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Reduced genetic diversity, increased isolation and multiple introductions of invasive giant hogweed in the western Swiss Alps

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Abstract

The giant hogweed (*Heracleum mantegazzianum*) has successfully invaded 19 European countries as well as parts of North America. It has become a problematic species due to its ability to displace native flora and to cause public health hazards. Applying population genetics to species invasion can help reconstruct invasion history and may promote more efficient management practice. We thus analysed levels of genetic variation and population genetic structure of *H. mantegazzianum* in an invaded area of the western Swiss Alps as well as in its native range (the Caucasus), using eight nuclear microsatellite loci together with plastid DNA markers and sequences. On both nuclear and plastid genomes, native populations exhibited significantly higher levels of genetic diversity compared to invasive populations, confirming an important founder event during the invasion process. Invasive populations were also significantly more differentiated than native populations. Bayesian clustering analysis identified five clusters in the native range that corresponded to geographically and ecologically separated groups. In the invaded range, 10 clusters occurred. Unlike native populations, invasive clusters were characterized by a mosaic pattern in the landscape, possibly caused by anthropogenic dispersal of the species via roads and direct collection for ornamental purposes. Lastly, our analyses revealed four main divergent groups in the western Swiss Alps, likely as a consequence of multiple independent establishments of *H. mantegazzianum*.

Keywords: Bayesian clustering, *Heracleum*, invasive species, microsatellites, plastid DNA, population genetics — empirical

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Introduction

Invasions are natural phenomena that have contributed to shaping the diversity of life on Earth (Vermeij 1991). However, during the past 500 years, humans have strongly contributed to these biological invasions by moving species from their original locations all over the world, thus breaching biogeographical barriers and homogenizing global biotas (Olden *et al*. 2004). Mainly due to their strong competitive abilities and their rapid spread, invasive alien species (IAS; *sensu* Richardson *et al*. 2000; Pyšek *et al*. 2004) are now considered a significant component of human-induced global environmental change (Elton 1958; Mack *et al*. 2000), and are one of the most important threats to biodiversity worldwide, second in impact only to the destruction and fragmentation of habitats (Wilcove *et al*. 1998; Sala *et al*. 2000). IAS cause ecological damages (e.g. Hawkes *et al*. 2005), health hazards (Soulé 1992) and have negatively impacted global economies, particularly in forestry, agriculture, fisheries as well as through management costs (Pimentel *et al*. 2000, 2005; Perrings *et al*. 2002).

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Much of the research done on IAS has focused on the species' ecology or on the community characteristics to identify common traits able to explain their invasion success (Lambrinos 2004; Richardson & Pyšek 2006). As yet, no universal factor explains species' invasiveness (Rejmánek & Richardson 1996; Kolar & Lodge 2001). Population and evolutionary genetics (Sakai *et al*. 2001; Lee 2002) could bring complementary information and help promote novel management practices (Hufbauer 2004). Upon introduction, invasive populations often undergo a reduction of genetic variation within populations and display increased differentiation among populations (Thulin *et al*. 2006; Dlugosch & Parker 2008) due to founder events and genetic drift (Husband & Barrett 1991; Amsellem *et al*. 2000; Parisod *et al*. 2005). However, after a lag period, rapid population expansion may help maintain substantial genetic variation within populations (Zenger *et al*. 2003; Bousset *et al*. 2004). Some IAS have been introduced several times, and such phenomena have been reported to increase genetic variation within invasive populations, thus leading to an increased potential for evolutionary change (Kolbe *et al*. 2004; Facon *et al*. 2006, 2008; Marrs *et al*. 2008; Rosenthal *et al*. 2008). Hybridization between individuals from two different subspecies or species in the invaded range may also act as a stimulus for the evolution of invasiveness by producing novel genotypes, which by chance may be better adapted to the local conditions (Ellstrand & Schierenbeck 2000; Abbott *et al*. 2003). These factors may act either separately or together to shape the fate of an invading species (Maron *et al*. 2004; Bossdorf *et al*. 2005). Besides genetic diversity, the organization of genetic variation among populations is likely to change during invasions. To document invasion history and assist management strategies, it is thus of interest to investigate the population genetic structure of IAS in both native and invasive ranges.

Heracleum mantegazzianum Sommier & Levier (Apiaceae) is one of the most important IAS in Europe, and it was addressed in the European project 'Giant Alien' (2002–2005), supported by the European Commission (Nielsen *et al*. 2005; http://www.giant-alien.dk). It has become a problematic species as it reduces native plant diversity (Pyšek & Pyšek 1995), increases erosion in river banks (which may, for instance, affect salmonid spawning; Caffrey 1999) and may become a health hazard as its sap contains furanocoumarins that can cause serious burns upon contact with human skin and subsequently exposed to UV rays (Drever & Hunter 1970; Tiley *et al*. 1996). In 2003, Walker *et al*. used four nuclear microsatellite loci and one plastid locus to investigate the population genetic structure of the species in northeast England. They found high genetic diversity, and attributed it to a large initial founding population or multiple introductions. These authors also suggested that the population structure seen in three river catchments was a result of genetic drift occurring during the initial founding, but they had no means of comparison with populations from the native range. In 2007, Jahodová *et al*. (2007b) used amplified fragment length polymorphism markers to characterize the genetic similarities of three invasive *Heracleum* species found at the continental scale in Europe and compared that to samples from their native ranges. They also found high levels of genetic diversity in the invaded range, and suggested that those populations were not affected by bottlenecks and possibly resulted from multiple introductions.

In the present study, we used microsatellite loci and plastid DNA markers coupled with Bayesian clustering algorithms to investigate and characterize the genetic diversity and population genetic structure of *H. mantegazzianum* populations at a regional scale in parts of their invasive (western Swiss Alps) and native (Caucasus) ranges. We characterized hundreds of individuals in many locations from each range to attain greater within population detail to explicitly address three main questions. (i) Do invasive populations display lower levels of genetic variation than native populations, characteristic of a founder event? (ii) How does population genetic structure differ in invasive and native ranges? (iii) Is there evidence for multiple introductions in the western Swiss Alps?

