

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

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Abstract An essential step in understanding biological invasions is the comparison of species' performance in the native and introduced ranges, especially for long-lived woody exotics. We explored causes for the higher density and abundance of invasive *Rosa rubiginosa* L. populations by comparing plant performance and habitat attributes in both ranges. Native shrubs in Spain

and Germany were, on average, taller than introduced shrubs in Central and Southern Argentina. Inside 100 m² plots rose-cover in Spain and Germany was significantly higher than in Central Argentina but comparable to that found in Southern Argentina. 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* 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 and lower abundance in the native range can therefore be attributed to management actions along with a lower level of viable habitat.

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Introduction

Until recently woody plants were underestimated as invasive exotic plants (Richardson and Rejmánek

2011). Common garden experiments are the method of choice to detect whether genotypic or environmental factors explain the invasion success of some exotic species (Kawecki and Ebert 2004). However, due to the predominant slow growth rates common garden experiments with woody perennials are few and have so far mainly been conducted with seedlings (Reinhart et al. 2005; Schumacher et al. 2009). Hierro et al. (2005) stated that in order to understand invasion processes, it is essential to study invasive species in their native and introduced ranges. This holds especially true for long-lived woody exotics, which are unpractical for short-term growth experiments.

Invasive plant species are known to grow in higher densities (Vilà et al. 2005) or are of a greater size in their introduced range (Jakobs et al. 2004), which can be due to biotic characteristics of the invasive species and its recipient community or to abiotic characteristics of the new environment (Catford et al. 2009).

However, evidence for an increased size in plants of introduced origin is still lacking (Thébaud and Simberloff 2001). For instance, the decreased regulation by natural enemies in the new range might explain the superior performance of non-native plants, as is proposed by the enemy release hypothesis (ER, Keane and Crawley 2002). Decreased impact by herbivores may also favor genotypes with reduced resource allocation to herbivore defenses and increased resource allocation to growth and reproduction (evolution of increased competitive ability hypothesis (EICA), Blossey and Nötzbold 1995). In accordance with the ER hypothesis, Adams et al. (2009) and de Walt et al. (2004) detected lower leaf damage in invasive populations of the tree *Acer platanoides* L. and the shrub *Clidemia hirta* L. respectively. Siemann and Rogers (2001) found a trade-off between poorer herbivore defenses and increased growth and reproduction in invasive *Sapium sebiferum* L. trees. However, common garden experiments with herbal species of Willis and Blossey (1999) and Willis et al. (2000) did not reveal a lower level of herbivore resistance, or failed to find post-invasion genetic changes. Blumenthal and Hufbauer (2007) did observe increased growth in invasive forb species, but only in non-competitive environments.

The establishment of invasive plant species is often linked to disturbance events, which may change community composition, resource availability and hence competition (Sher and Hyatt 1999; Pauchard

and Alaback 2004; Davis 2009). Soils with high nutrient availability seem to be more susceptible to non-native plants (Huenneke et al. 1990; Hoopes and Hall 2002), but there is also evidence that invasive species tolerate a wider range of nutrient availability (LeJeune et al. 2006). Invasive species often possess ruderal traits to exploit temporarily favorable conditions following disturbance, with a short-lived life cycle, rapid growth, high reproductive allocation, persistent soil seed-banks and rapid germination (Grime 1977; Blair and Wolfe 2004; Erfmeier and Bruelheide 2005).

In our study we explored these hypotheses through the example of native and invasive populations of *R. rubiginosa* L. (sweet briar). This spiny, long-lived shrub is native to Europe and was introduced to several countries over four continents (Meusel and Jäger 1965; Weber 2003), including the focus regions of our study in Argentina. Information on invasive species in the second largest country in South America is still widely lacking (Vázquez and Aragón 2002; Speziale and Lambertucci 2010). This shrub belongs to a family (Rosaceae) with a large amount of invasive species (Binggeli 1996; Hanspach et al. 2008; Richardson and Rejmánek 2011). *Rosa rubiginosa* has already invaded large areas in southern Argentina, building up monotypic stands with the potential for further expansion (Zimmermann et al. 2011). Other invasive species of the *Rosa* genus with similar life-strategies have proven to be very difficult to eradicate once they are successfully established (Loux et al. 2005; Bruun 2006; Isermann 2008). Moreover, at least in Patagonia, this species is already widely accepted as a typical local plant, thus its image can be found on postcards and its fruits are harvested to make teas, marmalade and rose oil (Damascos et al. 2008).

The low germination rates generally associated with the *Rosa* genus (Gordon and Rowe 1982; Younis et al. 2007) present a challenge to common garden experiments with the species. We therefore focused on field surveys complemented by greenhouse experiments to answer the following: (1) Do invasive *R. rubiginosa* plants outperform native plants in terms of growth and fitness? (2) Is the invasion success in Argentina due to a high-performing genotype or (3) to favorable conditions in the new environment, such as reduced competition by the surrounding vegetation, favorable edaphic conditions, or due to the release from enemies?

Methods

Study species

The shrub *R. rubiginosa* (Rosaceae, sect. *Caninae* (D.C.) Ser.; “dogroses”) grows up to 2–3 m in its native range (Montserrat and Silvestre 1998; Jäger and Werner 2002). The species is insect-pollinated but also produces apomictic seeds (Wissemann and Hellwig 1997; Werlemark 2000). Its fleshy rosehips are dispersed by birds, horses and cattle (Hatton 1989; Damascos et al. 2005) and individual shrubs spread vigorously by vegetatively producing root suckers (Zimmermann et al. 2010). *Rosa rubiginosa* naturally occurs within Europe’s temperate zone, has been introduced to North America and is classified as a noxious weed in South Africa, New Zealand, Australia and Chile (Meusel and Jäger 1965; Weber 2003; Bellingham et al. 2004; Nel et al. 2004; Parsons and Cuthbertson 2001). Further introductions in South America have occurred in Bolivia and Argentina (Seibert 1993; Henker 2000); to the latter it was introduced around the year 1900 from Central Europe to Patagonia (Hirsch et al. 2011) from where it was brought to Central Argentina (Zimmermann et al. 2010).

