

PHYLOGEOGRAPHY

Vicariance and dispersal in the alpine perennial *Bupleurum stellatum* L. (Apiaceae)Peter Schönswetter^{1,3} & Andreas Tribsch^{2,3}¹ Department of Biogeography, Institute of Botany, University of Vienna, Rennweg 14, A-1030 Vienna, Austria. peter.schoenswetter@univie.ac.at (author for correspondence)² Department of Systematic and Evolutionary Botany, Institute of Botany, University of Vienna, Rennweg 14, A-1030 Vienna, Austria. andreas.tribsch@nhm.uio.no³ NCB – National Centre for Biosystematics, The Natural History Museums and Botanical Garden, University of Oslo, P.O. Box 1172 Blindern, N-0318 Oslo, Norway.

Using Amplified Fragment Length Polymorphism (AFLP), we explored the intraspecific phylogeography of the alpine vascular plant *Bupleurum stellatum* (Apiaceae), disjunctly distributed in the Alps and Corsica. Within the Alps, the species' distribution area is also not contiguous, spatially isolated groups of populations occurring in the Dolomites (Italy) and the Montafon (Austria). A main goal of our study was to explore the degree of differentiation of the isolated populations in Corsica, the Dolomites and the Montafon from the populations in the main distributional area and to test for hypotheses of vicariance or dispersal. We also sought a better general knowledge of glacial refugia of low alpine silicicolous plants. Phenetic as well as cladistic analyses of the AFLP multilocus phenotypes reveal a substantial north-south split through the contiguous distribution area of *B. stellatum* in the Alps. The resulting phylogeographic groups can be related to glacial refugia in peripheral areas of the Alps that were recognised in previous studies. The disjunct populations in Corsica, the Dolomites and the Montafon, however, are less strongly differentiated. For example, the Corsican population clustered with high bootstrap support with populations from the Eastern Alps, suggesting immigration to Corsica from that region. Our study shows that deep phylogeographic splits resulting from old vicariance events can be concealed by presently contiguous distribution areas. In contrast, disjunctions, if they are due to dispersal events, need not be accompanied by genetic divergence.

KEYWORDS: AFLP, Alps, *Bupleurum stellatum*, Corsica, dispersal, phylogeography, Pleistocene, refugia, vicariance.

INTRODUCTION

Studies exploring the phylogeography of disjunctly distributed alpine, arctic, or arctic-alpine plant species have shown that the resulting patterns are often complex and not easily explained by either vicariance or dispersal events. Whereas in some taxa disjunctions appear to have originated from dispersal (Hagen & al., 2001), others coincide with vicariance events (e.g., Kropf & al., 2003), or are evidenced by deep genetic splits through contiguous distribution areas (Schönswetter & al., 2004).

The identification of long-distance dispersal as a major factor in the generation of broad distribution areas (e.g., Cain & al., 2000; Abbott & Brochmann, 2003; Brochmann & al., 2003) has challenged the traditional assumption that large, e.g., circumarctic, distributions are ancient (Valentine, 1972). Even taxa that lack adaptations for dispersal over long distances were found to be highly mobile. On a regional scale, relatively recent (late-glacial to postglacial) long-distance dispersal has

been detected as much between mountain ranges (Schönswetter & al., 2002) as within them (Tribsch & al., 2002).

Vicariance in isolated Pleistocene refugia has been shown to have led to the evolution of genetically separable lineages (e.g., Hewitt, 1996, 2000; Tribsch & Schönswetter, 2003) in most of the taxa investigated up to now (reviewed, e.g., in Taberlet & al., 1998; Comes & Kadereit, 1998; Widmer & Lexer, 2001). When the climate ameliorated at the end of the Pleistocene, the refugial populations acted as sources for the recolonisation of appropriate habitats. Whereas some taxa managed to obtain a wide and contiguous distribution, others still show disjunctions due to incomplete remigration. In phylogeographic investigations of Alpine plants, both situations have been detected, even within the same study taxa (e.g., Tribsch & al., 2002).

Our target species, *Bupleurum stellatum* L. (Apiaceae; Fig. 1) is a perennial herb forming dense tussocks. It is diploid with $2n = 14$ (Cauwet, 1967; Favarger &



Fig. 1. *Bupleurum stellatum* in its natural habitat near Passo Croce Domini (northern Italy, population 19).

