In Search of Similarities in Invasive Plant Species - Comparing Native and Invasive Populations of Six Clonal Plant Species in Germany and New Zealand

Kumulative Dissertation

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Q: What are the characteristics of a good invader?

A: It depends.

Q: Depends on what?

A: That depends too!

Biological invasion has become one of those rare themes so profound in its implications and scope that it cuts a broad path across the academic disciplines. From genes to ecosystems and economics and law, species incursions have confronted the global community with a most transcendent Gordian knot.

- ***James Drake***
Conceptual Ecology and Invasion Biology: Reciprocal Approaches to Nature

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Nomenclature

DE, GER	Germany
EICA	Evolution of increased competitive ability hypothesis
ERH	Enemy release hypothesis
GxE	Genotype-by-environment
LDMC	Leaf dry matter content
NZ	New Zealand
PSII	Photosystem II
ROS	Reactive oxygen species
SLA	Specific leaf area
UV-B	Ultraviolet-B radiation, 315 nm - 280 nm

Summary

Humans have introduced non-native species into almost every corner of the world. These, often invasive, alien species have caused severely negative ecological and economical consequences and are regarded to be one of the most problematic aspects of human caused global environmental change. In an attempt to explain why some species become invasive while others do not, invasion science could link some traits to the invasiveness of alien plant species. Clonal growth is such a beneficial trait as it contributes to resource foraging and habitat exploration, and indeed, many invasive plant species possess that ability. Notwithstanding, although the research efforts in invasions science have substantially increased during the last decades, there remains a clear need for further studies that investigate the specific contributions of different types of clonal growth to invasion success and that lead to a better understanding of invasion processes.

Biological invasions are often viewed as "natural experiments" that can provide insights into fundamental ecological processes. Since alien species are often exposed to new environmental conditions, they are also subjected to a different set of biotic (e.g. herbivory) and abiotic (e.g. UV-B radiation) environmental filters. These factors may alter the phenotype of plants but can also act as drivers for natural selection processes, eventually leading to alien populations that are distinctly different in comparison to native populations. Studies comparing native and alien populations can help to determine if these differences are based on phenotypic plasticity or evolutionary processes.

This thesis investigates the invasion of six clonal growing plant species in New Zealand: *Achillea millefolium* L., *Hieracium pilosella* L., *Lotus pedunculatus* Cav., *Leucanthemum vulgare* Lam., *Prunella vulgaris* L. and *Hypericum perforatum* L. These are all herbaceous, perennial grassland species native to Germany, that grow different types of clonal organs and that are of different invasive status in New Zealand. This thesis combines four comparisons of native (German) and alien (New Zealand) populations. The studies include a biogeographical multi-species comparison of field populations, a multi-species common garden experiment, a germination experiment including three study species and a UV-B experiment focusing on one species.

The outcomes of these studies show that the six investigated species present a current ecological threat to the alien range in New Zealand by showing distinctly different, often dominating population structures and by exhibiting higher clonal growth in the field. When grown from seeds, alien plants were less tolerant to simulated herbivory on clonal organs but the individual plant performance was not consistent with field observations. The germination experiment uncovered higher germination rates in alien populations of

three species in medium temperature conditions as well as changes in temporal development patterns. In another growth chamber experiment, *Hieracium pilosella* responded to increased UV-B intensities with high phenotypic plasticity and increased the length of foliar hairs. These physiological responses possibly increase the protection of leaf tissues from radiation and occurred regardless of the plant's origin.

From the biogeographical field comparison, this thesis concludes that multiple measures of plant performance applied at different spatial scales should be used when comparing native and alien populations of clonal species. As a practical recommendation, the measuring of population crowdedness is suggested to provide a quick and reliable method to uncover population differences between alien and native ranges. The outcomes of the common garden experiment indicate that local adaptation and contemporary evolution might be responsible for the observed lower tolerance of alien plants to simulated herbivory on clonal organs. In case of the germination and UV-B experiments, alternative explanations such as phenotypic plasticity or maternal effects are more likely to be the source of different responses. Overall, the inconsistencies in individual plant performance between field and common environment studies, emphasise the importance of the local environment when trying to fully understand patterns and processes involved during invasions. Through the different responses found for different types of clonal growth (e.g. guerrilla or phalanx forms), this thesis also emphasises the need to more explicitly address clonal growth in future studies in invasion science.

Zusammenfassung

In fast jedem Winkel der Welt wurden durch menschliche Aktivitäten nicht heimische Arten eingeschleppt. Diese, oft invasiven, gebietsfremden Arten haben bereits schwerwiegende, negative ökologische und ökonomische Konsequenzen hervorgerufen und gelten als einer der problematischsten Aspekte der vom Menschen verursachten globalen Umweltveränderungen. Um zu klären, warum manche Arten invasiv werden und andere nicht, konnte die Invasionswissenschaft einige Merkmale ausmachen, die mit der Invasivität gebietsfremder Pflanzenarten in Verbindung stehen. Klonales Wachstum ist solch ein nützliches Merkmal, da es zur Nährstoffaufnahme und Habitat-Exploration beiträgt. Tatsächlich besitzen viele invasive Pflanzenarten diese Fähigkeit. Obwohl die Forschungsanstrengungen in den Invasionswissenschaften in den letzten Jahrzehnten erheblich zugenommen haben, besteht weiterhin ein Bedarf an Studien, die zu einem besseren Verständnis von Invasionsprozessen führen und beipielsweise die spezifischen Beiträge verschiedener Typen von klonalem Wachstum zu Invasionserfolgen untersuchen.

Biologische Invasionen werden oft als "natürliche Experimente" angesehen, die Einblicke in grundlegende ökologische Prozesse geben können. Da gebietsfremde Arten häufig unter neuen Umweltbedingungen wachsen, werden sie auch anderen biotischen (z. B. Herbivorie) und abiotischen (z. B. UV-B-Strahlung) Umweltfiltern ausgesetzt. Diese Faktoren können einerseits den Phänotyp der Pflanzen verändern, können andererseits aber auch als Treiber für natürliche Selektionsprozesse wirken. Dies kann schließlich zu gebietsfremden Populationen führen, die sich von einheimischen Populationen deutlich unterscheiden. Studien, die solche einheimischen und gebietsfremden Populationen vergleichen, können feststellen, ob diese Unterschiede auf phänotypischer Plastizität oder evolutionären Prozessen beruhen.

Diese Dissertation untersucht die Invasion von sechs klonal wachsenden Pflanzenarten in Neuseeland: *Achillea millefolium* L., *Hieracium pilosella* L., *Lotus pedunculatus* Cav., *Leucanthemum vulgare* Lam., *Prunella vulgaris* L. und *Hypericum perforatum* L. Bei diesen Arten handelt es sich um krautige, mehrjährige, in Deutschland heimische Graslandarten, die verschiedene Typen klonaler Organe bilden und in Neuseeland einen unterschiedlichen invasiven Status haben. Diese Dissertation setzt sich aus vier Vergleichen einheimischer (deutscher) und gebietsfremder (neuseeländischer) Populationen zusammen. Die Studien beinhalten einen biogeografischen Vergleich von Feldpopulationen, einen *Common-Garden* Versuch, ein Keimungsexperiment sowie ein UV-B-Experiment.

Die Ergebnisse dieser Arbeit zeigen, dass die sechs untersuchten Arten eine aktuelle ökologische Bedrohung in Neuseeland darstellen, indem sie im Vergleich zu heimischen

Populationen deutlich unterschiedliche, oft dominierende Populationsstrukturen aufweisen und höheres klonales Wachstum zeigen. Im direkten experimentellen Vergleich waren gebietsfremde Pflanzen weniger tolerant gegenüber simulierter Herbivorie an klonalen Organen als native Pflanzen. Das individuelle Pflanzenwachstum im *Common-Garden* Versuch stimmte jedoch in vielen Fällen nicht mit den Feldbeobachtungen überein. Das Keimungsexperiment zeigte höhere Keimungsraten gebietsfremder Populationen von drei Arten bei mittleren Temperaturbedingungen und Veränderungen in den zeitlichen Entwicklungsmustern der Keimlinge. In einem weiteren Wachstumskammerexperiment reagierte *Hieracium pilosella* auf erhöhte UV-B-Intensitäten mit hoher phänotypischer Plastizität und bildete verlängerte Haare auf der Blattoberseite. Dies geschah ungeachtet der Herkunft der Pflanzen und erhöht möglicherweise den Schutz des Blattgewebes vor UV-B Strahlung.

Aus dem biogeographischen Feldvergleich schließt diese Arbeit, dass beim Vergleich von einheimischen und gebietsfremden Populationen klonaler Arten mehrere Messungen des Pflanzenwachstums auf verschiedenen räumlichen Skalen verwendet werden sollten. Als praktische Empfehlung wird die Messung der "population crowdedness" als schnelle und zuverlässige Methode zur Ermittlung von Populationsunterschieden zwischen gebietsfremden und nativen Regionen vorgeschlagen. Die Ergebnisse des *Common-Garden* Versuches weisen darauf hin, dass lokale Anpassung und evolutionäre Prozesse für die geringere Toleranz von gebietsfremden Pflanzen gegenüber simulierter Herbivorie an klonalen Organen verantwortlich sein könnten. Im Falle der Ergebnisse des Keimungs- und UV-B-Experiments sind alternative Erklärungen wie hohe phänotypische Plastizität oder maternale Effekte eher als Quelle beobachteter Unterschiede anzusehen. Insgesamt heben die Unstimmigkeiten im individuellen Pflanzenwachstum zwischen der Feldstudie und den experimentellen Untersuchungen die Bedeutung der lokalen Umweltbedingungen hervor. Die Ergebnisse dieser Arbeit, die für unterschiedliche Typen von klonalem Wachstum gefunden wurden (z. B. Guerilla- oder Phalanx-Formen), betonen auch die Notwendigkeit, klonales Wachstum in zukünftigen Studien eingehender zu untersuchen.

1 General Introduction

1.1 Biological invasions: research motivation and terminology

Research on biological invasions dates back to the 1950s when Charles Elton's book "The Ecology of Invasions by Animals and Plants" laid the foundations for the discipline of invasion science (Elton, 1958). Since then, and increasingly over the last three decades, invasion science flourished as a field of study (Richardson, 2011; Richardson & Ricciardi, 2013), but it has also become fragmented into smaller sub-disciplines that focus on specific species groups or regions. Therefore, invasion science has developed a large and partly redundant body of theory (Catford *et al.*, 2009), terminology (Davis & Thompson, 2001; Colautti & MacIsaac, 2004) and concept (Williamson & Fitter, 1996a; Richardson *et al.*, 2000; Downey & Richardson, 2016).

This thesis adopts the terminology suggested by Blackburn *et al.* (2011), who developed an attempt to unify the existing frameworks and terminologies (see Section1.2.1 and Figure 1.2.1 on page 19). This framework has become widely accepted in invasion science and has been modified by some authors to include aspects such as evolutionary processes (Zenni *et al.*, 2017) or natural range expansion (Hoffmann & Courchamp, 2016). According to the unified framework, for species that have been translocated outside their native range, the general term *alien* is used in this thesis. For species that are able to spread in their alien range without the help of human interference, which is the case for all species investigated in this thesis, the term *invasive* is used as well.

The wealth in theory and conceptualisations in invasion science underlines the efforts spent on understanding when and where biological invasions occur, which factors influence them and how they can be controlled or prevented. For example, we do know that only about 0.1 percent of all species that were introduced to a new area can establish themselves, start to spread and eventually become pests ("tens rule"; Williamson & Fitter, 1996b). Many species undergo a "lag phase" upon introduction before they spread and this phase varies considerably in length between species (e.g. Crooks, 2005; Hui & Richardson, 2017). We also know that some traits enhance the possibility to become invasive (e.g. clonal growth, Baker, 1974; prolific seed production, Richardson & Pyšek, 2006). Despite this knowledge, the question about *which species* these rules apply to remains largely open (Heger, 2016).

The main motivation behind the existing body of research in invasion science has likely been drawn from the impact invasive species have on biodiversity and human well-being

(e.g. Downey & Richardson, 2016; Walsh *et al.*, 2016). In fact, invasive alien species are one of the most important aspects of human caused global environmental change and they can lead to severely negative ecological (e.g. Palumbi, 2001; Butchart *et al.*, 2010; McGeoch *et al.*, 2010; Doherty *et al.*, 2016) and economical consequences (e.g. Vitousek *et al.*, 1996, 1997; Paini *et al.*, 2016).

While substantial parts of the natural world have been irrevocably lost through human activities, there are options to alter the velocity and impact of ongoing global change processes, such as are explored, for example, by international initiatives to mitigate climate change (e.g. Intergovernmental Panel on Climate Change, 2015). Alien plant species offer another opportunity to take action, given that their introduction into or spread within alien regions may be controlled (for possible directions see Hulme, 2015; Vanderhoeven *et al.*, 2017). However, the total eradication of alien species or the successful suppression of all new introductions remain unrealistic goals in most cases (but see Jones *et al.*, 2016, for successful mammalian eradication examples) and compromises and prioritisations have to be made (McGeoch *et al.*, 2016). In order to make such decisions meaningful and to be able to prevent, eradicate and control invasive organisms in the future, invasion science seeks for a better understanding of the processes involved during biological invasions (e.g. McLaughlan *et al.*, 2014).

Biological invasions are multifaceted processes and unravelling the exact impacts of alien species has proven to be difficult, especially for plants. Therefore, this thesis aims at broadening the understanding about how the invasion process of a set of plant species takes place and what environmental or ecological factors might be of importance for it. Based on the outcomes of the conducted studies, this thesis also explores whether generalisations for these and similar species are warranted.

1.2 Concepts and approaches in invasion science

1.2.1 The invasion process: a series of stages and environmental filters

According to Blackburn *et al.* (2011), the invasion process can be described as a series of stages that are separated by barriers (such as geography, survival, dispersal) which need to be overcome by a species in order to reach the next stage (Figure 1.2.1 on the next page). At the very beginning of the invasion process stands the accidental or intentional translocation of the species outside of its native range. This simply means that a native species is transformed into an alien species through human interference (stage "transport" in Figure 1.2.1). Such introduction events follow the fundamental principles of natural extra-range dispersal (Wilson *et al.*, 2009) but typically lack the potential for increased gene flow and the dependency on specific adaptations to dispersal pathways (e.g. wind, water, animals).

These early stages of biological invasions are largely dependent on human activities (e.g. the transportation of propagules along trade routes or the selection of ornamental

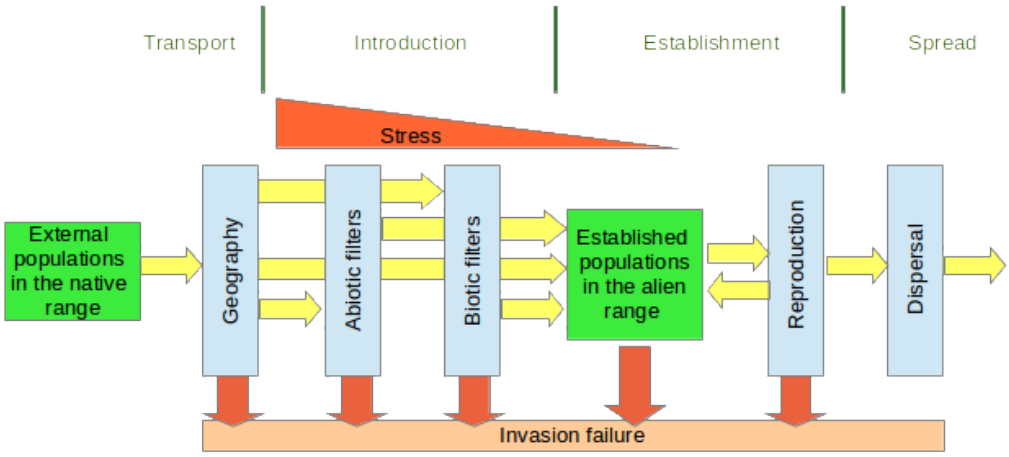

Figure 1.2.1: Schematic diagram describing the invasion process as a series of stages in which specific barriers or environmental filters (blue boxes) need to be overcome in order to reach the next stage (top row). Native source populations and established alien populations are depicted as green boxes (adapted from Fattorini & Halle, 2004; Blackburn *et al.*, 2011).

species), and thus, especially the "transport" stage can be influenced by legislation and policy (Sheppard *et al.*, 2016; Hulme *et al.*, 2017). However, during later stages of invasion (i.e. "introduction", "establishment" and "spread") ecological processes and environmental interactions are becoming more important and the potential impact of regulations on the success of invasions decreases. Notwithstanding, investigating these later stages of invasions may provide useful insights into fundamental ecological processes which may help to understand biological invasions from a scientific perspective.

The concept of environmental filters that shape community assembly in plant ecology dates back several decades (Mueller-Dombois & Ellenberg, 1974; Kraft *et al.*, 2015). According to this concept, processes like long range dispersal events will allow species to enter the established species pool of a local habitat or community after passing through a set of abiotic and biotic filters which are specific to that habitat (Fattorini & Halle, 2004). This concept is applicable in the context of biological invasions and abiotic and biotic filters, such as climate or competition, fit well into the unified framework for invasion ecology (Figure 1.2.1). Such filters may be regarded as barriers (sensu Blackburn et al., 2011) encountered during the introduction and establishment stages of an invasion event. If a species is able to "skip" an environmental filter or barrier such as herbivory, it may encounter more favourable conditions in the alien range.

However, the environmental filter concept adds another element: a gradient of stress which is getting lower with each filter a species passes. This is crucial when trying to understand an often ignored aspect in invasion biology: failed invasions (but see Zenni & Nuñez, 2013; Lavoie *et al.*, 2016). Theoretically, in most cases of failed invasions the benefits, if any, experienced through some kind of release will have been "outweighed" by

the stress caused by filters the species were unable to pass ("increase of constraints" in the sense of Erfmeier, 2013). Surprisingly, the role of environmental filters has received relatively little attention in invasion science, and if so mostly indirectly. However, in order to address one of the fundamental questions in invasion biology (i.e. "How do species become invasive?") it is crucial to investigate alien species of different status as well as failed invasions in connection with environmental filters they were or were not able to pass.

1.2.2 Biogeographical comparisons: collecting data from natural experiments

The understanding of invasions as "natural experiments" dates back to the early 20th century (Grinnell, 1919; Sax *et al.*, 2007) and at the very heart of this idea lies the assumption that species are exposed to new environmental conditions through the translocation into an area outside of their native range. However, biological invasions are constantly changing processes that extend over long periods of time (Strayer *et al.*, 2006), and often, very little information on the geographical origin and the introduction time of an alien species is available (but see Dray *et al.*, 2006; Zenni, 2014). This lack of knowledge on, as it were, "parameters" of these "natural experiments" can make it quite difficult, for example, to identify in which stage of the invasion process a species is currently in (Figure 1.2.1 on the preceding page).

Once introduced outside its native range, a species is exposed to a new environment, which presents itself as a different set of environmental filters or barriers (Chapter 1.2.1 on page 18). Studies in invasion science can investigate how plants have responded over long periods of time to these changed conditions and, this way, can enlighten what lies in the past of these alien species. In this context, it is of fundamental importance to comprehensively observe and describe the current state of alien species through monitoring their populations and spread. One way to appropriately do that is by conducting biogeographical comparisons (sometimes called transcontinental comparisons e.g. Shah *et al.*, 2014), which take into account a species' native *and* alien populations (e.g. Hejda *et al.*, 2017; Nielsen *et al.*, 2017). By comparing, for example, the population density or reproductive success between native and alien regions, possible differences can be effectively uncovered and described. The outcomes of such descriptive comparisons may indicate that the responses of a species to a new environment differ from those at home or hint at underlying changes that could have occurred in the alien populations and that may be good candidates for further experimental testing.

Furthermore, biogeographical comparisons allow to rigorously test long standing assumptions and hypothesis that have been developed in invasion science (e.g. Parker *et al.*, 2013). For example, it has been commonly assumed that alien plant species grow at much larger densities and have greater individual performance in the alien range. However, for a long time only few studies have actually validated these assumptions by quantitatively

comparing species populations in both ranges (but see Hierro *et al.*, 2005). Over the last decade, more and more studies have conducted biogeographical field comparisons (e.g. Hejda *et al.*, 2017; Nielsen *et al.*, 2017). Notwithstanding, up until today the overall outcomes of these studies remain ambiguous, with several species revealing higher population densities in the alien range (e.g. Alba & Hufbauer, 2012; Callaway *et al.*, 2012; Moroney & Rundel, 2013; Pal *et al.*, 2015) while others do not (e.g. Firn *et al.*, 2011; Kwong *et al.*, 2017). Some studies have even found contradictory results in biogeographical comparisons for the very same species (e.g. *Achillea millefolium;* Beckmann *et al.* 2009; Firn *et al.* 2011). Therefore, there remains a clear need for more biogeographical comparisons that measure population performance under field conditions in the native and alien range. Describing the *status quo* will allow for a more comprehensive identification of a species' status and may help detect real-world differences in performances.

1.2.3 Clonal growth in invasion science

Trying to understand certain aspects and principles of invasions, researchers have often taken a trait-centred perspective, focusing on specific abilities and traits of species (e.g., Pyšek & Richardson, 2007; Küster *et al.*, 2009). However, attempts to detect common traits among invasive plant species have led to the conclusion that there are no "invasive traits" per se which could fully explain plant species invasions (Hulme, 2008b; van Kleunen *et al.*, 2010a). Nevertheless, some features, that have more general implications, could be identified. For example, plant traits associated with reproduction seem to be of vital importance for successful plant invasions, meaning that species that reproduce fast and/or clonal are much more likely to develop into invasives compared to species that do not (e.g. Speek *et al.*, 2011).

The role of clonality during invasions has been discussed for decades (Baker, 1974; Sakai *et al.*, 2001; Yu *et al.*, 2016), and indeed, many invasive plant species possess that ability (Kolar & Lodge, 2001; Liu *et al.*, 2006). Organs of clonal growth (in this thesis the term "clonal organs" is used) allow plants to continuously explore habitat space that might be temporally unavailable to seeds or adult plants (de Kroon & Hutchings, 1995; Givnish, 2002). Thereby, clonality contributes to resource foraging (e.g. Roiloa *et al.*, 2016), especially in disturbed habitats of heterogeneous resource availability (Baruch & Gómez, 1996; Rejmánek & Richardson, 1996) where ramets are able to acquire and share resources through clonal integration (van Kleunen *et al.*, 2000). Such conditions have been suggested to be common during the early stages of invasions (Keser *et al.*, 2014).

In general, clonal growth appears to be associated with the invasiveness of alien plant species (Song *et al.*, 2013; Roiloa *et al.*, 2016). More specifically, traits and abilities associated with clonal growth, such as clonal integration, division of labour, resource sharing (You *et al.*, 2014; Elgersma *et al.*, 2015; Liu *et al.*, 2016; Roiloa *et al.*, 2016), or the ability to selectively position ramets (Keser *et al.*, 2014; Waters & Watson, 2015) are suggested to contribute to plant invasiveness.

Although clonal growth has been investigated as a relevant trait for successful plant invasions for a long time, the interplay of clonal growth with other potentially interacting factors such as herbivory, have yet to be addressed.

1.2.4 Adaptation and evolutionary processes during biological invasions

Similar to clonal growth, evolutionary processes have received much attention in invasion science and there is extensive evidence that such processes have led to alien populations that are phenotypically (e.g. Xu *et al.*, 2010), ecologically (e.g. Colautti & Barrett, 2013) and/or genetically (e.g. Chun *et al.*, 2011) different from native populations. In an attempt to place evolutionary aspects of the invasion process within the widely accepted unified framework for biological invasion (Blackburn *et al.*, 2011), Zenni *et al.* (2017) recently identified the most important evolutionary mechanisms for tree invasions. Thereby, the authors developed an extended conceptualisation of the unified framework for plant invasions (Blackburn *et al.*, 2011) that is, in large parts, applicable to plant invasions in general.

According to Zenni *et al.* (2017), pre-introduction evolutionary history in the native range often provides the basis for successful invasions through the evolution of local adaptations, symbiotic interactions (Zenni *et al.*, 2014) or large phenotypic plasticity (Lamarque *et al.*, 2015). The ability to respond in a plastic manner to a new environment allows species to express beneficial phenotypes in a wider set of environmental conditions (e.g. Donohue *et al.*, 2001; Richards *et al.*, 2006; Ghalambor *et al.*, 2007) and the particular importance of phenotypic plasticity in plant invasions was emphasised in several studies (e.g. Geng *et al.*, 2007; Ward *et al.*, 2008; Riis *et al.*, 2010).

During the transport, introduction and establishment stages of biological invasion, other evolutionary processes like sampling and founder effects come into play as filters (e.g. Kanarek & Webb, 2010; Schrieber & Lachmuth, 2017). Here it is crucial to understand whether the transportation into the alien range has been accidental or on purpose and if a selection for certain traits (e.g. for ornamental or cropping purposes) or genotype-by-environment (GxE) interactions have been made (e.g. Corliss & Sultan, 2016). There are numerous examples for silvicultural species that have undergone active selection of genotypes suitable for certain climatic conditions (e.g. Isaac-Renton *et al.*, 2014; Rieksts-Riekstins *et al.*, 2014). Furthermore, these filters limit the genetic diversity available in the alien range through the number of introduction events and the life-history of the species. However, while low genetic diversity can be a disadvantage for the establishment of populations in the alien range (Keller & Taylor, 2010) it is, by no means, necessarily a hindrance as successful invasions by single genotypes have shown (Hardesty *et al.*, 2012; Bhattarai *et al.*, 2017).

Once populations are established in the alien range, the directional selection of well adapted phenotypes might occur and the terms "rapid evolution" or "contemporary evolution" have been coined to describe such evolutionary processes (see Yoshida *et al.*, 2007).

Rapid evolution is considered to generally support invasions (Parker *et al.*, 2003) and has been observed in several invasive species (Hendry & Kinnison, 1999; Thompson, 1998; Erfmeier *et al.*, 2010; Schrieber *et al.*, 2017). However, recent advances have revealed that even epigenetic effects (i.e. inherited, non-DNA caused variation in gene expression; Richards, 2008) and second genomes (i.e. the genotypes of closely associated or symbiotic organisms; Crous *et al.*, 2017) may play important roles during invasions, but also add further levels of complexity.

Herbivory as an evolutionary driver during invasions is one of the most studied research topics in plant invasion science today (e.g. Bazzaz *et al.*, 1987; Baldwin, 1998; Liao *et al.*, 2016; Stastny & Sargent, 2017). Plant herbivore interactions have brought forward many hypotheses and frameworks (see Catford *et al.*, 2009; Thorpe *et al.*, 2011), with the enemy release hypothesis (ERH, Keane & Crawley, 2002), and the evolution of increased competitive ability hypothesis (EICA, Blossey & Nötzold, 1995) being the foremost addressed. It has even been demonstrated that release from selection pressure by insect herbivores can drive real-time evolution, detectable through molecular evidence within only a few generations (Agrawal *et al.*, 2012). While the release from herbivory might be the most obvious and well documented driver of rapid evolution, other kinds of release may act in a similar way. In a broader sense, a *release from constraints* (Erfmeier, 2013) may yield direct benefits but can also drive rapid evolution that ultimately allows a species to spread in the alien range.

Disentangling the potential contribution of evolutionary processes to invasion success has proven to be difficult (Dlugosch *et al.*, 2015). In many cases it remains unclear whether some abilities (e.g. phenotypic plasticity) are the outcome or the driver of selection processes in the alien range and it seems to be the most appropriate way to address such questions on a case-by-case basis. Therefore, more studies investigating aspects of evolutionary processes in the context of invasions are urgently needed.

1.2.5 Advances in multi-species studies in invasion science

The attempts to formulate and test hypotheses in invasion science vary greatly between individual studies. The majority of invasion research has focused on single species (e.g. Ebeling *et al.*, 2011; Hirsch *et al.*, 2012; Rosche *et al.*, 2017) which has the advantage that specific mechanisms or concepts can be investigated with high precision (van Kleunen *et al.*, 2014). For example, the effects of specific drivers of selection (e.g. herbivory; Bossdorf *et al.*, 2004; Eckberg *et al.*, 2012), responses at the population level (e.g. population genetics; Zimmermann *et al.*, 2010; Erfmeier *et al.*, 2013) or the effects of specific traits (e.g. germination; Erfmeier & Bruelheide, 2005; Perglova *et al.*, 2009) have been extensively explored in single species studies. However, in order to identify patterns *across species*, studies are needed that comparatively investigate multiple species.

A number of multi-species studies exist that either use species databases (e.g. the TRY database; Kattge *et al.*, 2011) or compare native and alien flora information to investigate

traits for which information is readily available (Thébaud & Simberloff, 2001; Prinzing *et al.*, 2002; van Kleunen *et al.*, 2007; Pyšek *et al.*, 2009a; Razanajatovo *et al.*, 2016). Furthermore, meta-analyses have become an important tool for synthesising patterns across invasive plant species (e.g. Song *et al.*, 2013; Oduor *et al.*, 2016). While these non-experimental multi-species studies provide valuable insights into biological invasions on a very broad scale and may help to formulate predictions, they lack information on whether the investigated species show *actual* similarities or differences under common environmental conditions.

Experimental multi-species studies, on the other hand, have greater potential to reveal such differences and allow for making generalisations (Kempel *et al.*, 2013; van Kleunen *et al.*, 2014) especially if they are able to detect similar patterns for a set of studied species (e.g. van Kleunen & Johnson, 2007; Schlaepfer *et al.*, 2010; Firn *et al.*, 2011; Erskine-Ogden *et al.*, 2016). For example, Schlaepfer *et al.* (2010) investigated the germination behaviour of 14 congeneric alien plant species pairs, that were all introduced to North America and half of them are being regarded as invasive. The authors conclude that, among other traits that confer high plant performance, fast germination may provide a preadaptation for species to become invasive. This way, Schlaepfer *et al.* (2010) reflect the findings of single species studies that also found increased or faster germination of alien origins (e.g. Hierro *et al.*, 2009; Perglova *et al.*, 2009), but were also able to draw the conclusion that these results provide some generality.

Experimental multi-species studies allow to address complex hypotheses and research questions and, thus, are an important step towards a more comprehensive understanding of biological invasions. For example, questions on the fundamental differences between alien and native species may be addressed using multi-species experiments (e.g. van Kleunen *et al.*, 2014). In a recent greenhouse experiment Liu & van Kleunen (2017) investigated whether or not common species may benefit more from environmental fluctuations in comparison to rare species. The authors found that, regardless of their rarity, alien species benefited most from nutrient fluctuations. Another recent multi-species study investigated the potential success of non-naturalized alien garden-plant species to invade native grasslands under simulated climate change conditions (Haeuser *et al.*, 2017). The authors and conclude that some alien plants may have greater colonisation success under a warmer climate and link this pattern to life-form and seed size.

These examples show that multi-species experiments can provide answers to questions concerning general patterns, rules and mechanisms in invasion science. Therefore, in order to allow for generalisations and to advance the current knowledge on mechanisms involved in the invasion process, further multi-species studies that investigate differences and similarities among several alien species are needed. Such upcoming studies should be combined with transcontinental comparisons and will be particularly meaningful if they are accompanied by single-species studies that focus on specific traits.

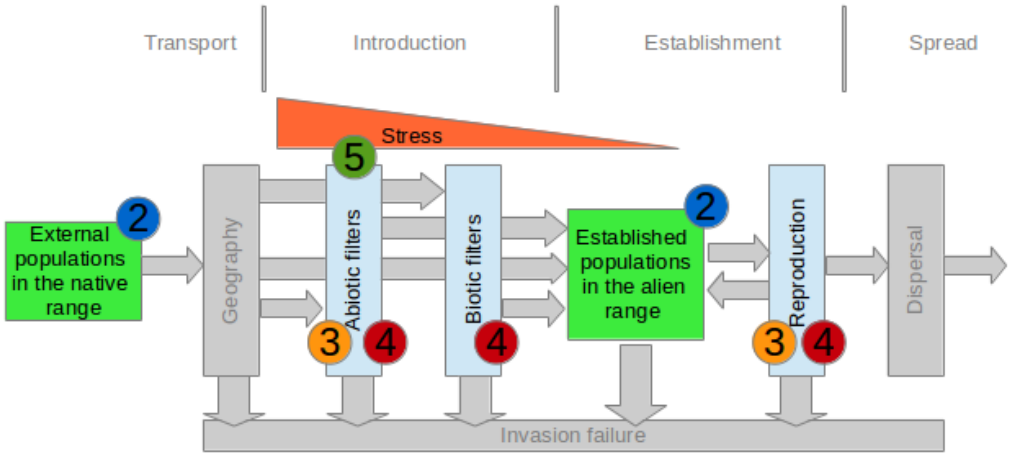

Figure 1.3.1: Schematic diagram describing the relation of the four main chapters of this thesis within the conceptual framework as outlined in Figure 1.2.1 on page 19. The invasion process is depicted as a series barriers or environmental filters which need to be overcome during the invasion process. Native source populations and established alien populations are shown as green boxes. The numbers in circles refer to the individual chapters of this thesis.

1.3 Structure and objectives of this thesis

This thesis aims at contributing to a better understanding about the mechanisms involved during the invasion of six study species in New Zealand. In doing so, this thesis follows the idea that biological invasions are "natural experiments" that allow to investigate ecological and evolutionary processes at a biogeographical scale. By focusing on a group of clonal growing species that possess different clonal growth strategies, this thesis addresses an often mentioned suggestion that the ability of clonal growth is beneficial for a species to become invasive in the first place (Baker, 1974; Sakai *et al.*, 2001; Perglova *et al.*, 2009).

The presented thesis combines several methods and approaches in an attempt to address closely connected aspects of biological invasions:

Chapter 2 provides a **biogeographical multi-species comparison** between the native and alien range investigating population structure in the field. As a starting point and the basis to test further hypotheses, Chapter 2 (Page 39) identifies whether the six study species differ in their performance in native and invasive populations. The comparative field study describes how the population structures, growth and clonal reproduction occur under natural conditions and examines the species' status in New Zealand. Furthermore, Chapter 2 addresses whether differences in performance could be detected at multiple scales, and whether the investigation of population structures at the

neighbourhood scale would allow to identify similarities across species.

