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Research article

Population genomics of *Tillandsia landbeckii* reveals unbalanced genetic diversity and founder effects in the Atacama Desert

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ABSTRACT

In hyper-arid habitats vegetation tends to be highly patchy with individual plant populations set widely apart from each other. In the Atacama Desert of northern Chile, rainfall is essentially absent, but fog occurring both at the coast and sometimes reaching inland areas supports patches of vegetation in an otherwise barren environment. *Tillandsia landbeckii* (Bromeliaceae), a epiarenic plant without functional roots, completely depends on fog as source for water, therefore it is found only in fog corridors. Here, we investigate the genetic connectivity within and between populations of *T. landbeckii*, using genome-wide single-nucleotide-polymorphisms (SNP) obtained through genotyping-by-sequencing (GBS). The 21 sampled populations from the Chilean Atacama Desert are distributed in three geographically ordered south to north clusters, with the southern cluster containing only one population that is genetically very distant from the others. From our study we obtained three genetic groups that corresponded to these three geographical clusters, with the exception of the two populations 16 and 18, where genetic affiliation lies at least in part with the central cluster. Further, our results show uneven distribution of genetic diversity among the populations with highest diversity in the central cluster. We found large amounts of shared heterozygous SNPs as well as negative values for the inbreeding coefficient F_{IS} in the populations of the north and south. They indicate that these populations are strongly affected by clonal reproduction, while the populations in the center are mostly reproducing sexually. We interpret these data as the result of genetic bottlenecks due to founder events involving few dispersing genotypes combined with strong geographical isolation for the northern and southern populations, following stepping stone dispersal of *Tillandsia* during more climatically favorable episodes.

1. Introduction

The Chilean Atacama Desert is regarded as one of the driest deserts on earth (Dunai et al., 2005). Where clouds from the Pacific Ocean meet the steep westward facing slopes of the coastal cordillera, they deliver fog as the only major and regular source of humidity. As a result, vegetation with a relatively high species diversity is restricted to these areas, called loma formations, “fertile belts” or “fog oases” (Johnston, 1929; Muñoz-Schick et al., 2001; Rundel et al., 1991). Corridors of increased humidity are found where gaps in the coastal cordillera allow for fog to permeate inland, which in turn allows for plant growth also in these areas (Muñoz-Schick et al., 2001; Pinto et al., 2006; Rundel et al., 1991). These fog corridors are very unevenly distributed and the lomas are often isolated from each other by large stretches of barren landscape.

Tillandsia landbeckii Phil. (Bromeliaceae; Tillandsioideae; *Tillandsia* subg. *Diaphoranthema*) is one of 14 species in the genus *Tillandsia* adapted to the extremely arid conditions of the Atacama and Peruvian Deserts (Rundel et al., 1997). It's geographic distribution stretches from the Coquimbo region in Chile (type locality Illapel, 31.65°S) to the north of Peru and possibly into Ecuador (Smith and Downs, 1977; Till, 1992a). It can grow epiphytically, but it is mostly known as an

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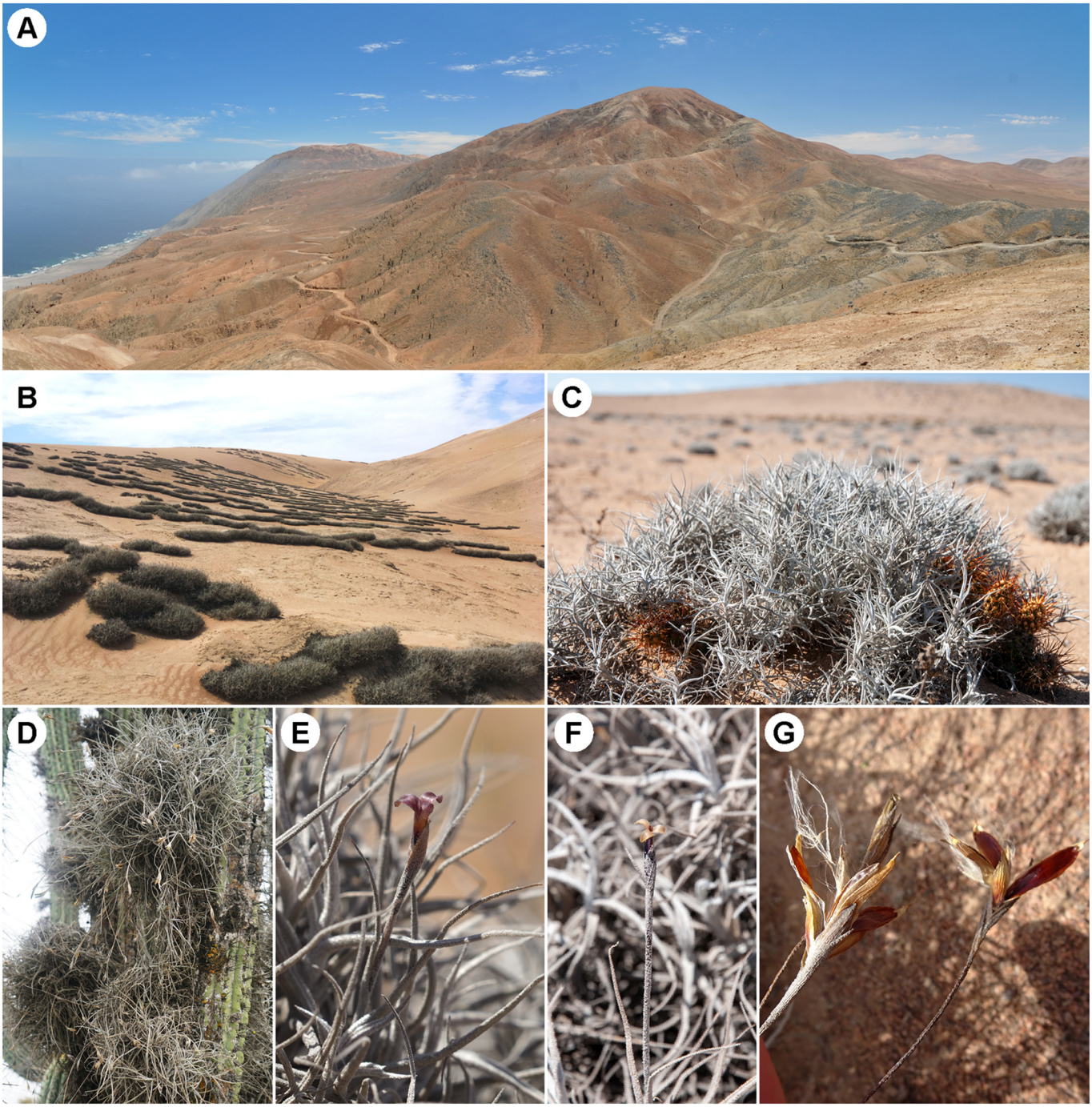

