

High genetic and morphological diversity despite range contraction in the diploid *Hieracium eriophorum* (Asteraceae) endemic to the coastal sand dunes of south-west France

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Endemic plants inhabiting coastal sand dunes show augmented extinction risks due to the dynamic nature of dunes and strong human pressure on coastal areas. To investigate the survival strategies and threats to long-term survival of such species, we combined genetic, morphological and biogeographical approaches, using the example of *Hieracium eriophorum* (Asteraceae) and its putative cryptic sister species *H. prostratum*, which are endemic to the longest coastal sand dune in Europe. An analysis of amplified fragment length polymorphism revealed high within-population genetic variability, and slight isolation by distance was the only indication of genetic population structure. Thus, no signs of genetic threats to survival were found. Furthermore, genetic and morphometric data provided no evidence for the existence of two species. Therefore, we propose to synonymize *H. prostratum* with *H. eriophorum* and provide a nomenclatural overview with typification. Finally, an analysis of historical distribution records showed that, during the last 100 years, the species was lost from its range margins, where its habitat became fragmented. Taken together, our results suggest that one successful survival strategy of narrow endemics may be the achievement of large local population sizes on a small geographical scale, thus avoiding the genetic problems inherent to small and fragmented populations. Dune management policies should thus take care that the current tendencies to allow more erosion will not result in too severe fragmentation of the remaining continuous stretches of dune habitat.

ADDITIONAL KEYWORDS: AFLP – Atlantic – coastal sand dunes – conservation – endemism – genetic structure – management – multivariate morphometrics.

INTRODUCTION

Species that are geographically restricted to a small area are often termed ‘narrow endemics’ (e.g. Kruckeberg & Rabinowitz, 1985). As a consequence of their limited range, narrow endemics have a high risk of extinction from a combination of stochastic, environmental and genetic factors (e.g. Ellstrand & Elam, 1993; Avise & Hamrick, 1996). Therefore, they are of high conservation priority (Primack, 1995).

Coastal habitats harbour many narrowly distributed plant species. For instance, along European seashores, 25% of all species are endemic to a province or a county (van der Maarel & van der Maarel-Versluys, 1996). Shorelines are under heavy pressure for industrial, agricultural and recreational use (e.g. Martinez & Psuty, 2004). As a consequence, 37% of the European littoral plants are endangered (van der Maarel & van der Maarel-Versluys, 1996). Many of the coastal endemics are specialists of sand dunes (vanden Berghen, 1964; Bakker, 1976; Géhu & Franck, 1985), a habitat that is particularly threatened by

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destruction due to urbanization and erosion (e.g. Géhu, 1989; Heslenfeld, Jungerius & Klijn, 2004).

Molecular markers have been used in coastal plants to elucidate modes of dispersal and phylogeography and to clarify the phylogenetic origin of endemics (e.g. Purdy, Bayer & McDonald, 1994; Purdy & Bayer, 1996; Chapman & Abbott, 2005; Kadereit *et al.*, 2005; Pillon *et al.*, 2007; Westberg & Kadereit, 2009). Such information is relevant for species conservation, as it helps to define conservation units and to preserve genetic diversity (Ellstrand & Elam, 1993; Primack, 1995; Avise & Hamrick, 1996). Investigations of genetic diversity and genetic population structure may also help to explain the high degree of endemism in this habitat. In fact, the high degree of endemism may seem surprising because sand dunes are dynamic habitats, potentially characterized by frequent cycles of extinction and re-colonization which may erode genetic diversity and exacerbate the threats to survival already imposed by the small geographical range (e.g. Gilpin, 1991; McCauley, Raveill & Antonovics, 1995; Jacquemyn *et al.*, 2008).

Here we study genetic diversity and genetic population structure of a sand dune endemic using the example of *Hieracium eriophorum* St.-Amans, a sand-dune specialist, which occurs exclusively along a narrow stretch of 80 km of the Atlantic sea coast in south-western France (Department of Landes; Favennec, 2002a). The species inhabits the longest continuous sand dune in Europe, which is only interrupted by a few towns and villages (Favennec, 1998). On the dune, it occurs in zones with moderate erosion (semi-fixed dune), where it experiences only low levels of interspecific competition and where it can form high-density stands of thousands of individuals together with other endemic plant species (Géhu & Franck, 1985; Favennec, 2002a; Forey *et al.*, 2008).

In the last 150–200 years, the distribution area of *H. eriophorum* has experienced large-scale transformations. The previous, up to 10-km-wide system of several parallel ridges of highly dynamic sand dunes was forested during the 19th century leaving only a single, 200- to 500-m-wide dune, which is actively managed to prevent erosion (Favennec, 2002b, 2002c). Based on historical maps, we estimate that 93% of potential habitat was lost (a reduction from c. 465 km² to 33 km², D. Frey, unpublished data). However, because the semi-stabilized dune is favoured by management practices, the actual degree of change in the amount of available habitat is unknown (Favennec, 2002d). Today, *H. eriophorum* is classified as ‘vulnerable’ (Dupont, 1995), but due to the uncertainties about habitat loss and the response of the species to dune management practices, this classification is only weakly supported by data (Lesouëf, 1986; Géhu, 1989). Today, the largest

threats to its survival are habitat loss and habitat fragmentation due to erosion (e.g. by trampling) and urbanization (Dupont, 1995; Favennec, 1998).