Küpfer, 1968). Favarger's (1954) count of $2n = 16$ was erroneous (Favarger & Küpfer, 1968). *Bupleurum stellatum* is an insect-pollinated outcrosser, the flowers are strongly proterandric, and the umbels shift from an exclusively male to an exclusively female stage (Hegi, 1925). Main habitats are open grassland communities covering dry, sunny, rocky outcrops or stabilised scree fields from 1700 up to 2650 (2800) m (Hegi, 1925; Pignatti, 1983). The species is confined to siliceous mountain ranges of the Alps mainly south of the main divide, and to Corsica. Within the Alps, *B. stellatum* is restricted to the Western Alps and to the southern part of

the middle Alps. It is most frequent in the middle part of its distribution area and becomes rare towards the southwest and the east (Pignatti, 1983). There are disjunct occurrences in the southwestern Dolomites (Cima d'Asta, Lagorai) that provide an island of alpine vegetation on silicates almost completely surrounded by limestone, and in the Montafon (Austria/Switzerland) where there is a group of populations that is isolated in spite of a lack of obvious barriers. The peculiar distribution pattern of *Bupleurum stellatum* L. (Apiaceae) offers the possibility for exploring patterns of vicariance and dispersal in a disjunctly distributed alpine plant (Fig. 2) and allows us to test the hypothesis that the phylogeographic pattern coincides with disjunctions.

Thus, a major goal of this study is to explore the history of the disjunct populations of *B. stellatum* in Corsica, the Dolomites and the Montafon. As in other phylogeographic studies based on molecular fingerprinting data, old vicariance is expected to result in significant genetic divergence whereas recent dispersal might lead to genetic depauperation due to founder effects but to little or no genetic divergence. Apart from this major goal, our study also contributes to a better understanding of glacial refugia of silicolous plants at the southern border of the Alps (Tribsch & Schönswetter, 2003).

MATERIALS AND METHODS

Sampling. — We sampled 23 populations of *B. stellatum* from the Alps (populations 2–24) and one population from Corsica (population 1; Fig. 2). The gap between populations 8 and 9 (Fig. 2) is a sampling artefact and does not reflect a break in the distribution. Fresh

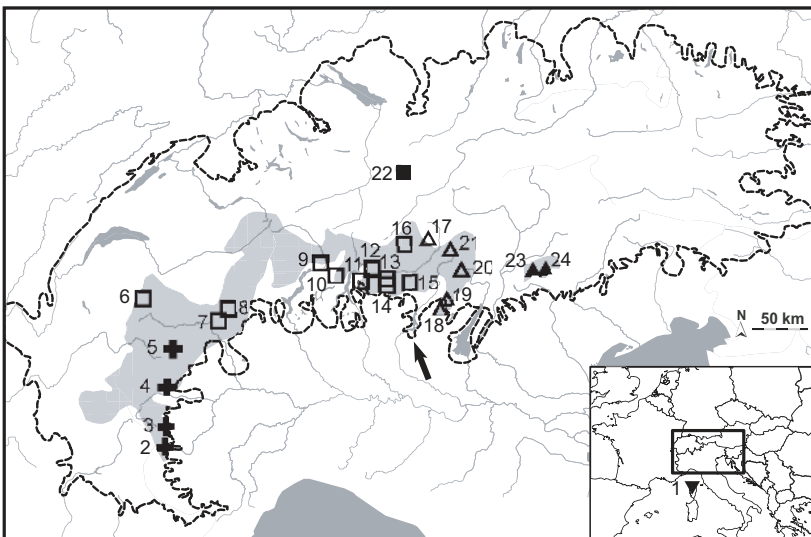


Fig. 2. Distribution (shaded in light grey) and sampled populations of *Bupleurum stellatum* in the European Alps and in Corsica along with the maximum extent of the Pleistocene ice shield during the last glacial period (broken line; taken from Jäckli, 1970; Van Husen, 1987; Voges, 1995). The arrow indicates the position of the glacier tongue in Val Camonica (see text). The symbols refer to population groups identified in the present study (+, W1; □, W2; △, E+Co excluding population 1 from Corsica) or to disjunct population groups (▼, population 1 from Corsica; ■, population 22 from Montafon; ▲, populations 23 and 24 from the Dolomites). Bottom right insert gives the location of population 1 from Corsica and indicates the position of the sampling area in Europe. Population numbers refer to Table 1.