Fig. 1. Habitat (A-B) and details (C-G) of *Tillandsia landbeckii.* A) Panorama of a typical *T. landbeckii* loma at Alto Chipana (Pop 5), the gray-shaded slopes indicate the presence of dense *Tillandsia* stands. B) View into the Río Lluta population (Pop 21) showing the characteristic banded pattern. C) *T. landbeckii* individual from the Caldera population (Pop 1) growing together with *Cumulopuntia leucophaea.* D) *T. landbeckii* growing epiphytically on *Eulychnia acida* at the type locality of both species near the town of Illapel. E) 1-flowered inflorescence of *T. landbeckii* with purple flower at the Caldera locality (Pop 1). F) Inflorescence of *T. landbeckii* at the Salar Grande population (Pop 6). G) Seed shedding capsules of *T. landbeckii.* Note the pseudo-pappus on the seeds, predestined for wind-dispersal. Images: F. F. Merklinger (B, D &G) & T. Böhnert (A, C, E & F). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

epiarenic species from the arid coastal regions of Chile and Peru, where it forms near-mono-specific *Tillandsia* lomas, also referred to as "Tillandsiales" (Latorre et al., 2011; Pinto et al., 2006; Rundel et al., 1997; Rundel and Dillon, 1998; Fig. 1). These "Tillandsiales" form a characteristic banded landscape pattern that in some cases can even be recognized with remote sensing and satellite imagery (Castro Avaria et al., 2014; Wolf et al., 2016). While in Chile, *T. landbeckii* sometimes grows in sympatry with *T. virescens* or *T. marconae,* the majority of these xerophytic, lomas-forming species of *Tillandsia* is native to Peru. *T. landbeckii* is thus one of the southernmost representatives of the genus, alongside *T. minutiflora* and *T. usneoides.*

Tillandsia landbeckii is a physiological specialist: it traps and absorbs fog and nutrients through highly specialized leaf trichomes unique to this plant family and most complex in xerophytic *Tillandsia* species. In addition, the species employs Crassulacean acid metabolism (CAM) for photosynthesis (Benzing, 2000).

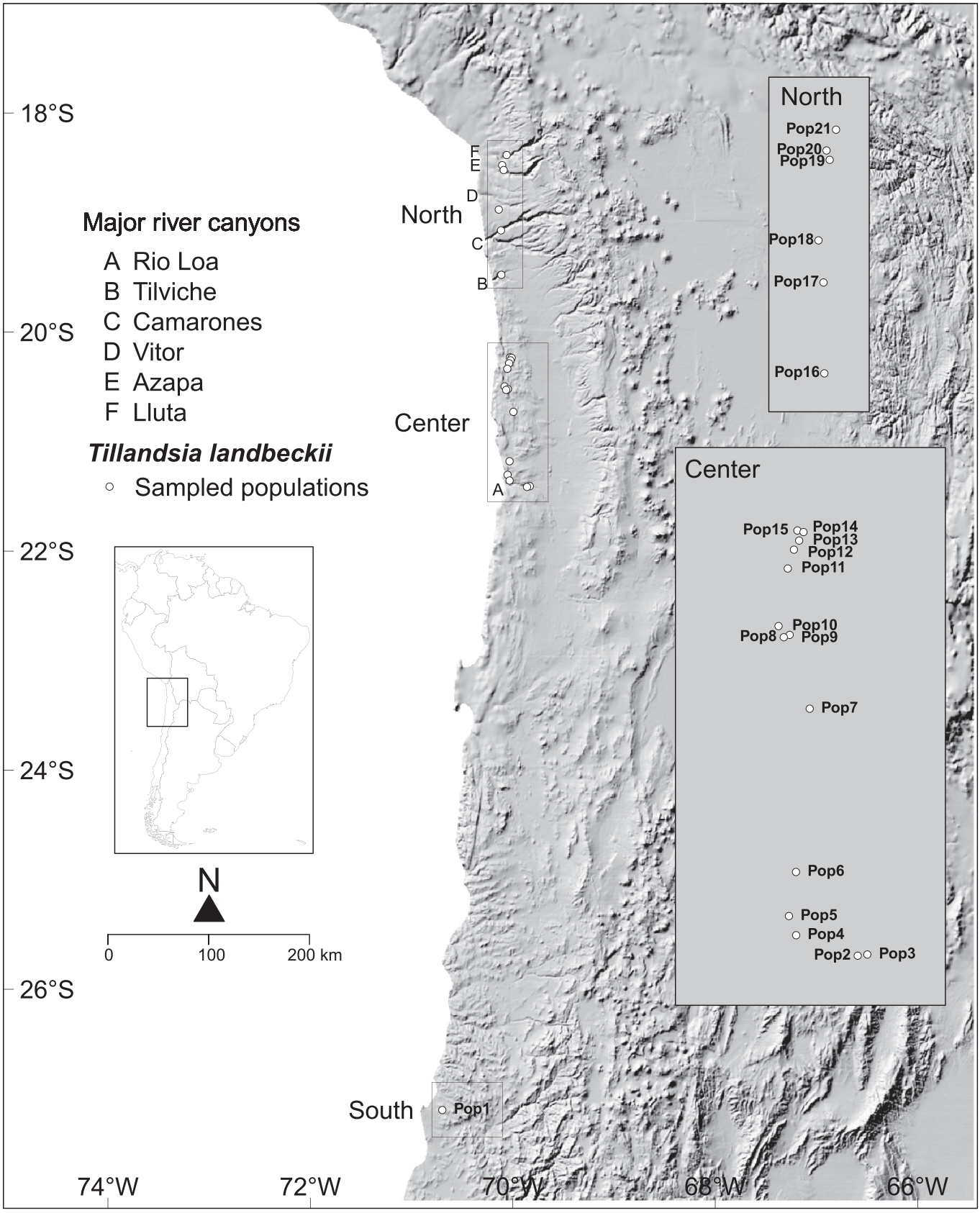

Fig. 2. The geographic location of sampling sites across the Atacama Desert, divided into three geographical clusters: north, center, south.