Chapter 3 addresses potential **adaptations to differences in germination conditions** that three of the study species might have encountered after introduction to New Zealand. In a multi-species growth chamber experiment the germination performance is compared between native and alien populations. In Chapter 3 (Page 53) it was specifically tested if non-native populations are characterised by different germination temperature requirements and higher and/or faster germination rates which could provide competitive advantages during the expansion of the species' ranges into new environments.

Chapter 4 investigates the potential **release from herbivory on clonal organs** and the importance of **clonal growth as a foraging behaviour**. Chapter 4 (Page 63) describes the results of a common-garden experiment conducted with all six study species and combining a nutrient treatment with simulated herbivory on clonal organs. Origin-dependent differences in sexual reproduction, plant growth and the production of clonal organs were investigated to test whether reduced tolerance to herbivory on organs of clonal growth is identifiable in alien genotypes.

Chapter 5 investigates the potential role of **UV-B radiation as an environmental filter** during biological invasions. Chapter 5 (Page 81) contains a growth chamber experiment and focuses on one species, *Hieracium pilosella*. This single species study addresses phenotypic plasticity and adaptation of leaf traits to higher levels UV-B radiation, which this species is exposed to in its alien range in New Zealand.

This thesis is concluded by a synthesis and outlook in Chapter 6 (Page 95).

1.4 Study species and study area

This thesis comprises a combination of multi- and single-species studies that have been conducted in naturally occouring field populations, common garden or growth chamber experiments. The studied species are *Achillea millefolium* L., *Hieracium pilosella* L., *Lotus pedunculatus* Cav., *Leucanthemum vulgare* Lam., *Prunella vulgaris* L. and *Hypericum perforatum* L. (see Table 1.4.1 for an overview of the study species).

Table 1.4.1: Overview of the study species. Information on range distribution refers to Rothmaler et al. (2005), time of first records in New Zealand (NZ) to Webb et al. (1988). Clonal growth syndrome combinations are given as the name and category number provided in the appendix of Klimeš et al. (1997), clonal growth type and lateral spread per year as given in the CLO-PLA database (Klimešova & De Bello 2009). Status in NZ as given in Howell (2008), numbers indicate the frequency of mentions in 13 checked weed lists therein.

	Achillea millefolium L.	*Hieracium pilosella* L.	*Hypericum perforatum* L.	*Leucanthemum vulgare* Cav.	*Lotus pedunculatus* Lam.	*Prunella vulgaris* L.
Native range	Europe, Siberia	Europe	Europe, Western Asia	Europe, Western Siberia	Eurasia	Eurasia
Introduced range	Americas, Australia, New Zealand	Americas, Australia, New Zealand, Southern Africa	Americas, Australia, New Zeeland	Americas, Australia, New Zealand	Americas, Australia, New Zealand	Americas, Australia, New Zealand
Clonal growth syndrome	*Aegopodium podagraria* (10), *Asperula odorata* (13)	*Fragaria vesca* (11), *Caltha palustris* (12)	*Rumex acetosella* (3)	*Rumex obtusifolius* (7), *Lycopodium annotinum* (5)	*Aegopodium podagraria* (10)	*Rumex obtusifolius* (7)
Clonal growth type	hypogeogenous stem (rhizome)	horizontal aboveground stem, epigeogenous stem	root-splitter, roots with adventitious buds	root-splitter, hypogeogenous stem (rhizome)	epigeogenous stem	horizontal aboveground stem
Lateral spread per year	> 25 cm	> 25 cm	> 25 cm	> 25 cm	1 - 25 cm	1 - 25 cm
First recorded in NZ	1867	1878	1869	1867	1867	1867
Status in NZ	naturalized (0)	invasive (7)	invasive (5)	naturalized (1)	invasive(8)	naturalized (1)

They were selected from a subset of 70 species that are all clonally growing, perennial,

Figure 1.4.1: Morphological characteristics of *Achillea millefolium* L. (drawing altered from Jäger & Werner, 1999)

herbaceous grassland species, native to Central Europe and introduced to the South Island of New Zealand where all fieldwork took place and all seeds used in the experiments were collected. The investigated species are of different invasive status in NZ, possess different types of clonal organs and are members of four different plant families. At the same time, these species are similar with respect to their traits and habitat preferences to a larger number of alien plant species present in NZ (see Section 1.4.2 on page 35 for further details). By including taxonomic and morphological differences among the study species and by comparing their native and alien populations, this thesis differs from studies such as Schlaepfer *et al.* (2010) that focus on taxonomically closely related species pairs.

The two study regions (Germany and New Zealand) provide the advantage of being situated on the Northern and the Southern Hemispheres and, therefore, being separated by large geographical distances. This makes natural range expansion of the species highly unlikely, while the exhibited climatic conditions are, to some extent, comparable. These conditions are also suitable for a large number of other native European plant species which have established wild populations throughout NZ. It is worth to note her that one environmental variable is distinctively different between Europe and the South Island of NZ: the intensity of ultraviolet-B radiation is about 50-60% higher in the study region on the Southern Hemisphere (see Figure 1.4.9 on page 37 and Section 5 on page 81 for further details). In order to account for some of the environmental variability that occurs along a latitudinal gradient, the locations of the populations used in this thesis were selected to cover similar geographic distances within both study regions (see Figure 1.4.8 on page 35).

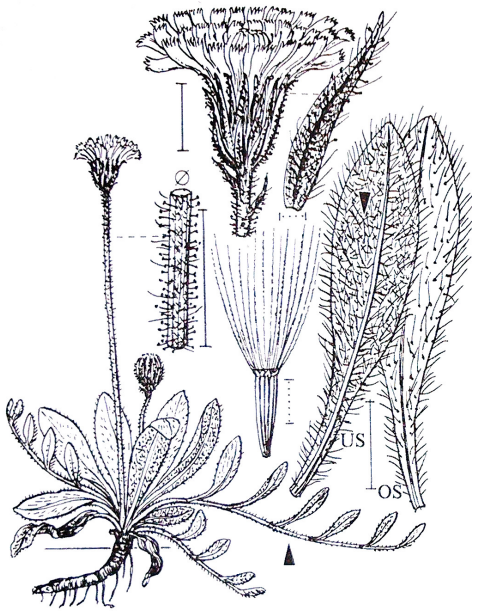

Figure 1.4.2: Morphological characteristics of *Hieracium pilosella* L. (drawing altered from Jäger & Werner, 1999)

1.4.1 Study species

Achillea millefolium L. (Common yarrow; Figures 1.4.1 on the preceding page) is a rhizomatous *Asteraceae* species that is widespread in the northern hemisphere. It is a drought tolerant perennial herb and grows on dry grasslands, along waysides, fresh meadows and pastures (Jäger & Werner, 2005a). *A. millefolium* can also been found in southern hemisphere countries including New Zealand and Australia, where it was introduced as a fodder plant and as an ornamental (Bourdot & Field, 1988). It was introduced to New Zealand in the mid-19th century (Webb *et al.*, 1988) and currently, it can be found throughout the country but it is more common in drier areas of the South Island where the species particularly grows in disturbed areas such as roadsides, lawns and pastures (e.g. Figure 1.4.7C on page 34). Although *A. millefolium* has been recognised as an alien species in many parts of the world, only rarely has it been studied as such, a notable exception being the works of Frances Johnston in the Kosciuszko National Park in the Australian Alps (e.g. Johnston & Johnston, 2004; Johnston, 2005; Johnston & Pickering, 2006).

The facultative apomict *Hieracium pilosella* L. (Mouse-ear hawkweed; *Asteraceae*; syn. *Pilosella officinarum*; Figure 1.4.2) is native to Europe and Northern Asia where it frequently occurs in dry grasslands, heathlands, open pine forests and along waysides (Jäger & Werner, 2005b). It has been introduced to North (Wilson *et al.*, 1997) and South America (Cipriotti *et al.*, 2010), New Zealand and Australia, where it has been successfully eradicated in Tasmania (Rudman & Goninon, 2002). In NZ it has been considered a "sleeper weed", as it was first recorded in the wild in 1878 (Webb *et al.*, 1988)

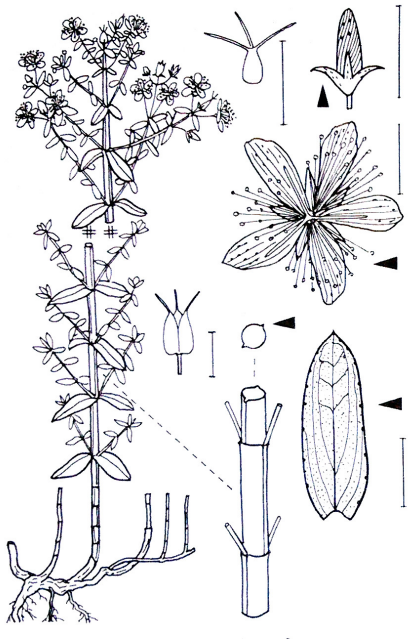

Figure 1.4.3: Morphological characteristics of *Hypericum perforatum* L., (drawing altered from Jäger & Werner, 1999)

but remained localised for around 80 years. After this "lag" phase the species suddenly increased its range (Groves, 2006). *Hieracium pilosella* has now spread and is a major invasive weed in in central and western regions of the North Island and can be found throughout the entire South Island where it is particularly frequent in eastern, dryer areas of the Southern Alps (e.g. Figure 1.4.7A and B on page 34). It infests native tussock grasslands, conservation areas as well as wastelands, pastures and areas along roadsides, commonly following rabbit grazing (Klöppel *et al.*, 2003; Groves, 2006). The plant has become an aggressive and troublesome weed and its invasion resulted in dramatic changes in native fescue grassland vegetation (Scott, 1984; Treskonova, 1991) by displacement of native species and forming of mono-specific patches through clonal growth (Norton *et al.*, 2006; Beckmann *et al.*, 2009). *Hieracium pilosella* affects soil properties and nutrient cycling in areas it inhabits (Saggar *et al.*, 1999; Knicker *et al.*, 2000; Beaumont *et al.*, 2009) and it is able to extract large proportions of moisture and nutrients from the surrounding soil, leaving drier and less favourable conditions for other species (McIntosh *et al.*, 1995). A study by Zidorn *et al.* (2005) has shown a positive correlation of concentrations of flavonoids and phenolic acids along an altitudinal gradient in NZ, arguing that this may be related to higher levels of UV-B radiation in higher altitudes. The systematics of the genus *Hieracium* is extremely complex, probably due to recent speciation, hybridization, polyploidy, and diverse reproductive strategies (Mráz & Szelag, 2004; Mraz *et al.*, 2007). In its native European range five cytopes of *Hieracium pilosella* have been identified, ranging from diploid to heptaploid, but the alien range is dominated by sexual tetraploids and asexual pentaploids (Trewick *et al.*, 2004). New Zealand populations are morphologically and genetically diverse, even though the initial introduction is thought

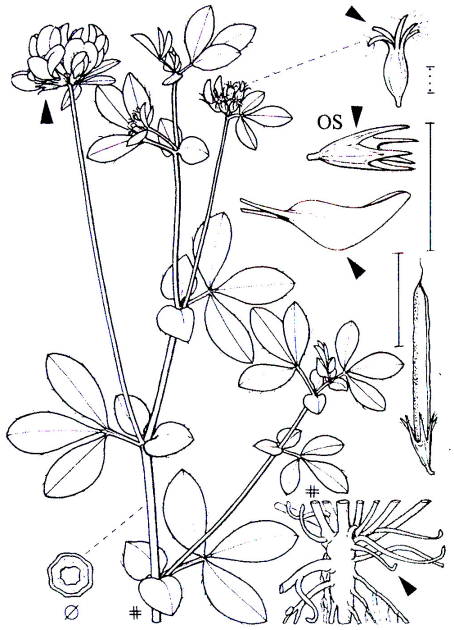

Figure 1.4.4: Morphological characteristics of *Lotus pedunculatus* Lam., (drawing altered from Jäger & Werner, 1999)

to have been by facultative apomictic tetra-, penta-, and hexaploids (Chapman *et al.*, 2003). Sexual plants have also been observed occasionally in NZ (Chapman & Bicknell, 2000; Houliston & Chapman, 2004). Similarly, the reproductive system of *Hieracium pilosella* in another part of its alien range in Patagonia was described as apomictic with a low degree of residual sexuality (Krahulec & Krahulcova, 2011). Hybrids with a related taxon have also occurred in NZ at least three times (Trewick *et al.*, 2004). Following Bräutigam & Greuter (2007), in Chapter 2 the terminology used in NZ is adopted and the name *Pilosella officinarum* is used for this species. Because of its immense impact on the native biodiversity in NZ (Moen & Meurk, 2001; Day & Buckley, 2011, 2013) and its unique set of leaf traits (see Section 5.3.1 on page 85 for details), *Hieracium pilosella* was chosen for an experimental study conducted in Chapter 5 and is, therefore, the only species addressed in all four chapters of this thesis.

Hypericum perforatum L. (St. John's Wort; Figure 1.4.3 on the facing page) is an erect, herbaceous plant of the *Hypericaceae* family. As a common rhizomatous perennial, it is native to Eurasia and Northern Africa where it grows in dry grasslands, heathlands, dry to fresh ruderal sites such as waysides or wastelands, outskirts of forests and forest clearings (Jäger & Werner, 2005b). *Hypericum perforatum* has been introduced to many regions around the globe including the Americas, Australia, Japan, New Zealand and South Africa. The species is adapted to a wide range of environmental conditions in its native and introduced range (Maron *et al.*, 2004b). *Hypericum perforatum* can grow on a variety of soils, from dry, rocky, shallow soils, to deep fertile soils, with it performing best in regions with greater than 760mm of precipitation a year (Buckley *et al.*, 2003a; Figure 1.4.7D on page 34). However, it is able to tolerate drought and disturbance events

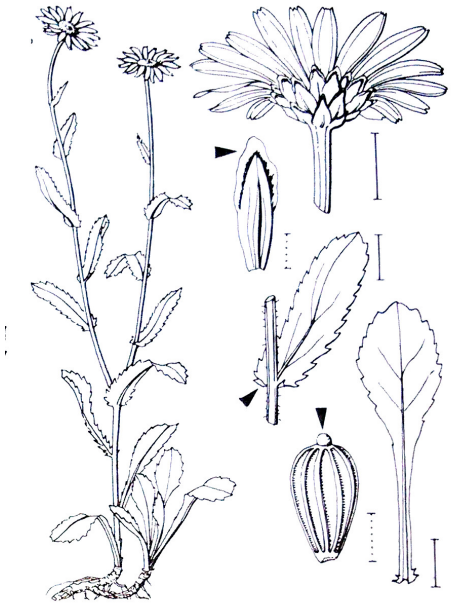

Figure 1.4.5: Morphological characteristics of *Leucanthemum vulgare* Cav., (drawing altered from Jäger & Werner, 1999)

by storing reserves in its roots (Buckley *et al.*, 2003a). *Hypericum perforatum* has been extensively studied as an invasive species in North America by the research groups of John Maron and Montserrat Vilà who have found support for the enemy release hypothesis (Vilà *et al.*, 2005) but not for the EICA hypothesis (Vilà *et al.*, 2003). The production of compounds toxic to pathogens is lower in North American populations which, therefore, have lower enemy resistance (Maron *et al.*, 2007, 2004a). *Hypericum perforatum* was first recorded in New Zealand in 1869 (Webb *et al.*, 1988). Today, it is distributed widely over the main islands of NZ and is most common on disturbed sites such as pastures, grassland, along roadsides or stony riverbanks. In the 1940s the chrysomelid beetle (*Chrysolina hyperici*) has been released in NZ as a biological control agent, a measure which is deemed to have been successful (Fowler *et al.*, 2000). *Hypericum perforatum* contains secondary compounds that cause severe photosensitizing reactions on the skin of mammals and are dangerous to livestock. St. John's wort is used as a herbal remedy, mainly for the treatment of depression (Whiskey *et al.*, 2001). UV-B radiation has shown to enhance the production of the medicinally relevant metabolite concentration in *Hypericum perforatum* (Brechner *et al.*, 2011).

Lotus pedunculatus Lam. (Greater Bird's-foot Trefoil; syn. *Lotus uliginosus*; Figure 1.4.4 on the previous page) is a member of the *Fabaceae*. It is a herbaceous perennial native to Europe where it occurs in a wide range of damp, open habitats. It is growing 20-80 cm tall, with leaflets 10-25 mm long and 10-20 mm broad. Its stem is always hollow and the peak flowering period in Germany is June and July (Jäger & Werner, 2005b). *Lotus pedunculatus* has been introduced to NZ where it was first recorded in 1867 (Webb *et al.*, 1988) and it is now commonly found throughout the North Island and is locally

Figure 1.4.6: Morphological characteristics of *Prunella vulgaris* L., (drawing altered from Jäger & Werner, 1999)

common to abundant throughout the South Island (Figure 1.4.7E on page 34).

Leucanthemum vulgare Cav. (ox-eye daisy; syn. *Chrysanthemum leucanthemum; Asteraceae*; Figure 1.4.5 on the facing page) is a widespread, perennial flowering plant native to Europe and the temperate regions of Asia and an alien plant in North America[1], Australia, and New Zealand as well as India (Chaujar, 2010). *Leucanthemum vulgare* is a grassland perennial, growing in meadows and fields, open forests and in disturbed areas. The species sprouts and spreads vegetatively through rhizomes and produces a seedbank that remains viable for 2 to 3 years (Cole, 1999). In some areas it is an invasive species forming dense colonies displacing native plants and modifying existing communities, and is classified as a noxious weed in many states in the USA and Canada. *Leucanthemum vulgare* is a host for the yellow dwarf virus of potatoes, indirectly causing severe economic damage (Smith *et al.*, 2012). *Leucanthemum vulgare* was first recorded in NZ in 1867 and can now be found throughout the country in grasslands, riverbeds, forest margins and along roadsides.

Prunella vulgaris L. (self-heal; Figure 1.4.6) is a perennial, herbaceous plant in the *Lamiaceae* family. *P. vulgaris* grows 5 to 30 cm high, with creeping, self-rooting, stems branching at leaf axis. The species is self-compatible, being capable of producing numerous seeds in the absence of pollinators (Winn & Werner, 1987). *P. vulgaris* is native to temperate regions in Europe, Asia and North America and it has been introduced to many regions in the Southern Hemisphere. It was first recorded in NZ in 1867 where it can now be found throughout the main islands in pastures and lawns, forest margins and clearings, dry banks and riverbeds (Figure 1.4.7F on the following page). *P. vul-*

[1] http://www.invasive.org/browse/subinfo.cfm?sub=5937

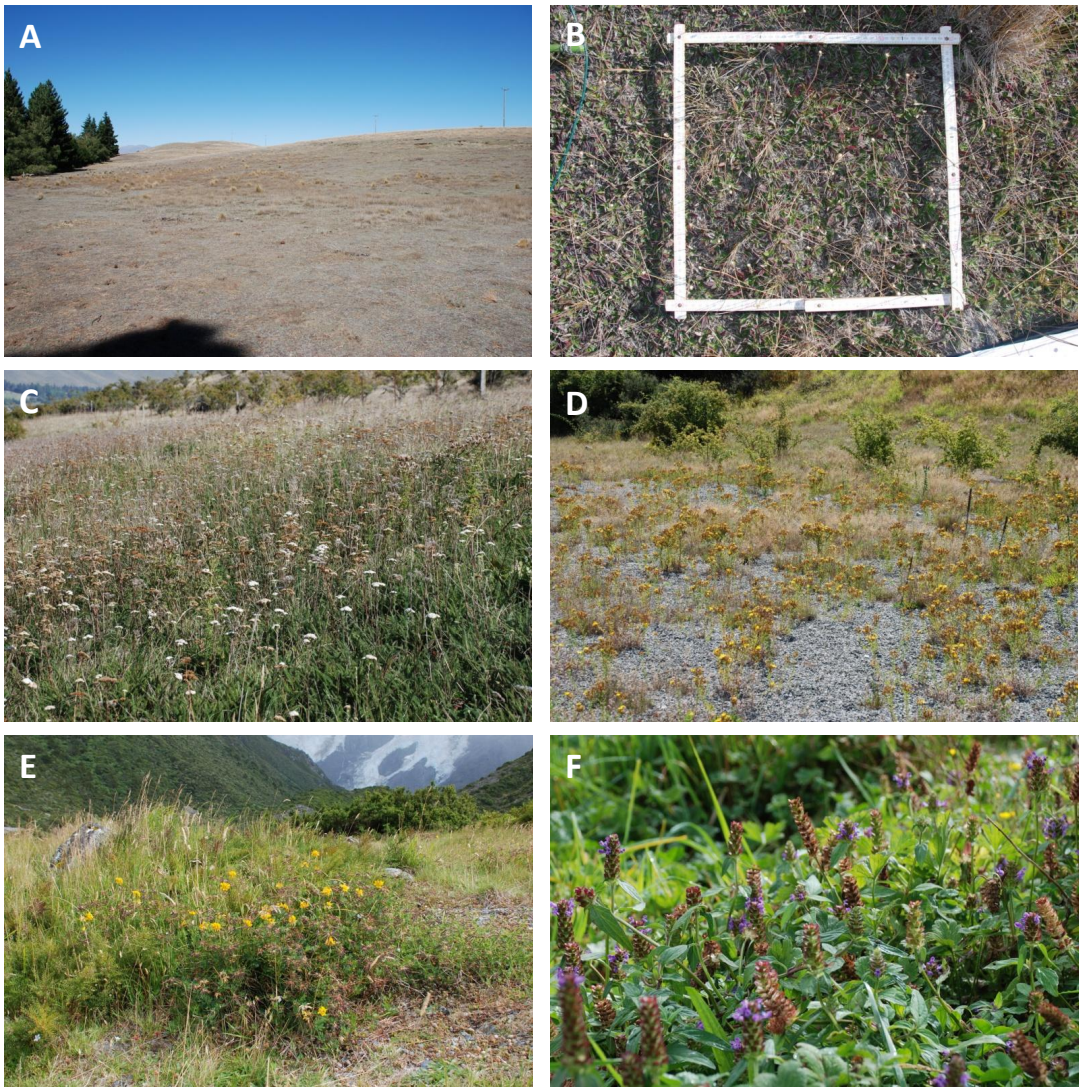

Figure 1.4.7: Examples of investigated populations in New Zealand. **A**, *Hieracium pilosella* in the McKenzie Country close to Lake Pukaki (NZHI802); **B**, close-up of *Hieracium pilosella* population NZHI802 demonstrating extreme high population densities; **C**, *Achillea millefolium* (NZAM803) in the Waihi River Gorge; **D**, *Hypericum perforatum* at the Lake Aviemore Dam (NZHY801); **E**, *Lotus pedunculatus* at Davies Flat (NZLP807); **F**, *Prunella vulgaris* in the Cobb Valley (NZPV804).

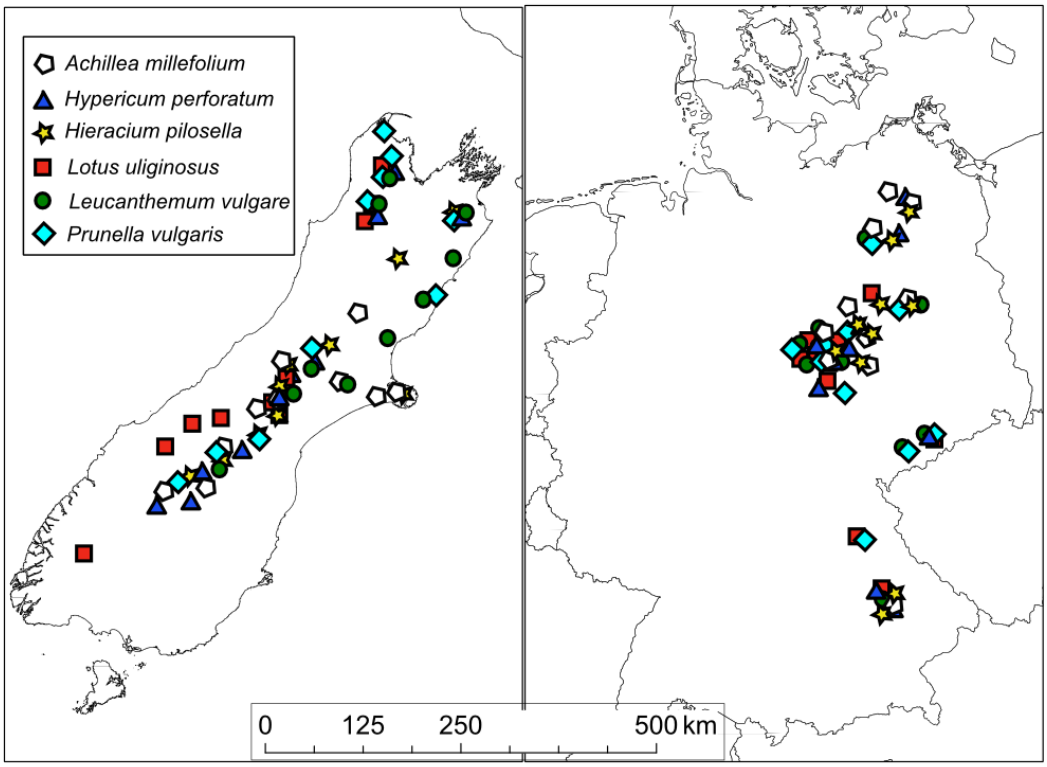

Figure 1.4.8: Map of all 120 population locations considered in this thesis. South Island of New Zealand (left) and in Germany (right). See Table A.2 on page 144 for further information.

garis has revealed high phenotypic plasticity to contrasting light environments (Winn & Evans, 1991). It has invaded parts of the South American temperate evergreen rainforest (Valdivian forest) by reducing its plastic responses to light variation, potentially as an outcome of rapid evolution (Godoy *et al.*, 2011b). *P. vulgaris* is edible and is used as a herbal remedy, mainly internally as a medicinal tea (Ryu *et al.*, 2000).

1.4.2 Study area and investigated populations

This thesis focuses on alien populations of six clonal growing species in New Zealand. In order to compare these populations with their respective native biogeographic regions and to be able to address the questions outlined in Section 1.3, also populations from the species' native range in Germany are included in this thesis. These two study regions exhibit both similarities and differences in their climatic and geographical conditions that have been incorporated in the study framework of this thesis.

Europe, the native range of the study species, has become a major area of plant invasions itself. According to the pan-European alien database DAISIE, there are about 5800 alien plant species found within Europe alone, 3800 of which are regarded as being naturalised (Pyšek *et al.*, 2009b), meaning that they are able to sustain wild populations. New Zealand (NZ), a much smaller part of the world which covers roughly 2.6 % of Europe's

land area, has recorded an astonishing number of 24744 alien plant species (Duncan & Williams, 2002; more recent estimations go as far as 35000 alien plant species[2]). About 2500 of these are regarded as being naturalised and up to 500 as serious environmental weeds. In NZ biological invasions also cause tremendous economic costs for prevention, eradication and caused losses: between NZ$2.1 and 3.3 billion annually (Giera, 2009). In Europe and elsewhere, alien species from all taxonomic groups negatively affect all ecosystem service types and, therefore, human well-being (Charles & Dukes, 2007; Vilà *et al.*, 2010; Vilà & Hulme, 2017). The total costs of alien species (i.e. covering those beyond the effects on ecosystem services as well) in Europe are estimated to reach more than €20 billion annually (Kettunen *et al.*, 2009).

For each of the six species studied in this thesis, 10 populations were investigated in the native and 10 in the alien range, resulting in a total of 120 investigated populations (Figure 1.4.8 on the previous page). The elevation of the sampled populations ranges from around 50m a.s.l. in both ranges to 700m a.s.l. in the native regions and to 1100m a.s.l. in the alien regions. Accordingly, the climatic conditions covered by the studied populations show some variability (see Table A.2 on page 144). For example, among the native populations the mean annual temperature ranges from 5.1°C to 9°C and in the alien populations between 5.2 and 12.7 °C (Hijmans *et al.*, 2005). Similarly, the mean annual precipitation ranges from ca. 500 mm per year to ca. 800 mm in the native range and up to 3300 mm in the investigated alien range.

While temperature and precipitation conditions are, at large, comparable between populations sampled in the native and alien regions, the intensity of UV-B radiation differs substantially between them. Local UV-B measurements in New Zealand and Germany at comparable latitude, altitude and meteorological season revealed that erythemally weighted irradiance in NZ is about 60% higher than in Germany (Seckmeyer & McKenzie, 1992; Beckmann *et al.*, 2014b; Figure 1.4.9 on the next page). Absorption of UV-B in the atmosphere is primarily due to the ozone layer but may be also influenced by other factors such as reflection by air pollutants (including aerosols) and clouds (McKenzie *et al.*, 2011). The differences in the UV-B intensities penetrating the Northern and Southern Hemispheres are partly attributable to the outer regions of the ozone hole over Antarctica reaching New Zealand, Southern Australia and Southern South America (Herman *et al.*, 1996). The inclination of the Earth's orbit leads to a smaller distance of the Earth to the sun during summer in the Southern Hemisphere (approx. 5 million km less) which further influences the amount of UV-B radiation reaching the surface (Godar, 2007; Hay *et al.*, 1997).

[2] http://www.nzpcn.org.nz/page.aspx?help_faqs_NZ_plants

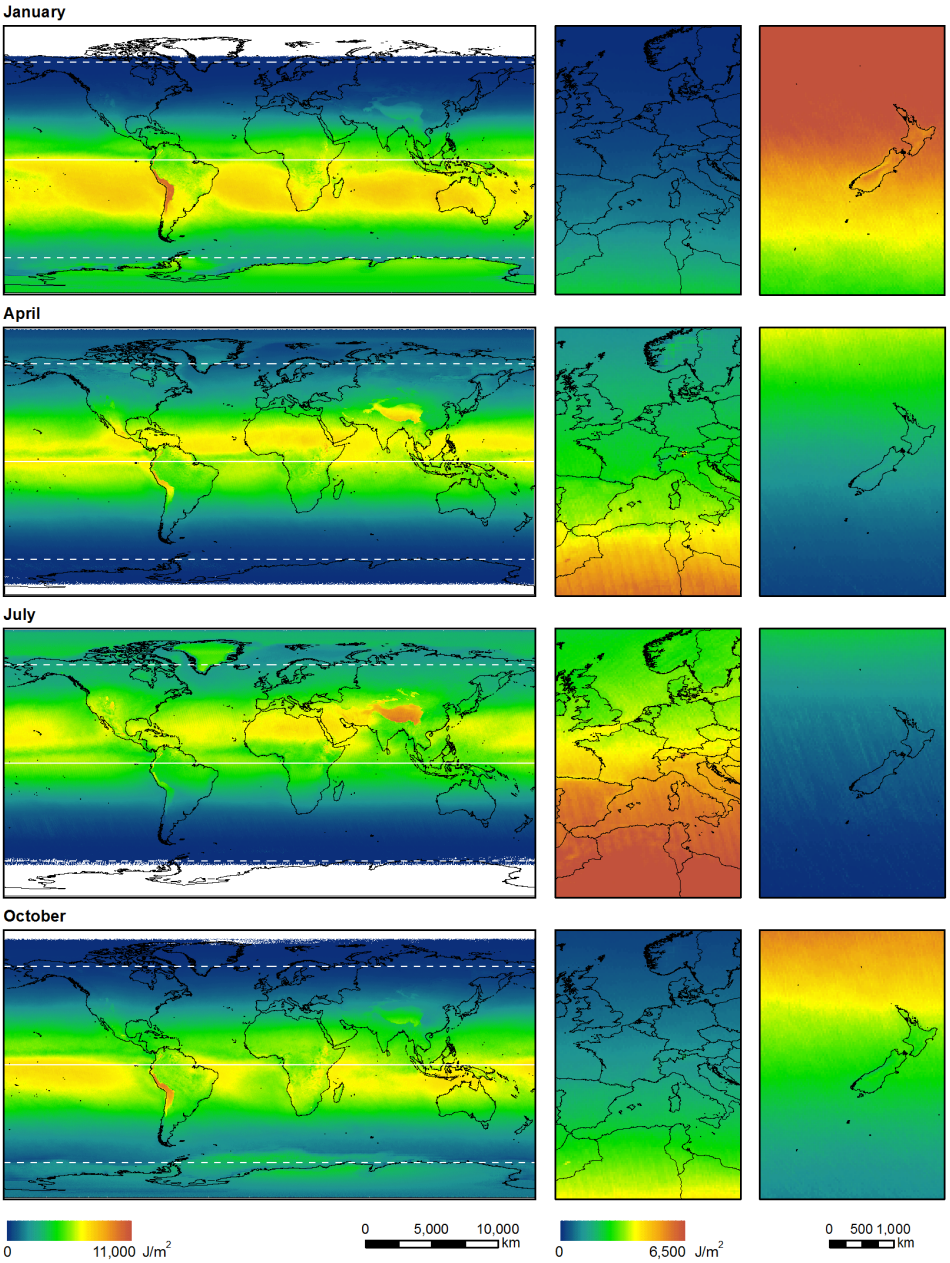

Figure 1.4.9: Examples of global monthly mean UV-B values in the study regions: January, April, July, October. The two insets on the right show finer scale variation in the data for the same latitudinal ranges between 30 and 60 degrees latitude on the Northern and Southern Hemispheres. The shown data is taken from the glUV dataset which is derived from direct satellite measurements of surface UV-B irradiation (Beckmann et al., 2014).

With the exception of Chapter 2, in which all 120 populations were investigated in the field, each of the individual chapters uses subsets of these populations. They were selected according to the hypotheses addressed within the chapter and the availability of collected seed material. Details on the used subsets can be found in the methods sections within each chapter.