Table 1. Numbering of populations, location, country (A = Austria; CH = Switzerland; F = France; I = Italy), co-ordinates; number of investigated individuals (N), number of AFLP fragments (Frag_{tot}) per population, percentage of fragments which exhibit intrapopulational polymorphism (%_{poly}), number of fragments that only occur in one population (Frag_{uni}), and frequency-down-weighted marker values (DW) of the 24 investigated populations of *Bupleurum stellatum* L. To even out the unequal sample sizes, the genetic diversity measures Frag_{tot}, %_{poly} and the divergence measures Frag_{uni} and DW were calculated with only four randomly chosen individuals.

	Location	Country	Co-ordinates (E/N)	N	Frag _{tot}	% _{poly}	Frag _{uni}	DW
1	Corsica, Monte d'Oro	F	8.97 / 42.13	4	133	30.08	7	14.87
2	Pian di Re	I	7.11 / 44.70	5	138	36.23	2	13.93
3	Punta Cialancia	I	7.12 / 44.87	5	148	47.30	1	12.57
4	Monte Palon	I	7.13 / 45.20	5	133	34.59	2	11.80
5	Val Savaranche	I	7.20 / 45.52	5	141	36.17	3	12.79
6	Le Brevent	F	6.85 / 45.93	5	152	41.45	4	16.65
7	Monte Nery	I	7.73 / 45.75	5	163	48.47	5	18.16
8	Vallone di Mos	I	7.85 / 45.85	5	149	40.27	5	16.12
9	Cima dell'Uomo	CH	8.95 / 46.22	4	153	41.83	2	13.75
10	Pizzo di Gino	I	9.13 / 46.12	5	152	41.45	1	11.03
11	Monte Legnone	I	9.42 / 46.08	5	141	36.17	0	8.85
12	Monte Spluga	I	9.55 / 46.18	5	149	37.58	1	11.16
13	Valle Vicime	I	9.72 / 46.10	5	146	41.78	1	10.29
14	Cima Cadelle	I	9.73 / 46.05	5	151	40.40	0	10.53
15	Bivacco Resnati	I	10.00 / 46.07	5	145	40.69	0	9.55
16	Bochetta delle Forbici	I	9.90 / 46.32	5	138	36.23	1	10.12
17	Monte Verva	I	10.22 / 46.42	4	152	36.84	0	10.16
18	Monte Colombine	I	10.36 / 45.85	4	148	37.16	1	10.04
19	Passo Croce Domini	I	10.43 / 45.93	5	144	37.50	1	10.15
20	Passo delle Toppette	I	10.60 / 46.17	5	146	37.67	0	9.93
21	Passo Gavia	I	10.47 / 46.33	5	147	31.29	3	12.43
22	Valisera	A	9.93 / 46.95	4	142	37.32	3	12.66
23	Monte Ziolera	I	11.45 / 46.17	5	139	35.25	3	12.27
24	Cima d'Asta	I	11.60 / 46.18	5	127	29.92	0	7.19

leaves were collected in the field and immediately stored in silica gel. Details of the sampling locations as well as the number of sampled individuals per population (four or five) are given in Table 1. Voucher specimens for all populations are deposited in the herbarium of the Institute of Botany of the University of Vienna (WU).

DNA isolation and AFLP fingerprinting. — Protocols for DNA isolation and for AFLP fingerprinting are described in Schönswetter & al. (2002, 2004). For the selective amplification, we used the fluorescence-labelled primer combinations *EcoRI* ACC (NED)-*MseI* CAT, *EcoRI* ACT (6-Fam)-*MseI* CTC, and *EcoRI* AGG (HEX)-*MseI* CAA. The selective amplification-products were separated on a 5% polyacrylamide gel with an internal size standard (GeneScan-500 [ROX], PE Applied Biosystems, Foster City, California, U.S.A.) on an automated sequencer (ABI 377, PE Applied Biosystems). Raw data were collected and aligned with the internal size standard using the ABI Prism GeneScan Analysis Software (PE Applied Biosystems). Subsequently, the GeneScan sample files were imported into Genographer (ver. 1.6.0, © Montana State University 1999; <http://hordeum.msu.montana.edu/genographer/>) for scoring of the fragments. The results of the scoring were exported as a presence/absence matrix and used for further analysis.