The conservation of *H. eriophorum* is complicated by the existence of a putative sister species, *H. prostratum* DC., reported to co-occur with *H. eriophorum* in the same region and habitat (e.g. de Candolle, 1813; Zahn, 1922; Sell & West, 1976). However, its taxonomic status is controversial, and it is unclear whether it represents a separate taxon or not. Although *H. prostratum* was mentioned in many standard floras and checklists (e.g. Sell & West, 1976; Kerguelen, 1993; van der Maarel & van der Maarel-Versluys, 1996; Greuter, 2006–2009), it was omitted in the *Red Book of France* (Dupont, 1995). As a consequence, no conservation status is currently assigned to this taxon, and it is not protected by law (Lesouëf, 1986; Dupont, 1995; Favennec, 1998).

In the current study, we assessed the genetic diversity and genetic population structure of *H. eriophorum* using amplified fragment length polymorphisms (AFLPs; Vos *et al.*, 1995) to investigate potential genetic signatures of extinction–recolonization dynamics and other signs of genetic drift and loss of genetic variation which may threaten the long-term survival of the species. Furthermore, to define unambiguous conservation units, we investigated the existence of the putative sister species *H. prostratum* using morphometric and genetic analyses. Such a combined approach has been successfully applied in other threatened species (e.g. de Oliveira *et al.*, 2008; May-Itza *et al.*, 2010). In *Hieracium* L., AFLPs have proved useful for discrimination between closely related species (Rich, McDonnell & Lledó, 2008; Ronikier & Szeląg, 2008) or detection of interspecific hybridization (Mráz, Chrtek & Fehrer, 2011). Finally, using historical and current distribution records, we attempted to elucidate whether *H. eriophorum* has suffered a recent range contraction and to help determine the conservation status and management priorities for this species and its habitat.

MATERIAL AND METHODS

STUDY SPECIES

Hieracium eriophorum is a perennial herb with a dense hair cover (indumentum, trichome cover) and a semi-prostrate habit. These characters are considered adaptations to a sand dune environment (Danin, 1996). As in other species of the genus, the achenes have a hairy appendix (pappus), which allows long-distance dispersal by wind. The genus has a holarctic distribution and shows widespread polyploidy and apomixis, which considerably complicates taxonomy (e.g. Sell & West, 1976). However, *H. eriophorum* is

diploid ($2n = 2x = 18$) (Merxmüller, 1975; Chrtek *et al.*, 2007), and diploid *Hieracium* spp. are obligately sexual and outbreeding (Mráz, 2003). Cross pollination is mediated by insects (Thomson, 1978). The putative sister species, *H. prostratum*, has been reported to differ from *H. eriophorum* by having a more prostrate habit and by being less hairy, especially on the involucre bracts (leaves surrounding the flower heads; Zahn, 1922; Sell & West, 1976). In spite of the close morphological and phylogenetic relationship of *H. eriophorum* and *H. prostratum* to section *Hieracioides* Dumort. (synonym *Umbellata* Fr.) (cf. Fehrer, Krak & Chrtek, 2009), traditional classifications treat both taxa within the separate section *Eriophora* (Arv.-Touv.) Zahn (e.g. Zahn, 1922; Stace, 1998).

GENETIC ANALYSES

Leaves were collected from eight individuals from each of the six populations (Table 1; Fig. 1). Vouchers are deposited in the Natural History Museum Fribourg (NHMF). Between 10 and 20 mg of dried material was ground with glass beads. Total DNA was extracted using the DNeasy Plant Mini Kit (Qiagen) following the manufacturer's instructions and stored at -20°C . The following AFLP protocol was used: *c.* 200–250 ng of genomic DNA was restricted with *EcoRI* and *MseI* (New England Biolabs) and ligated to the adaptors 5'-CTCGTAGACTGCGTACC-3'/3'-CATATGACGCATGGTTAA-5' and 5'-GACGATGAGTCCTGAG-3'/3'-TACTCAGGACTCAT-5' using 1.1 μL T4 DNA Ligase buffer 10 \times (Qiagen), 1.1 μL of 0.5 M

NaCl, 0.55 μL of bovine serum albumin (1 g L $^{-1}$), 5 μM *EcoRI* adaptor, 50 μM *MseI* adaptor, 5 units of *EcoRI* (New England Biolabs), 1 unit of *MseI* (New England Biolabs) and 0.99 units of T4 DNA ligase (New England Biolabs), all in a total volume of 11 μL . Reactions were then incubated at 37°C for 3 h. A pre-selective amplification of the restricted-ligated DNA was performed using 4 μL of 20 \times diluted restriction-ligation product, 0.2 μL of each of the two preselective primers (5'-GACTGCGTACCAATTCA-3' and 5'-GATGAGTCCTGAGTAAC-3'; each *c.* 29 μM), 2 μL 10 \times PCR buffer (Qiagen), 0.2 μL of each dNTP (10 mM each), 0.5 units of Taq Polymerase (Qiagen), all in a total volume of 10 μL with the following cycle profile: 94°C for 2 min; 94°C for 20 s, 56°C for 30 s and 72°C for 2 min (20 cycles); followed by 60°C for 30 min and 4°C thereafter. After a 20-fold dilution of pre-selective PCR products, the selective PCR step was carried out as a multiplex reaction using three fluorescent selective primers (*EcoRI*-6-FAM-CTA, *EcoRI*-NED-CG and *EcoRI*-HEX-CTC; Applied Biosystems, ABI) combined with *MseI*-CTA. These three primer combinations were selected from 12 combinations tested, as they gave the best reproducible and polymorphic profiles. The selective PCR was performed using the following profile: 94°C for 2 min; 94°C for 20 s, 66 to 56°C ($\Delta T = -1^{\circ}\text{C}$ per cycle), 72°C for 2 min (nine cycles); 94°C for 20 s, 56°C for 30 s, 72°C for 2 min (20 cycles); 60°C for 30 min and 4°C thereafter. Then, 1 μL of selective PCR product was mixed with 10 μL of HiDi formamide (ABI) and loaded for 40 min on an ABI 3130 Genetic Analyzer (ABI). One individual per population was replicated