2 Local performance of six clonal alien species differs between native and invasive regions in Germany and New Zealand

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2.1 Abstract

Exotic plant invasions are widely observed to have strong biogeographic patterns with invasive species occurring at higher abundances in their introduced range when compared to their native range. However, only few field studies have validated this assumption by comparing plant populations of multiple species in their native and introduced ranges and have evaluated to what extent changes in sexual and clonal reproduction potentially have contributed to the success of plant invasions. Here, we present the results of a comparative field study in both the native (Germany) and the introduced (New Zealand) ranges of six clonal plant species with different invasive status: *Achillea millefolium* L., *Pilosella officinarum* Vaill., *Hypericum perforatum* L., *Prunella vulgaris* L., *Leucanthemum vulgare* Lam. and *Lotus pedunculatus* Cav. We hypothesized that all six species show better performance in introduced NZ than in native German populations and tested if population structures investigated at different scales provide a useful tool to identify differences between native and introduced occurrences. In ten populations per species and country we assessed plant density and flowering proportion at the population scale and around individual plants, thereby identifying the "crowdedness" of the populations. Furthermore, we collected individual plants and determined the number of attached clonal organs and plant biomass. For all six species crowdedness in NZ populations was higher than in German populations. Additionally, overall population density of four species and the production of clonal organs (expressed as total number or per biomass ratio) of three species were higher in NZ than in Germany. When measured around individual plants, the flowering proportion was higher in native German populations of *Pilosella officinarum*, *Hypericum perforatum* and *Leucanthemum vulgare*.

Although the study species differed in their invasive status, our findings show that for all six species performance was better in introduced than in native populations. Furthermore, this study emphasizes that multiple measures of plant performance, different spatial scales and differences among species should be taken into account when trying to identify biogeographic differences in the performance of weed species.

Keywords: *Achillea millefolium* L., biological invasion, Germany, *Hieracium pilosella* L., *Hypericum perforatum* L., *Leucanthemum vulgare* Lam., local performance, *Lotus pedunculatus* Cav., New Zealand, *Prunella vulgaris* L., *Pilosella officinarum* Vaill., reproductive traits, vegetative reproduction

2.2 Introduction

How do naturalized species become invasive? This question has triggered many research approaches and prompted several hypotheses that try to explain it (Catford *et al.*, 2009). Two common approaches include studies that investigate introduced species exclusively in their introduced regions (for example Day & Buckley, 2011) or compare them with competing native species (e.g. Schlaepfer *et al.*, 2010). However, it is likely that in new regions, species may be subjected to different environmental selection regimes compared to the situation at home sites (e.g. Wilson *et al.*, 1992), and thus, might have become differentiated ecologically (e.g. Colautti *et al.*, 2010).

While recent concepts are based on the hypothesis of evolutionary shifts during invasions (see Bossdorf *et al.*, 2005 and Hierro *et al.*, 2005 for reviews), only a few studies have validated whether invasive species occur at higher abundances in their introduced range than in their native range by assessing population characteristics in the field. Hierro *et al.* (2005) state that "[...] the assumption of greater abundances and overall impacts of species in recipient than in native communities is based almost exclusively on non-quantitative observations [...and...] remain largely anecdotal". Studying the abundances of herbaceous species in native and invasive populations has produced mixed results. While population size and density may be higher in introduced populations of some species (e.g. Bastlova-Hanzelyova, 2001; Beckmann *et al.*, 2009; Callaway *et al.*, 2012; Moroney & Rundel, 2013) it also may not differ in others (Wolfe, 2002; Erfmeier & Bruelheide, 2004; Vilà *et al.*, 2005). In a large scale study, Firn *et al.* (2011) investigated 26 herbaceous species in native and introduced regions and concluded that substantially higher abundances in introduced regions are rather the exception. However, changes in population growth are difficult to detect and are usually only observed at the scale of individuals when invader impacts are extreme (e.g. Hejda *et al.*, 2009) or at the population scale when range expansion occurs rapidly (Engelkes *et al.*, 2008). Therefore, some of the inconsistency in findings between the multiple species study by Firn *et al.* (2011) and other studies may be resolved by distinguishing between strong and weak invaders (Ortega & Pearson, 2005), but also by accounting for scale- and, thus, method-dependent effects. In a large scale database analysis attempting to identify factors that explain inva-

sive species frequency at a regional scale, Speek *et al.* (2011) showed that life form, plant height and origin are highly correlated with regional frequency of exotic species. Yet, the authors concluded that regional frequency itself is no predictor of local dominance, where, in contrast, clonal growth and residence time were the best explanatory factors. Similarly, in a long term field study on weed species in New Zealand, the relevance of clonal growth for high abundance could be confirmed at the community level (Buckley & Freckleton, 2010). Other studies addressing seed rain, seed banks and clonal growth have also suggested that there is a direct effect on species abundance in the immediate vicinity of invasive plants (e.g. Güsewell *et al.*, 2006; Lortie *et al.*, 2010). This implies that measured differences in the performance of alien species may often be attributed to different levels of observations.

Clonal growth has been reported to be greater in introduced than in native populations (e.g. Jakobs *et al.*, 2004; Brown & Eckert, 2005; Beckmann *et al.*, 2009) and might be especially important in explaining local dominance of invasive species (Küster *et al.*, 2010; Speek *et al.*, 2011). The effects of clonal growth are most visible at a local scale as clonal propagation allows plants to explore habitats (de Kroon & Hutchings, 1995) and contributes to resource foraging (e.g. van Kleunen *et al.*, 2000) and sharing (Alpert, 1996). Therefore, investigating this local or neighborhood scale of introduced plants is particularly important for clonal species and may allow us to detect differences between native and introduced ranges. Enhanced sexual reproduction or more vigorous growth in introduced provenances has been described in several comparative field studies on single species (e.g. Woodburn & Sheppard, 1996; Bastlova & Kvet, 2002; Buckley *et al.*, 2003b; Jakobs *et al.*, 2004; Prati & Bossdorf, 2004; Stastny *et al.*, 2005; Ebeling *et al.*, 2008). However, for most plant species, it remains uncertain whether or not such traits differ between native and introduced populations (but see Thébaud & Simberloff, 2001; Hawkes, 2007). Therefore, there is a need for studies that measure plant growth and reproductive traits, preferably for a larger set of species under field conditions as they will help to detect differences in species performances in different geographical regions.

In this study, we compared plant densities at the population and the neighborhood level as well as individual growth of the following six species in their native and introduced ranges in Germany and in New Zealand (NZ): *Achillea millefolium* L., *Pilosella officinarum* Vaill., *Lotus pedunculatus* Cav., *Leucanthemum vulgare* Lam., *Prunella vulgaris* L. and *Hypericum perforatum* L. Ten populations of each species were investigated in each country. These species are all clonal growing, perennial herbaceous species of grasslands. They possess different habits of clonal growth ranging from short-stemmed mat-forming species to long-stemmed species with below-ground rhizomes (following the categorization proposed by Klimeš *et al.*, 1997) and they differ in their invasive status in protected areas of NZ (Howell, 2008). Recognizing different forms of clonal growth is important when trying to detect differences in individual plant performance and population structures, which has recently been demonstrated for grassland species in response to nitrogen fertilization (Gough *et al.*, 2012). However, investigating alien species of different

invasive status is equally important as this will contribute to the current knowledge on the determinants of invasiveness (van Kleunen *et al.*, 2010a). We tested the hypothesis that for all six species better performance will be displayed in introduced NZ populations compared to native German ones. Furthermore, we were interested in whether differences in plant performance between native and alien regions can be detected at multiple scales (i.e. at the individual, neighborhood or population scale), and whether the investigation of population structures at the neighborhood scale would allow us to identify any difference across species. The expected differences between native and introduced populations in density and/or traits are assumed to vary among species and will become evident at the population scale, the individual scale and/or the neighborhood scale.

2.3 Methods

2.3.1 Species selection

We compiled a list of 70 perennial, herbaceous grassland species that are native to Germany and that grow clonal organs (BIOLFLOR Database, www.biolflor.de, Klotz & Kühn, 2002). Suitable study species had to be introduced to NZ at least for 150 years (years of first records as given in Webb et al., 1988) and had to occur commonly in the South Island. Local distribution information was provided by the National Vegetation Survey Database of NZ[1]. Based on their frequency of occurrence and their similar phenology we selected *Achillea millefolium* (common yarrow; *Asteraceae*), *Hypericum perforatum* (St John's wort; *Hypericaceae*), *Pilosella officinarum* (mouse-ear hawkweed; *Asteraceae*), *Leucanthemum vulgare* (ox-eye daisy; *Asteraceae*), *Prunella vulgaris* (self-heal; *Lamiaceae*) and *Lotus pedunculatus* (greater bird's-foot trefoil; *Fabaceae*) as suitable study species (see Table A.1 on page 143 for detailed information on the study species). Following Bräutigam & Greuter (2007), we conform to the terminology used in NZ and refer to *Pilosella officinarum*, whereas, in other regions, the species is often described under its synonym *Hieracium pilosella*.

In order to estimate the species status in NZ we follow Howell (2008) who provided a consolidated weed list for NZ by checking 13 localized weed lists for the recording of alien plant species in protected areas. Based on the frequency of records in these lists we derived the species status as either naturalized or invasive, thereby following the unified terminology for alien species suggested by Blackburn et al. (2011). We categorized three of the six species as naturalized, since they were mentioned in none (*A. millefolium*) or one (*Leucanthemum vulgare* and *P. vulgaris*) weed list only, while we categorized the other species as invasive, since they were mentioned in five (*Hypericum perforatum*), seven (*P. officinarum*) or eight (*Lotus pedunculatus*) weed lists checked within Howell (2008).

[1] http://nvs.landcareresearch.co.nz/

2.3.2 Selection of sites and scale-dependent field sampling

A total of 120 populations were investigated during late summer and autumn of 2008 in the native range (Germany: August - September) and in the introduced range (New Zealand: February - March). Ten populations per species with similar geographical distances were examined in each country covering a range of environmental conditions (see Table A.2 on page 144 for a complete list of locations and information on annual mean temperature and annual precipitations). Suitable populations were selected in consideration of the species phenological status and of the accessibility of the sites. For three out of the six species, we were able to reassess several populations included in a previous study (Beckmann *et al.*, 2009). In the non-native range, the sampling took place in the drier regions of the South Island in NZ and the sites often contained further non-native vegetation. Sampled habitats included, for example, tussock grasslands, which are typical to these dry areas and which are commonly formed by species of the genera *Chionochloa*, *Festuca* or *Poa*. Further sampled habitats include braided riverbeds, subalpine heath- and shrubland. In the native range, the investigated species were sampled in dry to fresh (semi-)natural grasslands, where they typically occur and that are usually unaffected by invasions from non-native species. These sites included calcareous grasslands, meadows or forest clearings. The sampling design within populations followed Kluth & Bruelheide (2004) and Beckmann *et al.* (2009) with some adjustments.

We assessed species performance on three levels of scale: the population scale, the neighborhood scale and the individual scale. At the population scale, plant density and the proportion of flowering individuals were measured as the mean number of plants counted per metre squared within five, randomly positioned squares of 1 m x 1 m in size (subplots). For the number of plants, here, we refer to both genets and ramets, since in case of the densely growing and mat-forming species, distinct individual plants and genetically identical ramets could not be differentiated. The proportion of flowering plants was calculated as the ratio of flowering plants to all plants within each subplot as a relative measure of sexual reproduction in the populations.

For measurements at the neighborhood scale, adjacent to each subplot, the nearest plant of the target species that flowered or fruited was chosen for further investigations. In order to avoid multiple counting of the same area these plants had to be at least 60cm away from each other and from the subplots. Around each target plant, the plant density was determined within three distance classes. This was achieved by counting all flowering and non-flowering plants of the target species within three rings ranging from 0-20, 20-40 and 40-60 cm radius around each target plant. To clearly distinguish between plant density measurements taken around target plants at the neighborhood scale and those taken in random subplots at the population scale, we use the previously introduced term crowdedness (Beckmann *et al.*, 2009) to refer to the three distance classes. Assessing crowdedness as an additional measure allows quantifying different local expansion habits of the species at the individual level in their different ranges. The counted plants included

both genets and ramets. The means of all count-values were calculated to generate plant numbers per m^2.

To determine traits at the individual scale, all target plants, i.e., five individuals per population, were dug out and the number of stolons was counted on these individuals. Occasionally attached ramets were removed from these plants in order to allow for standardized biomass measurements. Plants were transferred to the lab for the determination of dry plant biomass after being dried for 48h at 80°C. Allocation to vegetative reproduction was determined by calculating the ratio of the number of stolons to total plant biomass (stolon-biomass ratio) as a proxy.

2.3.3 Statistical analysis

Since we were most interested in the effects of the range (native vs. introduced) for each species we analyzed the data separately by species. Due to a lack of normal distribution for most variables, data were square-root or log-transformed where appropriate to achieve normal distribution of residuals (as recommended by Zuur *et al.*, 2009). We used linear mixed models to test for differences between regions. "Country" (NZ, Germany) was implemented as a fixed and "population" as a random factor nested within "country" into the model. All analyses were conducted using R 2.9.1 (R Core Development Team, 2009; package "nlme", function "lme"; Pinheiro *et al.*, 2011).

2.4 Results

2.4.1 Population scale

Significant country effects that indicated greater performance in introduced populations with respect to the native range were found at the population scale for all species studied, except for *P. vulgaris* which displayed no significant differences between the countries at this level of observation (Table 2.4.1 on the facing page). Population density was significantly higher in NZ populations than in native German ones for *A. millefolium*, *P. officinarum*, *Hypericum perforatum* and *Lotus pedunculatus*, while *Leucanthemum vulgare* and *P. vulgaris* revealed no such trend (Fig. 2.4.1 a-f left on page 47, Table 2.4.1). The total number of flowering plants in randomly selected subplots was significantly higher for *A. millefolium*, *Lotus pedunculatus* and *Leucanthemum vulgare* in the introduced than in the native range (Fig. 2.4.2 a, d, e left on page 49) but lower for *P. officinarum* (Fig. 2.4.2 b left). Accordingly, the ratio of flowering plants was significantly lower in NZ populations of *P. officinarum* and higher for *Leucanthemum vulgare* and *Lotus pedunculatus* (Fig. A.3 b, d, e left on page 147, Table 1). For the other species no differences in the proportion of flowering plants were detected (Fig. A.3 on page 147).

Table 2.4.1: Means of populations by country for variables studied at different scales. Summarized results of mixed model analysis. Significance codes: $p < 0.001$ "***", $p < 0.01$ "**", $p < 0.05$ "*", $p < 0.1$ ".", $p < 1$ "n.s.". Bold numbers indicate higher means for significantly different values in direct comparisons between countries ($p<0.05$). Abbr.: NZ: New Zealand, DE: Germany.

	Achillea millefolium			*Hieracium pilosella*			*Hypericum perforatum*			*Lotus pedunculatus*			*Leucanthemum vulgare*			*Prunella vulgaris*		
	Mean NZ	Mean DE	p-value	Mean NZ	Mean DE	p-value	Mean NZ	Mean DE	p-value	Mean NZ	Mean DE	p-value	Mean NZ	Mean DE	p-value	Mean NZ	Mean DE	p-value
Population scale																		
Population density [plants m-^{2}]	**480.36**	61.36	***	**756.96**	320.48	**	**62.96**	27.6	***	**64.54**	27.92	***	12.56	11.52	n.s.	24.04	25.42	n.s.
Number of flowering plants[plants m-^{2}]	**74.32**	10.8	***	32.48	**41.28**	*	29.04	16.4	n.s.	**60.94**	22.8	***	**6.34**	2.62	**	21.22	21.74	n.s.
Ratio of flowering plants	0.16	0.25	n.s.	0.06	**0.14**	***	0.46	0.61	n.s.	**0.94**	0.81	***	**0.47**	0.23	***	0.88	0.86	n.s.
Neighborhood scale																		
Crowdedness, radius of 20cm [plants m-^{2}]	**755.03**	264.83	***	1016.43	902.98	n.s.	**199.26**	78.94	***	**165.04**	94.54	***	**62.87**	47.91	**	**121.75**	80.21	***
Crowdedness, radius of 40cm [plants m-^{2}]	**604.37**	118.2	***	**818.57**	358.29	***	24.4	21.22	n.s.	**85.04**	51.57	***	**36.34**	19.68	***	97.72	76.29	.
Crowdedness, radius of 60cm [plants m-^{2}]	**571.05**	76.27	***	**671.05**	496.18	**	18.84	9.17	n.s.	**119.46**	53.29	***	**70.38**	24.89	***	60.16	52.33	.
Number of flowering plants, radius of 20cm	199.26	157.24	.	51.57	**150.24**	***	68.75	61.75	n.s.	**146.11**	69.23	***	27.69	**32.79**	*	**69.87**	37.72	***
Number of flowering plants, radius of 40cm	**91.25**	40.53	**	16.13	**65.15**	***	16.76	11.67	n.s.	**74.01**	40.21	***	13.11	14.06	n.s.	49.45	43.71	n.s.
Number of flowering plants, radius of 60cm	**66.97**	22.79	***	16.68	**64.04**	***	**14.52**	3.95	*	**113.48**	48.48	***	**26.55**	12.26	**	**38.67**	28.39	*
Flowering ratio, radius of 20cm	0.26	**0.57**	***	0.12	**0.31**	***	0.5	**0.87**	***	**0.88**	0.74	***	0.44	**0.71**	***	**0.58**	0.49	*
Flowering ratio, radius of 40cm	0.17	0.32	n.s.	0.04	**0.35**	***	0.47	0.31	n.s.	**0.86**	0.77	**	0.37	**0.72**	***	0.52	0.55	n.s.
Flowering ratio, radius of 60cm	0.14	**0.34**	*	0.05	**0.38**	***	0.8	0.13	n.s.	**0.95**	0.9	*	0.4	0.49	.	**0.65**	0.53	**
Individual scale																		
Plant biomass [g]	2.74	3.57	.	0.59	0.66	n.s.	5.89	5.15	n.s.	1.91	**2.54**	**	7.03	5.99	n.s.	3.77	3.28	n.s.
Stolons per plant	**3.84**	2.18	*	0.46	0.73	n.s.	11.86	5.9	***	3.74	3.82	n.s.	6.9	5.66	.	4.96	3.86	.
Stolon-biomass ratio	**2.00**	0.65	**	0.87	1.35	n.s.	4.09	1.21	*	**2.39**	1.56	***	1.03	0.96	n.s.	1.34	1.21	.

2.4.2 Neighborhood scale

All species displayed significant differences between countries in some of the variables at the neighborhood scale. However, frequency and direction of significant effects differed among species. *Lotus pedunculatus* displayed higher values in NZ populations most often, whereas *Hypericum perforatum* had only very few variables that expressed differences at this scale. We observed a very clear trend for population crowdedness to be higher in introduced NZ populations (Fig. 2.4.1 a-f right on the next page, Table 2.4.1). This was most prominently detected for *A. millefolium*, *Leucanthemum vulgare* and *Lotus pedunculatus* where crowdedness was higher in NZ at all three measured rings (Fig. 2.4.1 a, d, e). The largest differences between countries were detected for *A. millefolium* and *Hypericum perforatum* with the crowdedness in NZ in the smallest ring (0-20 cm) being between a factor of 2.4 and 2.8 higher than in Germany. However, this tendency disappeared for *Hypericum perforatum* and also for *P. vulgaris*, when crowdedness was measured in the larger rings (20-40 and 40-60 cm; Fig. 2.4.1 c, f). *Pilosella officinarum*, in contrast, showed the opposite trend. Only when measuring crowdedness further than 20 cm away from a target plant was it significantly higher in NZ populations (Fig. 2.4.1 b).

The number of flowering plants measured in all three rings was lower in NZ populations for *P. officinarum* and higher for *Lotus pedunculatus* (Table 2.4.1, Fig. 2.4.2 b, e). *A. millefolium* showed greater numbers of flowering plants in NZ with distance to the target plants and this was also observed for *Hypericum perforatum*, *Leucanthemum vulgare* and *P. vulgaris* where the number of flowering plants was significantly higher in NZ when measured at a 60 cm radius only.

Similar to the number of flowering plants the proportion of flowering plants was higher in all three distance classes in NZ populations of *Lotus pedunculatus* (Fig. A.3 on page 147). This was also true for *P. vulgaris* with exception of the measurement ring ranging from 20 to 40 cm. All other species showed a lower flowering proportion in NZ populations at least in the 20 cm ring. Most conspicuous was the proportion of flowering plants of *A. millefolium* in NZ which reached only 10-20 % of the ratio measured in Germany.

2.4.3 Individual scale

Significant effects at the individual scale were found for three out of the six study species. Among the variables assessed at the individual scale, the number of stolons per plant as well as the stolon-biomass ratio displayed significantly higher values in NZ (Table 2.4.1, Fig. A.4 on page 148). However, none of the species displayed significantly higher individual plant biomass in the introduced range. In contrast, *Lotus pedunculatus* collected in NZ produced less biomass. Absolute stolon production per plant was significantly higher in NZ for *Hypericum perforatum* and *A. millefolium*, and, by trend, for *P. vulgaris* and *Leucanthemum vulgare*. *Pilosella officinarum* and *Lotus pedunculatus* did not differ in

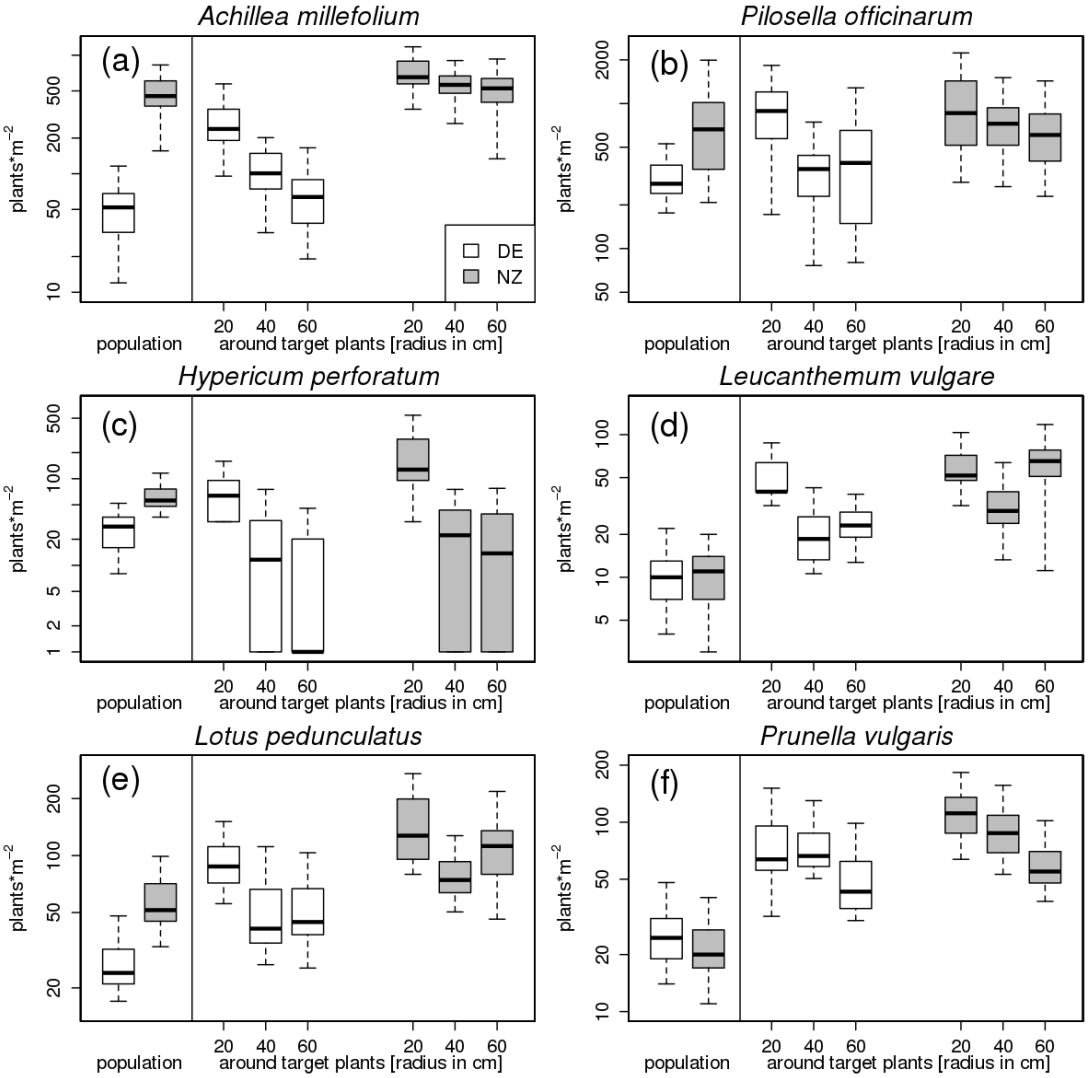

Figure 2.4.1: Population and neighborhood scale. Box and whiskers plots of plant density measurements by species (a-f) on logarithmic scales. The left part of each panel shows plant densities measured in randomly selected 1m² subplots, the right parts show plant density measured in three rings (20, 40 and 60 cm radius) placed around flowering target plants; (a) *Achillea millefolium*, (b) *Hieracium pilosella*, (c) *Hypericum perforatum*, (d) *Leucanthemum vulgare*, (e) *Lotus pedunculatus*, (f) *Prunella vulgaris*. Each box plot represents measurements taken in ten populations per species and country. Medians (solid lines), 25th and 75th percentiles (boxes) and 5th and 95th percentiles (whiskers) are shown. Abbreviations: NZ = New Zealand, DE = Germany. See Table 2.4.1 for statistical details.

stolon production between regions (Table 2.4.1 on page 45, Fig. A.4 on page 148). If related to biomass, however, *Lotus pedunculatus* produced more stolons in the introduced than in the native range. The same result of a higher stolon production per biomass was observed for *A. millefolium* and *Hypericum perforatum* (Table 2.4.1, Fig. A.4 on page 148), yet, not for the rest of the species.

2.5 Discussion

2.5.1 Overall better performance of invasive populations

The findings of our study demonstrated better performance either in clonal growth and/or in sexual reproduction for all of the investigated species in NZ populations and at least at one of the measured scales, therefore, confirming our main hypothesis that better performance will be evident in non-native populations of our study species. Better performance of introduced populations was most prominent at the neighborhood scale where all six species displayed significantly higher crowdedness, in one or more of the distance classes around target plants. Differences in abundance between biogeographical regions may be expected, in particular, for species that have been regarded as invasive or "strong invaders" (in the sense of Ortega & Pearson, 2005). In this study, however, those species classified as naturalized but not invasive ("weak invaders") have revealed greater abundances in alien populations, thereby clearly highlighting that low-impact alien species might also have experienced substantial changes during the invasion process and need to be included in biogeographical comparisons.

The apparently scale-dependent performance differences among the six studied species highlight the importance of considering population structures at different scales in order to determine any substantial differences between native and introduced populations. It might well be that ignoring such species-specific strategies hampers the detection of differences among native and introduced regions when comparing several species. Firn *et al.*, 2011 concluded that differences in species abundances between native and alien regions were rather unusual. However, conflicting results for three species also included in the present study (*A. millefolium*, *P. officinarum* and *P. vulgaris*) suggest that the generalizing approach used by Firn *et al.*, 2011 disregarded fine-scale differences. In fact, the discrepancy between study outcomes for the same species underlines the need to account for different scales when assessing and comparing population structures between native and naturalized regions.

Greater individual plant biomass production in introduced populations, as was described for *Solidago gigantea* (Jakobs *et al.*, 2004) or *Senecio inaequidens* (Prati & Bossdorf, 2004) seems to be of minor importance for our study species, at least with regard to traits associated with individual biomass. However, traits associated with allocation, and, in this case related to clonal growth, provide evidence of higher values in introduced populations: *A. millefolium*, *Hypericum perforatum* and *Lotus pedunculatus* displayed

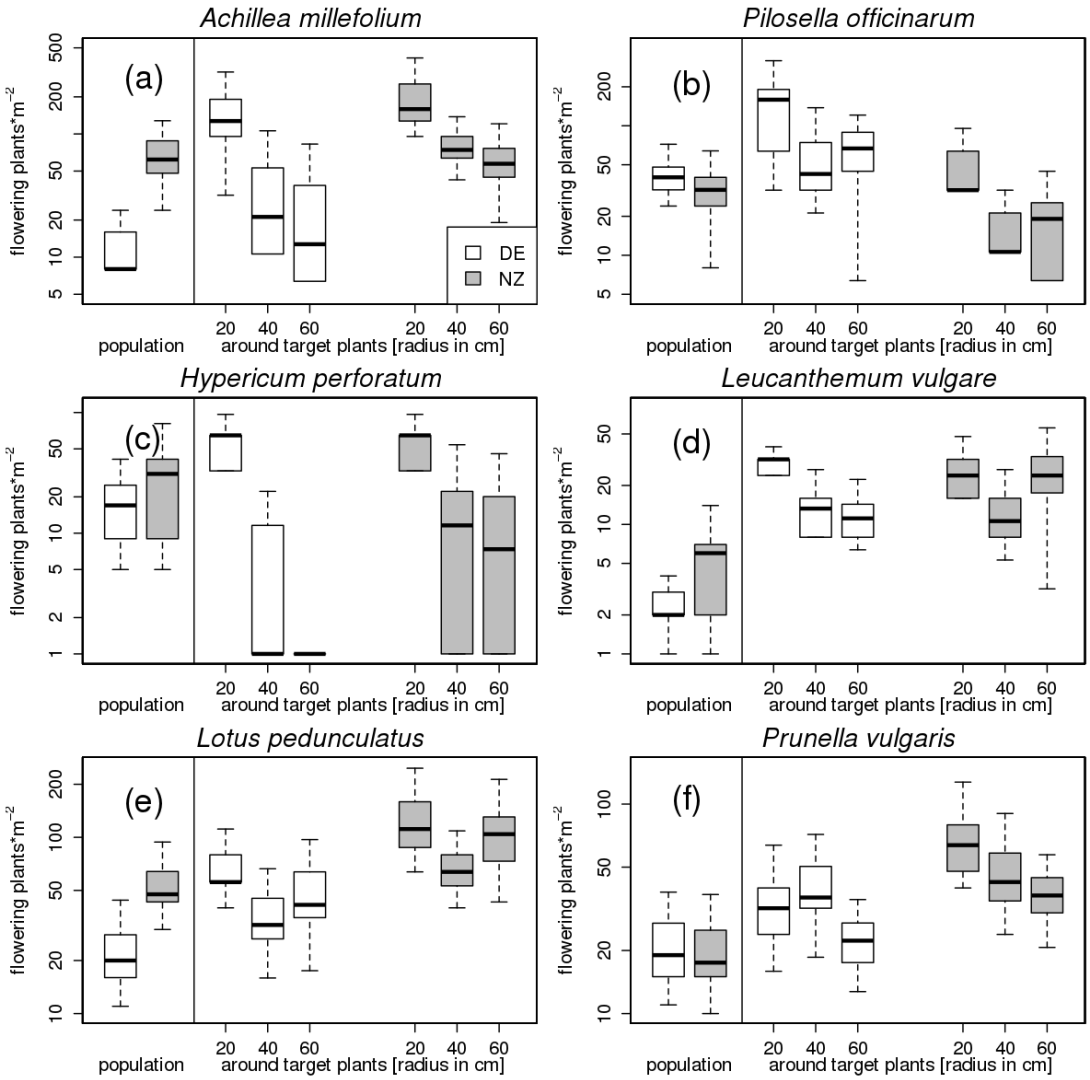

Figure 2.4.2: Box and whiskers plots of the number of flowering plants by species (a-f) on logarithmic scales. The left part of each panel shows the number of flowering plants in randomly selected 1m² subplots, the right parts show the number of flowering plants in three specified rings (20, 40 and 60 cm radius) placed around target plants; (a) *Achillea millefolium*, (b) *Hieracium pilosella*, (c) *Hypericum perforatum*, (d) *Leucanthemum vulgare*, (e) *Lotus pedunculatus*, (f) *Prunella vulgaris*. Each box plot represents measurements taken in ten populations per species and country. Medians (solid lines), 25th and 75th percentiles (boxes) and 5th and 95th percentiles (whiskers) are shown. Abbreviations: NZ = New Zealand, DE = Germany. See Table 2.4.1 for statistical details.

better individual performance as revealed by higher clonal organ production and/or a higher clonal output per biomass in NZ, which is in general accordance with previous studies (Jakobs *et al.*, 2004; Brown & Eckert, 2005; Beckmann *et al.*, 2009). Therefore, these three species present an overall higher allocation of biomass towards clonal growth in introduced populations. Whether these observations at the individual scale are plastic responses to differing environmental conditions (e.g., soil, precipitation, UV-B radiation, Beckmann *et al.*, 2012), effects of enemy release (e.g. as described for *Hypericum perforatum* in North America; Vilà *et al.*, 2005) or whether they demonstrate evidence for local adaptation (Yoshida *et al.*, 2007) was not the subject of this study and cannot be assessed with the data at hand. Furthermore, the lack of differences in clonal growth between Germany and NZ for two species that are considered as being invasive weeds in NZ (*P. officinarum* and *Lotus pedunculatus*; Howell, 2008), indicates that clonality alone is not the only effective recipe for successful plant invasion.

Variables related to sexual reproduction were mostly found to be higher in native populations when compared across species. German populations outperformed NZ populations in the flowering ratio when measured at the neighborhood scale in all species, except *Lotus pedunculatus* and *P. vulgaris*, whereas the ratio of flowering plants was lower in NZ. However, lower flowering ratios in alien populations may be the result of higher recruitment rates due to higher production or survival of seeds, thereby resulting in higher densities of young plants and, thus, rectifying the seemingly lower performance of alien populations. Therefore, both sexual and clonal reproduction seem to be of importance in introduced populations of these species.