Data analysis. — As a measure of within-population diversity, the number of AFLP fragments (Frag_{tot}) and the percentage of polymorphic fragments (%_{poly}) were calculated for all populations. The number of unique fragments (Frag_{uni}) was calculated as a measure of divergence. In order to detect divergent populations with many rare markers we avoided applying a subjective threshold defining the notion of “rare” (e.g., markers present in < 10 % of the investigated individuals; Stehlik & al., 2002; or in less than a certain number of individuals; Tribsch & al., 2002). We calculated an additional measure of divergence, i.e., “frequency-down-weighted marker values” (DW) equivalent to range-down-weighted species values in historical biogeographical research (Crisp & al., 2001). For each population, the number of occurrences of each AFLP marker in that population was divided by the number of occurrences of that particular marker in the total dataset. Finally these values were summed up. The value of DW is expected to be high in long-term isolated populations where rare markers should accumulate due to mutations whereas newly established populations are expected to exhibit low values, thus helping in distinguishing old vicariance from recent dispersal. To even out the unequal sample sizes, the genetic diversity measures and DW were calculated with just four randomly chosen individuals. We per-

formed a maximum parsimony analysis with PAUP 4.0 b10 (Swofford, 1998). Heuristic searches were done using a starting tree obtained by neighbour-joining and swapped to completion using TBR branch swapping, and MULTREES on (keeping multiple, shortest trees). A strict consensus tree of the 160 equally most parsimonious trees was constructed. Robustness of clades was estimated using the bootstrap approach (Felsenstein, 1985) with 500 replicates with random sequence addition (10 replicates) saving no more than 500 trees per replicate. Although the application of parsimony methods for fingerprinting data is not undisputed, empirical evidence has shown that with increasing amounts of AFLP data, all commonly used methods of reconstructing relationships with fragment data converge on the same tree and these estimates are robust (Beardsley & al., 2003). To underline this, we also performed a neighbour-joining analysis with TREECON 1.3b (Van de Peer & De Wachter, 1997) based on Nei & Li's (1979) genetic distance. The robustness of the branches was estimated with 500 bootstrap replicates.

A principal coordinate analysis (PCoA) based on inter-individual Jaccard similarities ($C_J = a / [a + b + c]$, where a is the number of fragments shared between two individuals and b and c are the numbers of fragments present in only one individual) was calculated and plotted with SPSS 10.0.7 (Norusis, 1999). Analyses of molecular variance (AMOVAs) were computed with ARLEQUIN 1.1 (Schneider & al., 1997).

RESULTS

With the three primer combinations used, 287 unambiguously scorable AFLP fragments were generated, 46 (16.0%) of which were monomorphic. The length of the fragments varied from 52 to 502 bp. All individuals had different multilocus genotypes. The Frag_{Tot} varied between 127 in population 24 and 163 in population 7 (mean 144.9, $SD = 7.8$; Table 1), $\%_{\text{poly}}$ ranged from 29.9 in population 24 to 48.5 in population 7 (mean 38.1, $SD = 4.5$; Table 1), and Frag_{Uni} varied between zero in populations 11, 14, 15, 17, 20 and 24 and seven in population 1 (mean 1.92, $SD = 1.89$; Table 1). The DW ranged from 7.19 in population 24 to 18.16 in population 7

(mean 11.96, $SD = 2.62$; Table 1).

The maximum parsimony analysis (Fig. 3) revealed the following structure: the population from Corsica (pop. 1 = group Co) formed a highly supported group (bootstrap support 97). It clustered with populations 17 to 21, 23 and 24 from the Eastern Alps (group E), again with very high support (bootstrap support 97). This group is henceforth referred to as E+Co.

The neighbour-joining analysis (Fig. 4) revealed essentially the same structure as the parsimony analysis. It differs mainly in that population 1 from Corsica clusters with high support (bootstrap support 100) with populations 17 to 21 from the Eastern Alps, and populations 23 and 24 from the Dolomites form a moderately (bootstrap support 70) supported sister group to that branch. Furthermore, populations 2 to 5 (except for one individual of population 3) from the southwestern Alps form one unsupported branch instead of two in the parsimony analysis.

