

CORRIGENDUM

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Follow-up analyses of the AFLP data published in Lachmuth *et al.* (2010) revealed that wrong peak height thresholds had been applied during genotyping of one of the AFLP primer combinations. This resulted in erroneous presences or absences at some loci. We have subsequently resubmitted a corrected AFLP data set to DRYAD (<http://dx.doi.org/10.5061/dryad.1813.2>).

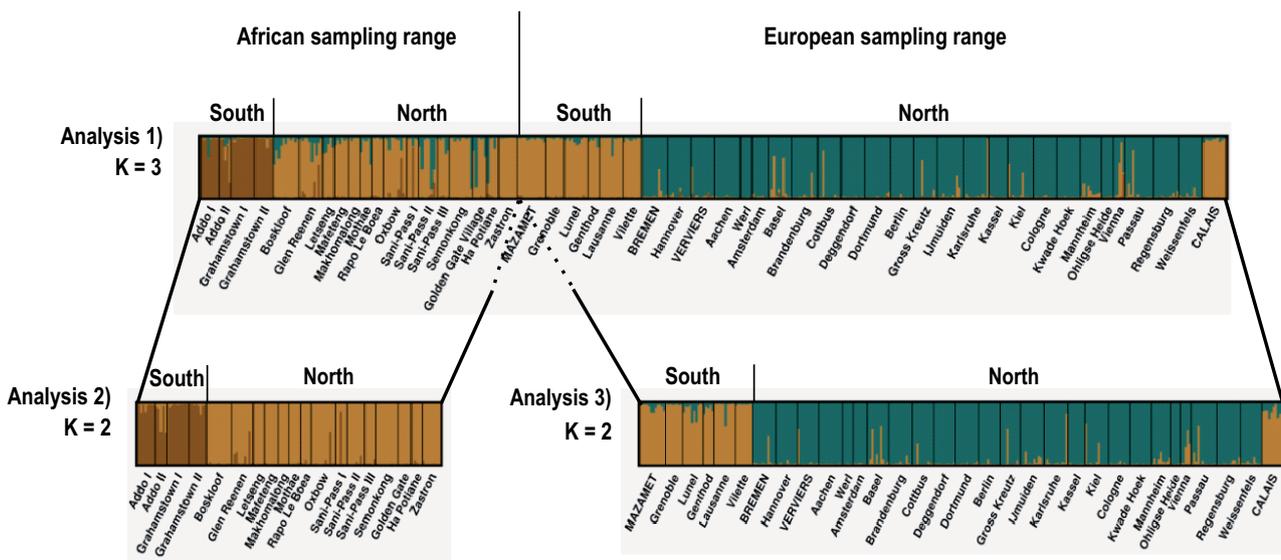
Re-analyses of the corrected data brought about changes in the results and the design of the STRUCTURE analyses as well as slight changes in the absolute values of measures of genetic diversities and parameter estimates of all statistical analyses. Despite these changes, all statistical analyses yielded qualitatively the same results as reported in the original publication. Consequently, the major interpretations and conclusions of this publication remain unaltered.

Changes in the AFLP genotyping and data

- 1 For loci obtained from primer combination ACT (FAM)-CAG, individual peak thresholds were corrected which yielded changes in the respective absence–presence data.
- 2 After discarding monomorphic markers, we now analysed presence–absence data for 187 polymorphic AFLP loci and 29 polymorphic microsatellite alleles of 437 samples. One sample was removed due to exceptionally low number of AFLP marker presence.

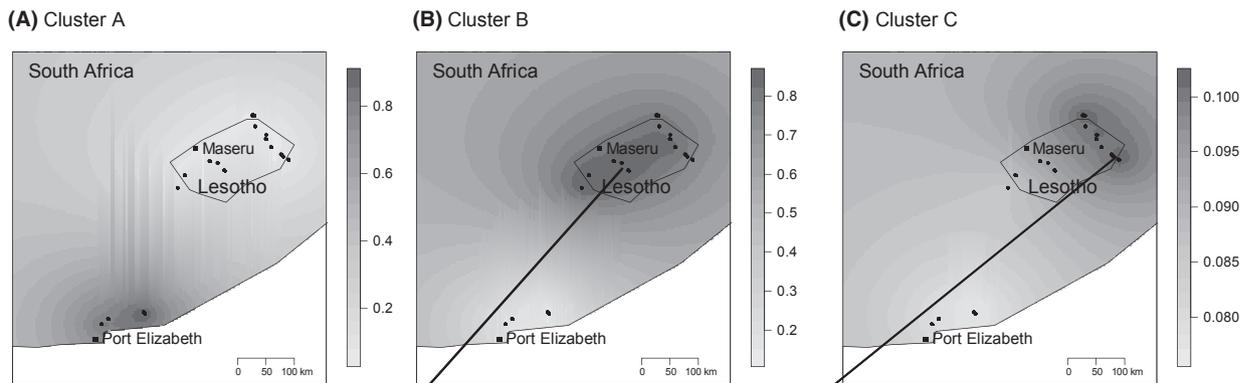
Synopsis of changes in results and interpretation

Re-analyses of the corrected data yielded slight changes in the measures of genetic diversity (see Original Table

