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TRACKING THE ORIGIN OF INVASIVE *ROSA RUBIGINOSA* POPULATIONS IN ARGENTINA

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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.

Online enhancement: appendix B.

Introduction

The discovery of America by Christopher Columbus in 1492 was a crucial event in human history and nature. Since the discovery of the New World, globalization of trade, transport, and emigration has been constantly growing, and humans have played an increasing role in the dispersal of species (Meyerson and Mooney 2007). As a consequence, many species have become introduced to areas where they could not have naturally dispersed. Some of these species became so successful after establishment that they are regarded as being invasive in their new ranges (Richardson et al. 2000).

It is predicted that most invasive populations develop from a few introduced individuals, and these initially small populations are generally expected to have a low genetic diversity because of founder effects and genetic drift (Dlugosch and Parker 2008*a*; Novak and Mack 2005). However, the magnitude of these effects depends on several factors, for example, the reproduction system (Novak and Mack 2005; Barrett et al. 2008), the ploidy level (Soltis and Soltis 2000; Prentis et al. 2008), or preadaptations to abiotic influences (Prinzing et al. 2002; Schlaepfer et al. 2010). Therefore, invasive species can be very successful despite having low genetic variability (Ahmad et al. 2008; Le Roux et al. 2008). Detailed insights into these aspects of invasion success can often be gained by comparing invasive and native populations of the invasive species (Bossdorf et al. 2005; Erfmeier and Bruelheide 2005; Hierro et al. 2005).

Identification of the exact geographic origin of source populations of invasive species provides important information about success, spread, and evolution of invasive species and creates opportunities for their biological control (e.g., host-specific pathogens; Guo 2006; Estoup and Guillemaud 2010). Molecular markers are appropriate tools for identifying the source populations of invasive species, since they enable the detection of pathways of introduction and allow for comparisons between the species' genetic variation in the native and invasive ranges (Barrett and Shore 1989; Sakai et al. 2001; Durka et al. 2005). Nonetheless, only a few studies have determined the source populations of invasive species (Milne and Abbott 2004; Gaskin et al. 2005; Goolsby et al. 2006). One example is the study by Novak and Mack (2001), who used allozyme electrophoresis techniques in combination with historical information to trace the native source region of invasive *Bromus tectorum* L. populations in North America as

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well as other naturalized ranges (Argentina, Chile, Canary Islands, Hawaii, and New Zealand). They revealed that its spread was closely related to patterns of European human immigration around the world. Similarly, Besnard et al. (2007) determined the origin of invasive olive trees (*Olea europaea* L.) in Australia and Hawaii on the basis of microsatellites and chloroplast markers as well as ITS sequences.

Rosa rubiginosa L. (Rosaceae), the sweet briar or eglantine rose, is native to Eurasia (Täckholm 1922; Meusel et al. 1965) and forms neophytic or even invasive populations in South Africa, Australia, New Zealand, and North and South America (Parsons and Cuthbertson 2001; Weber 2003; Bellingham et al. 2004; Nel et al. 2004; Lüttig 2006). In Argentina, populations of *R. rubiginosa* are mainly located in central Argentina and Patagonia. In Patagonia, the rose is widespread and populations most often take the form of dense stands that displace native species (Damascos and Gallopin 1992). Here, *R. rubiginosa* is already accepted as part of the local flora, and rose hips are harvested for private use or by small producers. In Chile, on the other hand, *R. rubiginosa* is already being exploited on a large scale for its seed oil by international cosmetic companies (Joublan and Rios 2005). In central Argentina, populations are smaller than in Patagonia but equally invasive (Zimmermann et al. 2010). The exact Eurasian origin of the Argentinean populations is unknown. In accordance with the predominant European origin of human immigrants, two scenarios are currently discussed in the literature: (1) *R. rubiginosa* was introduced to South America by Spanish immigrants (Joublan et al. 1996; Leuenberger 2005; Lüttig 2006) or (2) German immigrants brought *R. rubiginosa* to South America (Damascos 1992).

A comparison of 13 Argentinean and 20 native populations (Germany and Spain) using dominant random amplification of polymorphic DNA and codominant microsatellite markers by Zimmermann et al. (2010) revealed that genetic diversity of *R. rubiginosa* is highly reduced in the invasive range, but they were unable to detect the geographic origin of the invasive populations. However, one Argentine population was genetically very similar to German populations. In this study, we extended our sampling with the focus on Germany and its neighboring countries and Spain in the native range and therefore analyzed *R. rubiginosa* populations in a wider distribution range than in our previous study by using both fresh and herbarium plants. Herbarium material provides the additional advantage that genetic information from extinct populations can be used. Furthermore, we used nuclear microsatellite markers because of their expected higher genetic variability and good reproducibility (Litt and Luty 1989; Tautz 1989). We assessed the following questions: (1) Is it possible to track the European origin of the *R. rubiginosa* invasion in Argentina and to estimate how many introduction events occurred? (2) Can we confirm the low genetic diversity of *R. rubiginosa* in the invasive range?

Material and Methods

Study Species

Rosa rubiginosa is one of ~60 species of the section *Caninae* (DC.) Ser. (dog roses; Wissemann and Ritz 2007). Dog roses reproduce by xenogamy and autogamy, but apomixis has also been described (Wissemann and Hellwig 1997). The species of this section are characterized by an unusual meiotic system, the canina meiosis, first described by Täckholm (1920, 1922) and Blackburn and Harrison (1921). Their studies revealed that most dog roses, including *R. rubiginosa*, are pentaploid (2n=5x=35). The unique canina meiosis produces tetraploid egg cells (1n=4x=28)—which stabilizes this odd ploidy level, thus ensuring sexual reproduction—and haploid sperm cells (1n=1x=7). This leads to distinctive matroclinal inheritance (Ritz and Wissemann 2003; Wissemann et al. 2006; Wissemann and Ritz 2007) and renders analysis of heterozygosity and related genetic measures complicated.