The clustering of population 1 from Corsica is also supported by the direct comparison of the distribution of AFLP markers: all markers of that population except for its seven private fragments (Table 1) are shared with populations of E. This is not the case for W, in spite of the higher number of populations in that group. From the 287 scored fragments, 81 markers were private to W, 19 to E+Co, and 187 were found in both population groups.

The PCoA (Fig. 5) largely confirmed the pattern detected by the maximum parsimony analysis. Additionally, the first factor (explaining 27.2% of the total variation) revealed the internal structure of W, i.e., the separation between a southwestern group W_1 (populations 2–5) and the remaining populations, W_2 (populations 6–16). The individuals of population 22 from Montafon fall into group W_2 . Along the second factor, E+Co (24.0%) is separated from W. Whereas the individuals from the Dolomites (populations 23, 24) group with the other accessions from E, the Corsican individuals (population 1) are somewhat separated. The third factor (13.6%) separates nearly all individuals of W_1 from the rest of the dataset. From the fourth factor onwards, single populations are separated, such as population 6 along factor four (3.1%).

Non-hierarchical AMOVAs (Table 2) assigned 38.6% of the overall genetic variation to variation among

Table 2. Analysis of molecular variance (AMOVA) of the 24 investigated populations of *Bupleurum stellatum* L.

Source of variation	d.f.	Sum of squares	Variance components	% Total variance	F_{ST}^*
Among populations 1–24	23	1402.96	9.55	38.58	0.39
Within populations	91	1383.90	15.21	61.42	
Among E and W	1	371.94	6.48	22.92	0.46
Among populations	22	1030.06	6.60	23.32	
Within populations	91	1383.90	15.21	53.76	

*All P-values were < 0.001

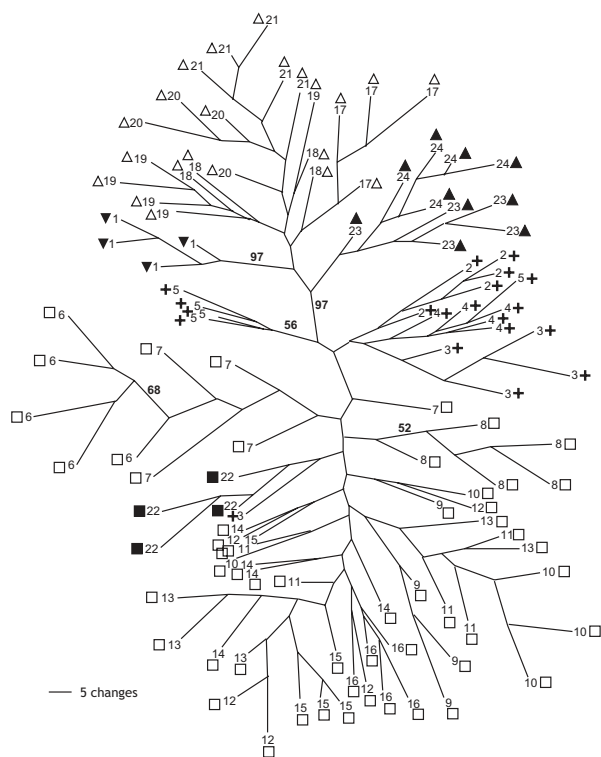


Fig. 3. Unrooted maximum parsimony network based on AFLP data of 115 individuals of *Bupleurum stellatum* from the Alps and Corsica. The bold numbers above the branches are bootstrap values above 50 (500 replicates). To enforce legibility, they are given only for branches with at least 4 individuals. The population numbers are given at the tips of the branches. Symbols as in Fig. 2.

the 24 populations. Hierarchical AMOVAs of the Alpine populations attributed 22.9% of the overall variation to variation among E and W, 23.3% to variation among the populations within the groups, and 53.8% to variation within populations.

