

“Causes for the invasion success of *Rosa rubiginosa* L. in Argentina”

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Kings um das Schloss aber begann eine Dornenhecke zu wachsen, die jedes Jahr höher ward, und endlich das ganze Schloss umzog und darüber hinauswuchs, dass gar nichts mehr davon zu sehen war, selbst nicht die Fahne auf dem Dach.

But round about the castle there began to grow a hedge of thorns, which every year became higher, and at last grew close up round the castle and all over it, so that there was nothing of it to be seen, not even the flag upon the roof.

Pero alrededor del castillo comenzó a crecer una red de espinos, que cada año se hacían más y más grandes, tanto que lo rodearon y cubrieron totalmente, de modo que nada de él se veía, ni siquiera una bandera que estaba sobre el techo.

Jakob und Wilhelm Grimm (1812) Dornröschen/Sleeping Beauty/La Bella Dormiente.
Kinder- und Hausmärchen



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Summary

With the globalisation of trade and travel, many species have been enabled in conquering natural boundaries with some regionally restricted species becoming successfully established outside their natural ranges. Numerous introduced species have become invasive, which not only affects ecosystem functioning but can also have negative economic consequences and effects on human health. Being placed far outside their natural range, the introduction of invasive species represents an unintentional anthropological experiment, enabling evolutionary and biogeographical processes to take place over grand scales.

Current theories on how such species can survive and spread in their new environments and how they can manage to outgrow their native congeners in number and size can be divided into three categories: propagule pressure, abiotic characteristics of the invaded ecosystem, or the biotic characteristics of the recipient community and the invading species. Comparative field studies in native and introduced populations allow us to pinpoint whether these differences in growth or abundance are due to only one or to a combination of these factors, and even for long-lived, slow growing plant species.

Therefore I adopted a comparative field study approach for the present thesis on the invasive, long-lived shrub *Rosa rubiginosa* L. (sweet briar), which assessed differences between native populations in Germany and Spain against introduced populations in Argentina. The overall conclusions for the study are drawn from five publications aimed at identifying the extent of each of the factors as drivers of the invasion success of the species.

Rosa rubiginosa invades natural plant communities and builds up large monotypic stands in its introduced range. In spite of being pentaploid, it is able to reproduce sexually due to its heterogamous meiotic system, but it also has the ability to produce apomictic seeds and spread vegetatively. Its ability to resprout after cutting or burnings and to build up a persistent seed-bank makes the eradication of this species very labour- and cost-intensive and, to date, no effective or risk-free biological control method has been found.

A literature review revealed that three invasive species of the same genus (*R. canina*, *R. multiflora*, *R. rugosa*) possess similar traits in respect of their growth, reproduction and adaptation to disturbance as *R. rubiginosa*, but with *R. rubiginosa* being the most invasive at the global scale.

The relationship between *R. rubiginosa* occurrence and specific biotic or abiotic predictors at the landscape scale was illustrated in a habitat invasibility map for the study area in Patagonia. *Rosa rubiginosa* occurrence was shown to be independent of habitat type and precipitation levels but connected to habitat disturbance. The model predicted that 36% of the study area is threatened by *R. rubiginosa* invasion, with populations being expected to possess sufficient propagule pressure to fulfil such a prediction.

The propagule pressure of an invasive species can also be defined through the number of introduction events that have occurred for a species in the invaded area, which were identified with molecular markers. Multiple introduction events increase the chances that individuals encounter favourable conditions and reduce founder effects. Two molecular studies revealed strong similarities between populations of southern and Central Argentina, indicating the transport of *R. rubiginosa* plants or seeds within Argentina. The exact source population was not found, but Spain could be excluded with Germany, the Czech Republic and Austria being probable source regions. Invasive populations in southern and Central Argentina were less genetically diverse than native populations, indicating a low number of introduction events, predominantly asexual reproduction and high phenotypic plasticity. The molecular studies raised the question as to whether an especially adapted genotype successfully invaded Argentina or if introduced populations benefit from new environmental conditions.

This was clarified by comparing invasive and native *R. rubiginosa* plants in terms of growth and fitness as well as habitat characteristics in both ranges. Results of the field surveys and common garden experiments did not point to an adaptive invasive genotype with higher growth rates or fitness, or to any benefit gained from soil conditions or vegetation structure. In addition, I found no evidence for the release of enemies in the introduced range, but discovered that recurrent trimming is responsible for the relatively small populations in Germany and Spain and that less habitat is available for the species in the old cultural landscape of Europe.

This thesis concludes that low levels of genetic diversity are compensated by primarily vegetative reproduction and a high phenotypic plasticity. *Rosa rubiginosa* tolerates a wide range of edaphic and climatic conditions and it benefits from single disturbance events supporting its establishment across different habitat types. However, recurring control of the species, as practiced for native populations, reduces population sizes. In the absence of species management, *R. rubiginosa* has a high potential to spread even further throughout its introduced range.

Resumen

Con la globalización del comercio y los viajes, las especies han dominado las barreras naturales y muchas de ellas, que antes estaban restringidas a un determinado rango, se han establecido exitosamente fuera de este. Numerosas especies introducidas se han convertido en especies invasoras, causando impactos indeseados en la economía, salud humana, y sobre la función de los ecosistemas. Estando establecidas fuera de su rango nativo, las especies invasoras constituyen un experimento humano accidental, el cual permite explorar procesos evolutivos y biogeográficos a gran escala. Las teorías sobre como estas especies pueden sobrevivir y proliferar en su nuevo ambiente, e incluso superar a su congéneres nativos en número y tamaño, pueden ser divididas en tres: presión de propagulo, características abióticas del ecosistema invadido y características bióticas de la comunidad receptora y las especies invasoras.

Los estudios comparativos de campo en las poblaciones nativas e introducidas de una especie invasora, permiten identificar si estas diferencias en el crecimiento o abundancia se deben a uno o varios de estos factores, incluso para especies longevas de crecimiento lento. Seguí este enfoque para el arbusto longevo *Rosa rubiginosa* L. (rosa mosqueta), mediante la comparación entre las poblaciones introducidas en Argentina, y las poblaciones nativas de Alemania y España. Mis conclusiones respecto de si el éxito de invasión de *R. rubiginosa* se debe a la presión de propagulo, condiciones bióticas y abióticas favorables en el nuevo ambiente o una rápida evolución adaptativa posterior a la introducción, es compilada en cinco publicaciones.

Rosa rubiginosa invade comunidades naturales de plantas y genera grandes parches monotípicos en su rango introducido. A pesar de ser penta ploide, es capaz de reproducirse sexualmente ya que posee un sistema meiótico heterógamo, además posee la habilidad de producir semillas apomícticas y propagarse vegetativamente. *Rosa rubiginosa*, posee la habilidad de rebrotar después de ser cortado y quemado, generando un banco de semillas persistente, lo que hace su erradicación costosa, intensiva y poco efectiva. Además, hasta ahora no se ha encontrado ningún método de control biológico libre de riesgo.

La revisión bibliográfica indica que las tres especies invasoras del mismo género (*R. canina*, *R. multiflora* y *R. rugosa*) poseen similares características relacionadas con el crecimiento, reproducción y la adaptación a las perturbaciones que posee *R. rubiginosa*, pero esta última es más invasora a escala global. Si la presencia de *R. rubiginosa* está

conectada con factores bióticos y abióticos específicos a escala de paisaje, fue ilustrado para el área de estudio en Patagonia, con un mapa de la invasibilidad del hábitat. La presencia de *R. rubiginosa* fue independiente del tipo de hábitat o nivel de precipitación, pero está relacionado con la perturbación del hábitat. El modelo predijo que el 36% del área de estudio está amenazado por la invasión de *R. rubiginosa*, y dada la presión de propagulo generada por las poblaciones de esta especie, se espera que la predicción se cumpla.

Además, la presión de propagulo es definida como el número de eventos de introducción, el cual fue identificado mediante el uso de marcadores moleculares. Múltiples eventos de introducción incrementan la chance de que los individuos encuentren condiciones favorables y por lo tanto se reduce el efecto fundador de las poblaciones. Dos marcadores moleculares estudiados revelaron una fuerte similaridad entre las poblaciones del Sur y Centro de Argentina, indicando la existencia de transporte de plantas o semillas de *R. rubiginosa* dentro del país. La fuente de origen exacta de la población no fue encontrada, pero España puede ser excluida, mientras que Alemania, República Checa y Austria fueron las fuentes de origen probables. Las poblaciones invasoras del Sur y Centro de Argentina fueron genéticamente menos diversas que las poblaciones nativas, indicando pocos eventos de introducción, una predominante reproducción asexual y una alta plasticidad fenotípica. Los estudios moleculares plantean la pregunta de si un genotipo especialmente adaptado invade exitosamente Argentina o si las poblaciones introducidas se benefician de las nuevas condiciones ambientales.

Esto fue aclarado al comparar plantas de *R. rubiginosa* invasoras y nativas en términos de su crecimiento y adecuación biológica, así también como las características del hábitat en ambos rangos de distribución. Los resultados de los muestreos en terreno y los experimentos de jardines comunes no indicaron un genotipo adaptativo invasor con mayor tasa de crecimiento o adecuación biológica. No encontré evidencia de liberación de enemigos, ni que las especies se beneficien de las condiciones del suelo o la estructura de la vegetación en el rango introducido. Yo concluyo que el corte recurrente de las poblaciones de *R. rubiginosa* en Alemania y España es el responsable de la disminución de las poblaciones y por lo tanto menos hábitat disponible para esta especie en el viejo paisaje cultural de Europa.

En consecuencia, mi tesis ha mostrado que un bajo nivel de diversidad genética es compensado principalmente por la reproducción vegetativa y una alta plasticidad fenotípica. *Rosa rubiginosa* tolera un amplio rango de condiciones edáficas y climáticas y se

beneficia de eventos de perturbación aislados para su establecimiento en los diferentes tipos de hábitats. Sin embargo, perturbaciones recurrentes, como las que se realizan en las poblaciones nativas (cortes recurrentes) reducen el tamaño de la población. Sin una práctica de manejo adecuada *R. rubiginosa* tiene un alto potencial de dispersión, incluso aun más, en su rango introducido.

