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DIPLOMARBEIT

Titel der Diplomarbeit

Is taxon diversity in prominent refugial areas overestimated? Phylogeny and taxonomy of the local endemic *Erigeron glabratus* subsp*. candidus* (Asteraceae)

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TABLE OF CONTENT

LIST OF FIGURES

LIST OF TABLES

LIST OF APPENDIX

INTRODUCTION

One of the most dramatic palaeoclimatic events, whose effects are still evident today, are the ice ages. They are caused by minimal fluctuations of the Earth's orbit resulting in a progressive accretion of the polar ice (Dynesius & Jansson, 2000). The subsequent climatic change had major impacts on biota in general and on mountain biota in particular, such as the Alps (Dynesius & Jansson, 2000; Schönswetter & Tribsch et al., 2004; Tribsch & Schönswetter, 2003; van Husen, 1997). Since the Alps were subjected to cumulative glaciation modifying landscapes, only ice-free habitats offered biota adequate living conditions: Peripheral areas such as marginal mountainous regions and lowlands as well as isolated mountain peaks protruding above the ice sheet also known as Nunataks have enabled survival (Comes & Kadereit, 1998; Hewitt, 1996; Hewitt, 1999; Schönswetter & Tribsch et al., 2004; Tribsch & Schönswetter, 2003).

The effects of climate fluctuations are reflected in distribution patterns and patterns of species diversity (Hewitt, 1999). For instance, disjunctive patterns can lead to allopatric separation of taxa and therefore to divergence and eventually speciation (Alvarez & Thiel-Egenter et al., 2009). Noticeable in this context is that disjunct distribution areas and endemism correlate with formerly unglaciated or only weakly glaciated regions of the Alps (Merxmüller, 1952; Schneeweiss & Schönswetter, 1999; Schönswetter & Tribsch et al., 2003). One of those enigmatic Pleistocene refugia is Koralpe, a mountain located in the eastern Central Alps of Austria. The rocks are mainly comprised of paragneiss and mica with marble belts in a few places (Widder, 1955). The isolated geographical situation of the mountain compared with the geological constitution and negligible glaciation during the ice ages is reflected in a high botanical diversity (Closs, 1927; Heritsch, 1921). It harbours several endemics and subendemics. These include *Doronicum cataractarum* WIDDER and *Erigeron glabratus* subsp. *candidus* WIDDER, both belonging to the family of Asteraceae. Whereas the taxonomic distinctness of *D. cataractarum* is beyond dispute, the taxonomic status of *E. glabratus* subsp. *candidus* has changed over time. Initially described as separate species *Erigeron candidus* (Widder, 1932), this taxon was reduced to a subspecies of *E. glabratus*, a species widespread from the Pyrenees to the Balkan Peninsula (Huber, 1993).

The genus *Erigeron* includes about 200 taxa worldwide and has its origin in the western North American ranges (Huber, 1993). In the Alps, HUBER (1993) distinguishes 9 taxa in total, occurring at higher elevations: *E. acer* L., *E. alpinus* L., *E. angulosus* GAUDIN, *E. atticus* VILL., *E. gaudinii* BRÜGGER, *E. glabratus* HOPPE & HORNSCH. ex BLUFF & FINGERH subsp. *glabratus*, *E. glabratus* subsp. *candidus* WIDDER, *E. neglectus* KERNER and *E. uniflorus* L.. Several of these species have distinct distributions and habitats, but are morphologically difficult to distinguish exhibiting only weakly expressed differential characteristics (Huber, 1993; Huber & Leuchtmann, 1992). Responsible

for this is the variability of morphological characters especially in contact areas where intermediate types frequently appear as a result of hybridizations (Huber & Leuchtmann, 1992; Utelli & Huber, 1996). *E. glabratus* subsp. *candidus* is one of those taxa that is difficult to determine. The taxon is distinguished from *E. glabratus* subsp. *glabratus* mainly by the color of the petals (completely white during anthesis) and its always one-headed habitus (Fischer & Oswald et al., 2008). Although these characteristics always occur in this combination in *E. glabratus* subsp. *candidus*, they are also found in *E. glabratus* subsp. *glabratus* individuals (for a more detailed morphological description see Material and Methods). The two taxa are also geographically separated, with *E. glabratus* subsp. *candidus* being restricted to higher altitudes of Koralpe and *E. glabratus* subsp. *glabratus* occurring frequently on limestone areas throughout the Alps (Fischer & Oswald et al., 2008; Huber, 1993).

The aim of this study is a clarification of differential characteristics of *E. glabratus* subsp. *candidus* against its closely related *E. glabratus* subsp. *glabratus* based on former works by Huber (1993); Utelli & Zopfi (1995); Utelli & Huber (1996). To this end, we infer phylogenetic relationship using molecular data (ITS sequencing) and investigate morphological as well as ecological differentiation from the widespread and closely related *E. glabratus* subsp. *glabratus.*

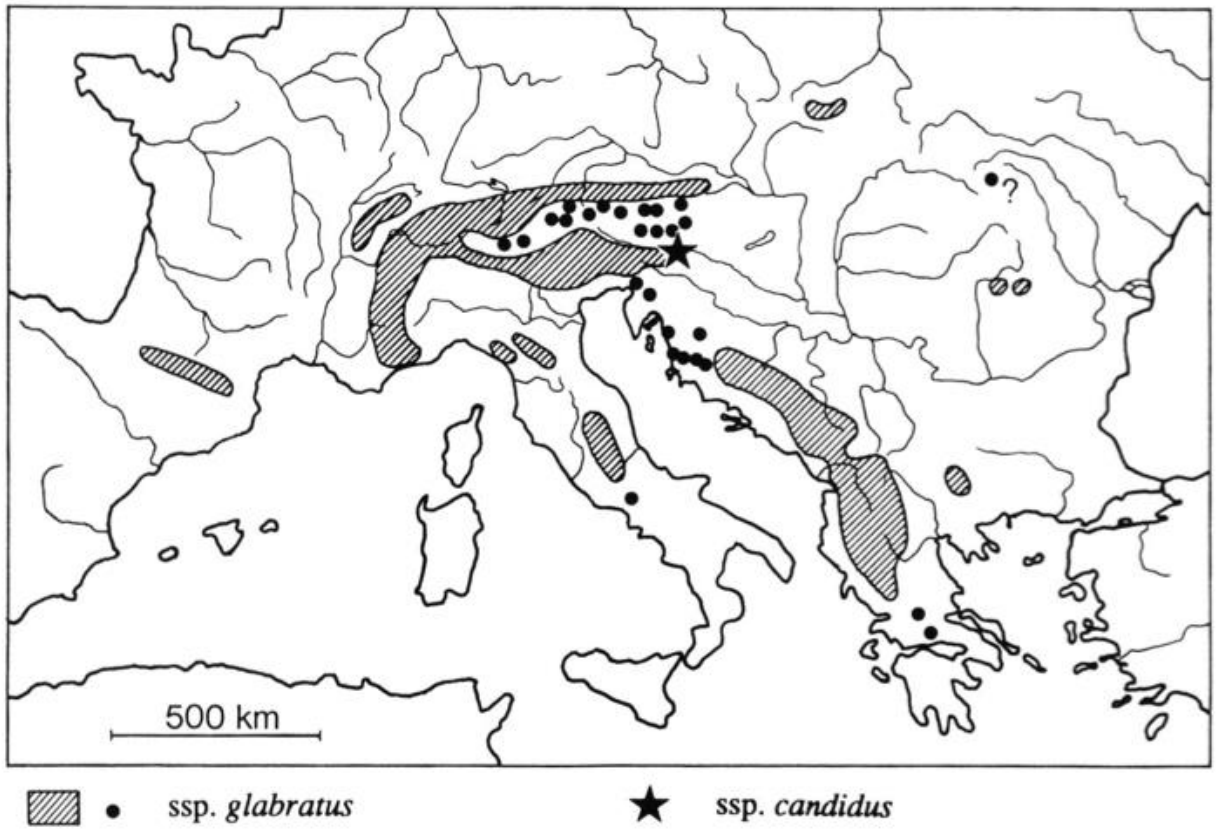

Fig. 1 Distribution area of *E. glabratus* subsp**.** *glabratus* (hatched areas and dots) and *E. glabratus* subsp. *candidus* (star). Following Meusel & Jäger et al. (1992), changed by Huber (1993).

MATERIAL AND METHODS

STUDY AREA AND STUDY SPECIES

The Eastern Alps have a characteristic composition of limestone and dolomites in the North and South (Northern and Southern Calcareous Alps) and siliceous bedrocks in higher altitudes in the central parts (Central Alps). The investigated areas were selected to cover all major areas of occurrence of *E. glabratus* subsp. *glabratus* maximally 130 km from the single site of *E. glabratus* subsp. *candidus* (**Fig. 2**). They were chosen using data from the Mapping of the flora of Austria project (Österreichs, 2001). The whole sample list is in the appendix (**TableS 1**).

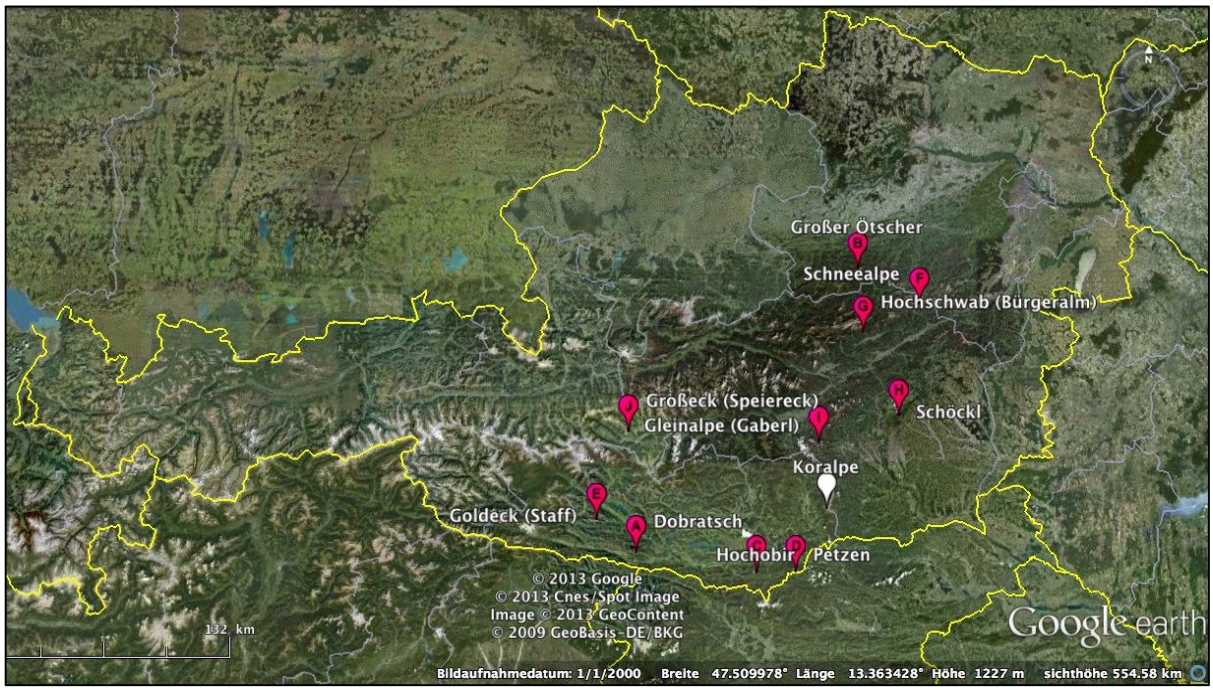

Fig. 2 Locations of sampled individuals; Dobratsch (A), Großer Ötscher (B), Hochobir (C), Petzen (D), Staff (E), Hochschwab (G), Schöckl (H), Gleinalpe (I), Speiereck (J); taken from Google earth (Patterson, 2007)

Erigeron glabratus subsp. *candidus* is distinguished from *Erigeron glabratus* subsp. *glabratus* mainly by the possession of exclusively single heads (versus one to six heads) with constantly white ligulate florets that may become purple at the basis after anthesis (versus predominately purple and only rarely white ligulate florets); by the almost glabrous lower leaves (versus glabrous to sparsely hairy leaves); by the sparsely to densely hairy involucral bracts with mostly purple tips (versus nearly glabrous to strongly hairy involucral bracts with only sometimes purple tips); and by the plant height of 3–30 cm (versus 5–40 cm; Fischer & Oswald et al., 2008). Huber (1993) mentions several further

characters, which weakly differentiate between the two taxa; these are listed in **Table 1.** Although none of the diagnostic characters is restricted to *Erigeron glabratus* subsp. *candidus* and each is also found in *E. glabratus* subsp. *glabratus*, the constant occurrence of the development of a single head and the white ligulate florets within the populations of *Erigeron glabratus* subsp. *candidus* has been suggested to indicate a certain discreteness (Huber, 1993). Both taxa grow on calcareous substrate (limestone, marble) mostly on rocks, screes and open grasslands (Fischer & Oswald et al., 2008).