Table 1. Sampling sites of *Hieracium eriophorum* for molecular and morphometric analyses and within-population genetic diversity measures based on AFLP data

Locality	Code	Lat. ($^{\circ}\text{N}$)	Long. ($^{\circ}\text{W}$)	N^*	Nbds \dagger	%Poly \ddagger	h^{\S}	IR \P
AFLP analysis								
Mimizan-Plage	MIMN	44 $^{\circ}$ 13'51.8"	1 $^{\circ}$ 17'33.0"	7	34	68	0.316	0.83
Petre Morue	PET	43 $^{\circ}$ 58'33.5"	1 $^{\circ}$ 21'19.0"	8	37	73	0.310	0.92
Huchet	HUCH	43 $^{\circ}$ 53'02.8"	1 $^{\circ}$ 22'56.8"	8	37	64	0.219	0.89
Plage de Soustons	PDS	43 $^{\circ}$ 46'16.2"	1 $^{\circ}$ 25'09.0"	7	38	75	0.325	1.06
Hossegor	HOSC	43 $^{\circ}$ 39'32.9"	1 $^{\circ}$ 26'37.4"	8	40	82	0.343	1.05
Tarnos-Plage	TARN	43 $^{\circ}$ 33'58.8"	1 $^{\circ}$ 29'36.9"	8	38	75	0.314	1.00
Morphometric analysis								
Biscarosse-Plage	BIS	44 $^{\circ}$ 27'8.6"	1 $^{\circ}$ 15'05.5"	14	–	–	–	–
Moliets-et-Maa	MOL	43 $^{\circ}$ 50'39.8"	1 $^{\circ}$ 23'43.4'	26	–	–	–	–
Tarnos-Plage	TAM	43 $^{\circ}$ 33'10.5"	1 $^{\circ}$ 30'14.9"	24	–	–	–	–

*Number of individuals analysed per population.

\dagger Total number of AFLP bands.

\ddagger Percentage of polymorphic bands.

\S Nei's gene diversity.

\P Index of rarity.

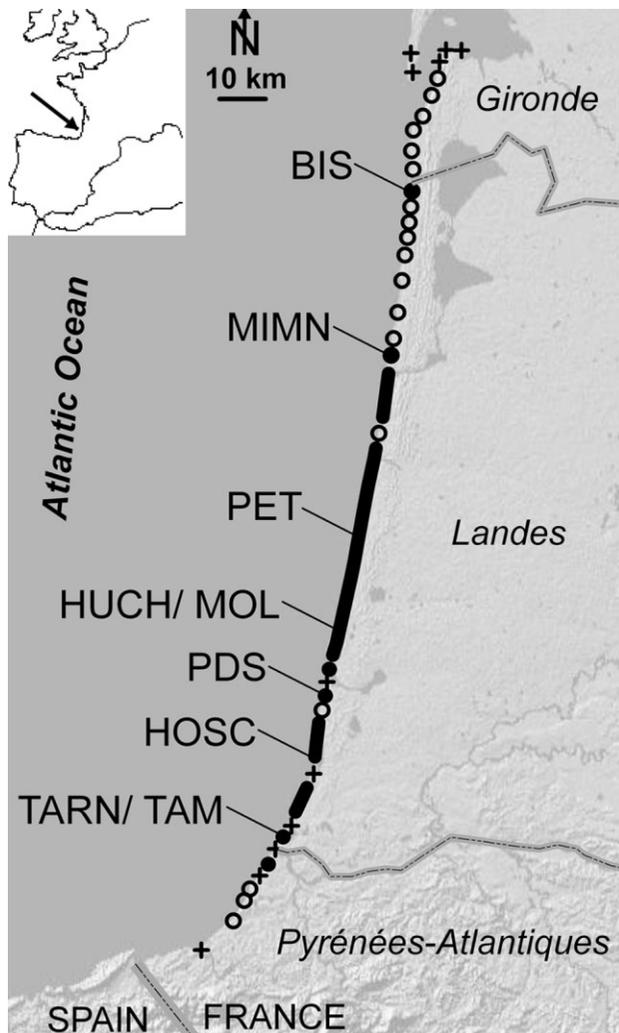


Figure 1. Historical and current distribution of *Hieracium eriophorum* and sampling sites (see Table 1). The thick line and the filled circles represent sites with presence records between 2001 and 2010 (the thick line representing the continuous distribution without gaps > 2 km). Empty circles show absence records collected between 2001 and 2010, but not all absence records are mapped to simplify the illustration. Crosses indicate extinctions, i.e. sites with former (1850–2000) records but confirmed absence between 2001 and 2010.

twice to assess the level of reproducibility. After removal of non-reproducible markers, the average overall reproducibility reached 98.3% (Bonin *et al.*, 2004). The presence and absence of the AFLP fragments were then scored manually with GeneMapper (version 4.1; ABI). Only polymorphic fragments were considered in the analyses.