Materials and methods

Study species

Historical accounts suggest that giant hogweed was discovered in the early 1890s in the Kliutsch Valley, Abkhazia (eastern part of the Republic of Georgia), where the plant occurs in clearings, meadows and forest margins of the upper forest belts up to 2000 m (Mandenova 1950). Seeds were brought to the Botanical Garden of the Horticultural Society for Plant Acclimation in Plainpalais (Geneva, Switzerland; Jeanmonod 1999) in 1892 and the plant was described as a new species named *Heracleum mantegazzianum* (Sommier & Levier 1895). From there, the plant was disseminated in botanical gardens throughout Europe (Perrier 2001) as well as alpine botanical gardens and private gardens in western Switzerland (E. Mottier, personal communication; Dessimoz 2006). However, contradictions among sources and dates of introduction of giant hogweed are found in the literature. These discrepancies are further enhanced by the fact that the genus *Heracleum* has not been fully revised. Many cases of later re-identification of specimens collected in the 19th and in the first half of 20th century suggest that earlier names were used indiscriminately (Stewart 1979). The first record of introduction of large *Heracleum* species to Europe comes from England, where in 1817 a plant under a name of *H. giganteum* appeared on the seed list of Kew Botanic Garden. It is

plausible to suggest that the introduced plant was *H. mantegazzianum* (Sommier & Levier 1895), since the first naturalized population of this species was documented in 1828 in Cambridgeshire (Perring *et al*. 1964). Introduction of *H. mantegazzianum* prior to its former description is also documented in the Czech Republic where the species is said to have been introduced in 1862 and the first herbarium voucher comes from 1877 (Holub 1997; Müllerová *et al*. 2005). These divergent historical records of introduction suggest that the species has been introduced multiple times at the continental scale, possibly from disparate source populations (Pyšek 1991; Jahodová *et al*. 2007b).

Heracleum mantegazzianum is characterized by many attributes common to successful invaders: it is a tall, herbaceous, short-lived perennial which is often dominant where established (Nielsen *et al*. 2005). Its vernacular name, giant hogweed, illustrates the dimensions of the plant: its stout stem can reach 5.5 m, its alternate leaves can measure 2.5 m in length and its inflorescences (compound umbels) can reach a diameter of 50 cm (Tiley *et al*. 1996), thus comprising thousands of flowers. Up to 10 inflorescences can be present on one stem. The typical life cycle lasts 3 to 5 years, with reproduction occurring in the last year (Tiley *et al*. 1996; Caffrey 1999; Pergl *et al*. 2006). Flowers are hermaphrodite, protandrous, insect-pollinated and self-compatible. The plant reproduces exclusively by seeds and a single individual can produce up to 50 000 seeds with an average of 10 000–20 000 (Pyšek *et al*. 1995; Perglová *et al*. 2006). The bulk of the seed set is dispersed around the plant's stalk by wind to a distance of about 10 m (Neiland *et al*. 1987), although some seeds may be found up to 50 m from mother plants (Caffrey 1994). Natural long-distance dispersal mainly occurs along watercourses, as seeds can float for up to 3 days (Clegg & Grace 1974). Long-distance dispersal can also occur via anthropogenic means mediated by vehicles and trains or by collection of seed heads for decorative purposes (Lündstrom 1984; Nielsen *et al*. 2005). Beekeepers are also said to have contributed to its spread as this plant was thought to produce high quantities of nectar (Reinhardt *et al*. 2003). The species has successfully established invasive populations in 19 European countries (Jahodová *et al*. 2007a) as well as Canada and the USA (Morton 1978; Dawe & White 1979) and has significantly increased its geographical range in recent years (Pyšek 1991, 1994; Tiley *et al*. 1996; Caffrey 1999; Jeanmonod 2005; Nielsen *et al*. 2008; Pyšek *et al*. 2008). In its invasive range, *H. mantegazzianum* occurs in riparian habitats such as river banks and moist meadows as well as along roadsides and in urban wastelands (Nielsen *et al*. 2005).