DISCUSSION

Vicariance within the continuous distribution area of *B. stellatum* in the Alps. — The Alpine populations of *Bupleurum stellatum* fall into two clearly divergent groups that are both characterised by a high number of private fragments and high bootstrap support (Figs. 3–5). Group W comprises populations from the western part of the Alps eastwards to the Bernina mountain range (Italy, Switzerland) and the Alpi Orobie (Italy) plus population 22 from the Montafon. Group E+Co encompasses populations from the easterly adjacent mountain ranges along with population 1 from Corsica. There appears to be no break in the distribution area between groups W and E+Co. As shown by the strong

separation of individuals from east and west of the main phylogeographic split (groups W₂ and E in the PCoA; Fig. 5), a possible hybrid zone was not sampled. The split between W and E+Co explains approximately a quarter of the overall genetic variation (Table 2). This comparatively low value (see e.g., Schönswetter & al., 2002, and Tribsch & al., 2002 for comparison) relates to the high intrapopulation genetic variation accounting for > 60% of the overall variation (Table 2; see also the diversity indices in Table 1). Moreover, this supports the assumption that the species is strongly outbreeding (Hegi, 1925). In other studies on alpine plants, however, much lower values for variation among groups were detected (e.g., Holderegger & al., 2002; Kropf & al., 2003).

The differentiation between W and E+Co, that cannot be paralleled with any taxonomical intraspecific variation (summarized in Hegi, 1925), is most likely due to a vicariance event, i.e., the disruption of a formerly continuous distribution area and survival in disjunct glacial refugia. This split appears to be older than the last glaciation, as group W is internally structured as revealed by the neighbour-joining analysis (Fig. 4) and the PCoA (Fig. 5). It falls into two subgroups, W₁ south of the Valle d'Aosta and W₂ north and east of it, a phylogeographic pattern similar to those observed in *Androsace alpina* Lam. (Schönswetter & al., 2003) and, less clearly, in *Ranunculus glacialis* L. (Schönswetter & al., 2004). The subgroups of W and the Alpine populations of group E+Co overlap with presumed refugia along the southern margin of the Alps (see Fig. 2 in Schönswetter & al., 2002), areas that have been less affected by the glaciations than more interior parts (reviewed in Tribsch & Schönswetter, 2003a). W₁ overlaps with the hypothetical refugia in the eastern Cotic and the eastern Grajic Alps, W₂ with the southern Penninic Alps and the Alpi Bergamasche, E+Co covers the southwestern Dolomites and the northern Alpi Giudicarie. Important barriers for the populations in the refugia south of the ice sheet during the Last Glacial Maximum and probably also during earlier glaciations might have been the large glacier tongue protruding from Val Camonica (to the west of populations 18 and 19; Jäckli, 1970; indicated by an arrow in Fig. 1) and carbonate mountain ranges at the periphery of the Alps that offered no potential growing sites for the strongly acidophilic *B. stellatum*. At present, there are no obvious ecological factors that maintain the observed genetic differentiation as the area between populations 16 and 17 (Fig. 2) provides more or less continuous suitable habitats. In conclusion, due to the unambiguous separation of only two large population groups, and the congruence of the split between W₁ and W₂ with previous studies, the results from the phylogeographic analysis of *B. stellatum* do not allow a finer separation of refugia in the Alps compared to previous studies but