As a measure of within-population genetic diversity, the proportion of polymorphic loci, Nei's gene diversity (Nei, 1987) and the 'index of rarity 1' (IR)

were calculated using the 'AFLPdat' script (Ehrich, 2006; see updated manual at <http://www.nhm.uio.no/english/research/ncb/aflpdat/>) within the R environment (R Development Core Team, 2009). The IR corresponds to the 'down-weighted value', a measure of the frequency of rare/private alleles in a population (Schönswetter & Tribsch, 2005). We used a neighbor-joining cluster algorithm (NJ) based on Euclidean distance computed from allele frequencies to estimate relatedness among populations, where a population was defined as one sampling location. NJ was performed also at the individual level and it was based on Jaccard's index of similarity computed from the presence and absence of bands. Statistical support of nodes was computed using 99 bootstrap replicates for analysis at the population level, and 999 replicates for analyses of individual plants. We also conducted a principal coordinate analysis (PCO) based on Jaccard's index of similarity. Analysis of molecular variance (AMOVA; Excoffier, Smouse & Quattro, 1992) was used to partition the genetic variance into within- and among-population components. Isolation by distance pattern (the correlation between Euclidean genetic and geographical distance between populations) was assessed using a Mantel test with 999 permutations. All analyses mentioned above and plotting were performed using the 'ade4', 'ape', 'pegas' and other basic packages (Chessel, Dufour & Thioulouse, 2004; Paradis, Claude & Strimmer, 2004; Paradis, 2010) within R environment. Population structure was further assessed using a Bayesian clustering algorithm implemented in STRUCTURE (version 2.3.3; Pritchard, Stephens & Donnelly, 2000; Falush, Stephens & Pritchard, 2007). We ran STRUCTURE for 900 000 iterations following a burn-in period of 100 000 iterations with $k = 1-10$ using the correlated allele frequencies model and assuming admixture (the default values). Every run was repeated five times with the exception of the last four runs ($k = 6-10$) in which fewer runs (two to four) were performed.

MORPHOMETRIC ANALYSES

The morphometric analysis was based on 14–30 plants collected from each of three distant sampling sites (Table 1), which were not included in the genetic analysis. One intact flowering stem per individual (i.e. not the entire plant) was sampled and subsequently deposited in the herbarium of the Natural History Museum Fribourg (NHMF). The height of the plant and the height of the first branching above the ground were directly measured in the field. Other characters were measured on the pressed herbarium material. In total, 28 characters were recorded (Table 2), including all characters considered

Table 2. Variables used for the morphometric analysis of *Hieracium eriophorum*

Variable	Description
Continuous quantitative characters	
HP	Plant height (mm): perpendicular distance between the ground and the base of the uppermost capitulum, measured in the field
HFB	Height of first branching (mm): perpendicular distance between the ground and the first ramification, measured in the field
DST	Stem diameter (mm): measured at the base of the stem
LST	Length of stem (mm): measured from the base to the basal part of the principal capitulum
LFB	Length of stem to the first branching (mm)
LIN	Length of synflorescence (mm): calculated as LST – LFB
LLL	Length of the longest stem leaf (mm)
WLL	Width of the longest stem leaf (mm)
LLT	Length of longest tooth of the longest stem leaf (mm)
LLB	Length of the longest lateral branch (mm)
LA	Length of acladium (mm)
LLBR	Length of the longest bract of the principal capitulum (mm) or another capitulum
LTB	Length of the longest eglandular trichome on bract (mm) of the principal capitulum or another capitulum
LTA	Length of the longest eglandular trichome on acladium (mm) or of another peduncle
LTUT	Length of the longest eglandular trichome in the upper third of the stem (mm)
LTMT	Length of the longest eglandular trichome in the middle third of the stem (mm)
LTSB	Length of the longest eglandular trichome at the stem base (mm)
LTLUT	Length of eglandular trichomes on the stem leaf (L1) of the upper third of the stem (mm): mean of four measures per leaf
LTLMT	Length of eglandular trichomes on the stem leaf (L2) of the middle third of the stem (mm): mean of four measures per leaf
LTLLT	Length of eglandular trichomes on the stem leaf (L3) from the lower third of the stem (mm): mean of four measures per leaf
LS	Length of seeds (mm): mean of four measures
LP	Length of longest pappus bristle (mm)
Discrete quantitative and semi-quantitative characters	
NL	Number of stem leaves (excluding small bract-like leaves)
NT	Number of teeth including ‘mucronate glands’ at the leaf margin of the longest leaf
NC	Number of capitula per stem
TDL1	Density of simple eglandular trichomes of L1: ± glabrous (1), scattered (2), moderate (3), dense (4), very dense (5)
TDL2	Density of simple eglandular trichomes L2: ± glabrous (1), scattered (2), moderate (3), dense (4), very dense (5)
TDL3	Density of simple eglandular trichomes L3: ± glabrous (1), scattered (2), moderate (3), dense (4), very dense (5)
Binary characters	
SC	Seed colour: various brown tints (1) or beige/greyish (0)
GH*	Glandular hairs on bracts: present (1) or absent (0)
Ratio characters	
LLL/WLL, NC/LIN	

*This character was not included in the PCA, because this trait was invariable in all individuals.

to discriminate between *H. eriophorum* and *H. prostratum* (De Candolle, 1813; Zahn, 1922). In addition, we tested for the correlation between pair-wise genetic distances (based on Jaccard's coefficient of similarity between individuals) and pair-wise pheno-

typic distances in hairiness (Euclidian distance in trichome density between individuals) measured on a stem leaf in the upper part of the plant, as this trait should discriminate between *H. eriophorum* and *H. prostratum* (e.g. Zahn, 1922). This Mantel test was

done using 35 of the 46 individuals included in the genetic analysis.

The results of the morphometric analysis were visualized using principal component analysis (PCA). We performed two PCAs, one including all variables and one including only the variables related to hairiness and plant habit, the putative discriminant characters between *H. eriophorum* and *H. prostratum*. Analyses were performed using the ‘ade4’ package implemented in R software. Confidence ellipses delineating the phenotypic spaces of three populations were constructed using the gravity centre and 1.5 standard deviations.