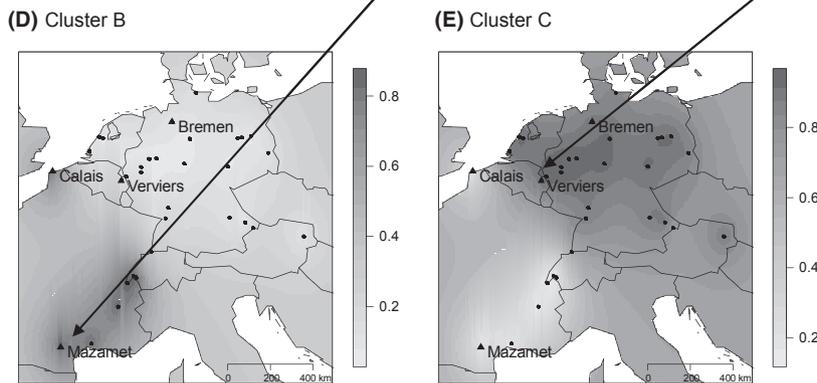


New Fig. 1 Average cluster assignment probability Q in nested STRUCTURE analyses of AFLP data for individuals from native African and invasive European populations of *Senecio inaequidens*. Each bar represents one individual, and populations are separated by black lines. Analysis 1: including all African and European samples. Analysis 2: comprising African samples only. Analysis 3: including all European samples.

Native African Sampling Range



Invaded European Sampling Range



New Fig. 2 Spatial interpolation (kriging) of assignment probabilities Q to single genetic clusters in the native African and invasive European range of *Senecio inaequidens*. All subplots show results of STRUCTURE analyses 1. Symbols indicate sampled populations (●) and sampled documented introduction sites (▲) as well as locations of bigger cities for orientation (■). Arrows connect these European sites to their most likely African origin.

1 and New Table 1) and in the STRUCTURE results. For the European range, only two clusters were identified, which contain the introduction sites Mazamet and Verviers, and their presumable descendent populations, respectively. The introduction site Calais is now largely assigned to the Mazamet cluster, whereas the Bremen introduction centre is completely allocated to the Verviers route. The four historically documented introductions to Verviers, Mazamet, Bremen and Calais thus show even stronger differences in invasion success than reported in Lachmuth *et al.* (2010). In all subsequent statistical analyses (Isolation by distance, AMOVA, variation in genetic diversity), the absolute values of parameter estimates and sometimes P -values changed. However, the analyses yielded qualitatively the same results as in the original publication (all effects that were previously significant at $P < 0.05$ remain significant). The main interpretations and conclusions of the original publication thus remain unaltered.

Comparison of the original analytical results to the re-analysis

After correction of the AFLP absence–presence data, the following results changed between the original analyses and the re-analyses of the data.

Structure analyses

For the European range (STRUCTURE analysis 3, see Original Fig. 1 and New Fig. 1), only two clusters ($K = 2$) were identified, which contain the introduction sites Mazamet (a subset of cluster B in analysis 1, Europe-S) and Verviers (a subset of cluster C in analysis 1, Europe-N), and their presumable descendent populations, respectively (New Fig. 1, New Fig. 2D, E). The introduction site Calais was largely assigned to the Mazamet cluster, but shows higher assignment to the Verviers cluster than the populations descending from Mazamet. The Bremen intro-

New Table 1 (selected columns): Properties of sampled populations including subregions and invasion routes derived from STRUCTURE analyses: country codes A: Austria, B: Belgium, CH: Switzerland, D: Germany, F: France, L: Lesotho, NL: Netherlands and ZA: South Africa; *N*, sample size; *H_j*, gene diversity; *PLP* (5) and *B_r* (5); polymorphic marker proportion and band richness, respectively, with sample size rarefied to five individuals

Country	Location	Region	Route	<i>N</i>	<i>H_j</i>	<i>PLP</i> (5)	<i>B_r</i> (5)
ZA	Addo I	Africa-S	—	8	0.178	0.430	1.349
ZA	Addo II	Africa-S	—	5	0.215	0.411	1.411
ZA	Boskloof	Africa-N	—	11	0.159	0.481	1.322
ZA	Glen Reenen	Africa-N	—	10	0.178	0.472	1.349
ZA	Golden Gate	Africa-N	—	6	0.189	0.383	1.348
ZA	Grahamstown I	Africa-S	—	8	0.208	0.509	1.406
ZA	Grahamstown II	Africa-S	—	10	0.209	0.570	1.424
L	Ha Potiane	Africa-N	—	5	0.206	0.346	1.346
L	Letseng	Africa-N	—	5	0.193	0.355	1.355
L	Mafeteng	Africa-N	—	6	0.149	0.276	1.252
L	Makhomalong	Africa-N	—	5	0.174	0.308	1.308
L	Mothae	Africa-N	—	5	0.183	0.327	1.327
L	Oxbow	Africa-N	—	10	0.188	0.537	1.382
L	Rapo-Le-Boea	Africa-N	—	5	0.174	0.318	1.318
L	Sani Pass I	Africa-N	—	5	0.210	0.407	1.407
L	Sani Pass II	Africa-N	—	8	0.182	0.453	1.359
L	Sani Pass III	Africa-N	—	5	0.214	0.421	1.421
L	Semonkong	Africa-N	—	10	0.171	0.458	1.324
ZA	Zastron	Africa-N	—	8	0.167	0.360	1.290
ZA	Elliot	—	—	9	NA	NA	NA
ZA	Lady Grey	—	—	6	NA	NA	NA
ZA	Langholm	—	—	8	NA	NA	NA
L	Malefiloune	—	—	5	NA	NA	NA
L	Masianokong	—	—	4	NA	NA	NA
L	Masuaneng	—	—	5	NA	NA	NA
L	Molumong	—	—	10	NA	NA	NA
D	Aachen	Europe-N	VER	11	0.181	0.472	1.348
N	Amsterdam	Europe-N	VER	7	0.169	0.336	1.291
CH	Basel	Europe-N	VER	10	0.163	0.421	1.305
D	Berlin	Europe-N	VER	10	0.171	0.411	1.311
D	Brandenburg	Europe-N	VER	11	0.165	0.416	1.307
D	Bremen	Europe-N	VER	11	0.172	0.449	1.330
F	Calais	Europe-N	MAZ	10	0.153	0.346	1.262
D	Cologne	Europe-N	VER	10	0.179	0.458	1.340
D	Cottbus	Europe-N	VER	10	0.162	0.402	1.299
D	Deggendorf	Europe-N	VER	10	0.125	0.257	1.193
D	Dortmund	Europe-N	VER	11	0.173	0.430	1.319
CH	Genthod	Europe-N	MAZ	5	0.142	0.210	1.210
F	Grenoble	Europe-N	MAZ	8	0.174	0.369	1.300
D	Gross Kreutz	Europe-N	VER	10	0.152	0.364	1.267
D	Hanover	Europe-N	VER	10	0.167	0.444	1.312
N	Ijmuiden	Europe-N	VER	11	0.160	0.407	1.297
D	Karlsruhe	Europe-N	VER	11	0.161	0.416	1.298
D	Kassel	Europe-N	VER	8	0.169	0.369	1.299
D	Kiel	Europe-N	VER	11	0.155	0.402	1.285
N	Kwade Hoek	Europe-N	VER	10	0.134	0.290	1.219
CH	Lausanne	Europe-S	MAZ	10	0.111	0.252	1.183
F	Lunel	Europe-S	MAZ	10	0.158	0.421	1.306
D	Mannheim	Europe-N	VER	9	0.159	0.379	1.290
F	Mazamet	Europe-S	MAZ	12	0.162	0.481	1.323
D	Ohligse Heide	Europe-N	VER	5	0.174	0.290	1.290
D	Passau	Europe-N	VER	5	0.185	0.313	1.313
D	Regensburg	Europe-N	VER	12	0.157	0.425	1.302