Study region

We sampled 13 invasive *R. rubiginosa* populations in Argentina, 11 native populations in Germany and 7

native populations in Spain (Fig. 1; Table 1). Populations were located using local floras (Montserrat and Silvestre 1998; Fukarek and Henker 2005) and expert knowledge (see acknowledgments). Sampling covered a broad climatic range within diverse habitat types (Table 1). Within Argentina, we focused on two regions over 1,000 km apart. We investigated populations in Central Argentina ($N = 6$) in the province of Córdoba, and in Patagonia ($N = 7$) in the provinces of Neuquén and Río Negro. In Córdoba, populations were situated in the main mountain chain (1,000–1,700 m a.s.l.), the Sierras Grandes de Córdoba and an adjacent mountain range; the climate in the Córdoba mountains is temperate humid with an annual precipitation of 670 mm/a and an average temperature of 12 °C at 1,500 m a.s.l. (Hijmans et al. 2005; Table 1). Rains occur during the summer and snow events are rare. Sampled populations were in distinct habitats like high-montane shrub-grassland communities, a pine plantation and an evergreen *Fagaya coco* Engl. forest.

Rosa rubiginosa populations in Patagonia were studied around the town of San Carlos de Bariloche and in the surrounding Nahuel Huapi National Park. In contrast to Córdoba, snow events are frequent with a temperate climate and an average temperature of 8 °C. Precipitation values varied considerably from 831 to 1,252 mm/a (Table 1), with precipitation decreasing with distance from the Andes. Thus the vegetation types change accordingly from the drier Patagonian steppe to conifer forests to more wet broad-leaved forests (De Fina 1972).

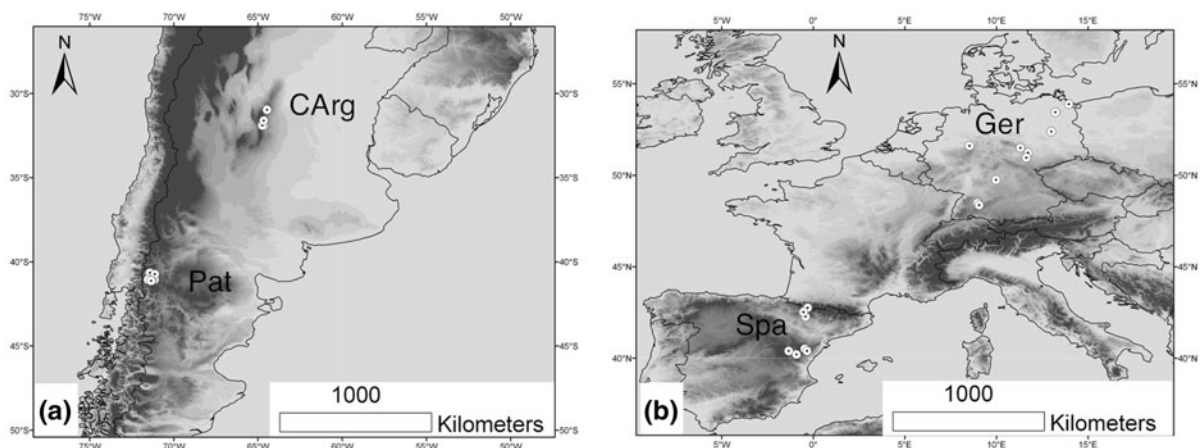


Fig. 1 **a** Sampled invasive populations in Patagonia (Pat) and Central Argentina (CArg) and **b** sampled native populations in Spain (Spa) and Germany (Ger)

Table 1 Sampled *R. rubiginosa* populations

Range	Region	Province	Lat	Long	Altitude	Habitat	Precip.	Tmean	Tmin	Tmax
I	Central Argentina	Córdoba	-31.60	-64.67	1,529	High-montane shrub-grassland	663	12.7	-0.5	26.3
I	Central Argentina	Córdoba	-31.63	-64.68	1,668	High-montane shrub-grassland	671	12.0	-1.1	25.6
I	Central Argentina	Córdoba	-31.88	-64.76	1,433	Montane shrub-grassland	661	13.1	-0.2	27.0
I	Central Argentina	Córdoba	-31.91	-64.68	1,136	Pine plantation	658	14.5	1.0	28.3
I	Central Argentina	Córdoba	-30.91	-64.49	1,542	Evergreen broad-leaved forest	676	12.5	-0.5	25.8
I	Central Argentina	Córdoba	-30.95	-64.47	1,433	Montane shrub-grassland	676	12.9	-0.1	26.2
I	Patagonia	Río Negro	-41.05	-71.54	840	<i>Nothofagus</i> forest with bamboo	1,252	8.2	-0.7	21.4
I	Patagonia	Río Negro	-41.12	-71.36	845	Urban area	921	7.5	-2.2	20.9
I	Patagonia	Río Negro	-41.13	-71.32	969	<i>Austrocedrus chilensis</i> forest	924	8.1	-1.6	21.6
I	Patagonia	Neuquén	-41.04	-71.15	819	Shrub-grass steppe	831	8.5	-1.4	22.3
I	Patagonia	Neuquén	-40.72	-71.14	930	River bed	835	8.2	-1.7	22
I	Patagonia	Neuquén	-40.67	-71.31	1,046	Pasture	932	7.5	-2.2	21.1
I	Patagonia	Neuquén	-40.65	-71.43	932	<i>Nothofagus</i> forest	1,077	7.7	-1.8	21.2
N	Germany	Brandenburg	52.39	12.97	29	Hedge along path	563	9.2	-3.0	23.9
N	Germany	Sachsen-Anhalt	51.22	11.72	200	Dry grassland	546	8.5	-2.7	22.7
N	Germany	Thüringen	51.49	11.29	238	Shrub-grassland	538	8.5	-2.9	22.5
N	Germany	Thüringen	50.96	11.61	292	Meadow/mixed forest	611	8.0	-3.2	22.0
N	Germany	Niedersachsen	51.61	8.51	170	Former stone quarry	860	8.7	-1.8	21.5
N	Germany	Bayern	49.74	9.96	281	Shrub-grassland	627	9.3	-2.8	23.8
N	Germany	Baden-Württemberg	48.49	8.94	360	Field edge	784	9.0	-3.1	23.5
N	Germany	Baden-Württemberg	48.36	9.04	670	<i>Juniperus</i> sp. heathland	989	7.6	-4.3	22.0
N	Germany	Mecklenburg-Vorpommern	53.44	13.20	65	Shrub-grassland	569	8.1	-3.2	21.7
N	Germany	Mecklenburg-Vorpommern	53.88	13.93	1	Firs plantation	550	8.7	-3.4	22.4
N	Germany	Mecklenburg-Vorpommern	54.00	13.85	8	Coastal pine forest	551	8.6	-3.2	22.0
N	Spain	Aragon	40.21	-0.92	1,104	Field edge	503	10.4	-1.2	25.5
N	Spain	Aragon	40.53	-0.48	1,200	Montane ruderal	641	9.3	-3.3	22.6
N	Spain	Aragon	40.40	-0.35	1,447	Montane ruderal	705	7.8	-2.2	23.5
N	Spain	Aragon	40.43	-1.39	1,085	River bed	491	10.0	-2.4	25.4