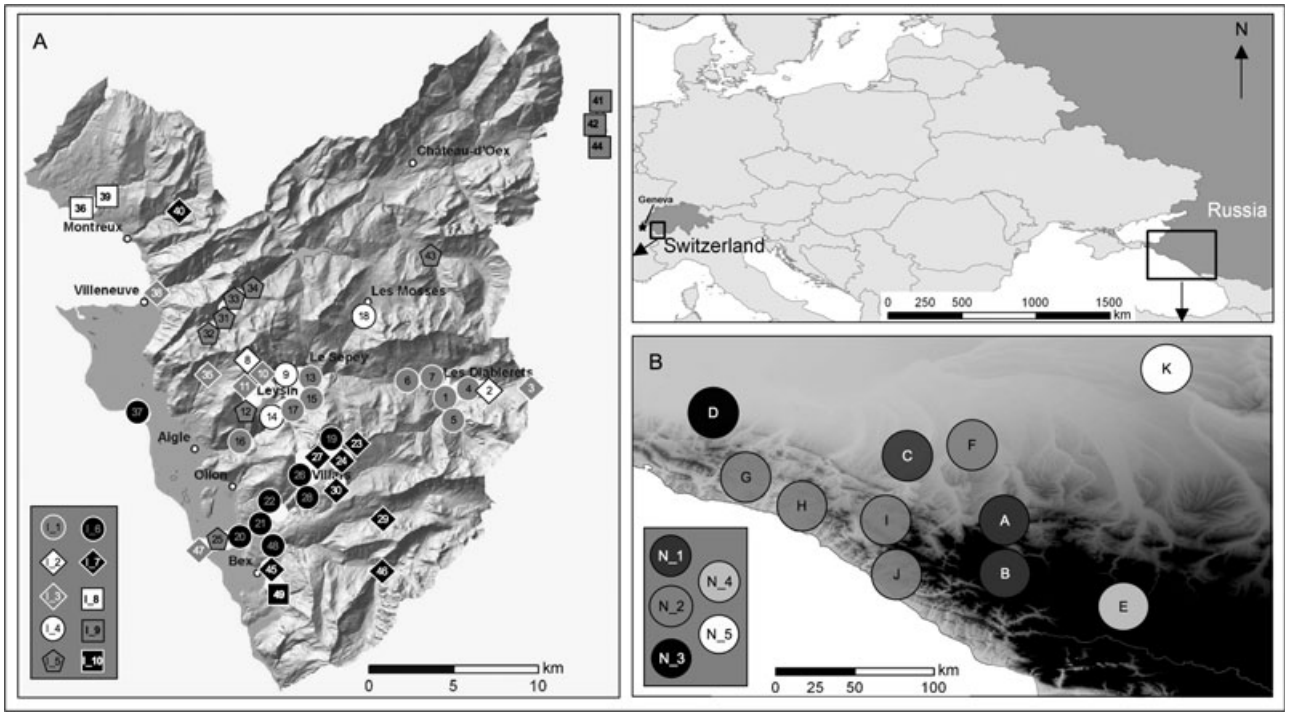

Fig. 1 Location of *Heracleum mantegazzianum* populations sampled: A. invasive populations from Switzerland; B. native populations from the Caucasus. Based on nuclear data, invasive populations were grouped into ten distinct clusters (I_1-10) with a Bayesian inference (Guillot *et al.* 2005; Corander *et al.* 2008), while native populations were grouped into five clusters (N_1-5). These different clusters are represented by different symbols. Invasive clusters I_8, I_9 and I_10 possibly arose from separate sources and are thus represented by distnict symbols.

Study area

The western Swiss Alps (Fig. 1) are a low-lying mountain range made of calcareous bedrock ranging in altitude from 372 to 3210 m above sea level (a.s.l.). The climate is cool and wet, with abundant rainfall (up to 2400 mm per year) that increases with elevation. The average yearly temperatures range from –3 °C to 10 °C. Climatic conditions (WORLDCLIM database, Hijman *et al*. 2005) here are very similar to those of the native range of *H. mantegazzianum* in the Caucasus. This area has recently been invaded by *H. mantegazzianum*, and its expansion is now leading to hazards for rural economy, tourism, public health and native biodiversity. In the western Swiss Alps, *H. mantegazzianum* populations occur near villages, roadsides, railway embankments, farmlands, meadows and riparian habitats at considerable distances from human settlements (Jeanmonod 1999) from an altitude of 380–1980 m a.s.l.

Sampling and DNA extraction

Leaf material from 724 individuals belonging to 49 *H. mantegazzianum* populations from the western Swiss Alps were collected in summer 2005 and 2006 (Fig. 1; Table 1). Populations were defined as patches isolated in the landscape by at least 100 m, as this is twice the natural maximal seed dispersal distance (Caffrey 1994). A horizontal transect was run through each sampled population, and a section of 10 cm^2 of leaf material was collected from individual plants at a minimum of 10 m apart. Leaves were desiccated in silica gel until completely dried. We characterized between six and 16 plants per population.

Additionally, leaf material from 129 individuals originating in 11 Caucasian populations (Russia) representing about one-third of the distribution of *H. mantegazzianum* in its native range (Fig. 1; Table 2; Pyšek *et al*. 2007) were also sampled. Between six and 14 individuals per population were characterized. Although historical accounts suggest that the origin of invasive *H. mantegazzianum* populations is the Kliutsch Valley, Abkhazia (currently Republic of Georgia), samples from this region could not be collected in the present study.

Twenty milligrams of leaf material from each individual was ground in 2-mL Eppendorf tubes using a Tissuelyser (QIAGEN) with two tungsten carbide beads in each tube. DNA was extracted using the DNeasy Plant mini kit (QIAGEN) according to the manufacturer's protocol.

Molecular markers and plastid DNA sequencing

Each individual was characterized by means of eight nuclear microsatellites (SSR): *A43, C52* (Walker *et al*. 2003), *HMNSSR-131, HMNSSR-132 A, HMNSSR-132B, HMNSSR-140, HMNSSR-206* and *HMNSSR-211* (Henry *et al*. 2008). Polymerase chain reaction (PCR) was performed in a total volume of 25 μL containing 1× reaction buffer (Colorless GoTaq reaction buffer, Promega; 1.5 mM $MgCl_2$, pH 8.5), 0.2 mM of each dNTP, 0.4 μM of forward and reverse primers, template DNA (about 20–100 ng) and 1 U GoTaq DNA polymerase. Each forward primer was labelled with one fluorescent dye (HEX, NED or 6-FAM). Cycling was performed in a T3 Thermocycler (Biometra). Cycling parameters were used as described by Walker *et al*. (2003) and Henry *et al*. (2008). PCR products were loaded on an ABI PRISM 3100 with GeneScan 350 size standard, and alleles were sized using GeneMapper (version 3.7; Applied Biosystems).

To investigate the population genetic structure for a maternally inherited genome, six plastid DNA (cpDNA) loci were screened on all samples: *ccmp5*, *ccmp10* (Weising & Gardner 1999), *trn-TL-indel1*, *trn-TL-indel2*, *trn-TL-indel3* and *trn-TL-indel4* (Henry *et al*. 2008). Genotyping procedures were identical to those previously described for nuclear loci. These markers were combined to obtain a multilocus profile (or chlorotype) for each individual. This method enables rapid and cheap screening of chlorotypes in different populations (Parisod & Besnard 2007). In addition, for every different multilocus genotype found in each native population, the *trn*T-*trn*L intergenic spacer was PCR-amplified following Taberlet *et al*. (1991), then sequenced to confirm chlorotype identification and detect possible additional polymorphism. Thirty-three native individuals were thus analysed. In the invasive range, the *trn*T-L spacer was also sequenced on 16 individuals (e.g. eight individuals for both multilocus profiles detected; see below). Sequencing was performed using the Big Dye 3.1 Terminator cycle sequencing kit (Applied Biosystems) according to manufacturer's instructions; sequences were run on an ABI PRISM 3100 genetic analyser (Applied Biosystems). Sequences were deposited in the EMBL databank under Accession numbers AM998493 to AM998530 and FM160625 to FM160633.