New Table 1 Continued

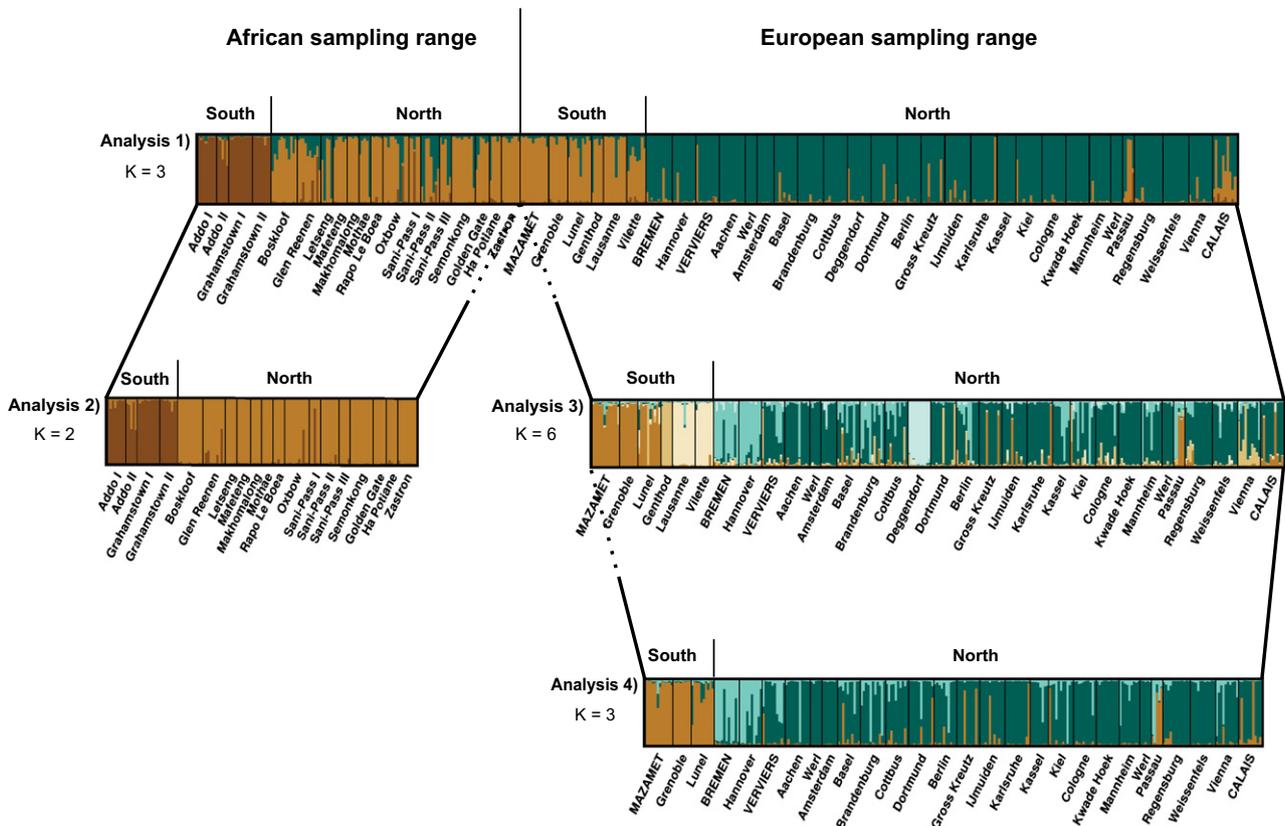
Country	Location	Region	Route	N	H _j	PLP (5)	B _r (5)
B	Verviers	Europe-N	VER	10	0.186	0.453	1.351
A	Vienna	Europe-N	VER	10	0.170	0.407	1.307
CH	Vilette	Europe-S	MAZ	8	0.138	0.271	1.219
D	Weissenfels	Europe-N	VER	11	0.147	0.369	1.267
D	Werl	Europe-N	VER	5	0.171	0.271	1.271