Table 1 continued

Range	Region	Province	Lat	Long	Altitude	Habitat	Precip.	Tmean	Tmin	Tmax
N	Spain	Huesca	42.53	-0.54	1,092	Pine woodland	842	8.3	-2.8	22.2
N	Spain	Huesca	42.61	-0.48	960	Pine woodland	915	7.7	-3.3	21.4
N	Spain	Huesca	42.76	-0.32	1,290	High-montane shrub-grassland	1,150	5.0	-5.4	18.0

Latitude (Lat) and longitude (Long) are given in decimal degrees and altitude in m a.s.l. Climate data was obtained from Hijmans et al. (2005)
I introduced, *N* native, *Tmin* mean minimum temperature of coldest month (°C), *Tmax* mean maximum temperature of warmest month (°C), *Tmean* annual mean temperature (°C),
Precip. annual precipitation (mm)

In Germany, we studied 11 populations ranging from the Baltic Sea to the Swabian Alps in southern Germany. The overall climate is temperate but differences in topography (11–791 m a.s.l.) and continentality alter annual precipitation values (538–989 mm/a, Table 1), with habitat types varying from dry grassland to heathland.

In Spain, three populations were visited in the Pyrenees Mountains and four populations were located 200 km to the southeast in the mountain range of Aragón (Table 1). In the Pyrenees (960–1,290 m a.s.l.), annual mean temperatures vary from 5 to 8.3 °C for our study sites, and annual precipitation values are high (915–1,150 mm/a). Populations were situated in pine woodlands and high-montane shrub-grassland. In the mountain range of Aragón (1,100–1,500 m a.s.l.), annual precipitation values may be as low as 491 mm/a. Here, *R. rubiginosa* individuals were found along roads and montane pastures.

Field measurements

In South America, random coordinates were located with a GPS in areas that contained *R. rubiginosa* populations. There we established study units of 50 × 50 m (0.25 ha) and measured plant size and density and monitored performance in 25 plots of 100 m² (Table 2). The percentage of missing, damaged or infested leaf area on 20 randomly leaflets on each shrub was assessed in two subsequent years (Table 2). Furthermore, we determined each plots' vegetation characteristics (Table 2).

In Europe, we conducted the same measurements; however, population density was sparse and we consequently sampled every individual over the maximum population extension (0.09–9 ha). Although we studied 18 populations in the native range compared to 13 in the introduced range, there were only 81 *R. rubiginosa* shrubs in the native range compared to 210 in the invasive populations (325 plots: 13 grids á 25 plots, of which 210 were occupied, with even more shrubs growing beyond the study grid). In order to compare measurements between South America and Europe, we also established a 100 m² plot around each *R. rubiginosa* individual and conducted the same measurements as described above for the invasive populations.

Growth rate measurements were conducted by tagging one branch of each individual and measuring

Table 2 Overview of sampling, analysis and main results

Sampling	Analysis	Result
<i>In population</i>		
Soil parameters		
Mixed topsoil samples (10 cm depth)	Conductivity, pH, calcium carbonate, phosphorus, C/N, Ca, Mg, K	<i>Rosa rubiginosa</i> tolerates wide range of pH conditions, phosphorus- and nitrogen supply levels/favourable pH values, Ca and K levels in native populations
<i>In 100 m² plots</i>		
Plant performance		
<i>Rosa rubiginosa</i> cover	Boxplot, type III Anova with log-transformed data post hoc Tukey test	Central Argentina least cover ($p < 0.05$)
Habitat characteristics		
Cover and height of: trees > 2 m, trees < 2 m, remaining shrubs, herbs, grasses, ferns, open soil, stones, rocks, inclination	Generalized linear model response variable = invasive/native model validation with AUC value	Differences between habitats of invasive and native plots weak, AUC = 0.4
<i>One shrub inside 100 m² plot</i>		
Plant performance		
Longest stem ^a	Boxplot, type III Anova, post hoc Tukey test	Invasive shrubs on average smaller ($p < 0.05$)
Cover	Boxplot, type III Anova, post hoc Tukey test	Central Argentina least cover ($p < 0.05$)
Shrub volume ^b (height × crown diameter, may exceed 100 m ² plot)	Boxplot	Largest volume in Patagonia
Number of rosehips: 0, 1–10, 11–50, 51–100, 101–500, 501–1,000, >1,000	Barplots, boxplots	In highest category (>1,000 rosehips) mostly Patagonian individuals
Seed number and seed weight in 10 rose hips (random subset of individuals)	Boxplot, type III Anova, post hoc Tukey test	Highest number of seeds per rosehip in Patagonia
Growth of tagged branches	Boxplot, type III Anova, with rank-transformed data, post hoc Tukey test	No difference between regions ($p > 0.05$)
Diameter of biggest stem	Correlation with growth ring numbers	Oldest rose stems in invasive range
Enemy release	Mixed effects model	No difference between invasive and native range
Percentage of missing, damaged or infested leaf area on 20 random leaflets ^c		
<i>Experiments</i>		
Reciprocal seed bank experiment (900 days)	Ancova, post hoc Tukey test	Higher seed survival in Central Argentina ($p < 0.001$) in Germany and Central Argentina seeds still viable after 900 days
Biomass of native and invasive <i>R. rubiginosa</i> plants under same conditions in growth chamber	Boxplot, type III Anova with log-transformed data, post hoc Tukey test	Native plants more biomass ($p < 0.001$)

Table 2 continued

Sampling	Analysis	Result
Height of native and invasive <i>R. rubiginosa</i> plants after 215 days grown on three different substrate types in greenhouse ^d	Ancova with square root transformed data, post hoc Tukey test	No range effect ($p > 0.05$)
Germination experiment with seeds from 3 populations of each region ^e $n = 180$ seeds per population	Boxplot, Anova, post hoc Tukey test	Seeds from Central Argentina higher germination rate ($p < 0.001$)

Patagonia and Central Argentina represent the invasive range, Germany and Spain the native range. Sampling was conducted in seven populations in Patagonia, six populations in Central Argentina, seven populations in Spain and 11 populations in Germany. All seed and plant material for the experiments originates from these populations. Inside populations 100 m² plots were placed and habitat characteristics were measured as well as one random *R. rubiginosa* shrub

^a Longest stem of *R. rubiginosa* that could be regarded as established (at least 40 cm tall or shoot diameter at least 1 cm)

^b One shrub was considered a continuous unit

^c The upper and lower side of each leaflet as 100 % leaf area. Leaf area was regarded as damaged or infested if necrosis, fungi or leaf sucking insects were present

^d All substrates were sterilized at 90 °C degrees and filled into 1 dm³ pots. silty substrate = 60 % volume silt (<0.063 mm), sandy substrate = 68 % sand (0.2–2 mm), gravely substrate = 33 % gravel (>2 mm)

^e Prior to germination experiments, we tested all seeds for viability by submerging them in water for 15 min discarding floating seeds (pers. comm. V. Wissemann)

its growth over a 2-year period (Table 2). In some cases, tags could not be found the following year. This happened in 29 % of all cases in Germany, in 10 % of all cases in Spain and in 14 % of those in Patagonia. In Central Argentina all tags were rediscovered. In Europe, in at least 10 cases the whole shrub, or parts of it, was cut down. In Patagonia, only the tags were missing and all shrubs could still be rediscovered.