Nuclear data analyses

Deviation from Hardy–Weinberg equilibrium and genotypic disequilibrium. We calculated, separately for invasive and native populations, deviation from Hardy–Weinberg equilibrium within each population and overall as well as genotypic disequilibrium among all pairwise combinations of nuclear loci using FSTAT 2.9.4 (Goudet 2005; unless otherwise stated, all following calculations were conducted using FSTAT). All tests implemented in FSTAT are randomization-based, where randomizing the appropriate unit generates the distribution of each statistic under the null hypothesis: the observed statistic is then compared to this distribution to provide an unbiased estimator of the *P* value (Goudet 1995). Sequential Bonferroni corrections

Table 1 Information concerning invasive populations for: (A) all populations; (B) clusters of populations. ID, name of sampled populations; Alt., altitude in metres above sea level, *N*, number of individual sampled; H_O, mean observed heterozygosity overall loci; H_S, mean gene diversity overall loci; R_S, mean allelic richness; F_{ST}, mean pairwise genetic differentiation between populations; F_{IS}, inbreeding coefficient; HWE, deviation from Hardy–Weinberg equilibrium as calculated using 10 000 permutations in FSTAT 2.94 (Goudet 2005): *$P < 0.05$; NS, $P > 0.05$; Cluster, group to which sample has been assigned using Geneland (Guillot *et al*. 2005); chloro, chlorotype present in sample (A)

ID	Alt.	Latitude	Longitude	*N*	H_O	H_S	R_S	F_{ST}	F_{IS}	HWE	Cluster	Chloro
1	1169	46°35′55.3′N	7°13′11.3′E	16	0.234	0.306	2.007	0.413	0.235	NS	I_1	HM1
4	1263	46°33′57.3′N	7°16′31.3′E	16	0.469	0.459	2.429	0.18	–0.02	NS	I_1	HM1,2
5	1217	46°25′14.4′N	7°11′08.7′E	16	0.391	0.279	1.684	0.359	–0.4	NS	I_1	HM1
6	1129	46°30′08.4′N	7°04′93.7′E	16	0.242	0.292	1.726	0.305	0.173	NS	I_1	HM1
7	1197	46°31′90.6′N	7°07′16.2′E	16	0.32	0.412	2.173	0.282	0.222	NS	I_1	HM1
13	948	46°28′81.7′N	7°02′22.5′E	16	0.289	0.354	1.927	0.372	0.183	NS	I_1	HM1,2
15	803	46°34′51.2′N	7°04′31.1′E	16	0.484	0.413	2.097	0.293	–0.17	NS	I_1	HM1
16	619	46°35′04.7′N	7°02′02.9′E	10	0.375	0.312	1.748	0.323	–0.2	NS	I_1	HM2
17	807	46°44′97.1′N	6°88′30.6′E	16	0.438	0.416	2.182	0.237	–0.05	NS	I_1	HM1,2
2	1343	46°35′13.1′N	7°17′91.3′E	16	0.297	0.451	2.303	0.321	0.341	*	I_2	HM1
8	1967	46°35′16.9′N	7°03′67.9′E	13	0.258	0.526	2.957	0.357	0.51	NS	I_2	HM1
3	1424	46°26′86.4′N	7°00′22.4′E	16	0.477	0.423	2.339	0.211	–0.13	NS	I_3	HM1
10	1316	46°35′98.0′N	7°22′66.6′E	15	0.375	0.305	1.859	0.297	–0.23	NS	I_3	HM1
11	1406	46°33′75.9′N	7°00′46.9′E	15	0.3	0.255	1.837	0.294	–0.18	NS	I_3	HM1
35	1196	46°39′21.5′N	7°09′64.9′E	16	0.217	0.232	1.815	0.34	0.064	NS	I_3	HM2
38	437	46°36′57.6′N	7°00′60.1′E	16	0.217	0.248	2.011	0.306	0.125	NS	I_3	HM1,2
47	404	46°25′30.5′N	7°02′39.9′E	16	0.334	0.286	1.982	0.294	–0.17	NS	I_3	HM2
9	1040	46°34′99.0′N	7°16′94.9′E	16	0.359	0.357	2.187	0.287	–0.01	NS	I_4	HM1,2
14	856	46°33′97.7′N	7°03′52.7′E	16	0.258	0.279	1.847	0.362	0.074	NS	I_4	HM1,2
18	1414	46°34′85.6′N	7°04′49.7′E	16	0.242	0.247	1.728	0.341	0.02	NS	I_4	HM1
12	1232	46°35′83.6′N	6°97′51.7′E	16	0.125	0.175	1.48	0.396	0.285	NS	I_5	HM1
25	405	46°34′85.5′N	7°15′86.7′E	16	0.328	0.344	1.969	0.273	0.045	NS	I_5	HM2
31	1440	46°39′39.2′N	6°99′08.2′E	16	0.383	0.401	2.255	0.245	0.043	NS	I_5	HM2
32	1489	46°38′13.9′N	6°97′70.9′E	16	0.292	0.401	2.183	0.239	0.273	NS	I_5	HM2
33	1459	46°39′48.6′N	6°99′10.8′E	16	0.35	0.348	2.016	0.285	–0.01	NS	I_5	HM2
34	1426	46°39′98.9′N	6°99′69.2′E	16	0.339	0.358	2.14	0.266	0.054	NS	I_5	HM2
43	1158	46°42′29.4′N	7°14′67.2′E	6	0.35	0.213	1.5	0.375	–0.65	NS	I_5	HM2
19	1798	46°31′14.7′N	7°07′69.4′E	16	0.29	0.351	2.305	0.248	0.173	NS	I_6	HM1
20	444	46°26′80.6′N	6°99′08.5′E	16	0.328	0.392	2.413	0.287	0.162	NS	I_6	HM1,2
21	478	46°26′39.2′N	6°97′12.8′E	16	0.344	0.457	2.472	0.224	0.248	NS	I_6	HM1,2
22	1004	46°28′82.1′N	7°02′26.6′E	16	0.32	0.336	2.227	0.234	0.047	NS	I_6	HM1
26	1265	46°31′09.3′N	7°05′95.1′E	16	0.422	0.416	2.293	0.251	–0.02	NS	I_6	HM1
28	1202	46°35′73.9′N	7°04′73.4′E	16	0.273	0.405	2.373	0.212	0.324	*	I_6	HM1
37	387	46°35′59.4′N	7°15′43.9′E	16	0.433	0.466	2.625	0.253	0.07	NS	I_6	HM2
48	515	46°28′01.1′N	7°11′02.6′E	16	0.4	0.397	1.95	0.342	–0.01	NS	I_6	HM1
23	1595	46°30′35.6′N	7°05′54.2′E	16	0.313	0.329	1.995	0.261	0.051	NS	I_7	HM1
24	1654	46°31′27.5′N	7°07′98.9′E	16	0.336	0.319	2.004	0.299	–0.05	NS	I_7	HM1
27	1142	46°40′21.8′N	6°93′53.7′E	16	0.352	0.334	2.158	0.273	–0.05	NS	I_7	HM1
29	1262	46°24′44.5′N	7°02′77.6′E	12	0.273	0.511	2.958	0.36	0.465	NS	I_7	HM1
30	1389	46°29′87.7′N	7°07′50.1′E	15	0.273	0.39	2.474	0.298	0.299	NS	I_7	HM1
40	984	46°44′74.3′N	6°95′21.6′E	16	0.242	0.275	1.78	0.295	0.12	NS	I_7	HM1
45	453	46°26′38.3′N	7°02′66.5′E	16	0.411	0.497	2.487	0.246	0.174	NS	I_7	HM1
46	1255	46°34′52.2′N	7°00′98.5′E	16	0.317	0.399	2.31	0.285	0.205	NS	I_7	HM1
36	393	46°26′71.3′N	6°98′14.9′E	16	0.242	0.311	2.114	0.343	0.223	NS	I_8	HM1
39	417	46°44′77.6′N	6°88′00.3′E	16	0.242	0.186	1.599	0.493	–0.3	NS	I_8	HM1
41	1218	46°50′65.5′N	7°28′43.6′E	16	0.45	0.547	2.852	0.303	0.177	NS	I_9	HM1
42	1278	46°50′32.8′N	7°28′50.1′E	10	0.575	0.503	2.565	0.326	–0.14	NS	I_9	HM1
44	1250	46°50′55.9′N	7°28′34.3′E	8	0.304	0.473	2.306	0.367	0.358	NS	I_9	HM1
49	472	46°33′61.5′N	6°92′44.2′E	16	0.4	0.448	2.286	0.346	0.108	NS	I_10	HM2