Fig. 3 Habitus of the two investigated taxa: (A) *E. glabratus* subsp. *candidus*, (B) *E. glabratus* subsp. *glabratus* on the right side; taken from Huber (1993).

Table 1 Morphological characters tentatively differentiating *E. glabratus* subsp. *glabratus* and *E. glabratus* subsp. *candidus* (based on Huber 1993).

Characteristics	***Erigeron glabratus* subsp. *glabratus***	***Erigeron glabratus* subsp. *candidus***
Pubescence of the stem (lower part) [hairs/mm^2]	< 8	< 5
Length of basal leaves [cm]	1 – 10	1 – 6
Width of basal leaves [cm]	0.3 – 1	0.3 – 0.8
Pubescence of the lower basal leaves [hairs/mm^2]	0 – 5	almost glabrous
Pubescence of the upper basal leaves [hairs/mm^2]	0 – 5	0 – 2
Pubescence of the outer involucral leaves [hairs/mm^2]	1 – 8	3 – 8
Length of ray floret [mm]	5 – 7	3 – 4
Anthesis*	July – September	July – August

FIELDWORK

Ten populations of *E. glabratus* subsp. *glabratus* from the Eastern Alps and the single population of *E. glabratus* subsp. *candidus* were investigated during summer 2013 (**Table 2**; **Fig. 2**; **TableS 1**). Ten individuals were collected per population except in too small populations of the widespread *E. glabratus* subsp. *glabratus* and in the single population of the locally distributed *E. glabratus* subsp. *candidus* (five individuals as requested by the collecting permit; **Table 2**). From each sampled individual, a herbarium voucher (to be deposited in WU) suitable for morphometric measurements was made after one cauline leave was removed and dried in silica gel for genetic analyses. For genetic analysis, *Erigeron alpinus* and *E. uniflorus* were included as outgroups.

In a circular plot with 20 cm radius centered at the focal *Erigeron* individual, several abiotic (altitude, exposition, inclination; Appendix **TableS 1**) and biotic parameters (vegetation coverage, accompanying species; Appendix **TableS 2**) were recorded. Identification and nomenclature of the accompanying species is based on Fischer & Oswald et al. (2008). Species not identified in the field were taken to the Institute of Botany of the University of Vienna (Austria) either to compare them with Herbarium vouchers or to obtain the expertise of Mag. Dr. Gerald Schneeweiss, Dr. Luise Ehrendorfer-Schratt and Dr. Josef Greimler.

Table 2 Locations of the populations including sample size, averages altitude [m], average northing and average easting [decimal degree]; for further details see Appendix **TableS 1**.

Pop.	Species	Sampled Individuals	Location	Altitude Average	Northing Average	Easting Average
A	*Erigeron glabratus* subsp. *glabratus*	10	Dobratsch (SW Zehnernock) Carinthia	1809.50	46.593086	13.700669
B	*Erigeron glabratus* subsp. *glabratus*	10	Großer Ötscher Lower Austria	1736.20	47.857567	15.192547
C	*Erigeron glabratus* subsp. *glabratus*	10	Hochobir Carinthia	1831.80	46.503951	14.501537
D	*Erigeron glabratus* subsp. *glabratus*	10	Petzen (Kniepsattel) Carinthia	2043.90	46.504456	14.759840
E	*Erigeron glabratus* subsp. *glabratus*	6	Goldeck (Staff) Carinthia	2151.00	46.735545	13.435113
F	*Erigeron glabratus* subsp. *glabratus*	10	Schneealm Styria	1782.70	47.696097	15.609572
G	*Erigeron glabratus* subsp. *glabratus*	8	Hochschwab (Bürgeralm) Styria	1531.10	47.572884	15.222883
H	*Erigeron glabratus* subsp. *glabratus*	10	Schöckl Styria	1433.30	47.197724	15.460560
I	*Erigeron glabratus* subsp. *glabratus*	7	Gleinalpe (Gaberl) Styria	1648.60	47.081849	14.919619
J	*Erigeron glabratus* subsp. *glabratus*	8	Großeck (Speiereck) Salzburg	2124.40	47.131390	13.639965
K	*Erigeron glabratus* subsp. *candidus*	5	Koralpe (Seekar) Styria	1990.30	46.790887	14.979092

MORPHOMETRIC ANALYSES

In agreement with previous investigations by Utelli & Huber (1996); Utelli & Zopfi (1995) ten morphological characters were measured for all sampled individuals, for 165 selected herbarium specimens (from WU and GZU; complete lists in Appendix **TableS 3**), and for seven non-collected individuals of *E. glabratus* subsp. *candidus*. We restrict ourselves to quantitative characters because this greatly facilitates statistical analysis and because the only qualitative diagnostic character (flower color) could not be assessed anymore in late collected plants. The measured characters are (**Fig. 4**): A, Distance from the uppermost cauline leaf to the flowering head, hereinafter referred to as scape length [cm] ("Distance"); H, plant height measured as the distance from the base of the rosette to the apex of the involucral bacts [cm] ("Height"); Z, number of heads including pre- and post-anthetic ones ("Heads"); F, shape of the upper basal leaves expressed as the ratio of leaf length to distance from base to maximal width [cm] ("ShapeLeaf"); I, leaf index of the upper basal leaves expressed as the ratio of leaf length to leaf width [cm] ("IndexLeaf"); L, involucrum length [cm] ("LenghtInv"); O, pubescence of the upper basal leaves [hairs/mm^2] ("PubUpper"); U, pubescence of the lower basal leaves [hairs/mm^2] ("PubLower"); B, pubescence of the outer bracts [hairs/mm^2] ("PubBracts"); S, pubescence of the stem [hairs/mm^2] ("PubStem"). For an accurate evaluation of the pubescence, hairs were counted three times on the upper side of the leaf beside the main nerve in a 1mm^2 plot and then averaged (Utelli & Zopfi,1995).

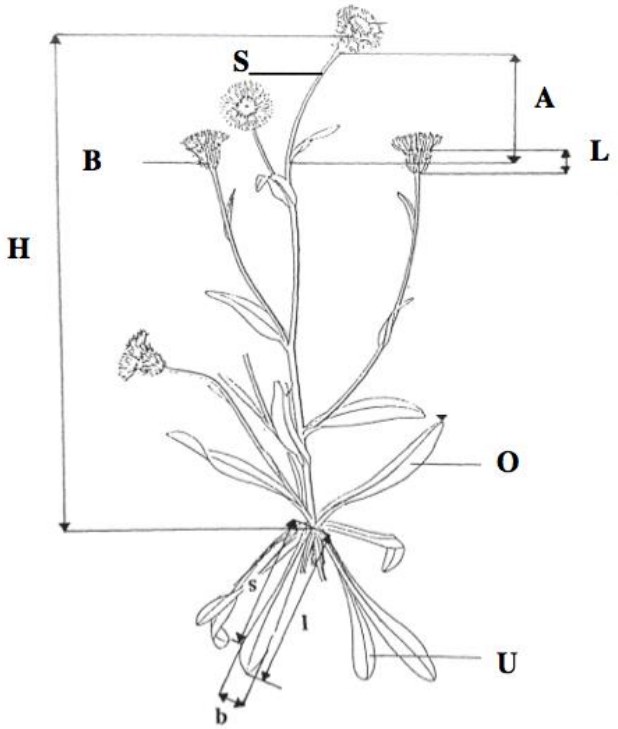

Fig. 4 Scheme of an *Erigeron* plant taken from Utelli & Zopfi (1995) and modified; including the landmarks descriped in text; b= width, l= lenght from the base to the tip, s= distance from leaf base to the max. width.

Statistical analyses were all done using R 3.0.1 GUI (Venables & Smith, 2010). Principal component analysis (PCA) was done using the functions PRINCOMP or PRCOMP; principal coordinate analysis (PCO) was performed with the package ECODIST (Goslee & Urban, 2007) using an Euclidean dissimilarity matrix. Putative differences between the two subspecies with respect to the morphometric characters were assessed via Wilcoxon rank sum tests. Data exploration was achieved via scatterplot matrices generated with GGPLOT2 (Wickham, 2008) and GGALLY (Schloerke & Crowley et al., 2011).

ECOLOGICAL ANALYSES

The habitats were characterized using the indicator values of Landolt (1977). To this end, for each sample plot the averages of the indicator values moisture (F), dispersity (D), light (L), continentality (K), reaction (R), humus (H), nutrients (N) and temperature (T) of the accompanying species were calculated. Species for which at least one indicator value is lacking were removed from this analysis (see Appendix **TableS 2** for details).

All statistical tests and visualisations were done using R. For PCA, PCO and the generating of scatterplot matrices the same functions and packages were used as for the morphometric data. Putative differences between the two subspecies with respect to the ecological data were assessed using non-parametric Wilcoxon rank sum test.

DNA ISOLATION AND ITS SEQUENCING

Total genomic DNA was extracted from roughly similar amounts of silica gel dried leaf-material following the CTAB-protocol (Doyle & Doyle, 1987) with minor modifications. The quality of the DNA was checked on a 1% TAE agarose gel run for 20 min at 90 V; the quantity was checked via NanoDrop (Peqlab).

One randomly selected individual of each *E. glabratus* population and of the two outgroup taxa were used for generating sequences of the internal transcribed spacer (ITS) region of the nuclear ribosomal DNA. Altogether, ten individuals of *E. glabratus* subsp. *glabratus* (A3, B3, C1, D2, E2, F2, G3, H9, I4, J0), one of *E. glabratus* subsp. *candidus* (K0), one of *E. alpinus* (L3) and one of *E. uniflorus* (M4) were sequenced. The ITS region was amplified by polymerase chain reaction (PCR) using the primers ITS4 and ITS5 (Noyes, 2006; White & Bruns et al., 1990) with the sequences 5'-TCCTCCGCTTATTGATATGC-3' (ITS4, reverse) and 5'-GGAAGTAAAAGTCGTAACAAGG-3' (ITS5, forward). The PCR reactions were performed in 15 µl volumes containing 1 µl of the DNA

extract, 4.8 µl REDTaq ReadyMix (Sigma-Aldrich, Vienna), 7.4 µl ddH_2O, 0.6 µl DMSO and 0.15 µl each of forward and reverse primers. Cycling conditions were: 1 min at 95°C followed by 35 cycles with each 30 s at 95°C, 30 s at 52°C and 90 s at 72°C, followed by an extension period of 7 min at 72°C. 2 µl of the PCR products were checked on 1.5% TAE agarose gel run for 20 min at 90 V. For enzyme cleanup 2 µl of an ExoI-FastAP mastermix (150 µl ddH_2O, 100 µl FastAP and 50 µl ExoI; Fisher Scientific, St. Leon-Rot, Germany) was added to the samples following the manufacturer's instructions. The PCR reactions for cycle sequencing were performed in 10 µl volumes containing 1 µl Big Dye, 1 µl 3.2 µM primer, 2 µl ddH_2O and 6 µl PCR product. The products were cleaned with a total amount of 600 µl Sephadex following the manufacturer's instructions. After preparation of the Sephadex plates the cycle sequencing products and 10 µl ddH_2O were added on top of the columns and centrifuged for 5 minutes. Subsequently, the supernatant comprised the purified DNA (cycle sequencing product) and was sequenced on an ABI 3770 DNA Analyzer (PE Applied Biosystems).

PHYLOGENETIC ANALYSES

The ITS sequences were assembled with SeqMen (Swindell & Plasterer, 1997) and aligned manually with Bioedit (Hall, 2001). This alignment also included sequences from 33 additional species (obtained from GenBank; Benson & Karsch-Mizrachi et al. (2010); **Table 3**) from *Erigeron* clade VI (Noyes, 2006) that contains *E. uniflorus*. Phylogenetic analyses using maximum parsimony were conducted using PAUP 4.0b8 (Swofford, 1993).

