species were also grouped into distinct genetic clusters in a STRUCTURE analysis, although no private alleles were observed. Adding the mixed population data to the analyses provided evidence for extensive hybridization among species, predominantly between P. cruenta and P. echinata, and between P. cruenta and P. tussilaginis, and morphological and genetic signals were congruent. The mixed populations were geographically located in between the uniform populations and were found in road verges significantly more often than the uniform populations. The observed distribution strongly suggests that hybridization between originally isolated species is recent, promoted by secondary contact due to human disturbance and the construction of roads.

Keywords: AFLP, conservation, endemic plants, homoploid hybridization, island biogeography, *Pericallis*

Appendix 12

Deconvolution of the invasive meadow knapweed hybrid complex (*Centaurea ×moncktonii* C.E. Britton) in eastern North America: associations between genomic ancestry, genome size and capitula morphology

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Abstract

Background and aims. Plant invasions are prime opportunities for studying hybridization and the nature of species boundaries, but hybrids also complicate the taxonomic treatment and management of introduced taxa. In this study, we use population genomics to estimate the extent of genomic admixture and test for its association with morphology and genome size in a hybrid complex of knapweeds invasive to North America: meadow knapweed (*Centaurea ×moncktonii*) and its parental species (*C. jacea* and *C. nigra*).

Methods We sampled 20 populations from New York and Vermont, USA, and used genotyping-by-sequencing to identify single nucleotide polymorphisms in order to estimate genome-wide ancestry and classify individuals into hybrid genotype classes. We then tested for association between degree of genomic introgression and variation in a subset of traits diagnostic for the parental taxa, namely capitula morphology and monoploid genome size.

Key results. Genomic clustering revealed two clearly-defined lineages, as well as many admixed individuals forming a continuous gradation of introgression. Individual assignments to hybrid genotype classes revealed many advanced generation intercrosses and backcrosses, suggesting introgression has been extensive and unimpeded by strong reproductive barriers between taxa. Variation in capitula traits between the two unadmixed, presumed parental, lineages exhibited continuous, and in some cases transgressive, segregation among introgressed hybrids. Genome size was also divergent between lineages, although advanced generation hybrids had smaller genomes relative to additive expectations.

Conclusions. Our study demonstrates deep introgression between the porous genomes of a hybrid invasive species complex. In addition to strong associations among genomic ancestry, genome size, and morphology, hybrids expressed greater variation in capitula traits and genome size, indicating transgressive segregation, as well as a bias towards smaller genomes, possibly due to genomic downsizing. Future studies will apply these results to experimentally test how introgression, transgressive segregation, and genome size reduction interact to confer invasiveness.

Keywords: Asteraceae, black knapweed, brown knapweed, *Centaurea jacea*, *Centaurea nigra*, genomic admixture, genotyping by sequencing, introgression, single nucleotide polymorphisms

Appendix 13

Phenotypic variability along a climatic gradient in a perennial afrotropical rainforest understorey herb

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Abstract

Plants evolved in response to climatic conditions, which shaped their geographic distribution, functional traits and genetic composition. In the face of climatic changes, plants have to react by either genetic adaptation, phenotypic plasticity or geographic range shift. Their reaction potential depends on their phenotypic and genetic variability which can be evaluated through regional scale trait estimates, however, little is known here about tropical African plants. To start filling this gap of knowledge, the aim of this study was to estimate the phenotypic variability in a widespread perennial herb from the understorey of tropical African rainforests: *Sarcophrynium prionogonium* (Marantaceae). We surveyed 211 individuals from eight populations distributed across four sites in Cameroon covering largely the climatic range of the study species. Fourteen key functional traits were measured monthly for 18 months (2013–2014). Individuals of the study species persisted under a wide range of environmental conditions and there was considerable intraspecific variability within and across populations. Still, plant vegetative growth decreased with dryness. Productivity was positively related to a combination of high temperatures and precipitation and under these favourable conditions strongly shaped by light. Seasonal patterns of flower and fruit development were strongly associated with seasonal rainfall. Thus, the predicted increased dryness in tropical Africa might be disadvantageous for the study species. In the past, plants reacted to such aridification tendencies (e.g. during the Pleistocene glacial cycles) by retracting to moist refugia. The current climatic changes, however, being much faster and larger might provide new challenges.