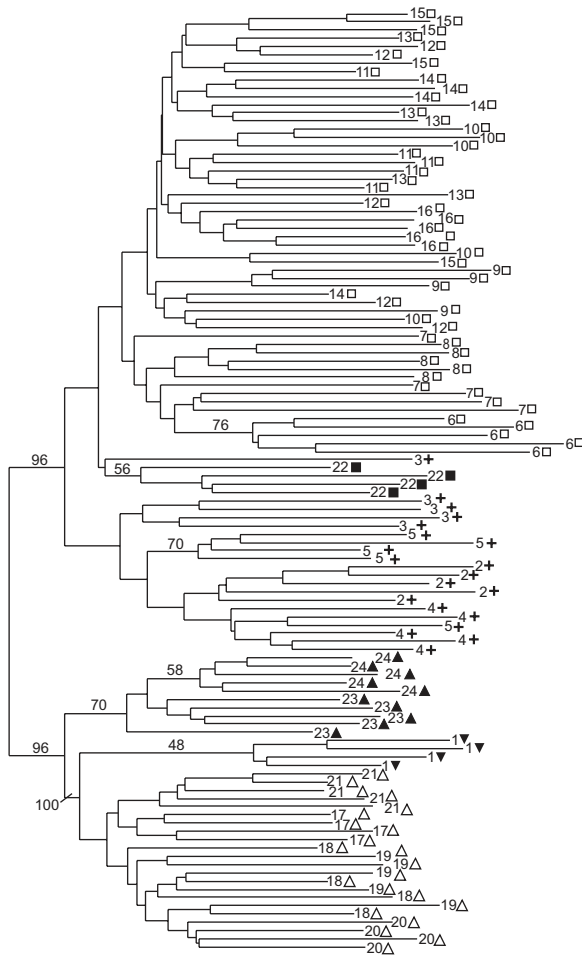


Fig. 4. Neighbour-joining tree based on AFLP data of 115 individuals of *Bupleurum stellatum* from the Alps and Corsica. The bold numbers above the branches are bootstrap values above 50 (500 replicates). As in Fig. 3, they are given only for the major branches. The population numbers are given at the tips of the branches. Symbols as in Fig. 2.

rather corroborate already known patterns.

The populations in the Montafon and the Dolomites are not clearly divergent. — Our results indicate a close relationship of the population in Montafon to group W and that of the populations in the Dolomites to E+Co (Figs. 3 to 5). Although the diversity and divergence measures presented in this paper should be treated with caution due to the low number of investigated individuals per population, the level of genetic differentiation and diversity of the Montafon and Dolomites populations are not above average (DW, %_{poly}; Table 1). The lack of strong divergence resulting from long-term isolation fits well to the very strong glaciation of the Montafon during the Last Glacial Maximum (LGM; van Husen, 1987), *a priori* excluding long-term survival of the low-alpine *B. stellatum* on nunataks in that region.

The southwestern Dolomites, in contrast, had already been identified as a glacial refugium in previous studies (Schönswetter & al., 2002, 2003b). Although glacial survival of populations 23 and 24 in that region could hypothetically have been possible, the two investigated populations from that area do not appear to be strongly divergent (Table 1) and their moderate bootstrap support in the neighbour-joining analysis (Fig. 4) but not in the maximum parsimony analysis (Fig. 3) could well be explained by their low genetic diversity. Thus, for the isolated groups of populations in the Montafon and probably also in the Dolomites, recent, late or postglacial dispersal is a possible scenario.

Dispersal from the Eastern Alps to Corsica.

— Population 1 from Corsica originated via dispersal from source populations in the Eastern Alps. It groups with Eastern Alpine populations with high bootstrap support (Figs. 3, 4) and shares all of its markers except for seven private fragments with the other populations of group E+Co. In contrast to the maximum parsimony analysis (Fig. 3) that provides no resolution in this respect, the neighbour-joining analysis (Fig. 4) suggests a highly supported sister-relationship of the Corsican population to populations 17 to 21, and not to the populations from the Dolomites. The differentiation of the Corsican and the Alpine populations can hardly be related to the “Messinian event”, the desiccation of the Mediterranean sea after the closure of the strait of Gibraltar in the late Miocene (c. 5.9 mya; e.g., Butler & al., 1999) for three reasons: (1) although it is impossible to date genetic fingerprinting data, we expect separation since the Tertiary to result in much stronger genetic differentiation; (2) migration of an alpine plant through former ocean-floor during a comparatively warm time period appears highly unlikely; (3) the Corsican populations relate to the Eastern Alpine populations instead of the geographically more close populations of the Western Alpine group W, suggesting long-distance dispersal rather than continuous migration. However, above-average level of divergence as expressed with DW (Table 1) and the presence of several private fragments, some of which are fixed (Table 1), indicate that the colonisation of Corsica from the Alps is not due to a Holocene dispersal event as argued, e.g., for the westernmost Alpine populations of *Saponaria pumila* Janchen (Tribsch & al., 2002) but rather dates back to the Pleistocene.