duction centre is assigned completely to the Verviers route. Thus, only two separate clusters (see New Table 1; see Original Fig. 2 and New Fig. 2) were distinguished as random effect in subsequent analyses. Also, with the updated AFLP genotyping, STRUCTURE analysis 3 no longer identified four strongly bottlenecked populations (Deggenndorf, Genthod, Lausanne, Vilette) as separate clusters. This means that the previous STRUCTURE analysis 4 (without these bottlenecked populations) was no longer necessary. However, these populations still have low values of genetic diversity (see New Table 1).

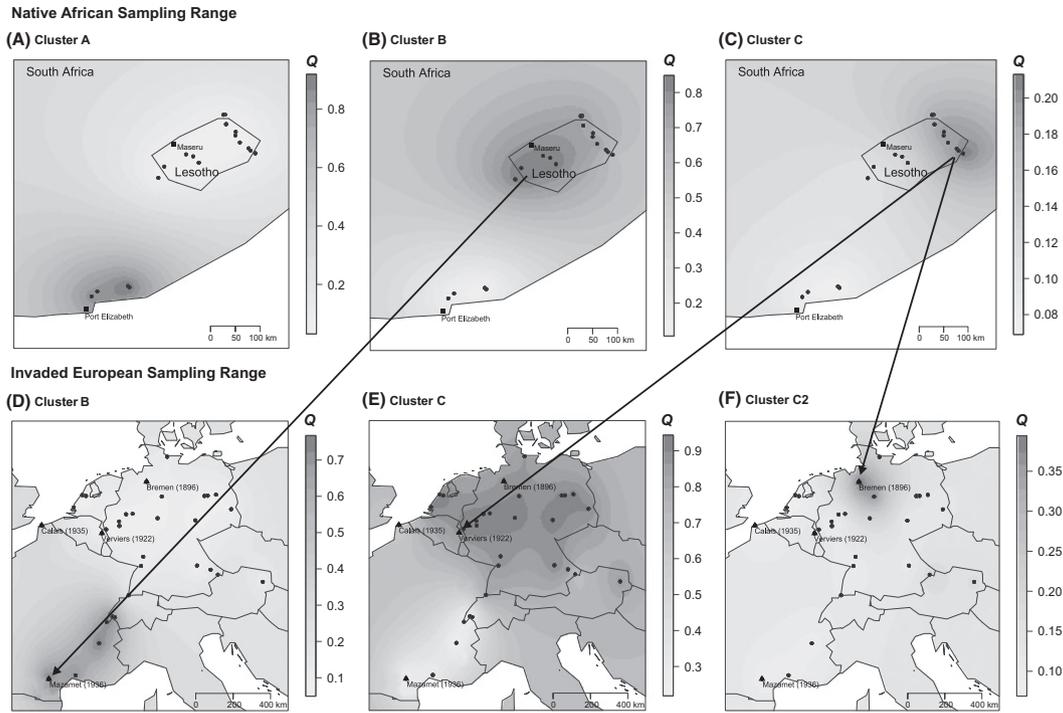
Interpretation: The four historically documented introductions to Verviers, Mazamet, Bremen and Calais show even stronger differences in invasion success than reported in Lachmuth *et al.* (2010). The previously identified ‘strongly bottlenecked’ populations still have low genetic diversity, but seem less differentiated from the other populations.

Intraspecific climatic differentiation

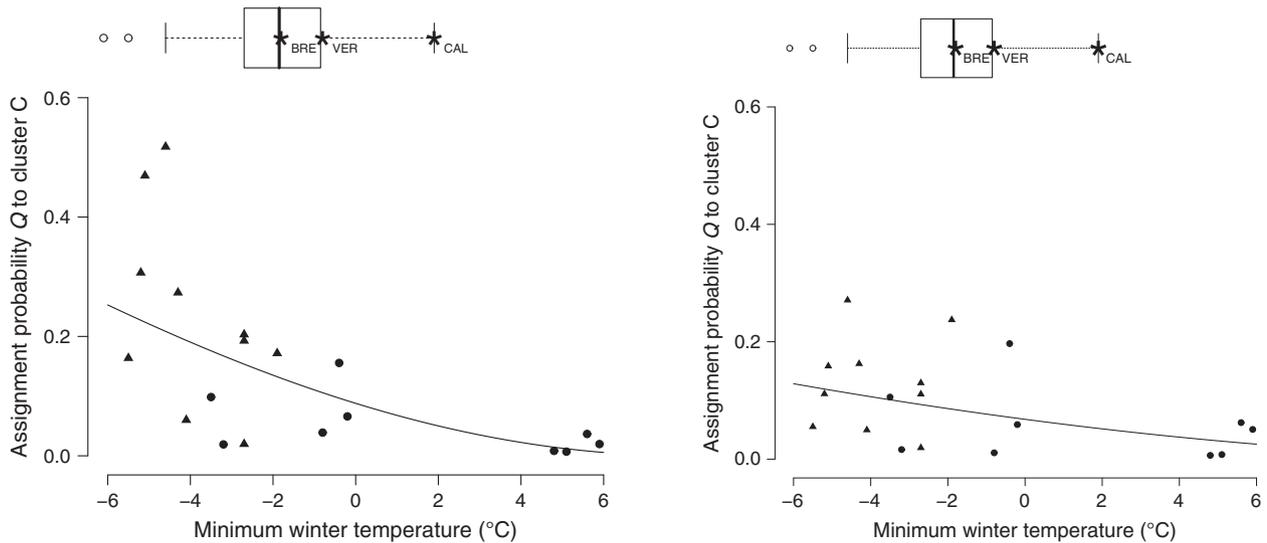
Old result: In the African range, the probability of population assignment (Q) to cluster C increases as