We cut at least one random stem in each population for growth ring counting, and cuttings from two Argentinean and one German population served as plants for an initial reciprocal common garden experiment (see online appendix). Mixed topsoil samples were collected at all populations over the whole population dimension (Table 2).

Soil analyses

We measured conductivity and pH of the soil samples. For soil samples with a pH above 6.5, calcium carbonate content was analysed with the Scheibler method. Phosphorus content was analysed photometrically (Eppstein) following extraction with Ca-Lactat at pH 3.6. In addition, we measured the total carbon and nitrogen content by combustion in a CN Analyser (Vario EL, Elementar, Germany) and analysed exchangeable soil cations with atomic absorption spectrometry (Ca, Mg) and flame spectrometry (K, AAS Vario 6 Analytik, Jena) following extraction with 0.2 N BaCl₂.

Germination and common garden experiments

Inside our study units achenes of 10 randomly sampled rosehips were counted and weighted for each individual (from here on we refer to the achenes inside the rosehip as seeds). Seeds of selected populations were used for germination experiments (Tables 2, 3).

For each population, we placed 180 seeds (30 seeds per Petri-dish and 6 replicates) on filter paper moistened with deionized water. Germination started after approx. half a year after being placed in water. At the end of the experiment, all remaining seeds were tested for viability with a TTC-test. The percentage of germinated seeds is based on the number of viable seeds at the end of the experiment.

After germination, seedlings were planted in 1 dm³ pots filled with standardized soil ("Einheitserde Typ 0", Einheitserde Werksverband e.V.) and placed in a

Table 3 Temperatures and relative humidity for germination and growth experiments

Experiment	Temperature (°C)		Relative humidity (%)	
	Darkness	Light	Darkness	Light
1. Germination chamber	4	8	–	–
2. Germination chamber	10	20	–	–
3. Germination chamber	20	30	–	–
Growth chamber	10	20	65	80
Greenhouse	6	19	60	70

An initial test with seeds from one native and one invasive population revealed that germination rates are highest if seeds are first stratified for 12 weeks at 20/30 °C followed by 12 weeks at 4/8 °C and then placed in the third germination chamber (see also Werlemark et al. 1995). The day–night cycle was 12 h for all experiments

growth chamber (Tables 2, 3). Due to the difference in germination and survival rates, seedling numbers were unbalanced, with 91 seedlings originating from the introduced range and 109 seedlings from the native range. The number of seedlings per population also varied strongly, rendering an analysis at the population level not possible. Plants were measured and harvested on the same day and, due to differing germination dates, growth periods varied from 105 to 181 days. We tested for the influence of the different growing periods by including time as a covariate (see below). After harvesting, above- and below-ground biomass was dried (24 h at 105 °C) and weighed.

We carried out a seedbank experiment over 900 days to detect differences in seed survival between ranges (Table 2). The experiment took place in common garden experiment sites in Central Argentina and Germany. Ten nylon bags—each containing 100 seeds from Germany, Central-Argentina and Patagonia respectively—were buried 10 cm in the ground. Every 90 days we checked for the percentage of non-viable seeds (number of floating seeds in water) in one bag per origin.

We performed an additional growth experiment with three different substrate types because we observed predominantly silty soils in the introduced range and sandy, gravelly soils in the native range. This growth experiment was conducted with 96 plants on three substrate types (8 replicates per substrate and plant origin), with 24 plants originating from Germany

(2 populations), Spain (3 populations), Central Argentina (3 populations) and Patagonia (3 populations). All pots were irrigated at the same time interval with 200 ml of water. Every 2 weeks, Algoflash Compo® rose fertilizer (200 ml, 20 % dilution) was added to all pots. All plants were placed in the same greenhouse cabin (Table 3) and pots were replaced randomly inside the cabin every 2 weeks. After 215 days, all plants were measured for their final height.

Statistical analysis

All statistical analyses were performed with the R software (R 2.11.1, R Development Core Team 2010; Table 2). We inspected differences of *R. rubiginosa* individuals in size, cover, growth rates, fruit-set and differences in soil conditions with boxplots or barplots and tested for significant differences with type III Anovas and post hoc Tukey tests (packages: car & multcomp, Hothorn et al. 2008; Fox and Weisberg 2010). Data from the germination, greenhouse and seedbank experiments were balanced and were therefore analyzed with Anovas or Ancovas. Rose cover values and biomass values from the growth chamber experiment were log-transformed and height measurements of the greenhouse experiment, as well as phosphate- and potassium values, were square-root-transformed to achieve a normal distribution of errors. Due to negative values in the branch growth data, analysis was performed on rank-transformed data. In all regions, negative annual growth rates were detected due to broken or dead branches.

Percentage of leaf damage was analyzed with a mixed effects model (package: lme4, Bates and Maechler 2010) with Poisson distribution of errors. In order to identify on which spatial scale most of the variance in leaf damage originated, we included the individual rose shrubs ($N = 256$), populations ($N = 29$), regions (Patagonia, Central Argentina, Spain and Germany) and range (native or introduced) as random effects in the model. To assess if range (introduced or native) and sampling year differed significantly we included the interaction of range and year as a fixed effect in a full model and tested it against a model with only random effects. Only rose individuals that were present in both years were included in this analysis.

Growth ring counts were correlated with stem width and the estimate of this regression was used to

calculate the age of each measured rose stem. In Patagonia, 33 shrubs were too dense and therefore inaccessible for stem measurements. We performed the correlation separately for Patagonia, Central Argentina, Germany and Spain.