Tillandsia landbeckii plants trap airborne sand, leading to the formation of conspicuous dune systems (Borthagaray et al., 2010; Latorre et al., 2011; Pinto et al., 2006; Rundel et al., 1997; Westbeld et al., 2009). Attempts in dating subfossil remains of *Tillandsia* from within such dunes using radiocarbon methods showed that some dunes are at least 2500 to 3500 years old (Jaeschke et al., 2019; Latorre et al., 2011). Individual "Tillandsiales" often occupy several square kilometers, forming distinct, geographically isolated units (Fig. 1). These individual "Tillandsiales" are treated here as distinct populations. The *T. landbeckii* populations we studied are found between the town of Caldera in the Atacama region (27.07°S) and the town of Arica in the Arica and Parinacota region (18.48°S) stretching over a geographical distance of almost 1000 km (Fig. 2) and can be roughly grouped into three main geographical clusters. While each cluster comprises several populations in close proximity to each other, there are major gaps between these clusters, likely due to the lack of suitable habitats. The southernmost *Tillandsia* loma (Caldera, Pop 1) is particularly remote (600 km) from its closest known neighbor at the northern banks of the Río Loa (Pop 2; 21.41°S).

Studies of vegetation patterns in arid ecosystems indicate that abiotic factors (geomorphology and topography) are the main drivers of pattern formation because they regulate the water and nutrients available to plants (Borthagaray et al., 2010; Deblauwe et al., 2008; Rietkerk, 2004; von Hardenberg et al., 2001; Wolf et al., 2016). However, from a biotic perspective it is also important to take into account dispersibility and gene flow. If long-distance seed dispersal and pollen transfer are rare, the lomas in different areas might be effectively isolated and distant lomas could establish through propagule dispersal of few or single genets, thus consisting of one or very few genotypes only (Latorre et al., 2011; Rundel et al., 1997). The seeds of *T. landbeckii* are adapted to wind-dispersal with a plumose appendage called pseudopappus (Benzing, 2000; Magalhães and Mariath, 2012; Smith and Downs, 1977; Szidat, 1922). Although this indicates the possibility of long-distance dispersal, such a dispersal mode would be heavily influenced by prevailing wind patterns and subsequent germination success. In contrast, also clonal populations could play a role, as *T. landbeckii* is capable of vegetative reproduction. Colonizers may reproduce this way, forming mostly clonal populations if only few individuals or genotypes were able to arrive and establish at a new locality.

The breeding system of plant species can contribute importantly to gene flow and is crucial for the amount of genetic diversity within and between populations. In *Tillandsia* subgenus *Diaphoranthema* autogamy (including cleistogamy, an extreme form of selfing) has been reported (Donadío, 2013; Donadío et al., 2015; Gilmartin and Brown, 1985; Till, 1989, 1992b, 1992a). There are no published data on the breeding system of *T. landbeckii*, but Till (1992a, 1992b) suggested the occurrence of cleistogamy also in this species. This is supported by the reduced petal size and usually inconspicuous petal color, pointing to autogamy (as well as cleistogamy) rather than pollinator attraction. As far as we are aware, no pollinator has so far been reported for *T. landbeckii.* Further, the position of the anthers very close to the stigma, forming a hood above it to prevent cross-pollination strengthens the case for autogamous behavior in this species. Autogamy, combined with fast life cycle may be responsible for the successful colonization of extreme habitats (Till, 1992b).

To understand the genetic structure of *T. landbeckii* populations we investigate here (1) the genetic diversity within populations in order to test if reproduction within individual populations is predominantly sexual or asexual; (2) whether genetic distance and differentiation correlates with geographical distance or the presence of dispersal barriers; (3) whether the distribution pattern we see today is the result of long-distance dispersal events, or if the outlying populations are relics of an ancient, more widespread distribution.

To address these questions, we employed genotyping-by-sequencing (GBS), a method that has become widely used in population genetics because of its ability to screen large numbers of single-nucleotide polymorphisms (SNPs) across the genome. GBS has also been useful for the study of genetic diversity within populations, gene flow between populations, and of mating type and hybridization, without the need of a completely sequenced reference genome (Elshire et al., 2011; Narum et al., 2013; Nemati et al., 2019; Pannell, 2012; Pannell and Fields, 2014; Wendler et al., 2014).

2. Materials and methods

2.1. Study system

There is a large distribution gap of approximately 600 km without known *Tillandsia* lomas between the southernmost population situated in Caldera (Pop 1; 27.06°S) and the closest one to the north near the Río Loa (Pop 2; 21.41°S). Only individual epiphytic specimens rather than specimens belonging to extensive populations have been recorded in this intervening area (Johnston, 1929; Rundel et al., 1997; Smith and Downs, 1977). The northernmost population sampled for this study was the one at the Río Lluta valley (Pop 21;18.37°S), close to the town of Arica near the Chilean border with Peru. We were unable to confirm previous reports of populations at the edge of Quebrada Honda and Quebrada La Higuera (18.32°S and 18.68°S, Pinto et al., 2006). Because this study formed part of the Collaborative Research Center 1211 (sfb1211.uni-koeln.de) with focus on the mutual evolutionary relationships between Earth surface processes and biota in the Chilean Atacama Desert, sampling did not extend into Peru. In Chile, the highest population density is found between the Río Loa and the town of Iquique. According to Pinto et al. (2006) a total of over 30 individual populations are known of which 21 were sampled for the present study. These can be roughly assigned to three geographical clusters (Fig. 2): Cluster 1 (Caldera), cluster 2 (Río Loa to Iquique) and cluster 3 (Quebrada Tiliviche to Arica).