Zusammenfassung

Im Zuge der Globalisierung des Güter- und Personenverkehrs haben Arten natürliche Barrieren überwunden und manche regional beschränkten Arten konnten sich erfolgreich außerhalb ihres nativen Areals etablieren. Zahlreich dieser Arten haben sich invasiv ausgebreitet, mit unerwünschten Auswirkungen auf die Wirtschaft, Gesundheit und Ökosystemfunktionen. Weit außerhalb ihres natürlichen Areals stellen invasive Arten auch ein unbeabsichtigtes vom Menschen geschaffenes Experiment dar, welches es ermöglicht, auf großem Maßstab evolutionäre und biogeographische Prozesse zu untersuchen. Theorien, wie diese Arten in ihrer neuen Umwelt überleben, sich ausbreiten und sogar größer und zahlreicher wachsen als ihre nativen Verwandten, können in drei Themengebiete unterteilt werden: Diasporendruck, abiotische Eigenschaften des neuen Ökosystems und biotische Eigenschaften der aufnehmenden Artengemeinschaft und der invasiven Art.

Ob diese Unterschiede in Wachstum und Abundanz durch einen oder mehrere dieser Faktoren bedingt sind, lässt sich, selbst für langlebige, langsam wachsende Pflanzen, durch vergleichende Feldstudien in nativen und eingeführten Populationen feststellen. Ich habe diesen Untersuchungsansatz für den langlebigen Strauch *Rosa rubiginosa* L. (Weinrose) gewählt, indem ich eingeführte Populationen in Argentinien mit nativen Populationen in Deutschland und Spanien verglichen habe. Meine Erkenntnisse zur Ursache des Invasionserfolg in Abhängigkeit vom Diasporendruck, günstigeren abiotischen oder biotischen Bedingungen im neuen Areal und der Einführung folgender rascher Evolution von adaptiven Merkmalen, sind in fünf Veröffentlichungen zusammengefasst.

Rosa rubiginosa dringt außerhalb ihres natürlichen Areals in indigene Pflanzengesellschaften ein und bildet große Dominanzbestände. Obwohl die Art pentaploid ist, kann sie sich aufgrund einer heterogamen meiotischen Vererbung sexuell fortpflanzen, wobei sie außerdem apomiktische Samen produziert und sich vegetativ fortpflanzt. Ihre Fähigkeit nach Schnitt und Brand erneut auszutreiben und der Aufbau einer dauerhaften Samenbank machen die Beseitigung der Art arbeits- und kostenintensiv und keine effektive oder risikofreie biologische Kontrollmethode wurde bisher gefunden.

Eine Literaturrecherche ergab, dass drei Arten der selben Gattung (*R. canina*, *R. multiflora*, *R. rugosa*) ähnliche Wachstums-, Reproduktionseigenschaften und Anpassungsformen an Störungen wie *R. rubiginosa* besitzen, aber letztere ist weltweit am häufigsten invasiv.

Ob das Vorkommen von *R. rubiginosa* mit bestimmten biotischen oder abiotischen Prädiktoren auf der Landschaftsebene zusammenhängt, wurde für Patagonien modelliert. Demnach war das Vorkommen von *R. rubiginosa* unabhängig von Habitattypen oder Niederschlagswerten, aber abhängig von Habitatstörungen. Anhand dieser Modellierung sind 36% des Untersuchungsgebietes von einer Invasion durch *R. rubiginosa* bedroht und es ist zu erwarten, dass Populationen über ausreichend Diasporendruck verfügen, um diese Vorhersage zu verwirklichen.

Unter Diasporendruck versteht man außerdem die Anzahl der Einführungsereignisse einer Art, welche mit molekularen Markern bestimmt wurden. Mehrfache Einführungen einer Art steigern die Wahrscheinlichkeit, dass Individuen auf günstigere Bedingungen treffen und sie minimieren Gründungseffekte. Zwei molekulare Studien enthüllten die starken Ähnlichkeiten zwischen Populationen in Süd- und Zentral-Argentinien. Diese Ähnlichkeiten deuten auf den Transport von *R. rubiginosa* Pflanzen oder Samen innerhalb Argentiniens hin. Die genaue native Ursprungspopulation konnte nicht ermittelt werden, aber Spanien konnte ausgeschlossen werden, wohingegen Deutschland, Tschechien und Österreich als mögliche Ursprungsregionen in Frage kommen. Invasive Populationen in Süd- und Zentral-Argentinien waren weniger genetisch divers als native Populationen, was auf wenige Einführungsereignisse, eine vorwiegende asexuelle Fortpflanzung und eine hohe phänotypische Plastizität hinweist. Die molekularen Studien warfen die Frage auf, ob sich ein besonders angepasster Genotyp in Argentinien ausbreitet oder ob die eingeführten Populationen von bestimmten neuen Umweltbedingungen profitieren.

Dies wurde durch den Vergleich von invasiven und nativen *R. rubiginosa* Pflanzen in Bezug auf Wachstum und Fitness sowie der Habitatseigenschaften in beiden Arealen geklärt. Aus den Feldstudien und den Verpflanzungsexperimente ergaben sich keine Hinweise auf einen angepassten Genotyp mit gesteigertem Wachstum und Fitness, oder Anzeichen für die Befreiung von Frassfeinden. Außerdem profitiert die Art nicht von den Bodenbedingungen oder der Vegetationsstruktur im neuen Areal. Ich komme zu dem Schluss, dass wiederholte Pflegemaßnahmen für die relativ kleinen Populationen in Deutschland und Spanien verantwortlich sind und dass in der alten europäischen Kulturlandschaft weniger Habitate für diese Art zur Verfügung stehen.

So konnte ich mit meiner Dissertation zeigen, dass niedrige genetische Diversität durch vorwiegende vegetative Fortpflanzung und hohe phänotypische Plastizität kompensiert wird. *Rosa rubiginosa* toleriert einen weiten Bereich an edaphischen und klimatischen Bedingungen und profitiert bei ihrer Etablierung über Habitattypen hinweg

von einmaligen Störungsereignissen. Jedoch führen wiederholte Störungsereignisse, wie sie im nativen Areal vorkommen zu reduzierten Populationsgrößen. Bleiben Pflegemaßnahmen aus, so besitzt *R. rubiginosa* ein großes Potential, um sich weiter in ihrem neuen Areal auszubreiten.

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General Introduction

Biological invasions: threat and challenge

Understanding invasion processes is crucial for the management of introduced exotic species. After being deliberately or accidentally introduced into a new ecosystem, some exotic species spread vigorously in their new range causing multiple problems (Vitousek et al. 1997a; Mack et al. 2000). Based on global biodiversity scenarios developed by Sala et al. (2000), by the year 2100 biodiversity loss caused by biotic exchange will be equal to that caused by climate change. Case studies confirm a significant decline in native species richness due to invasive species (Gaertner et al. 2009). For example, an analysis of the Red List Index showed that invasive species drive declines in the biodiversity of animal taxa (McGeoch et al. 2010). Invasive plants may reduce species richness in resident species through the displacement of established native plants or by preventing native plant colonization. For instance, invasive shrubs and trees restrain shade-intolerant native species by shading them out (Starfinger et al. 2003; Isermann 2008). Furthermore, it has been shown that exotic grasses, herbs, lianas and shrubs reduce the establishment of native plant seedlings (Yurkonis et al. 2005). A comparison between an exotic invasive and a highly dominant native species proved that the exotic plant species had an even greater impact at the community level (Hovick et al. 2011). Moreover, exotics can also cause extinction through hybridization (Rhymer and Simberloff 1996; Ayres et al. 1999).

Exotic plant species permanently alter ecosystems and sometimes transform entire habitats (Crooks 2002) by altering ecosystem processes, such as hydrology (Görgens and Wilgen 2004) or fire regimes (Brooks et al. 2004). The introduction of N-fixating plants changes soil properties (Vitousek and Walker 1989), but other plant species can also change soil-mineral composition or even increase erosion (Crooks 2002; Ehrenfeld 2003; Vanderhoeven et al. 2005). In addition, the provision of predator protection coupled with increased food supply by introduced plants can result in the disturbance of entire ecosystem food-chains (Dutra et al. 2011).

In addition, invasive plants can either directly cause human health problems or enhance the proliferation of diseases (Mack 2010). Examples include the invasive weed *Heracleum mantegazzianum* SOMMIER & LEVIER, which causes phytophotodermatitis (Tiley et al. 1996), and *Ambrosia spp.* pollen, which is the major cause of pollen-sensitive allergies (Makra et al. 2005). The invasive water hyacinth *Eichhornia crassipes* (MART.) SOLMS hosts mosquito larvae which can transmit malaria (Seabrook 1962) and the invasive shrub

Lantana camara L. attracts tsetse flies which transmit sleeping sickness (Syed and Guerin 2004). Mast seeding of invasive bamboo species in the United States represent a potential food supply for rodents infected with the Hantavirus, which can be lethal for humans (Mack 2010).

Thus, biological invasions can reshape ecosystems in many ways and, as invasions obliterate the regional distinctiveness of Earth's biota, we are in the process of losing unique ecosystems (Vitousek et al. 1997a; Chapin III et al. 2001). Human activities often trigger the extinction of rare species and assist in the introduction of already widespread species, thereby contributing to a homogenization of the biosphere (McKinney and Lockwood 1999). Homogenization of a flora has already been observed between regions in Europe (Winter et al. 2009), as well as throughout continents (Winter et al. 2010).

The economic implications of eradicating and preventing biological invasions runs into the billions (Pimentel et al. 2000; Scalera 2010), yet such high levels of public investment into species management programs will be necessary in order to avoid paying the ultimate price of losing unique ecosystems.

Vascular plants spread much faster in their introduced ranges than they would otherwise by natural forces or seed dispersal (Mack and Lonsdale 2001). Humans bear a responsibility for managing invasive species given our historic role in accelerating biological invasion rates by several orders of magnitudes (Vitousek et al. 1997b). Our approach to handling biological invasions is a topic of much debate (Haider and Jax 2007; Davis et al. 2011; Simberloff 2011); however, understanding such processes is a necessary precursor to establishing any potential solutions or effective discussion among the scientific community and the public (Rodewald 2011).