2.5.2 Different species – different strategies

Despite the interpretation of clonal growth being mainly a "foraging behaviour" that allows plants to collect and share resources (see de Kroon and Hutchings, 1995), clonal connections may also permit a plant to explore space that is temporally not available to seeds or adult plants (Givnish, 2002) which may result in a competitive advantage compared to the surrounding vegetation (e.g. Turkington *et al.*, 1991; see Callaway *et al.*, 2003 for review). Two main clonal growth strategies have been postulated: the guerrilla type that produces relatively long internodes and the phalanx type with relatively short internodes (Doust, 1981), and both types can be found among our study species. The guerilla strategists *P. officinarum* and *Lotus pedunculatus* produce long stem-derived clonal organs of similar type and, while both grow in denser and more crowded populations in NZ, only *L. peduculatus* displayed higher clonal organ production. *Prunella vulgaris* and *Leucanthemum vulgare* produce short-stemmed clonal organs and display features of phalanx-strategists. Accordingly, the latter two species displayed differences in clonal growth most notably at the neighborhood scale. The other two species (*A. millefolium* and *Hypericum perforatum*) combine characteristics of both strategies with intermediately long below-ground spacers either derived from roots or stems and show

enhanced vegetative characteristics at the individual and the population scale. Enhanced clonal growth, therefore, can be accounted as an important strategy for several of the species in our study, however, clearly differentiated by the observation scale. In summary, for both sexual and clonal reproduction, the response is different among plants of different clonal growth form. These differences need to be more seriously considered when searching for generalizations about changes in reproduction strategies in clonal plant species during invasions.

2.5.3 Implications & Conclusions

The observed differential performance of several clonal species across scales results in three further implications: First, appropriately rating the status of an introduced species requires the consideration of several spatial scales. Shifts in performance could be observed at the individual, the neighborhood and the population scale. Restricting field observations to only one scale ignores the presence or absence of shifts in performance at other scales. Second, multiple measures of population and individual growth and reproduction should be used. If we had measured only population densities or plant biomass we would have had to draw very different conclusions on the performance of the six study species in NZ. Third, measuring plant densities at the neighborhood scale is a very effective way to identify differences in plant species performance between regions. Using a target-plant approach provided consistent results for the six studied species, regardless of the three distances used. Nevertheless, the species-specific differences encountered between native and alien populations, suggest that different strategies might operate during alien species spread in NZ.

Our conclusions are consistent with growing concern about the possibility of generalizations across species as there is no evidence for a general "invasive ability" in successfully invasive plant species (Hulme, 2008b; van Kleunen *et al.*, 2010a). Additionally, alien species do not necessarily need to become visually "super-abundant" or "gigantic" to perform better in their introduced ranges than in their native range. Therefore, by acting at the neighborhood scale, plant invasions might often happen in a much more subtle way than expected. This finding also needs to be taken into account when modeling species distribution against scenarios of climate change. The results of this study suggest that for *A. millefolium* and *Leucanthemum vulgare*, which are not yet considered as environmental weeds in NZ (Howell, 2008), an upgrade of their status is appropriate. Comparing plant densities between native and introduced ranges of these two species made clear that they have become super-abundant in NZ, at least at the neighborhood scale. For comparable life- and growth-forms, we recommend measuring the population crowdedness as an appropriate tool to detect differences in the performance of introduced plant species where other measures based solely on the plant individual or the population might fail to provide relevant information.

Acknowledgments

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3 Germination responses of three grassland species differ between native and invasive origins

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3.1 Abstract

The germination stage is critical in plant lifehistory and is also a key process during the expansion of species' ranges into new environments. In this study we investigated the germination patterns of three plant species (*Achillea millefolium*, *Hieracium pilosella* and *Hypericum perforatum*) that are invasive to New Zealand (NZ) and native to Central Europe. We asked whether the species show differences in germination temperature requirements, germination speed and maximum germination rates, and thus, whether they display evidence of adaptation to different conditions in the invasive range. Seeds from three populations per species and region were subjected to three different temperature regimes to compare germination rates among origins and across temperature conditions. For *Achillea millefolium* and *Hypericum perforatum*, germination rates were significantly higher for invasive NZ provenances than for native German ones. Seeds from invasive populations of all three species displayed increased maximum germination at medium temperature conditions when compared to native populations, which indicates altered germination strategies in the invaded range. Changes in temporal development patterns were most conspicuous for invasive *Hieracium pilosella* and *Hypericum perforatum* populations. These findings imply that adaptation in germination patterns towards different climatic conditions in invasive populations has occurred. Our study emphasises the importance of the germination stage during plant invasion and its role in explaining range expansion of these species.

Keywords: Biological invasion, Germination rates, Germination velocity, *Achillea millefolium*, *Hieracium pilosella*, *Hypericum perforatum*

3.2 Introduction

Invasive plant species are widely recognised to be a serious threat to native species diversity and community structure (Meyerson & Mooney, 2007; Pimentel, 2009). In many parts of the world, large numbers of non-native species have been introduced during the last centuries, and a considerable number of them have succeeded to persist in the wild. New Zealand (NZ) alone, for example, has been exposed to more than 25,000 nonnative plant species, of which more than 2,200 have been estimated to have successfully established populations in the wild (Williams & Cameron, 2006). One of the most prominent tasks in invasion ecology research is to find an answer to the question why some species become invasive while others do not (Rejmánek *et al.*, 2005). In recent years, attempts to detect general patterns focused on identifying common traits among invasive plant species (e.g. Pyšek & Richardson, 2007; Küster *et al.*, 2008, 2009; Pyšek *et al.*, 2009a). A common conclusion, if applicable at all, seems to be that there are no "invasive traits" per se that explain plant species invasion (Hulme, 2008a; van Kleunen *et al.*, 2010b). Nevertheless, a general feature seems to be that plant traits associated with reproduction are of vital importance for successful plant invasions (Mandák, 2003; Erfmeier & Bruelheide, 2005; Mihulka *et al.*, 2006; Abraham *et al.*, 2008).

The ability of a species to germinate rapidly under a wide set of environmental conditions has been regarded as an important trait for invasive species since Baker (1974). For example, Perglova *et al.* (2009) showed that two invasive species of *Impatiens* germinated faster and had a higher total germination rate when compared to the native *I. noli-tangere*. Comparisons of native and invasive populations provided further evidence for shifts in reproductive traits during range expansion. Thereby, several studies found increased sexual or clonal reproduction in invasive populations (Noble, 1989; Brown & Eckert, 2005; Buschmann *et al.*, 2005; Meyer & Hull-Sanders, 2008; Beckmann *et al.*, 2009).

Research focusing on shifts in germination patterns in invasive species may increase our knowledge of genetic differentiation between native and invasive populations as suggested by Bossdorf *et al.* (2005), in particular as germination characteristics are not only environmentally triggered, but also under genetic control (Huang *et al.*, 2010). However, only a few studies have investigated seed germination patterns between native and invasive populations. As one example, Kudoh *et al.* (2007) found seed dormancy to be higher in invasive, Japanese populations of *Cardamine hirsuta* when compared to seeds from native European populations. The authors suggested that this change in germination patterns might help to explain the rapid invasion of *C. hirsuta* in Japan during the last decades because it enhances germination in autumn and enables longer transportation of dormant seeds. In their germination experiment, Erfmeier & Bruelheide (2005) found no differences in maximum germination rates or temperature optima between native and invasive origins of *Rhododendron ponticum*. They revealed, however, that invasive seeds germinated earlier than those of native provenances, thus contributing

to rapid range expansion. In a series of common garden experiments, Hierro *et al.* (2009) recently demonstrated genetic differentiation between native and invasive populations of *Centaurea solstitialis*. The authors suggested that "the degree of risk experienced at early developmental stages could exert an important control over the germination strategy of *C. solstitialis* populations". Thus, rapid adaptations in germination strategies might contribute to the success of other invaders. However, examples supporting this idea mostly refer to single species studies, and, so far, no across-species comparisons have been carried out for species that grow in similar habitats.

The present study addresses germination patterns of *Hieracium pilosella*, *Achillea millefolium* and *Hypericum perforatum* between native and invasive origins of the seeds. We compared seeds of populations from NZ, where the species have been introduced in the nineteenth century and from their native provenances in Germany. Although germination ecology of these species has been studied before (e.g. Oomes & Elberse, 1976; Bishop *et al.*, 1978; Campbell, 1985), a direct comparison of the germination performance between native and invasive populations has not been the subject of research so far.

In this comparative experimental approach, we aimed to determine differences in (1) germination temperature requirements, (2) germination speed and (3) maximum germination rates of seeds from native populations in Germany and from invasive populations in NZ of *Hieracium pilosella*, *Achillea millefolium* and *Hypericum perforatum*. In particular, we hypothesised that germination speed and germination rates were higher in invasive populations. Our goal was to investigate whether shifts in germination characteristics during range expansion might help explain exotic species' invasion success.

3.3 Materials and Methods

3.3.1 Study species

Achillea millefolium (Common yarrow) is a rhizomatous *Asteraceae* species that is widespread in the northern hemisphere. It is a perennial herb that grows in dry grasslands, along waysides and in pastures (Rothmaler *et al.*, 2005). *A. millefolium* was introduced to NZ in the mid-nineteenth century. First records date back to 1867 (Webb *et al.*, 1988). Currently, it can be found throughout the country, but it is more common in drier areas of the South Island where the species particularly grows in disturbed areas such as roadsides, lawns and pastures. *A. millefolium* seeds are not dormant and germinate under a large variety of soil, temperature and light conditions. The germination process is known to be relatively insensitive to drought (Oomes & Elberse, 1976; Robocker, 1977).

The facultative apomict *Hieracium pilosella* (Mouseear hawkweed; *Asteraceae*) is native to Europe and northern Asia where it frequently occurs in dry grasslands, heathlands, open pine forests and along waysides. It is a major invasive weed in NZ as it infests tussock grasslands and reduces species richness in local communities (Scott, 1993). *Hieracium pilosella* was first recorded in NZ in 1878 (Webb *et al.*, 1988). The species can

be found throughout the entire South Island where it is particularly frequent in eastern, dryer areas of the Southern Alps. *Hieracium pilosella* seeds show no dormancy and germinate quickly under suitable conditions (Koltunow *et al.*, 1998). However, seedling survival in natural populations is relatively low with about 1% (Bishop *et al.*, 1978). *Hypericum perforatum* (St. John's Wort) is an erect, herbaceous plant of the *Hypericaceae* family. It is native to Eurasia and Northern Africa where it grows in dry grasslands, heathlands and in dry to fresh ruderal sites (Rothmaler *et al.*, 2005). *Hypericum perforatum* was introduced to NZ in 1869 (Webb *et al.*, 1988) and is today distributed widely over both islands. *Hypericum perforatum* seeds have shown to germinate preferably under relatively warm conditions (Campbell, 1985).

3.3.2 Germination experiment

We collected mature seeds in three populations of every species in each country, leading to seed samples from 18 populations (Table 3.3.1 on the next page). Seeds were sampled in February/March (NZ) and July/August (Germany) 2006 across multiple individuals and pooled for each population. Seed material was kept dry at approximately 15C until the beginning of the germination experiment, which took place in autumn 2006 at the Institute of Biology/Geobotany and Botanical Garden, Halle. Three different temperature conditions were applied in germination cabinets with a night/day cycle of 4/8C, 10/20C and 20/32C, and a photo- and thermoperiod of 12 h. From each population, 30 randomly chosen seeds were placed in petri dishes on filter paper. Three replicates of each population were exposed to each temperature regime resulting in a total of 162 dishes. The dishes were watered every week or more often where necessary. Germination was monitored regularly, and germinated seeds were removed from the dishes. After 40 days, germination tests were stopped. Cumulative germination rates were calculated and used for statistical analysis.

3.3.3 Statistical analysis

Since germination rates lacked normal distribution, we used rank transformed data for subsequent analyses (as recommended by Quinn & Keough, 2002). All analyses were done with SAS 8.2 (SAS Institute, Cary, NC). Maximum germination rates were analysed separately for each species using a two-factorial nested ANOVA design. "Temperature" and "country" were introduced as fixed factors ($3 \cdot 2$ levels) and with random factor "populations" nested within "country" into a generalised linear mixed model (SAS proc glm). Ryan-Einot-Gabriel-Welsh post-hoc tests were performed in order to indicate the direction of differences between categories of each factor. The results of the germination experiment were analysed for temporal development patterns using a logistic regression model (SAS proc nlin) following Erfmeier & Bruelheide (2005). We calculated the times when 10, 50 and 90% of the maximum germination occurred for every species and population separately, and analysed these variables using the same nested ANOVA design as

Table 3.3.1: Locations of sampled populations in New Zealand and Germany. Seeds were collected at these sites during Summer 2006 in both countries. Latitude and longitude are presented as decimal degrees. Mean temperature of wettest quarter, mean temperature of driest quarter and temperature seasonality values are long-term means and were extrapolated from the climate model provided by Hijmans et al. (2005). Range: GER = Germany, NZ = New Zealand.

Range	Species	Latitude	Longitude	Location	Mean Temperature of Wettest Quarter [°C]	Mean Temperature of Driest Quarter [°C]	Temperature Seasonality (standard deviation *100)
GER	*A. millefolium*	51.28876°	11.26469°	Oberheldrungen	16.6	0.3	634.5
GER	*A. millefolium*	51.42243°	11.06866°	Kyffhäuser	16.6	0.3	636.5
GER	*A. millefolium*	51.28926°	10.53344°	Menteroda	15.5	0.2	631.1
NZ	*A. millefolium*	-43.28337°	171.53615°	Rakaia	5.8	12.8	376.3
NZ	*A. millefolium*	-44.20826°	170.07684°	Ohau-Pukaki-Canal	7.1	12.8	433.6
NZ	*A. millefolium*	-44.64558°	168.93137°	Treble Cone Skifield	7	14.6	432.3
GER	*Hieracium pilosella*	51.52677°	11.30211°	Grillenberg	16.2	0.7	633.3
GER	*Hieracium pilosella*	51.65257°	11.75753°	Rothenburg	17.1	1.5	644
GER	*Hieracium pilosella*	52.72566°	12.12735°	Rehberger Berge	17.2	1.3	653.3
NZ	*Hieracium pilosella*	-44.01337°	170.50053°	Lake Tekapo	6.2	12.1	437.8
NZ	*Hieracium pilosella*	-44.15848°	170.22020°	Lake Pukaki	6.9	12.7	433.3
NZ	*Hieracium pilosella*	-44.58540°	169.65372°	Lindis Pass	4.3	0.7	446.7
GER	*Hypericum perforatum*	51.53070°	11.89119°	Lunzberge	17.4	1.6	646.8
GER	*Hypericum perforatum*	51.65086°	11.75768°	Rothenburg	17.1	1.5	644
GER	*Hypericum perforatum*	51.27164°	11.22357°	Heldrungen	16.8	0.4	637
NZ	*Hypericum perforatum*	-44.66327°	170.36404°	Lake Aviemore Dam	15	4.4	417
NZ	*Hypericum perforatum*	-44.25984°	169.99175°	Lake Ohau Dam	7.1	12.8	433.5
NZ	*Hypericum perforatum*	-44.73373°	169.28222°	Tasman Valley	10.7	15.7	443

described above. All figures were generated using R 2.10 (R Core Development Team, 2009).

3.4 Results

All species displayed significantly different germination patterns at the different temperature levels applied, with low germination at cold temperatures and highly increased germination at warmer temperatures (Table 3.4.1 on page 59). Maximum germination rates differed between the species, with *Achillea millefolium* and *Hypericum perforatum* reaching significantly higher germination rates with a median of 80% and 90%, respectively (Fig. 3.5.1 a, b, e, f on page 61), compared to *Hieracium pilosella* with a median germination rate of 7% (Fig. 3.5.1c, d).

Maximum germination of *Achillea millefolium* was significantly higher for invasive NZ populations than for native German populations as indicated by a significant country

effect (Table 3.4.1 on the facing page; Fig. 3.5.1 on page 61). Maximum germination was also higher at warm and medium temperatures when compared to cold temperature (Table 3.4.1 on the facing page). A significant interaction between temperature and country displayed that seeds from NZ germinated better in the warm and medium temperature environments than those from native German populations (Table 3.4.1; Fig. 3.5.1). Temporal development patterns of *Achillea millefolium* were affected by the temperature levels but displayed no effects of interaction with the country (Table 3.4.2 on the next page).

Maximum germination rates of *Hieracium pilosella* were very similar under all three temperature regimes when compared between regions, yet differed significantly between temperatures (Table 3.4.1 on the facing page). NZ seeds reached 10% of maximum germination at the medium temperature earlier than German seeds, but showed no such differences between countries at cold and warm temperatures, which resulted in a significant country · temperature interaction effect (Table 3.4.2 on the next page). For later stages of germination (i.e. 50 and 90% of maximum germination) no differences in germination speed were detected.

Maximum germination rates of *Hypericum perforatum* were found to be marginally significantly different between countries (Table 3.4.1 on the facing page). For native populations, the highest maximum germination was detected under warm conditions, whereas for invasive populations it was under medium temperature conditions (Fig. 3.5.1 e, f on page 61). Analysis of temporal development patterns revealed that NZ seeds reached 50 and 90% of maximum germination later than German seeds as indicated by a significant effect of country and significant country · temperature interactions (Table 3.4.2 on the facing page).

3.5 Discussion

With this study we found evidence for differences in seed germination temperature requirements between German and NZ populations for *Achillea millefolium* and *Hypericum perforatum*, confirming our general hypothesis for these species. For the third study species, *Hieracium pilosella*, a similar, yet not statistically significant trend could be observed (Table 3.4.2 on the next page). Differences in germination in invasive populations were also found by Kudoh *et al.* (2007), who described suppressed germination at higher temperatures for invasive, Japanese populations of *Cardamine hirsuta* compared to native European populations. The authors linked these differences in seed dormancy to an adaptation to climatic conditions in Japan. In another recent common garden experiment, Hierro *et al.* (2009) found that germination patterns of *Centaurea solstitialis* varied between two climatically different regions of introduction. They explained these results with the degree of risk *C. solstitialis* experiences at early developmental stages and suggested that rapid adaptations in germination strategies contribute to the success of invasive species.

Table 3.4.1: ANOVA results for the analysis of maximum germination rates. Bold numbers indicate significant effects ($P < 0.05$). Analysis was performed separately for the three species. Bold numbers indicate significant country- and temperature-effects or interactions ($P < 0.05$). Results of the Ryan–Einot–Gabriel–Welsh post-hoc tests indicate the direction of significant differences between categories of each factor. Abbr.: SS = sum of squares, d.f. = degrees of freedom, NZ = New Zealand, DE = Germany, w = warm (20/32°C), m = medium(10/20°C), c = cold(4/8°C).

	Achillea millefolium					*Hieracium pilosella*					*Hypericum perforatum*				
Source of variation	d. f.	Type III SS	F	P	post-hoc	d. f.	Type III SS	F	P	post-hoc	d. f.	Type III SS	F	P	post-hoc
Temperature	2	35018.69	74.66	**<0.001**	w,m>c	2	6408.12	10.71	**<0.001**	w,m>c	2	141687.79	293.56	**<0.001**	w,m>c
Country	1	6424.46	27.39	**<0.001**	NZ>DE	1	966.89	3.23	0.079	n.s.	1	1520.04	6.3	**0.016**	NZ>DE
Temp*country	2	5450.29	11.62	**<0.001**		2	348.45	0.58	0.563		2	852.69	1.77	0.183	
Population(Temp*country)	4	3305.48	3.52	**0.014**		4	12445.18	10.4	**<0.001**		4	487.93	0.51	0.732	
Residual	53	60517.83				53	33329.47				53	155166.86			

Table 3.4.2: ANOVA results for the time elapsed to 10, 50 and 90 percent of maximum germination. Analysis was performed separately for the three species. Bold numbers indicate significant effects or interactions ($P < 0.05$). Results of the Ryan–Einot–Gabriel–Welsh post-hoc tests indicate the direction of significant differences between categories of each factor Abbr.: SS = sum of squares, d.f. = degrees of freedom, NZ = New Zealand, DE = Germany, w = warm (20/32°C), m = medium(10/20°C), c = cold(4/8C).

	Achillea millefolium					*Hieracium pilosella*					*Hypericum perforatum*				
Source of variation	d. f.	Type III SS	F	P	post-hoc	d. f.	Type III SS	F	P	post-hoc	d. f.	Type III SS	F	P	post-hoc
10.00%															
Temperature	2	32255.79	44.78	**<0.001**	w>m>c	2	22441.07	28.27	**<0.001**	w>m,c	2	24232.11	29	**<0.001**	w>m
Country	1	462.22	1.28	0.264	n.s.	1	293.6	0.74	0.376	n.s.	1	821.78	0.98	0.33	n.s.
Temp*country	2	309.46	0.43	0.654		2	3202.79	4.03	**0.03**		2	841	1.01	0.324	
Population(Temp*country)	4	1112.45	0.77	0.549		3	5511.98	4.63	**0.01**		4	4504.22	1.35	0.277	
Residual	52	49654.3				34	52951.47				35	53794			
50.00%															
Temperature	2	52949.68	131.96	**<0.001**	w>m>c	2	20571.85	19.27	**<0.001**	w>m>c	2	15047.11	51.11	**<0.001**	w>m
Country	1	205.55	1.02	0.317	n.s.	1	305.41	0.57	0.456	n.s.	1	1067.11	3.62	0.067	n.s.
Temp*country	2	589.51	1.47	0.241		2	604.45	0.57	0.575		2	1272.11	4.32	**0.047**	
Population(Temp*country)	4	1306.76	1.63	0.1845		3	1930.19	1.21	0.327		4	7399.44	6.28	**0.001**	
Residual	52	63749.25				34	54237.67				35	33028.56			
90.00%															
Temperature	2	58464.42	244.06	**<0.001**	w>m>c	2	14191.43	19.13	**<0.001**	w>m>c	2	5801.36	31.81	**<0.001**	w>m
Country	1	21.67	0.18	0.673	n.s.	1	138.45	0.37	0.547	n.s.	1	1013.36	5.56	**0.026**	n.s.
Temp*country	2	80.8	0.34	0.716		2	398.17	0.54	0.591		2	812.25	4.45	**0.044**	
Population(Temp*country)	4	494.54	1.03	0.402		3	6266.38	5.63	**0.004**		4	68.7.44	9.33	**<0.001**	
Residual	52	64163.19				34	50876.79				35	19540.31			

Differences in germination temperature requirements, as we detected in the present study, might be interpreted as an adaptation to climatic conditions in both regions and to the potential risk the seedlings have to take under these conditions. Compared to native German populations, seeds from invasive NZ populations benefited from medium temperature conditions (10/20C), which corresponds well with the mean temperature of the wettest quarter of the year in NZ when germination can be expected to occur (Table 3.3.1 on page 57). This would, consequently, result in greater establishment rates in invasive populations at such temperatures. While the assumption of genotypic differentiation between native and invasive populations is justified according to this finding, it cannot be validated with the data at hand. A thorough test of this assumption would require reciprocal field trials with more than one generation. Nevertheless, a genetic shift in invasive populations has been demonstrated previously (e.g. Willis *et al.*, 1999; Siemann & Rogers, 2003). Other studies have proven genetic differences in invasive plant species with respect to different climatic patterns, such as oceanic or continental conditions or altitudinal (e.g. Alexander *et al.*, 2009) and latitudinal clines (e.g. Maron *et al.*, 2007). Regional genetic variation has been addressed within non-native regions (Meyer & Allen, 1999; Erfmeier *et al.*, 2010; see Bossdorf *et al.*, 2005 for review) as well as between native and non-native regions (Maron *et al.*, 2007; Leger & Rice, 2007). In the case of our study, the question as to whether the differences between regions reflect genetic differences, effects of the parental environment or maternal effects (or combinations of these factors) cannot be resolved and needs to be addressed in future studies. Furthermore, it cannot be excluded that the observed differences result from stochastic events (see Keller & Taylor, 2008) as only three populations per species and country were incorporated in our study. A greater number of populations sampled within a wider climatic range would be advisable in order to overcome these shortcomings.

Temporal development of germination has rarely been addressed in previous studies on invasive plant species. It has been proven, however, to be significantly different between native and invasive regions at least in one case. Erfmeier & Bruelheide (2005) showed that invasive populations of *Rhododendron ponticum* germinated earlier and faster than native ones. In the present study, germination speed did also differ between regions for *Hieracium pilosella* and *Hypericum perforatum*. The slightly increased germination speed of NZ seeds of *Hieracium pilosella* was only relevant in the beginning at medium temperature, but might contribute to a "head start" in establishment for this species under beneficial temperatures. Nevertheless, the investigation of temporal development patterns may provide contrasting results for other species and at different temperatures. Thus, both effects of temporal dynamics in germination and of environmental variation should be taken into account in future studies.

In general, invasion success has been ascribed to high germination rates (Radford & Cousens, 2000; McAlpine *et al.*, 2008). Accordingly, high germination rates do apply for *Achillea millefolium* and *Hypericum perforatum*. In contrast, for clonal growing species it has been suggested that they do not have to rely exclusively on the production of

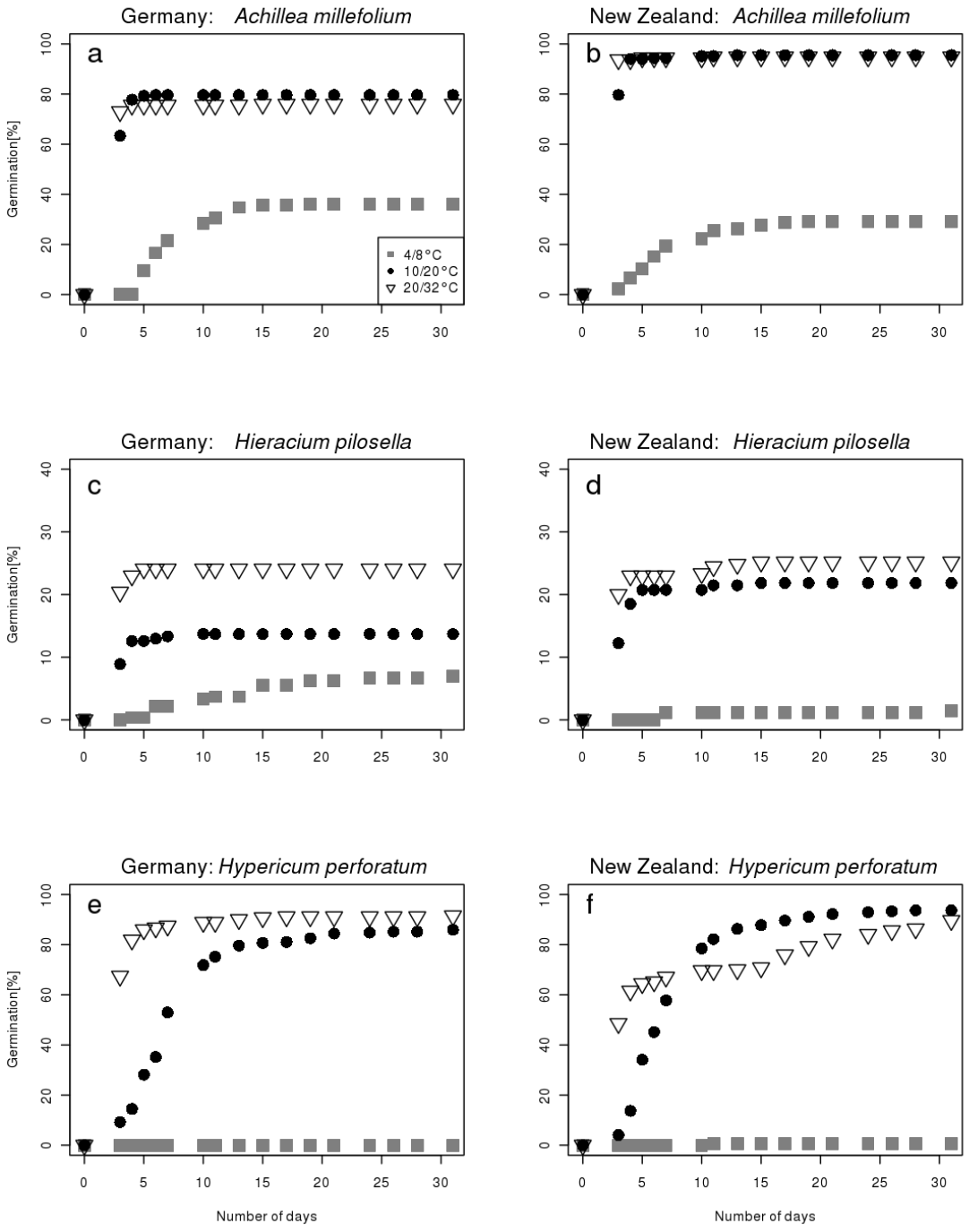

Figure 3.5.1: Mean germination rates of *Achillea millefolium* (a,b), *Hieracium pilosella* (c,d), *Hypericum perforatum* (e,f) seeds from Germany (left) and New Zealand (right) across three different temperature regimes with the time. For statistical details see Table 3.4.1 and Table 3.4.2 on page 59.

seeds in order to successfully invade new areas (Olesen *et al.*, 2004). Nevertheless, in a related field study, we found that *Hieracium pilosella* benefits more from increased sexual reproduction in its invaded range, even though its overall germination rates are comparatively low (Beckmann *et al.*, 2009). That germination is under genetic control has recently been demonstrated by Huang *et al.* (2010) who showed that germination phenology of *Arabidopsis thaliana* is linked to particular regions on chromosomes by performing a quantitative trait-loci analysis. Additionally, maternal effects and the parental environment are known to influence seed germination patterns (Galloway, 2001; Donohue *et al.*, 2005). For minimising these effects, F1 or later generation seeds from plants grown under identical conditions would be necessary (Baskin & Baskin, 2001).

Despite our knowledge on seed germination being an important stage in plant life-history, comparative studies between native and invasive populations remain the exception. Future studies should enable more precise conclusions about the importance of shifts in germination patterns in the invasion success of invasive plant species. As already suggested by Hierro *et al.* (2009), we, therefore, recommend testing for differences in germination patterns, particularly in invasive species that have expanded into different regions with contrasting environmental conditions.

Acknowledgements

We thank the New Zealand Department of Conservation (Te Papa Atawhai) for providing distribution data on the study species, Mary Korver from Manaaki Whenua Landcare Research Institute for shipping assistance, Christine Voigt for her help carrying out the experiment, and Henrik von Wehrden and two anonymous reviewers for useful comments. The study was financially supported by a travel grant from the German State.

4 Reduced tolerance to herbivory on clonal organs in alien genotypes – a multi-species experiment with native and introduced origins.

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4.1 Abstract

Clonal growth may increase the likelihood for alien plants becoming invasive, as it is an efficient foraging and spatial exploration strategy. Here, we investigated the effect of artificial herbivory on organs of clonal growth and its potential to drive post- introduction evolutionary change. Based on the assumption that tolerance traits are costly and that clonal alien species may benefit from investing freed resources into growth, fecundity or nutrient acquisition, we tested the hypothesis of lower tolerance to herbivory on organs of clonal growth in alien plants. In a common-garden experiment we studied divergence in plants from native German and alien New Zealand populations of six species with different clonal growth forms. A nutrient treatment testing the plant's acquisition abilities, was combined with artificial herbivory on clonal organs. We investigated origin-dependent differences in sexual reproduction, plant growth and the production of clonal organs. For aboveground and clonal organ biomass, alien plants showed lower tolerance to artificial herbivory on clonal organs than native plants. In the combined herbivory and nutrient treatment, alien plants of four species grew fewer clonal organs when compared to the nutrient treatment alone. Alien plants of the other two species produced more clonal organs, regardless of treatment. All species revealed significant differences in flower production between origins, with five of them producing more flowers on alien than on native plants. The results support the hypothesis that a release of herbivory on clonal organs has lead to subtle evolutionary changes in tolerance of alien plants and to a species-dependent increase in plant vigour, clonal growth and/or sexual reproduction that may enhance their invasive success.

Keywords: Artificial herbivory, Clonal plants, Germany, New Zealand, Plant invasions, Resistance, Tolerance

4.2 Introduction

The role of herbivory is one of the most prominent research topics in plant invasion ecology and changes in plant-herbivore interactions are the basis for many hypotheses and frameworks for alien plant species success (see Catford *et al.*, 2009; Thorpe *et al.*, 2009). Investments in mechanisms of defence against herbivory are logical from an evolutionary perspective (e.g. Bazzaz *et al.*, 1987; Baldwin, 1998) and it has been demonstrated that herbivory can even drive evolutionary divergence within a few generations after suspension of selection pressure by insect herbivores (Agrawal *et al.*, 2012). In light of these recent advances in evolutionary ecology, research on plant-herbivore interactions within the realm of plant invasion ecology gains evermore importance (Erfmeier, 2013).

Among the most prominent theories in plant invasion research are the enemy release hypothesis (ERH, Keane & Crawley, 2002) and the evolution of increased competitive ability hypothesis (EICA, Blossey & Nötzold, 1995). ERH proposes a loss of herbivory-related constraints as an ecological explanation for successful invasion. EICA predicts that in the absence of herbivores, natural selection favours genotypes that invest fewer resources into mechanisms of defence. Although originally not explicitly addressing tolerance, the EICA hypothesis has since been extended (see Atwood & Meyerson, 2011) and separates resistance (i.e. the ability to protect from herbivore damage) and tolerance (i.e. the ability to compensate for herbivore damage; Strauss & Agrawal, 1999). These two alternatives have been repeatedly addressed as outcomes of post-introductory evolution in plant invasions. For example, Oduor *et al.* (2011) showed that alien populations of *Brassica nigra* had lower tolerance to herbivory than natives. However, upon herbivore exclusion, invasive populations produced more seeds than native ones, indicating a shift from defence towards increased sexual reproduction. In contrast, other studies detected increased tolerance in plants grown from alien populations if compared to native ones (e.g. Stastny *et al.*, 2005; Zou *et al.*, 2008; Carrillo *et al.*, 2014). Similarly, many studies failed to confirm the EICA hypothesis in a general approach while not explicitly testing for effects on tolerance and/or resistance (e.g. Willis *et al.* 2000; Maron *et al.* 2004b; but see Buschmann *et al.*, 2005). Based on these inconclusive results, we argue that for the evolution of tolerance in the alien range, both paths are possible and highly dependent on the specific conditions encountered. This duality and the fact that most previous studies have relied on single-species approaches show that there is a need for further research addressing tolerance in alien plant species, preferably on a multispecies basis.