Sampling Scheme

On the basis of the two currently discussed scenarios regarding the origin of invasive *R. rubiginosa* populations in South America, we focused our sampling in the native range on Spain (42 samples) and Germany (201 samples). According to recommendations by Muirhead et al. (2008), we also increased the population sampling with other countries of the native range, with the majority of samples from the Czech Republic (30 samples) and Austria (16 samples) followed by Italy (5 samples), France and Scotland (2 samples, respectively) and single samples from five more countries (Belgium, Croatia, Slovakia, Sweden, and Ukraine), which was realized by using both herbarium and fresh leaf material (see apps. A, B [app. B is in the online edition of the *International Journal of Plant Sciences*]). Since we aimed to cover a wide geographical range, leaf material was collected from a large number of regions (32) and populations (131), while the number of individuals per population was relatively low (sample sizes between 1 and 15 individuals per population; for similar strategies, see Clausing et al. 2000; Lambracht et al. 2007; Prinz et al. 2009). In the invasive range we mainly sampled populations in Argentina (90 samples), but we also included a few populations from Chile (6 samples), South Africa (1 sample), Australia (1 sample), and New Zealand (16 samples; see app. B). Herbarium material was collected from herbaria in Germany and Austria dating from 1927 to 2002 (see apps. A, B). Fresh leaf material was sampled randomly from areas within the invasive ranges no larger than 2500 m^2, and the minimum distance between populations was 1 km. Because of the small population sizes in the native range, the number of sampled individuals per population was often lower than 10 and usually covered the whole population area (area sizes between 0.009 and 0.09 km^2; for detailed information, see Zimmermann et al. 2010). Altogether, 417 samples from 29 invasive and 102 native populations were studied (see fig. 1; app. B). To test whether herbarium material was suited for microsatellite analyses, we tested both herbarium (1–2 years old) and fresh material from 10 individuals, which yielded identical results.

DNA Extraction

DNA extraction from silica gel–dried leaf material was performed with the DNeasy Plant Mini Kit (QIAGEN, Hilden) following the manufacturer's instructions. To increase