2.2. Population sampling

Stem and leaf tissue from a total of 21 populations and 307 individuals was sampled and silica-dried. An accession number was assigned to each population (Fig. 2, Table 1). All populations were sampled with 15 individuals each, apart from Pop 6 and Pop 2, which only consisted of 8 and 14 individual plants, respectively (Table 1).

Sampling was carried out along a transect crossing the population diagonally in order to gather plant material from different dunes and for the best possible coverage of the entire population. At least one voucher specimen from each population was deposited at the herbarium of the Nees Institute for Biodiversity of Plants, University of Bonn, Germany (BONN) and the herbarium of the La Serena University, Chile (ULS).

2.3. DNA extraction

DNA was isolated from silica-dried leaf and stem material, following the Macherey Nagel Nucleo Mag 96 protocol (Macherey Nagel, Düren, Germany). After homogenization and lysis, the samples were transferred into 96 Square Well Blocks to be processed by a Thermo Fisher Scientific KingFisher Flex benchtop system (Thermo Fisher Scientific, Waltham, MA, United States), binding DNA to NucleoMag C-beads and eluting at 55 °C into 150 µl MC6 elution buffer.

Extracted DNA was electrophoresed on 1% agarose gels using Lonza GelStar Nucleic Acid Gel Stain (100×) for testing the quantity and quality of the isolated products. A sample of 20 ng linear, double-stranded Lambda DNA (New England Biolabs, N3011S) was used to assess quality and quantity of the genomic DNA. Based on the agarose-gel images, Qubit 2.0 Fluorometer (Life Technologies, Carlsbad, CA, United States) measurements of selected individuals were taken, in order to assign a numerical value to the agarose-gel readings. Samples were then standardized to 20 ng/µl and a sample amount of 15 µl for

Table 1
Geographic and genetic summary for the 21 sampled populations. Geographic cluster (GC). Number of sampled individuals (n). Sum of haplotype diversity ($\Sigma\pi$). Individual level diversity (ID). Ratio individual level diversity/haplotype diversity (ID/π ratio). Number of SNPs (#SNPs). Observed haplotype diversity ($\Sigma\pi$ /s). Expected haplotype diversity (expected $\Sigma\pi$/s). Normalized version of observed haplotype diversity – the expected haplotype diversity (Tajima's D). Total F_{IS} per population (Total F_{IS}). Mean F_{IS} per population (Mean F_{IS}).

Pop	Locality	Latitude	Longitude	Elev. (m)	GC	Voucher	n	$\Sigma\pi$	ID	ID/π ratio	# SNPs	$\Sigma\pi$/s	expected $\Sigma\pi$/s	Tajima's D	Total F_{IS}	Mean F_{IS}
1	Caldera	−27.10049	−70.675983	340	S	FL 3888 (BONN)	15	403.54	70.86	0.18	994	0.4060	0.2524	2.3793	−559.27	−0.56
2	Rio Loa 2	−21.41230	−69.837087	980	C	FFM 2017–11 (BONN)	14	245.85	97.88	0.40	751	0.3274	0.2570	1.0813	−201.94	−0.27
3	Rio Loa 1	−21.40911	−69.810407	1021	C	FFM 2017–10 (BONN)	15	243.93	208.10	0.85	846	0.2883	0.2524	0.5564	30.71	0.04
4	Alto Chipana - Rio Loa	−21.35518	−70.008463	950	C	FL 3429 (BONN)	15	281.39	286.04	1.02	1107	0.2542	0.2524	0.0277	61.30	0.06
5	Alto Chipana	−21.30233	−70.028094	1000	C	FL 3426 (BONN)	15	378.55	368.90	0.97	1539	0.2460	0.2524	−0.0997	22.92	0.01
6	Salar Grande	−21.17943	−70.008580	940	C	FL 3430 (BONN)	8	485.34	317.00	0.65	1263	0.3843	0.3014	1.2076	−250.07	−0.20
7	Cerro Pajonal	−20.72587	−69.970655	960	C	FL 3432 (BONN)	15	260.11	143.87	0.55	1018	0.2555	0.2524	0.0482	−108.99	−0.11
8	Salitrera San Lorenzo 2	−20.52704	−70.042713	1183	C	FFM 2017–13 (BONN)	15	317.43	327.90	1.03	1785	0.1778	0.2524	−1.1566	118.15	0.07
9	Salitrera San Lorenzo 1	−20.52079	−70.026417	1204	C	FFM 2017–14 (BONN)	15	421.46	372.12	0.88	1710	0.2465	0.2524	−0.0920	−15.10	−0.01
10	N Salitrera San Lorenzo	−20.49637	−70.057147	1206	C	FFM 2017–15 (BONN)	15	497.45	505.21	1.02	2180	0.2282	0.2524	−0.3757	12.98	0.01
11	Cerro Guanaco	−20.33597	−70.031656	1040	C	FL 3433 (BONN)	15	425.17	306.69	0.72	1433	0.2967	0.2524	0.6868	−162.42	−0.11
12	Cerro Carpas	−20.28434	−70.014092	1000	C	FL 3434 (BONN)	15	405.64	374.83	0.92	1525	0.2660	0.2524	0.2108	−16.03	−0.01
13	E of Alto Hospicio	−20.25889	−70.00000	1049	C	FFM 2017–18 (BONN)	15	307.55	333.75	1.09	1465	0.2099	0.2524	−0.6585	122.71	0.08
14	NE of Alto Hospicio 2	−20.23537	−69.987869	1049	C	FFM 2017–17 (BONN)	15	356.45	373.42	1.05	1619	0.2202	0.2524	−0.4999	101.46	0.06
15	NE of Alto Hospicio 1	−20.23059	−70.004541	1023	C	FFM 2017–16 (BONN)	15	419.83	390.81	0.93	1856	0.2262	0.2524	−0.4064	−9.73	−0.01
16	Quebrada Tilivice	−19.47631	−70.090870	1064	N	FFM 2017–66 (BONN)	15	382.19	317.72	0.83	1354	0.2823	0.2524	0.4631	−83.89	−0.06
17	N edge of Camarones	−19.07064	−70.094111	1112	N	FFM 2017–58 (BONN)	15	504.93	318.21	0.63	1629	0.3100	0.2524	0.8927	−311.21	−0.19
18	Quebrada Vitor	−18.88194	−70.116794	1030	N	FL 3442 (BONN)	15	264.53	65.84	0.25	669	0.3954	0.2524	2.2127	−331.94	−0.50
19	N edge of Azapa	−18.52052	−70.066858	1093	N	FFM 2017–60 (BONN)	15	524.84	426.12	0.81	1822	0.2881	0.2524	0.5531	−158.01	−0.09
20	Pampa 2 Cruces	−18.47623	−70.084514	1000	N	FL 4002 (BONN)	15	450.93	213.40	0.47	1321	0.3414	0.2524	1.3791	−375.69	−0.28
21	N edge of Rio Lluta	−18.38547	−70.038438	1145	N	FFM 2017–59 (BONN)	15	471.38	263.92	0.56	1476	0.3194	0.2524	1.0383	−362.13	−0.25