We analyzed whether native roses occupied different habitat types than invasive roses with generalized linear models with binomial error distribution. Of a total of 17 vegetation characteristics, eight were redundant (spearman coefficient > 0.5, variance inflation factors > 10) and therefore not tested in the model. The cover of the upper (1) and lower (2) tree-layers, the shrub (3), herb (4) and grass-cover (5), and the height of grasses (6) were included, as well as the proportion of stones (7) and litter (8) and the plot inclination (9). We tested for a significant relationship ($p < 0.05$) between these parameters and whether the plot was in the native or invasive populations (binary coded, 0/1) by incorporating all nine parameters and their interactions into a full model, which was then reduced to the minimum adequate model through backward selection. Finally, the minimum adequate model was validated with the AUC-value (area under the curve) by randomly dividing the dataset into two equal parts.

Results

Plant performance and genotypic effects

Rosa rubiginosa shrubs in the introduced range had a higher variance in size (Fig. 2; Table 2). However, native shrubs were, on average, taller (mean 2.31 vs. 1.84 m). These differences were significant between Germany and Central Argentina ($p < 0.001$) as well as Patagonia ($p = 0.03$) and between Spain and Central Argentina ($p = 0.02$). There was also a marginally significant difference between rose height between regions in the introduced range ($p = 0.046$).

Growth ring counts and stem diameters significantly correlated ($p < 0.01$, r^2 between 0.7 and 0.8) for all regions. Overall, rose stems in the introduced range were older than stems in the native range (Fig. 3; Table 2). The oldest rose stem was measured in Central Argentina at 29 years, followed by Patagonia with 26 years, Spain with 24 years and Germany with 16 years.

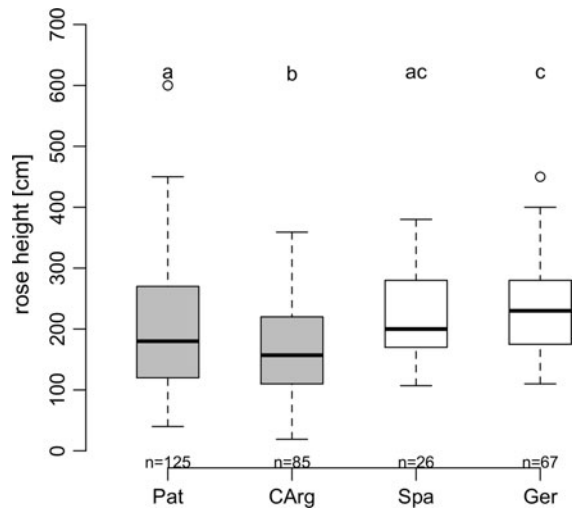


Fig. 2 Height of *Rosa rubiginosa* shrubs in Patagonia (Pat), Central Argentina (CArg), Spain (Spa) and Germany (Ger). *Rosa rubiginosa* individuals reach their greatest height in the invasive range, but the smallest individuals can also be found here. Different letters indicate significant differences ($p < 0.05$). The boxes show the location of the middle 50 % of the data (interquartile range) and the solid horizontal line represents the median. The dashed lines show the maximum values or 1.5 times the interquartile range if the data has outliers. Outliers are represented by dots (more than 1.5 times the interquartile range)

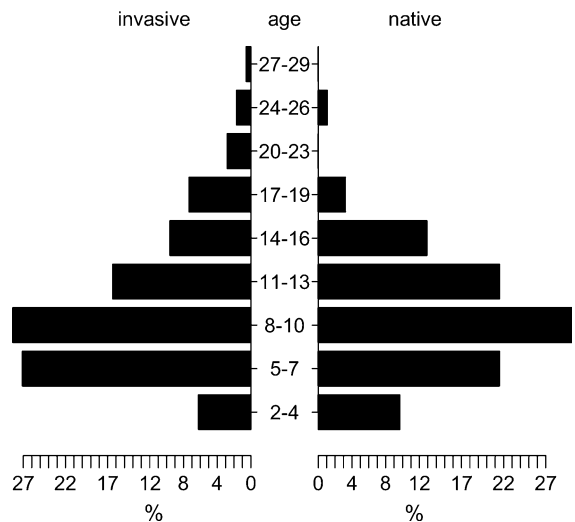


Fig. 3 Age structure of all invasive ($N = 177$) and native ($N = 93$) shrubs

Rose cover was lowest in Central Argentina (3 %) and significantly differed from that of the other regions (Fig. 4, $p < 0.001$, Table 2).

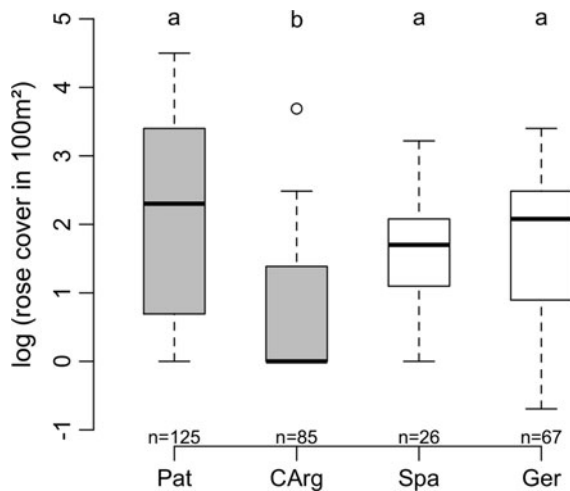


Fig. 4 Log-transformed cover of *R. rubiginosa* shrubs in 100 m² plots. Different letters indicate significant differences ($p < 0.05$). Patagonia (Pat), Central Argentina (CArg), Spain (Spa) Germany (Ger)

The mixed effects model attributed 76 % of the variance in percentage of damaged leaf area within individual rose shrubs and the remaining variance of 24 % within populations. Percentage of damaged or infested leaf area did not differ significantly between ranges or years.

Annual growth of marked branches was slightly higher in the native range than in the introduced range ($p = 0.03$, Fig. 5), while regions did not differ significantly.

Native roses gained on average more biomass in the growth chamber than invasive roses (+19 %, $p < 0.001$, online appendix 2), and this effect was independent from differences in growth time.

We found no range or region effect ($p > 0.05$) in the greenhouse experiment between different substrate types (Table 2), but we detected an interaction between substrate and range: *R. rubiginosa* plants of native origin grew less in silty substrate (median = 0.4 cm) than in gravel ($p < 0.0001$, median = 4.4 cm), and plants of invasive origin grew less in silty substrate (median = 1.1 cm) than in gravel (median = 2.9 cm) or sand ($p < 0.001$, median = 6.7 cm).