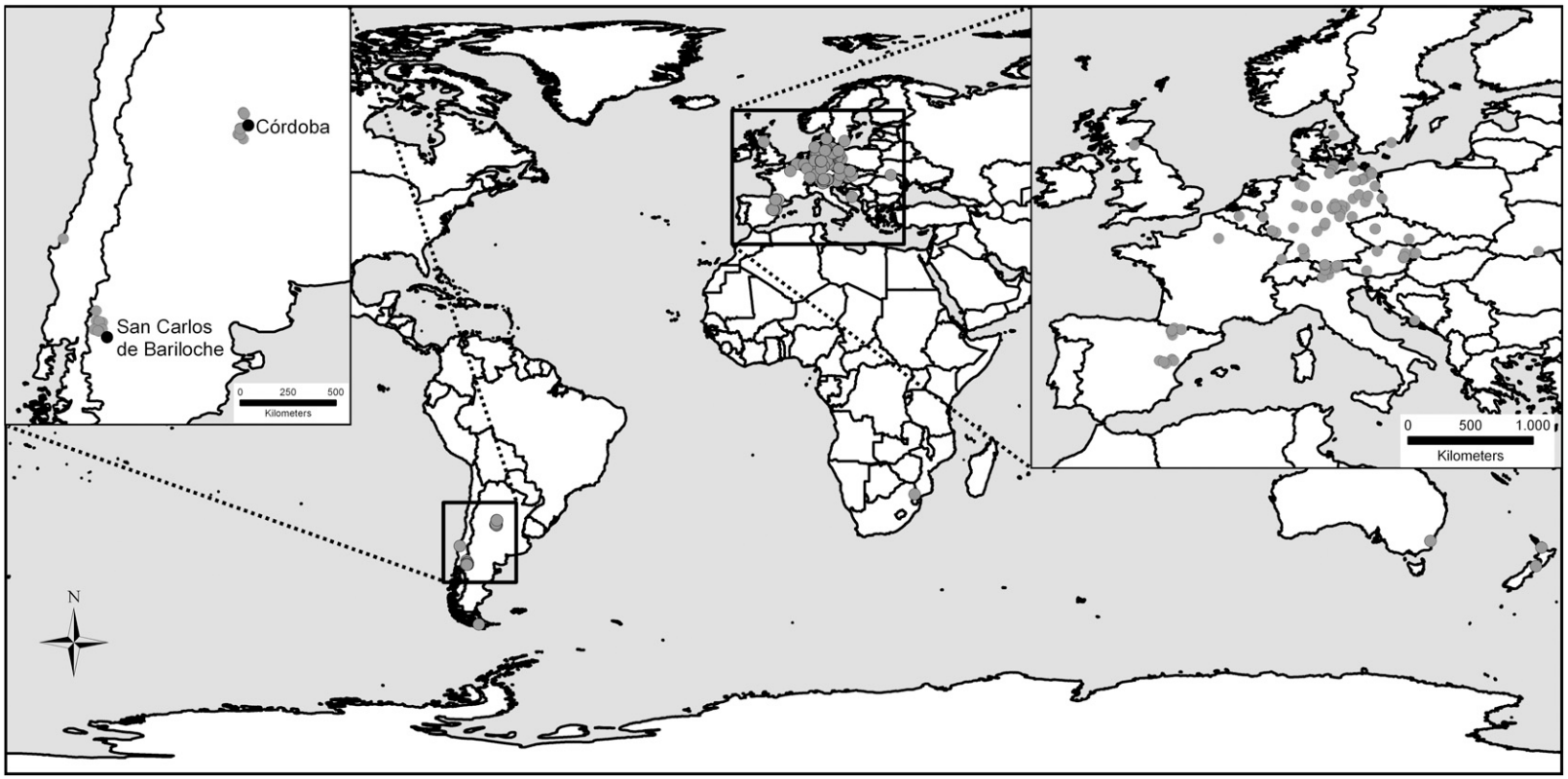

Fig. 1 Sampled populations (102 native and 29 invasive) of *Rosa rubiginosa*. Details of Europe and Argentina are enlarged. Argentinean populations around Córdoba are referred to as central Argentinean populations and those around San Carlos de Bariloche as Patagonian populations. Note that only a few populations from South Africa, Australia, and New Zealand (countries not enlarged) were sampled (see app. B in the online edition of the *International Journal of Plant Sciences*).

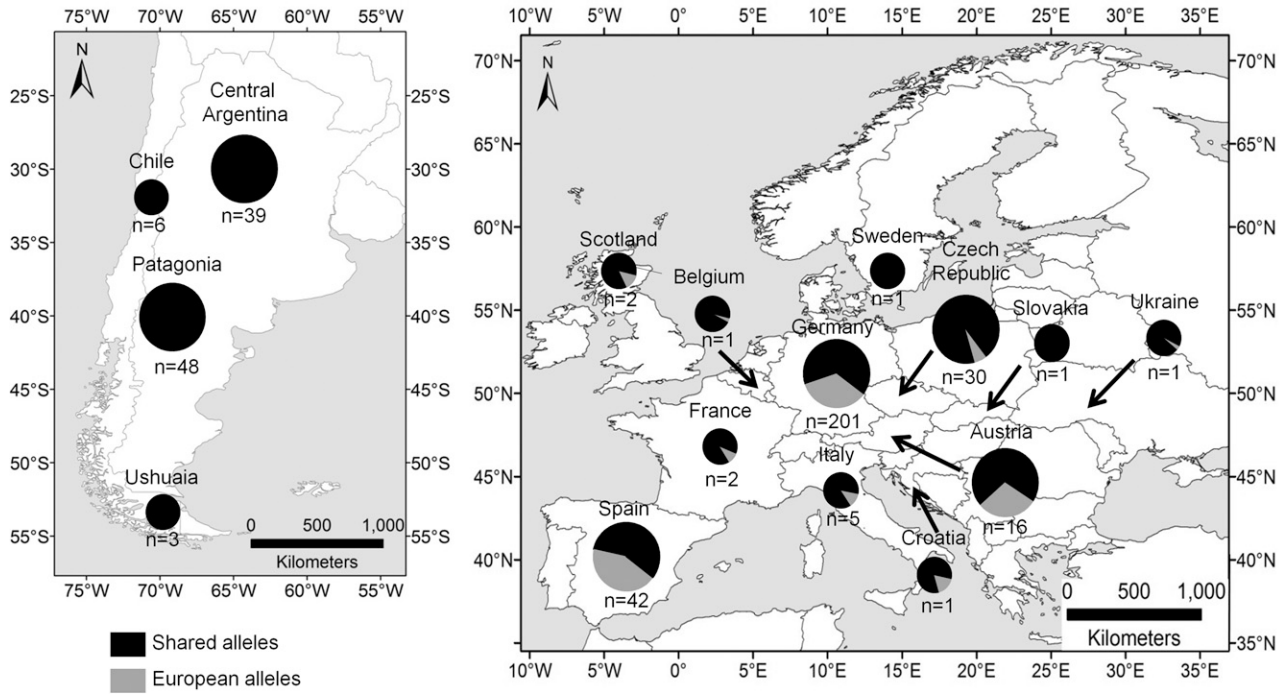

Fig. 2 Allele frequencies of *Rosa rubiginosa* in Europe and South America (black = alleles found in both Europe and South America, gray = alleles found exclusively in Europe). Individuals sampled within a country are pooled (n = sample size). Countries with sample sizes less than 10 are characterized by having smaller diagrams. The other invasive ranges are excluded because of their small sample sizes. Spain is characterized as having the highest proportion of exclusively European alleles, followed by Germany and Austria. No exclusive alleles were detected in South America.

the final DNA concentration, we used a longer elution time (10 min) for the herbarium samples in accordance with Drábkova et al. (2002).

Microsatellite Analysis

For the analyses of sequence-tagged microsatellite sites of *R. rubiginosa*, we used eight primer pairs (RhD201, RhD206, RhD221, RhB303, RhEO506, RhP519, RhE2b and RhAB26) isolated by Esselink et al. (2003). PCR assays were set up in final volumes of 25 μL, containing 10 ng of genomic DNA, 1 μL of each primer (5 pmol/μL; Metabion, Martinsried), 2.5 μL dNTPs (2.5 mM; Q-Biogene, Heidelberg), 1 U Taq DNA polymerase (Fermentas, St. Leon-Rot), 2.5 μL incubation mix T. Pol with 1.5 mM $MgCl_2$ (Q-Biogene) and 16.8 μL H_2O_{bidest}. One primer of each pair was labeled at the 5′ end with 6-FAM or HEX fluorescent dyes. PCR was performed in a Mastercycler gradient or Mastercycler epgradient (Eppendorf, Hamburg) under the following temperature regime: initial denaturation at 94°C for 3 min; 28 cycles (35 cycles for primer RhD201 and RhE2b) with 30 s denaturation at 94°C, 30 s annealing at 50°C, and 60 s elongation at 72°C, and a final elongation step for 3 min at 72°C. PCR products (fresh leaf material 1 : 5 and herbarium leaf material 1:1 diluted) were used for separation on a MegaBace 1000 system (Amersham Bioscience, Uppsala) with MegaBace-ET Rox 400 (Amersham Bioscience) as a size standard. The genotyping was performed with the MegaBace Fragment Profiler software 1.2 (Amersham Bioscience).