Table 1 *Continued*

(B)

Cluster	ID	*N*	H_O	H_S	R_S	F_{ST}	F_{IS}	Chloro
I_1	1,4,5,6,7,13,15,16,17	138	0.361	0.362	1.997	0.238	–0.004	HM1,2
I_2	2,8	29	0.278	0.489	2.63	0.277	0.4255	HM1
I_3	3,10,11,35,38,47	94	0.321	0.292	1.97	0.232	–0.085	HM1,2
I_4	9,14,18	48	0.286	0.294	1.92	0.243	0.029	HM1,2
I_5	12,25,31,32,33,34,43	102	0.309	0.321	1.93	0.246	0.007	HM1,2
I_6	19,20,21,22,26,28,37,48	128	0.351	0.403	2.33	0.174	0.125	HM1,2
I_7	23,24,27,29,30,40,45,46	123	0.315	0.382	2.27	0.244	0.1515	HM1
I_8	36,39	32	0.242	0.2485	1.86	0.35	–0.037	HM1
I_9	41,42,44	34	0.443	0.508	2.57	0.314	0.13	HM1,2
I_10	49	16	0.4	0.448	2.29	0.339	0.108	HM1

Table 2 Information concerning native populations for: (A) all populations; (B) clusters of populations. ID, name of sampled populations, Alt., altitude in metres above sea level, *N*, number of individual sampled; H_O, mean observed heterozygosity overall loci; H_S, mean gene diversity overall loci; R_S, mean allelic richness; F_{ST}, mean pairwise genetic differentiation between populations; F_{IS}, inbreeding coefficient; HWE, deviation from Hardy–Weinberg equilibrium as calculated using 10 000 permutations in FSTAT 2.94 (Goudet 2005): *$P < 0.05$; NS, $P > 0.05$; Cluster, group to which sample has been assigned using Geneland (Guillot *et al.* 2005); chloro, chlorotype present in sample

(A)