Table 3 Taxa included in the molecular data set with GenBank accession numbers and sequence lengths.

Species	Genbank	bp	Species	Genbank	bp
Conyza apurensis	AF118482	623	*Erigeron kachinensis*	AF118480	625
Conyza canadensis	AF046987	623	*Erigeron karvinskianus*	AF118487	626
Conyza ramosissima	AF118484	623	*Erigeron leiomerus*	AF118492	622
Erigeron acris	AF118496	622	*Erigeron leptorhizon*	AF118483	623
Erigeron annuus	AF118489	626	*Erigeron lonchophyllus*	AF118505	625
Erigeron argentatus	AF118506	622	*Erigeron pinnatisectus*	AF118501	625
Erigeron borealis	AF118495	622	*Erigeron pulchellus*	AF118500	625
Erigeron caespitosus	AF118481	625	*Erigeron religiosus*	AF118486	627
Erigeron cinereus	AF118502	625	*Erigeron scopulinus*	AF118497	625
Erigeron divergens	AY871317	624	*Erigeron simplex*	AF118493	622
Erigeron flettii	AF118503	625	*Erigeron speciosus*	AF118479	625
Erigeron formosissimus	AF118478	625	*Erigeron strigosus*	AF118490	626
Erigeron glabellus	AF118498	624	*Erigeron tenuis*	AF118488	626
Erigeron glaucus	AF118499	624	*Erigeron uniflorus*	AF046988	622
Erigeron grandiflorus	AF118494	622	*Erigeron ursinus*	AF118491	622
Erigeron grandiflorus	AF118494	622	*Erigeron utahensis*	AF118507	626
Erigeron humilis	AF118504	625			

All characters were equally weighted and multistate positions were interpreted as uncertainty; gaps were treated as missing. Heuristic searches included 500 random sequence addition replicates keeping maximally 100 trees per replicate and TBR branch swapping. Branch support was assessed via bootstrap analysis using 1000 bootstrap replicates and heuristic search settings with 10 random sequence addition replicates.

RESULTS

MORPHOMETRIC ANALYSES

Correlations of morphological characters are given in **Table 4** and **FigureS 1** (Appendix). The following characters are significantly positively correlated: "Distance" – "Height" (Pearson's r = 0.362, p < 0.001), "Distance"– "IndexLeaf" (r = 0.133, p = 0.033), "Height" – "Heads" (r = 0.253, p < 0.001), "Height" – "IndexLeaf" (r = 0.491, p < 0.001), "Heads" – "IndexLeaf" (r=0.125, p=0.046), "ShapeLeaf" – "PubBracts" (r = 0.142, p = 0.022), "PubUpper" – "PubLower" (r = 0.604, p < 0.001), "PubUpper" – "PubBracts" (r = 0.422, p < 0.001), "PubLower" – "PubBracts" (r = 0.343, p < 0.001) and "PubStem" – "PubBracts" (r = 0.178, p = 0.004); these are significant negatively correlated: "Distance" – "PubStem" (r = -0.22, p < 0.001), "Height" – "PubStem" (r = -0.192, p = 0.002), "ShapeLeaf" – "IndexLeaf" (r = -0.134, p = 0.022) and "IndexLeaf" – "PubUpper" (r = -0.138, p = 0.026).

Table 4 Correlation coefficients (upper triangle) and associated p-values (lower triangle) of the morphometric data.

	Distance	Height	Heads	Shape Leaf	Index Leaf	Lenght Inv	Pub Upper	Pub Lower	Pub Bracts	Pub Stem
Distance	x	**0.362**	-0.037	0.087	**0.133**	-0.028	0.043	0.047	0.005	**-0.220**
Height	**0.000**	x	**0.253**	-0.049	**0.491**	0.003	0.054	0.027	0.121	**-0.192**
Heads	0.560	**0.000**	x	0.065	**0.125**	-0.038	0.023	0.004	-0.042	-0.037
ShapeLeaf	0.166	0.439	0.301	x	**-0.134**	0.007	0.003	0.057	**0.142**	0.041
IndexLeaf	**0.033**	**0.000**	**0.046**	**0.032**	x	0.051	**-0.138**	-0.115	0.024	-0.057
LenghtInv	0.717	0.962	0.547	0.910	0.416	x	0.069	-0.018	0.055	0.017
PubUpper	0.492	0.387	0.713	0.965	**0.026**	0.268	x	**0.604**	**0.422**	0.014
PubLower	0.458	0.664	0.952	0.363	0.067	0.778	**0.000**	x	**0.343**	0.015
PubBracts	0.939	0.053	0.502	**0.022**	0.703	0.379	**0.000**	**0.000**	x	**0.178**
PubStem	**0.000**	**0.002**	0.554	0.516	0.367	0.783	0.828	0.808	**0.004**	x

The scatterplot matrix in **FigureS 2** (Appendix) represents another way for visualizing the collected morphological data, offering a comparison of the investigated taxa with respect to their morphological characteristics. As apparent from the matrix, the greatest variability between the two species concern "Distance", where *E. glabratus* subsp. *candidus* has longer scapes than *E. glabratus* subsp. *glabratus*. Furthermore, *E. glabratus* subsp. *candidus* is exclusively one-headed while in *E. glabratus* subsp. *glabratus* the number of heads varies from one to five. Minor differences exist concern indumentum characteristics ("PubUpper" and "PubLower") in that *E. glabratus* subsp. *glabratus* has more hairs than *E. glabratus* subsp. *candidus*. There are no differences with respect to the remaining characteristics.

Wilcoxon tests exhibit significant differences between the two taxa with respect to the following characters (**Table 5**): "Distance" ($p < 0.001$), "Height" ($p < 0.001$), "Heads" ($p < 0.001$), "IndexLeaf" ($p = 0.001$), "LenghtInv" ($p < 0.001$), "PubUpper" ($p < 0.001$), "PubLower" ($p < 0.001$) and "PubBracts" ($p < 0.001$). The number of flowering heads per plant ("Heads") is the most strongly discriminating character with p-values of $3.013e^{-10}$. The other parameters show no significant differences between the species. The within and between group variances are listed in **Table 5**. Measurement "PubStem" has the greatest within group variance (213.727), followed by the factors "Height" (17.864), "PubBracts" (6.311), "PubUpper" (4.063), "IndexLeaf" (3.882), "PubLower" (1.393), and "Distance" (1.282). The greatest between group variance has the parameter "Height" with a variance of 1.213.

Table 5 Results of Wilcoxon rank sum tests of the morphometric data (p-values), within and between group variances as well as group means of the two taxa.

Morphometrics	p-value Wilcoxon	Within groups variance	Between groups variance	Group means *E. cand*	Group means *E. glab*
Distance	**0.000**	1.282	0.168	1.859	1.262
Height	**0.000**	17.864	1.213	10.228	8.583
Heads	**0.000**	0.341	0.091	1.000	1.432
ShapeLeaf	0.373	0.005	0.000	1.232	1.243
IndexLeaf	**0.001**	3.882	0.229	9.214	8.494
LenghtInv	**0.000**	0.221	0.000	0.631	0.623
PubUpper	**0.000**	4.063	0.693	1.988	3.192
PubLower	**0.000**	1.393	0.207	0.630	1.291
PubBracts	**0.000**	6.311	0.852	5.750	7.093
PubStem	0.850	213.727	0.000	29.602	30.944

The first and second axes of the principal coordinate analysis explain 19.8% and 18.3% of the total variation (**Fig. 5B**). Along these two axes, there is no separation between the two subspecies. The first and second axes of the principal component analysis explain 19.8% and 18.3%, respectively, of the total variation (**Fig. 5A**) and give qualitatively identical results to the PCO. The loadings of each character on the PCA axes are given in **Table 6**.

Table 6 Loadings of the morphometric characters on the PCA axes.

Characters	Comp 1	Comp 2	Comp 3	Comp 4	Comp 5	Comp 6	Comp 7	Comp 8	Comp 9	Comp 10
Distance		-0.424	0.474		0.301	-0.218	0.574	0.124	-0.336	
Height		-0.641	-0.114						0.731	0.168
Flowers		-0.256	-0.263	0.534	-0.409	0.497	0.241	0.185	-0.268	
ShapeLeaf	-0.136		0.200	0.736	0.474		-0.246	-0.292	0.105	-0.125
IndexLeaf	0.164	-0.494	-0.405	-0.116		-0.201	-0.281	-0.459	-0.405	-0.232
LenghtInv			-0.281	-0.307	0.633	0.630	0.130			0.100
PubUpper	-0.598			-0.154	-0.155	0.149			0.140	-0.734
PubLower	-0.573		0.122		-0.208			-0.521		0.563
PubBracts	-0.500		-0.245		0.186	-0.265	-0.345	0.596	-0.252	0.188
PubStem	-0.122	0.285	-0.577	0.175	0.113	-0.406	0.572	-0.140	0.122	
Stand. dev.	1.404	1.352	1.071	1.035	1.014	0.969	0.817	0.744	0.627	0.603
Prop. var.	0.198	0.183	0.115	0.108	0.103	0.094	0.067	0.056	0.039	0.036
Cum. prop.	0.198	0.381	0.496	0.604	0.707	0.801	0.869	0.924	0.964	1.000

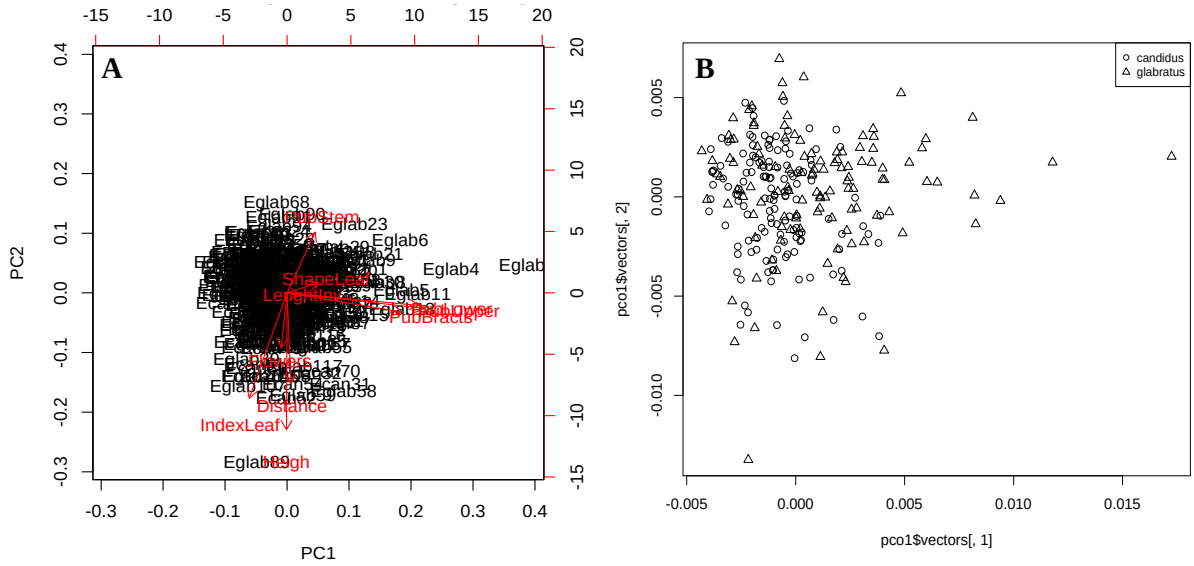

Fig. 5 Results of (A) PCA and (B) PCO analyses of standardized morphometric data from *Erigeron glabratus* subsp. *glabratus* and *E. glabratus* subsp. *candidus*.

ECOLOGICAL ANALYSES

The scatterplot matrix (Appenidx, **FigureS 3**) visualizes pairwise correlations for the indicator values. Correlations coefficients and their p-values are listed in **Table 7**. The largest significantly positive correlations with $r > 0.4$ and p-values < 0.001 concern "Light" – "Temperature" ($r = 0.680$), "Continentality" – "Light" ($r = 0.586$), "Temperature" – "Nutrients" ($r = 0.566$), "Continentality" – "Dispersity" ($r = 0.480$) and "Dispersity" – "Reaction" ($r = 0.429$). The largest significantly negative correlations with $r > -0.4$ and p-values < 0.001 are "Continentality" – "Moisture" ($r = -0.723$), "Humus" – "Dispersity" ($r = -0.648$), "Nutrients" – "Dispersity" ($r = -0.642$), "Light – Humus" ($r = -0.555$), "Temperature" – "Exposition" ($r = -0.553$), "Temperature" – "Dispersity" ($r = -0.491$), "Light" – "Nutrients" ($r = -0.457$) and "Reaction" – "Humus" ($r = -0.436$).