How species become invasive

The number of theories currently explaining invasion success are manifold and even the terminology surrounding invasion biology is a subject of much discussion and dispute (Davis et al. 2001; Pyšek et al. 2004; Davis 2009). In the current thesis, the term "invasive" is used as defined by Richardson et al. (2000), which maintains that an invasive plant species is a non-native (non-indigenous, alien, exotic) species that produces reproductive offspring some distance from the site of introduction, and thus has the potential to spread over a considerable area into semi-natural and natural habitats. Catford et al. (2009) summarized 29 leading hypotheses on plant invasion and broke them down into three

interdependent major themes: 1) Propagule pressure, 2) Abiotic characteristics of the invaded ecosystem, and 3) The biotic characteristics of the invading species and the recipient community.

The number of individuals introduced (propagule size) over the sum of the introduction events (propagule number) represents the propagule pressure (Lockwood et al. 2009). Propagule pressure has been positively correlated with invasion success because high propagule pressure increases the chance that an individual will encounter favourable environmental conditions (Lockwood et al. 2005), and multiple introduction events increase genetic diversity of populations, thus reducing founder effects, which could enable species to invade diverse habitats (Lockwood et al. 2005; Novak and Mack 2005). The term 'propagule pressure' is also used for the extent of spread and reproduction of established non-native populations, in which invasion success is facilitated by the production and dispersal of high amounts of seed or other plant propagules (von Holle and Simberloff 2005; Lambrinos 2006).

Environments differ in their capacity to be invaded (invasibility), for example, invasive plant species across growth forms benefit from high soil nutrients levels (Huenneke et al. 1990; Milberg et al. 1999; Allcock 2002; Hoopes and Hall 2002; Leishman and Thomson 2005), and light availability (Gurevitch et al. 2008; Schramm and Ehrenfeld 2010). Fluctuations in resource and space availability create windows of opportunity for invasive species to establish (Crawley et al. 1999; Davis et al. 2000; Shea and Chesson 2002). Correspondingly, increased invasibility is linked to disturbance events, which change the physical and chemical resource flux of an ecosystem (Sher and Hyatt 1999). Thus, invasibility is not a static condition of an environment (Davis et al. 2000).

Accordingly, many invasive plant species possess traits adapted to disturbance events. They are r-strategist ruderals adapted to exploit temporarily favourable conditions, characterised by their short-lived life cycle, rapid growth, high productive allocation, persistent soil seed-banks and rapid germination (Grime 1977; Rejmánek and Richardson 1996; Grotkopp et al. 2002; Blair and Wolfe 2004; Burns 2004). These characteristics together with plant traits like plasticity, self-compatibility, early flowering, vegetative reproduction, the ability to germinate in a wide range of conditions and to widely disperse, have all been integrated into the ideal weed hypothesis (Baker 1965). It has also been shown that invasive plant species are adapted to a wide range of edaphic and climatic conditions (Forcella and Wood 1984; Scott and Panetta 1993; LeJeune et al. 2006). However, an application of these traits as predictors of invasiveness for plants in general

could not be substantiated in experiments, because invasiveness results from the interaction of particular traits with particular environmental conditions (Richardson and Pyšek 2006; Davis 2009).

Biotic characteristics of the recipient community involve processes like competition, predation and parasitism. According to the 'empty niche hypothesis', invasive species profit from spare resources not used by the native species pool (Elton 1958; MacArthur 1970), for example, resources in soil horizons accessible only to deep-rooting invaders but inaccessible to native competitors (Borman et al. 1992; Dukes 2002). Invasive species may also benefit from other circumstances in the new range. For example, the 'Enemy Release' (ER) hypothesis states that species lose their natural enemies with the introduction to a new range and reallocate resources previously used for defence to growth and reproduction (Keane and Crawley 2002). Empirical support for this hypothesis, including the observation of reduced herbivory, fungal attacks and viral pathogens, has been found for some invasive plant species (Connor et al. 1980; Schierenbeck et al. 1994; Wolfe 2002; DeWalt et al. 2004b; Agrawal et al. 2005; Adams et al. 2009).

Changes in biotic constraints following introduction may also lead to biotic changes in the introduced species. The release from enemies, for example, may trigger the selection for genotypes with such attributes, as described by the 'Evolution of Increased Competitive Ability' (EICA) hypothesis (Blossey and Nötzbold 1995). Rapid adaptive evolution in invasive plants has been observed in common garden experiments, as manifested in growth, phenology and reproduction (Weber and Schmid 1998; Kollmann and Banuelos 2004; Maron et al. 2004; Barrett et al. 2008). On the other hand, introduced species may theoretically be threatened by new enemies and they might face the disadvantage that their populations have low genetic diversity, which can restrict their capacity for future adaptations ('Increased susceptibility hypothesis', Colautti et al. 2004).

Instead of a transformation of the invasive species after introduction, a pre-adaptation to the new environment may also facilitate naturalization. Duncan and Williams (2002) found higher naturalization rates for invasive genera that have native congeners in the New Zealand flora. They postulated that these genera share traits with their close relatives that enable survival in the new environment that outweigh the potential disadvantage of facing stronger competition. However, the importance of new functional traits for successful invasion has also been shown (Ordonez et al. 2010), as well as a decrease in herbivory with mean phylogenetic distance in a common garden experiment (Hill and Kotanen 2009). Results of studies on the pre-adaptation hypothesis vary because

they depend on the phylogenetic and spatial scales, the actual observed niche overlap of exotics and their native congeners as well as the specific stage of invasion (Diez et al. 2008; Thuiller et al. 2010). Diez et al. (2008) conclude that species specific traits or processes are more important than phylogenetic patterns for predicting invasion.

Invasive shrubs

According to the “global invasive species database” (GISD, <http://www.issg.org/database/welcome/>, accessed 23.05.2011) 22 out of 100 of the world’s worst invasive alien species – which are selected in accordance with their impact on biological diversity and on human activities - are trees and shrubs, with only 10 being either herbs, grasses or vines. However, scientific case studies on the causes of invasion success of exotic herbs, grasses and vines exceed those on invasive shrubs or trees by 32% (fig. 1). Grasses in particular seem to be over represented with 149 case studies but only 3 entries in the top 100 invasive species list (53 entries in the entire global invasive species database). Shrubs, on the other hand, are highly represented in the global invasive species database (111 entries), but they have been subject to scientific research less than any other life form except for vines (fig. 1). They generally have a strong impact on their recipient community by forming dense thickets, thereby shading out native species. In fact, four out of five herbal species belonging to the 100 worst invaders have shrub-like characteristics. They are perennials, such as *Fallopia japonica* (HOUTT.) RONSE DECR. or *Hedychium gardnerianum* SHEPARD EX KER-GAWL, which grow over 1 m tall forming dense stands.

Invasive shrubs have mostly been intentionally introduced as ornamentals for their attractive flowers, such as *Lantana camara* L. and *Buddleja davidii* FRANCHET (MORTON 1994; TALLENT-HALSELL AND WATT 2009), but also as windbreakers, such as *Tamarix* species (Di Tomaso 1998), and as living fences, including *Rosa multiflora* THUNB. EX. MURR. and *Ulex europaeus* L. (Amrine 2002; Isern 2007). The escape from cultivation and successful spreading of such species has long been ignored, and feasible opportunities for eradication may already have been missed (Mack and Lonsdale 2002). The impact of these unwary intentional introductions presents a hard learned lesson on the careless transfer of non-native species.

One reason for the unbalanced research focus might be the longevity and slow growth rates of shrubs compared to that of herbaceous species, which makes them an impractical study object for experiments. Greenhouse or common garden experiments

have been confined to a few fast growing shrubs that flower within the same year of germination (DeWalt et al. 2004a; Feng et al. 2007; Tallent-Halsell and Watt 2009). Common garden experiments with invasive tree species are also scarce and restricted to experiments on tree seedlings lasting from only a few months to a year (Siemann and Rogers 2003; Gleason and Ares 2004; Reinhart et al. 2005; Iponga et al. 2009; Schumacher et al. 2009). The majority of case studies on invasive trees are based on field observations, and the number of publications is twice as much as that on invasive shrubs (fig. 1). Therefore, another reason for the unbalanced research focus may be the economical relevance of some life forms, such as grasses for livestock grazing (McClaran and Anable 1992; Badgery et al. 2005; HilleRisLambers et al. 2010) and trees for forestry (Richardson 1998; Křivánek et al. 2006; Becerra and Bustamante 2008; Ross et al. 2009).

Field studies that allow for short periods of observation or monitoring at subsequent time intervals are the appropriate approach for woody, long-lived invasive species. In order to fully understand invasion processes, field studies should be conducted on both invasive and native populations of the respective species (Hierro et al. 2005).

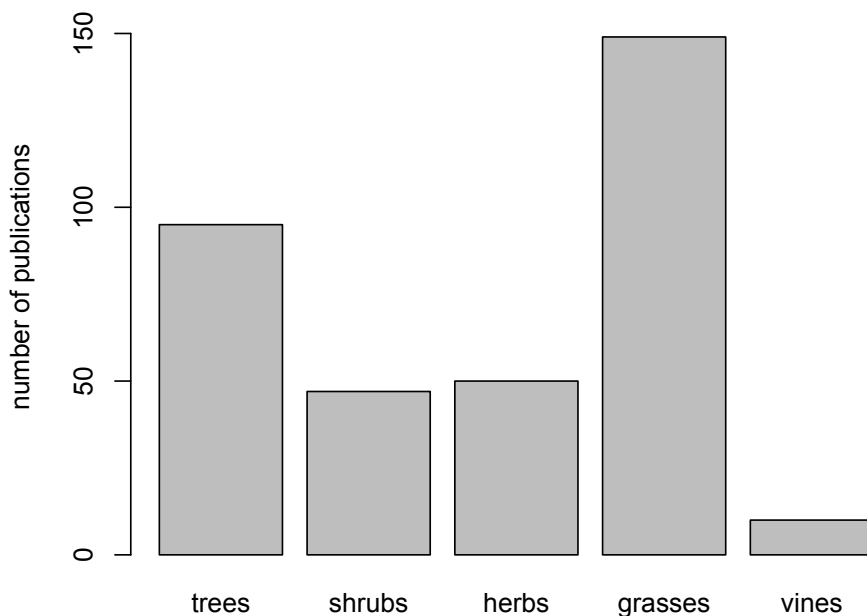


Fig. 1. Number of publications on invasive species divided by life form. The search was conducted in the Web of Science database (23.05.2011) with the search criteria "invasive species" OR "alien species" OR "exotic species", document type = article. Within the 8,046 hits, I searched for each life-form separately ("tree", "shrub", "herb and herbaceous", "grass", "vine") and checked each publication for its relevance.