Data Analysis

The eight primer pairs used in the PCR yielded 69 polymorphic alleles. Only four or fewer alleles per locus were detected in any individual at any of the scored loci, which is in accordance with previous results of Nybom et al. (2004) on several dog roses, including *R. rubiginosa*. The assessment of the exact allelic configurations using microsatellite DNA counting–peak ratios in accordance with Esselink et al. (2004) was not successful as a result of significant deviations between observed and expected microsatellite DNA counting–peak ratios. Possible reasons for these deviations include base substitution in the primer binding sites or reaction times exceeding the exponential phase during PCR (Esselink et al. 2003, 2004). Therefore, statistical analysis had to be based on the allelic phenotypes, since the number of allele copies remained unknown.

We calculated the proportions of shared alleles (i.e., alleles occurring in both the native range and the invasive range South America) and exclusively European alleles (i.e., alleles restricted to the native range). This method was previously described by Durka et al. (2005) and assumes that a high proportion of shared alleles indicates the possible source region, whereas unlikely source regions are characterized by a high proportion of exclusively European alleles. Moreover, the proportion of allelic phenotypes was also used as a measure of genetic diversity. In order to reveal genetic similarity between samples, a principal coordinate analysis (PCoA) using square root–transformed Jaccard dissimilarities (equivalent to Jaccard distance, which is obtained by subtracting the

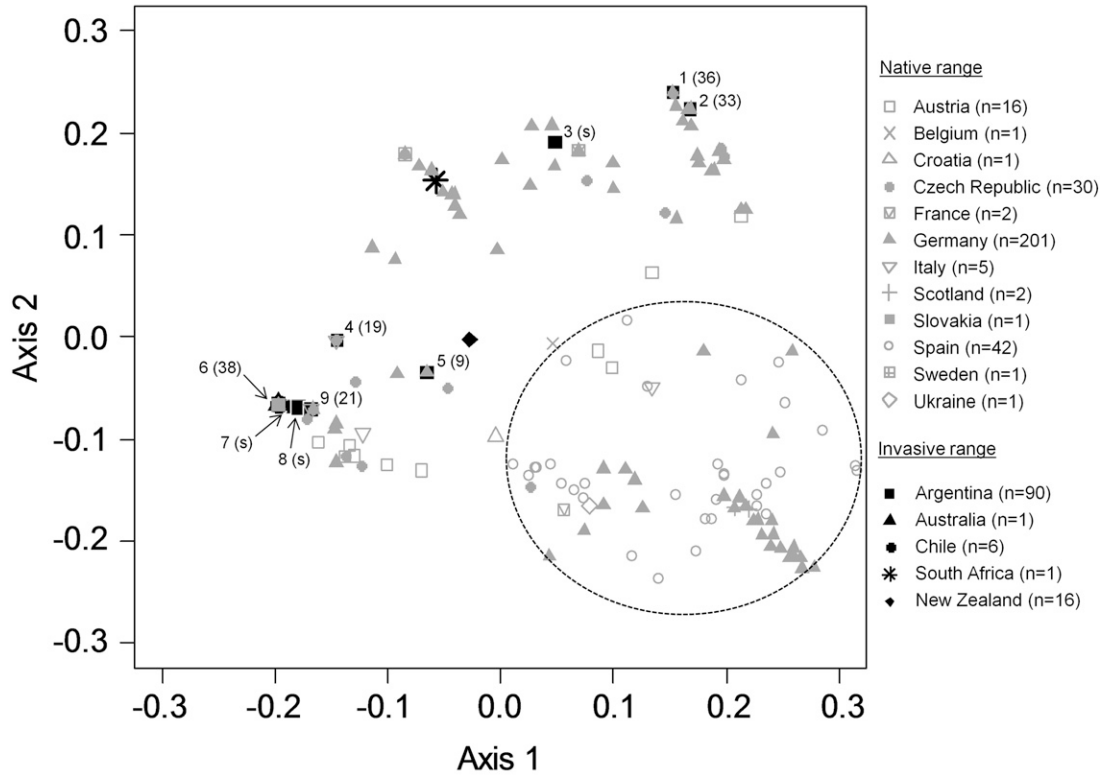

Fig. 3 Principal coordinate analysis (PCoA) of microsatellite data for *Rosa rubiginosa* (417 samples; PCoA based on square root–transformed Jaccard dissimilarity; explained variance axis 1 = 22.1%, axis 2 = 19.4%). Each point represents an individual and is coded with a unique symbol for the corresponding country (black = countries in the invasive range, gray = countries in the native range). Note that Argentinean samples are accumulated in only nine visible points (visualized by numbers 1–9; numbers in parentheses correspond to the group ID of groups with identical allelic phenotypes in table 2; *s* = single allelic phenotype) and show a high similarity or even identicalness with samples from Austria, the Czech Republic, Germany, Italy, and Slovakia. Note that three of the Argentinean groups (groups 1–3; represented by samples from two central Argentinean populations) are grouped separately from the remaining South American samples. Samples from Spain (circled with dashed line) are clearly separated from invasive samples.