ANALYSIS OF THE HISTORICAL AND ACTUAL DISTRIBUTION

Historical and actual distribution data were taken from (1) herbarium specimens, (2) available literature and (3) records of the French National Forestry Office (ONF) (Favennec, 2002a; J. Favennec, unpubl. data), the environmental agency managing most of the sand dunes in the study region. In addition, our own distribution records from fieldwork in 2009 and 2010 (including absence data) were included. No distinction was made between *H. eriophorum* and *H. prostratum*. The ArcGIS software (version 9.3; ESRI) was used to map all presence and absence data.

1. Herbarium records and specimens were checked from 13 herbaria (AIX, ANG, AUT, AV, G, G-DC, GRM-ARV, LISU, LMS LY, MPU, P, TL; abbreviations according to Thiers, 2011). Only specimens with unambiguous information on sampling site and sampling date were considered. Only a single record per year and site was retained. In total, 103 of 313 specimens collected between 1804 and 1998 were used for the analysis.
2. The existing literature on sand dune vegetation was screened for information on the presence and absence of the species. Absence data were taken into account only for studies covering sand dune habitats within 60 km to the south and 125 km to the north from the current distribution of the species, as there are no indications that the species ever occurred outside this region (e.g. Grenier & Godron, 1850; Lloyd & Foucaud, 1886; Rey, 1960; Jeanjean, 1961; Aseginolaza Iparragirre *et al.*, 1984; Favennec, 1998). Presence/absence records of the following sources were used: vanden Berghen (1964), Lahondère (1979), Géhu (1981), Lesouëf (1986) and Royaud & Lazard (1998).
3. Two ONF vegetation monitoring data sets from 1997 and 2003 were screened for presence and absence records of the species (Favennec, 2002a). These data cover 230 km of French Atlantic sand

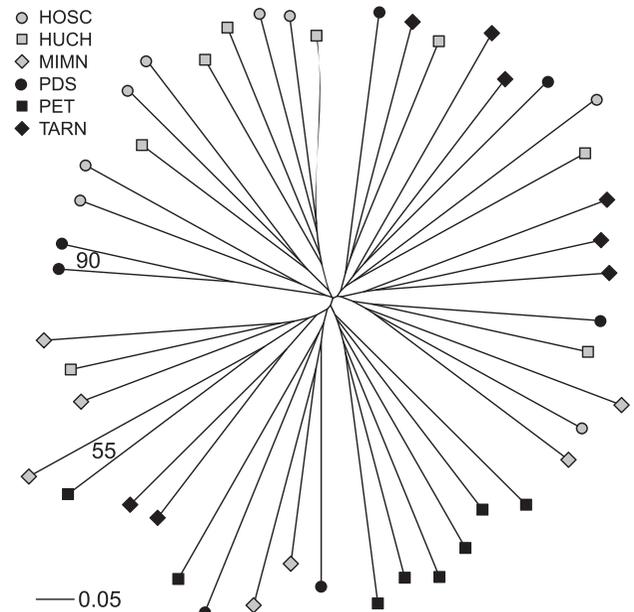


Figure 2. Unrooted neighbor-joining tree of 46 *Hieracium eriophorum* individuals based on Jaccard's distances (scale) based on AFLP data. Bootstrap values > 50% are indicated.

dunes, including 51 to 52 geo-referenced transects across the current and historically documented range of the species (Favennec, 2002a).

RESULTS

AFLP

The three primer combinations yielded 44 polymorphic and reproducible fragments ranging from 70 to 500 bp. Each of the 46 individuals had a unique multilocus genotype (Fig. 2). The NJ tree (Fig. 2) and the PCO (Supporting Information, Fig. S1) showed no clustering of plants from the same population and populations did not cluster together (supporting Fig. S3). Bayesian clustering analyses implemented in STRUCTURE, indicated that the most likely number of populations (K) was one (supporting Fig. S2). According to the AMOVA analysis, 92.2% of the overall genetic variation occurred within sampling sites and only 7.8% among sampling sites (Table 3). This small but significant ($P < 0.01$) amount of genetic differentiation between populations was positively correlated with distance among sampling sites (Mantel-test, $r = 0.4$; $P = 0.02$; Fig. 3). Generally, the genetic diversity was similar and high at each sampling site (Table 1). Only the proportion of rare alleles (index of rarity) was somewhat higher at southern compared with northern sampling sites (Table 1).

Univariate statistics of quantitative characters (mean, SD, minimum, maximum, 5% and 95% percentiles) are given in supporting Table S1. Both PCA analyses revealed a similar pattern: most individuals from the three sampling sites formed a single cluster, but a few individuals from the northernmost site (BIS) were somewhat separated along both axes (Fig. 4). In the PCA including all variables, the first two components accounted for 26.8 and 12.4%, respectively, of the total variation (Fig. 4A). Hairiness (TDL1, LTA and LTUT), stem length (LST) and leaf form (LLL, WLL) were most correlated with the first axis, whereas stem diameter (DST), length of the inflorescence (LIN) and number of capitula (NC) contributed most to the second axis (supporting Table S2). In the PCA including only characters related to habit and hairiness, the first two axes accounted for 39.5 and 16.0%, respectively, of the total variation (Fig. 4B). Whereas variation along the first PCA axis was explained mainly by traits related to