ID	Alt.	Latitude	Longitude	*N*	H_O	H_S	R_S	F_{ST}	F_{IS}	HWE	Cluster	Chloro
A	1363	44°00′36.5′N	40°02′44.6′E	7	0.588	0.623	3.832	0.139	0.057	NS	N_1	HM1,2,3
B	1260	44°08′60.1′N	40°04′00.0′E	6	0.396	0.521	3.898	0.139	0.24	NS	N_1	HM2
C	148	44°28′04.1′N	39°26′17.7′E	12	0.656	0.629	4.096	0.11	–0.04	NS	N_1	HM2
F	256	44°33′04.4′N	40°00′09.7′E	12	0.352	0.32	2.348	0.202	–0.1	NS	N_2	HM6
G	0	44°21′34.6′N	38°31′24.4′E	10	0.534	0.487	3.346	0.111	–0.1	NS	N_2	HM2,7,10
H	30	44°17′14.9′N	38°54′03.5′E	14	0.455	0.444	3.123	0.121	–0.03	NS	N_2	HM2,4,8,11
I	16	43°57′57.7′N	39°16′41.7′E	12	0.438	0.432	3.147	0.139	–0.01	NS	N_2	HM2,4,8
J	269	44°04′33.9′N	39°20′47.0′E	10	0.471	0.541	3.776	0.092	0.13	NS	N_2	HM2,8
D	20	44°24′48.8′N	38°30′17.4′E	12	0.58	0.612	3.629	0.123	0.052	NS	N_3	HM1,1a,2,7
E	1800	43°39′22.0′N	41°25′07.4′E	8	0.455	0.51	3.135	0.24	0.109	NS	N_4	HM1,1b,5
K	800	44°46′40.1′N	42°00′54.8′E	14	0.663	0.621	3.209	0.186	–0.07	NS	N_5	HM9

(B)

Cluster	ID	*N*	H_O	H_S	R_S	F_{ST}	F_{IS}	Chloro
N_1	A,B,C	25	0.547	0.591	3.942	0.114	0.0751	HM1,2,3
N_2	F,G,H,I,J	58	0.45	0.4448	3.148	0.142	0.0516	HM2,4,6,7,8,10,11
N_3	D	12	0.58	0.612	3.629	0.126	0.109	HM1,1a,2,7
N_4	E	8	0.455	0.51	3.135	0.157	0.102	HM1,1b,5
N_5	F	14	0.663	0.621	3.209	0.179	–0.0691	HM9

were applied to adjust the *P* value for multiple comparisons according to Rice (1989).

Comparison of genetic diversity and composition between invasive and native ranges. To estimate genetic diversity at the population level in native and invasive ranges, observed and expected heterozygosities (H_O and H_S; Nei 1987), and allelic richness (R_S, a metric that uses a rarefaction index to take into account differences in sample size; El Mousadik & Petit 1996) were calculated for all populations independently. The inbreeding coefficient (F_{IS}) was also calculated for invasive and native population separately. Tests for significant differences between native and invasive populations were ascertained using comparisons among groups

of samples as implemented in FSTAT with 10 000 permutations of individuals among groups tested.

Comparison of population genetic structure between invasive and native ranges. Analyses of population genetic structure traditionally consider *a priori* population delimitations to calculate metrics of genetic differentiation (Wright 1921). We calculated pairwise F_{ST} values (Weir & Cockerham 1984) for each sampled population in the invaded and native ranges separately. Pairwise F_{ST} were then averaged for populations in each range. Tests for the significant differences of the F_{ST} values between native and invasive populations were ascertained using comparisons among groups of samples as implemented in FSTAT with 10 000 permutations of individuals among groups tested. Isolation by distance (IBD) was tested by regressing genetic distances (F_{ST}) against geographical distances between all pairwise combinations of populations in the invasive and native ranges separately. Significance was tested by a Mantel test with 10 000 permutations implemented in IBDWS 3.15 (Jensen *et al*. 2005).

A more objective and *a posteriori* treatment of population genetic structure can be achieved with the use of Bayesian algorithms to cluster individual samples into populations at Hardy–Weinberg equilibrium with linkage equilibrium between loci (HWLE). The Bayesian clustering algorithm implemented in the R package Geneland 3.1.4 (Guillot *et al*. 2005) was used to estimate the most likely number of clusters of populations at HWLE and their geographical limits in invasive and native populations separately. Ten independent runs using the nonspatial model and uncorrelated allele frequencies between samples with 1 million iterations of the Markov chain Monte Carlo procedure were used (saving every thousandth iterations). Independently, we used a different algorithm, specifically the cluster groups of individuals module implemented in BAPS 5.2 (Corander *et al*. 2008) to support our findings using the above approach. The native clusters identified above were then used as reference populations in GeneClass 2 (Piry *et al*. 2004) to assign individuals from invasive populations. For this purpose, we used the frequency-based method of Paetkau *et al*. (1995) and Monte-Carlo resampling to compute assignment probability with the simulation algorithm of Paetkau *et al*. (2004). This latter step was undertaken to shed light on the relationship between invasive and native samples as well as to potentially identify the source of the invasive samples.

Chloroplast DNA variation and structure. For cpDNA variation, the phylogenetic relationship between the distinct chlorotypes evidenced in *H. mantegazzianum* was investigated based on the *trn*T-L sequences and length variation at *ccmp5* and *ccmp10*. A median-joining haplotype network with a maximum parsimony postprocessing was constructed using Network 4.112 (Bandelt *et al*. 1999).

In a similar manner as for nuclear loci, we calculated H_S, R_S and F_{ST} for invasive and native populations separately. Once again, significance of differences between invasive and native ranges was assessed using comparisons among groups of samples in FSTAT with 10 000 permutations.

Results

Nuclear microsatellites, genotypic disequilibrium and Hardy–Weinberg equilibrium

Tests for genotypic disequilibrium were all nonsignificant after sequential Bonferroni correction except for the combination of three loci in the invasive sample and two loci in the native sample (invasive: *HMNSSR-132A/HMNSSR-132B, HMNSSR-132A/HMNSSR-206, HMNSSR-132B/HMNSSR-206*; native: *HMNSSR-132A/HMNSSR-206, HMNSSR-132B/HMNSSR-206*). Tests of deviation from Hardy–Weinberg equilibrium based on 10 000 permutations were all nonsignificant after standard Bonferroni corrections, except for two populations (ID2 and ID28).

The eight nuclear microsatellite loci used in this study harboured between 2 and 36 alleles with 130 alleles across all loci. Observed and expected heterozygosities (H_O and H_S) over all loci and populations were 0.421 and 0.561 (Table S1, Supporting information).