Jaccard similarity from 1) was performed with the package vegan (Oksanen et al. 2008) in R (ver. 2.8.1; R Development Core Team 2008). We used the load on the first three axes of every yielded point in the PCoA and the "find clones" option of GenAlEx 6.1 (Peakall and Smouse 2006) to identify the groups of individuals with identical allelic phenotypes and the sizes of these groups.

Furthermore, we analyzed genetic similarities between populations with pairwise F'_{ST} values, and as a measure of genetic diversity within ranges, the mean Jaccard dissimilarities within the native as well as the invasive range were calculated. For these analyses, only data from populations with three or more sampled individuals (native range, 239 samples; invasive range, 101 samples; see app. B) were selected. Pairwise F'_{ST} values were calculated with the software FDASH. This program was developed by Obbard et al. (2006) for codominant marker analysis of polyploid species with unknown allelic configurations. On the basis of pairwise F'_{ST} values and geographic distances, we performed a Mantel test (Mantel 1967) with the package vegan in R to test for isolation by distance patterns among Argentinean populations as well as among European populations. Mean Jaccard dissimilarity was calculated (999 permutations; package vegan in R) per country and for both the invasive and the native ranges. Sample number in the native range was more than twice as high as for the invasive range, so the native range mean Jaccard dissimilarity was bootstrapped in order to account for unbalanced sampling.

Results

The geographical allele distribution (fig. 2) shows high proportions of European alleles in samples from Germany, Spain, and Austria (29.6%–43.1%). In contrast, the Czech Republic is characterized by only 5.9% of European-specific alleles. No exclusive alleles were detected in the invasive range.

The 96 South American samples were clustered in nine groups of individuals with identical allelic phenotypes in the PCoA (fig. 3). Two central Argentinean populations were grouped separately, while the seven remaining groups clustered closely and contained samples from both Argentinean regions as well as Chile. The PCoA revealed a clear distinction between the Spanish and Argentinean *Rosa rubiginosa* samples. In contrast, several Argentinean allelic phenotypes were very similar or even identical to allelic phenotypes from Germany, the Czech Republic, Austria, Italy, and Slovakia.

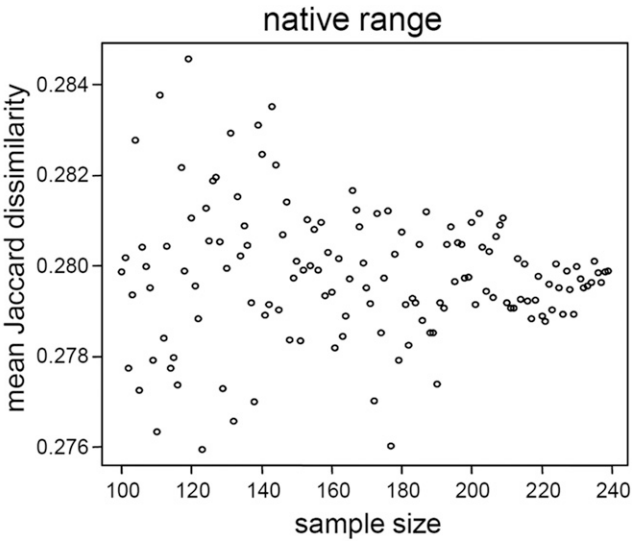

Fig. 4 Bootstrapped mean Jaccard dissimilarity for sample sizes between 100 and 239 in the native range to account for unbalanced sampling between native (239 samples) and invasive (101 samples) range. Jaccard dissimilarity is equivalent to Jaccard distance, which is obtained by subtracting the Jaccard similarity from 1. Mean Jaccard dissimilarity was calculated for the reduced data set, which contains populations with only three or more samples (see app. B in the online edition of the *International Journal of Plant Sciences*). Bootstrapped values show a very low variation at only less than 0.01, which excludes a significant influence of sample size on the mean Jaccard dissimilarity.

The Chilean, Australian, and several allelic phenotypes from New Zealand were identical to most Argentinean allelic phenotypes. These results are confirmed by the ranges of Jaccard dissimilarities between European countries and countries from the invasive range (table 1). We detected no exact match between European allelic phenotypes and the single sample from South Africa (table 1).

Levels of pairwise F'_{ST} values between the South American populations of *R. rubiginosa* were very low (0.00–0.04; data not shown). The only exceptions were two central Argentinean populations, which also grouped separately in the PCoA; they shared values between 0.19 and 0.49 with other South American populations. Pairwise F'_{ST} values between these two central Argentinean populations and the New Zealand population were 0.26 and 0.30, while the values between the New Zealand population and the remaining South American populations were only between 0.00 and 0.10. Among European populations, we found pairwise F'_{ST} values between 0.00 and 0.93. In accordance with the PCoA, the Mantel test revealed no isolation by distance relationship among the European populations (Mantel statistic $r = 0.135$, $P = 0.058$) or the South American populations ($r = 0.014$, $P = 0.259$).

Calculation of the mean Jaccard dissimilarity per range revealed that diversity in the native range was 4.7 times higher (0.28) than that in the invasive range (0.06). Bootstrapped native range estimates show a very low variation of less than 0.01 (fig. 4). The low genetic variability in the invaded South American and New Zealand ranges was also reflected by the large number of individuals clustered in only few groups of samples with identical allelic phenotypes (table 2; fig. 3). The European allelic phenotypes showed a more diverse pattern. The invasive range also had a smaller number of alleles as well as lower mean Jaccard dissimilarities and a smaller number of allelic phenotypes per locus at the country level than in the native range, except for Italian populations (table 3).