Original Fig. 1 Average cluster assignment probability *Q* in nested STRUCTURE analyses of AFLP data for individuals from native African and invasive European populations of *Senecio inaequidens*. Each bar represents one individual, and populations are separated by black lines. Analysis 1: including all African and European samples. Analysis 2: comprising African samples only. Analysis 3: including all European samples. Analysis 4: European samples without bottlenecked populations (Deggenndorf, Genthod, Lausanne, Vilette). Populations are sorted alphabetically within clusters (as derived from analyses 1 and 4).

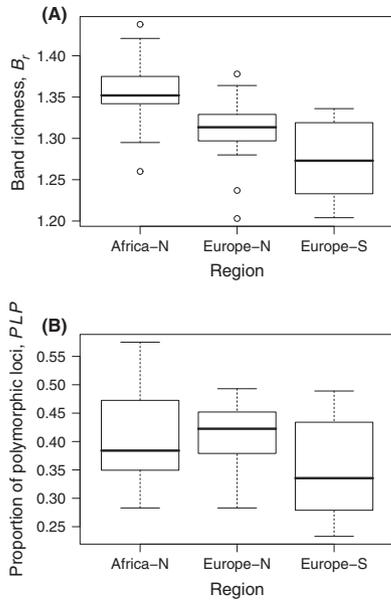


Original Fig. 2 Spatial interpolation (kriging) of assignment probabilities Q to single genetic clusters in the native African and invasive European range of *Senecio inaequidens*. Subplots (A)–(E) show results of STRUCTURE analyses 1, whereas (F) shows results of analysis 4 (see Fig. 1). Symbols indicate sampled populations (●) and sampled documented introduction sites (▲) as well as locations of bigger cities for orientation (■). Arrows connect these European sites to their most likely African origin.



Original Fig. 3 Relationship between the mean minimum winter temperature of African populations and their mean assignment probability to cluster C invading Central Europe (Europe-N). Triangles (▲) mark the Eastern highlands within the Africa-N region which show the highest assignment probability to this cluster. The remaining African populations are indicated by points (●). Stars indicate the introduction sites in this cluster, and the boxplot shows the temperature range of European populations assigned to this cluster (bold line: median, box: interquartile range, whiskers: typical range, points: outliers). Population assignment is based on STRUCTURE analysis 1.

New Fig. 3 Relationship between the mean minimum winter temperature of African populations and their mean assignment probability to cluster C invading Central Europe (Europe-N). Triangles (▲) mark the Eastern highlands within the Africa-N region which show the highest assignment probability to this cluster. The remaining African populations are indicated by points (●). Stars indicate the introduction sites in this cluster and the boxplot shows the temperature range of European populations assigned to this cluster (bold line: median, box: interquartile range, whiskers: typical range, points: outliers). Population assignment is based on STRUCTURE analysis 1.



Original Fig. 4 Band richness B_r (5) (A) and proportion of polymorphic loci PLP (5) (B) of populations in the Africa-N source region and European subregions. The definition of regions was derived from the results of STRUCTURE analysis 1. Both measures were rarefied to the minimum sample size of five individuals. See Fig. 3 for an explanation of the statistics indicated by the boxplots.

minimum winter temperature decreases ($F_{1,17} = 14.1$, $P < 0.01$, Akaike's information criterion AIC: -10.8 , Original Fig. 3).

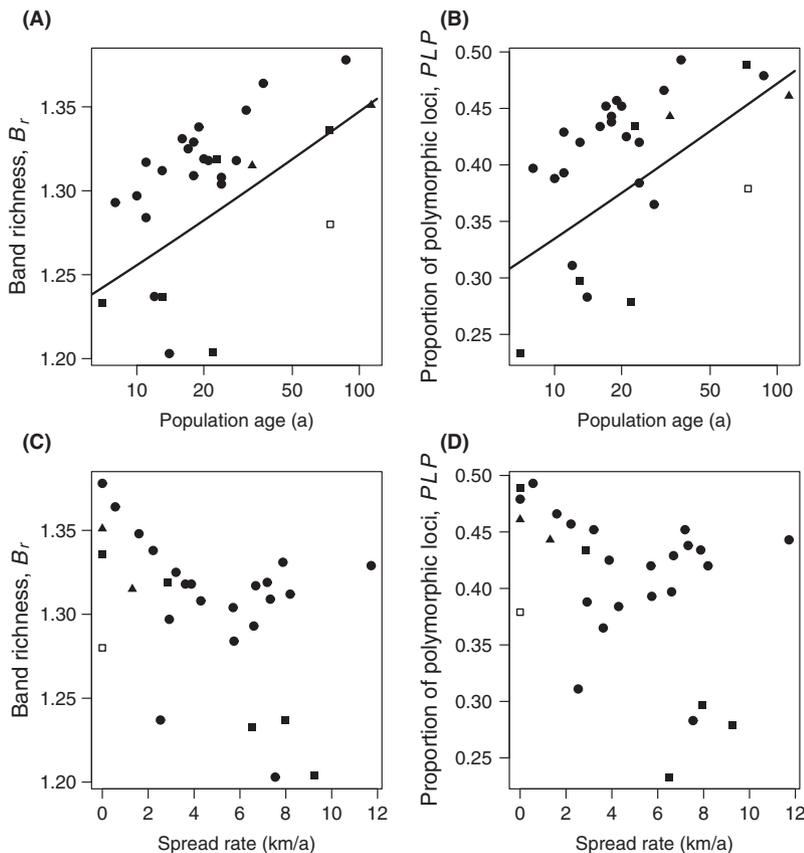
New result: In the African range, the probability of population assignment (Q) to cluster C increases as minimum winter temperature decreases ($F_{1,17} = 4.7$, $P < 0.05$, Akaike's information criterion AIC: -19.6 , New Fig. 3).