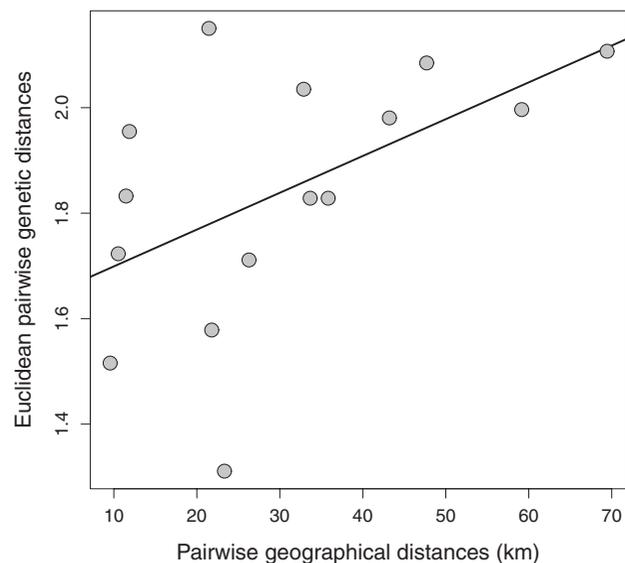


Figure 3. Correlation between genetic and geographical distances for all pairs of populations of *Hieracium eriophorum* (Mantel test, $r = 0.528$, $P = 0.02$).

Table 3. Analysis of molecular variance of *Hieracium eriophorum* based on AFLP data

Source of variance	d.f.	Sums of squares	Mean square	Variance components	% total variance*
Among populations	5	2.014	0.403	0.02060	7.8
Within populations	40	9.799	0.245	0.24497	92.2
Total	45	11.813	0.262	0.26557	

* $P < 0.01$.

hairiness (TDL1, LTLUT, more negative values indicating stronger hairiness), the traits related to habit (HFB, HP, LST) were most positively correlated with the second principal component (supporting Table S2). The individuals from the BIS site which did not fall into the main cluster tended to show a denser hair cover and a more erect habit than the remaining individuals from the same site and the individuals from the other two sites (Fig. 4). The Mantel test between genetic distance and phenotypic distance in hairiness did not reveal a significant correlation ($N = 35$, $r = 0.02$, $P = 0.38$).

DISTRIBUTION DATA

In total, we obtained 284 dated presence/absence records (103 from herbarium specimens, 30 from the literature, 194 from the ONF and 45 from our own observations; supporting Tables S3 and S4). These records cover the period between 1804 and 2010. The data after 1985 cover the entire potential range of the species (Fig. 1), but the data prior to 1946 come mainly from three easily accessible sites. We found that *H. eriophorum* currently occurs only in the Department of Landes, where its presence has been documented since the early 19th century. In the neighbouring departments (Gironde, Pyrénées-Atlantiques), the species was present in the 19th century, but records are lacking for the last three decades, except for four individuals on a golf course in Anglet (Pyrénées-Atlantiques), just across from the border of Landes, found by us in 2010. Thus, a latitudinal range contraction took place in the second half of the 20th century at the southern and northern margins of the historically documented distribution (Fig. 1). The range contraction was probably more pronounced than implied by the extinction records in Figure 1 because it is likely that most absence records also represent extinctions. The species was described as being continuously distributed along the coast of Landes and on the dunes of the adjacent departments during the 19th century (e.g. Grenier & Godron, 1850; Rey, 1960), but no exact dates or locations were given, so these sites were not included as formerly occupied in our analysis. The range contraction coincides with

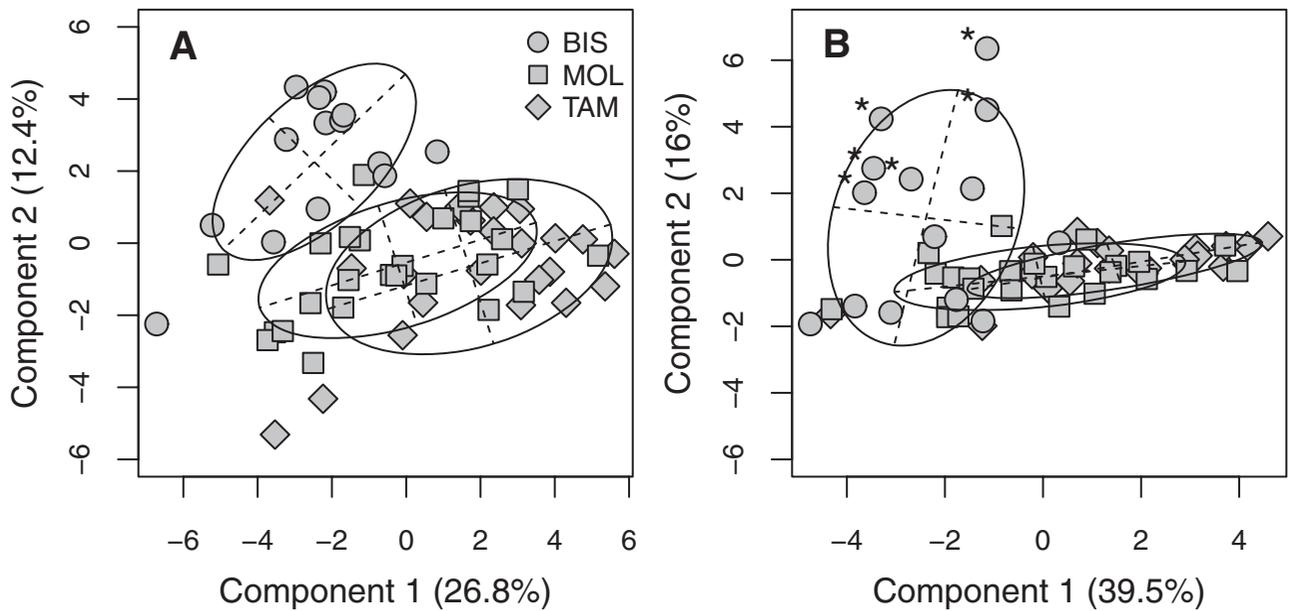


Figure 4. Principal components analyses of 64 plants originated from three populations (BIS, MOL, TAM) of *Hieracium eriophorum* based on (A) all 31 morphological variables and (B) 14 characters related to habit and hair cover. Shown are the first two principal components (PC1 and PC2) and the percentage of variation explained by each PC. Ellipses show 1.5 standard deviations around the gravity centre of each sampling population. The asterisks in B show the plants that grew inside shrubs and that also had an erect habit.