Discussion

Identification of the Source Region

Several authors assume that *Rosa rubiginosa* was introduced to South America by Spanish emigrants (Joublan et al. 1996; Leuenberger 2005; Lüttig 2006); however, this assumption is apparently based on largely unreliable evidence. In contrast, our PCoA and the ranges of Jaccard dissimilarities clearly distinguish between invasive Argentinean populations and native Spanish populations (table 1; fig. 3), suggesting that the origin of the species in Argentina is not Spanish. The results indicate exact or close similarity between Argentinean samples and those from Germany, the Czech Republic, Austria, Italy, and Slovakia. In accordance, populations in Spain had the

Table 1

Ranges of Jaccard Dissimilarities between European Countries and Countries in the Invasion Range

Country	Argentina	Australia	Chile	New Zealand	South Africa
Austria	.00–.41	.00–.39	.00–.39	.00–.39	.04–.34
Belgium	.11–.29	.17	.17	.17–.30	.23
Croatia	.27–.44	.30	.30	.30–.31	.35
Czech Republic	.00–.35	.00–.32	.00–.32	.00–.39	.11–.31
France	.14–.39	.23	.23	.23–.35	.17–.34
Germany	.00–.44	.00–.36	.00–.36	.00–.42	.04–.39
Italy	.00–.39	.04–.34	.04–.34	.04–.35	.11–.29
Scotland	.23–.31	.26–.28	.26–.28	.26–.34	.31–.33
Slovakia	.00–.26	.00	.00	.00–.21	.14
Spain	.07–.61	.11–.59	.11–.59	.11–.59	.04–.61
Sweden	.07–.17	.11	.11	.11–.18	.04
Ukraine	.14–.36	.20	.20	.20–.32	.31

Note. Jaccard dissimilarity is equivalent to Jaccard distance, which is obtained by subtracting the Jaccard similarity from 1. Values of 0 indicate the occurrence of identical allelic phenotypes between two countries.

Table 2

Groups of Identical Allelic Phenotypes and Geographic Origin of Samples in Each Group

Group ID	Group size	Native range	Invasive range
1	2	ES (2)	
2	2	ES (2)	
3	2	DE (2)	
4	2	DE (2)	
5	2	DE (1), GB (1)	
6	2	ES (2)	
7	2	ES (2)	
8	2	DE (2)	
9	2	DE (1)	AR (1)
10	2	DE (2)	
11	2	DE (2)	
12	2	DE (2)	
13	2	DE (2)	
14	2	ES (2)	
15	2	ES (2)	
16	3	DE (3)	
17	3	ES (3)	
18	3	DE (3)	
19	3	CZ (1), IT (1)	AR (1)
20	3	CZ (2), DE (1)	
21	3	IT (2)	AR (1)
22	3	DE (2), FR (1)	
23	3	DE (3)	
24	4	AT (2), CZ (2)	
25	4	ES (4)	
26	5	CZ (5)	
27	6	DE (6)	
28	7	DE (7)	
29	7	DE (7)	
30	7	DE (7)	
31	8	CZ (8)	
32	8	NZ (8)	
33	9	DE (6)	AR (3)
34	11	DE (11)	
35	13	DE (13)	
36	26	CZ (6), DE (17)	AR (3)
37	63	AT (1), DE (60), ES (1), SE (1)	
38	104	AT (4), CZ (1), DE (5), SK (1)	AR (78), AU (1), CL (6), NZ (8)

Note. Group size indicates the number of individuals that share the same allelic phenotype. Origin of samples is separated and arranged alphabetically by native range (AT = Austria, BE = Belgium, CZ = Czech Republic, DE = Germany, ES = Spain, FR = France, GB = Great Britain/Scotland, HR = Croatia, IT = Italy, SE = Sweden, SK = Slovakia, UA = Ukraine) as well as invasive range (AR = Argentina, AU = Australia, CL = Chile, NZ = New Zealand). Numbers in parentheses indicate samples represented from the corresponding country.

highest proportion of exclusively European alleles, whereas populations from the Czech Republic, Italy, Slovakia, Belgium, Croatia, Scotland, Sweden, Ukraine, and France had relatively small proportions of European alleles. However, the latter six countries were excluded as possible origin regions by the PCoA (fig. 3), while sample sizes of Italian and Slovakian populations were too small to draw any significant conclusions. German and Austrian populations show comparatively high proportions of exclusively European alleles, but they cannot be excluded as possible source regions because of the similarity between some of their samples and South American samples in the PCoA and according to the Jaccard dissimilarity ranges. The allele distribution result for the Czech Republic is in agreement with the PCoA. Furthermore, it is important to mention that the proportion of exclusively European alleles appears to be influenced by the sample size (the smaller the sample size, the higher the proportion of exclusively European alleles), except for the Czech Republic. Therefore, we emphasize the importance of comparing the results of the allele proportions with other statistical analyses that are based on a more exact relation of allelic phenotypes.

Combining all results, we are able to exclude a Spanish origin of the South American populations, and we assume that Central Europe—in particular, Germany, the Czech Republic, Austria, Slovakia, and Italy—constitutes the most probable source region for the South American populations. Narrowing down the geographical range would require more extensive sampling, especially from Austria, Slovakia, and Italy.

Table 3

Number of Alleles, Average Allelic Phenotypes per Locus, and Mean Jaccard Dissimilarity (999 Permutations) per Country for the Reduced FDASH Data Set

Country	*n*	No. alleles	Average allelic phenotypes per locus	Mean Jaccard dissimilarity
Native range:				
Czech Republic	30	34	2.50	.19
Germany	167	47	5.25	.22
Italy	3	29	1.12	.03
Spain	39	58	8.25	.38
Invasive range:				
Argentina	81	33	2.00	.04
Chile	5	27	1.00	.00
New Zealand	15	29	1.37	.10

Note. n = sample size of each country. FDASH data set includes 340 samples (see app. B in the online edition of the *International Journal of Plant Sciences*).