Interpretation: As in the original study, we find a significant relationship between the assignment probability of native populations to cluster C and minimum winter temperature.

Mantel tests for isolation by distance

Original results: Entire African sample, $r = 0.6$, Mantel- $P < 0.01$, slope = 0.0001; Africa-N region, $r = 0.4$, Mantel- $P < 0.01$, slope = 0.0002; Entire European sample: $r = 0.3$, Mantel- $P < 0.05$, slope = 0.00006; Europe-N region, $r = 0.3$, Mantel- $P < 0.05$, slope = 0.00005.

New results: Entire African sample, $r = 0.6$, Mantel- $P < 0.01$, slope = 0.0002; Africa-N region, $r = 0.4$, Mantel- $P < 0.01$, slope = 0.0004; European sample, $r = 0.3$, Mantel- $P < 0.05$, slope = 0.0001; Europe-N region, $r = 0.3$, Mantel- $P < 0.01$, slope = 0.0001.



Original Fig. 5 Influence of population age (A and B) and spread rate (C and D) on band richness B_r (5) (A and C) and proportion of polymorphic loci PLP (5) (B and D) in the European range of *S. inaequidens*. Symbols represent invasion routes (▲: Bremen, □: Calais, ■: Mazamet, ●: Verviers), and the line indicates the prediction of the corresponding linear mixed-effects models for the significant effect of population age. Note that the x-axis of (A and C) is plotted on a log scale. Both measures of genetic diversity were rarefied to the minimum sample size of five individuals and show a complex relationship to spread rate with initial steep decline and greater scatter at higher spread rates.

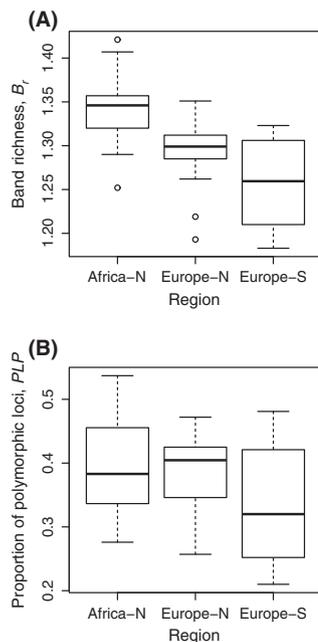
Original Table 1 (selected columns): Properties of sampled populations including sub-regions and invasion routes derived from STRUCTURE analyses: country codes A: Austria, B: Belgium, CH: Switzerland, D: Germany, F: France, L: Lesotho, NL: Netherlands and ZA: South Africa; *N*, sample size; *H_j*, gene diversity; *PLP*; polymorphic marker proportion; *B_r*, Band richness

Country	Location	Region	Route	<i>N</i>	<i>H_j</i>	<i>PLP</i>	<i>B_r</i>
ZA	Addo I	Africa-S	—	8	0.185	0.44	1.36
ZA	Addo II	Africa-S	—	5	0.217	0.41	1.406
ZA	Boskloof	Africa-N	—	11	0.172	0.50	1.346
ZA	Glen Reenen	Africa-N	—	10	0.196	0.50	1.377
ZA	Golden Gate	Africa-N	—	6	0.192	0.38	1.347
ZA	Grahamstown I	Africa-S	—	8	0.212	0.52	1.411
ZA	Grahamstown II	Africa-S	—	10	0.218	0.58	1.436
L	Ha Potiane	Africa-N	—	5	0.206	0.34	1.338
L	Letseng	Africa-N	—	5	0.196	0.35	1.352
L	Mafeteng	Africa-N	—	6	0.155	0.28	1.26
L	Makhomalong	Africa-N	—	5	0.196	0.35	1.352
L	Mothae	Africa-N	—	5	0.195	0.35	1.347
L	Oxbow	Africa-N	—	10	0.210	0.58	1.421
L	Rapo-Le-Boea	Africa-N	—	5	0.186	0.34	1.338
L	Sani Pass I	Africa-N	—	5	0.231	0.44	1.438
L	Sani Pass II	Africa-N	—	8	0.194	0.46	1.373
L	Sani Pass III	Africa-N	—	5	0.220	0.41	1.411
L	Semonkong	Africa-N	—	10	0.187	0.48	1.352
ZA	Zastron	Africa-N	—	8	0.172	0.37	1.295
D	Aachen	Europe-N	VER	11	0.191	0.49	1.364
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D	Brandenburg	Europe-N	VER	11	0.174	0.43	1.317
D	Bremen	Europe-N	BRE	11	0.185	0.46	1.351
F	Calais	Europe-N	CAL	10	0.169	0.38	1.28
D	Cologne	Europe-N	VER	10	0.185	0.47	1.348
D	Cottbus	Europe-N	VER	10	0.168	0.42	1.312
D	Deggendorf	Europe-N	VER	10	0.131	0.28	1.203
D	Dortmund	Europe-N	VER	11	0.183	0.46	1.338
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D	Gross Kreutz	Europe-N	VER	10	0.166	0.40	1.293
D	Hanover	Europe-N	BRE	10	0.170	0.44	1.315
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D	Werl	Europe-N	VER	5	0.187	0.29	1.292