increased fragmentation of the dune in these areas due to urbanization after World War II and also due to natural and human-induced erosion (Duffaud *et al.*, 1997; Favennec, 1998; Prat, 2002). In contrast to the latitudinal range, it was not possible to document the probable longitudinal range contraction due to the forestation of the inland dunes in the 19th century because the localities indicated on the labels of the herbarium specimens lacked precision. Now, the species exclusively inhabits the single, unforested dune located next to the coast.

DISCUSSION

TAXONOMY

Multivariate morphometrics revealed a high degree of variation in morphological characters, in particular in those which presumably differentiate between the two putative sister species. About eight individuals from the BIS site fit the original description of *H. eriophorum*, as they had a more erect habit than the remaining individuals from BIS and the two other sites, and they also had a denser hair cover and longer trichomes than the average. However, the majority of plants which had a prostrate habit do not fully fit the description of *H. prostratum*, because their habit was not correlated with trichome length or density, which is considered, with habit, to be impor-

tant for discrimination between *H. prostratum* and *H. eriophorum*. Indeed, the PCA failed to reveal two distinct morphological clusters of individuals, which would be expected if the sampled individuals belonged to two different species. Rather, the morphological variation was continuous with a particularly large spread in individuals from the BIS site, which showed all possible trait combinations of hairiness and habit. Similarly, high morphological variation was found, although not to the same extent, at the two other sampling sites. Although the individuals from the BIS site had on average a denser hair cover, longer trichomes and a more erect habit, this might be explained by environmental factors. In fact, all but one of the BIS plants that showed an unusually upright habit grew inside shrubs, contrasting with a prostrate or semi-prostrate habit of plants growing in close vicinity but not inside shrubs (Fig. 4B). Similar observations have been reported by other authors (Granereau, 1985; Favennec, 1998), suggesting that the erect habit of these individuals is explained by shading or mechanical support (Skálová & Krahulec, 1992; van Hinsberg & van Tienderen, 1997). The explanation of the variation in hairiness is less straightforward, but strong intraspecific variation in this character is also known to occur in another diploid, *Hieracium umbellatum* L. (e.g. Turesson, 1922). In addition to the purely morphological data,

the lack of a correlation between phenotypic distance in hairiness and genetic distance among individuals also suggests that the sampled individuals belong to a single species. Due to complete or partial reproductive isolation, different species should differ not only in morphological characters, but also in neutral genetic markers. Thus, based on morphometric data (morphological distribution does not fall into two clearly distinct clusters) and genetic data (morphologically dissimilar individuals do not show particularly great genetic distances) we find no evidence for the existence of these two putative sister species, but rather strong within-species morphological variation in both hairiness and habit partly influenced by the environment. Therefore, for the remainder of the discussion, we will treat all individuals as belonging to the same species. Moreover, based on the above reasoning, we propose to synonymize *H. prostratum* with *H. eriophorum* (see nomenclatural overview in the Appendix).

GENETIC STRUCTURE AND DIVERSITY

The results of our AFLP study revealed similar high levels of genetic diversity within sampling sites and only weak genetic differentiation between populations. Individuals sampled from the same sites showed almost as many genetic differences as individuals sampled from different sites (Fig. 2). Thus, the observation of low population differentiation was not due to lack of statistical power, but was also observed in absolute terms. This indicates that it is unlikely that higher sample sizes at each site would have substantially changed the observed patterns. Hence, our results suggest that levels of genetic drift and drift-related inbreeding are low, and that genetic bottlenecks (e.g. due to extinction–recolonization dynamics) are rare because all these processes would decrease within-population diversity and increase genetic differentiation among populations (e.g. Gilpin, 1991; McCauley *et al.*, 1995; Jacquemyn *et al.*, 2008). Thus, it is likely that the species exists as a single, outcrossing population with only low degrees of isolation by distance. This finding is consistent with the nearly continuous distribution of the species and its great abundance where its optimal habitat is still largely intact and continuously present (albeit only as a single rather than as several parallel dunes). In this large and continuous population, gene flow via pollen and/or seeds appears to be almost unrestricted except for the longest distances, as evidenced by the weak isolation by distance. A similar genetic structure has also been found in *Cakile maritima* Scop. (Brassicaceae) and *Eryngium maritimum* L. (Apiaceae), two non-endemic dune species studied in the same study region by Westberg & Kadereit (2009). These species

are common, and at least one of them occurs in a large and continuous population, similar to *H. eriophorum*. However, in contrast to *H. eriophorum*, the seeds of both species disperse efficiently via sea currents, which may explain their larger (i.e. non-endemic) range (Kadereit *et al.*, 2005; Westberg & Kadereit, 2009).

In contrast to the regions where it is continuously distributed, *H. eriophorum* has disappeared from those regions where the coastal dune has become fragmented due to urbanization and increased erosion (Favennec, 1998; Prat, 2002). This suggests that *H. eriophorum* may be vulnerable to habitat fragmentation, small population size and, perhaps, genetic factors, such as inbreeding depression, which are known to most strongly influence species that otherwise live in large and diverse populations (e.g. Ellstrand & Elam, 1993). Thus, our results suggest that one successful survival strategy for narrow endemics may be the achievement of large local population sizes on a small geographical scale, perhaps helped by low levels of competition in a highly specialized habitat. By achieving large local population sizes, these species may avoid the genetic problems inherent to small and fragmented populations. An alternative strategy for endemic species might be to find a way to cope with low genetic diversity and high genetic drift (Cole, 2003), but this appears not to be the case in our study species. The continuity and abundance of dune habitats in our study region before the forestation may also have favoured a similar strategy in other sand dune endemics.