Thesis objectives and structure

The objective of this thesis is to evaluate whether invasion success can be attributed to the number of introduction events, favourable conditions in the new range or characteristics of the invasive species based on native and invasive populations of a single study species. I chose a shrub of the Rosaceae family, *Rosa rubiginosa* L., as my study species as it has invaded several regions across four continents, including the focus country of this thesis, Argentina in South America.

The first publication of this thesis reviews the state of knowledge on the distribution, impact and management of invasive *Rosa* species in general. By comparing *R. rubiginosa* with species of the same genus with comparable traits, initial clues as to its invasion success are derived (Publication 1). The results of the review are completed by a regional prediction model which is employed to clarify whether the occurrence of *R. rubiginosa* depends on certain biotic or abiotic predictors and to quantify the invasion potential of the study species at the landscape scale (Publication 2).

The number of individuals introduced over the sum of the introduction events, i.e. propagule pressure, and the introductory pathway are identified using molecular markers (Publications 3 & 4). By quantifying the number of introduction events, it is possible to evaluate founder effects. Identifying source populations can provide important information on the release of specific constraints and evolution processes since immigration. Therefore, the identification of the exact source population may also help to identify biological control methods. An insight into the genetic diversity of native and invasive populations also indicates which mode of reproduction dominates in the native or invasive range.

Finally, a comparison on the ecology of native and invasive populations is made in order to detect genotypic and environmental effects on the invasion success (Publication 5). Germination experiments and the quantification of reproductive output show whether populations differ in terms of their fitness and information on individual size and age reveals differences in growth. Differences between the new and native environments are quantified for vegetation cover, soil nutrients and amount of leaf herbivory and assessed against their invasion success. Furthermore, the performance of individuals of native and invasive origin is monitored in the field and in common garden experiments in order to detect rapid adaptive evolution.



Fig. 2. *Rosa rubiginosa* can be distinguished from other dog roses by its pink flowers, glandular flower and hip stems. Sepals are persistent on the ripe rosehip and spines at the stem base are both hook and needle shaped (photos, H. Zimmermann).

Study species

Rosa rubiginosa (Syn: *R. eglanteria*, sweet-briar, eglantine rose) is a long-lived, spiny shrub (fig. 2). The species belongs to the family of Rosaceae in the section *Caninae* (D.C.) SER., commonly known as dogroses. Because of the unique meiotic behaviour of this section and the species' ability to hybridize with other *Rosa* species, the taxonomy of the genera is difficult to assess (Wissemann and Hellwig 1997; Wissemann and Ritz 2005). However, in comparison to other species of dogroses, *R. rubiginosa* is the most distinct taxon concerning its genetic constitution and morphological characteristics (Olsson et al. 2000). One of its defining characteristics is the sticky glands on the bottom side of the leaflets that secrete a strong, sweet-smelling apple-like fragrance. In addition to the defining characteristics of rosehips, the species' leaf-shape and spines can be clearly distinguished from other dogroses (fig. 2). The species is insect pollinated (autogamy and xenogamy), may also produce apomictic seeds and it spreads vegetatively by root suckers (Wissemann and Hellwig 1997; Werlemark 2000). *Rosa rubiginosa* achenes (hereafter referred to as seeds) have a hard bony pericarp, and when the hip is ripe, seeds are in both exogenous and endogenous dormancy (Gudin et al. 1990). In order to germinate, the pericarp has to be weakened, which usually occurs in nature during passage through the gut, but it can also be achieved through temperature treatment (Werlemark et al. 1995). It takes at least 6 months for seeds to germinate under experimental conditions (Werlemark et al. 1995) and



Fig. 3. *Rosa rubiginosa* (rosa mosqueta) products advertised in San Carlos de Bariloche, Argentina (photos H. Zimmermann).

plants need three years before they flower for the first time (Molloy 1964). However, time periods of 10 years or more before first flowering have been observed in the field (Molloy 1964).

With 150-200 morphospecies, the genus *Rosa* is distributed throughout the holarctic temperate region (Wisseman and Ritz 2005; Wisseman and Ritz 2007). *Rosa rubiginosa* is native to Europe and has been introduced to North America and several countries in the Southern Hemisphere; specifically, Argentina, Bolivia, Chile, South Africa, New Zealand and Australia (Seibert 1993; Timmermann and Müller 1994; Henker 2003; Weber 2003). It was probably introduced intentionally due to its ornamental properties (Kahle 1924; Mack and Erneberg 2002), and due to its edible hips, which are rich in vitamin C (Werlemark 2009). Nowadays, *R. rubiginosa* is being exploited on a large scale in Chile by the cosmetic industry because of the essential oils contained in its seeds (Joublan and Rios 2005; <http://www.weleda.de/Themenwelten/WeledaPflanzen/Wildrose/Index.html>, 16.05.2011). In Southern Argentina *R. rubiginosa* is already accepted as part of the local flora and its rosehips and seeds are harvested for private use or by small producers (fig. 3, Damascos 1992, <http://www.aceiterosamosqueta.com.ar/>, 16.05.2011). Given the popularity of the species, it is important to also raise awareness of the multiple problems caused by its introduction. *Rosa rubiginosa* builds up large monotypic thickets in its introduced range, thereby replacing native species (Damascos and Gallopin 1992; Weber 2003), and the extent to which native flora are outcompeted by pollinator and seed-disperser competition has not yet been fully investigated. However, insects frequently visit *R. rubiginosa* flowers in introduced populations (fig. 4, Morales and Aizen 2002; Aizen et al. 2008) and its fleshy hips are eaten by an array of dispersers including birds, horses and

cattle (fig. 4, Hatton 1989; Damascos et al. 2005). Furthermore, the flowering and fruiting period as well as the amount of fruit sets exceeds that of some native woody species (Cavallero and Raffaele 2010). Especially in Southern Argentina, *R. rubiginosa* hips represent a new resource during the winter period when food supply is rare (Damascos et al. 2005). These thickets also offer a new habitat for rodents, as they provide food and protection. In southern Argentina, some rodents carry a fatal virus called Hantavirus, which is transmitted to humans by inhalation of aerosols of infected rodent excretions (Pini 2004). So far, an outbreak of Hantavirus has been connected to rodent eruptions, which are triggered by periodical bamboo blooming and subsequent mast seeding (Jaksic and Lima 2003; Piudo et al. 2005). With the end of the mast seeding, rodent numbers decline again; but in the future, the availability of rosehips could stabilize large rodent populations.

Interspecific crosses of dogroses produce fertile hybrids, which are distinguishable from the mother plants if hips are present (Wissemann and Hellwig 1997; Ritz and Wissemann 2003; Wissemann and Ritz 2007; Ritz and Wissemann 2011). The hybridization of introduced *R. rubiginosa* individuals with native *Rosa* species only poses a potential threat in North America, since the genera is not native to the remaining regions of introduction in the Southern Hemisphere.

Eradication of this species is difficult, as has already been proven with other invasive species of the genus *Rosa* with similar life-strategies (Loux et al. 2005; Bruun 2006; Isermann 2008), and estate values in Southern Argentina have been known to fall when covered with *R. rubiginosa* (pers. comm. M. Damascos). Because the plant has to be removed with its roots, eradication is most effective at the early stages of establishment (Weber 2003). Moreover, it has been suggested that a combination of grazing by goats and



Fig. 4. A horse eating rose hips and a bee visiting a flower of a *Rosa rubiginosa* shrub in Argentina (photos H. Zimmermann).

herbicide treatment might be effective (Weber 2003). Burning is not an effective management method because *R. rubiginosa* resprouts readily after fire and seems to have a competitive advantage over native woody species on post-burned sites (Cavallero and Raffaele 2010).

Identification of the exact geographic origin of this species could help to understand the introduction histories, evolution and spread patterns of invasive populations and may help in the identification of biological control methods (Guo 2006; Estoup and Guillemaud 2010). The identification of source populations can be achieved with molecular markers (Milne and Abbott 2000; Milne and Abbott 2004; Durka et al. 2005). However, the interpretation of molecular markers is challenging in this species due to its odd ploidy level and the fact that one allele is always present in two identical copies (Nybom et al. 2004; Nybom et al. 2006). Like most dogroses, *Rosa rubiginosa* is pentaploid ($2n = 5x = 35$) and, despite its uneven ploidy level, it can reproduce sexually because of the unique canina meiosis, typical for this section (Täckholm 1920; Blackburn and Harrison 1921; Täckholm 1922). The pentaploid dogrose genome has a hybridogenic origin between non-dogroses and the now extinct Protocaninae (Ritz et al. 2005). These high ploidy levels and sexual reproduction are probably the reasons why dogroses were evolutionary successful in Europe across a broad range of different habitats following the end of the last glacial period in Europe (Ritz et al. 2011). Canina meiosis causes a pronounced maternal overload and nuclear markers may, in this case, behave similar to the strictly uniparentally inherited organelle DNA (Olsson et al. 2000; Nybom et al. 2001). During canina meiosis, two pairing genomes form bivalents and an additional three nonpairing genomes form univalents. The subsequent migration of the chromosomes in female and male meioses differ insofar as the functional egg cell is tetraploid, with one bivalent genome and three univalent genomes ($2n = 4x = 28$), whereas the pollen grain is haploid, with one bivalent genome ($n = x = 7$).