Some experimental tests of EICA include the simulation of herbivory by clipping a defined quantity of plant parts (e.g. van Kleunen & Schmid, 2003; Meyer *et al.*, 2005) or measuring the amount of damage inflicted on the plants by herbivores (e.g. Buschmann *et al.*, 2005; Meyer & Hull-Sanders, 2008; Joshi & Vrieling, 2005). Most of these studies

focused on leaves or roots, while the impact of herbivory on other parts of the plant, such as organs of clonal growth, has only recently received more attention (e.g. He *et al.*, 2014; Yang *et al.*, 2014). Clonal growth has long been suggested to increase the likelihood of plant species to become invasive in the first place (Baker, 1974; Sakai *et al.*, 2001; Perglova *et al.*, 2009), and indeed, many invasive plant species possess that ability (e.g. Kolar & Lodge, 2001; Liu *et al.*, 2006). In general, organs of clonal growth (in the following, we use the term "clonal organs") allow plants to continuously explore habitat space that might be temporally unavailable to seeds or adult plants (de Kroon & Hutchings, 1995; Givnish, 2002). Therefore, clonal growth contributes to resource foraging, especially in disturbed habitats with heterogeneous resource availability (Baruch & Gómez, 1996; Rejmánek & Richardson, 1996; van Kleunen *et al.*, 2000) where ramets are able to acquire and share resources through clonal integration (e.g. Alpert, 1996). Given the fact that clonal plants have the ability to re-allocate resources to and from their clonal organs Buschmann *et al.* (2006), they should respond differently to herbivory than non-clonal plants. Furthermore, in clonal plants, alternative paths for the evolution of plant traits, e.g. somatic mutations or epigenetic inheritance, may be more important than in non-clonal plants (as discussed in McKey *et al.*, 2010).

Clonal alien plant species may benefit from a loss of herbivory and the predicted freed resources by enhanced overall growth, but also by increased clonal growth, with the consequences of increased spatial exploration and nutrient acquisition (Fig. 4.2.1 on the next page). In contrast to many tests of EICA on non-clonal species (e.g. Strauss & Agrawal, 1999; Fornoni, 2011), we assume that, alien plants of clonal species will show reduced tolerance to herbivory but increased growth and/or fecundity as the outcome of short-term evolution. To our knowledge, these specific effects of loss of herbivory on clonal organs have not yet been explicitly addressed in alien plant species. In order to extend the EICA framework to clonal plant species, we have to assume that under natural conditions all plant parts, including clonal organs, may be subject to herbivory and thus to the evolution of reduced resistance or tolerance to it (Scenario II in Fig. 4.2.1). While there is only scarce knowledge of effects of herbivore damage on clonal organs (but see Scheidel *et al.*, 2003), experiments on clonal integration indicate that herbivory on clonal organs might have strong outcomes: e.g. severing the connections between mother plants and their offspring may lead to changes in growth of the mother-plants (e.g. Alpert, 1996; Wang *et al.*, 2008). In general, all groups of herbivores that also feed on other plant parts can be regarded as potential agents for herbivore damage on clonal organs in grassland species (de Kroon & van Groenendael, 1997): i.e., specialist and generalist herbivorous insects (e.g. aphids), mammals (e.g. small rodents) and other invertebrates (e.g. slugs).

Based on these considerations, we test the extension of EICA as outlined in Fig. 4.2.1 on the following page and hypothesize that clonal plants from alien populations display reduced tolerance to herbivory on clonal organs, if compared with plants from native populations. Theoretically, resources shifted away from investment in tolerance should be allocated toward traits that might provide benefits in the new range, including ei-

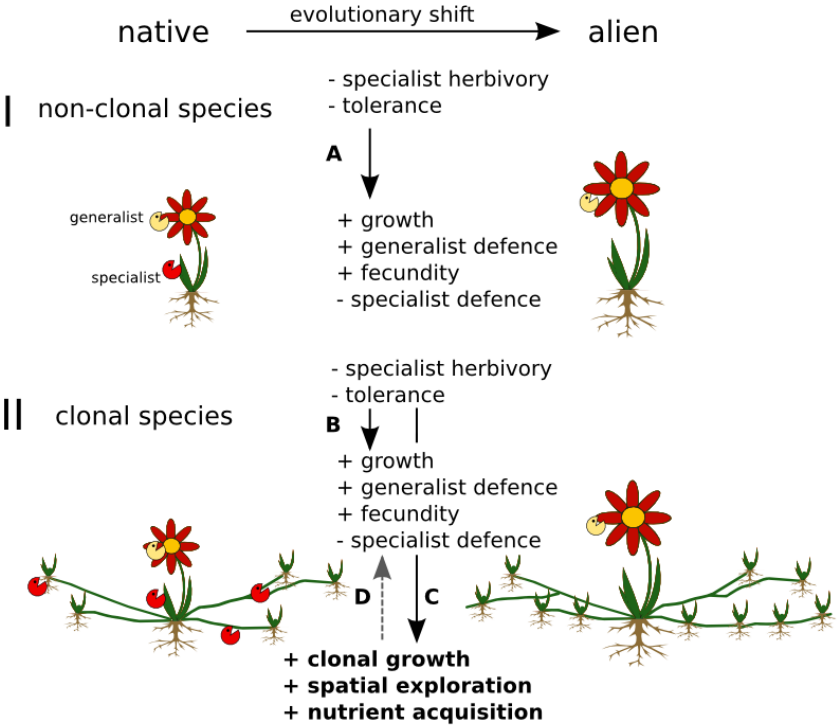

Figure 4.2.1: Illustration of the proposed conceptual framework extending the EICA hypothesis to clonal plant species: demonstration of potential clonal plant species' responses during the introduction into new ranges and upon enemy release. Hypothetically, all alien plant species experience a release from specialist (but not generalist) enemies upon introduction (Scenario I) which may result in a loss of tolerance to herbivory due to the selection of less tolerant specimen in the new range. The resources freed by reduced herbivory and reduced tolerance may be translated into growth, generalist tolerance/resistance and fecundity (a). In clonal species (Scenario II), similar processes may be encountered (b). However, in clonal species, surplus resources may be also allocated to clonal growth which may foster spatial exploration and/or nutrient acquisition (c). This, in turn, may feed back into further (clonal) growth, spatial exploration and nutrient acquisition (d).

ther: (I) in- creased sexual reproduction, (II) increased plant growth and vigour, and (III) increased clonal growth that result in enhanced spatial exploration and nutrient acquisition—or a combination of some of them. We tested these predictions on plants of six clonally growing species native to Europe and that were naturalized in New Zealand (NZ): *Achillea millefolium* L., *Hieracium pilosella* L., *Lotus pedunculatus* Cav., *Leucanthemum vulgare* Lam., *Prunella vulgaris* L. and *Hypericum perforatum* L. These species were all introduced to NZ during the same period of time in the 19th century (Table 4.3.1 on page 68) and possess different types of long-lived organs of clonal growth (according to Klimeš *et al.*, 1997). In a common garden approach, plants from each eight populations by species and country (in total 96 populations) were grown in long boxes to allow lateral spread of clonal organs. The plants were subjected to either equalized or one-sided nutrient distribution treatments which enabled us to observe their spatial

exploration and foraging behaviour through clonal growth. Additionally, we simulated herbivory on clonal organs in combination with the nutrient treatment. We analysed the differences in biomass production, flower production, quantitative and qualitative clonal growth between native and alien origins to identify evolutionary shifts in clonal growth among ranges.

4.3 Materials and Methods

4.3.1 Study species and seed material

Seeds were collected during a field survey of six clonally growing study species, i.e. *A. millefolium* L., *Hieracium pilosella* L., *Lotus pedunculatus* Cav., *Leucanthemum vulgare* Lam., *P. vulgaris* L. and *Hypericum perforatum* L. (Beckmann *et al.*, 2014a), that were also used to carry out the present experiment. Populations were selected from similar geographical distances within Germany and NZ and which comprise a comparable range of environmental conditions (see Table A.2 on page 144 for a complete list of locations and information on altitude, annual mean temperature and annual precipitations). A more detailed description of the selection procedure is given in Beckmann *et al.* (2014a). Seeds were gathered from 15 to 20 plants per population and pooled samples were stored at room temperature until the beginning of the experiment.

Physiologically, clonal organs of the six species represent rhizome, stem and root splitter based forms and vary considerably in their length and position (Klimešová & De Bello, 2009; see Table 4.3.1 on the next page for further information). In a comparison of insect herbivore infestation between NZ and UK populations, Fenner & Lee (2001) describe a release from herbivores in NZ populations of *Hieracium pilosella* and *Leucanthemum vulgare*, whereas for *A. millefolium*, the authors did not record differences in infestation (none in both regions). For the other three species, currently no comparative information on herbivore loads in NZ is available. In the native range, mammalian herbivory on the species is commonly being caused by rabbits, sheep, voles, deer (Bishop & Davy, 1994; Rothmaler *et al.*, 2005). Herbivory on clonal organs, specifically, is rarely addressed, but Bishop & Davy (1994) describe that rabbits feed on the stolons of *Hieracium pilosella*.

4.3.2 Experimental setup

Seeds were sown and germinated in early spring of 2009 in the greenhouse at the Botanical Garden in Halle, Germany. Four weeks after sowing, seedlings were transferred into small (5 x 5 cm) pots with a sand-compost mixture (1:3) and grown further till mid April, when they were planted into containers and placed outside. Altogether 64 plants per species were included in the experiment resulting in a total of 384 (6 species x 2 origins x 8 populations x 4 treatments) individuals studied. We used long plastic boxes (flower window boxes, 20 x 100 cm, volume 16 L, with drain holes) in order to investigate lateral spread through clonal growth of every single planted individual in the centre. The

Table 4.3.1: Overview of the study species. Description of distribution refers to Rothmaler et al. (2005), time of first records in NZ to Webb et al. (1988). Clonal growth type or type combinations and lateral spread per year as given in the CLO-PLA database (Klimešova & De Bello 2009).

	Achillea millefolium	*Hieracium pilosella*	*Hypericum perforatum*	*Lotus pedunculatus*	*Leucanthemum vulgare*	*Prunella vulgaris*
Native range	Europe, Siberia	Europe	Europe, Western Asia	Eurasia	Europe, Western Siberia	Eurasia
Alien range	Americas, Australia, New Zealand	Americas, Australia, New Zealand, Southern Africa	Americas, Australia, New Zealand	Americas, Australia, New Zealand	Americas, Australia, New Zealand	Americas, Australia, New Zealand
Clonal growth type	hypogeogenous stem (rhizome)	horizontal above-ground stem, epigeogenous stem	root-splitter, roots with adventitious buds	root-splitter, hypogeogenous stem (rhizome)	epigeogenous stem	horizontal above-ground stem
Lateral spread per year	> 25 cm	> 25 cm	> 25 cm	> 25 cm	1 - 25 cm	1 - 25 cm
First recorded in NZ	1867	1878	1869	1867	1867	1867

boxes were separated into three zones: a central zone of 16 cm length where the plants were placed and two approximately 42 cm long zones on opposite sides into which the plants were able to expand. These zones were marked by a waterproof pen and were subsequently used for nutrient fertilization and artificial herbivory treatments and referred to for separating the above- and below-ground biomass during harvest. The boxes were filled with 16 L of a mixture of sterilized standard soil that contained only a minimum level of nutrients (Einheitserde Typ O, Hamel/Tucher, Sinnthal-Jossa, Germany) and sand (2:1). Subsequently, 9.6 g of a nitrogen-phosphate- potassium complex fertilizer (Basacote 6M, Compo, Münster, Germany) with controlled continuous nutrient release over a period of 6 months were added manually to each box. Altogether, each box contained 553 approximately 1536 mg nitrogen, 768 mg phosphate and 1152 mg potassium. A directional nutrient treatment was created by adding the fertilizer in half of the boxes, i.e. 192, to only one (randomly selected) side (termed: one-sided nutrient treatment), while in the remaining 192 boxes, the same amount of fertilizer was equally distributed over both sides (termed: homogeneous nutrient treatment). Within the central zone of 8 cm in both directions around each plant no nutrient pellets were added in any of the boxes. Calculated daily release of nutrients in the one-sided nutrient treatment was 0.53 mg N, 0.27 mg P and 0.5 mg K per litre soil. Herbivore exclusion was crucial for our experiment to avoid uncontrolled herbivory on other than clonal organs. We excluded insect herbivores by applying a systemic, long term effective insecticide (Perfekthion, active ingredient dimethoate, BASF, Schwarzheide, Germany). This was done at the beginning of the experiment and after the 2nd and 4th month. In order to exclude slug herbivory we distributed snail repellents between the boxes every 3 weeks (Schneckenkorn, active

ingredient metaldehyde, Bayer, Leverkusen, Germany).

All boxes were positioned randomly in 16 rows on a flat non-shaded area (appr. 15 x 40 m) in the Botanical Garden of Halle (N 51.489712°, E 11.961108°). We allowed 20 cm of distance between boxes and 60 cm between rows in order to reduce the potential effects of shading among plants and to provide access to the boxes. The boxes and the surrounding area were weeded regularly.

The experimental setup was subjected to natural rainfall and additional water was provided to avoid drought stress. During the course of the experiment, some plants started to grow above-ground organs sideways away from the boxes (especially *Hieracium pilosella* and *Lotus pedunculatus* plants); in these cases we used small wooden sticks that were placed along the outer side of the boxes in order to restrict lateral spread only to the two directions provided by the boxes. This was controlled for and repeated, if necessary, once a week.

The artificial herbivory treatment took place on July 31st, 15 weeks after the start of the experiment. In a fully crossed design, half of the experimental units, i.e. 192 boxes, were assigned to the artificial herbivory treatment aimed at mimicking non-selective natural herbivory. For all these plants, we counted the total number of clonal organs and subsequently cut off 50 % of clonal organs on both sides of the box; in case of unequal numbers we rounded up in favour of cutting. The cutting took place approx. 8 cm away from the plant centre. In the case of plants with below- ground clonal organs (i.e., *Hypericum perforatum, Lotus pedunculatus* and *A. millefolium*), we carefully removed the top soil in order to count and cut the clonal organs. Prior to the harvest, we quantified plant growth by measuring height and counting the number of units of sexual reproduction (*Hypericum perforatum*: flowers or capsules; *A. millefolium*: disk flowers; *Lotus pedunculatus*: flower buds; *Hieracium pilosella*, *Leucanthemum vulgare*: flower heads; *P. vulgaris*: inflorescence clubs, henceforth we refer to all of them simply as "flowers"). Clonal organs were counted separately for the two sides of the boxes and, if necessary, using the method described above to access clonal organs below-ground.

Harvesting of above ground biomass began on September 17th 2009 and was done separately for the three zones described above. Above-ground clonal organs were separated and all samples were dried for 2 days at 80 °C and weighed. The below-ground root biomass and below-ground clonal organ biomass were harvested by separating the soil block with a knife into three parts according to the three zones. From the resulting 1152 samples, soil was shaken off and the root and clonal organs containing lumps were washed individually to remove any leftover soil. Clonal organs and roots were separated if applicable. Samples were dried and weighed as described above.

4.3.3 Tolerance calculation

Tolerance to herbivory is a measure of compensatory growth and plant fitness and therefore relies on information about reproductive success. In this study, we followed Pan & Price (2001), who argue that in clonal species, fitness is not only measurable in sexual reproduction but also in clonal growth. Therefore, we calculated tolerance as the proportion of clonal organ-, below- and above-ground-biomass of damaged (i.e. plants that received artificial herbivory treatment) vs. undamaged plants. Tolerance quantifies compensatory growth: a tolerance value of 1 indicates that damaged and undamaged plants had the same fitness (i.e. complete compensation of herbivory damage took place); whereas lower and higher values indicate an under- or overcompensation, respectively (i.e. damaged plants have a reduced or higher fitness than undamaged plants). We therefore, calculated tolerance by dividing biomass measurements of control plants (i.e. plants that were not treated with artificial herbivory) by biomass of clonal organs of plants that had been subjected to herbivory treatment.

4.3.4 Statistical analysis

Calculated tolerance data were square-root trans- formed and analysed with a mixed-model using R (R 2.15.1, package "lme4", function "lmer"; Bates *et al.*, 2012). Country of origin (Germany, NZ), nutrient treatment (homogeneous nutrients, one-sided nutrients) and species were implemented as fixed factors. Populations nested within species and origins were considered random. Since the number of clonal organs and the clonal organ biomass were determined on two sides of the boxes we calculated their means by box and used these values for the statistical analysis. All variables measured (number of clonal organs, number of flowers, above-ground biomass, root biomass and clonal organ-biomass) were then checked for normality of distribution and log or square-root transformed where appropriate (as recommended by Zuur *et al.*, 2009). The resulting data were analysed with mixed models ("lmer") in two ways: as a full model and separately for each species. The full model contained country of origin, species identity, nutrient treatment, artificial herbivory treatment and their interactions as fixed factors and populations nested within species and country as random factor. The species-specific model was run accordingly without the fixed factor species. Linear mixed-effects models were fitted using restricted maximum likelihood (REML). For all models, the "anovaTAB" function from the MixMod package (Kuznetsova & Brockhoff, 2012) was used to derive type III sum of squares, F values and the "summary" function to derive variances of random intercepts and p values from these models.

Table 4.4.1: Results of a linear mixed model analysis on the tolerance to herbivory on clonal organs for entire set of the six study species. Herbivory tolerance was calculated based on clonal organ biomass, above ground biomass and below ground biomass. Bold numbers indicate significant country, species or treatment effects or their interactions; denDF = Denominator degrees of freedom; numDF = Numerator degrees of freedom; *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$.

			Clonal organ biomass		Above ground biomass		Below ground biomass	
	denDF	numDF	F-value	p-value	F-value	p-value	F-value	p-value
Country	86	1	5.759	**0.019***	7.779	**0.007***	0.372	0.544
Nutrient treatment	82	1	0.518	0.474	6.952	**0.010***	0.454	0.502
Species	86	5	1.132	0.284	0.145	0.985	0.1	0.954
Country × nutrient treatment	82	1	1.033	0.321	0.712	0.401	0.038	0.845
Species × nutrient treatment	82	5	1.827	0.12	2.286	0.054	1.744	0.134

4.4 Results

4.4.1 Tolerance to artificial herbivory on clonal organs

Country of origin had a significant effect on plant tolerance to artificial herbivory on clonal organs when analysed together for all species for two of the tolerance measurements (Table 4.4.1; Fig. 4.4.1 on the next page). When tolerance was calculated based on biomass of clonal organs and above ground biomass, plants from NZ (alien) populations had lower tolerance (indicated by a mean tolerance <0) and therefore did undercompensate for experimental herbivory on clonal organs. German (native) plants showed a tendency to overcompensate for artificial herbivory (Fig. 4.4.1a, b). This pattern was influenced by the nutrient treatment when tolerance was calculated for above ground biomass alone but not by species identity (Table 4.4.1). Tolerance calculated for belowground biomass indicated no significant difference between origins (Fig. 4.4.1c).

4.4.2 General effects on clonal organs, biomass and sexual reproduction

The analysis of the full model showed consistent significant effects of the treatments (artificial herbivory, nutrients) for most of the variables and revealed strong differences among the target species in number of clonal organs, clonal organ biomass, above ground biomass, root biomass, number of flowers per plant (Table 4.4.2 on page 73). Variables related to clonal organs (number and biomass) displayed significant country x artificial herbivory interactions, thus indicating an overall different response to artificial herbivory depending on the native vs. invasive origin of the plants across all species. While for root biomass and the number of flowers, a significant country effect displayed an overall increased invasive performance across species, significant species x country interactions in four response variables indicate that the species did not respond consistently between the countries of origin. In addition, the artificial herbivory and nutrient treatments had

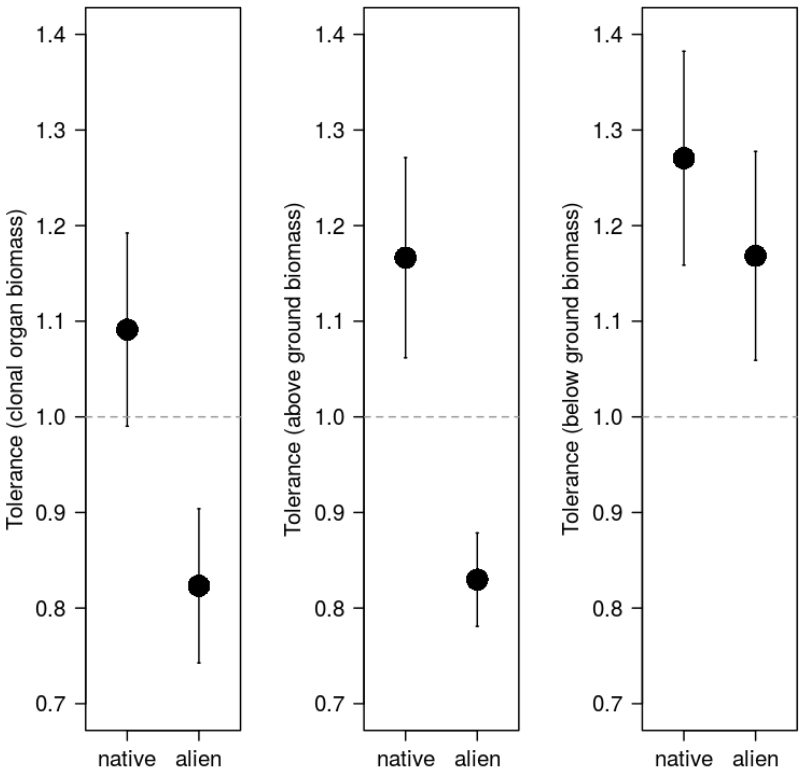

Figure 4.4.1: Tolerance to herbivory on clonal organs. Tolerance was calculated as the proportion of biomass on untreated plants versus plants that received herbivory treatment. (a) Tolerance calculated for clonal organ biomass; (b) tolerance calculated for above ground biomass; (c) tolerance calculated for below ground biomass. Native origins refer to German and alien origins to New Zealand populations. See text for statistical details

different effects on the different species as indicated by significant species x treatment interactions.

4.4.3 Species-specific responses: clonal organs

Species-specific analysis revealed that invasive NZ plants of *Hypericum perforatum*, *Leucanthemum vulgare* and *P. vulgaris* produced more and *Lotus pedunculatus* fewer clonal organs regardless of the artificial herbivory treatment (Table 4.4.3 on page 75; Fig. 4.4.2c-f). In the other two species, the production of clonal organs on NZ plants was reduced only when the herbivory was simulated: i.e. non-herbivory treated *A. millefolium* and *Hieracium pilosella* plants did not differ in the production of clonal organs between countries while, in these species, the artificial herbivory treatment reduced the production of clonal organs in plants from NZ (Fig. 4.4.2a, b; Table 4.4.3). Furthermore, the one-sided nutrient treatment resulted in a significantly reduced production of clonal organs in all species but *Hypericum perforatum* (Fig. 4.4.2 on page 74). For *Lotus pedunculatus*, in ad-

Table 4.4.2: Summary table of the full mixed-model analysis on the number of clonal organs, clonal organ-biomass, above-ground biomass, root biomass and the number of flowers. Bold numbers indicate significant country, species or treatment effects or their interactions; ***, $p < 0.001$; **, $p < 0.01$; * $p < 0.05$; denDF = Denominator degrees of freedom; numDF = Numerator degrees of freedom.

	Number of clonal organs per plant	Clonal organ biomass	Above-ground biomass	Root biomass	Number of flowers per plant
	F-value	F-value	F-value	F-value	F-value
Country	0.08	2.06	1.65	4.03*	**18.68*** **
Species	**16.62*** **	**67.89*** **	**64.18*** **	**14.58*** **	**133.39*** **
Herbivory treatment	0.15	**14.68*** **	**15.99*** **	**8.94** **	**5.28***
Nutrient treatment	**50.5*** **	**4.32***	**10.36** **	**6.25***	**5.56***
Country*Species	**9.1*** **	**2.48***	**4.96*** **	1.47	**9.96*** **
Country*Herbivory treatment	**7.0** **	**4.61***	2.94	0.19	0.25
Species*Herbivory treatment	**4.74*** **	1.85	1.56	**3.46** **	1.4
Country*Nutrient treatment	0.42	0.01	0.97	0.01	0.02
Species*Nutrient treatment	**4.89*** **	**3.78** **	**7.15*** **	0.98	**2.77***
Nutrient treatment*Herbivory treatment	**7.59** **	0.15	1.3	0.01	0.05
Country*Species*Herbivory treatment	1.26	1.61	1.19	2.22	0.19
Country*Species*Nutrient treatment	0.95	0.84	1.36	0.25	0.1
Country*Nutrient treatment*Herbivory treatment	**8.73** **	0.27	2.24	0.46	1.05
Species*Nutrient treatment*Herbivory treatment	**2.54***	1.88	**2.82***	1.89	0.49
Country*Species*Nutrient treatment*Herbivory treatment	1.16	1.45	0.35	0.35	1.71

dition, the combination of the one-sided nutrient and simulated herbivory treatment led to a strong reduction in the number of clonal organs. The analysis of the overall clonal organ biomass per pot revealed partially contrasting results (Table 4.4.3, Figure A.5 on page 149 in electronic supporting information). There were no significant country effects except for *Lotus pedunculatus* with lower biomass values in NZ plants. Overall, significant effects of artificial herbivory were encountered for *A. millefolium*, *Hypericum perforatum* and *Lotus pedunculatus* with reduced clonal organ biomass in response to simulated herbivory (Table 4.4.3 on page 75, Figure A.5 on page 149). However, *Hieracium pilosella* and *Hypericum perforatum* displayed a significant country by herbivory interaction, indicating higher clonal organ biomass of NZ plants without simulated herbivory but lower or similar values when herbivory was simulated, whereas German populations of these species displayed no such trend.

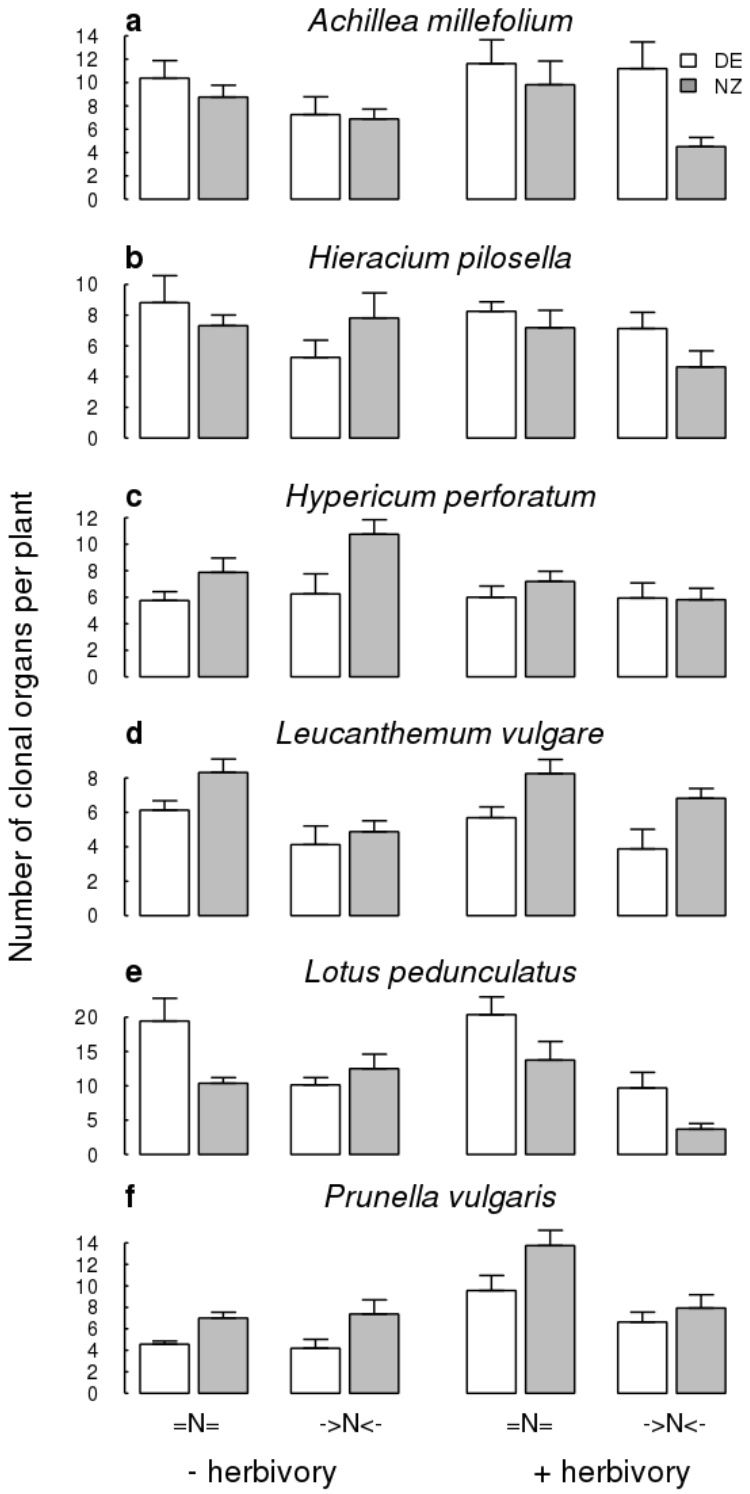

Figure 4.4.2: The number of clonal organs of *Achillea millefolium* (a), *Hieracium pilosella* (b), *Hypericum perforatum* (c), *Leucanthemum vulgare* (d), *Lotus pedunculatus* (e) and *Prunella vulgaris* (f) in response to the artificial herbivory treatment. Bars show means per pot and standard errors. Abbreviations for nutrient treatments: ->N<- one-sided nutrients, =N= homogeneous nutrients. DE refers to native German origins and NZ to alien origins from New Zealand

Table 4.4.3: Summary table of the mixed-model analysis on the number of clonal organs, clonal organ-biomass, above-ground biomass, root biomass and the number of flowers. The analysis was conducted separately for each species using subsets of 64 pots each. Bold numbers indicate significant country or treatment effects or their interactions; ***, $p < 0.001$; **, $p < 0.01$; * $p < 0.05$; denDF = Denominator degrees of freedom, numDF = Numerator degrees of freedom.

	den DF	num DF	*Achillea millefolium* F-value	*Hieracium pilosella* F-value	*Hypericum perforatum* F-value	*Leucanth. vulgare* F-value	*Lotus pedunculatus* F-value	*Prunella vulgaris* F-value
Number of clonal organs per plant								
Country	14	1	2.58	0.73	**5.46***	**15.3*****	**9.92****	**7.72***
Herbivory treatment	42	1	0.06	0.26	3.16	0.06	**5.96***	**14.05*****
Nutrient treatment	42	1	**10.46****	**10.41****	0.08	**16.21*****	**26.38*****	**8.78****
Country*Herbivory treatment	42	1	**4.26***	**6.33***	3.79	1.46	2.53	1.89
Country*Nutrient treatment	42	1	1.08	0.01	0.23	**5.28****	0.32	0.12
Herbivory treatment*Nutrient treatment	42	1	0.09	0.01	2.36	0.02	**11.05****	0.54
Country*Herbivory treatment*Nutrient treatment	42	1	4.47	2.16	2.05	0.75	3.75	0.32
Clonal organ biomass								
Country	14	1	1.58	0.26	0.44	0.01	**12.06****	0.7
Herbivory treatment	42	1	**8.98****	1.35	**16.62*****	0.11	**6.73***	0.22
Nutrient treatment	42	1	0.53	3.14	**10.17****	**7.19****	0.07	**4.84***
Country*Herbivory treatment	42	1	0.02	**5.87***	**8.28****	0.13	0.56	2.87
Country*Nutrient treatment	42	1	1.52	1.63	0.66	0.06	0.01	1.42
Herbivory treatment*Nutrient treatment	42	1	0.17	0.37	**4.45***	2.37	1.1	0.29
Country*Herbivory treatment*Nutrient treatment	42	1	0.14	1.93	0.45	2.03	0.13	2.21
Above-ground biomass								
Country	14	1	1.34	0.16	0.7	**11.23****	**5.03***	1.08
Herbivory treatment	42	1	0.3	0.85	**8.12****	**8.44****	**12.81*****	0.24
Nutrient treatment	42	1	2.91	2.99	1.36	**11.57****	**7.35****	2.12
Country*Herbivory treatment	42	1	0.85	**5.29***	2.72	1.46	**5.77***	0.47
Country*Nutrient treatment	42	1	1.66	2.81	0.84	0.15	2.9	2.81
Herbivory treatment*Nutrient treatment	42	1	0.01	1.93	**8.27****	0.03	**10.3****	1.91
Country*Herbivory treatment*Nutrient treatment	42	1	1.97	0.76	2.66	0.01	3.19	0.12
Root biomass								
Country	14	1	0.98	0.51	0.33	**6.14***	3.81	0.83
Herbivory treatment	42	1	1.83	0.01	0.89	**11.22****	**4.75***	0.35
Nutrient treatment	42	1	2.3	1.03	1.76	3.99	0.13	1.89
Country*Herbivory treatment	42	1	1.03	0.01	**5.95***	3	0.31	0.8
Country*Nutrient treatment	42	1	0.21	0.94	0.01	0.66	0.76	0.86
Herbivory treatment*Nutrient treatment	42	1	1.52	0.27	0.48	1.54	0.04	1.32
Country*Herbivory treatment*Nutrient treatment	42	1	0.14	1.62	0.75	0.09	2.49	0.51

Table 4.4.3 continued

	den DF	num DF	*Achillea millefolium* F-value	*Hieracium pilosella* F-value	*Hypericum perforatum* F-value	*Leucanth. vulgare* F-value	*Lotus pedunculatus* F-value	*Prunella vulgaris* F-value
Number of flowers per plant								
Country	14	1	**4.37***	2.04	**4.51***	**28.53*****	**62.68*****	**4.98***
Herbivory treatment	42	1	0.29	2.2	2.45	0.01	2.53	1.47
Nutrient treatment	42	1	0.76	**8.42****	**4.32***	0.31	0.48	0.12
Country*Herbivory treatment	42	1	0.81	0.6	0.06	0.82	0.01	1.19
Country*Nutrient treatment	42	1	1.24	0.01	0.01	0.6	0.05	0.05
Herbivory treatment*Nutrient treatment	42	1	2.6	**3.98***	0.09	0.04	0.47	1.55
Country*Herbivory treatment*Nutrient treatment	42	1	0.74	**4.15***	1.64	2.16	1.14	1.88

4.4.4 Species-specific responses: sexual reproduction and growth

Five of the six study species revealed significant differences between countries in the production of flowers per pot (Table 4.4.3 on the preceding page; Fig. 4.4.3a, c-f). While *A. millefolium, Hypericum perforatum, Lotus pedunculatus* and *P. vulgaris* showed generally higher flower production on NZ plants, it was lower on NZ plants of *Leucanthemum vulgare* (Fig. 4.4.3e). NZ genotypes of *Lotus pedunculatus* and *Leucanthemum vulgare* also showed an overall increased above- ground biomass production, whereas for *Leucanthemum vulgare*, root biomass production was significantly greater in invasive populations (Table 4.4.3, Fig. A.6 on page 150).