Table 7 Correlation coefficients (upper triangle) and associated p-values (lower triangle) of the ecological data.

	T	K	L	F	R	N	H	D	Alt	Ex	In	Cov
T	x	0.009	-0.398	-0.314	-0.060	0.566	0.273	-0.491	-0.373	-0.553	-0.197	-0.089
K	0.901	x	0.586	-0.723	0.165	-0.389	-0.384	0.480	-0.078	0.114	-0.029	-0.006
L	**0.000**	**0.000**	x	-0.397	0.217	-0.457	-0.555	0.680	0.202	0.354	0.143	0.014
F	**0.000**	**0.000**	**0.000**	x	-0.261	0.368	0.194	-0.360	0.046	-0.020	0.126	-0.080
R	0.390	**0.018**	**0.002**	**0.000**	x	-0.301	-0.436	0.429	0.191	0.098	-0.145	-0.110
N	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	x	0.276	-0.642	-0.350	-0.398	-0.055	-0.189
H	**0.000**	**0.000**	**0.000**	**0.005**	**0.000**	**0.000**	x	-0.648	-0.241	-0.112	-0.170	0.092
D	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	x	0.396	0.384	0.256	0.040
Alt	**0.000**	0.268	**0.004**	0.517	**0.006**	**0.000**	**0.001**	**0.000**	x	0.202	0.246	0.005
Ex	**0.000**	0.106	**0.000**	0.778	0.163	**0.000**	0.110	**0.000**	**0.004**	x	0.172	0.144
In	**0.005**	0.681	**0.041**	0.073	**0.038**	0.431	**0.015**	**0.000**	**0.000**	**0.014**	x	0.051
Cov	0.206	0.931	0.838	0.252	0.118	**0.007**	0.191	0.569	0.941	**0.040**	0.471	x

As apparent from the scatterplot matrix (Appendix, **FigureS 4**), *Erigeron glabratus* subsp. *candidus* has lower T- and R-values but higher F-values than its close relative. Furthermore, *E. glabratus* subsp. *glabratus* shows a broader distribution with respect to the parameter "Nutrients". The remaining indicator values feature no differences between the two taxa. Minor differences also exist in "Altitude" and "Exposition": *E. glabratus* subsp. *glabratus* has wide amplitudes while *E. glabratus* subsp. *candidus* occurs around average values. "Coverage" features higher values for *E. glabratus* subsp. *candidus*, while "Inclination" shows no differences.

Table 8 lists the p-values of the Wilcoxon rank sum tests as well as the within and between group variances and the group means of the two investigated taxa. The indicator values "Temperature", "Moisture" and "Reaction" have p-values < 0.001, indicating highly significant differences in the ecological preferences of the two taxa. The parameters "Altitude" and "Inclination" are significantly different too (p-values < 0.05), whereas the remaining parameters do not differ significantly (p-value > 0.05). The within and between group variances are listed in **Table 8**. "Dispersity" (0.301) and "Temperature" show the greatest within group variance, "Continentality" (0.051) and "Light" (0.053) the lowest. With values of < 0.001, the lowest between group variances are given by "Continentality", "Light", "Nutrients", "Dispersity", "Coverage" and the abiotic parameter "Exposition". "Humus" has a value of 0.004. Therefore, *E. glabratus* subsp. *glabratus* and *E. glabratus* subsp. *candidus* occupy habitats with similar altitudes and inclinations but different expositions and total coverage of the accompanying vegetation.

Table 8 Results of Wilcoxon rank sum tests of the ecological data (p-values), within and between group variances as well as group means of the two taxa.

Indicator values	p-value Wilcoxon	Within groups variance	Between groups variance	Group means E. candidus	Group means E. glabratus
Temperature (T)	**0.000**	0.102	0.117	1.763	2.255
Continentality (K)	0.238	0.051	0.000	3.395	3.467
Light (L)	0.436	0.053	0.000	4.134	4.193
Moisture (F)	**0.000**	0.056	0.045	2.731	2.424
Reaction (R)	**0.000**	0.082	0.053	3.424	3.760
Nutrients (N)	0.676	0.068	0.000	2.208	2.239
Humus (H)	0.413	0.072	0.004	2.680	2.798
Dispersity (D)	0.825	0.301	0.000	3.417	3.339
Altitude	**0.004**	43960.990	16462.650	1990.308	1798.472
Exposition	0.641	8175.404	0.000	196.077	174.405
Inclination	**0.003**	180.780	113.628	32.538	16.944
Coverage	0.516	605.179	0.000	71.923	65.61798

In the PCO (**Fig. 6B**), *Erigeron glabratus* subsp. *candidus* is separated along the second axis, which explains 17.1% of the total variance; the first axis explains 34.3%. Qualitatively similar results are obtained from the principal component analyses (**Fig. 6A**; **Table 9**), where *Erigeron glabratus* subsp. *candidus* is weakly differentiated from *Erigeron glabratus* subsp. *glabratus* along the second axis (17.1% of the total variance; the first component explains 34.3% of the total variation).

Table 9 Loadings of the ecological data on the PCA axes.

	Comp 1	Comp 2	Comp 3	Comp 4	Comp 5	Comp 6	Comp 7	Comp 8	Comp 9	Comp 10	Comp 11	Comp 12
T	0.278	-0.470		0.142	0.302		0.261	0.220		-0.246		0.634
K	-0.298	-0.429	0.185	0.205	-0.159	-0.110			-0.230	0.694	0.206	0.165
L	-0.396			0.208	-0.237		-0.203	0.330	0.703		-0.228	0.142
F	0.223	0.525	-0.217		-0.185	0.286	-0.177			0.287	0.155	0.607
R	-0.227	-0.156	-0.423	-0.475	0.219	0.241	0.456	-0.132	0.295	0.315		
N	0.377		-0.221	0.285		0.272	0.130	0.547		0.158	0.381	-0.391
H	0.334		0.387	-0.174		-0.485	0.187	-0.127	0.522	0.135	0.354	
D	-0.448							-0.114		-0.409	0.767	
Alt	-0.212	0.313	-0.236		0.486	-0.517	-0.198	0.467		0.177		
Ex	-0.251	0.291	0.286	-0.130	-0.356		0.619	0.394	-0.257			0.121
In	-0.107	0.294		0.719	0.283		0.399	-0.319	0.113	0.117	-0.121	
Cov			0.624	-0.118	0.540	0.504	-0.102	0.137				
Stand. dev.	2.028	1.434	1.136	1.030	0.943	0.846	0.783	0.688	0.538	0.467	0.431	0.309
Prop. var.	0.343	0.171	0.108	0.088	0.074	0.060	0.051	0.039	0.024	0.018	0.015	0.008
Cum. prop.	0.343	0.514	0.622	0.710	0.784	0.844	0.895	0.934	0.958	0.977	0.992	1.000

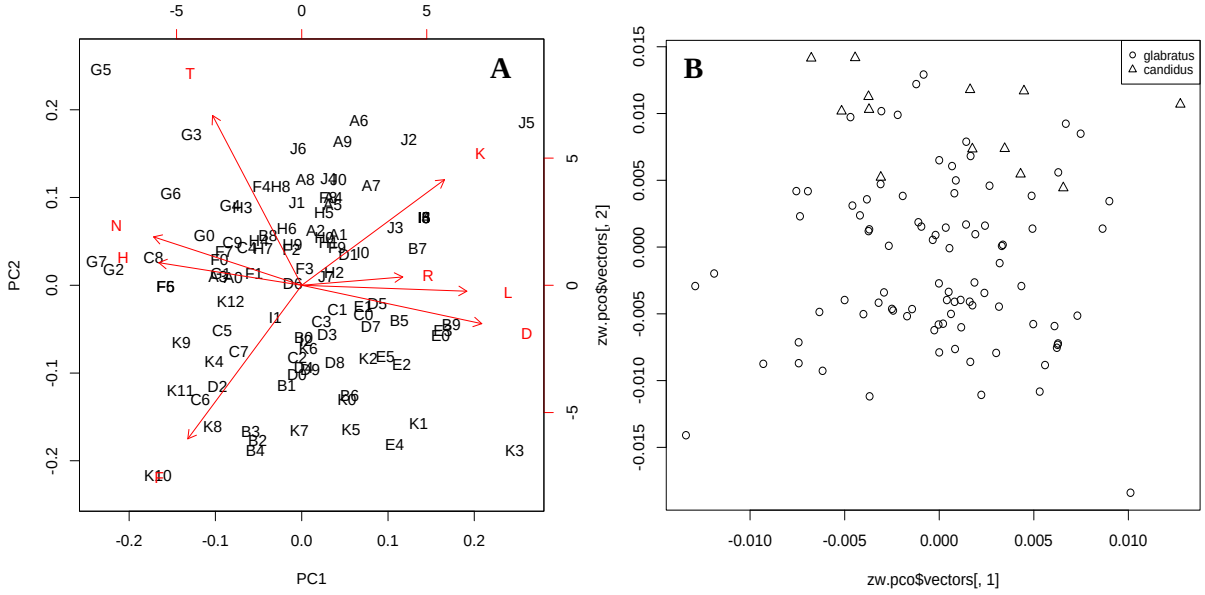

Fig. 6 Results of (A) PCA and (B) PCO analyses of standardized ecological data from *Erigeron glabratus* subsp. *glabratus* and *E. glabratus* subsp. *candidus*.

DNA ANALYSES

Newly obtained ITS sequences were 622–623 bp long (expect populations A and C, which did not work); aligned sequences were 630 bp long. Of these, 125 were variable and 75 were parsimony-informative. Heuristic search resulted in 724 equally parsimonious trees (length= 186; R.I = 0.892; R.C. = 0.700, C.I. = 0.785); the majority rule consensus tree is shown in **Fig. 7**. *Erigeron glabratus* subsp. *glabratus*, *E. glabratus* subsp. *candidus*, *E. alpinus*, *E. acris* and *E. borealis* constitute a moderately supported clade (bootstrap [BS] 65) that is sister to a paraphyletic *E. uniflorus* (BS 91). *Erigeron glabratus* subsp. *glabratus* is paraphyletic because of the nested position of *E. alpinus*, *E. acris* and *E. borealis*. *Erigeron glabratus* subsp. *candidus* has the same ITS sequences as *E. glabratus* subsp. *glabratus* from populations F, H, I, J, thus including all populations of *E. glabratus* subsp. *glabratus* from the Central Alps. The remaining populations of *Erigeron glabratus* subsp. *glabratus* constitute a distinct clade (BS 61) differing by a single synapomorphy.