Study region

This thesis focuses on invasive *R. rubiginosa* populations in Central and Southern Argentina (figs. 5 & 6). In Australia, New Zealand and South Africa *R. rubiginosa* has already been recognized as a noxious weed (Parsons and Cuthbertson 2001; Bellingham et al. 2004; Nel et al. 2004), but information on invasive species for Argentina, the second largest country in South America, is still widely lacking (Vázquez and Aragón 2002; Speziale and Lambertucci 2010). I compared Argentinean invasive populations with populations from

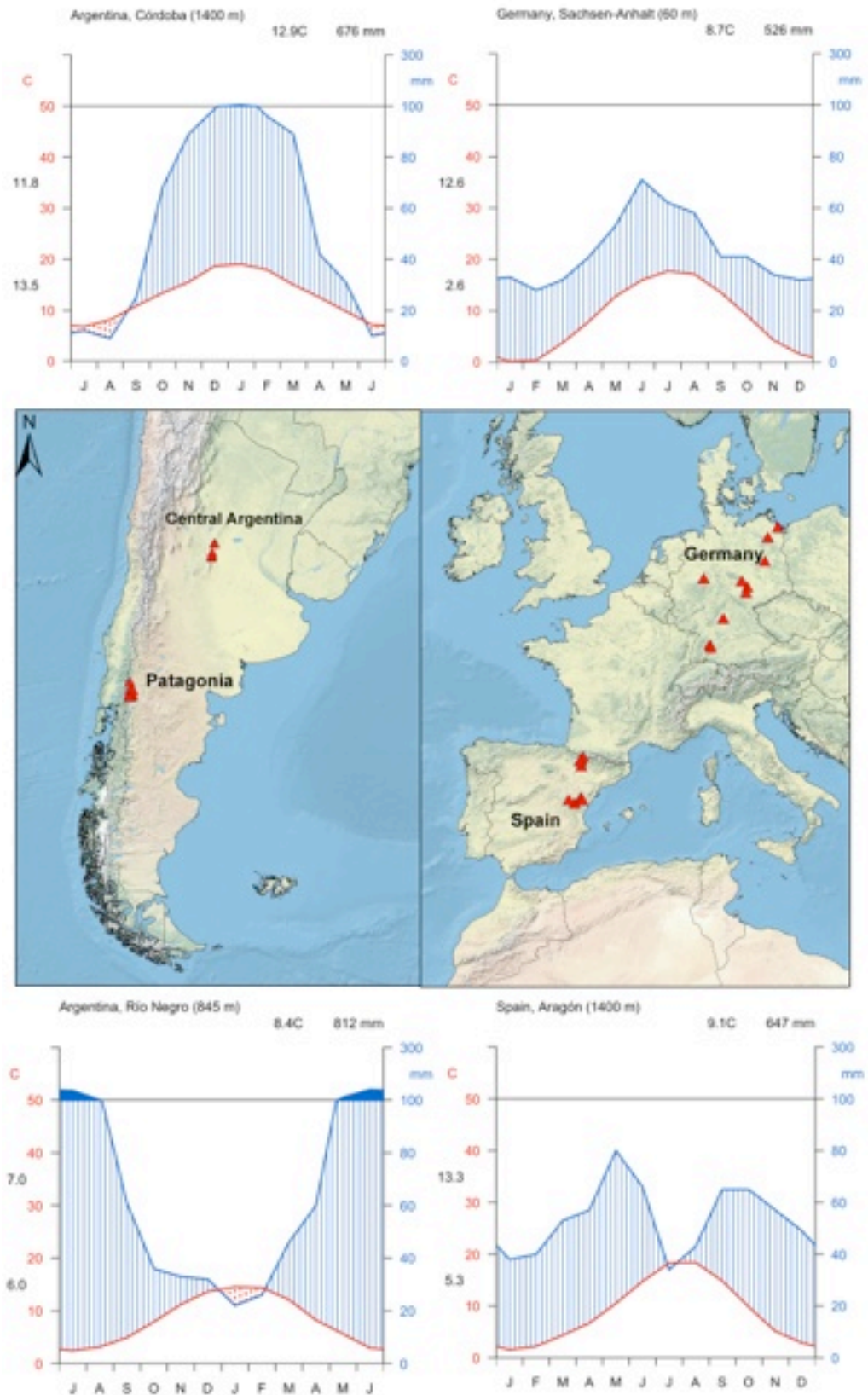


Fig. 5. Study sites in Central Argentina, Patagonia, Spain and Germany represented by red triangles and four Walter-Lieth climate diagrams of selected study sites in each region. From the top left clockwise: the climatic diagram of a study site in Central Argentina, Germany, Spain and Patagonia (climate data obtained from a global climate data source; Hijmans et al. 2005, map drafted by H. von Wehrden).



Fig. 6. *Rosa rubiginosa* populations in Argentina and Europe. (a) *Rosa rubiginosa* thicket in Patagonia, (b) *R. rubiginosa* with red rose hips in the foreground and more shrubs in the background in Central Argentina at 1700m a.s.l., (c) study site in Patagonia (*R. rubiginosa* shrubs in green-yellow), (d) *R. rubiginosa* shrub in the Pyrenees at 1300 m a.s.l., (e) *R. rubiginosa* population on a small summit inside an agriculture field, (f) *R. rubiginosa* shrub in a protected area in Germany and (g) *R. rubiginosa* shrub in the foreground at 1500 m a.s.l in the mountain range of Aragón, Spain (photos, H. Zimmermann).

the native range. So far, it has been assumed, that *R. rubiginosa* was introduced to South America by Spanish emigrants at the beginning of the 19th century (Joublan et al. 1996). However, I studied populations in Spain as well as in Germany, because Argentinean *R. rubiginosa* populations are often found close to settlements with German descendants. Populations are distributed over a broad climatic range within diverse habitat types, both, in the native and the introduced range (figs. 5&6). Germany has an overall temperate climate, but regarding the microclimate of our study sites annual precipitation varies considerably (538-989 mm/a; Weischet 2000; Hijmans et al. 2005). Monthly mean temperatures range from -4 °C for the coldest month to 24 °C for the warmest month (Hijmans et al. 2005). Studied *R. rubiginosa* populations occur on dry grasslands, heath land, in hedges along fields and roads (fig. 6). In Spain study sites were situated in the Pyrenees Mountains (960-1290 m a.s.l.) and further South in the mountain range of Aragón (1100-1500 m a.s.l.; fig. 5). The Pyrenees receive high precipitation throughout the year, with a slight summer minimum, towards the South precipitation decreases and summers are dry with high radiation (Weischet 2000). Our study sites in the Pyrenees receive high annual precipitation values (915-1150 mm/a), whereas sites in the central mountain range of Aragón have lower precipitation values (491-705 mm/a; Hijmans et al. 2005). Monthly mean temperatures range from -5 °C to 25 °C in our Spanish populations. *Rosa rubiginosa* populations in these regions were found in open pine woodlands, high-montane shrub-grasslands, along roads and montane pastures.

In Europe, population densities are sparse and often consist no more than 10 individuals. In contrast, populations in Argentina consist of hundreds of individuals forming dense thickets (fig. 6). Within Argentina, the climate differs considerably between our study areas in Central and Southern Argentina, which are over 1000 km apart (fig. 5). In Central Argentina, our studied populations are situated in the province of Córdoba, in the main mountain chain the Sierras Grandes de Córdoba (1000-1700 m a.s.l.) and in the adjacent mountain range, the Sierras Chicas (1000-1500 m a.s.l.). The climate in the Córdoba mountains is temperate-humid, with predominant summer rains, an annual precipitation of 670 mm/a and an average temperature of 12 °C at 1500 m a.s.l. (Cabido et al. 1987; Hijmans et al. 2005). Annual precipitation values vary between 658-676 mm/a and monthly mean temperatures range from -1 to 28 °C at our study sites (Hijmans et al. 2005). Studied populations were situated in high-montane shrub-grassland communities, a pine plantation and evergreen *Fagaria coco* ENGL. forest.

The predominant climate in Southern Argentina in Patagonia is temperate with frequent snow events and an average temperature of 8 °C (Weischet 1996; Hijmans et al. 2005). Our study sites were situated around the town San Carlos de Bariloche, in the province of Río Negro, and inside the Nahuel Huapi National Park, which borders the town and extends into the province of Neuquén. San Carlos de Bariloche (845 m a.s.l.) is located 40 km east of the Andes' main chain, at the shores of the grand Nahuel Huapi lake. Annual precipitation values decrease dramatically with distance to the Andes. Our study sites receive 831-1252 mm/a precipitation and mean monthly temperatures range from -2 to 22 °C (Hijmans et al. 2005). *Rosa rubiginosa* populations are distributed along the whole precipitation gradient. Study sites were sited in steppe vegetation with bunch-grasses and spiny shrubs as well as conifer *Austrocedrus chilensis* (D. DON) PIC. SERM. & BIZZARI forests at the lower precipitation levels, and in gaps within broad-leafed *Nothofagus dombeyi* MIRB. (OERST.) forest with bamboo (*Chusquea culeou* DESVAUX) understory at the highest precipitation levels (De Fina 1972; Veblen et al. 1992).

1. Publication

Some dark sides and their addressing

In: Wild Crop Relatives--Genomic & Breeding Resources: *Rosa*. (ed. C Kole). Springer-Verlag, Berlin-Heidelberg

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Roses have a long history as horticultural plants and have as such been introduced into several countries outside their native range. Unfortunately, some of these *Rosa* species escaped gardens or parks and invaded natural habitats and threatened the native flora. Four *Rosa* spp. are so far known to be invasive globally (*R. canina*, *R. multiflora*, *R. rugosa* and *R. rubiginosa*). Management is cost-intensive, since once established as alien plants *Rosa* spp. are difficult to eradicate due to their ability to resprout after cutting, browsing or even fire.