Our study confirms the general fact that the exact native source region of an invasive species is difficult to determine, even if advanced molecular tools are applied. Durka et al. (2005), looking for the progenitors of North American invasive *Alliaria petiolata* (M. Bieb.) Cavara and Grande, also identified a relative wide-ranging area (British Isles, Northern Europe and Central Europe) as a possible source region. Milne and Abbott (2004) showed that invasive *Ligustrum robustum* populations in the Mascarene Islands originated in Sri Lanka, but it was not possible to detect the exact origin location within Sri Lanka. Even the tracing of source regions at much smaller spatial scales can be complicated. Neither Prinz et al. (2009) nor Esfeld et al. (2008) were able to identify the exact colonization source of newly established populations from former mining areas. Studies using a combination of uni- and biparentally inherited DNA sequences seem to be more successful. For instance, Milne and Abbott (2000) identified the Iberian Peninsula as the source region of the invasive *Rhododendron ponticum* L. populations on the British Isles via chloroplast and nuclear ribosomal DNA restriction fragment length polymorphisms. Combining mitochondrial DNA and microsatellite markers, Rugman-Jones et al. (2007) identified Coatepec Harinas in Mexico as the most likely source region of the invasive Californian populations of the avocado thrips (*Scirtothrips perseae* Nakahara). However, in the case of *R. rubiginosa*, we expect that an analysis with maternally inherited DNA would not show a more informative result than the matroclinal inherited microsatellites. Olsson et al. (2000) assume a conservative force in the maternal-biased inheritance of nonorganelle DNA markers in the section *Caninae* that leads to a comparability of matroclinal and uniparental inheritance. Our assumption is also confirmed by the results of Wissemann and Ritz (2005), who show that established chloroplast DNA markers are not suitable to find differentiations within and between the subsections *Rubiginae* (including *R. rubiginosa*) and *Vestitae*.

On the basis of historical evidence, it is assumed that *R. rubiginosa* was introduced to Patagonia ~1900 (Damascos 1992). The hypothesis that Spanish emigrants introduced the rose is probably based on the fact that most ancestors of the Argentineans were Spanish. However, the Argentinean government promoted the immigration of other Europeans to Argentina following the end of Spanish colonial rule in 1816 (Oelsner 2007). Thus, especially Italian, French, German, Austrian, British, Belgian, and Swiss emigrants reached Argentina during a mass immigration in the second half of the nineteenth century. For example, 21,831 Germans, 26,335 Austrians, and 838,267 Italians arrived in Argentina in the years between 1877 and 1897 (Oelsner 2007). It is most likely that emigrants from the region of today's Czech Republic were among the Austrians, since this area was, at the time, part of the Austro-Hungarian monarchy, and all citizens of this region travelled with Austrian passports, rendering any estimation of more detailed proportions difficult (U. Prutsch, personal communication).

An introduction to Argentina via Chile cannot be excluded, because central European immigrants began arriving in Chile prior to arriving in Argentina (Liga Chileno-Alemana 1950; Bernecker 1997). This idea of indirect introduction—or the so-called bridgehead effect (Estoup and Guillemaud 2010; Lombaert et al. 2010)—is supported by the identical allelic phenotypes between the Chilean and most of the Argentinean samples. Surprisingly, we also detected identical allelic phenotypes between the Australian, New Zealand, and South American samples and low pairwise F'_{ST} values between the New Zealand population and most South American populations. We assume a mixed introduction history in these regions, but additional investigations would be required to arrive at any definitive conclusions.

Identical allelic phenotypes across Argentina suggest a joint origin of Patagonian and central Argentinean populations, which has also been discussed in previous work by Zimmermann et al. (2010). It is assumed that *R. rubiginosa* was first introduced to Patagonia and later transported to central Argentina. Furthermore, we suggest that *R. rubiginosa* was introduced to Argentina at least twice, considering that two of the central Argentinean populations were separated in the PCoA (fig. 3). Both populations are located only 13 km away from Villa General Belgrano, a village with descendants mainly of German, Swiss, and North Italian origin. It is possible that their ancestors introduced *R. rubiginosa* independently from the introduction in Patagonia. Usage of *R. rubiginosa* as living livestock fences due to its dense growth form as well as the traditional usage of rose hips for the production of jam

and tea are given as possible reasons for the introduction in areas outside of the native range (Damascos 1992; Joublan et al. 1996).

Genetic Diversity and Structure

The comparison of mean Jaccard dissimilarities, groups with identical allelic phenotypes, number of alleles, average number of allelic phenotypes per locus, and pairwise F'_{ST} values between native and invasive ranges confirms a very low genetic variability for invasive *R. rubiginosa* populations in Argentina and New Zealand, which is in accordance with the previous study by Zimmermann et al. (2010). We assume that this lack of variability in invasive Argentinean *R. rubiginosa* populations is due to the low number of introduction events and predominantly clonal growth or apomixis (Novak and Mack 2005). For instance, Xu et al. (2003) detected an extremely low genetic diversity in invasive populations of alligator weed (*Alternanthera philoxeroides* (Mart.) Griseb) in China and suggested that they originated from only a very low number of introduced clones. Furthermore, Prentis et al. (2009) showed that invasive *Macfadyena unguis-cati* (L.) A. H. Gentry populations in Africa, Australia, Europe, North America, and the Pacific Islands are characterized by very low genetic diversity, and they assume a single or, at best, a few introductions in the invasive range. To estimate the introduction events in New Zealand, more samples would be needed from this range. Nevertheless, *R. rubiginosa* is one of the examples that introduced species can develop successful invading populations despite reduced genetic diversity (Dlugosch and Parker 2008*b*).