In response to the artificial herbivory treatment, *Lotus pedunculatus* and *Leucanthemum vulgare* displayed an overall reduction both of above-ground and root biomass production, whereas *Hypericum perforatum* reduced only above-ground biomass when treated with simulated herbivory on clonal organs (Table 4.4.3 on the preceding page). Furthermore, for *Hypericum perforatum*, *Hieracium pilosella* and *Lotus pedunculatus*, significant country x herbivory interactions in either above-ground or root biomass production revealed that less above- or belowground biomass was

4.5 Discussion

4.5.1 Loss of tolerance to artificial herbivory on clonal organs in alien populations

For a majority of the studied species, we found undercompensation of artificial herbivory in alien plants when compared to native origins, thereby confirming our main hypothesis that populations in the introduced range in NZ have become less tolerant to herbivory on clonal organs. In the context of biological invasions, changes in tolerance can be addressed in the framework provided by the EICA hypothesis (Blossey & Nötzold, 1995), which more specifically predicts that a release from specialist herbivores is most beneficial

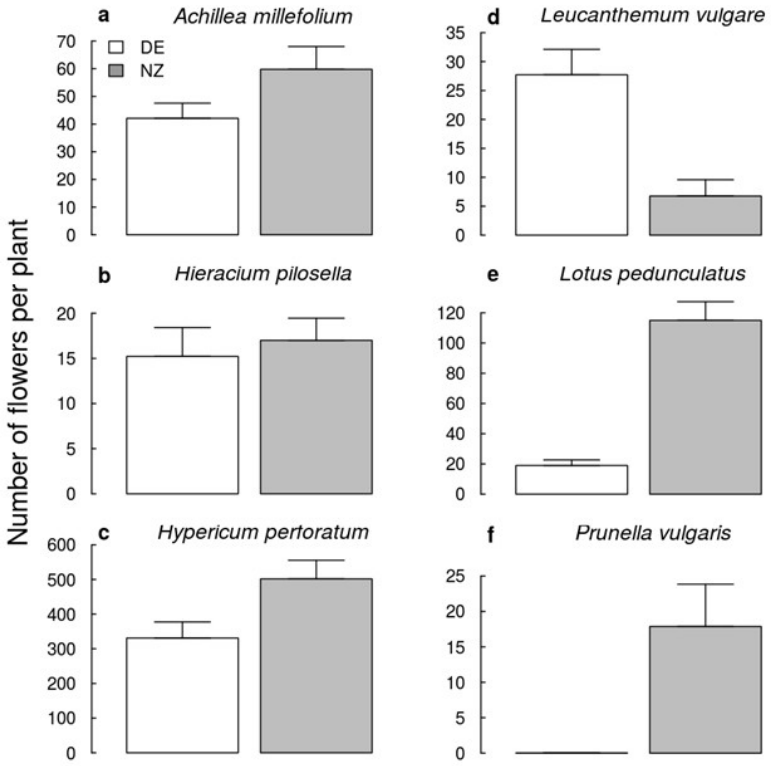

Figure 4.4.3: Number of flowers per plant of *Achillea millefolium* (a), *Hieracium pilosella* (b), *Hypericum perforatum* (c), *Leucanthemum vulgare* (d), *Lotus pedunculatus* (e) and *Prunella vulgaris* (f). Bars show means per pot and standard errors.

during plant invasion and may potentially lead to changes in tolerance (Fornoni, 2011). However, understanding the role of tolerance during plant invasions is complicated by the fact that not only increased, but also decreased tolerance in alien populations may be interpreted as being beneficial when invading new areas: the absence of specialist herbivores potentially induces decreased tolerance to specialists and can lead to the evolution of increased resistance or tolerance to generalists (e.g. Joshi & Vrieling, 2005; Liu & Stiling, 2006; Huang *et al.*, 2010) but can also induce more vigorous or more fecund plants. (Oduor *et al.*, 2011) described a loss of tolerance in invasive *Brassica nigra* which may have enabled the relocation of resources into growth or fecundity. Based on experiments conducted on the same species, Lankau (2007) concluded that specialist and generalist herbivores possess differential selective value on chemical defence traits.

Nevertheless, not all differences between native and invasive provenances can be ascribed to post- introductory evolutionary change and fit into the EICA framework. The fact that sampling of native populations was restricted to Germany and did not cover the entire native range might have hindered capturing some of the differences between native and introduced populations over their entire distribution ranges. Furthermore, plants from native populations might have benefited from local adaptation to non-identified environmental differences between the two countries despite our standardised selection

of populations with environmental conditions comparable between countries. An alternative explanation is the introduction of pre-adapted genotypes from the native range; where phenotypic differentiation reflects prior-introduction divergence rather than recent evolution (Montague *et al.*, 2008; Bossdorf *et al.*, 2008). However, most previous examples have attributed such findings to climate-associated factors (e.g. altitudinal and latitudinal clines) that act as a pre-selective barrier to colonization (Theoharides & Dukes, 2007). Whether pre-selection is as important for more dynamic factors, such as encountered in plant-herbivore interactions, remains to be tested.

4.5.2 Shift towards sexual reproduction or growth

Increased sexual reproduction of introduced populations was found for four species in the present study, which confirms this common outcome of observational studies (e.g. Woodburn & Sheppard, 1996; Bastlova & Kvet, 2002; Erfmeier & Bruelheide, 2004) and of experimental studies (e.g. Blumenthal & Hufbauer, 2007; Daws *et al.*, 2007; Morrison & Mauck, 2007; Meyer & Hull-Sanders, 2008). However, only for *Hieracium pilosella*, the observed increase in sexual reproduction was exclusively related to artificial herbivory. Thus, *Hieracium pilosella*, one of the most abundant invaders of dry grasslands in the South Island of NZ, provides some evidence for a release from clonal-related herbivory and enhanced sexual reproduction. Notwithstanding, increased sexual reproduction might be attributable to alternative drivers of differentiation such as differences in competition or environmental conditions (Beckmann *et al.*, 2012). Furthermore, in agreement with several other studies (Willis *et al.*, 2000; Thébaud & Simberloff, 2001; Maron *et al.*, 2004b) we did not find evidence for increased biomass production of alien populations, and therefore no indication for a shift in resource reallocation from tolerance to growth in general. In contrast, shifts in resource allocation towards clonal growth have been found for the majority of the species. Here, alien populations showed increased clonal growth when only the nutrient treatment was applied but performed worse in comparison to native populations when the artificial herbivory was additionally applied.

4.5.3 The role of the clonal growth form

In this study on the effects of herbivory on clonal organs, we found considerable variation in responses to simulated herbivory as displayed by the six study species. Three species showed reduced growth in clonal organs in alien plants, while native plants displayed increased or similar levels in response to the herbivory treatment. Shifts from tolerance to artificial herbivory towards growth and reproduction were only observed in species with long and fast growing clonal organs (*A. millefolium*, *Hieracium pilosella*, *Hypericum perforatum*, *Lotus pedunculatus*). For species that produce relatively short clonal organs (*Leucanthemum vulgare*, *P. vulgaris*), such shifts were not detected. These results indicate that the type of clonal growth form should be considered when addressing clonal alien species, as different types of clonal growth may vary in their responses to

new environments. Increased numbers of clonal organs in alien plants (at least in the absence of artificial herbivory) indicate that alien populations can profit from enhanced foraging. Similarly, although not interpreted as such by the authors, Chun (2011) showed potentially increased foraging of invasive populations of *Lythrum salicaria* by increased shoot production of invasive populations in a high nutrient treatment only. Based on the results of the present and further studies that detected increased clonal growth of alien populations (e.g. Jakobs *et al.*, 2004; Brown & Eckert, 2005; Barney *et al.*, 2009), it seems that changes in clonal growth are quite common during plant invasions. We thus suggest that future studies should also take clonal integration and aspects of competition of clonal organs more explicitly into account as these may interact both on intra- and inter-specific levels.

4.5.4 Conclusions

Even though we conducted an experiment involving a set of artificial constraints (e.g. confinement to boxes, unlimited resources, absence of competition, herbivore exclusion, early life stage of perennial plants) far from those encountered in natural populations of these species, we argue that the results allow for generalizations as we found some consistency in responses across a set of species from different taxonomic groups and for different types of clonal growth. The observed reduction of tolerance to artificial herbivory on clonal organs might help explain the high success of clonal species among plant invaders (e.g. Sakai *et al.*, 2001; Liu *et al.*, 2006). In order to further test the extension of the EICA framework for clonal invasive species that we propose in this study, field observations that quantify herbivory effects on clonal organs between native and alien regions are needed. These studies should also investigate the role of generalist and specialist herbivores on clonal species and consider other forms of clonal growth, e.g. short-lived clonal organs or bulbs.

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5 The role of UV-B radiation in the invasion of *Hieracium pilosella* - a comparison of German and New Zealand plants

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5.1 Abstract

Intensity of ultraviolet-B radiation (UV-B) differs between northern and southern hemispheres. Therefore, exotic plants species that originate from the northern hemisphere provide an opportunity to study the effects of UV-B on plant physiology and growth, and their implications for the role of adaptation and phenotypic plasticity during plant invasion on the southern hemisphere.

We conducted a growth-chamber experiment with and without UV-B on *Hieracium pilosella* plants from Germany, where the species occurs natively and New Zealand (NZ), where it is invasive. We tested the hypothesis that: (i) *Hieracium pilosella* plants respond to UV-B with high phenotypic plasticity, demonstrating the ability to react to changes in UV-B, and (ii) NZ plants are better adapted to UV-B than German plants as a result of directional selection of well adapted phenotypes.

Consistent with our first hypothesis *Hieracium pilosella* plants reacted plastically to UV-B by producing longer foliar hairs and a higher leaf dry matter content (LDMC) when they were treated with UV-B regardless of their origin. Additionally, irrespective of the treatment, plants from NZ displayed a higher LDMC and grew less but longer leaves than German plants. Plants showed typical stress responses and a reduction in growth caused by the UV-B treatment: below-ground biomass and production of ramets were reduced when plants were treated with UV-B. *Hieracium pilosella* proved to be particularly well predisposed to grow in areas of high UV-B radiation.

Our findings hint at the necessity to consider UV-B radiation in future research on mechanisms of invasions in regions with high UV-B irradiation. Species that provide the

ability to respond directly to UV-B might have an advantage to invade these areas. As UV-B intensity is likely to change in the future due to ongoing ozone depletion, research addressing the effects of UV-B during plant invasions is of increasing importance.

Keywords: Adaptation, Biological invasions, Global change, *Hieracium pilosella*, Phenotypic plasticity, Ultraviolet radiation

5.2 Introduction

The increase of ultraviolet-B (UV-B, 280–315 mm) radiation penetrating the biosphere (Erickson *et al.*, 2000; McKenzie *et al.*, 2007) as a result of stratospheric ozone reduction might have a – yet unknown – impact on other aspects of global change, such as the spread of exotic plant taxa. However, these interactions remain widely unstudied (Environmental Effects Assessment Panel, 2008). Biological invasions are the outcome of the anthropogenic range expansion of organisms, and their ecological and economical impacts pose a great challenge for future generations (Vilà *et al.*, 2010). Various studies have demonstrated that introduced populations often experience new abiotic and biotic conditions they have to cope with (Callaway & Ridenour, 2004). In many regions of the southern hemisphere these populations are coincidentally subjected to, by trend, higher UV-B exposure when compared to the northern hemisphere (Godar, 2007). Therefore, it can be expected that many introduced populations have been growing under high levels of UV-B for a relatively long period of time. Comparing plants from these populations with plants from similar latitudes, altitudes and climatic conditions on the northern hemisphere provides an opportunity to study the effects of differences in UV-B on selection regimes and plant performance during invasion. Based on this scenario, our hypothesis is that plants from invasive populations (high UV-B) would show better adaptation to UV-B than plants from native populations (lower UV-B).

The amount of radiation that penetrates the atmosphere differs fundamentally between northern and southern hemispheres (Godar, 2007). Among other factors, this may be attributable to the distribution of atmospheric dust particles, the inclination of the earth and the elliptical orbit the planet follows (Herman *et al.*, 1997; McKenzie *et al.*, 2011). The earth is farthest away from the sun when there is summer on the northern hemisphere but winter on the southern hemisphere and vice versa when it is closest to the sun (Hay *et al.*, 1997). In consequence, many regions of the southern hemisphere have historically been subjected to higher UV-B irradiation when compared to the same meteorological season and latitude on the northern hemisphere. Additionally, the outer regions of the ozone hole over Antarctica reach as far as New Zealand, Southern Australia and Southern South America (Herman *et al.*, 1996). Seckmeyer & McKenzie (1992) quantified the difference in UV-B in Lauder, New Zealand (NZ), and Neuherburg, Southern Germany, at comparable season, latitude and altitude and detected an almost twofold higher amount of UV-B that reaches the surface in NZ. Nevertheless, the determination of UV-B doses has proven to be complex and is influenced by a great number of factors, therefore,

presumptions of historical UV-B doses contain some uncertainty (McKenzie *et al.*, 2011).

During the last two decades a growing number of studies have investigated the effects of UV-B on plant responses and our understanding of processes involved has made a tremendous leap forward. UV-B has proven to induce negative effects at multiple organisational levels of plant performance. Reactive oxygen species (ROS), which are formed by UV-B, have been identified as a main source of stress (Parsons & Fry, 2010) as they inflict damage to plants at a cellular and molecular level (Björn, 1996; Brosché & Strid, 2003). Plant cells respond to UV-B damage with reparative and protective processes, for example by increasing the production of antioxidant enzymes and flavonoids (see Harborne & Williams, 2000; Jenkins, 2009; Kuhlmann & Müller, 2010, for an overview) or decreases growth regulating phytohormone concentrations (Yang *et al.*, 2004), which, represent typical responses to stress as they can also be encountered in response to herbivore damage (e.g. Schmelz *et al.*, 2003). UV-B can also impact photosynthetic performance of plants by reducing maximum photosynthetic yield (Xiong & Day, 2001; Jansen *et al.*, 2010; Albert *et al.*, 2011).

A morphological response of plants to UV-B has been suggested by several studies. Yang *et al.* (2008), for example, found leaves of *Hippophae rhamnoides* to be thicker, denser and smaller under UV- B exposure, a pattern that has also been previously described by Day & Vogelmann (1995), reviewed in Jansen *et al.* (1998) and Pollastrini *et al.* (2011). Leaf dry matter content (the ratio of leaf dry mass to saturated fresh mass, LDMC), which is associated with the density of leaf tissue, is known to be higher during summer and spring when amounts of radiation and temperature are higher (Al Haj Khaled *et al.*, 2005). Plants can also respond to UV-B by reducing their size and overall biomass (e.g. Xiong & Day, 2001; Sangtarash *et al.*, 2009; for review see Caldwell *et al.*, 2007).

The understanding of biological invasions as "natural experiments", due to the exposure of taxa to new environmental conditions, dates back to the early 20th century (Grinnell, 1919 as cited in Sax *et al.*, 2005). This approach has triggered increasing research during the last two decades (see Pyšek *et al.*, 2008) and two main adaptive mechanisms that are encountered during plant invasions in new environments have been identified: rapid evolution and phenotypic plasticity. The ability to respond in a plastic manner allows species to express beneficial phenotypes in a wider set of environmental conditions (e.g. Donohue *et al.*, 2001; Richards *et al.*, 2006; Ghalambor *et al.*, 2007) and the particular importance of phenotypic plasticity in plant invasions was emphasized in several studies (e.g. Geng *et al.*, 2007; Ward *et al.*, 2008; Riis *et al.*, 2010). Alternatively, the directional selection of well adapted phenotypes is considered to support invasions (Parker *et al.*, 2003) and the term "contemporary evolution" has been coined to describe such evolutionary processes on a relatively short time-scale (see Yoshida *et al.*, 2007). Contemporary or rapid evolution has been observed in several, invasive species (e.g. Hendry & Kinnison, 1999; Thompson, 1998; Erfmeier & Bruelheide, 2010). To the best of our knowledge, the role of UV-B stress in eliciting rapid evolution or plastic responses in introduced plants

species has not previously been tested.

As a consequence of human colonization, many regions, particularly in the southern hemisphere, have suffered from biological invasions (e.g. Arroyo *et al.*, 2000; Meyerson & Mooney, 2007). Earliest herbarium records of European plant species in New Zealand date back to the mid-19th century (Webb *et al.*, 1988). Invasive plant species, European in origin and introduced to New Zealand, allow us to investigate to what extent responses to high levels of UV-B are involved in the process of invasion, and whether these responses are a feature from the native range, where species may have already been pre-adapted to high levels of UV-B, or if they have evolved after introduction in the new range as the outcome of directional selection (van Kleunen *et al.*, 2010a). In other words: do potential responses to high levels of UV-B reflect attributes of phenotypic plasticity rather than short-term evolutionary effects or a combination of the two?

We set out to study combined effects of two aspects of global change research: increased levels of UV-B and biological invasions. We designed a growth chamber experiment in which *Hieracium pilosella* L. plants grown from native populations in Germany and from invasive populations in NZ were exposed to radiation treatments with and without UV-B. Our goal was to quantify UV-B caused stress responses which would manifest in treatment effects on plant traits that translate into plant fitness. We hypothesized, first, that *Hieracium pilosella* plants respond to UV-B with high phenotypic plasticity which would be reflected in significant differences in functional UV-B response traits between UV-B treated and non-UV-B treated plants. This should be observed independent of origin; alternatively, if phenotypic plasticity differs between countries, with significant country × treatment interactions. Second, we hypothesized that plants from New Zealand are better adapted to UV-B than plants from Germany as the outcome of directional selection. This would result in significant interactions between origin and UV-B treatment in addition to significant country effects. Although addressing two possible mechanisms, these hypotheses are not regarded as being mutually exclusive.

5.3 Materials and Methods

5.3.1 Study species and material collection

Hieracium pilosella, mouse-ear hawkweed (*Asteraceae*), is frequently encountered in its native range in Europe in dry grasslands, heathlands, open pine forests, and along waysides (Rothmaler *et al.*, 2005). The species has been introduced to New Zealand in the late 19th century, first records from wild plants date back to 1878 (Webb *et al.*, 1988). It has become a major invasive weed in NZ as it grows densely in native tussock grasslands, where it reduces species richness (Scott, 1993). Population densities of *Hieracium pilosella* have been shown to be two to three times higher in NZ when compared to native populations (Beckmann *et al.*, 2009). The species is common in dryer areas in the North Island but more prevalent throughout eastern, dryer areas of the Southern Alps in the

Table 5.3.1: Overview on *Hieracium pilosella* seed origins and locations of the populations used in the experiment.

Country	Latitude [dec. °]	Longitude [dec.°]	Place
NZ	44.58540° S	169.65372° E	Lindis Pass
NZ	43.26180° S	171.69778° E	Porters Heights
NZ	43.71457° S	172.78298° E	Levy Saddle
NZ	42.00933° S	172.95406° E	Molesworth Road
NZ	43.84927° S	170.11037° E	Mt. Cook road
DE	52.94307° N	12.12941° E	Klein Leppin
DE	53.64323° N	13.34552° E	Rossow
DE	51.27164° N	11.22357° E	Heldrungen
DE	49.03042° N	11.61379° E	Wolfsberg
DE	51.50378° N	11.92790° E	Halle

Coordinates are shown as decimal degrees. Abbreviations: NZ = New Zealand, DE = Germany.

South Island of NZ.

Hieracium pilosella is known to display distinctive responses in stressful environments: facing drought situations *Hieracium pilosella* leaves roll inwards and present the white, felt-like lower surface upwards to increase the amount of radiation reflection (Hunt et al., 2002). We collected seeds in five populations of each country during summer and autumn 2008 in New Zealand (March–April) and Germany (July–September; see Table 5.3.1). Population characteristics were comparable in latitude, vegetation type and abiotic soil conditions (see Beckmann *et al.*, 2009 for more information on selection criteria). Seeds were pooled per population and stored in a dark, dry place at room temperature. The seeds were sown in mid-December of 2009 in trays with a compost-sand mixture (2:1) in the greenhouse at the Institute of Biology/Geobotany and Botanical Gardens in Halle at 25°C and 60% relative humidity. The majority of the seeds germinated within one week and grew for two more weeks until they were piqued into 9 × 9 cm^2 sized pots with the same soil mixture. Plants were allowed to grow in the greenhouse for two more weeks prior to the experimental treatment.

5.3.2 Experimental setup and UV-B treatment

We used two growth-chambers of type VB 1514 (Vötsch Industrietechnik, Germany). Both were equipped with the identical set of fluorescent lamps (27x Osram Lumilux 30W/830 and 6X Osram Fluora L30W/77). In order to increase UV-B lighting, we added two TL20W/12 RS SLV fluorescent tubes (Phillips, The Netherlands) that were controlled independently from outside in one of the growthchambers. All lamps were positioned at a distance of 65 cm to the surface of the pots.

Day conditions were set to 25°C and 65% relative humidity and lasted 8 h. Night conditions were simulated at 12°C and 80% relative humidity at complete darkness, also for 8 h. In between day and night, dusk and dawn were simulated for 4 h each by gradually increasing or decreasing temperature, humidity and lighting intensity.

Without prior information on the effects of UV-B exposure on our study species, we assumed increasing robustness of plants with time and size. Thus, we increased the

time of daily irradiation with UV-B over the course of the experiment. The first two weeks UV- B lamps were switched on for 2 h during mid-day which equals approximately 1.44 kJ*m²*d^{-1}, the next 2.5 weeks the dose was increased to 3 h a day (2.16 kJ*m²*d^{-1}) and for the last 3.5 weeks plants were exposed to UV-B for 12 h every day (8.64 kJ*m²*d^{-1}). UV-B was measured using a custom made UV-B meter (UV-Design, Brachttal, Germany).

In each of the two chambers we randomly placed eight pots per population with *Hieracium pilosella* plants. All 80 pots were repositioned randomly at weekly intervals within each growth-chamber in order to counteract potential effects of unequal illumination. Plants were supplied with water regularly. The experiment ran for nine weeks from February to April 2010.

In order to test the effectiveness of our UV-B treatment we mea- sured effective quantum yield (Y =△F/Fm , following Genty et al., 1989) of photochemical energy conversion in photosynthesis as a measure of the efficiency of photosystem II (PSII) with a mobile fluorometer (Mini-PAM, Heinz Walz, Effeltrich, Germany). Measurements were undertaken in the third, fifth, seventh and eighth week of the experiment. PSII efficiency measurements took place after half of the daily UV-B dose had been received by the plants. Leaves were darkness-adapted for 10 min prior to the measurements. These measurements showed that plants of either origin revealed a reduced PSII efficiency after an increase of UV-B dosage. However, plants quickly adapted to the change in UV-B as the effect had been resolved until the following measurements (results not shown).

5.3.3 Trait selection, data collection and analysis

We selected two groups of traits: (i) traits associated with plant growth and fitness, and therefore, overall plant performance and (ii) traits that facilitate functional plant responses to UV-B. As fitness-related traits we measured plant biomass (below- and aboveground), the number of leaves per plant, the number of ramets per plant and the number of leaves per ramet. Accordingly, leaf-length, specific leaf area (SLA), leaf dry matter content, the number of hairs per leaf and the length of these hairs were chosen as traits potentially showing direct functional responses to UV-B.

We monitored all plants every two weeks by counting the numbers of leaves, inflorescences and ramets. At the end of the experiment, three fresh, similarly sized and healthy leaves per plant were weighed and SLA was determined with a commercial leaf-scanning program (Win FOLIA Pro S, Regent Instruments, Canada). Afterwards leaves were dried for 48 h at 60°C and weighed again. Using the calibrated images derived for SLA determination we counted the number and measured the length of all hairs within a 10 × 10 mm square on the upper surface of the leaves excluding the rachis. Mean SLA, LDMC, number and length of hairs were calculated per plant. Additionally, plants were harvested and dried for 48 h at 60°C in a drying oven to determine above- and belowground biomass.

All collected data were checked for normality of distribution and log or square-root transformed where appropriate (as recommended by Zuur *et al.*, 2009). We used a linear mixed model approach (R 2.10.1, package "nlme", function "lme"; Pinheiro *et al.*, 2011) to analyse the data. Country of origin (NZ, DE) and treatment (+UV-B, −UV-B) were implemented as fixed factors. Population was considered random nested within country, and the "summary" function was used to derive estimates, variances of random intercepts and p-values from the model. Although we performed multiple tests we did not attempt at Bonferroni correction (Rice, 1989) in order to test for the potential of type I errors. Bonferroni correction has been considered as too conservative (e.g. Moran, 2003; García, 2004) and type I errors are generally regarded to be of minor concern in ecological studies. We believe that in this early stage of research on the potential effects of UV-B during plant invasion it is appropriate to present raw p-values and acknowledge that multiple tests were performed upon their interpretation.

5.4 Results

5.4.1 Growth and leaf traits

The analysis of traits related to plant growth, and thus, those that directly translate into fitness, such as belowground biomass, the number of ramets produced as well as the number of leaves per ramet, revealed a significant treatment effect with lower values encountered on UV-B treated plants than on the control plants that grew without UV-B (Table 5.4.1 on the following page, Fig. 5.5.1(a), (d), (e) on page 90). In contrast, aboveground biomass revealed no significant difference between the treatment levels (Table 5.4.1, Fig. 5.5.1(b)). The number of leaves per plant was lower on NZ plants, regardless of UV-B treatment as indicated by a significant country effect (Table 5.4.1, Fig. 5.5.1(c)).

5.4.2 Functional UV-B response traits

For one of the UV-B response traits studied, statistical analysis revealed significant differences between the origin of the plants (Fig. 5.5.2(c) on page 91, Table 5.4.1 on the next page). In addition, we found significant treatment effects (Fig. 5.5.2(c) and (e), Table 5.4.1). Leaves were marginally longer on NZ plants; however, the specific leaf area showed no differences between origins (Fig. 5.5.2(b)). Among traits associated with functional responses to UV-B leaf dry matter content was most responsive and displayed both significant effects of origin and treatment. We found a significantly higher LDMC on NZ plants as well as a higher LDMC for UV-B treated plants (Table 5.4.1 on the following page).

Whereas the number of hairs that grew on the leaves was significantly different neither for country nor for treatment (Table 5.4.1), the length of foliar hairs on the upper surface of leaves differed between treatments (Fig. 5.5.2(e)). When plants were treated with

Table 5.4.1: Analysis of variance of plant growth variables related to fitness and functional response traits to UV-B of *Hieracium pilosella.*

Response	Source	F-value	p-value
Traits of plant fitness			
Below ground biomass [g]	country	1.72	0.227
	treatment	5.27	**0.023**
	country x treatment	0.24	0.627
Above ground biomass [g]	country	0.02	0.893
	treatment	1.24	0.267
	country x treatment	0.22	0.637
Number of ramets per plant	country	0.37	0.56
	treatment	5.57	**0.02**
	country x treatment	0.47	0.496
Number of leaves per ramet	country	0.37	0.358
	treatment	5.57	**0.007**
	country x treatment	0.47	0.503
Number of leaves per plant	country	11.05	**0.011**
	treatment	1.19	0.277
	country x treatment	0	0.944
Functional responses to UV-B			
Leaf-length [cm]	country	3.83	0.086
	treatment	0.23	0.633
	country x treatment	0.04	0.845
Specific leaf area (SLA) [dm^2/kg]	country	0.67	0.438
	treatment	2.6	0.109
	country x treatment	0.03	0.872
Leaf dry matter content (LDMC) [%]	country	7.93	**0.023**
	treatment	4.98	**0.027**
	country x treatment	0.89	0.346
Number of hairs per [cm^2] leaf area	country	0	0.961
	treatment	0.66	0.418
	country x treatment	0.6	0.438
Length of foliar hairs [mm]	country	0.11	0.751
	treatment	19.87	**<0.001**
	country x treatment	0.03	0.87

The table shows F-statistics and analysis of variance results.
Fixed effects were country of origin and UV-B treatment. Random effects were population nested within country. Significant effects ($p < 0.05$) of country, treatment or their interaction are indicated in bold.

UV-B, hairs grew about 20% longer than under the control treatment (Fig. 5.5.2(f)). However, hair length was neither affected by origin nor by origin × treatment interactions (Table 5.4.1).

5.5 Discussion

5.5.1 Stress responses caused by UV-B

Our expectation of stress related responses to UV-B has been confirmed, pointing to increased stress levels induced by the UV-B treatment. Growth related traits, by the majority, proved to be directly negatively affected by UV-B. Among leaf traits, LDMC and length of foliar hairs displayed increased values under UV-B, also indicating a stress response. Measurements of PSII efficiency also revealed that plants suffered from photoinhibition after increased UV-B exposure (see methods). Since the experimental setup ensured that other stress factors known to decrease PSII efficiency (e.g. drought, nutrient availability; Marshall *et al.*, 2000; Godoy *et al.*, 2011a) had been excluded, photoinhibi-

tion has to be interpreted as a response to UV-B, therefore confirming the effectiveness of our experimental setup.

Reduction in growth is one of the most common responses to UV-B. In a three-year field-experiment, e.g., Rinnan *et al.* (2005) showed that below ground biomass of *Vaccinium uliginosum* is reduced under ambient UV-B when compared to sites where UV- B has been filtered. This also seems to apply for *Hieracium pilosella* in this study. In a recent meta analysis on UV-B studies in polar regions, Newsham & Robinson (2009) showed that UV-B exposure resulted in a mean 10% reduction of plant height and biomass. As the growth form of *Hieracium pilosella* leads to rather horizontally than vertically expanded plants, plant height is not a suitable measurement; however, we found comparable results when considering the number of ramets and the number of leaves attached to them as a proxy for growth and height.

When comparing native and invasive plant populations, increased general plant growth and productivity has been observed in introduced populations for a number of species (e.g. Güsewell *et al.*, 2006; Zou *et al.*, 2007). In a study on 14 species, Blumenthal & Hufbauer (2007) found plants grown from invasive populations to be generally larger compared to native conspecifics. UV-B treatment, however, results in a converse pattern. These opposing mechanisms might explain why, in regions with high levels of UV-B exposure the increased vigour of introduced plants might be offset by UV-B, and in consequence, increased growth rates may not be detected. Accordingly, in an earlier comparative field study in Germany and NZ (Beckmann *et al.*, 2009) no evidence for increased vigour in NZ populations of *Hieracium pilosella* under natural conditions could be provided.

5.5.2 Plasticity and adaptation

We found evidence for both phenotypic plasticity – as indicated by significant treatment effects of functional response traits – and genetic differentiation between origins – as indicated by significant country effects. Such differences do not necessarily indicate recent adaptation, as they might have been evoked by historical pre-selection prior to introduction (Henery *et al.*, 2010). The ultimate evidence for better adaptation to UV-B would have been significant interaction effects between UV-B treatment and origins in combination with significant origin effects. However, such effects were not found in this study.

Traits that are associated with functional responses to UV-B displayed significant treatment effects and suggest some evidence for high phenotypic plasticity. This was most prominent in the length of foliar hairs that grow on the upper surface of the leaves. *Hieracium pilosella* responded directly and strongly to UV-B by increasing the length of these hairs and, as a result, reducing the amount of solar radiation that reached the epidermis and parenchyme. Although the average increase in hair-length of 0.8 mm might seem little, the net benefit results from increased reflected or absorbed radiation or

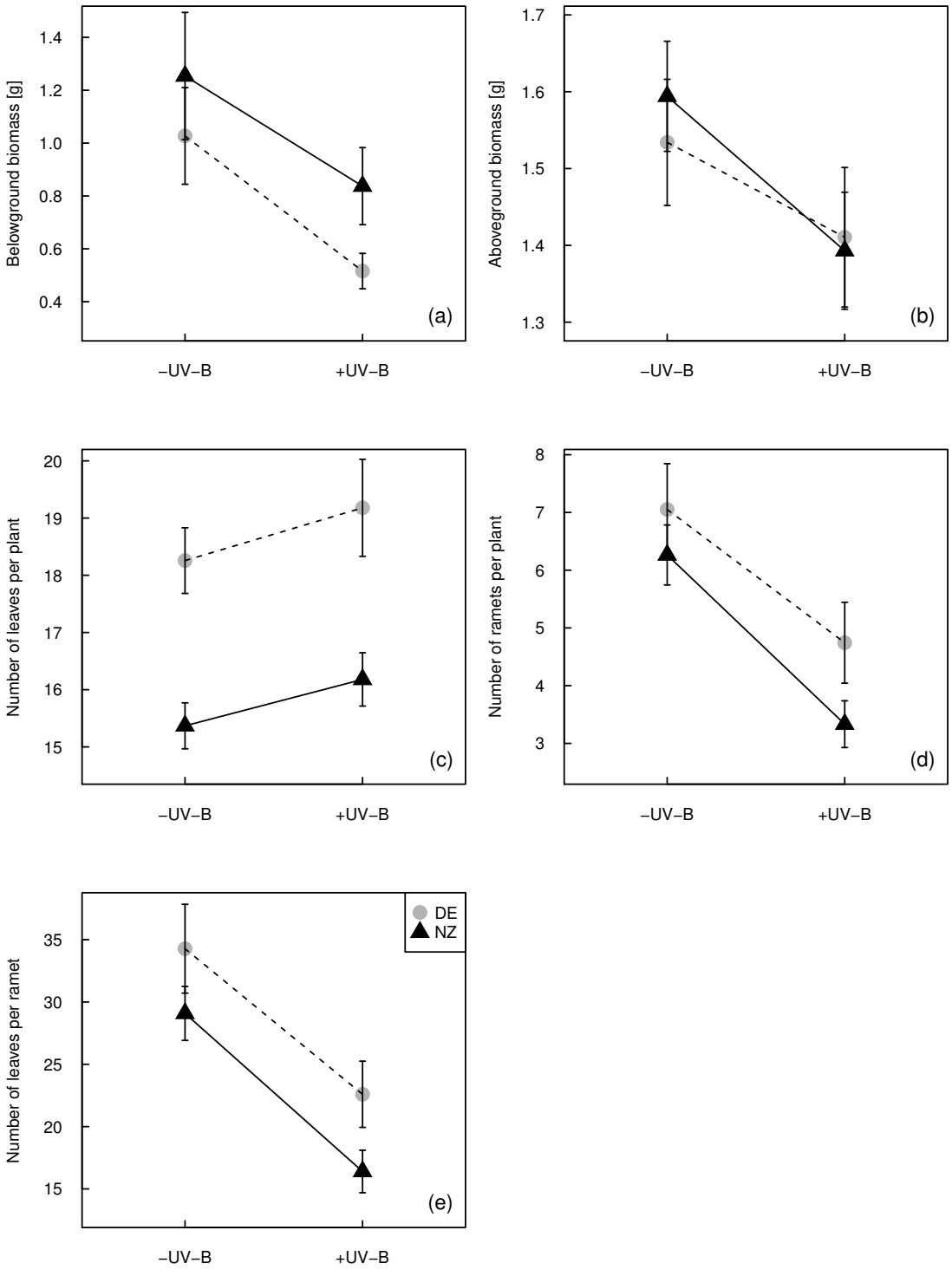

Figure 5.5.1: Reaction norms of growth of *Hieracium pilosella* plants from German (dashed) and New Zealand populations (solid line) to UV-B radiation (right) vs. no UV-B radiation treatment (left); (a) below ground biomass, (b) above ground biomass, (c) number of leaves per plant, (d) number of ramets per plant, (e) number of leaves per ramet. Bars represent ± 2 SE. Abbr.: DE = Germany, NZ = New Zealand.