each individual was used for library preparation and sequencing.

2.4. Library preparation and genotyping-by-sequencing

For library preparation 200 ng of genomic DNA were used and digested with the restriction enzymes *Pst*I-HF (New England Biolabs, R3140S) and *Msp*I (New England Biolabs, R0106S). Library preparation, individual barcoding, and single-end sequencing on the Illumina HiSeq 2500 followed Wendler et al. (2014). The library was size-selected to a range of 200–600 bp with a SYBR gold stained electrophoresis gel. Fragment size distribution and DNA concentration were evaluated on an Agilent BioAnalyzer High Sensitivity DNA Chip and using the Qubit DNA Assay Kit in a Qubit 2.0 Fluorometer (Life Technologies, Carlsbad, CA, United States). Finally, the DNA concentration of the library was checked by a quantitative PCR run. Cluster generation on Illumina cBot and sequencing (1 × 100 bp) on the Illumina HiSeq 2500 platform followed Illumina's recommendations and included 1% Illumina PhiX library as internal control.

Barcoded reads were de-multiplexed using the CASAVA pipeline 1.8 (Illumina, Inc.). The obtained raw sequence reads (0.5–4 million per individual) were adapter trimmed and quality trimmed (phred score > 25) with CUTADAPT v1.16 (Martin, 2011), and reads shorter than 65 bp after adapter removal were discarded. Sequence reads for the GBS Illumina runs were deposited in the European Nucleotide Archive under the study accession PRJEB35036.

2.5. Analysis of genotyping-by-sequencing data

A de novo assembly of the GBS data of 307 *Tillandsia* individuals was carried out using IPYRAD v0.7.19 (Eaton, 2014). The minimal number of samples per locus was set to 200, the maximum cluster depth within samples was set to 0.85. Based on data by Koch et al. (unpublished), *T. landbeckii* is assumed to be diploid, so the ploidy level was set to diploid. For the other parameters the default settings of parameter files generated by IPYRAD were used. VCFTOOLS v0.1.14 (Danecek et al., 2011) was used to filter out the SNP positions with a depth below six and to produce a filtered vcf file for downstream analyses.

In order to document the intra-population genetic variability, we calculated the following statistics per population: (1) Haplotype diversity π, i.e., the average number of different nucleotides between two random haploid genomes. (2) average genotype diversity $\bar{g}$, a measure of genotype difference between two randomly chosen individuals, defined as:

$\bar{g} = \frac{2}{n(n-1)} \sum_{i=1}^{n-1} \sum_{j=i+1}^{n} x_{ij}$, where n is the number of individuals sampled and

$$x_{ij} = \left\{ \begin{matrix} 0 \\ 0.5 \\ 2 \end{matrix} \right\} \text{ if genotypes } i \text{ and } j \text{ share } \left\{ \begin{matrix} 2 \\ 1 \\ 0 \end{matrix} \right\} \text{ alleles.}$$

(3) Tajima's D (Tajima, 1989). (4) The inbreeding coefficient F_{IS}. (5) Number of nucleotides that are heterozygous in 1, 2, …, n individuals, where n is the sample size. (6) Number of positions that are homozygous for one allele in at least x individuals, and homozygous for a different allele in at least x other individuals; x equals 1, 2 or 3. For (5) and (6), a subset of SNPs was used so that every locus is represented only by its most (globally) variable site.

In a structured population, the expectations of π equals $4N\mu$, where N is the population size of the analyzed population plus other populations with which it has substantial gene flow, and μ is the mutation rate. Under Hardy-Weinberg Equilibrium and neutral evolution, individual level diversity is expected to equal π.

Population structure was examined through a sparse Non-Negative Matrix Factorization algorithm (SNMF) using the R-package LEA v2.4.0 (Frichot and François, 2015) in an initial run for K = 2 to K = 21 clusters and 20 repetitions. SNMF provides a STRUCTURE-like output.

In parallel, fastSTRUCTURE v1.0 (Raj et al., 2014) was employed to approximate ancestry estimates, i.e. to identify the proportion of ancestry contributed by different populations averaged across the entire genome (Padhukasahasram, 2014). A maximum likelihood analysis was conducted with RAxML v. 8 (Stamatakis, 2014) using the population consensus sequences under the GTRCAT + I model (GTR model, approximate Gamma rate heterogeneity and a proportion of invariable sites). Bootstrap values were calculated based on 100 replicates. Average F_{ST} across all loci was calculated based on pairwise comparisons between populations and correlated to geographical distance between each pair of populations using a Mantel test with the R package VEGAN v.2.5–4 (Oksanen et al., 2019). F_{ST} was also calculated between groups of populations defined by the LEA analysis with K = 3.