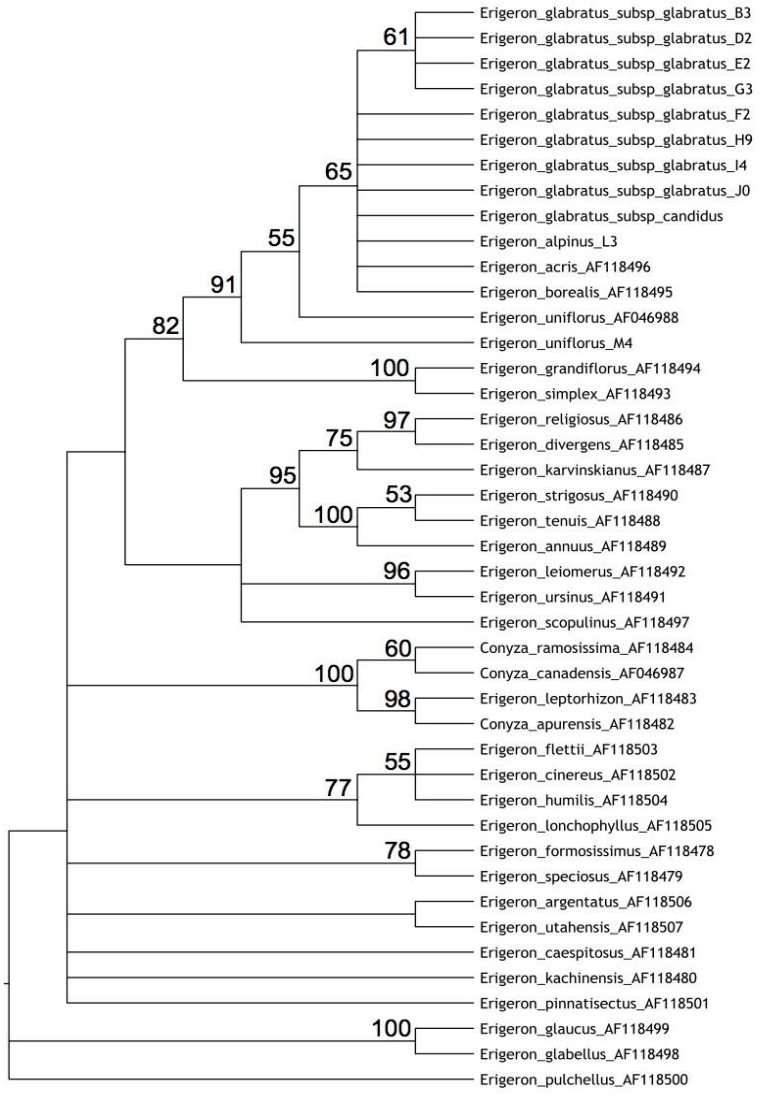

Fig. 7 Majority rule consensus tree

DISCUSSION

Erigeron glabratus subsp. *candidus* is an endemic of Mt. Koralpe, where it is restricted to marble belts embedded within crystalline rocks, while its close relative *E. glabratus* subsp. *glabratus* is a common species of higher altitudes within the Calcareous Alps and in limestone areas of the Central Alps (**Fig. 1**). These two subspecies mainly differ with respect to the number of flowering heads and the flower color of perianth, but none of the diagnostic features of *E. glabratus* subsp. *candidus* is restricted to this taxon (Huber, 1993). Here, we combine phylogenetic, morphometric and ecological analyses to address whether *E. glabratus* subsp. *candidus* constitutes a taxonomically distinct entity.

Erigeron glabratus subsp. *candidus* does not differ from *E. glabratus* subsp. *glabratus* with respect to its nuclear ITS sequences (**Fig. 7**). As *E. borealis*, *E. acris* and *E. alpinus* do not differ from *E. glabratus* subsp. *glabratus* either, ITS sequences obviously lack sufficient variation to distinguish among those closely related species. Intraspecific sequence variation in *E. glabratus* subsp. *glabratus* is geographically structured: all populations from the Central Alps (Schöckl, I; Gleinalpe, H; Speiereck, J) plus one from the northern Calcareous Alps (Schneealpe, F) possess the same ribotype as *E. glabratus* subsp. *candidus*, while the remaining populations of *E. glabratus* subsp. *glabratus* have distinct ITS-sequences (Appendix, **TableS 4**).

The two subspecies differ slightly with respect to their habitat conditions as inferred from indicator values of the accompanying vegetation (**Fig. 6 A & B**). Specifically, sites of *E. glabratus* subsp. *candidus* are slightly moister, more acidic and cooler. This is likely the result of the different substrate types the two taxa are growing on. Whereas *E. glabratus* subsp. *glabratus* usually occurs on limestone (as the case for the sampled populations), *E. glabratus* subsp. *candidus* is limited to marble, rich in other minerals such as pegmatite (Kieslinger 1928). Marble has smaller pore sizes (Graves & Monk, 1985) and thus can hold more water resulting in moister soils. The narrow marble belts on Koralpe are embedded within a geological matrix of crystalline rocks. Thus, acidophilic plants are frequent in the surrounding vegetation, some of which may marginally enter the sampling plots of *E. glabratus* subsp. *candidus* (e.g. *Juncus trifidus*, *Vaccinium gaulteroides*, *Vaccinium myrtillus*). Higher T-values for *E. glabratus* subsp. *glabratus* might be the result of our sampling strategy that focused on populations geographically close to *E. glabratus* subsp. *candidus* and which often are at relatively low altitudes (e.g., Gaberl 1646 – 1655 m; Schöckl 1426 – 1442 m). Generally, *E. glabratus* subsp. *glabratus* occupies a wider altitudinal amplitude than *E. glabratus* subsp. *candidus* (Fischer & Oswald et al., 2008).

The two taxa differ morphologically to some extent (**Fig. 5 A & B**). The main difference between *E. glabratus* subsp. *candidus* and *E. glabratus* subsp. *glabratus* is the number of flowering

heads. While *E. glabratus* subsp. *candidus* is constantly one-headed, its close relative possesses one to several heads. This characteristic is well known and constitutes together with flowering color the major diagnostic features (e.g. Huber, 1993; Fischer & Oswald et al., 2008-). A further difference concerns the length of the scape (i.e., the stem between the uppermost cauline leaf and the flowering head), which is longer in *E. glabratus* subsp. *candidus*. Scape length correlates significantly positively with plant height, which can strongly vary within and between populations. To some extent, this might, however, be due to the extent of grazing, because localities of *E. glabratus* subsp. *glabratus* are more strongly affected by grazing than the single locality of *E. glabratus* subsp. *candidus* on Koralpe. Finally, *E. glabratus* subsp. *glabratus* tends to be more strongly hairy than *E. glabratus* subsp. *candidus* as already found by Huber (1993). None of these diagnostic differences are, however, exclusive, and all morphological features of *E. glabratus* subsp. *candidus* can also be found in individuals of *E. glabratus* subsp. *glabratus*, although not in all individuals of the entire population.

Erigeron glabratus subsp. *candidus* is phylogenetically not and morphologically and ecologically only weakly differentiated from *E. glabratus* subsp. *glabratus*. *Erigeron glabratus* subsp. *candidus* probably evolved by vicariance. As Koralpe was only weakly glaciated during the ice ages and thus acted as a Pleistocene refugium, *E. glabratus* probably survived glacial periods *in situ*. The morphological and ecological homogeneity of *Erigeron glabratus* subsp. *candidus* likely is due to a population bottleneck and the small population sizes on Koralpe, which fostered fixation of morphological characters found more rarely in *Erigeron glabratus* subsp. *glabratus*. Therefore, the rank as a subspecies is adequate.

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APPENDIX

TableS 1 Sampled individuals including altitude [m], northing and easting [decimal degrees], exposition and inclination [°degree] and coverage of the accompanying species.

Pop	Location Mountain	Altitude [m]	Northing	Easting	Exposition [°Degree]	Inclination [°Degree]	Coverage [%]
A0	Dobratsch (SW Zehnernock)	1806	46.59308	13.70047	141	16	90
A1	Dobratsch (SW Zehnernock)	1807	46.59306	13.70044	155	19	95
A2	Dobratsch (SW Zehnernock)	1801	46.59306	13.7005	163	16	90
A3	Dobratsch (SW Zehnernock)	1803	46.59311	13.70056	187	15	90
A4	Dobratsch (SW Zehnernock)	1804	46.59319	13.70056	143	2	80
A5	Dobratsch (SW Zehnernock)	1804	46.59061	13.70083	165	15	85
A6	Dobratsch (SW Zehnernock)	1808	46.59361	13.70092	148	26	65
A7	Dobratsch (SW Zehnernock)	1813	46.59364	13.70097	129	26	75
A8	Dobratsch (SW Zehnernock)	1824	46.59375	13.70072	155	20	80
A9	Dobratsch (SW Zehnernock)	1825	46.59375	13.70072	147	27	95
B0	Großer Ötscher	1732	47.85756	15.19281	248	33	85
B1	Großer Ötscher	1760	47.85792	15.19369	281	6	90
B2	Großer Ötscher	1767	47.85814	15.19406	282	32	95
B3	Großer Ötscher	1769	47.85808	15.19406	298	26	100
B4	Großer Ötscher	1802	47.85903	15.19653	111	20	90
B5	Großer Ötscher	1791	47.85847	15.19517	81	22	50
B6	Großer Ötscher	1761	47.85797	15.19367	131	0	45
B7	Großer Ötscher	1685	47.85672	15.18964	307	7	60
B8	Großer Ötscher	1648	47.85589	15.18792	220	0	50
B9	Großer Ötscher	1647	47.85589	15.18792	244	0	45
C0	Hochobir	1826	46.50372	14.502	166	26	70
C1	Hochobir	1827	46.50375	14.50197	251	25	30
C2	Hochobir	1828	46.50369	14.502	55	23	10
C3	Hochobir	1828	46.50367	14.50203	102	22	20
C4	Hochobir	1826	46.50381	14.5025	207	15	95
C5	Hochobir	1830	46.50425	14.50178	80	11	80
C6	Hochobir	1829	46.50431	14.50178	178	18	85
C7	Hochobir	1828	46.50431	14.50172	176	12	70
C8	Hochobir	1848	46.504	14.49978	130	33	80
C9	Hochobir	1848	46.504	14.49981	0	8	55
D0	Petzen (Kniepsattel)	1927	46.50394	14.76247	260	11	65
D1	Petzen (Kniepsattel)	1990	46.50397	14.7625	252	24	90
D2	Petzen (Kniepsattel)	2031	46.50439	14.75964	250	13	75
D3	Petzen (Kniepsattel)	2049	46.50436	14.75953	299	3	95
D4	Petzen (Kniepsattel)	2052	46.50439	14.7595	231	28	50
D5	Petzen (Kniepsattel)	2068	46.50439	14.7595	249	18	60
D6	Petzen (Kniepsattel)	2078	46.50478	14.75872	141	11	70
D7	Petzen (Kniepsattel)	2081	46.50478	14.75881	48	7	75
D8	Petzen (Kniepsattel)	2081	46.50478	14.75881	37	9	80
D9	Petzen (Kniepsattel)	2082	46.50478	14.75892	230	12	95
E0	Staff (Goldeck)	2149	46.73547	13.43492	318	32	20
E1	Staff (Goldeck)	2121	46.73544	13.43492	333	26	15
E2	Staff (Goldeck)	2151	46.73547	13.43492	315	48	40
E3	Staff (Goldeck)	2151	46.73547	13.43492	285	17	20

Pop	Location Mountain	Altitude [m]	Northing	Easting	Exposition [°Degree]	Inclination [°Degree]	Coverage [%]
E4	Staff (Goldeck)	2164	46.73567	13.43539	308	20	15
E5	Staff (Goldeck)	2170	46.73575	13.43561	350	10	65
F0	Schneealpe	1799	47.69606	15.60939	180	39	95
F1	Schneealpe	1790	47.69614	15.60942	180	46	90
F2	Schneealpe	1786	47.69603	15.6095	150	43	100
F3	Schneealpe	1782	47.69608	15.60958	144	49	70
F4	Schneealpe	1781	47.69608	15.60958	167	33	30
F5	Schneealpe	1777	47.69608	15.60961	164	14	35
F6	Schneealpe	1777	47.69608	15.60961	184	29	40
F7	Schneealpe	1778	47.69614	15.60967	240	25	45
F8	Schneealpe	1778	47.69614	15.60967	130	50	45
F9	Schneealpe	1779	47.69614	15.60969	220	18	70
G0	Hochschwab (Bürgeralm)	1536	47.57278	15.22333	0	7	20
G1	Hochschwab (Bürgeralm)	1525	47.57306	15.22361	0	5	60
G2	Hochschwab (Bürgeralm)	1528	47.57278	15.22278	0	6	30
G3	Hochschwab (Bürgeralm)	1527	47.57278	15.22278	72	34	45
G4	Hochschwab (Bürgeralm)	1536	47.57278	15.22278	0	0	75
G5	Hochschwab (Bürgeralm)	1527	47.57278	15.22278	0	5	10
G6	Hochschwab (Bürgeralm)	1534	47.57278	15.22278	0	0	35
G7	Hochschwab (Bürgeralm)	1536	47.57333	15.22222	0	0	45
H0	Schöckl	1426	47.19778	15.46056	205	11	75
H1	Schöckl	1435	47.19778	15.46056	225	11	75
H2	Schöckl	1442	47.19778	15.46056	207	11	55
H3	Schöckl	1435	47.19778	15.46056	210	11	90
H4	Schöckl	1433	47.19778	15.46056	208	10	50
H5	Schöckl	1434	47.1975	15.46056	201	5	85
H6	Schöckl	1433	47.19778	15.46056	209	6	95
H7	Schöckl	1429	47.1975	15.46056	198	10	85
H8	Schöckl	1435	47.19778	15.46056	0	8	55
H9	Schöckl	1431	47.19778	15.46056	211	16	30
I0	Gleinalpe (Gaberl)	1655	47.08183	14.91958	294	4	75
I1	Gleinalpe (Gaberl)	1649	47.08183	14.91958	290	4	80
I2	Gleinalpe (Gaberl)	1647	47.08183	14.91958	267	29	75
I3	Gleinalpe (Gaberl)	1648	47.08192	14.91961	281	16	85
I4	Gleinalpe (Gaberl)	1647	47.08186	14.91967	178	15	90
I5	Gleinalpe (Gaberl)	1648	47.08186	14.91967	280	17	75
I6	Gleinalpe (Gaberl)	1646	47.08181	14.91964	280	13	85
J0	Speiereck (Großeck)	2125	47.13139	13.64	144	37	80
J1	Speiereck (Großeck)	2127	47.13139	13.64	140	19	65
J2	Speiereck (Großeck)	2130	47.13139	13.64	153	9	50
J3	Speiereck (Großeck)	2127	47.13139	13.64	190	4	20
J4	Speiereck (Großeck)	2119	47.13139	13.63972	173	14	95
J5	Speiereck (Großeck)	2123	47.13139	13.64	0	3	75
J6	Speiereck (Großeck)	2125	47.13139	13.64	160	12	85