CONSERVATION AND MANAGEMENT IMPLICATIONS

Our results do not provide evidence for the existence of a sister-species relationship and indicate low levels of population subdivision. Hence, *H. eriophorum* should be treated as a single conservation unit. Furthermore, our results suggest that *in situ* conservation of this species may depend on the maintenance of large, continuous stretches of its optimal habitat, the semi-stabilized dune. In earlier times (i.e. before the forestation of the inland dunes), large areas of semi-stabilized dune probably occurred at any given time in the formerly much larger range for *H. eriophorum*. After forestation, the semi-stabilized dune was favoured by the stabilization of the remaining coastal dune, hence offering an ideal habitat to *H. eriophorum* and other species adapted to low levels of erosion and concurrence (Favennec, 2002b, d; Forey *et al.*, 2008). However, current dune management practices aim at maintaining a more dynamic equilibrium (i.e. allowing more natural erosion; Favennec, 2002c). As a consequence, the semi-stabilized dune may become fragmented, which may threaten *H. eriophorum* and

other specialists of the semi-stabilized dune. For instance, we observed that individuals at the BIS site occurred in a strongly eroding dune sector at the edge of the forest and that many individuals at this site were dead due to root and rhizome exposure (D. Frey, pers. observ., 2010). While the new management policies might not favour species of the semi-stabilized dune, they may of course favour species that can more easily cope with erosion. Thus, we suggest that these new management policies should be implemented in some parts of the region, whereas other (large and continuous) parts should be stabilized, unless inland dunes can be re-established at least in part of this, the largest dune system in Europe.

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APPENDIX. NOMENCLATURAL OVERVIEW OF *HIERACIUM ERIOPHORUM*

Symbols used: ‘≡’ a nomenclatural synonym, ‘=’ taxonomic synonym.

***Hieracium eriophorum* St.-Amans** Bull. Sci. Soc. Philom. Paris 3: 26, 1801.

Ind. loc.: ‘Sur les dunes maritimes de sable quartzeux pur et mobile des environs de la tête de Buch [La Teste-de-Buch], département de la Gironde’.

Lectotype (designated here): Plate II, Fig. 1 in St.-Amans Bull. Sci. Soc. Philom. Paris 3, 1801.

≡ *Hieracium umbellatum* subsp. *eriphorum* (St.-Amans) Bonnier, Fl. Ill. Fr. 7: 14, 1924.

= *Hieracium eriophorum* var. *intermedium* Arv.-Touv. Hier. Gall. Hisp. Cat.: 443, 1913.

Ind. loc.: ‘France occid.-mériod.: Gironde: Arcachon: dune du cap Ferret (avec le type); Basses-Pyrénées: Biarritz, à la Chambre d’Amour, etc’.

Lectotype (designated here) [the plant on the right]: ‘France occidentale-mériod. (Gironde): Arcachon: dunes du cap Ferret (avec le type); (Basses-Pyrénées): Biarritz, à la Chambre d’Amour’, 2 août 1902 et 4 août 1901 (Hieraciotheca Gallica no. 1036, GRM-ARV: MHNGr.1914.36006, leg. J. Neyraut, det. C. Arvet-Touvet ut ‘*Hier. eriophorum* var. *intermedium*’).

= *Hieracium eriophorum* var. [β] *umbrosum* Rouy Fl. France, 9: 402, 1905.

Ind. loc.: ‘dunes herbeuses près d’Arcachon’.

Neotype (designated here): ‘France, Gironde, dunes boisées à Arcachon’, 15 septembre 1895 (LY-Rouy, leg. G. Rouy, not determined). (note: no suitable material for lectotypification could be traced.)

= *Hieracium prostratum* DC. in Mém. Agric. Soc. Agric. Dépt. Seine 11: 78, 1808.

Ind. loc.: ‘Vallons de dunes à Bayonne, près de l’embouchure de l’Adour’.

Lectotype (designated here): Bayonne, 30 août 1804 (G-DC, leg. et det. A.P. De Candolle ut ‘*Hieracium* nouveau, tige couchée’).

≡ *Hieracium eriophorum* var. [β] *prostratum* (DC.) Gren. & Godr. Fl. France, 388, 1850.

≡ *Hieracium eriophorum* subsp. [*] *prostratum* (DC.) Fr. Uppsala Univ. Årsskr. 1862: 132, 1862.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1. Principal coordinate analysis of the AFLP data from 46 individuals from six sampling sites, based on Jaccard's similarity distances. The first two principal coordinates axes are plotted.

Figure S2. Log-likelihood probability of the number of inferred clusters (K) estimated using STRUCTURE (Pritchard *et al.*, 2000).

Figure S3. Neighbor-joining tree of the six sampling locations, based on Euclidean distance of allele frequencies.

Table S1. Univariate statistics of measured/scored quantitative characters of *Hieracium eriophorum*. Character abbreviations and units are explained in Table 3. Min., minimum; 5%, 5% percentile; SD, standard deviation; Max., maximum; 95%, 95% percentile.

Table S2. Eigenvector values showing correlations of characters measured on *Hieracium eriophorum* with the first two principal components for the PCA based on all traits (PCA A), and the PCA based on the reduced set of traits (PCA B).

Table S3. List of herbarium records.

Table S4. Absence and presence records used for maps.