2. Publication

Habitat invasion risk assessment based on Landsat 5 data, exemplified by the shrub *Rosa rubiginosa* in southern Argentina

Austral Ecology (2010) doi: 10.1111/j.1442-9993.2010.02230.x

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Abstract

Prediction of invasive species spread helps to plan management actions. We performed a risk assessment by quantifying habitat invasibility, predicted the potential distribution of an invasive species using the Maxent modelling program and confirmed patterns using detailed field studies. Our study was conducted in southern Argentina, Patagonia, where large areas are already invaded by the European shrub *Rosa rubiginosa*. A total of 163 *R. rubiginosa* locations served as ground truth data, and predictors were obtained from the spaceborne sensor Landsat 5. Based on the Maxent Method (area under the receiver operating characteristic curve 0.8), the habitat invasibility map covered about 5000 km². Our model revealed that *R. rubiginosa* has the potential to invade 36 % of the area along a steep precipitation gradient (target region 600–1400 mm per year). The Tasseled Cap brightness index and the normalized vegetation index explained most of the variance in our model, followed by the Tasseled Cap greenness and wetness indices, which can be interpreted as indicators of disturbance. Highest levels of invasibility were predicted for urban areas, along roads and rivers, on pastures, in *Austrocedrus chilensis* forests and inside *Nothofagus dombeyi* forest gaps. Detailed field assessments of rose cover performed in seven habitat types supported these results: rose cover significantly decreased with increasing tree cover ($P < 0.01$). Our data revealed that the occurrence of *R.*

rubiginosa is not connected to a certain habitat type, but that it thrives in open patches following habitat disturbance. Our approach is a widely applicable, cost-free remote sensing method that can serve as a risk assessment tool for alien plant species invasion of habitats.

Key words: alien species, Patagonia, presence-only, remote sensing, Rosaceae.

3. Publication

Highly reduced genetic diversity of *Rosa rubiginosa* L. populations in the invasive range

International Journal of Plant Sciences (2010) 171(4): 435–446

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Abstract

Rosa rubiginosa (Rosaceae) populations introduced to Argentina successfully invade various habitats, forming extensive impenetrable thickets. To investigate the consequences of founder events and to track the native origin of Argentinean populations, the genetic diversity of invasive *R. rubiginosa* populations was compared with that of native populations in Europe, and genetic similarity was assessed between groups. We sampled 13 Argentinean populations and 20 native populations in Germany and Spain, and we applied two molecular marker techniques (simple sequence repeats and random amplification of polymorphic DNA [RAPD]). Genetic diversity within the invasive range was clearly lower than it was in the native range. Principle coordinate analysis and between-class analysis did not reveal the exact European origin of the invasive populations, but our data suggest that at least one Argentinean population originated in Germany. Overall, the strong similarity of RAPD and allelic phenotypes throughout Argentina suggests a limited number of introduction events, that the species spread through human transport, and that the few genetic phenotypes present in the species were conserved largely unaltered as a result of mainly asexual reproduction.

4. Publication

Tracking the origin of invasive *Rosa rubiginosa* populations in Argentina

International Journal of Plant Sciences (2011) 172(4):530–540

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Abstract

The exact geographic origin of invasive species populations is rarely known; however, such knowledge is vital to understanding species' invasion success, spread, and evolution as well as for assessing any biological control options. We investigated the shrub *Rosa rubiginosa* L., focusing on the presumed European origin of invasive populations in Argentina. We analyzed eight polymorphic microsatellite loci among 102 native (European) and 29 invasive (mainly central Argentinean and Patagonian) populations. Genetic diversity in the invasive range was clearly lower than in the native range, possibly because of a low number of introductions. Contrary to earlier hypotheses, the interpretation of principal coordinate analysis results and Jaccard dissimilarities contradicts the idea of the Argentinean populations having a Spanish origin. Instead, we found a close similarity between Argentinean samples and those from Germany, the Czech Republic, and Austria. We therefore assume that these neighboring countries are the most probable source regions for the Argentinean populations, which in some cases may also have arrived via Chile. According to historic information, emigrants from these regions may have introduced *R. rubiginosa* to South America in the nineteenth century on at least two occasions, either for food or as rootstock material for propagating living fences.

Keywords: biological invasions, microsatellites, native origin, bridgehead effect, polyploidy, Rosaceae.

5. Publication

Shrub management is the principal driver of differing population sizes between native and invasive populations of *Rosa rubiginosa* L.

Biological Invasions (under review)

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Abstract

An essential step in the understanding of biological invasions is the comparison of species' performance in the native and introduced ranges. *Rosa rubiginosa* L. is acknowledged as a noxious weed only outside of its native range. By comparing native *R. rubiginosa* populations in Spain and Germany with invasive populations in Central and Southern Argentina, we found that native shrubs were, on average, taller than introduced shrubs. At the 100 m² plot scale, rose-cover in Spain and Germany was significantly higher than in Central Argentina but comparable to that found in Patagonia. At the population scale, native populations were less dense and smaller than their invasive counterparts. Growth rates of marked branches did not differ between ranges, but marked shrubs indicated that native *R. rubiginosa* stems are cut regularly, with the oldest rose stems being found in Argentina. Seeds from the introduced range did not have higher germination rates overall, and low seedling numbers in the field underline the general importance of vegetative growth for the species. Leaf damage did not differ between regions and soil analyses proved that *R. rubiginosa* may tolerate a wide range of soil conditions without necessarily benefiting from any one in particular. No differences were observed in vegetation structure, pointing to favorable conditions in the introduced range, and greenhouse experiments showed that plants of invasive origin do not outgrow native roses.

The smaller population sizes in the native range can therefore be attributed to management actions along with a lower level of viable habitat.

Key words: woody exotic, Rosaceae, South America, plant performance, enemy release

Synthesis

General discussion

The defining keys to the invasion success of *R. rubiginosa* are its biotic characteristics and the availability of vegetation gaps triggered by habitat disturbance. Thus, the species' successful invasion is caused by its high phenotypic plasticity, predominant asexual reproduction and its ability to tolerate a wide range of edaphic and climatic conditions. Furthermore, it benefits from a high availability of vegetation gaps as entry vectors in Argentina. Instead of the common assumption that invasive plants perform better in their new range (Blossey and Nötzbold 1995; Keane and Crawley 2002), the relative smaller size of *R. rubiginosa* populations in the native range was due to management practice. Human-mediated dispersal was the starting point for its introduction to Argentina and responsible for long distance dispersal within Argentina. However, following the incremental approach by Catford et al. (2009; fig. 7), propagule pressure, i.e. the number of individuals over all introduction events, along with the biotic characteristics of the invaded communities did not contribute to its invasion success.

Our approach to conduct a habitat invasion risk assessment involved using *R. rubiginosa* locations as ground truth data and remote sensing data as predictors and pinpointed the invasion potential and the importance of habitat disturbance for the establishment of the species. This method is widely applicable and recommendable as a starting point for invasive species studies in general. Forest gaps, pastures, river- and roadsides have a high probability of being invaded by *R. rubiginosa*. The importance of roadsides for the distribution of exotic species was also revealed by Pauchard & Alaback

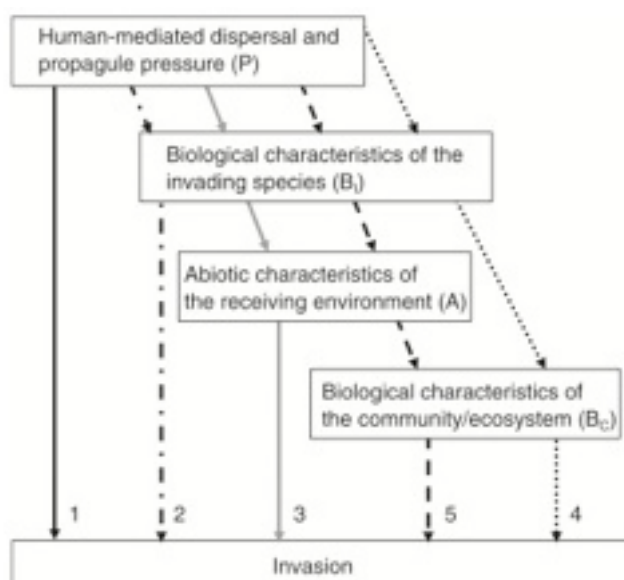


Fig. 7. This figure from Catford et al. (2009) illustrates their proposed top-down incremental approach to study invasion processes.

(2004) for national parks in Chile. Two other invasive rose species also benefit from habitat disturbance. Robertson et al. (1994) did not observe invasive *R. multiflora* populations inside mature forests in North America, which was confirmed by Lundgren et al. (2004) and Yates et al. (2004), who found a correlation between *R. multiflora* abundance and human disturbance on the landscape scale, with *R. multiflora* being most frequent along roads and urban areas followed by former fields and forest edges. *Rosa rugosa* seedling emergence and survival was positively related to vegetation gaps in a small-scale disturbance experiment (Kollmann et al. 2007). This is in line with other studies, indicating the relevance of gap dynamics for the colonization of invasive species. While transplanted exotic species may survive in both undisturbed plots and vegetation gaps, seedlings only establish in disturbed plots (Jesson et al. 2000). Invasive species not only benefit from disturbance through reduced competition and higher resource availability (Burke and Grime 1996; Lake and Leishman 2004) but also through the slower colonization rate of local species (Williams et al. 2010). Manipulative experiments in forest communities with other woody exotics and an exotic grass underline the importance of increased light availability for seedling establishment and growth (Gurevitch et al. 2008; Schramm and Ehrenfeld 2010). Comparison of *R. rubiginosa* phenology with native species on burned sites in Patagonia proved that the invasive shrub has a competitive advantage over native trees but not over a native shrub following fire (Cavallero and Raffaele 2010).

In conclusion, disturbance events are windows of opportunity for *R. rubiginosa* to establish (Crawley et al. 1999) as it does not occur underneath closed canopies and it benefits from increased light availability accompanying habitat destruction.

The molecular studies of this thesis disproved the common assumption that Argentinean *R. rubiginosa* populations originated in Spain. Although we were not able to locate the exact source region, we can pinpoint the place of origin to Central Europe, which is also in line with the origin of a large proportion of emigrants in the 19th century (Oelsner 2007). I expect the chances of finding the exact source region in the future with an enhanced sampling scheme in the native range to be small, since genetic structures in European *R. rubiginosa* are not well linked to geographical patterns, and the population of origin may have already gone extinct. The most probable reason for the distribution pattern of *R. rubiginosa* genotypes across Europe could be that the species rapidly dispersed during the postglacial recolonization of Europe and that genotypes were conserved via self-fertilization or apomixis. This is also in line with the observed preservation of only a few genotypes during the present colonization of Argentina. Other

European plant species, like *Abies normanniana* (STEV.), *Salix caprea* L., *Crateagus laevigata* (POIR.) DC. and *C. monogyna* JACQ. (Palmé et al. 2003; Fineschi et al. 2005; Hansen et al. 2005), are also known to show a lack of phylogeographic structure. All mentioned species are invasive outside their native range (Hunter and Mattice 2002; Howell and Sawyer 2006; Aslam et al. 2010).