Pop	Location Mountain	Altitude [m]	Northing	Easting	Exposition [°Degree]	Inclination [°Degree]	Coverage [%]
J7	Speiereck (Großeck)	2119	47.13139	13.64	0	0	90
K0	Koralpe	1941	46.79333	14.98083	230	25	85
K1	Koralpe	1932	46.79369	14.98086	170	31	25
K2	Koralpe	1934	46.79378	14.98076	165	40	90
K3	Koralpe	1934	46.79375	14.98081	160	81	90
K4	Koralpe	1933	46.79372	14.98083	117	53	75
K5	Koralpe	1990	46.79194	14.97919	287	42	60
K6	Koralpe	2018	46.79194	14.97919	266	14	85
K7	Koralpe	2022	46.79156	14.97942	283	14	100
K8	Koralpe	2036	46.78794	14.97756	165	18	70
K9	Koralpe	2035	46.78794	14.97756	165	40	55
K10	Koralpe	2031	46.78794	14.97761	138	3	65
K11	Koralpe	2030	46.78694	14.97672	258	32	80
K12	Koralpe	2038	46.78706	14.97686	145	30	55

TableS 2 Accompanying species; * = removed from ecological analyses

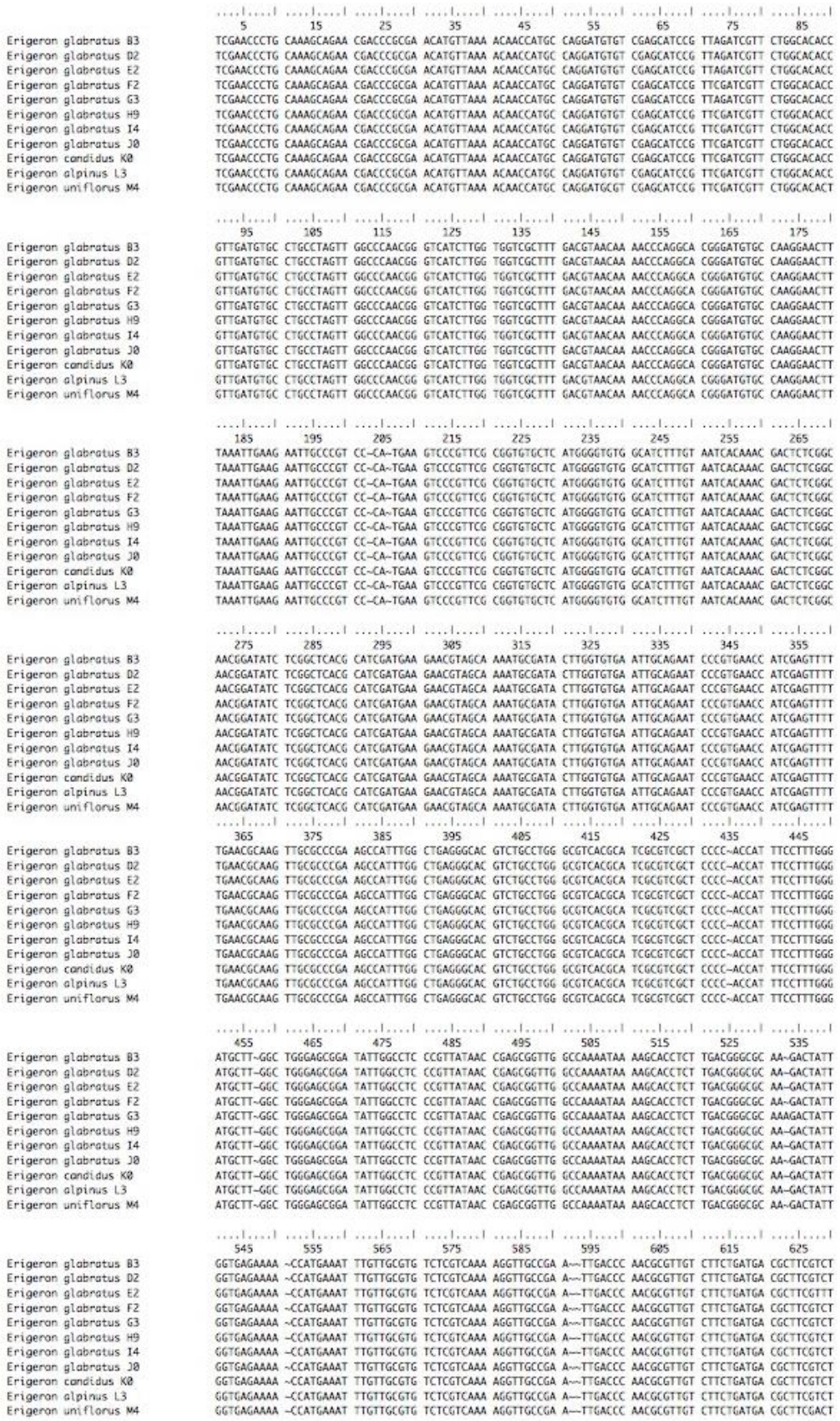
Accompanying species	*E. candidus*	*E. glabratus*	Accompanying species	*E. candidus*	*E. glabratus*
Achillea clavennae		x	*Gnaphalium hoppianum*	x	
Achillea millefolium	x	x	*Gypsophila repens*		x
Acinos alpinus		x	*Helianthemum alpestre*		x
Agrostis alpina		x	*Helianthemum glabrum*		x
Agrostis capillaris		x	*Helianthemum montanum*		x
Alchemilla alpina agg.		x	*Heliosperma alpestre*		x
Alchemilla confer. fissa	x	x	*Helleborus niger*		x
Alchemilla flabellata		x	*Hieracium pilosella*		x
Alchemilla glaucescens		x	*Hippocrepis comosa*		x
*Alchemilla sp.**		x	*Homogyne alpina*	x	x
Anemone narcissiflora		x	*Homogyne discolor*		x
Anthyllis vulneraria		x	*Juncus trifidus*	x	
Anthyllis vulneraria subsp. *alpicola*		x	Koeleria pyramidata		x
Aposeris foetida		x	*Leontodon hispidus*	x	x
Arabis alpina		x	*Leontodon incanus*		x
Arabis cilliata		x	*Leucanthemum atratum*		x
Arabis vochinensis		x	*Leucanthemum halleri*		x
Asplenium viridis	x		*Loiseleuria procumbens*	x	
Aster bellidiastrum		x	*Lolium perenne*		x
Astragalus alpinus cf.	x		*Lotus corniculatus*		x
Astragalus australis	x		*Minuartia sedoides*		x
Athamanta cretensis		x	*Myositis alpestris*		x
Avenella flexuosa		x	*Nardus stricta*		x
Avenula versicolor	x		*Nigritella rhellicani*		x
Bartsia alpina		x	*Oxytropis montana*		x
Bellidiastrum michelii		x	*Parnassia palustris*	x	x
Betonica alopecuros		x	*Pedicularis rostratocapitata*		x
Bistorta vivipara		x	*Phleum hirsutum*	x	x
Botrychium lunaria	x	x	*Phyteuma orbiculare*	x	x
Briza media		x	*Picea abies* *		x
Campanula alpina	x		*Pinus mugo**		x
Campanula cespitosa		x	*Plantago major*		x
Campanula cochleariifolia	x	x	*Plantago media*		x
Campanula scheuchzeri		x	*Poa alpina*	x	x
Cardaminopsis halleri	x		*Polygala camaebuxus*		x
Carex atrata	x	x	*Potentilla aurea*	x	x
Carex capillaris		x	*Potentilla crantzii*		x
Carex digitata		x	*Primula elatior*	x	
Carex ferruginea		x	*Primula minima*		x
Carex firma		x	*Prunella grandiflora*		x
Carex flacca		x	*Pulsatilla alpina*	x	
Carex ornithopoda	x	x	*Pyrola sp.**		x
Carex sempervirens	x	x	*Ranunculus alpestris*		x
Carlina acaulis	x	x	*Ranunculus breyninus*		x
Cerastium arvense		x	*Ranunculus carinthiacus*		x
Cerastium arvense subsp. stricta		x	*Ranunculus hybridus*		x
*Cerastium fontanum**	x		*Ranunculus montanus*		x
Coronilla vaginalis		x	*Rhinanthus glacialis*		x
Crepis aurea		x	*Rhinanthus pulcher**	x	
Cystopteris fragilis	x		*Rubus idaeus*		x
*Deschampsia cespitosa**	x	x	*Sagina saginoides*		x
Dianthus alpinus		x	*Salix repens*		x
Doronicum calcareum		x	*Saponaria pumila*	x	
Draba aizoides		x	*Saxifraga aizoides*	x	x
Draba confer. dubia	x		*Saxifraga oppositifolia*	x	
Dryas octopetala		x	*Saxifraga paniculata*	x	x
Erica carnea		x	*Scabiosa lucida*	x	x
Erigeron candidus	x		*Sedum atratum*		x
Erigeron confer. atticus	x		*Selaginella selaginoides*		x
Erigeron glabratus		x	*Sesleria albicans*	x	x
Euphrasia minima		x	*Silene acaulis*		x
Euphrasia officinalis subsp. picta		x	*Silene vulgaris*	x	
Euphrasia salisburgensis		x	*Soldanella alpina*		x
*Euphrasia sp.**	x		*Soldanella minima*		x