Original Table 2 Hierarchical analyses of molecular variance among and within the native and invaded regions of *S. inaequidens*

Source of variation	Over all F_{ST}	Percentage of variation		
		Among populations	Within populations	
Both continents pooled	0.17	17.01	82.99	
Africa	0.14	13.54	86.46	
Europe	0.16	16.23	83.77	
		Among continents	Among populations within continents	Within populations
Africa + Europe	0.19	4.15	14.8	81.05
Africa-North + Europe-North	0.16	4.6	11.09	84.31
Africa-North + Europe-South	0.17	2.43	14.39	83.19
		Among regions	Among populations within regions	Within populations
Africa: North + South	0.20	12.88	7.62	79.5
Africa: North	0.10		9.61	90.39
Africa: South	0.06		6.01	93.99
Europe: North + South	0.20	6.25	13.65	80.1
Europe: North	0.12		12.39	87.61
Europe: South	0.26		25.65	74.35

Significance was tested on 1000 permutations. All differences are significant at $P < 0.001$.



New Fig. 4 Band richness B_r (5) (A) and proportion of polymorphic loci PLP (5) (B) of populations in the Africa-N source region and European subregions. The definition of regions was derived from the results of *STRUCTURE* analysis 1. Both measures were rarefied to the minimum sample size of five individuals. See Fig. 3 for an explanation of the statistics indicated by the boxplots.

Interpretation: As in the original study, all regions show patterns of isolation by distance.

Population structure (AMOVA)

See Original Table 2 and New Table 2.

Interpretation: Although the absolute values change slightly, the interpretation of AMOVA results remains unaltered.

Private alleles

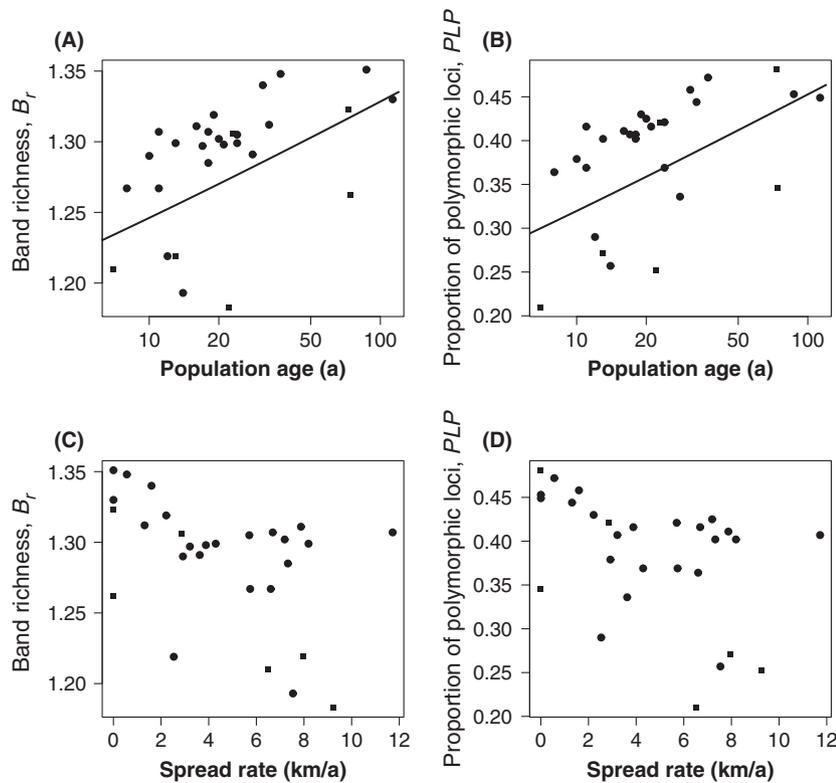
Old values: Africa-N, 0; Africa-S, 4; Europe-N, 1; Europe-S, 1.

New values: Africa-N, 0; Africa-S, 3; Europe-N, 2; and Europe-S, 1.

Interpretation: Numbers of private alleles for the different subregions were low in both the original analysis and the re-analysis. Thus, population differentiation mainly resulted from shifts in band frequencies.

Genetic diversity within populations

Original results: Genetic diversity of populations (H_j , PLP and B_r) varied between 0.12–0.23 (mean 0.18), 0.23–0.58 (mean 0.41) and 1.20–1.44 (mean 1.33) per population, respectively (Original Table 1). European



New Fig. 5 : Influence of population age (A and B) and spread rate (C and D) on band richness B_r (5) (A and C) and proportion of polymorphic loci PLP (5) (B and D) in the European range of *S. inaequidens*. Symbols represent invasion routes (■: Mazamet, ●: Verviers), and the line indicates the prediction of the corresponding linear mixed-effects models for the significant effect of population age. Note that the x -axis of (A and C) is plotted on a log scale. Both measures of genetic diversity were rarefied to the minimum sample size of five individuals and show a complex relationship to spread rate with initial steep decline and greater scatter at higher spread rates.