Both the PCoA and the Mantel test showed that genetic structures in European *R. rubiginosa* are not linked to geographical patterns. Such a result might indicate an intensive gene flow, but this is unlikely because of the large distances between the European populations and the partly high pairwise F'_{ST} values. A more likely scenario is that some genotypes had rapidly and homogeneously dispersed during the postglacial recolonization of Europe and were conserved via self-fertilization or apomixis. A microsatellite analysis by Ritz and Wissemann (2011) revealed a high level of genetic identity between open pollinated offspring and mother plants of *R. rubiginosa*. This result is in line with that of Olsson (1999), who also indicated *R. rubiginosa* as an unusually homogenous species. Consequently, self-fertilization might play an important role in native populations and could also explain the successful establishment of *R. rubiginosa* in spite of its reduced genetic variability.

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Appendix A

Source of Specimens from Public Herbaria

Each entry includes voucher number, the number that corresponds to the serial number in the complete population list (see app. B in the online edition of *International Journal of Plant Sciences*), locality (administrative classification, region, country), sampling year, and herbarium code from the herbarium where the material was collected (B = Herbarium of the Free University Berlin; W = Herbarium of the Natural History Museum Vienna). Entries are arranged alphabetically by country and region (E = east, N = north, NE = northeast, NW = northwest, S = south, SW = southwest, W = west).

Taxon; voucher number; serial number corresponding to appendix B; collection locale; sampling year; herbarium.

Rosa rubiginosa L.; 1957-9916; 10; Río Negro, Patagonia, Argentina; 1945; W. *R. rubiginosa* L.; 1986-04693; 31; Spittal an der Drau, Kärnten, Austria; 1985; W. *R. rubiginosa* L.; 2004-17296; 32; Bruck an der Leitha, Lower Austria, Austria; 1979; W. *R. rubiginosa* L.; 2005-13042; 33; Vienna, Lower Austria, Austria; 2001; W. *R. rubiginosa* L.; 2003-04737; 34; Wiener Neustadt, Lower Austria, Austria; 2002; W. *R. rubiginosa* L.; 2006-10460; 35; Wiener Neustadt, Lower Austria, Austria; 2005; W. *R. rubiginosa* L.; B100400004; 36; Linz (city), Upper Austria, Austria; 1950; B. *R. rubiginosa* L.; 1984-04895; 37; Imst, Tyrol, Austria; 1983; W. R. rubiginosa L.; 1992-14972; 38; Imst, Tyrol, Austria; 1991; W. *R. rubiginosa* L.; 1991-05721; 39; Innsbruck-Land, Tyrol, Austria; 1990; W. *R. rubiginosa* L.; B100400005; 40; Innsbruck-Land, Tyrol, Austria; 1939; B. *R. rubiginosa* L.; 1989-04417; 41; Innsbruck-Land, Tyrol, Austria; 1988; W. *R. rubiginosa* L.; 1981-08425; 42; Innsbruck, Tyrol, Austria; 1980; W. *R. rubiginosa* L.; 1984-04894; 43; Landeck, Tyrol, Austria; 1983; W. R. rubiginosa L.; 1981-08426; 44; Landeck, Tyrol, Austria; 1980; W. *R. rubiginosa* L.; 1996-02949; 45; Reutte, Tyrol, Austria; 1990; W. *R. rubiginosa* L.; 1991-05737; 46; Reutte, Tyrol, Austria; 1990; W. *R. rubiginosa* L.; B10040006; 25; New South Wales, SW Australia, Australia; 1967; B. *R. rubiginosa* L.; 1983-04453; 47; Vlaams Brabant, S Flanders, Belgium; 1955; W. *R. rubiginosa* L.; B100121112; 27; Región del Bío-Bío, Central Chile, Chile; 2002; B. *R. rubiginosa* L.; 1956-1257; 48; Splitsko-Dalmatinska, S Croatia, Croatia;

1927; W. *R. rubiginosa* L.; 1962-13708; 54; Oise, N France, France; 1960; W. *R. rubiginosa* L.; B100400010; 55; Haut-Rhin, E France, France; 1989; B. *R. rubiginosa* L.; B100400003; 56; Sachsen-Anhalt, Middle Germany, Germany; 1980; B. *R. rubiginosa* L.; B100400002; 72; Brandenburg, NE Germany, Germany; 1972; B. *R. rubiginosa* L.; B100400009; 73; Brandenburg, NE Germany, Germany; 1955; B. *R. rubiginosa* L.; B100400001; 74; Brandenburg, NE Germany, Germany; 1953; B. *R. rubiginosa* L.; B100400013; 75; Brandenburg, NE Germany, Germany; 1989; B. *R. rubiginosa* L.; B10040012; 76; Brandenburg, NE Germany, Germany; 1989; B. *R. rubiginosa* L.; B100052063; 103; Baden-Württemberg, S Germany, Germany; 1994; B. *R. rubiginosa* L.; 2000-05437; 111; Nordrhein-Westfalen, W Germany, Germany; 1985; W. *R. rubiginosa* L.; 1981-11830; 115; Sondrio, Tyrol, Italy; 1980; W. *R. rubiginosa* L.; 1961-16176; 30; Limpopo, NE South Africa, South Africa; 1960; W. *R. rubiginosa* L.; B100400007; 125; Huesca, Pyrenees, Spain; 1994; B. *R. rubiginosa* L.; 1956-8640; 130; Blekinge län, S Sweden, Sweden; 1949; W. *R. rubiginosa* L.; B100400008; 131; Chernivtsi, W Ukraine, Ukraine; 1992; B.

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