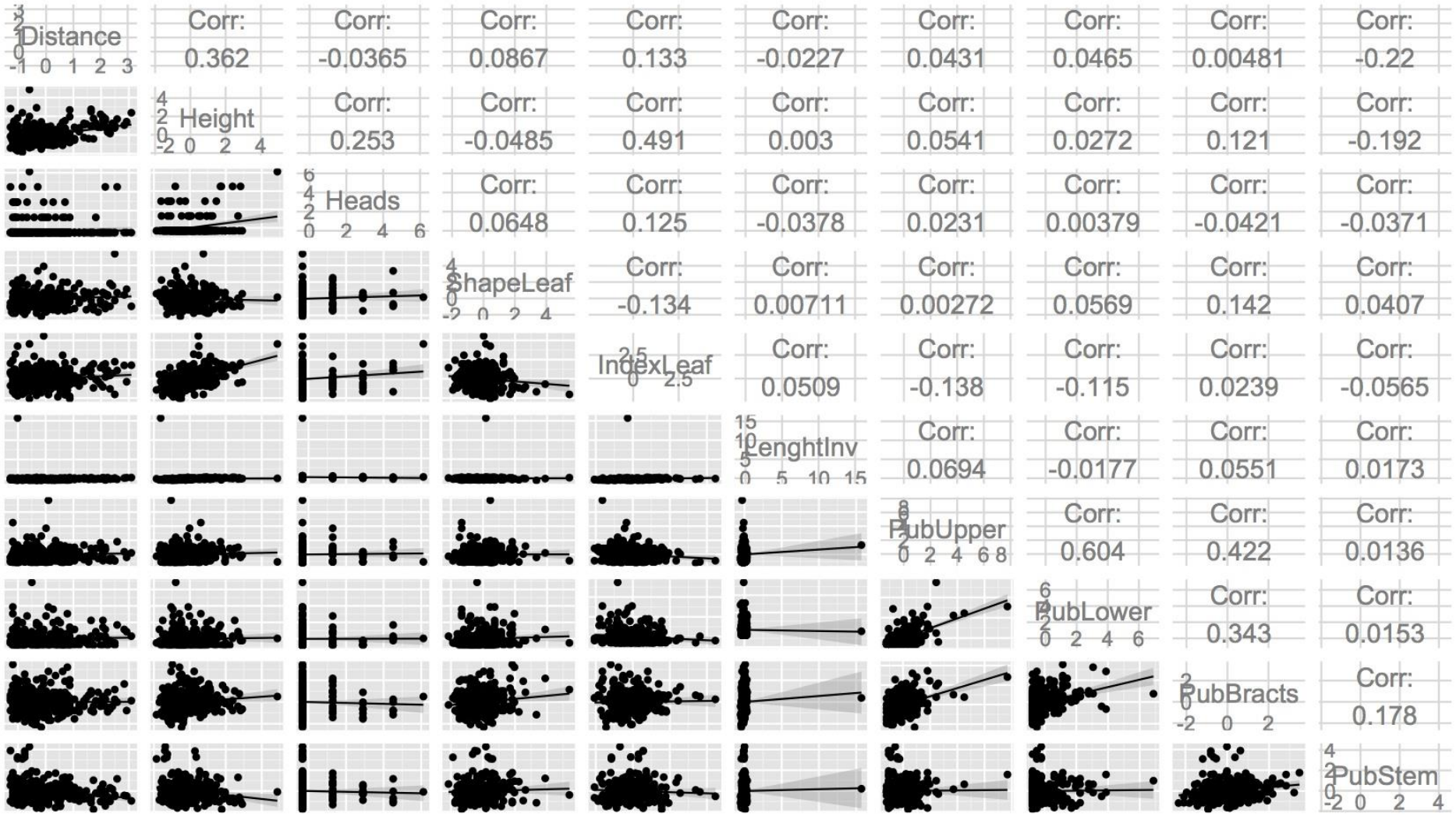
Accompanying species	*E. candidus*	*E. glabratus*	Accompanying species	*E. candidus*	*E. glabratus*
Festuca alpina		x	*Tanacetum corymbosum* subsp. *subcorymbosum*	x	
Festuca confer. picturata	x		*Taraxacum officinale agg.**	x	x
Festuca nigrescens		x	*Thesium alpinum*		x
Festuca nitida		x	*Thymus alpestris*		x
Festuca norica		x	*Thymus praecox*		x
Festuca pumila	x		*Thymus pulegioides*		x
Festuca rupicola		x	*Tofieldia calyculata*		x
*Festuca sp.**		x	*Trifolium pratense*		x
Festuca varia	x		*Trifolium pratense subsp. nivale*	x	x
Festuca versicolor subsp. brachystachys		x	*Trifolium repens*		x
Gallium anisophyllum	x	x	*Trisetum alpestre*		x
Gentiana clusii		x	*Trollius europaeus*		x
Gentiana nivalis	x	x	*Tussilago farfara*		x
Gentiana verna		x	*Vaccinium gaulteroides*	x	
Gentianella anisodonta		x	*Vaccinium myrtillus*	x	x
Gentianella germanica	x		*Vaccinium vitis-idaea*		x
Globularia cordifolia		x	*Veronica fruticans*	x	
Globularia nudicaulis		x	*Viola biflora*	x	x

TableS 3 Analyzed herbarium specimens.

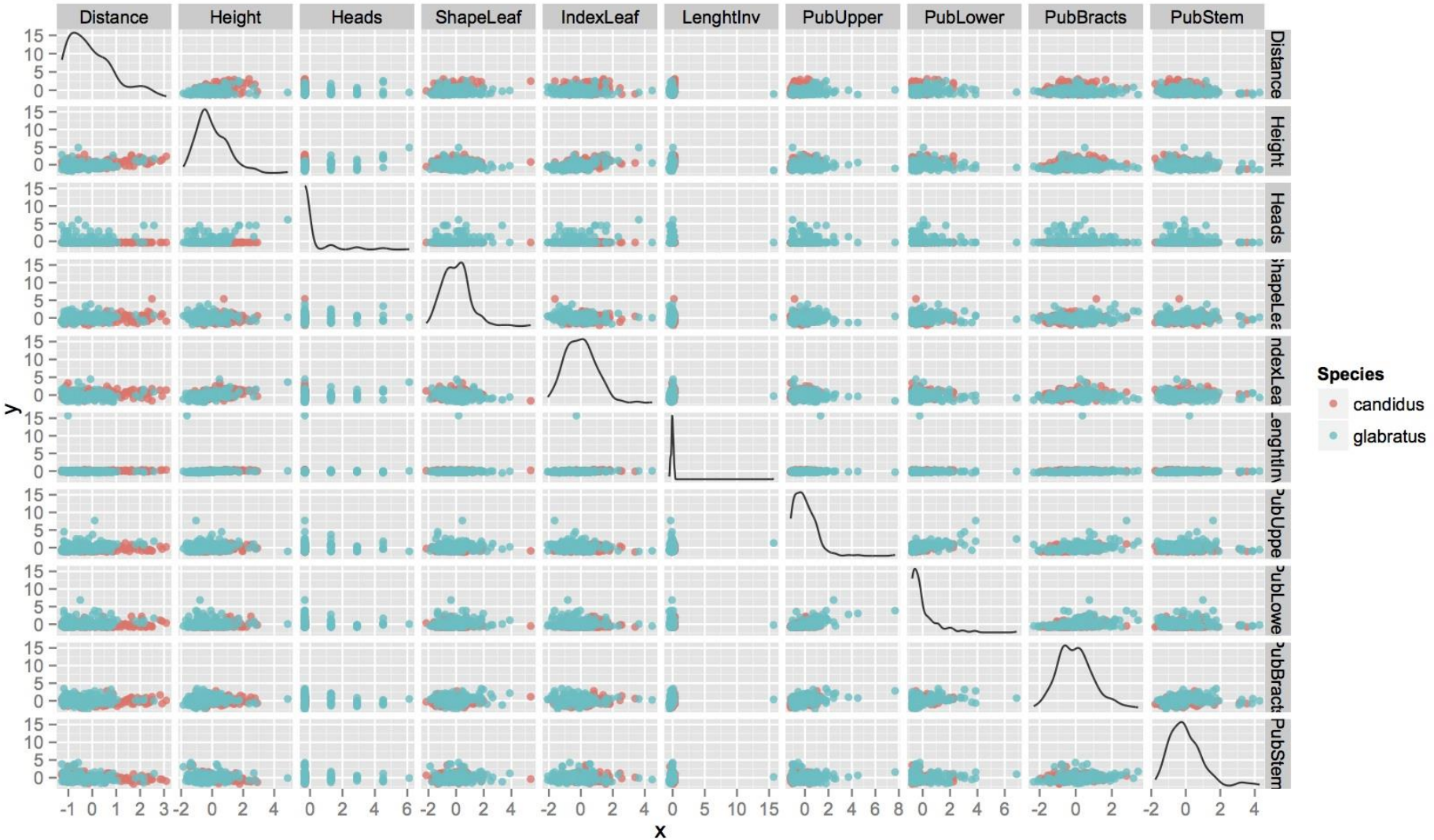
Ind	Herbarium	DigiBota ID	Nr.	Ind	Herbarium	DigiBota ID	Nr,	Ind	Herbarium	DigiBota ID	Nr.
Egc1	WU	x	5093	Egc56	GZU	161423	x	Egc111	GZU	167195	x
Egc2	WU	x	5093	Egc57	GZU	161423	x	Egc112	GZU	167195	x
Egc3	WU	x	4365	Egc58	GZU	161423	x	Egc113	GZU	167195	x
Egc4	WU	x	4365	Egc59	GZU	161423	x	Egc114	GZU	167195	x
Egc5	WU	x	4365	Egc60	GZU	161397	x	Egc115	GZU	167195	x
Egc6	WU	x	3102	Egc61	GZU	161397	x	Egc116	GZU	167195	x
Egc7	WU	x	3102	Egc62	GZU	161397	x	Egc117	GZU	161485	x
Egc8	GZU	161466	x	Egc63	GZU	161474	x	Egc118	GZU	161485	x
Egc9	GZU	161466	x	Egc64	GZU	161474	x	Egc119	GZU	161485	x
Egc10	GZU	161466	x	Egc65	GZU	161478	x	Egc120	GZU	161485	x
Egc11	GZU	161466	x	Egc66	GZU	161478	x	Egc121	GZU	161485	x
Egc12	GZU	161466	x	Egc67	GZU	161478	x	Egc122	GZU	161495	x
Egc13	GZU	161466	x	Egc68	GZU	161478	x	Egc123	GZU	161495	x
Egc14	GZU	x	215	Egc69	GZU	161478	x	Egc124	GZU	161490	x
Egc15	GZU	x	215	Egc70	GZU	161478	x	Egc125	GZU	161493	x
Egc16	GZU	x	215	Egc71	GZU	161478	x	Egc126	GZU	161493	x
Egc17	GZU	161445	x	Egc72	GZU	161478	x	Egc127	GZU	161493	x
Egc18	GZU	161445	x	Egc73	GZU	161481	x	Egc128	GZU	161493	x
Egc19	GZU	161445	x	Egc74	GZU	161481	x	Egc129	GZU	161493	x
Egc20	GZU	161451	8901	Egc75	GZU	161481	x	Egc130	GZU	161493	x
Egc21	GZU	161451	8901	Egc76	GZU	161481	x	Egg1	GZU	5154	x
Egc22	GZU	161451	8901	Egc77	GZU	161484	x	Egg2	GZU	5154	x
Egc23	GZU	161451	8901	Egc78	GZU	161484	x	Egg3	GZU	4924	x
Egc24	GZU	161457	x	Egc79	GZU	161488	x	Egg4	GZU	4924	x
Egc25	GZU	161457	x	Egc80	GZU	161488	x	Egg5	GZU	4883	x
Egc26	GZU	161454	x	Egc81	GZU	161488	x	Egg6	GZU	4760	x
Egc27	GZU	161454	x	Egc82	GZU	161488	x	Egg7	GZU	4760	x
Egc28	GZU	161454	x	Egc83	GZU	161488	x	Egg8	GZU	4760	x
Egc29	GZU	161454	x	Egc84	GZU	161488	x	Egg9	GZU	4760	x
Egc30	GZU	161468	x	Egc85	GZU	161488	x	Egg10	GZU	4760	x
Egc31	GZU	161470	x	Egc86	GZU	161500	x	Egg11	GZU	2436	x
Egc32	GZU	161470	x	Egc87	GZU	161492	x	Egg12	GZU	2436	x
Egc33	GZU	161470	x	Egc88	GZU	161492	x	Egg13	GZU	2896	x
Egc34	GZU	161427	x	Egc89	GZU	161492	x	Egg14	GZU	2896	x
Egc35	GZU	161427	x	Egc90	GZU	161492	x	Egg15	GZU	2896	x
Egc36	GZU	161427	x	Egc91	GZU	161492	x	Egg16	GZU	2896	x
Egc37	GZU	161427	x	Egc92	GZU	161492	x	Egg17	GZU	2896	x
Egc38	GZU	161435	x	Egc93	GZU	161498	x	Egg18	GZU	2896	x
Egc39	GZU	161435	x	Egc94	GZU	161498	x	Egg19	GZU	5093	x
Egc40	GZU	161435	x	Egc95	GZU	161499	x	Egg20	GZU	x	x
Egc41	GZU	161435	x	Egc96	GZU	161499	x	Egg21	GZU	x	x
Egc42	GZU	161435	x	Egc97	GZU	161499	x	Egg22	GZU	x	x
Egc43	GZU	161441	x	Egc98	GZU	161473	x	Egg23	GZU	x	x
Egc44	GZU	161441	x	Egc99	GZU	161473	x	Egg24	GZU	x	x
Egc45	GZU	161441	x	Egc100	GZU	161473	x	Egg25	GZU	x	x
Egc46	GZU	161402	x	Egc101	GZU	161473	x	Egg26	GZU	4102	x
Egc47	GZU	161402	x	Egc102	GZU	161477	x	Egg27	GZU	2331	x
Egc48	GZU	161413	x	Egc103	GZU	161477	x	Egg28	GZU	2827	x
Egc49	GZU	161413	x	Egc104	GZU	161477	x	Egg29	GZU	2827	x
Egc50	GZU	161413	x	Egc105	GZU	161477	x	Egg30	GZU	2827	x
Egc51	GZU	161413	x	Egc106	GZU	161477	x	Egg31	GZU	4365	x
Egc52	GZU	161415	x	Egc107	GZU	161482	x	Egg32	GZU	5093	x
Egc53	GZU	161415	x	Egc108	GZU	167194	x	Egg33	GZU	5093	x
Egc54	GZU	161415	x	Egc109	GZU	167194	x	Egg34	GZU	5093	x
Egc55	GZU	161415	x	Egc110	GZU	167194	x	x	x	x	x

TableS 4 Alignment of newly obtained ITS sequences.