Most Patagonian *R. rubiginosa* shrubs carried over 1,000 rosehips (38 %), whereas only 3 % of the Central Argentinean roses had similarly high reproductive output (Fig. 6; Table 2). In the native range in Spain, most shrubs had 100 to 500 rosehips (42 %), while in Germany the majority had only 50 to 100

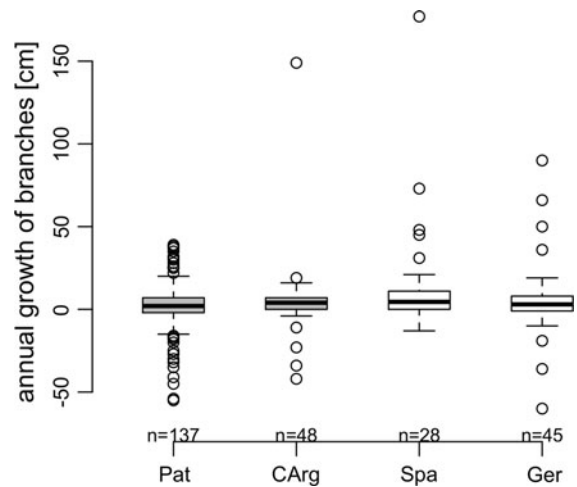


Fig. 5 Annual growth rates of marked branches as a function of region. No significant differences at $p < 0.05$. Patagonia (Pat), Central Argentina (CArg), Spain (Spa), Germany (Ger)

(33 %, Fig. 6). Rosehip numbers increased with increasing shrub volume in both ranges (Fig. 7) and rosehips from invasive shrubs contained more seeds than native shrubs, but this effect was only significant for rosehips from Patagonian populations ($p < 0.0001$, Fig. 8). Moreover, seeds from Patagonia and Central Argentina were significantly heavier than seeds from Germany ($p < 0.001$, Fig. 8).

Not a single seed germinated during the 24 weeks of stratification. On average, 12 % of seeds from the invasive range and 4 % of seeds from the native range were not viable at the end of the experiment (difference invasive—native, $p < 0.001$). Seeds from Central Argentina had significantly higher germination rates (on average twice as high or higher) than seeds from Germany, Patagonia or Spain ($p < 0.001$, Table 2; online appendix 3).

A higher number of seeds buried in Central Argentina survived ($p < 0.001$) irrespective of the seeds' origin (Table 2). In both gardens, 1–13 % of seeds per bag were still viable after 900 days.

Habitat characteristics

The final model explaining rose occurrence based on vegetation characteristics had a low AUC-value of only 0.4. The cover of shrubs other than *R. rubiginosa* was slightly higher in the introduced range.

Sites in the introduced range had significantly lower pH values than in the native range ($p < 0.001$,

Fig. 6 Proportion of rose shrubs in each rosehip category for each region (N = number of individuals)

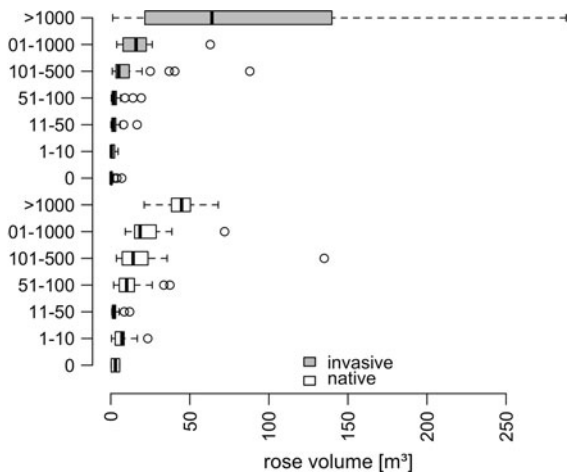
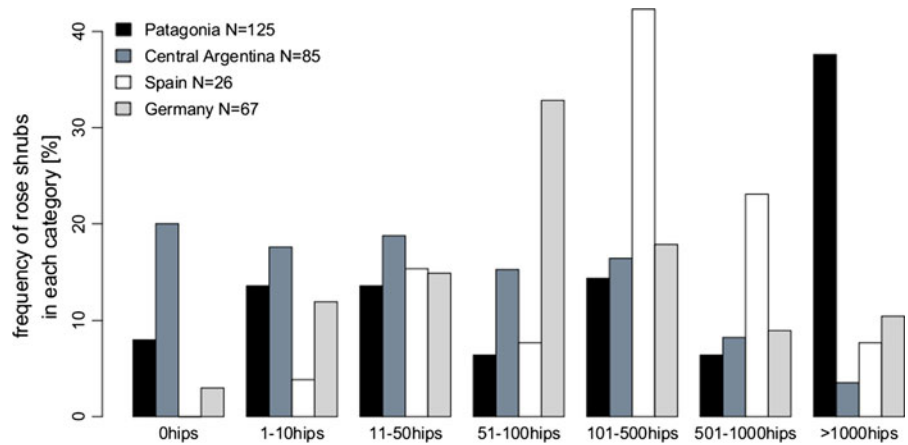


Fig. 7 Rosehip numbers on the y-axis (0 to >1,000) for invasive and native *R. rubiginosa* shrubs plotted against shrub volume

Table 4). Sites in Germany had slightly acidic to neutral soils and differed significantly from Spanish sites, which had neutral to weakly alkaline soils ($p < 0.001$). They both differed from Patagonian and Central Argentinean sites ($p < 0.001$), which were strongly acidic to neutral (Table 4). Accordingly, conductivity and calcium carbonate content were higher in Europe than in Argentina. Soil samples from all regions did not differ in their carbon/nitrogen ratio, nor in their phosphorus or magnesium content ($p > 0.05$). The mean C/N ratio over all samples was 14.3. The phosphorus content over all samples reached at most 0.4 mg/100 g soil, and in about half of the samples phosphorus content was not detectable with our method. Soil samples from the native range contained more calcium; however, for Spanish and

Patagonian samples, the difference was not significant (Table 4). Potassium contents differed weakly between Spain and Patagonia ($p = 0.03$, Table 4).

Discussion

No benefit through resource allocation to growth or reproduction

Invasive *R. rubiginosa* populations were more abundant and of greater density than native populations, but we could not confirm the general assumption that plants grow bigger in their introduced range (Siemann and Rogers 2001; Jakobs et al. 2004; Ebeling et al. 2008). Instead, native rose shrubs were on average taller and growth rates were slightly higher in the native range.

Comparison of *R. rubiginosa* cover values at the 100 m² plot level confirm results on rose height, with cover values in the introduced range not exceeding cover values in the native range; values in Central Argentina are even significantly lower than in the remaining regions. However, when considering the number of plots per population, populations in the introduced range were denser than native populations (see methods) and, given the higher number of smaller shrubs, they are further expanding.