Our studies revealed an overall low genetic diversity across Argentinean populations. Thus, we can assume that high propagule pressure accompanied by genetic variation usually associated with successful invasion (Novak and Mack 2005; Lavergne and Molofsky 2007; Lockwood et al. 2009; Simberloff 2009) does not contribute to the invasiveness of this species. Dlugosch and Parker (2008) also documented reduced genetic diversity in founder populations of the invasive shrub *Hypericum canariense* L., but in contrast to *R. rubiginosa*, common garden experiments nonetheless proved the evolution of adapted invasive genotypes following introduction.

In order to enhance our understanding of the invasion history of *R. rubiginosa* on a global scale, more samples from other areas of introduction would be desirable. Samples from Australia and New Zealand, for example, have already revealed a strong similarity to Argentina, pointing to a joint origin for these introduced populations.

By comparing leaf damage, plant size, growth rates, reproductive output, germination and age structure of native and invasive *R. rubiginosa* populations we were able to reject the ER and the EICA hypotheses (Blossey and Nötzbold 1995; Keane and Crawley 2002) for our study species. In common with other studies that disproved these hypotheses by comparing the abundance of natural enemies and the effect on productivity between phylogenetically related native and invasive plant species (Parker and Gilbert 2007; Lombardero et al. 2008), we did not observe any difference in leaf damage between *R. rubiginosa* shrubs of both ranges, nor did we observe increased plant performance or fitness in the invasive range. Despite these facts, population density and size were still larger in the invasive range. Our insights from the molecular analysis and field surveys contradict the Increased Susceptibility hypothesis (Colautti et al. 2004), given that no evidence was found for an increased susceptibility to new enemies, despite *R. rubiginosa* populations having a low level of genetic diversity.

Seeds from both ranges underwent a dormancy period lasting over six months during which they were placed in water, and no plant flowered within the same year of germination. This confirmed that this invasive species does not possess two traits typical for r-strategists and many invasive plant species alike, namely, a short life cycle and rapid

germination (Grime 1977; Blair and Wolfe 2004; Erfmeier and Bruelheide 2005). However, other characteristics assigned to r-strategists (Grime 1977) and to the Ideal Weed hypothesis (Baker 1965) do apply. For example, our molecular study proved that *R. rubiginosa* possesses a high phenotypic plasticity and reproduces predominantly asexually, and the soil-seed bank was persistent in both ranges over two years. We were not able to detect favourable edaphic conditions or differences in vegetation cover in the introduced range, but we confirmed that invasive species tolerate a wide range of edaphic conditions (LeJeune et al. 2006).

Populations in both ranges were situated in habitats with open canopies, and the cover of shrubs other than *R. rubiginosa* was even higher in the introduced range. Although it was not investigated in detail as to whether *R. rubiginosa* occupies an empty niche in Argentina (Elton 1958; MacArthur 1970), the empty niche hypothesis seems unlikely given the high cover values of plants with the same life-form in the invasive range. A detailed comparison of climatic conditions was also not undertaken for this study; however, climatic differences can probably be neglected given the large differences within the invasive range concerning seasonality and precipitation.

A notable observation was that individuals in the native range are regularly cut back; a measure that certainly keeps populations small by controlling both the number and size of individuals. This was underlined by the fact that the oldest rose stems were found in invasive populations. Thus, this is the first population ecology study (to my knowledge) that has revealed land-use as a limiting factor for an invasive species in its native range. The invasive shrub *Rhododendron ponticum* L. is also endangered in its place of origin, but its status is due to climatic constraints (Mejías et al. 2002). Here, the native populations are relicts from a formerly wider distribution. Species with a wider native distribution range tend to be more successful invaders (Forcella and Wood 1984; Scott and Panetta 1993), which also holds true for *R. rubiginosa*, whose range spans from the lowlands to the subalpine and from the Atlantic to the Mediterranean (Timmermann and Müller 1994). However, despite its wide distribution, *R. rubiginosa* is restricted to only a few viable habitats inside this range and it is increasingly endangered in its native range due to anthropogenic land-use changes (Ludwig and Schnittler 1996; Poppendieck et al. 1998; Rennwald 2000; Seitz et al. 2004).

This thesis underlines the relevance of field studies in exploring the invasion biology of long-lived exotic species and the importance of examining multiple factors simultaneously, such as genetic shifts following introduction in the new range, plant

performance and edaphic conditions in both ranges (Guo 2006; Davis 2009). Common garden experiments are an unsuitable tool given the limited time frame of this thesis and the species' slow germination and growth rate. While the reciprocal transplantation experiment with root cuttings bypassed the germination period, the survival of cuttings during transport represents another challenge. Furthermore, common garden experiments may be biased by maternal effects (Roach and Wulff 1987), which can be minimized by an acclimation period of plants for two to three generations (Kawecki and Ebert 2004). Such an approach would however not be feasible for *R. rubiginosa* as it has a reproduction cycle of at least three years (Molloy 1964). Available resources of parental plants are primarily expressed in the nutrition status of the seeds. Thus, equal seed mass is also used as an indicator for the absence of maternal effects (Callaway et al. 2005; Blumenthal and Hufbauer 2007). Differences in seed mass among populations were detected in our studies, but since we did not detect a conclusive relationship between seed mass and seedling performance, maternal effects are expected to be minimal. Finally, *R. rubiginosa* plants of invasive origin did not perform better in the common garden experiments. Consequently, neither genetic nor maternal effects are responsible for the invasion success of *R. rubiginosa* in Argentina.

Implications for nature conservation

By identifying the factors responsible for a successful invasion, this study can support decision-making processes and evaluate the suitability of certain management techniques (Catford et al. 2009). Given the insights of this thesis, I make the following recommendations for the management of *R. rubiginosa*:

- 1) First of all, it is important to raise public awareness regarding the impact of this invasive species. This measure could prevent further intentional transport of *R. rubiginosa* within Argentina and could ensure eradication of newly established populations. Recently established individuals can still be easily removed with its complete root system. I started to inform the public in Córdoba by passing out leaflets with information for the identification, general impact and eradication of this species (fig. 8). Moreover, scientists from the University of Córdoba and members of the nature conservation organization Ecostimas Argentinos (<http://www.ecosistemasarg.org.ar>) have already written and distributed some books and leaflets to inform the public about biological invasions in general. Their efforts to address schools in environmental education represent a particularly promising investment for the future awareness of biological invasions. Weed

control management of this species is already practiced by government agencies in other countries including Australia (<http://www.dpi.nsw.gov.au/agriculture/pests-weeds/weeds/profiles/sweet-briar>), New Zealand (http://weedbusters.co.nz/weed_info/detail.asp?WeedID=61) and South Africa (http://www.arc.agric.za/uploads/images/0_sapia_news_no_3.pdf). Argentinean government agencies and NGOs may therefore learn from their experience.

2) It is essential to assign funding to management practices. As our review has shown, rose eradication is labour and cost-intensive and, to date, no appropriate biological control agent has been found. Moreover, without any proof for enemy release, biological control agents are not promising. While invasive populations with high levels of genetic diversity have a high potential to evolve new traits, due to recombination and rapid adaptive evolution (Lavergne and Molofsky 2007; Williams and Grosholz 2008) it is not expected that management has to adapt to changes in this species' biology due to the low genetic diversity observed in invasive *R. rubiginosa* populations.

Invasión de la rosa mosqueta
(*Rosa rubiginosa* L.)

¿Qué es una invasión biológica?
Las especies invasoras exóticas son uno de los problemas ambientales más preocupantes a nivel mundial. Argentina no escapa a esta situación.....

...la introducción de especies animales o vegetales exóticas por parte del hombre se ha convertido en una amenaza para la biodiversidad de nuestros ecosistemas. Algunas de estas especies se multiplican y crecen descontroladamente, desplazando a las especies nativas y modificando de manera irreversible nuestros ecosistemas. La pérdida de esta biodiversidad implica también la pérdida de un legado histórico y cultural relacionado con el uso de plantas medicinales, especies exóticas invasoras producen cambios en el suelo y en el clima y alteran el ciclo del agua. Su erradicación o control puede resultar muy costoso. En Argentina, las especies invasoras más comunes son: el árbol de la caña, el algarrobo, el eucalipto, el pino, la robla, la acacia, la lechuga, y también, la rosa mosqueta.

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¿Cómo puedes ayudar?

- Difundir la información de este folleto.
- Plantar especies nativas en tu terreno.
- No traigas más rosas mosquetas u otras plantas y animales exóticos.
- Cuando veas una rosa mosqueta, elimínala de raíz cuando todavía es pequeña.
- Y lo más importante: preservar los bosques nativos. En un ambiente sano, la rosa mosqueta tiene menos oportunidades de crecer.

Nuestro estudio
El objetivo es determinar si la rosa mosqueta es invasora en Argentina y no en su lugar de origen debido a cambios genéticos, de clima o del ambiente que favorecen su dispersión. Relevamientos a campo, análisis genéticos y de nutrientes del suelo, análisis de las condiciones climáticas y el registro de factores como el sobrepastoreo, erosión, incendios y urbanización nos ayudarán a comprender las causas de la invasión de la rosa mosqueta, y prevenir futuras invasiones. La rosa mosqueta está invadiendo estepas, pastizales y bosques. Tenemos cuatro regiones de estudio: Alemania, España, centro y sur Argentina.