Chlorotype identification

We found 11 cpDNA multilocus profiles in our sample (Table S2; Fig. S1, Supporting information). All were detected in native populations from Caucasus, while only two (HM1 and HM2) were observed in Switzerland. In the Caucasian populations, chlorotype HM2 was the most common (45% of all individuals sampled). In contrast, in the invasive Swiss populations HM2 occurred in only 24% of individuals and was found mostly in the northwest, while HM1 occurred mostly in the southern parts of the study area. In the invasive range, sequencing of the *trn*T-L spacer confirmed the distinction between the two multilocus profiles and no additional polymorphism was found to distinguish new chlorotypes. In the native range, sequencing of the *trn*T-L spacer for each multilocus profile confirmed the distinction between chlorotypes. However, compared to multilocus profiles, two new chlorotypes were revealed based on sequences in populations D and E (further named HM1a and HM1b). In fact, in each of these populations, one individual displayed the multilocus profile HM1 but the *trn*T-L spacer sequence displayed, respectively, one and two nucleotide substitutions compared to all other HM1 sequences. Overall, sequencing confirmed that the use of multilocus profiles was efficient to discriminate chlorotypes.

Table 3 Summary statistics comparing invasive and native populations for both plastid and nuclear DNA markers. *N*, number of individual sampled; R_S, mean allelic richness; H_O, mean observed heterozygosity overall loci; H_S, mean gene diversity overall loci; F_{ST}, mean pairwise genetic differentiation between populations; F_{IS}, inbreeding coefficient, *N* chloro, number of chlorotypes. Values in brackets are standard errors. All comparisons were significantly different at the 5% nominal level based on permutation tests in FSTAT 2.94 (Goudet 2005), except F_{IS} (indicated in italic)

		Nuclear microsatellite					Plastid DNA			
Range	*N*	R_S	H_O	H_S	F_{IS}	F_{ST}	*N* chloro	R_S	H_S	F_{ST}
Invasive	724	**2.10** (0.82)	**0.328** (0.31)	**0.353** (0.28)	*0.071 (0.045)*	**0.315** (0.012)	2	**1.142** (0.05)	**0.054** (0.02)	**0.854** (0)
Native	129	**3.41** (0.5)	**0.514** (0.12)	**0.522** (0.09)	*0.016 (0.036)*	**0.162** (0.029)	13	**2.087** (0.28)	**0.299** (0.08)	**0.635** (0.115)

Genetic diversity in invaded and native ranges

Mean gene diversity and allelic richness values based on nuclear microsatellite data were significantly lower in invasive populations from the western Swiss Alps compared to the native Caucasian populations (Table 3). Results from cpDNA are concordant with the signal from the nuclear genome as both gene diversity and allelic richness were significantly lower in invasive populations (Table 3). In the native range, 64% of populations were made up of more than one chlorotype. In contrast, 84% of invasive populations were made up of a single chlorotype, while the other 16% were characterized by the two chlorotypes HM1 and HM2 (Tables 1 and 2; Fig. S1). Based on nuclear data, F_{IS} values were not significantly different in populations from the invasive and native ranges (Table 3).

Population genetic structure in invaded and native ranges

Sampled populations were significantly differentiated from each other in both ranges, yet F_{ST} values were significantly higher in the invasive range than in the native range (Table 3). Mantel tests indicated that isolation by distance was evident in both ranges, with a weak correlation between genetic and geographical distances found in the invaded range ($r^2 = 0.072$, $P = 0.002$) and a higher correlation in the native range ($r^2 = 0.35$, $P = 0.026$). Bayesian analyses based on two different algorithms identified 10 clusters in the invasive range and five clusters in the native range (Fig. 1; Tables 1, 2). The 10 invasive clusters of populations were not clumped in one specific area as would be expected under natural dispersal, but rather represented a mosaic in the landscape. While most of the clusters of invasive populations were characterized by F_{ST} values ranging from 0.1 to 0.25, three clusters of populations (I_8, I_9 and I_10) were highly differentiated from each other with F_{ST} values larger than 0.3 (Table 1).

In the native range, the five clusters displayed a pattern of population structure generated by isolation by distance with clear geographical separation of clusters. The three peripheral populations D (N_3), E (N_4) and K (N_5) each made up a separate cluster, while the central populations formed two clusters representing a lower-elevation southwestern group of five populations (N_2) and a higher-elevation northeastern group (N_1) of three populations (Fig. 1; Table 2). It is important to note that removing the loci that diverged from the assumption of the Bayesian clustering algorithm (Hardy–Weinberg equilibrium and genotypic disequilibrium) from the analyses yielded identical results to that obtained with the entire dataset; we thus retained all eight loci and populations in these analyses.

Lastly, the proportion of invasive individuals assigned to the five native clusters ranged from close to 0% for clusters N_3, N_4 and N_5, to 13 and 12% for cluster N_1 and N_2, respectively.

Discussion

Evidence for founder events in invasive populations from Switzerland

Invasive populations often exhibit substantially lower levels of genetic diversity compared to native populations (Baker 1974), which is often attributed to a founder event. Yet, a range of situations can be found in the literature (Dlugosch & Parker 2008): a single clone can successfully invade large areas (e.g. Amsellem *et al*. 2000; Hollingsworth & Bailey 2000), invasive populations may exhibit similar genetic diversity as natives ones (Genton *et al*. 2005), or invasive populations may display substantially higher genetic diversity than native populations (Kolbe *et al*. 2004). Although differing genetic patterns are often reported for distinct invasive species in their invaded range (i.e. increase, maintenance or decrease in genetic diversity), such differences can also occur within the same species, depending on the spatial scale studied (Ward 2006) or on the local history of introduction (e.g. Besnard *et al*. 2007).