The alpine flora of Corsica is poor in otherwise exclusively Alpine taxa. Out of 2518 taxa native to Corsica, of which 21 are regarded as oreophilous Central and Southern European elements (Contandriopoulos, 1962), Gamsans (1991) lists only two species that are exclusively shared by Corsica and the Alps. One of them is our study taxon, *B. stellatum*, and the second is *Viola nummularifolia* All. (Violaceae) that, in the Alps, is

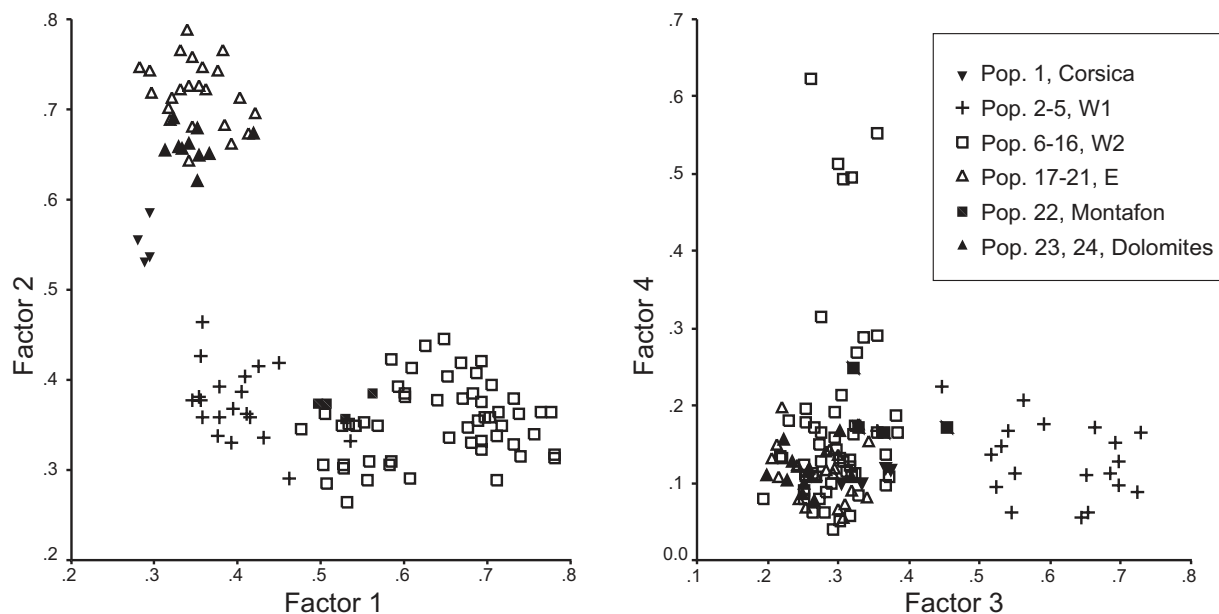


Fig. 5. Principal Coordinate Analysis (first four factors cumulatively explaining 67.9% of the total variation) based on AFLP data of 115 individuals of *Bupleurum stellatum* from the Alps and Corsica. Symbols as in Fig. 2.

restricted to the southwesternmost part (Alpes Maritimes) geographically closest to Corsica. Additionally, *Ranunculus kuepferi* (Ranunculaceae) occurs both in Corsica and in the Alps. Its diploid sexual cytodeme, subsp. *kuepferi*, is restricted to the Alpes Maritimes, whereas the tetraploid apomictic subsp. *orientalis* is more widespread from the Alpes Maritimes to Hohe Tauern (Huber, 1988) and occurs locally in Corsica (Huber, 1989). Since the polyploid apomict is most likely a derivative of subsp. *kuepferi*, dispersal has probably gone in parallel both in southerly and northerly direction. A further taxon that illustrates Corsica's floristic links with the Alps or Carpathians is *Alnus alnobetula* C. Koch (syn. *Alnus viridis* DC.; Betulaceae), with subspecies *suaveolens* (Req.) J. Lambinon & M. Kerguelen endemic to Corsica and the type subspecies distributed throughout the Alps and major parts of the Carpathians. A parallel case to *B. stellatum* was found in a phylogenetic study of the genus *Phyteuma* (G. Schneeweiss, P. Schönswetter, A. Tribsch, unpubl.) where sequences of nuclear and chloroplast markers as well as AFLP data suggest a highly supported sister relationship of the Corsican endemic *P. serratum* Viv. with the East Alpine/ Carpathian *P. confusum* Kern. Further studies covering alpine taxa shared by Corsica and the Eastern Alps region should clarify whether the unexpected biogeographic connection detected in our study taxon *B. stellatum* is an idiosyncrasy of the investigated plant species or indicates a more general biogeographic pattern.

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