Invasion can be facilitated when exotics supply high amounts of seeds, including under conditions of strong local biotic resistance (Lambrinos 2006). In Patagonia, propagule supply was highest, with most shrubs containing more than 1000 rosehips and more seeds per rosehip than the remaining regions.

Fig. 8 (left) Invasive *R. rubiginosa* individuals in Patagonia (Pat) have significantly more seeds per rosehip ($p < 0.0001$) than shrubs in Central Argentina (CArg), Spain (Spa) or Germany (Ger). (right) Mean seed weight is significantly higher in Patagonia and Central Argentina than in Germany ($p < 0.0001$)

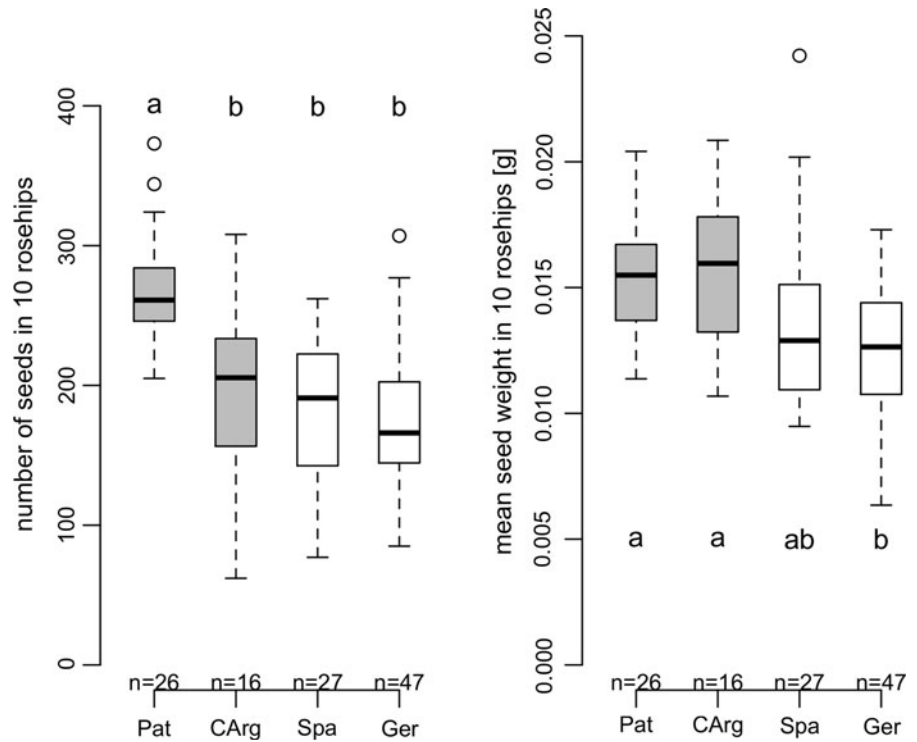


Table 4 Sites in Germany and Spain differed significantly in their pH values from each other and from Patagonia and Central Argentina (type III ANOVA, post hoc Tukey, $p < 0.001$). Soils from German sites had significantly higher calcium contents than soil from Patagonia or Central Argentina

	Patagonia	Central Argentina	Spain	Germany	<i>P</i>
pH					
Min	5.6	4.8	7.5	6.4	
Mean	6.0 ^a	5.6 ^a	7.8 ^b	7.1 ^c	**
Max	6.4	7.0	8.0	7.2	
Ca (μmol/g)					
Min	65.21	34.26	136.50	55.95	
Mean	131.10 ^{ac}	121.00 ^a	252.50 ^{cb}	286.10 ^b	*
Max	246.10	315.60	358.70	512.20	
K (μmol/g)					
Min	1.54	0.01	2.32	3.11	
Mean	3.46 ^a	5.74 ^{ab}	9.32 ^b	7.81 ^{ab}	*
Max	6.09	9.55	21.86	12.24	

Calcium contents of Spanish soil samples differed only to those from Central Argentina ($p < 0.01$). Potassium content only differed between soil samples from Patagonia and Spain ($p = 0.03$). Different letters indicate significant differences

* $p < 0.05$; ** $p < 0.01$

However, this cannot be interpreted as an allocation of resources to reproduction as proposed by the EICA hypotheses (Blossey and Nötzel 1995), nor by higher nutrient availability. Instead, the high number of rosehips per shrub can be explained by the higher number of big shrubs in Patagonia, which is not so much expressed in the height of each individual but by the thickets' volume.

Propagule pressure does not result from propagule supply alone but from successfully germinating seeds (e.g. Eschtruth and Battles 2011). Seed weight can be an indicator of fitness, as heavy seeds may have higher germination rates (Tripathi and Khan 1990; Seltmann et al. 2007), but whether seedlings from larger seeds with more resources are also better competitors is still under debate (Kidson and Westoby 2000; Leishman 2001, Moles and Westoby 2004). Our results on seed weight are not in line with our results on germination rates or growth rates. While Central Argentinean populations had the highest germination rates and relatively heavy seeds, Patagonian seeds were heavier than seeds from Europe but had low germination rates. Furthermore, seedlings derived from heavy seeds did not perform better in the growth chamber. Germination rates averaged for each region were equivalent to

or higher (14–49 %, online appendix 3) than those reported in a study of *R. rubiginosa* seeds of Swedish origin in which 19 % of seeds germinated (Werlemark et al. 1995). In a meta-analysis, Kolar and Lodge (2001) found no relationship between seed mass and invasiveness but found a correlation between the ability to reproduce vegetatively and invasiveness. Correspondingly, clonal growth has been documented as a common trait of invasive species across families (e.g. Hollingsworth and Bailey 2000, Loomis and Fishman 2009, Roiloa et al. 2010). This is all in line with an earlier study conducted by our study group that already emphasized the importance of clonal growth for the expansion of *R. rubiginosa* (Zimmermann et al. 2010). It also corresponds with the observed lateral root growth in our common garden experiment in Argentina and Germany (online appendix). Two other invasive species of the same genus, *R. rugosa* and *multiflora*, are also known for pronounced vegetative growth that has been shown to have detrimental effects on native vegetation (Epstein and Hill 1999, Bruun 2006, Isermann 2008).

We did not conduct seedling counts in our populations because we hardly found any seedlings during the 3 years of study. Engler et al. (2011) also found few seedlings in introduced populations of the successful invader *Fallopia japonica*, which is also known for its clonal growth. Seeds from both ranges had a long dormancy period, as is typical for seeds from the *Rosa* genus (Gordon and Rowe 1982; Younis et al. 2007). As such, rapid germination is not a trait of this invasive species that can explain its invasion success.