Keywords: Adaptation, climatic gradient, intraspecific trait variation, Marantaceae,Tropical Africa

Appendix 14

Environmental gradients shape the genetic structure of two medicinal *Salvia* species in Jordan

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Abstract

Environmental gradients, and particularly climatic variables, exert a strong influence on plant distribution and, potentially, population genetic diversity and differentiation. Differences in water availability can cause among-population variation in ecological processes and can thus interrupt populations' connectivity and isolate them environmentally. The present study examines the effect of environmental heterogeneity on plant populations due to environmental isolation unrelated to geographic distance. Using AFLP markers, we analyzed genetic diversity and differentiation among 12 *Salvia spinosa* populations and 13 *Salvia syriaca* populations from three phytogeographical regions (Mediterranean, Irano-Turanian and Saharo-Arabian) representing the extent of the species' geographic range in Jordan. Differences in geographic location and climate were considered in the analyses. For both species, flowering phenology varied among populations and regions. Irano-Turanian and Saharo-Arabian populations had higher genetic diversity than Mediterranean populations, and genetic diversity increased significantly with increasing temperature. Genetic diversity in *Salvia syriaca* was affected by population size, while genetic diversity responded to drought in *S. spinosa*. For both species, high levels of genetic differentiation were found as well as two well-supported phytogeographical groups of populations, with Mediterranean populations clustering in one group and the Irano-Turanian and Saharo-Arabian populations in another. Genetic distance was significantly correlated to environmental distance, but not to geographic distance. Our data indicate that populations from moist vs. arid environments are environmentally isolated, where environmental gradients affect their flowering phenology, limit gene flow and shape their genetic structure. We conclude that environmental heterogeneity may act as driver for the observed variation in genetic diversity.

Keywords: AFLP, drought, flowering phenology, genetic diversity, phytogeographic regions, *Salvia spinosa*, *Salvia syriaca*

Appendix 15

Local adaptation to different phytogeographic regions: habitat-related variations in seed germination in response to temperature and salinity for two medicinal *Salvia* species from Jordan

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Abstract

Salvia spinosa L. and *Salvia syriaca* L. are perennial medicinal herbs that occur in the Mediterranean, Irano-Turanian and Saharo-Arabian phytogeographic regions of Jordan. With respect to the seed germination requirements, prevailing environmental conditions in each phytogeographic region may promote local adaptation and consequently affect the distribution range of the species. Using seeds of both species collected from populations across the three regions, we tested responses to variations in temperature and salinity under laboratory conditions. Both species showed significant differences in cumulative germination percentages and germination rates (modified Timson Index) with temperature, while origin only significantly affected *S. spinosa* seeds. Both species germinated best under the highest temperature regime (32/20°C). The low temperature regime (8/4°C) completely inhibited germination in *S. syriaca*, wheras it led to 80% to 95% germination in *S. spinosa*, with significant variation being recorded between the phytogeographic regions. For both species, salt solutions of 0, 25 and 50 mM NaCl yielded the highest germination percentages and rates, which sharply and significantly declined at higher concentrations (100 and 200 mM NaCl). Our results provide evidence of local adaptation of the study species to salinity and temperature in the respective maternal environments, particularly in the Irano-Turanian and Saharo-Arabian regions. Such differentiation should be accounted for in future conservation planning.

Keywords: germination percentage, germination rate, phytogeographic region, *Salvia spinosa, Salvia syriaca*

Appendix 16

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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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 tradeoff 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 1) invasive populations evolved lower resistance and higher performance, 2) this evolutionary change is indeed adaptive, and 3) there is a negative genetic correlation between performance and resistance (i.e. a tradeoff) in native and introduced individuals. Moreover, 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 ʻanimal modelsʼ that account for population co-ancestry to quantify the amount of variance in traits explained by non-adaptive versus 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 versus 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 tradeoff 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 tradeoff, and that various selective agents (including resource availability) interact in shaping both traits and in weakening negative genetic correlations in the invaded habitat.