3. Results

3.1. Genetic diversity and inbreeding coefficient F_{IS}

The genetic diversity at haplotype level (π) and individual level (ID) are shown in Table 1. Here we see that while π has a 2.15-fold variation, individual level diversity has the highest (505.2) being 7.67 times as large as the lowest (65.8). The values obtained for Tajima's D are strongly positive in populations that have a more negative F_{IS}, indicating an excess of intermediate-frequency alleles (in the case of the all-heterozygous SNPs, the frequencies are 50%).

The inbreeding coefficient analysis (Table 1) shows the lowest mean F_{IS} for the southernmost population Pop 1 (Caldera) with a value of −0.56, followed by population 18 (Vitor) with a value of −0.50. Negative values were also obtained from other northern populations, including Pop 20 (Pampa dos Cruces), Pop 21 (Rio Lluta) and Pop 17 (Camarones), with values of −0.28, −0.25 and − 0.19 respectively. In the central cluster around Iquique and the Rio Loa, population Pop 2 (Rio Loa) showed the lowest negative value (−0.27), followed by Salar Grande (Pop 6) with −0.20, Cerro Pajonal (Pop 7) and Cerro Guanaco (Pop 11), both with a value of −0.11 and Salitrera San Lorenzo 1 (Pop 9), Cerro Carpas (Pop 12) and Alto Hospicio 1 (Pop 15) with a mean F_{IS} of −0.01. The other populations in this area generally indicated values close to zero. Populations with strongly negative F_{IS} are also likely to have a lower individual level diversity than π. The correlation between mean F_{IS} and individual-diversity-to-haplotype-diversity ratio is 0.94.

3.2. Heterozygosity analysis

Four populations showed excessively high numbers of shared heterozygous SNPs among all individuals (Table 2). In particular Pop 1 (Caldera) showed 439 heterozygous SNPs for all 15 individuals, followed by Pop 18 (Vitor) with 230 heterozygous SNPs for 15 individuals, Pop 21 (Rio Lluta) 127 heterozygous SNPs for 15 individuals and Pop 2 (Rio Loa 2) with 103 heterozygous SNPs for 14 individuals. Populations 20, 7 and 17 shared 59, 51 and 48 heterozygous SNPs. In summary, seven populations out of 21 shared a large number of heterozygous SNPs while the other 14 populations shared less than eight heterozygous SNPs. Additionally, some populations show atypical “peaks” in the number of heterozygotes shared by x and n-x individuals: for example, $x = 3$ for Pop 21, and $x = 2$ for Pop 20. The populations with an excessive number of shared heterozygous SNPs also have the most negative F_{IS} values and there is an inverse relationship between F_{IS} and shared heterozygous SNPs (Fig. S1).

3.3. Genetic structure among populations

Evaluation of population structure through a sparse Non-Negative Matrix Factorization algorithm (SNMF) in LEA resulted in a decreasing cross entropy curve as values for increasing K. LEA results for K = 2–9 are shown in Fig. 3. The analysis obtained from fastSTRUCTURE revealed an optimal K = 8.

The separations of the populations obtained at each value for K revealed a geographical pattern (Fig. 3). At K = 3 the three resulting genetic groups roughly correspond with the three geographical clusters with the exceptions of Pop 18 and Pop 16 that are geographically in the northern cluster (Fig. 2), but genetically fall into the central group. This grouping is also reflected in the ML-tree from the RaxML analysis (Fig. S2). At K = 8 populations from the central group at the Río Loa (Pop 3, Pop 2) and Cerro Pajonal (Pop 7) clearly separate from the rest. Within the northern group populations Vitor (Pop 18), Lluta and Azapa (Pop 21 and Pop 19) separate from the others.

Genetic distances expressed by F_{ST} were small to moderate (< 0.3), but a trend was observed between the three geographical clusters of populations (Fig. 4 and supplementary Table S1). Between populations belonging to the central genetic group, mean F_{ST} was comparatively low (e.g., between Pop 9 and Pop 10 = 0.025). Mean F_{ST} was also very low between populations from the northern geographic cluster (e.g. between Pop 20 and Pop 17 = 0.028), while the F_{ST} between populations of the central and northern geographic clusters was comparatively high (e.g., between Pop 7 and Pop 21 = 0.163). Consistently large mean F_{ST} was detected between the southernmost population and the northern geographic cluster (e.g., between Pop 1 and Pop 17 = 0.193; Pop 1 and Pop 20 = 0.222, etc.; see heat map Fig. 5 and Table S1). F_{ST} showed a positive correlation to geographical distance $r = 0.72$ (Fig. 4) supported by Mantel test ($P < .001$). When F_{ST} was compared between groups of populations resulting from the SNMF analysis with K = 3 (see above) similar trends were observed. Relatively low F_{ST} values were obtained between the central genetic group and both the northern and the southern genetic groups (0.031 and 0.037 respectively), while a greater F_{ST} value was obtained between the northern and southern genetic groups (0.103). An overall pattern of genetic separation in three geographic clusters is evident. However, we would like to emphasize that there are some incongruences between genetic groups and geographic clusters, particularly Pop 16 (Tiliviche) and Pop 18 (Vitor), are genetically more similar to the central genetic group, albeit geographically belonging to the northern cluster.

4. Discussion

4.1. Sexual reproduction versus clonality

A high number of shared heterozygous SNPs was found in several populations sampled in this study. In a sexually reproducing population, the probability of finding such shared heterozygous SNPs is extremely low (for each SNP, at most ~1/30,000 in 15 sampled individuals), independent of mating system. The very low F_{IS} values and the high differences between diversity at haplotype (π) and individual level show that the individuals of these seven populations are very similar to each other. In a sexually reproducing population, crossing of two individuals with a shared heterozygous SNP would result in 50% homozygous offspring. With 15 samples per population, we would therefore expect to find more homozygous individuals than we actually see in our results. The same holds true if we assumed reproduction purely by selfing (including cleistogamy), as the proportion of heterozygous loci would be halved in each successive generation. The only possible explanation for the presence of such high numbers of shared heterozygous SNPs in some populations is therefore that these populations predominantly reproduce vegetatively, i.e. are mostly clonal. In *Tillandsia,* the importance of vegetative reproduction has been reported for *T. latifolia,* a lomas-forming species from southern Peru (Masuzawa, 1986) and has been suggested for *T. landbeckii* at a local scale (Rundel et al., 1997). Observations by Till (1992a) suggested that populations in Chile produce flowers that do not open but instead self-pollinate. He further noted, that in the Peruvian coastal deserts many populations do not produce flowers at all anymore. However, our own observations do not confirm this, rather did we find several of the Chilean populations in full bloom. It may thus be that flowering occurs irregularly and

Table 2
Count of sites by heterozygosity based on one SNP per locus. Each column indicates the number of sites for which *x* individuals in a population share heterozygous SNPs. Populations with > 10 all-heterozygous sites are shown in bold. We also included count of sites that are homozygous for two different alleles, in at least one, two or three individuals. Column GC indicates the geographical cluster to which the populations belong.