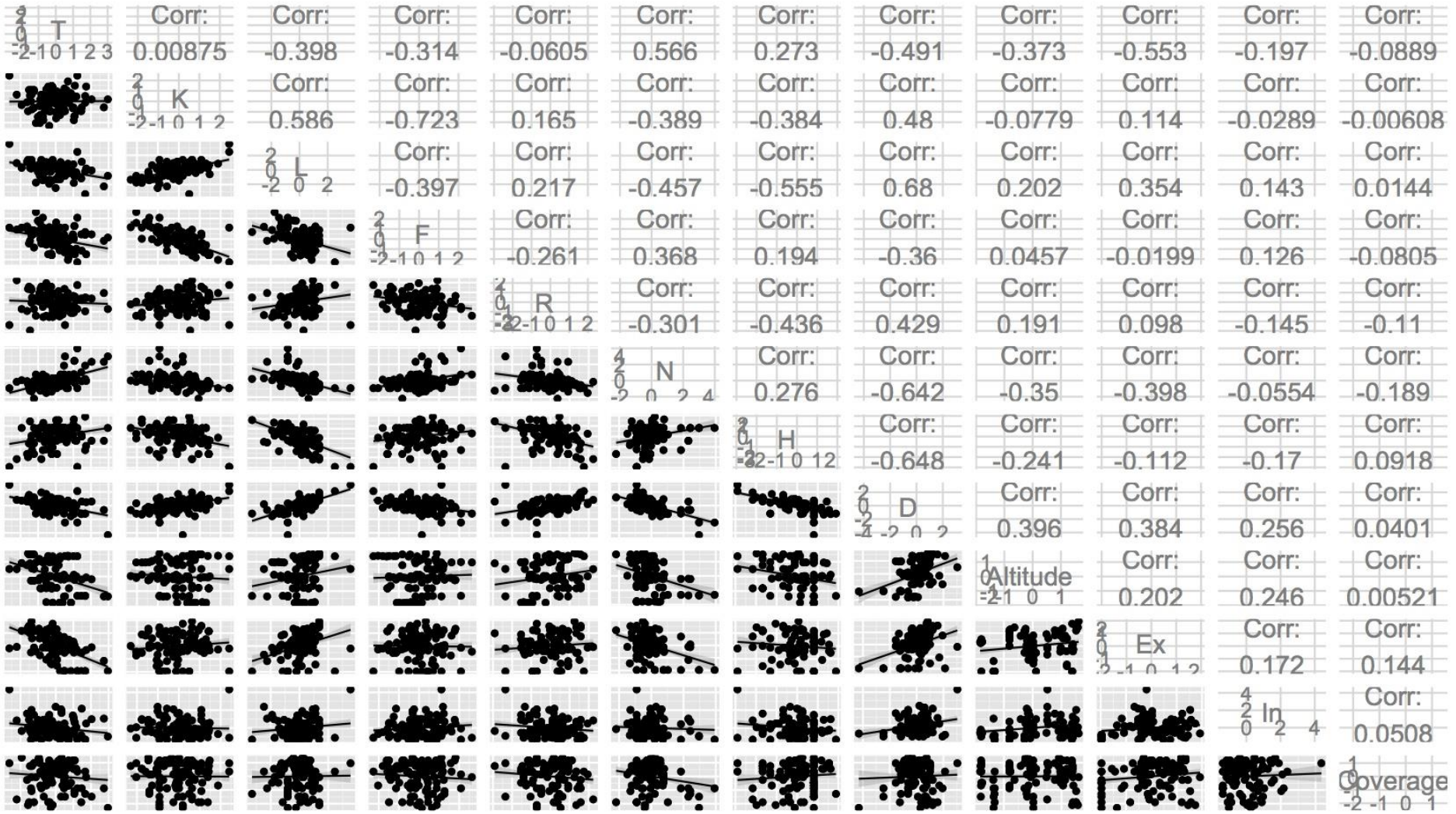




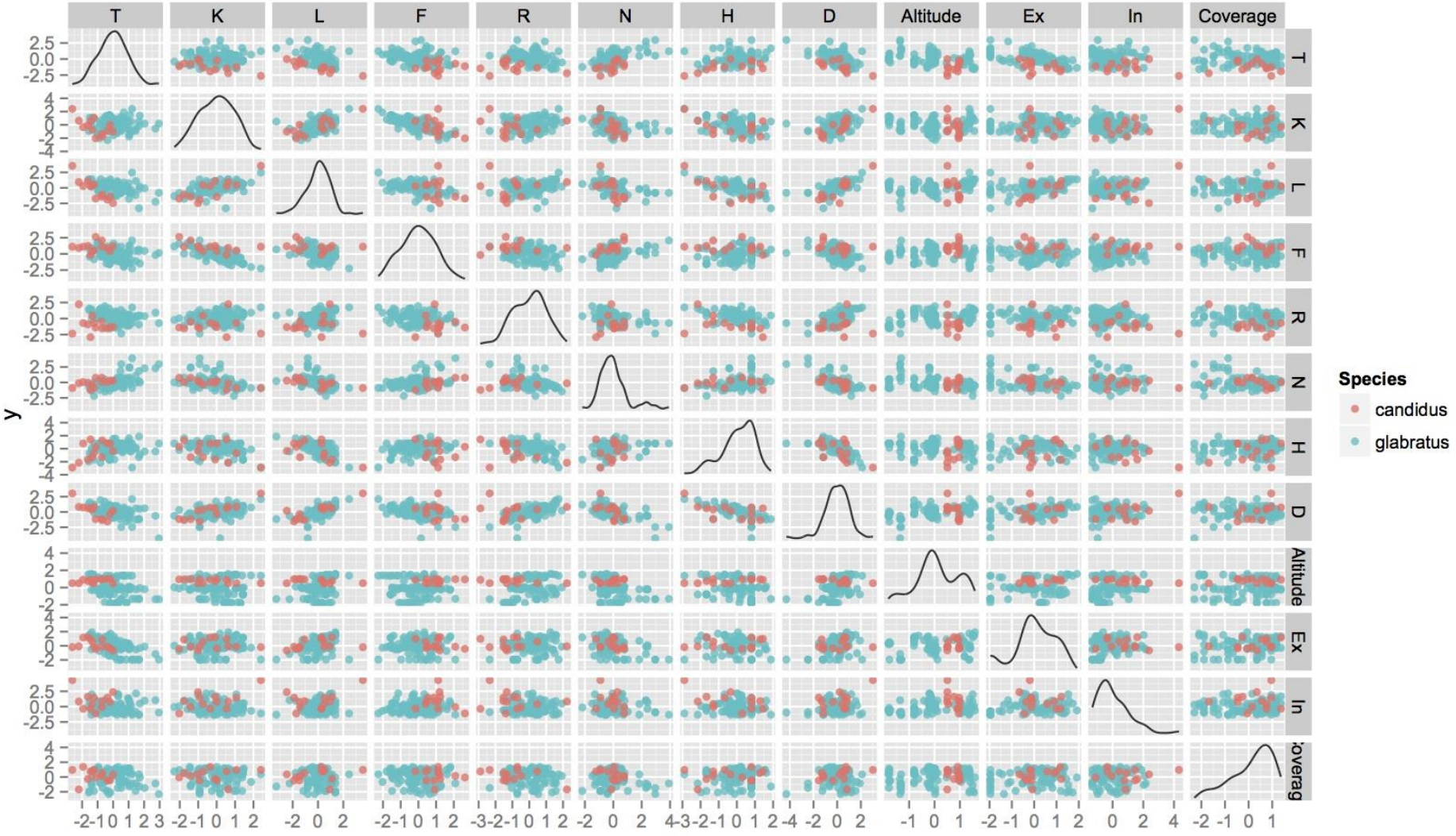
FigureS 1 Scatterplot matrix and correlations of standardized morphological data.



FigureS 2 Scatterplot matrix of standardized morphological data; function for calculation from http://gastonsanchez.wordpress.com /2012/08/27/scatterplot-matrices-with-ggplot/ (accessed 7. Oct. 2013)



FigureS 3 Scatterplot matrix and correlations of standardized ecological data.



FigureS 4 Scatterplot matrix of standardized ecological data; function for calculation from http://gastonsanchez.wordpress.com /2012/08/27/scatterplot-matrices-with-ggplot/ (accessed 7. Oct. 2013)

ABSTRACT

Climate fluctuations during the Pleistocene had major impacts on the alpine flora, especially in relation to their distribution. During glacial periods plants were repeatedly forced into ice-free locations (refugia), which supposedly facilitated allopatric divergence and speciation. One of these refugia is Koralpe, a mountain in the eastern Central Alps. It harbours two locally endemic taxa, both of which belong to the family of Asteraceae: *Doronicum cataractarum* and *Erigeron glabratus* subsp. *candidus*. Whereas the taxonomic distinctness of *D. cataractarum* is beyond dispute, the taxonomic status of *E. glabratus* subsp. *candidus* has changed over times. However, neither the phylogenetic position nor the morphological and/or ecological differentiation of *E. glabratus* subsp. *candidus* from its presumably closest relative *E. glabratus* subsp. *glabratus*, widespread in the Alps and beyond, has been sufficiently investigated. This is the motivation of the present study, which attempts to clarify relationships of, and morphological and/or ecological differentiation between *E. glabratus* subsp. *candidus* and *E. glabratus* subsp. *glabratus*. *Erigeron glabratus* subsp. *candidus* possesses identical ribotypes as Central Alpine populations of *Erigeron glabratus* subsp. *glabratus*, but is morphologically weakly differentiated by having exclusively single heads with completely white ligulate florets. Ecological differentiation is weak and may be due to the peculiar habitats on Koralpe, where habitats suitable for *Erigeron glabratus* subsp. *candidus* (on narrow marble belts) are embedded within a matrix of acidiphilic vegetation.

ZUSAMMENFASSUNG

Pleistozäne Klimaschwankungen hatten immense Auswirkungen auf die alpine Flora, vor allem in Bezug auf ihre Verbreitung. Während der glazialen Kälteperioden konnten Taxa nur an eisfreien Standorten, sogenannten Refugialorten, überdauern. Eines dieser Refugien ist die Koralpe, ein in den östlichen Zentralalpen Österreichs gelegener Berg. Die Koralpe beherbergt zwei lokalendemische Taxa, welche der Familie der Asteraceae angehören: *Doronicum cataractarum* und *Erigeron glabratus* subsp. *candidus*. Die taxonomische Eigenständigkeit von *D. cataractum* steht außer Frage, wohingegen der taxonomische Status von *E. glabratus* subsp. *candidus* mehrere Male geändert wurde. Dies deutet auf die Unsicherheit der taxonomischen Einstufung dieser Sippe innerhalb der Gattung *Erigeron* innerhalb der Alpen hin. Weder Verwandtschaftsgrad, morphologische Differenzierung noch ökologische Differenzierung von *E. glabratus* subsp. *candidus* sind ausreichend bekannt. Ziel dieser Studie ist es daher, Kriterien zur eindeutigen Differenzierung zwischen *E. glabratus* subsp. *candidus* und dem nächstverwandten *E. glabratus* subsp. *glabratus*, der in den Alpen und darüber hinaus weit verbreitet ist, zu finden. Dafür werden molekular-phylogenetische Analysen (ITS Sequenzierung) sowie morphometrische und ökologische Daten verwendet. *E. glabratus* subsp. *candidus* besitzt identische Ribotypen wie zentral alpine Populationen von *E. glabratus* subsp. *glabratus*, jedoch sind morphologische Differentialmerkmale nur schwach ausgeprägt (z.B. bildet *E. glabratus* subsp. *candidus* stets nur einen Korb mit weißen Zungenblüten aus). Ökologisch differenzieren sich die beiden Taxa ebenfalls nur schwach. Dies könnte an den besonderen Standortsbedingungen der Koralpe liegen. *E. glabratus* subsp. *candidus* besiedelt dort ausschließlich schmale Marmorbänder, wo sich die Art in eine vorwiegend acidophile Vegetation mosaikartig einbettet.

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