La rosa mosqueta
Es originario de Eurasia y su nombre científico es *Rosa rubiginosa* L. Posee espinas curvas en sus tallos, flores rosadas muy vistosas y frutos de un intenso color rojo. Su característica más llamativa es la fragancia dulce, similar a una manzana, que despiden sus hojas al ser tocadas.
En Europa la rosa mosqueta crece hasta 3 m de altura y una población se compone de no más que 20 arbustos. Sus frutos son apetecidos y dispersados por diversas aves, insectos y también por el ganado.

En la Patagonia puede crecer hasta 10 m de altura, trepando arriba de árboles, y formando matas impenetrables de grandes extensiones.

En el centro Argentino la rosa mosqueta posee sitios con poblaciones de más de 100 individuos, afortunadamente, todavía no ocupan grandes extensiones.

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Fig. 8 Leaflet created by the author with information on the identification, general impact and eradication of *Rosa rubiginosa*. This leaflet was distributed in Central Argentina, where the general public is largely unaware of the species' presence.

3) The most important task is to preserve the remaining intact forests because the disturbance and fragmentation of these ecosystems enables the establishment of *R. rubiginosa*. Eradication measures should start along roads and rivers, in order to minimize possible invasion corridors. Once rose thickets have been removed, managed sites have to be monitored for re-colonization. As our seed-bank experiment has shown, seeds remain viable in the soil for over two years, and only a few vegetatively spreading individuals are sufficient to establish a new population.

4) It is important to offer native plants as alternatives to *R. rubiginosa* given that the economic exploitation of *R. rubiginosa* in Argentina as already practiced in Chile is somewhat imminent. There are many Argentinean native plants whose fruits or leaves are being harvested to prepare teas or sweets or that can be processed for their high levels of essential oils. For example, the fruits of *Berberis microphylla* G. FORST. (Calafate) in Patagonia are rich in Vitamin C and other antioxidants (von Baer et al. 2010), dried leaves of *Minthostachys spp.* (Peperina) are used to prepare a popular tea in Córdoba (Bustos and Bonino 2005; Schmidt-Lebuhn 2008) and the Central Argentinean tree *Schinus molle* L. produces essential oils useful for the cosmetic industry (Zahed et al. 2011).

Concerning the status of *R. rubiginosa* in its native range, nature conservation agencies in Germany have the directive to spare *R. rubiginosa* when clearing grasslands from shrubs (pers. comm.). However, this is often not accomplished because experience in distinguishing the different *Rosa* species is lacking. The same holds true for Red Listed data assessment (Seitz et al. 2004). Therefore, native *R. rubiginosa* shrubs are constantly cut back, and in the fragmented landscape of Europe, viable habitats are scarce. In a way, the situation of *R. rubiginosa* in its native and invasive range reflects the situation of the human emigrants who brought this species to the New World. Just like them, *R. rubiginosa* escaped from persecution in its home range, found refuge in Argentina, successfully established and spread, but not without leaving a lasting impact on its new home.

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Publications of the dissertation

1. Publication

Zimmermann H and I Hensen (in print) **Some dark sides and their addressing**. In: Wild Crop relatives: Genomic & Breeding Resources. ed. C. Kole. Springer, Heidelberg, Berlin, New York, Tokyo

2. Publication

Zimmermann H, H von Wehrden, M Damascos, D Bran, E Welk, D Renison and I Hensen(2010) **Habitat invasion risk assessment based on Landsat 5 data, exemplified by the shrub *Rosa rubiginosa* in southern Argentina**. *Austral Ecology*: doi 10.1111/j.1442-9993.2010.02230.x

3. Publication

Zimmermann H, CM Ritz, H Hirsch, D Renison, K Wesche and I Hensen (2010) **Highly reduced genetic diversity of *Rosa rubiginosa* L. populations in the invasive range**. *International Journal of Plant Sciences* 171 (4): 435-446

4. Publication

Hirsch H, Zimmermann H, CM Ritz, V Wissemann, von Wehrden H, D Renison, K Wesche, E Welk and Hensen (2011) **Tracking the origin of invasive *Rosa rubiginosa* populations in Argentina**. *International Journal of Plant Sciences* 172(4): 530-540

5. Publication

Zimmermann H, H von Wehrden, D Renison, K Wesche, E Welk, MA Damascos and I Hensen (under review) **Shrub management is the principal driver of differing population sizes between native and invasive populations of *Rosa rubiginosa* L.** *Biological Invasions*

Curriculum vitae and full publication list

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subject biology (botany, genetics, limnology, soil science)
Diploma thesis: "Regeneration-niche of *Polylepis australis* in the
Sierras Grandes de Córdoba, Argentina"

Professional career

Sept. 2003: part time scientific staff member, competition
experiments, UFZ (Centre for environmental research), Halle
May-July 2005: part time scientific staff member, project Alternet, UFZ, Halle
Sept.-Nov. 2005: part time scientific staff member, project Leda, UFZ, Halle
July-Nov. 2006: layout artist of the "Multivariate Statistik in der Ökologie,
Springer" textbook
Sept. 2006-June 2011: employment as Biologist at the Institute of Geobotany,
Halle Germany
2009: Paternal leave

Grant

2006-2008: German Academic Exchange Service scholarship

Field trips

- 2002: short fieldtrip, Mongolia
- 2003: three months fieldwork for diploma thesis, Argentina
- 2005: three months participation within the project
"Vegetation mapping of southern Mongolian protected areas",
Mongolia
- 2005-2008: three times for three month fieldwork for PhD in Argentina
- 2006-2007: 2 times for 2 weeks fieldwork for PhD in Spain

Teaching

- 2005-2011: several seminars on the "Introduction to R--The Foundation for Statistical Computing"
- Jun. 2006: practical course "Basic plant ecology"
- Mar.-July 2006: practical course "Plant classification"
- 2006-2007 excursion-"Plant determination in the field"

conferences

- Zimmermann H, D Renison, R Suarez, I Leyer and I Hensen (2006). Effects of livestock exclusion on the regeneration of *Polylepis australis* BITT in the mountains of Central Argentina. Poster Plant Population Biology conference in Halle, organized by Martin Luther-University, UFZ Halle/Leipzig and GfÖ.
- Zimmermann H, I Hensen, D Renison, K Wesche and E Welk (2007). Invasive *Rosa rubiginosa* L. shrubs outgrow their European ancestors in number and size. Poster 37. Jahrestagung der Gesellschaft für Ökologie (GfÖ), Marburg
- von Wehrden H, H Zimmermann, J Hanspach, K Ronnenberg, K Wesche (2007). Predicting the occurrence of plant species and communities in an arid southern Mongolian mountain range. In: Becker U (ed.): Verhandlungen der Gesellschaft für Ökologie, Band 37, Marburg, Deutschland.
- Zimmermann H, D Renison, MA Damascos, E Welk, K Wesche and I Hensen (2008). Density and growth of *Rosa rubiginosa* L.; invasive in Argentina and declining in Europe. In: Stadler J, Schöppe F, Frenzel M (eds.): Verhandlungen der Gesellschaft für Ökologie, Band 38, Leipzig, Deutschland.

Zimmermann H, H von Wehrden, H Hirsch, M Damascos M, D Bran, E Welk, K Wesche, C Ritz C, V Wissemann, D Renison and I Hensen (2010). The invasion success of *Rosa rubiginosa* across diverse ecosystems and climates despite its highly reduced genetic diversity. In: Kollmann J, van Mólken T, Ravn HP (eds.): 16th Neobiota conference, Biological Invasions in a changing world, from science to management, Copenhagen, Denmark.

publications

Zimmermann H, D Renison, I Leyer and I Hensen (2009) Do we need livestock grazing to promote *Polylepis australis* tree recruitment in the Central Argentinean Mountains? *Ecological Research* 24: 1075-1081.

von Wehrden H, H Zimmermann, J Hanspach, K Ronnenberg and K Wesche (2009) Predictive mapping of plant species and communities by using GIS and Landsat data in a southern Mongolian mountain range. *Folia Geobotanica* 44: 211-225.

von Wehrden H and H Zimmermann (2009). Plant communities of the Dund Sayhan peak region, southern Mongolia. *Candollea* 64: 49-67.

Zimmermann H, H von Wehrden, M Damascos, D Bran, E Welk, D Renison and I Hensen(2010) Habitat invasion risk assessment based on Landsat 5 data, exemplified by the shrub *Rosa rubiginosa* in southern Argentina. *Austral Ecology*: doi 10.1111/j.1442-9993.2010.02230.x

Zimmermann H, CM Ritz, H Hirsch, D Renison, K Wesche and I Hensen (2010) Highly reduced genetic diversity of *Rosa rubiginosa* L. populations in the invasive range. *International Journal of Plant Sciences* 171 (4): 435-446.

Hirsch H, Zimmermann H, CM Ritz, V Wissemann, von Wehrden H, D Renison, K Wesche, E Welk and Hensen (2011) Tracking the origin of invasive *Rosa rubiginosa* populations in Argentina. *International Journal of Plant Sciences* 172(4): 530–540

Zimmermann H and I Hensen (in print) Some dark sides and their addressing. In: Wild Crop relatives: Genomic & Breeding Resources. ed. C. Kole. Springer, Heidelberg, Berlin, New York, Tokyo

Zimmermann H, H von Wehrden, D Renison, K Wesche, E Welk, MA Damascos and I Hensen (under review) Shrub management is the principal driver of differing population sizes between native and invasive populations of *Rosa rubiginosa* L. *Biological Invasions*

Eigenständigkeitserklärung

Hiermit erkläre ich, dass diese Arbeit nicht bereits zu einem früheren Zeitpunkt der Naturwissenschaftlichen Fakultät I Biowissenschaften der Martin-Luther-Universität Halle-Wittenberg oder einer anderen wissenschaftlichen Einrichtung zur Promotion vorgelegt wurde.

Darüber hinaus erkläre ich, dass ich die vorliegende Arbeit eigenständig und ohne fremde Hilfe verfasst sowie keine anderen als die im Text angegebenen Quellen und Hilfsmittel verwendet habe. Textstellen, welche aus verwendeten Werken wörtlich oder inhaltlich übernommen wurden, wurden von mir als solche kenntlich gemacht.

Im Übrigen erkläre ich, dass ich mich bisher noch nie um einen Doktorgrad beworben habe.

Lüneburg, den