			Homozygotes	Heterozygotes															
Population	GC	Count	1 + 1	2 + 2	3 + 3	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	**S**	**15**	**83**	**20**	**7**	**29**	**13**	**7**	**4**	**1**	**1**	**1**	**0**	**2**	**2**	**1**	**3**	**6**	**21**	**439**
2	**C**	**14**	**104**	**37**	**9**	**102**	**5**	**7**	**6**	**3**	**2**	**0**	**2**	**3**	**2**	**5**	**38**	**130**	**103**	
3	C	15	170	64	33	59	52	21	10	10	2	2	1	96	131	26	10	7	5	0
4	C	15	219	98	59	29	26	25	392	29	37	23	35	21	17	6	3	1	0	1
5	C	15	268	115	60	89	221	56	31	212	50	122	57	30	18	7	2	0	1	0
6	C	8	184	48	2	206	18	29	43	74	285	51	0							
7	**C**	**15**	**153**	**33**	**10**	**209**	**50**	**5**	**5**	**6**	**1**	**1**	**4**	**5**	**2**	**4**	**13**	**118**	**81**	**51**
8	C	15	325	115	55	481	153	84	61	30	18	34	30	30	45	20	16	11	3	0
9	C	15	279	142	60	144	108	131	292	48	16	12	9	61	42	56	34	15	16	8
10	C	15	356	178	120	145	292	152	264	163	74	66	61	34	15	16	4	8	1	0
11	C	15	271	72	28	160	71	70	47	17	20	18	77	65	60	87	96	68	21	3
12	C	15	367	149	63	101	90	120	112	94	90	84	81	71	32	28	12	7	1	0
13	C	15	359	141	71	247	139	98	96	81	67	47	23	32	10	3	2	3	0	0
14	C	15	393	161	70	239	140	120	88	80	74	60	54	38	19	7	3	4	2	0
15	C	15	307	182	57	160	412	60	70	72	46	79	37	58	40	46	18	16	6	1
16	N	15	242	146	38	100	80	98	38	99	47	83	47	43	67	41	32	28	4	7
17	**N**	**15**	**175**	**92**	**25**	**36**	**306**	**15**	**104**	**7**	**3**	**1**	**6**	**6**	**20**	**313**	**7**	**106**	**2**	**48**
18	N	**15**	**42**	**20**	**13**	**28**	**5**	**3**	**6**	**1**	**3**	**5**	**1**	**4**	**4**	**4**	**11**	**24**	**49**	**230**
19	N	15	263	73	42	109	102	47	136	51	120	283	35	37	16	29	31	35	28	7
20	**N**	**15**	**148**	**89**	**11**	**26**	**220**	**8**	**8**	**6**	**5**	**5**	**4**	**4**	**3**	**4**	**23**	**382**	**13**	**59**
21	N	**15**	**127**	**56**	**39**	**33**	**22**	**359**	**2**	**2**	**3**	**0**	**2**	**2**	**0**	**13**	**314**	**2**	**5**	**127**

perhaps in response to certain climatic conditions only, which would mean that *T. landbeckii* may be capable of rapidly shifting its reproductive strategy. Interestingly, petal color varied between the southernmost population 1 (Caldera) and other populations further north. We do not know whether this can be related to reproductive strategies. Further studies would be needed to fully understand this species' breeding system including potential pollinators. In summary, *T. landbeckii* appears to maintain a mixed-mating system including clonal reproduction.

Seven out of 21 populations showed a high number of shared heterozygous SNPs, of which four exhibit an extremely high amount (Table 2). The four populations with the largest numbers of shared heterozygous SNPs and the lowest F_{IS} values are all geographically farthest away from the central cluster. However, populations 2 and 7 also have high numbers of shared heterozygous SNPs. These two populations occur in the central cluster, that is composed of a genetic group otherwise dominated by highly admixed populations reflected in high F_{IS} values and zero to maximum eight shared heterozygous SNPs in the whole of the sampled populations.

The reason why some populations appear to reproduce sexually and others almost exclusively by cloning remains unknown. There are, however, two possible processes that may serve as an explanation for this phenomenon, namely long-term isolated relic populations and founder effects, which in both cases result in strongly reduced diversity of the gene pool of a population. The first scenario implies a formerly continuous metapopulation that became fragmented, while the second scenario would be based on the colonization of outlier populations from a source gene pool.

4.2. Fragmentation versus founder effects

In a scenario of a former more continuous distribution range of *T. landbeckii* along the coastal Atacama Desert, one needs to look for mechanisms which could have led to fragmentation and subsequent isolation of populations such as (1) directional climatic changes causing expansions of arid regions leading to local extinction and thus contraction and isolation of their floras and (2) geological changes to the land surface leading to gene flow barriers.