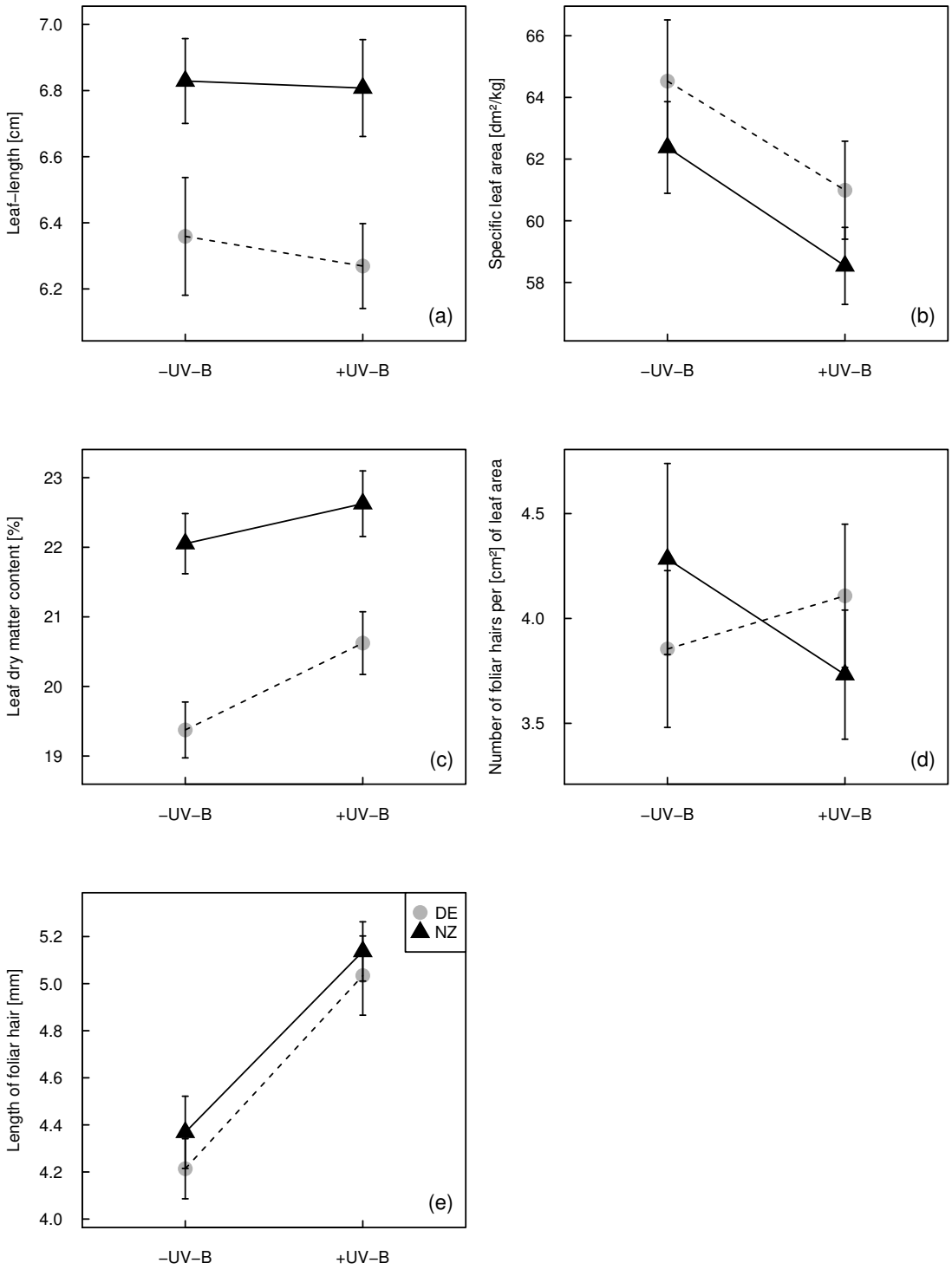

Figure 5.5.2: Reaction norms of functional response traits to UV-B radiation of *Hieracium pilosella* plants from German (dashed) and New Zealand populations (solid line) to UV-B radiation treatment (right) vs. no UV-B radiation (left); (a) leaf-length, (b) specific leaf area, (c) leaf dry matter content, (d) number of foliar hairs, (e) length of foliar hairs. Bars represent ± 2 SE. Abbr.: DE = Germany, NZ = New Zealand.

shaded area per hair by about one fifth (19%). The effectiveness of leaf hairs in protecting leaf tissue from excess radiation has been evaluated before: experimental removal of leaf hair of *Verbascum speciosum*, e.g., resulted in increased photoinhibition due to increased UV-B (Manetas, 2003). Accordingly, Filella & Peñuelas (1999) demonstrated that sun leaves of *Quercus ilex* produced more adaxial hairs than shade leaves.

Adaptive plasticity of traits may in itself be subject to rapid evolution which has recently been demonstrated for shade tolerance in *Prunella vulgaris* (Godoy *et al.*, 2011b). However, this does not seem to be the case in this study as the seen in the absence of treatment × origin interactions. Some functional responses to UV-B depend on the availability of particular traits (e.g. hairs or trichomes) that are not necessarily present in all species, whereas other responses, such as the increase of LDMC and phenolic compounds are of more generic nature and can be encountered in numerous species. Ultimately, all these responses represent trade-offs between defence and growth because they involve costs for the plant, and therefore, may result in decreased growth.

Increased LDMC of UV-B treated plants also emphasizes the importance of phenotypic plasticity in the UV-B response of *Hieracium pilosella*. High values of LDMC have been linked to higher radiation doses received by plants during different times of the year (Al Haj Khaled *et al.*, 2005), and this appears to be valid also for *Hieracium pilosella* in our experiment. Besides increased LDMC towards UV-B treatment, *Hieracium pilosella* also revealed significantly higher LDMC in NZ plants. The direction of the response, however, was the same for both native and invasive plants, and therefore, interpretation for local adaptation fails. Albeit overall higher LDMC in NZ populations might point towards adaptation to higher levels of UV-B in NZ, the evidence provided in this study remains insufficient, as higher LDMC alone may also be interpreted, for example, as an adaptation to warmer conditions (e.g. Garnier *et al.*, 2007).

5.5.3 Conclusion

In summary, we might conclude that *Hieracium pilosella* showed the anticipated stress responses to UV-B in traits related to plant fitness, as well as a highly plastic reaction in UV-B response traits, most prominently in the length of leaf hairs and LDMC. Evidence for local adaptation to higher levels of UV-B in the introduced range was not found. As plastic responses to UV- B are a feature of both, native and invasive origins, *Hieracium pilosella* appears to be particularly well equipped to grow under high levels of UV-B.

We believe that the investigation of UV-B related effects in the context of biological invasions presents an opportunity to study the importance of phenotypic plasticity and local adaptation as a response to new environments. Until now, UV-B has been overlooked as an environmental variable that may be encountered in different intensities in new ranges of introduced plant species. Naturally, this calls for studying further introduced species in NZ and other parts of the southern hemisphere in comparison with their native provenances. Upcoming studies should incorporate analyses of the effects of UV-B

on plant chemistry, morphology and acclimatization to unravel underlying mechanisms of UV-B triggered phenotypic responses. To allow generalizations about the possibility of UV-B being a relevant environmental filter during plant species invasions, these studies should include several species differing in their native or invasive status and which possess specific traits particularly associated with UV-B protection.

Acknowledgements

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6 Synthesis

6.1 Main results

With this thesis I tried to add to the existing knowledge on some of the mechanisms involved during plant invasions. To do so, I used observational and experimental approaches to compare alien with native populations of six clonal plant species at a biogeographical scale. In the four preceding chapters I collected the following main results:

Chapter 2. In this field study I compared wild populations in the native and alien range at three levels: the population structure, the immediate neighbourhood of plants and the individual plant performance. **Better performance of alien populations was consistently detected for all six species at the neighbourhood scale** which revealed generally more crowded populations. At the same time, performance at the population and individual scale varied between species. Clonal growth was higher in alien populations of three species while measures of sexual reproduction were higher in native population in three species as well.

Chapter 3. This experiment addressed whether three of the study species show differences in germination requirements between native and alien populations. I found that **alien populations have increased maximum germination at medium temperature conditions**. Further, seeds from alien populations of *Hieracium pilosella* had increased, while those of *Hypericum perforatum* had decreased germination velocity.

Chapter 4. In this common garden experiment I investigated the potential release from herbivory on clonal organs and the importance of clonal growth as a foraging behaviour. I could show that **alien origins of all six species were consistently less tolerant to simulated herbivory on clonal organs**. In a combined herbivory and nutrient treatment, alien plants of four species grew fewer clonal organs while the other two species produced more clonal organs, regardless of the treatment. In the absence of herbivory alien plants grew generally higher numbers of clonal organs and five species produced more flowers on alien plants regardless of the treatment.

Chapter 5. This growth chamber experiment compared the effect of UV-B radiation on native and alien plants of *Hieracium pilosella*. I found that this species is well

predisposed to grow in areas of high UV-B radiation as it **produced longer foliar hairs when treated with UV-B** regardless of the population origins. Furthermore, all plants showed typical responses to UV-B caused stress, such as higher leaf dry matter content and a reduction in below ground biomass. However, physiological differences between native and alien origins where not directly attributable as functional responses to the UV-B treatment.

6.2 Overall discussion

The studies I have presented in this thesis offer excellent opportunities for examining many aspects of the invasion process and their role during plant invasions. According to the conceptual framework used in this thesis (Figures 1.2.1 on page 19 and 1.3.1 on page 25), the six studied species are in the last stage of invasion. They are well established and continue to spread throughout large areas of NZ. However, the studies I conducted, did not focus on the spread of these species but on the stages of introduction and establishment. I investigated if and how these species have been able to overcome environmental filters, and how this has potentially helped them to reach the final stage of spread.

In each of the four main chapters of this thesis, several hypotheses or research questions have been addressed and could be partly confirmed or rejected. In the following discussion I will not deal with these questions individually and instead focus on the discussion of three linking aspects: (1) clonal growth, (2) abiotic filters in the form of temperature, nutrient and UV-B conditions and (3) adaptation and evolution.

6.2.1 Clonal growth

The importance of clonality for plant invasions has been supported by the present and other studies that detected increased clonal growth of invasive populations under natural and experimental conditions (e.g. Jakobs *et al.*, 2004; Brown & Eckert, 2005; Barney *et al.*, 2009; Roiloa *et al.*, 2016). As described in Chapter 2 (page 39), differences in clonal growth in the six studied species are detectable in wild populations in the field and according to Chapter 4 (page 63) these may also be detectable when growing the plants in a common environment. However, these observations are neither consistent between the species within the two chapters nor are they consistent for the same species across the chapters.

For example, in Chapter 2 I found both higher and non-different clonal organ growth in alien populations. In the specific case of *Achillea millefolium,* Chapter 2 revealed a *higher* amount of clonal organs in alien populations under field conditions. However, the plants grown from seeds collected in these populations, showed (depending on the experimental treatment) no differences in clonal organ production between native and alien populations or even significantly lower clonal organ production on plants from alien

populations (Chapter 4). Similar discrepancies were detected for other species as well.

When grouping the studied species by the types of clonal organs they grow and the clonal growth strategies these represent, some further distinctions can be made. According to Lovett-Doust (1981) the six studied species can be categorised as guerrilla, phalanx or a combined type, each showing advantages under certain conditions. These types of clonal growth can affect a species' abilities for spatial exploration, nutrient collection and sharing (You *et al.*, 2014; Elgersma *et al.*, 2015; Liu *et al.*, 2016; Roiloa *et al.*, 2016). While not resolving all between-study differences among species, these three groups do reduce some between-group differences:

- *Prunella vulgaris* and *Leucanthemum vulgare* are **phalanx-strategists** with comparatively short-stemmed clonal organs. In the phalanx growth form, connections between ramets are short, resulting in closely packed ramets which have been regarded as beneficial in homogeneous nutrient conditions (Ye *et al.*, 2006). Accordingly, I found higher clonal growth of alien plants from these species under controlled conditions (Chapter 4, Figure 4.4.2 on page 74). However, both species did not show significantly higher numbers of clonal organs in alien populations in field conditions (Table 2.4.1 on page 45), meaning that the direct comparison of the results from the two chapters fails to provide consistent interpretations. Nevertheless, both species do show higher densities in alien populations most notably at the neighbourhood scale. While this might be interpreted as an indirect measure of the success of the phalanx growth form, it could also be the result of higher recruitment rates of plants from seeds.

- *Hieracium pilosella* and *Lotus pedunculatus* are **guerrilla-strategists** which produce long, stem-derived clonal organs of similar type. The guerrilla growth form develops long connections between ramets which can help to compensate environmental stress (Wang *et al.*, 2017) and are believed to be most beneficial in heterogenous nutrient conditions as they allow the "exploration" of habitat (Saiz *et al.*, 2016). Both species grow in denser and more crowded populations in their alien range where *Lotus pedunculatus* also produces more clonal organs per total plant biomass (Chapter 2, Table 2.4.1 on page 45). On the contrary, under controlled conditions (Chapter 4, Figure 4.4.2 on page 74), *Lotus pedunculatus* and *Hieracium pilosella* plants from NZ did grow overall *less* clonal organs than plants from the native range. However, in the heterogeneous nutrient treatment and in absence of simulated herbivory, these two species showed similar or even higher numbers of clonal organs when originating in the alien range (Figure 4.4.2 on page 74). Presumably, these conditions better resemble those encountered in alien populations. The patterns observed in Chapter 4 indicate that clonal growth in these species might take shape mainly as a "foraging behaviour" that allows plants to collect and share resources (sensu de Kroon & Hutchings, 1995; Wang *et al.*, 2016; Portela & Roiloa, 2017) or to explore temporally unavailable space (Givnish, 2002; Furman

et al., 2017). Potentially, this provides a competitive advantage in comparison with the present vegetation (Callaway *et al.*, 2003).

- With intermediately long below-ground clonal organs, *A. millefolium* and *Hypericum perforatum* **combine characteristics of the phalanx and guerrilla strategies**. Both species show enhanced clonal growth in alien populations under field conditions (Chapter 2, Table 2.4.1 on page 45). However, these outcomes are not detectable when growing them in a common environment (Chapter 4, Figure 4.4.2 on page 74), where only alien plants of *Hypericum perforatum* showed enhanced clonal growth in absence of herbivory, whereas *A. millefolium* revealed even reduced clonal growth when herbivory was present. It may be assumed that the conditions encountered in NZ populations are more similar to the no-herbivory treatment applied in Chapter 4 which, thus, may more closely reflect the patterns of higher clonal growth observed in alien populations. Yet, given the lack of information on actual herbivore loads on clonal organs in the field in either region, such interpretations remain highly speculative.

At first glance, the discrepancies between the findings of field and the common garden studies may raise concerns. However, it has to be taken into account that such comparisons have to be done cautiously as the conditions found in wild populations cannot be fully replicated in common garden or growth chamber experiments (nor did I intend to do so). Experimental studies often fail when trying to replicate findings of wild populations (e.g. see meta analyses by van Kleunen *et al.*, 2010b; Vilà *et al.*, 2011). Many reasons may be held accountable for this disparateness, ranging from environmental conditions such as confinement (spatial, temporal), temperature, precipitation and radiation to biotic conditions such as the lack or presence of herbivores or competitors. In addition, maternal effects may also influence the performance of plants grown in a common environment (see Section 6.2.3 on page 102 for further details). Notwithstanding, both, field comparisons and common environment approaches have their merits and will be needed when trying to better understand the invasion process in the future.

The insights on the role of clonal growth during invasions gathered by this thesis, indicate that the type of clonal growth form should be considered more explicitly when addressing clonality among alien plant species. The, so far mainly used, simple "clonal or not" approach might be insufficient and is likely to ignore important differences between clonal growing species. As demonstrated in Chapters 2 and 4, different types of clonal growth may enable very different responses to new environments in alien species. Future studies should consult tools such as the CLO-PLA database of clonal growth in plants[1] (Klimešová & De Bello, 2009) and select specific clonal growth forms present in alien plant species and phrase their research hypothesis with these here presented implications in mind.

[1] http://clopla.butbn.cas.cz/

Ultimately, this thesis provides little basis for general conclusions on the role of clonal growth during invasions. If consistent patterns across species, such as the higher population crowdedness in Chapter 2 or the loss of tolerance to herbivory on clonal organs in Chapter 4, were detected, they relate only indirectly to clonal growth. Contradictory results, as I collected for important clonal growth traits within the individual chapters, further reduce the potential for generalisations. Therefore, the importance of clonal growth for plant invasions has not been finally clarified yet and future research must continue to seek for more general answers.

6.2.2 Abiotic filters

In the Chapters 3, 4 and 5 of this thesis I addressed research questions related to the role of environmental factors during the invasion process of the study species in different life-history stages. Chapter 3 focuses on the early establishment of plants and their germination requirements, whereas Chapters 4 and 5 were conducted during the first growing season of these perennial species.

Germination temperature requirements

The ability of a species to germinate rapidly and under a wide set of environmental conditions has long been regarded as an important trait for invasive species (Baker, 1974). Chapter 3 describes differences in seed germination temperature requirements between native and alien populations for two of the three tested study species *(Achillea millefolium* and *Hypericum perforatum*). Differences in germination between ranges were also found by Hirsch *et al.* (2012), who found faster germination of alien, North American populations of *Ulmus pumila* when compared to native populations and revealed an overall negative relationship between precipitation and germination speed. Similarly, Hierro *et al.* (2009) found that germination patterns of *Centaurea solstitialis* varied between two climatically different regions of introduction and explained this with the degree of risk *C. solstitialis* experiences at early developmental stages. Both studies concluded that short term evolutionary change in germination strategies contribute to the success of the investigated invasive species.

While a similar conclusion could also be drawn from the results presented in Chapter 3, where the differences in germination temperature requirements might be interpreted as an adaptation to climatic conditions in both regions, other possible explanations should be carefully considered (see Section 6.2.3 on page 102 for further details). For example, as mentioned in Section 1.4.2 (page 35), the populations sampled in this thesis vary considerably in the climatic conditions they are exposed to. As the seeds used in Chapter 3 grew in these conditions, their germination preferences as detected in the growth chamber experiment, might have been influenced by the environment of the mother plants through maternal effects (e.g. as described in Alba *et al.*, 2016).

However, potential inaccuracies in the referenced environmental data (WorldClim, Hi-

jmans *et al.*, 2005) may also exist. WorldClim provides spatially interpolated data that is prone to errors in mountainous areas where large elevation changes are occurring over relatively small distances (Hijmans *et al.*, 2005; Benham & Witt, 2016). This has certainly been the case in many of the populations sampled within the Southern Alps in NZ and, judging from my personal observations of the present conditions and vegetation cover, the annual precipitation values provided by WorldClim seem to overestimate the amount of actual rainfall in these areas. Potentially, higher resolution climate data, such as provided by the CliMond dataset (Kriticos *et al.*, 2012), or data directly measured in the investigated populations (e.g. through data loggers) might be explored in the future to accurately identify how the maternal environments might differ.

UV-B radiation and its potential role in the invasion process

Based on the observation that NZ receives approximately 60% more UV-B than Germany (Seckmeyer & McKenzie, 1992; Beckmann *et al.*, 2014b), in Chapter 5, I investigated the response of *Hieracium pilosella* to a UV-B treatment. I found that exposure to UV-B reduced growth related traits, which seems to be a general effect UV-B exposure has on plants and confirms the outcomes of many previous studies (e.g. Rinnan *et al.*, 2005; Newsham & Robinson, 2009; Chen *et al.*, 2016).

However, in invasion science it has also often been reported that plant growth and productivity is higher in alien populations (e.g. Güsewell *et al.*, 2006; Zou *et al.*, 2007; Blumenthal & Hufbauer, 2007; Hinz *et al.*, 2012). Bringing these two obviously contradictory observations of reduced growth under UV-B and increased growth of alien plants together, could help explain why I was unable to find evidence for increased growth in alien populations of *Hieracium pilosella* (or any other investigated species) in Chapter 2, and in another comparative field study (Beckmann *et al.*, 2009). Theoretically, in regions with high levels of UV-B exposure the increased vigour that alien plants might possess could be offset by the UV-B caused reduction in growth. Notwithstanding, other explanations are certainly possible, especially since several counterexamples exist that show indifferent or even smaller growth of alien plants and that cannot be linked to overall higher UV-B radiation in the alien range (e.g. Jakobs *et al.*, 2004; Alba & Hufbauer, 2012). It remains an open question if and how much UV-B accounts for differences in alien plant size, a question that could be tackled through reciprocal transplantation experiments (see Section 6.3 on page 104 for possible future directions).

Although the potential impact of UV-B goes beyond a reduction in growth, the general role of UV-B as a potential abiotic filter during biological invasions in regions of high UV-B intensity might have been overlooked so far. Recently, Barnes *et al.* (2017) tested whether native and alien species growing in the alpine zone of Hawaii differed in their UV-B screening capabilities and found that flexibility in screening is a mechanism employed by some species to cope with varying solar UV-B exposures along elevation gradients. The authors further speculate that *Verbascum thapsus,* a species not native to tropical alpine

climate, is able to invade such areas due to its tolerance to high UV-B. In another study I recently co-authored (Václavík *et al.*, 2017), we used historical herbarium specimens of *Hieracium pilosella* and *Echium vulgare* and examined whether UV-B exposure explains the geographical distribution of leaf traits such as length of foliar hairs in the native and the alien range. We found that UV-B explained geographical distribution of hair length in *Hieracium pilosella* best. Together with Chapter 5, these results suggest that, also under field conditions, foliar hair length of *Hieracium pilosella* can respond to higher UV-B intensities in a plastic manner, potentially offering some protection against detrimental levels of radiation. However, these findings neither confirm nor reject that a selection of genotypes that are particularly well adapted to high levels of UV-B, has occurred. One way or another, these outcomes show that UV-B may help to enhance the spread of exotic taxa possessing functional UV-B response traits, such as the foliar hair in *Hieracium pilosella*, into areas of high UV-B - similar to what Barnes *et al.* (2017) suggested for *Verbascum thapsus*.

Nutrient availability and foraging behaviour

The availability of resources such as nutrients can also play an important role for plant species when colonising a new area. However, nutrient availability acts at much finer scales than climatic conditions such as temperature or UV-B radiation as described above. Still, resource competition has been regarded as a potential determinant of the successful establishment, spread and persistence of alien plant species (Eckstein *et al.*, 2012; Gioria & Osborne, 2014). For example, it has been demonstrated by several studies that clonal integration can provide benefits to alien plant species (e.g. Peltzer, 2002; Otfinowski & Kenkel, 2008; You *et al.*, 2014; Liu *et al.*, 2016). However, in Chapter 4 I did not investigate clonal integration directly. Instead, I explored related aspects of the nutrient acquisition behaviour by subjecting the study species to a simplified heterogeneous or homogeneous nutrient treatment. I could show that clonal growth of alien populations outperformed native populations in heterogeneous nutrient conditions when herbivory was absent (see Figure 4.4.2 on page 74). While this supports the general expectation that clonality provides benefits to invaders in heterogeneous conditions (e.g. Jaafry *et al.*, 2016), these outcomes also are in contrast to Keser *et al.* (2014) who did not detect a link between nutrient availability and indicators of clonal growth in invasive species. However, comparability between studies might be reduced as Keser *et al.* (2014) compared closely related invasive and non-invasive species pairs and not native and alien plants from the same species as has been done in Chapter 4. In summary, it remains open if and how potential benefits for nutrient uptake provided by clonal growth translates into invasion success of the six study species.

6.2.3 Adaptation and evolution

Approximately two decades ago, studies in invasion science started to increasingly investigate the potential contribution of evolutionary processes to the successful invasion of plant species. Back then, experiments that identified differences between plants grown from native and alien populations in a controlled environment, were considered to provide sufficient proof that the selection of well adapted genotypes or other evolutionary processes have occurred. One of the most influential studies has been conducted by Blossey & Nötzold (1995), who proposed the EICA hypothesis, stating "that under controlled conditions, individuals of a species taken from an area where they have been introduced will produce more biomass than individuals taken from the species' native range" and linked that observation to the directional selection of genotypes that invest more in growth and less in herbivore defence. The authors also mention, but quickly dismiss, possible alternative explanations such as maternal effects or phenotypic plasticity.

If the same standards would still apply today, I could state with great confidence that Chapters 3, 4 and 5 provide solid evidence that the selection of genotypes better adapted to the growing conditions in NZ has occurred. In all three chapters I conducted experiments growing plants from native and invasive populations under controlled conditions and found differences in growth between these origins. However, since the first concepts on invasions and evolution were published in the 1990s, we have learned much more about possible alternative explanations and I am hesitant to draw such a simple conclusion that would clearly overstate the results.

Not all differences between native and invasive provenances can be interpreted as post-introductory evolutionary change and there are several possible alternative explanations that can be applied to all three experiments here. First of all, maternal effects could possibly explain all observed differences between native and alien origins and have done so, for example, in germination (e.g. Alba *et al.*, 2016) or growth experiments (e.g. Campbell *et al.*, 2015). In fact, it is quite likely that the detected growth responses "echo" the environmental conditions of the mother plants to some degree. To fully account for maternal environmental effects, studies have to grow plants for a single generation in common environmental conditions (e.g. in a greenhouse) and use seeds collected from this generation for further experiments (e.g. Bayliss *et al.*, 2017). For reasons of feasibility I did not account for maternal effects in the experiments conducted in this thesis and, therefore, I cannot finally rule out that the observed differences between regions or even populations could be explained by maternal effects.

Another potential explanation of the observed differences between regions is the selection of the included populations. Since, typically, plant individuals are not genetically the same across their entire distribution range, it remains unclear how representative of either native or alien region the used seed material really was (e.g. the sampling of populations was restricted to a portion of the native range only). Potentially, the purposeful or accidental introduction of pre-adapted genotypes from the native range provides an

alternative explanation for phenotypic differences uncovered between native and alien populations (Bossdorf *et al.*, 2008; Montague *et al.*, 2008).

These and other potential alternative explanations hamper the ability of this thesis to finally conclude that any of the observed differences can be assuredly attributed to genetic differentiation between native and alien populations caused by the selection of well adapted genotypes. However, if adaptation or evolution has occurred, can be concluded with different degrees of uncertainty for each individual chapter:

Entirely uncertain. The differences in growth as detected in the field study (**Chapter 2**) cannot be linked to adaptation or evolution at all. Basically, any differences in environmental conditions (e.g. precipitation, temperature, solar radiation, herbivory, soil properties) could explain the observed differences of growth and reproduction between regions. For these reasons, observational field comparisons such as conducted in Chapter 2 are largely unsuitable for investigating evolutionary processes.

Very uncertain. If adaptation or evolutionary processes account for differences in germination preferences, as discovered in **Chapter 3,** cannot be concluded - even though the experiment was conducted in controlled environmental conditions. Especially since previous studies have shown that maternal effects can influence germination in several invasive species (e.g. Espeland & Hammond, 2013; Alba *et al.*, 2016), this thesis can neither rule out nor confirm if evolutionary processes explain these differences.

Quite uncertain. Of the ten in **Chapter 5** investigated growth and UV-B response traits, two showed significantly different responses between origins. One possible explanation is that these differences are the outcome of directional selection. Yet again, maternal effects might explain these results, but to my knowledge, no previous study has specifically investigated the role of the maternal environment of plants on their LDMC or leaf length. Given the complex genetics of *Hieracium pilosella* (Chapman & Bicknell, 2000; Chapman *et al.*, 2003; Houliston & Chapman, 2004; Trewick *et al.*, 2004), genetic changes are certainly possible, if not likely, but the degree to which these are related environmental conditions as evolutionary drivers remains an open question.

Less uncertain. In this thesis the strongest support for evolutionary processes being involved during invasion has been provided by **Chapter 4**. The undercompensation of simulated herbivory on clonal organs in alien plants of all six study species could very well be explained by directional selection in the alien range. These results support the hypothesis that herbivory is a major driver in the evolution of tolerance-related traits in plants (Fornoni, 2011) and point out that post-introductory evolution can be observed in the studied species,

a result which has been described in several other studies as well (e.g. Joshi & Vrieling, 2005; Liu & Stiling, 2006; Huang *et al.*, 2010; Oduor *et al.*, 2011). The major problem with this interpretation is the lack of evidence that the experimentally simulated herbivory on clonal organs is actually comparable to conditions in wild populations. As Prior *et al.* (2015) argue, enemy release can only occur if enemies effect plants in the native range - a question that remains unclear due to a lack of the relevant field data. Furthermore, recent studies on the milkweed-monarch-butterfly-relationship found that simulated herbivory does not have equivalent effects as actual herbivory (Agrawal, 2017; A. Agrawal, personal communication).

Ultimately, to fully prove that evolutionary processes have been at play during invasions, genetic evidence on a molecular level is needed. Such evidence should be able to clarify the link between functional traits and the specific DNA sequences (contrasting typical $Q_{ST} - F_{ST}$ studies; Chun *et al.*, 2009). Given the immense depth of molecular understanding needed for such analyses, so far only very few studies were able to show real time evolution has occurred (e.g. Agrawal *et al.*, 2012; Gervasi & Schiestl, 2017). However, the ongoing development of new, fast and affordable technologies for sequencing and molecular analysis suggest that, in the future, such direct approaches will become more common and will allow invasion science to investigate the role of adaptation and evolution with much more precision.

6.3 Outlook

This thesis underpins the urgency to develop approaches that enhance the knowledge in areas of research that might increase in importance in the foreseeable future. Five future directions of research in invasion science are identified in the following.

Reciprocal transplantation experiments

Many of the open questions related to the role of adaptation and evolution raised in this thesis could be approached through biogeographical transplantation experiments. Such studies transfer plants from populations in the native range to the alien range and vice versa (e.g. Erfmeier & Bruelheide, 2010; Colautti & Barrett, 2013; Li *et al.*, 2015; Siemann *et al.*, 2017) and can directly test for evidence of local adaptation. If local populations reveal better fitness in reciprocal transplantation experiments, this can be regarded as direct evidence for local adaptation (Colautti & Lau, 2015).

Reciprocal transplantation experiments are superior to other approaches in invasion science that have focused on the detection of local adaptation of invasive species. For example, $Q_{ST} - F_{ST}$ studies (population comparisons based on quantitative traits and neutral genetic loci to infer past selection; e.g. Chun *et al.*, 2009) may often claim that rapid adaptive evolution has occurred in alien populations, but it remains unclear if

the differences in neutral genetic loci can be interpreted as adaptation to current local conditions.

While classic reciprocal transplantation experiments are conceptually simple, they are relatively rarely undertaken. One possible reason for this lack of reciprocal transplantation experiments may be the comparatively large logistical and financial efforts needed to conduct such studies, especially if they include several native or alien regions or are conducted across hemispheres. Another obstacle reciprocal transplantation approaches have to recognise, are local laws that prohibit the introduction of alien plant or seed material, restrict its use to confined areas (e.g. greenhouses) and may require the destruction of plants before they reach flowering. This way, important scientific questions may not be fully addressed. Notwithstanding, such regulations are crucial to avoid the accidental release of new genetic material to the alien range.

Reciprocal transplantation experiments remain one of the greatest next challenges in invasion science and large reciprocal transplants are urgently needed to rigorously test for adaptive evolutionary responses to ecological differences between the native and alien range. Based on the outcomes of this thesis, it would be worthwhile exploring the relationship between growth of alien species and UV-B radiation in a reciprocal transplantation experiment. It would be interesting to see how well alien and native populations might be able compensate detrimental effects caused by UV-B. Such experiments should also investigate shifts in plant-herbivore interactions and competition.