In the case of *Heracleum mantegazzianum*, Walker *et al*. (2003) identified levels of genetic diversity in British populations that were intermediate between our invasive and

native samples ($H_S = 0.493 \pm 0.03$). They interpreted their results as a high level of genetic diversity resulting from multiple introductions or a large initial founding population. In contrast with the interpretation of Walker *et al*. (2003), we identified a significant reduction of genetic diversity on both nuclear and plastid genomes in invasive populations. This discrepancy in genetic diversity measured may arise because our study area in the invaded range is about half the size as the one used by Walker *et al*. (2003) and/or because we used different genetic markers. Although our sample from the native range represented about one-third of the entire native distribution of *H. mantegazzianum* spread over an area 10 times larger than our study site in the invasive range, both nuclear and chloroplast genomes point to evidence that a founder event has occurred during the introduction of *H. mantegazzianum* to the western Swiss Alps.

Population genetic structure of H. mantegazzianum *in the invaded and native ranges*

The only previous estimate of population differentiation between invasive *H. mantegazzianum* populations based on F_{ST} values were provided by Walker *et al*. (2003). They found higher between-catchments differentiation in northeast England ($F_{ST} = 0.28 \pm 0.1$) compared to within-catchment estimates ($F_{ST} = 0.11 \pm 0.08$). Their overall estimate of genetic differentiation ($F_{ST} = 0.24 \pm 0.013$) is once again intermediate between our estimate in the invasive and native range (Table 3). They suggest that high population differentiation could have resulted from high selfing rates in the invaded range. Although our values of F_{IS} were not significantly different in invasive and native populations, invasive populations displayed a fourfold increase in F_{IS}, which is in agreement with the interpretation of Walker *et al*. (2003). We found mean pairwise F_{ST} values that were significantly higher in invasive populations compared to native populations, although the geographical scale was 10 times smaller in Switzerland than in the Caucasus. High population differentiation observed in the invasive range compared to the native range could have been generated by sequential founder events; while the species was first introduced to the Botanical Garden for Plant Acclimation in Geneva, it is highly probable that seeds were disseminated to Alpine botanical gardens in the western Swiss Alps and to other private gardens. The invasive populations sampled in the present study are thus possibly descendants of plants that escaped from these gardens or were transferred to other areas. Bayesian clustering analyses support this idea as the invasive populations displayed a mosaic pattern. This pattern was possibly generated by the collection of plant material from initial sites of introduction and dispersal at random to distant areas. Other anthropogenic means than direct collection can also be proposed as generators of the observed structure, such as dispersion by vehicles on main roads between Aigle and Les Diablerets (I_1) and Bex and Villard (I_6, I_7) as well as a smaller road between Aigle and Les Mosses (I_5). In some cases, natural features in the landscape (rivers and streams) can be identified as the factor that generated the observed population genetic structure (I_8, I_9), but this pattern is the exception rather than the rule in the invaded range. In contrast, native populations clustered in geographically (peripheral populations) and ecologically separate groups (high- vs. low-elevation populations), reflecting a natural long-distance dispersal mediated by rivers.

Evidence for multiple introductions in the western Swiss Alps derives from the Bayesian clustering. While majority of invasive clusters retained low genetic differentiation, the three most peripheral clusters were highly differentiated from other invasive clusters (based on F_{ST} values). We thus hypothesize that our invasive samples are the result of independent introductions; three peripheral introductions (I_8, I_9 and I_10 represented by distinct symbols in Fig. 1) and one major introduction in the centre of the study area. This pattern was suggested by Jahodová *et al*. (2007b) as they also unveiled substantial genetic differentiation between native and invasive *H. mantegazzianum* populations, and attributed it to multiple introductions, drift due to founder events, or rapid evolution in the new range. It is important to note that the source population(s) for any of the independent introductions hypothesized in the present study was not found in our sample from the native range and thus warrants further investigation with a broader geographical sample from the native range.

Conclusion

Although founder events have been suggested in previous work, the present study was the first to explicitly test and identify it occurring during the invasion process of *H. mantegazzianum* at the population level. Our results suggest that anthropogenic dispersal may be a main factor contributing to the successful invasion of *H. mantegazzianum* in the western Swiss Alps. Moreover, the identification of four divergent clusters in the invaded range indicates that the species may have been introduced multiple times in the study area, possibly from disparate source populations. If this study was repeated over a larger geographical area in Switzerland, we expect that more evidence for independent introductions of the species could be found. As time goes by, and as each introduced population expands its range, chances for genetic exchanges between populations originating from independent introductions would increase, leading to admixture events that may possibly further inflate the genetic pool of *H. mantegazzianum* and contribute to increase the success of this already successful invader. In order to reduce the possibility of admixture events between

plants originating from different regions, management strategies for the invasion of giant hogweed should be aimed at public awareness in order to limit the dissemination of the plant for ornamental purposes. Eradication plans should be particularly targeted at populations found along roadsides and river banks, since they contribute to long-distance dispersals in the invaded range.

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Supporting information

Additional supporting information may be found in the online version of this article:

Fig. S1 Distribution of chlorotypes found in invasive and native *Heracleum mantegazzianum* population clusters identified with Bayesian inferences (Guillot *et al.* 2005; Corander *et al.* 2008) A. Two chlorotypes are found in Switzerland. B. Median-joining haplotype network (Bandelt *et al.* 1999) constructed based on sequences from trnT-trnL intergenic spacer and length variation at ccmp5 and ccmp10. Short lines across the network illustrate single-step mutations while white squares represent missing (ancestral) nodes. The sizes of the circles are proportionate to the number of individuals representative

of each chlorotype. C. Thirteen chlorotypes are found in the Caucasus.

Table S1 Mean values of polymorphism metrics at each locus overall for all populations. Loci are represented in the columns. Rows represent number of alleles (N_a), observed heterozygosity (H_O) and expected heterozygosity (H_S). Standard deviation is indicated in brackets

Table S2 Plastid DNA haplotypes identified using the six ptDNA loci. For each locus, the fragment size is given in bp. Each haplotype is characterized by a specific multilocus profile

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