New Table 2 Hierarchical analyses of molecular variance among and within the native and invaded regions of *S. inaequidens*

Source of variation	Percentage of variation			
	Over all F_{st}	Among populations	Within populations	
All populations	0.17	17.07	82.93	
Africa	0.14	13.99	86.01	
Europe	0.16	16.20	83.80	
		Among populations within continents	Within populations	
	Among continents			
Africa + Europe	0.19	3.98	14.95	81.07
Africa-North + Europe-North	0.15	4.51	10.9	84.6
Africa-North + Europe-South	0.17	2.53	14.92	82.55
		Among populations within regions	Within populations	
	Among regions			
Africa: North + South	0.21	13.39	7.80	78.82
Africa: North	0.10		9.83	90.17
Africa: South	0.07		6.80	93.20
Europe: North + South	0.20	6.56	13.49	79.94
Europe: North	0.12		11.99	88.01
Europe: South	0.27		26.86	73.14

Significance was tested on 1000 permutations. All differences are significant at $P < 0.001$.

populations showed a decrease in H_j and B_r compared to the Africa-N source populations (H_j : $F_{1,45} = 16.3$, $P < 0.001$, B_r : $F_{1,45} = 14.6$, $P < 0.001$, see also Original Fig. 4A). This also held after omitting the four strongly bottlenecked European populations (Deggendorf, Genthod, Lausanne, Vilette, Table 1). In contrast, *PLP* did not differ significantly between native and invasive populations ($F_{1,45} = 0.4$, $P > 0.05$, see also Original Fig. 4B). Within Africa, the lowland populations (Africa-S) were slightly more diverse than the highland populations (Africa-N), but the difference was not significant. In Europe, southern populations (Europe-S) were significantly less diverse than the Central European (Europe-N) ones except for *PLP* (H_j : $F_{1,30} = 6.2$, $P < 0.05$, B_r : $F_{1,30} = 4.7$, $P < 0.05$, *PLP*: $F_{1,30} = 3.2$, $P > 0.05$; Original Fig. 4). The different diversity measures showed the same temporal development along the four European invasion routes. All of them increased with population age (H_j : $\chi^2_{(1)} = 9.4$, $P < 0.01$, B_r : $\chi^2_{(1)} = 11.7$, $P < 0.001$, *PLP*: $\chi^2_{(1)} = 11.5$, $P < 0.001$, Original Fig. 5A, B), whereas spread rate was dropped from the minimum adequate model. A comparison of models containing either log-transformed population age or spread rate as explanatory variable further established the higher explanatory power of population age for all three measures (AIC differences: H_j : 2.4, B_r : 4.1, *PLP*: 5.6, note that population age and spread rate were correlated (Spearman $\rho = -0.63$, $P > 0.001$)). Still, spread rate as a single explanatory variable did have a significant negative effect on genetic diversity (H_j : $\chi^2_{(1)} = 9.4$, $P < 0.01$, B_r : $\chi^2_{(1)} = 11.7$, $P < 0.001$, *PLP*: $\chi^2_{(1)} = 5.86$, $P < 0.05$, Original Fig. 5C, D).

New results: Genetic diversity of populations (H_j , *PLP* and B_r) varied between 0.11–0.22 (mean 0.17), 0.21–0.57 (mean 0.39) and 1.18–1.42 (mean 1.31) per population, respectively (New Table 1). European populations showed a decrease in H_j and B_r , compared to the Africa-N

source populations (H_j : $F_{1,45} = 15.2$, $P < 0.001$, B_r : $F_{1,45} = 14.8$, $P < 0.001$, see also New Fig. 4A). In contrast, *PLP* did not differ significantly between native and invasive populations ($F_{1,45} = 0.66$, $P > 0.05$, see also New Fig. 4B). Within Africa, the lowland populations (Africa-S) were more diverse than the highland populations in terms of B_r (Africa-N, ($F_{1,17} = 5.8$, $P < 0.05$)). In Europe, southern populations (Europe-S) were significantly less diverse than the Central European (Europe-N) ones except for *PLP* (H_j : $F_{1,30} = 5.3$, $P < 0.05$, B_r : $F_{1,30} = 4.6$, $P < 0.05$, *PLP*: $F_{1,30} = 2.7$, $P > 0.05$; New Fig. 4). The different diversity measures showed the same temporal development along the two European invasion routes. All of them increased with population age (H_j : $\chi^2_{(1)} = 9.0$, $P < 0.01$, B_r : $\chi^2_{(1)} = 11.6$, $P < 0.001$, *PLP*: $\chi^2_{(1)} = 11.9$, $P < 0.001$, New Fig. 5A, B), whereas spread rate was dropped from the minimum adequate model. A comparison of models containing either log-transformed population age or spread rate as explanatory variable further established the higher explanatory power of population age for all three measures (AIC differences: H_j : 1.0, B_r : 3.9, *PLP*: 4.6, note that population age and spread rate were correlated (Spearman $\rho = -0.63$, $P > 0.001$)). Still, spread rate as a single explanatory variable did have a significant negative effect on genetic diversity (H_j : $\chi^2_{(1)} = 8.0$, $P < 0.01$, B_r : $\chi^2_{(1)} = 8.6$, $P < 0.01$, *PLP*: $\chi^2_{(1)} = 7.4$, $P < 0.01$, New Fig. 5C, D).

Interpretation: The interpretation remains the same as in the original study.

Reference

- Lachmuth S, Durka W, Schurr FM (2010) The making of a rapid plant invader: genetic diversity and differentiation in the native and invaded range of *Senecio inaequidens*. *Molecular Ecology*, **19**, 3952–3967.