No rapid adaptive evolutionary change

Common garden experiments supported our field measurements as we found no evidence for a better performing invasive genotype, nor did we find evidence for release from natural enemies. The successful establishment of *R. rubiginosa* across climates and habitats is therefore probably due to inherent phenotypic plasticity and ecological flexibility, as opposed to rapid adaptive evolutionary change. A common garden experiment with introduced *Verbascum thapsus* L. populations also underlined that some invasive plants have high environmental tolerance, rather than them having rapidly evolving physiological traits (Parker et al. 2003). Our reciprocal

common garden experiments in Central Argentina and Germany—although partly flawed by differing growth length—did not point to a high-performing invasive genotype (see online appendix). On this basis, performing further reciprocal common garden experiments would not have offered any more insight. Moreover, experiments in the growth chamber and the greenhouse did not reveal a better performance of plants from the invasive range when grown under identical growing conditions, as is conversely proposed by Blossey and Nötzbold (1995). In our growth chamber study, plants from the native range performed better, and in the greenhouse experiment we did not find a range effect at all. Although we observed predominately silty soils in the introduced range, all plants performed worse on this substrate type in the greenhouse experiment.

The lack of differences in leaf damage between invasive and native populations was primarily due to a uniformly high abundance of sap-feeding insects, like aphids. For woody plants in particular, sap-feeding insects reduce plant performance in terms of growth and photosynthesis even more than defoliators (Zvereva et al. 2010). Also in contrast to the EICA hypothesis, Bossdorf et al. (2008) discovered that introduced *Senecio inaequidens* DC. Populations have greater herbivory defense than native populations and they relate its invasion success to a pre-adapted and plastic genotype. Despite the fact that roses in Argentina also grow on pastures, larger herbivores avoid the spiny leaves and only eat the rosehips thereby contributing to seed dispersal (pers. obs.). Possible negative effects of soil biota were not investigated, which is shown to be important for some invasive species (Callaway et al. 2004; Scharfy et al. 2010).

No favorable conditions in the introduced range

Contrary to a recent study by Erfmeier and Bruelheide (2010), we did not detect favorable edaphic conditions in terms of nutrient supply in the introduced range or differences in canopy cover. Differences between habitats of invasive and native roses with respect to the surrounding vegetation and other site characteristics were weak, as the discrimination of our model was worse than in a random classification. Invasive roses do not have a competition advantage over native roses in respect of the presence of other shrub species, as

shrub cover values were even slightly higher in the introduced range. A regional study restricted to Patagonia showed that *R. rubiginosa* cover decreased with increasing tree cover (Zimmermann et al. 2011), but tree cover did not differ between ranges.

Soil analyses of invaded and native *R. rubiginosa* sites proved that this rose tolerates a wide range of pH conditions, from strongly acidic to alkaline soils, as well as a wide range of nitrogen and phosphorus supply levels. C/N ratios of 9–12 are common for topsoil samples, and higher ratios, which indicate poorer nitrogen availability, were found for all regions. Cabido et al. (1987) detected similar C/N ratios close to our study sites in the Sierras Grandes de Córdoba. Phosphorus values were low but very variable across sites, which was also observed by Blanck et al. (2010) in Patagonia.

Significant differences between regions were found in pH values, calcium content and potassium contents of soil samples, but these results cannot explain the invasion success as they point to more favorable conditions in the native range. With increasing acidity, like observed in the introduced range, phosphorus, calcium, magnesium and potassium availability is lowered (Kuntze et al. 1996). Critical calcium values below 2 $\mu\text{mol/kg}$, which lead to calcium deficiency in plants (Rowell 1997), were not detected in any of the samples. Potassium is also an important macro-element, e.g. as it regulates stomata activity; however, the only significant effect we found was higher potassium values in Spain.

We did not investigate the effect of different climatic conditions on plant performance, but in respect of our study sites we can conclude that this species tolerates a wide range of climatic conditions (Table 1), and species that are adapted to a wide climatic niche tend to be more invasive (Forcella and Wood 1984; Scott and Panetta 1993). We do not suspect favorable climatic conditions to be the driver of invasion in this species since seasonality, precipitation and temperatures also vary greatly within the introduced range.

Land-use explains size of invasive populations

Without proof of a superior performing invasive genotype or more favorable biotic or abiotic conditions in the introduced range, the difference in land-use might explain the observed pattern. In both ranges,

populations were close to human settlements or roads, but management actions only took place in the native range where shrubs are pruned or cut down by public or private landowners. Moreover, in Germany these management actions are partly conducted by nature conservation agencies in order to keep grasslands containing rare herbal species free from shrubs (Milton et al. 1997; Seitz et al. 2004; Trost et al. 2008). In Argentina, all studied *R. rubiginosa* populations grew on sites that had formerly been disturbed by man-made fires, logging or road construction; but such disturbance events occurred once, thereby creating a window of opportunity for this species to establish (Shea and Chesson 2002, Zimmermann et al. 2011). In Germany, *R. rubiginosa* is classified as endangered in five out of 16 federal provinces (Ludwig and Schnittler 1996). We conducted our field studies in one of the five provinces where the species is red-listed (Mecklenburg-Vorpommern). Contrary to their status, the studied populations were denser here than in the other provinces, which revokes any potential sampling bias. Moreover, in the old cultural landscapes of Europe, which were dominated by agricultural fields and urban areas, there was simply less habitat available for this species to occur.

The experiment with tagged branches deserves further interpretation. In native *R. rubiginosa* populations, some marked individuals were completely cut down or at least partly cut down the following year, which did not occur with tagged invasive populations. This is supported by the fact that invasive populations possess a higher number of old stems. Herrera et al. (2011) also discovered that the oldest *Genista monspessulana* L. shrubs in invasive populations were 2 years older than the oldest native shrubs, yet differences between invasive and native *R. rubiginosa* ramets were up to eight times greater, and potentially even more if dense thickets of great volume and presumably higher age in Patagonia had been accessible for measurement.

Both the extent of invasive and native populations can be explained by human influence. In the introduced range, anthropogenic disturbance facilitated the establishment of *R. rubiginosa* populations while in the native range this species is constantly cut back keeping populations small, which is broadly demonstrated by the younger age of the native rose stems. The invasive shrub *Rhododendron ponticum* L. is endangered in its place of origin due to climatic

constraints (Mejías et al. 2002), but to our knowledge this is the first study showing that native populations of an invasive species are endangered because of human influence.

This apparent success of control measures in the native range implies that management seems promising for *R. rubiginosa* populations, although a complete eradication of *R. rubiginosa* in its introduced range remains doubtful because it would be labor and cost intensive and only successful over several growing seasons with best results occurring on recently established populations (Weber 2003; Zimmermann and Hensen 2011).

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