Multiple alien regions

Many plant species have been introduced to, or are invasive in, several geographically distinct regions worldwide (gloNAF database; van Kleunen *et al.*, 2015). However, studies in invasion science predominantly focus on one alien region alone. Many important research questions may be addressed by incorporating several alien regions in one study. Multiple alien regions can be incorporated in field comparisons (e.g. Taylor *et al.*, 2016), experimental studies under controlled conditions (e.g. Hierro *et al.*, 2009, 2017) or reciprocal transplant experiments (see above). Albeit the outcomes generated by such studies may be more complex to interpret, the potential gain in knowledge is enormous. Incorporating multiple alien regions will allow studies to link their outcomes to different environmental conditions encountered in different regions and to their role in local adaptive evolution. Furthermore, different introduction histories may be compared and the influence of the originating native population(s) for the invasion success may be investigated by including multiple alien regions.

Interaction effects of clonal growth

The interaction between clonal growth and invasion has received considerable attention in invasion science (Yu *et al.*, 2016). However, the interaction between clonality, invasions and aspects of climate change has only recently started to gain interest. Understanding

interactions that involve clonal growth can help to predict the impacts of global change in natural environments. For example, Liu *et al.* (2017) performed a meta-analysis to assess whether there are general differences in alien and native plant performance in response to global change. Such an approach could be extended to investigate the potential interactions of global change with plant traits like clonal growth. In addition, the interaction of herbivores with clonal organs (as investigated in Chapter 4 using simulated herbivory) has yet to be validated with actual herbivory and under field conditions. Future studies should also take clonal integration and aspects of competition of clonal organs into account as these may show intra- and inter-specific interactions.

Under-researched environmental conditions

Many studies in invasion science have addressed environmental conditions such as precipitation or temperature and their influence on the invasion process, however, other environmental conditions have received much less attention. This is the case for UV-B radiation, which until now, has been largely overlooked as an environmental variable that may be encountered in different intensities in new ranges of introduced plant species (but see Barnes *et al.*, 2017). Similar to other environmental factors, UV-B radiation could act as a selection pressure and drive local adaptation in the alien range. Ideal conditions to investigate the interaction between plant invasions and UV-B radiation can be found in areas of the Southern Hemisphere such as New Zealand, Tasmania or Argentina. In these regions the long-term development of the native flora under high UV-B can be investigated as well as the short term response of alien plant species to higher levels of UV-B. Future studies should continue to investigate whether UV-B related plant responses are the outcome of phenotypic plasticity or local adaptation. Upcoming studies should also incorporate analyses of the effects of UV-B on plant chemistry, morphology and acclimatization to unravel underlying mechanisms of UV-B triggered phenotypic responses. To allow generalizations about the possibility of UV-B being a relevant environmental filter during plant species invasions, these studies should include several species differing in their native or invasive status and which possess specific traits particularly associated with UV-B protection. Furthermore, UV-B may potentially prevent the spread of UV-B-sensitive species. Thereby, future predictions of spreading exotic species may be enhanced and refined by implementing information on UV-B intensity such as provided by the glUV dataset (Beckmann *et al.*, 2014b).

Another environmental aspect that has received little attention in invasion science is wind. The dispersal of many plant species is dependent on or affected by wind, yet relatively little is known about the role wind might play for the establishment or spread of alien plant species (but see Quick *et al.*, 2017). Future studies should address the role of these and other under-researched environmental factors during biological invasions, for example, by applying correlative species distribution models that try to explain the distribution or spread patterns of invasive organisms.

Invasive plants in ecosystems of the future

Especially in areas of continuous human disturbance, such as agricultural or silvicultural production systems, new communities composed of alien species originating from various regions as well as native species, have emerged worldwide (Hobbs *et al.*, 2009). In fact, the six study species investigated in this thesis are mostly growing in such communities in New Zealand. Given that the total eradication of alien species currently remains an unrealistic goal for most plant invaders, it is likely that alien species will contribute to local species pools in the long run. It is even likely that global trade will continue to increase pressures caused by the accelerating transport of species into new regions in the future (Pace & Gephart, 2017). Therefore, it is crucial for future research in invasion science to increasingly focus on such communities and ecosystems rather then on individual alien species. As many previous studies in invasion science have shown, things are usually more complicated than expected and often, the devil lies in the detail. There are many open questions related to invasions and "novel ecosystems" that might be good candidates for future research: Are there similar communities present in isolated regions worldwide? If so, how are they formed? Are the same alien species in different communities originating from the same native regions? Are ecological processes or human activities the predominant drivers that form these communities? Answering these and other questions requires to approach invasions from a more holistic community or ecosystem perspective and should make use of the methodological tool-sets developed in classic ecology. Eventually, this change in perspective may help unravel some of the dynamics and processes that are going on in these novel ecosystems.

6.4 Conclusions

This thesis has shown that the six studied species *Achillea millefolium* L., *Hieracium pilosella* L., *Lotus pedunculatus* Cav., *Leucanthemum vulgare* Lam., *Prunella vulgaris* L. and *Hypericum perforatum* L. present a current ecological threat to the alien area in New Zealand. Based on the comparisons of native and alien populations conducted in this thesis, it is clear that: (1) for all six species performance is better in alien, New Zealand populations than in native populations; (2) multiple measures of plant performance applied at different spatial scales should be used when comparing native and alien populations of clonal species; (3) measuring population crowdedness might provide a quick and reliable way to do so; (4) the germination strategies of three species differ between native and alien range, possibly as a result of maternal effects or local adaptation; (5) lower tolerance to simulated herbivory on clonal organs consistently found for all six alien species from different taxonomic groups may be the outcome of local adaptation to a loss of herbivory on clonal organs; (6) inconsistencies in individual plant performance between field and common garden studies emphasise the importance of the local environment encountered by plants in the field; (7) types of clonal growth (e.g.

guerrilla or phalanx forms) have shown different responses and should be considered when addressing clonality among alien plant species in the future; and (8) plastic responses of *Hieracium pilosella* to UV-B indicate that functional UV-B response traits, such as the foliar hair, may offer protection against detrimental levels of radiation and the possession of such traits could help to enhance the spread of taxa into areas of high UV-B radiation.

Ultimately, in search for similarities in six clonal alien plant species, this thesis answered some and raised many new questions. It now remains for future studies to continue to illuminate the patterns and processes involved in the invasion of the study species. I am hopeful that upcoming research can draw from the results gathered here and that the studies conducted in this thesis will contribute to the prevention of further invasions of these and other species in the future.

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Supporting Information

Table A.1: Overview of the study species. Information on range distribution refers to Rothmaler et al. (2005), time of first records in New Zealand (NZ) to Webb et al. (1988). Status in NZ is derived from Howell (2008), see methods section for detailed description). Clonal growth type or type combinations are given as the name and category number provided in the appendix of Klimeš et al. (1997).

	Achillea millefolium	*Pilosella officinarum*	*Hypericum perforatum*	*Leucanthemum vulgare*	*Lotus pedunculatus*	*Prunella vulgaris*
Native range	Europe, Siberia	Europe	Europe, Western Asia	Europe, Western Siberia	Eurasia	Eurasia
Introduced range	Americas, Australia, New Zealand	Americas, Australia, New Zealand, Southern Africa	Americas, Australia, New Zealand	Americas, Australia, New Zealand	Americas, Australia, New Zealand	Americas, Australia, New Zealand
Clonal growth type	below-ground stems, *Aegopodium podagraria* (10), *Asperula odorata* (13)	above-ground stems, *Fragaria vesca* (11), *Caltha palustris* (12)	below-ground rhizomes, *Rumex acetosella* (3)	above-ground stems, *Rumex obtusifolius* (7), *Lycopodium annotinum* (5)	below-ground stems, *Aegopodium podagraria* (10)	above-ground stems, *Rumex obtusifolius* (7)
First recorded in NZ	1867	1878	1869	1867	1867	1867
Status in NZ	naturalized	invasive	invasive	naturalized	invasive	naturalized

Table A.2: Detailed list of sampled populations. The column ID shows codes for country (NZ = New Zealand, DE = Germany) and species (HI = *Pilosella officinarum*, AM = *Achillea millefolium*, HY = *Hypericum perforatum*, LP = *Lotus pedunculatus*, LV = *Leucanthemum vulgare*, PV = *Prunella vulgaris*). Values on altitude, mean annual temperature and annual precipitation were extracted from the Worldclim database (Hijmans et al. 2005) and represent long-term means.

ID	Latitude	Longitude	Name	Altitude (m)	Mean annual temperature (°C)	Annual precipitation (mm)
NZHI801	-44.01337	170.50053	Lake Tekapo	792	8.4	728
NZHI802	-44.15848	170.22020	Lake Pukaki	586	9.3	658
NZHI803	-44.58540	169.65372	Lindis Pass	1025	6.8	1285
NZHI804	-43.26180	171.69778	Porters Heights	1014	7	1918
NZHI805	-43.31328	171.69010	Lake Lyndon	998	7.1	1789
NZHI806	-43.71457	172.78298	Levy Saddle	493	9.4	998
NZHI807	-44.46152	169.71924	Ahuriri River	885	7.6	1221
NZHI808	-42.00933	172.95406	Molesworth Road	1457	5.2	1823
NZAM801	-44.58137	170.12060	Otamatata-Omarama	423	9.8	504
NZAM802	-44.20826	170.07684	Ohau-Pukaki-Canal	553	9.4	808
NZAM803	-44.00227	171.15365	Waihi River Gorge	291	10.4	1037
NZAM804	-43.28336	171.53609	Lake Colridge	751	8.3	1467
NZAM805	-43.71444	172.78300	Port Lewis Pass	493	9.4	998
NZAM806	-41.52009	173.61115	Wairau River	173	12	1205
NZAM807	-41.19950	172.79389	Grahams Valley	382	10.8	1861
NZAM808	-44.46268	169.71938	Ahuri Valley rd	885	7.6	1221
NZHY801	-44.66327	170.36404	Lake Aviemore Dam	315	10.2	518
NZHY802	-44.25984	169.99175	Lake Ohau Dam	538	9.5	794
NZHY803	-44.73373	169.28222	Tasman Valley	306	10.3	635
NZHY804	-43.28051	171.54055	Lake Colridge	751	8.3	1467
NZHY805	-42.00933	173.41032	Molesworth, North	810	8.6	820
NZHY806	-41.47763	173.81347	Renwick	47	12.7	936
NZHY807	-41.03490	172.85502	Harwood Lookout	663	9.5	2216
NZHY808	-44.46272	169.71994	Ahuri Valley	885	7.6	1221
NZLP801	-44.03760	171.08176	Te Moana River	507	9.4	924
NZLP802	-44.00227	171.15365	Waihi River Gorge	291	10.4	1037
NZLP803	-41.13081	172.62274	Cobb Valley	1226	6.6	2756
NZLP804	-41.03601	172.86624	Takaka Hill	663	9.5	2216
NZLP805	-41.18907	172.74390	Mt. Arthur Walkway	1024	7.7	2368
NZLP806	-41.99788	171.89621	Sandfly River Bridge	130	11.8	2135
NZLP807	-44.13399	169.33567	Davies Flat	1089	6.6	3277
NZLP808	-44.45991	169.71851	Ahuri Valley	885	7.6	1221
NZLV801	-43.06859	172.75067	Waipara Riverbed	71	11.8	627
NZLV802	-41.47737	173.81338	Renwick	47	12.7	936
NZLV803	-41.52025	173.61098	Wairau River	173	12	1205
NZLV804	-41.19950	172.79389	Grahams Valley	382	10.8	1861
NZLV805	-41.03601	172.86624	Takaka Hill	663	9.5	2216
NZLV806	-41.19785	172.71236	Mt. Arthur Walkway,	1024	7.7	2368
NZLV807	-43.83798	172.19576	Little Rakaia	25	11.6	651
NZLV808	-43.72451	171.97665	North of Rakaia	129	11.1	731

Table A.2 continued

ID	Latitude	Longitude	Name	Altitude (m)	Mean annual temperature (°C)	Annual precipitation (mm)
NZPV801	-44.27428	169.85017	Lake Middleton	536	9.5	985
NZPV802	-43.06859	172.75067	Waipara	71	11.8	627
NZPV803	-40.62199	172.67774	The Innlet	61	12.7	2420
NZPV804	-41.13081	172.62274	Cobb Valley	1226	6.6	2756
NZPV805	-41.03601	172.86624	Takaka Hill	663	9.5	2216
NZPV806	-44.45918	169.71522	Ahuri River	885	7.6	1221
NZPV807	-44.88991	168.27081	Caples Track	758	7.5	1783
NZPV808	-45.54152	167.88206	Mararoa Riverbed	376	8.6	1068
DEAM801	51.48616	11.88889	Lintbusch	99	9	481
DEAM802	52.59311	12.48337	Gräninger See	37	9	544
DEAM803	51.28876	11.26469	Oberhelldrungen	210	8.4	539
DEAM804	51.42243	11.06866	Kyffhäuser	195	8.5	545
DEAM805	53.46016	12.80039	Schwarzenhof	89	7.9	579
DEAM806	51.65257	11.75753	Rothenburg	127	8.8	500
DEAM807	53.45685	12.42981	Malchow	86	8.1	583
DEAM808	49.03042	11.61379	Wolfsberg	427	8.1	719
DEHI801	51.53070	11.89119	Lunzberge	94	9	482
DEHI802	53.45685	12.42981	Malchow	86	8.1	583
DEHI803	52.94307	12.12941	Klein Leppin	43	8.7	554
DEHI804	51.65086	11.75768	Rothenburg	127	8.8	500
DEHI805	53.64323	13.34552	Rossow	51	8.1	568
DEHI806	51.27164	11.22357	Heldrungen	179	8.5	523
DEHI807	49.03042	11.61379	Wolfsberg	427	8.1	719
DEHI808	48.93777	11.68951	Kohlmühle	424	8.1	724
DEHY801	51.52677	11.30211	Grillenberg	270	8.1	576
DEHY802	51.65257	11.75753	Rothenburg	127	8.8	500
DEHY803	52.72566	12.12735	Rehberger Berge	39	8.8	544
DEHY804	52.98859	12.79405	Neuruppin	60	8.5	568
DEHY805	50.78559	10.63528	Schmalwasser Talsperre	634	6.4	792
DEHY806	49.03014	11.61386	Wolfsberg	427	8.1	719
DEHY807	51.27498	11.22050	Heldrungen	179	8.5	523
DEHY808	48.93772	11.68960	Kohlmühle	424	8.1	724
DELP801	50.68920	13.13736	Heinzebank	614	6.1	733
DELP802	51.61078	11.10248	Neundorf	423	7.2	695
DELP803	50.82975	13.77541	Bärenhecke	522	6.2	691
DELP804	51.67255	11.19872	Selketal	346	7.6	641
DELP805	50.70206	13.14666	Stausee Obervorwerk	614	6.1	733
DELP806	51.52049	11.07214	Schwederschwende	420	7.3	687
DELP807	51.58731	10.96013	Stolberg	477	6.9	753
DELP808	48.93747	11.69251	Kohlmühle	424	8.1	724
DELV801	50.72418	13.62466	Holzhau	747	5.1	783
DELV802	51.67204	11.19898	Selketal	346	7.6	641
DELV803	50.70206	13.14666	Stausee Obervorwerk	614	6.1	733
DELV804	51.51993	11.07281	Schwederschwende	420	7.3	687
DELV805	51.58552	10.95552	Stolberg	482	6.9	764

Table A.2 continued

ID	Latitude	Longitude	Name	Altitude (m)	Mean annual temperature (°C)	Annual precipitation (mm)
DELV806	48.93737	11.69421	Kohlmühle	424	8.1	724
DELV807	52.94318	12.12984	Klein Leppin	43	8.7	554
DELV808	51.52661	11.30075	Grillenberg	270	8.1	576
DEPV801	50.70228	13.14668	Neuzehnhain 2	614	6.1	733
DEPV802	50.72418	13.62466	Holzhau	747	5.1	783
DEPV803	48.93758	11.69093	Riedenburg	424	8.1	724
DEPV804	51.67216	11.18889	Selketal	346	7.6	641
DEPV805	51.50754	11.07593	Agnesdorf	420	7.3	687
DEPV806	51.58731	10.96013	Stolberg	477	6.9	753
DEPV807	51.72238	11.01779	Friedrichsbrunn	405	7.3	708
DEPV808	51.42243	11.06866	Kyffhäuser	195	8.5	545

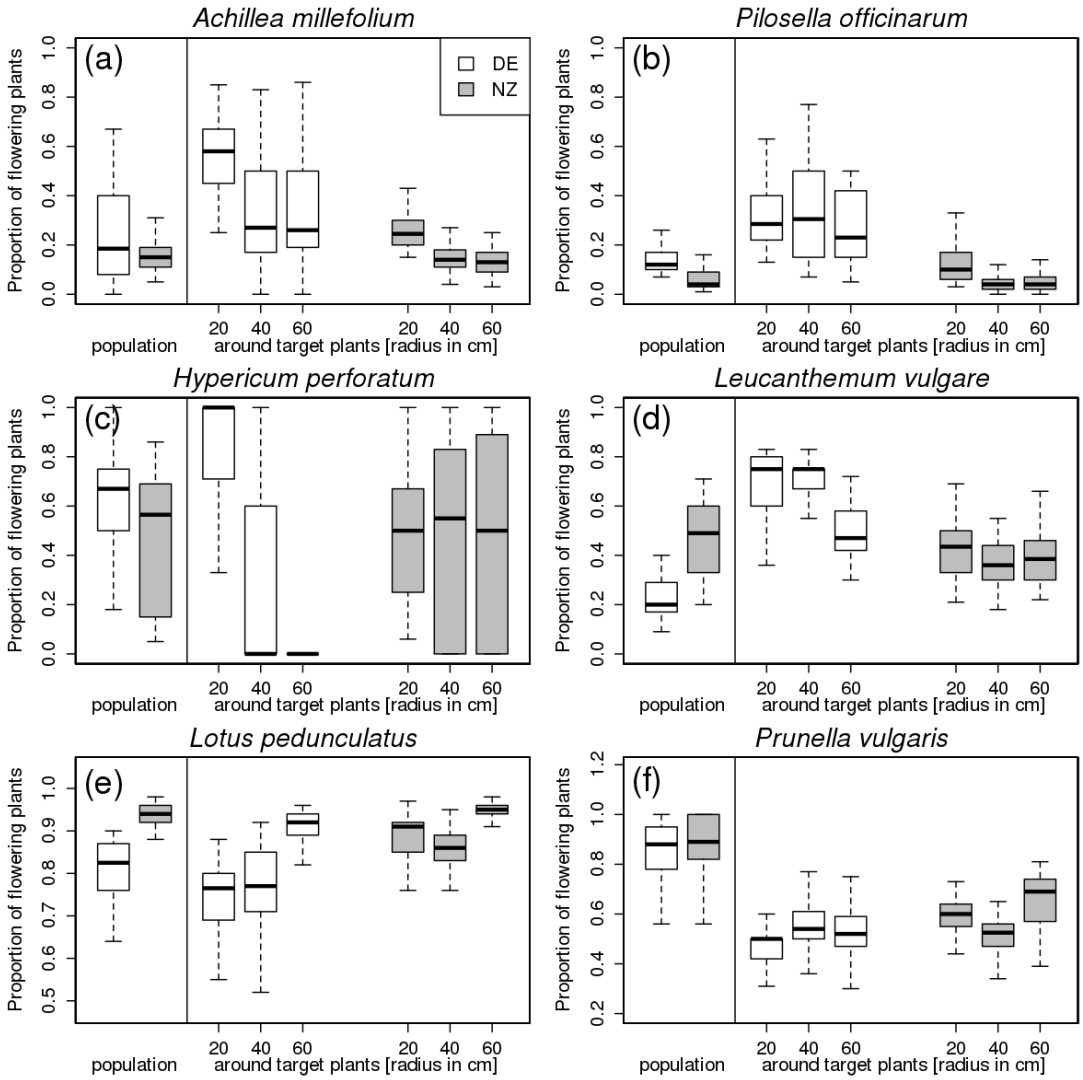

Figure A.3: Population and neighborhood scale. Box and whiskers plots of the proportion of flowering plants by species (a-f). The left part of each panel shows the proportion of flowering plants in randomly selected 1m² subplots, the right parts show the proportion of flowering plants measured in three specified rings (20, 40 and 60 cm radius) placed around target plants; (a) *Achillea millefolium*, (b) *Pilosella officinarum*, (c) *Hypericum perforatum*, (d) *Leucanthemum vulgare*, (e) *Lotus pedunculatus*, (f) *Prunella vulgaris*. Each box plot represents measurements taken in ten populations per species and country. Medians (solid lines), 25th and 75th percentiles (boxes) and 5th and 95th percentiles (whiskers) are shown. Abbreviations: NZ = New Zealand, DE = Germany. See Table 2.4.1 on page 45 for statistical details.

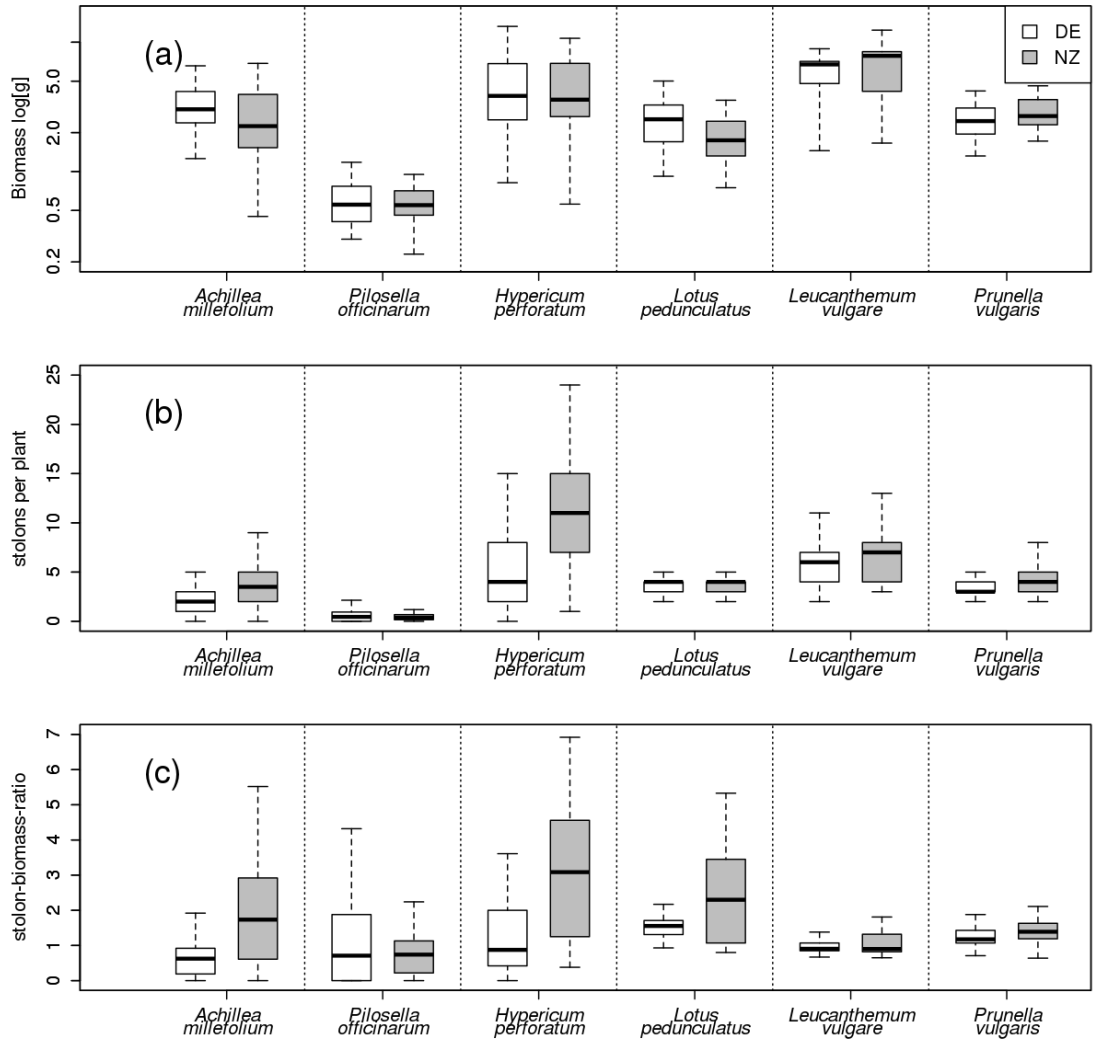

Figure A.4: Individual scale. Box and whiskers plots of plant biomass (a), the number of stolons per plant (b) and the stolon-biomass-ratio (c) of *Achillea millefolium*, *Pilosella officinarum*, *Hypericum perforatum*, *Leucanthemum vulgare*, *Lotus pedunculatus* and *Prunella vulgaris*. Each box plot represents measurements taken on five plants in ten populations per species and country. Medians (solid lines), 25th and 75th percentiles (boxes) and 5th and 95th percentiles (whiskers) are shown. Abbreviations: NZ = New Zealand, DE = Germany. See Table 2.4.1 on page 45 for statistical details.

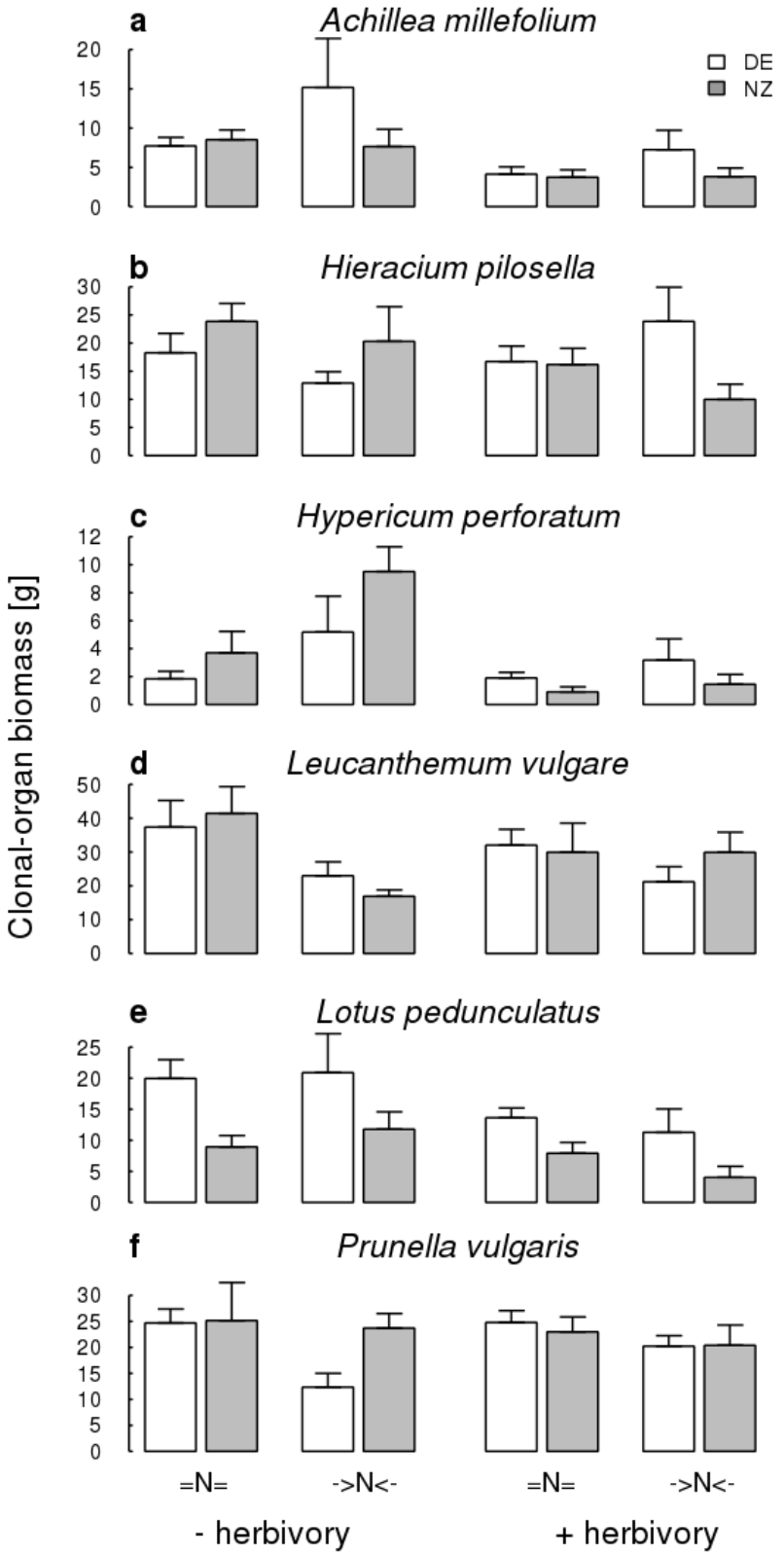

Figure A.5: Clonal-organ biomass of *Achillea millefolium* (a), *Hieracium pilosella* (b), *Hypericum perforatum* (c), *Leucanthemum vulgare* (d), *Lotus pedunculatus* (e) and *Prunella vulgaris* (f). Bars show means per pot and standard errors.

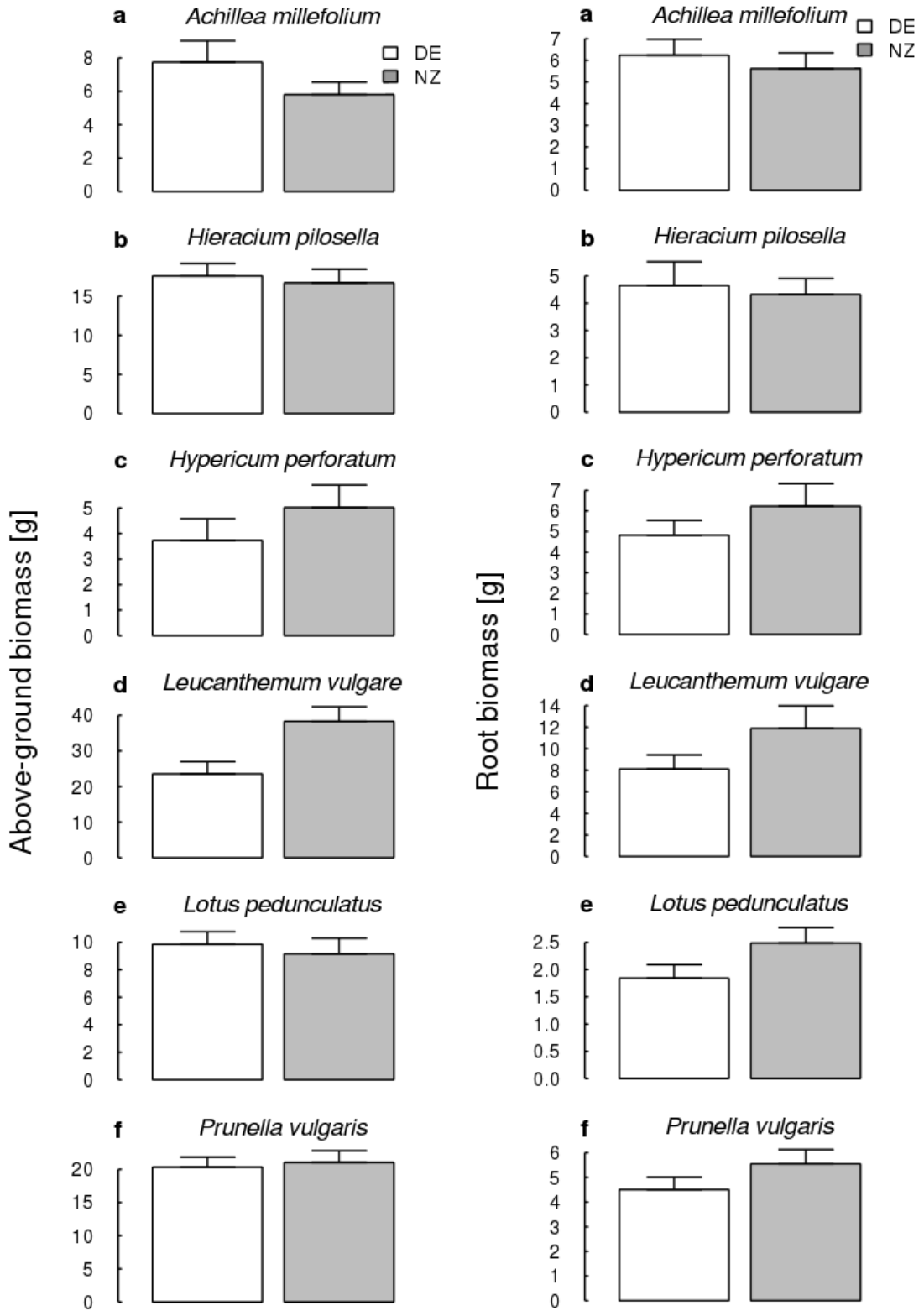

Figure A.6: Above-ground and root biomass of *Achillea millefolium* (a), *Hieracium pilosella* (b), *Hypericum perforatum* (c), *Leucanthemum vulgare* (d), *Lotus pedunculatus* (e) and *Prunella vulgaris* (f). Bars show means per pot and standard errors.

Eigenständigkeitserklärung

Hiermit erkläre ich, dass ich die vorliegende Dissertation - abgesehen von der Beratung durch meine Betreuerin Prof. Dr. Alexandra Erfmeier - selbstständig und ohne fremde Hilfe angefertigt, keine anderen als die angegebenen Quellen und Hilfsmittel benutzt und die den benutzten Quellen wörtlich oder inhaltlich entnommenen Stellen als solche kenntlich gemacht habe. Die Arbeit ist unter Einhaltung der Regeln der guten wissenschaftlichen Praxis der Deutschen Forschungsgemeinschaft entstanden. Diese Arbeit hat in gleicher oder ähnlicher Form noch keiner anderen Institution oder Prüfungsbehörde vorgelegen und ich habe bisher keine erfolglosen Promotionsversuche unternommen. Da es sich bei der vorliegenden Arbeit um eine kumulative Dissertation handelt wurden die einzelnen Kapitel in wissenschaftlichen Journals veröffentlicht. Dies ist entsprechend gekennzeichnet.

Kiel, den

Michael Beckmann