The core Atacama has been predominantly hyper arid since the Miocene, possibly even the Oligocene/Eocene (Dunai et al., 2005; Ritter et al., 2018). However, aridity was subsequently interrupted repeatedly by wetter phases (Evenstar et al., 2017; Jordan et al., 2010). These climatic fluctuations during the Pleistocene (Stuut and Lamy, 2004) caused expansions and contractions of the arid regions and the associated floras, leading to alternating phases of isolation and secondary contact of populations. Molecular clock dating analyses suggest an origin of diversification within *Tillandsia* subg. *Diaphoranthema* at the Miocene/Pliocene boundary, around 5 Ma (Givnish et al., 2011). Since *T. landbeckii* is nested in subg. *Diaphoranthema* (Barfuss et al., 2016;Donadío, 2013;Donadío et al., 2015) the split from its sister species is certainly more recent and likely coincident with Pleistocene climatic fluctuations. The genetic signature left by this process may be indistinguishable from that left by continuous gene flow (Barton and Hewitt, 1985; Strasburg et al., 2012), which is at odds with the apparent limitation to gene flow between geographical clusters in *T. landbeckii.* However, divergence time estimations would need to be carried out, perhaps based on more recent studies by Donadío et al. (2015), Barfuss et al. (2016) or Granados Mendoza et al. (2017) which indicate *T. landbeckii* as sister to *T. usneoides* and *T. mollis.*

Habitat fragmentation and subsequent isolation of plant populations may also have been caused by geological changes to the land surface, including the evolution of surface rivers such as the Río Loa, with the maximum age of its incision dated to 274 ± 74 ka (Ritter et al., 2018). Such a major change in the landscape may pose a substantial barrier to gene flow by influencing the spread of wind-dispersed pollen and seed and/or vegetative propagules. However, Evenstar et al. (2017) also show, that the incision of the northern rivers such as Quebrada Camarones, Quebrada Azapa and Río Lluta are much older, dating back to ~15 Ma and ~11 Ma. Given the phylogenetic divergence age of *Tillandsia* subg. *Diaphoranthema* in northern Chile (< 5 Ma, Givnish et al., 2011), population fragmentation of *T. landbeckii* therefore must postdate landscape fragmentation, and dispersal across already extant barriers is the only explanation for its current range. This is also supported by population 16 (Quebrada Tiliviche), which is situated in the northern geographical cluster but genetically belongs to the central cluster. Quebrada Tiliviche is the youngest surface river of the northernmost river systems, with its incision dated at ~6.4 Ma (Evenstar et al., 2017). It is also the narrowest river valley of the four

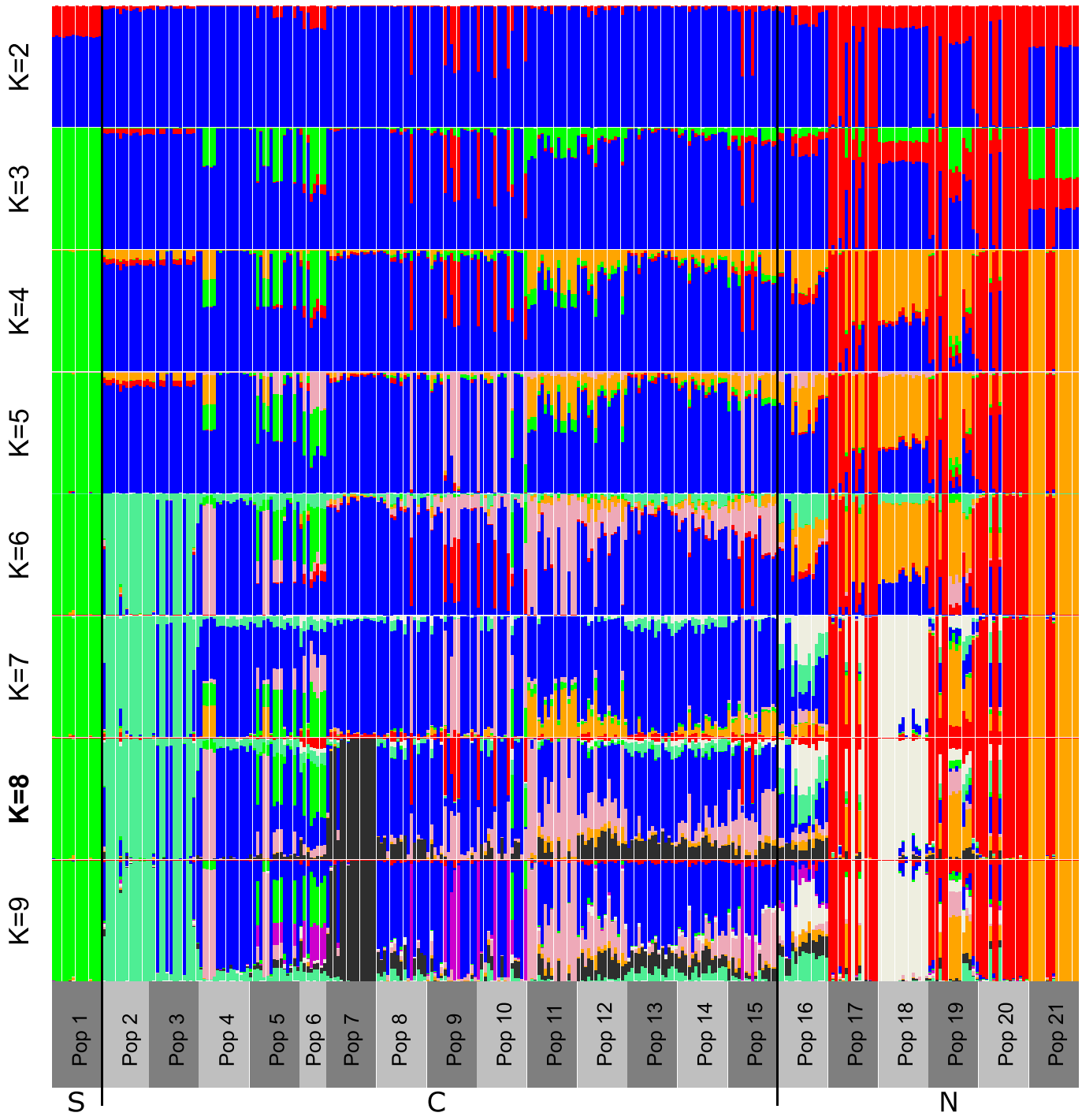

Fig. 3. Output of Non-Negative Matrix Factorization algorithm from the R package LEA. Number of clusters, K from 2 to 9 are shown. The fastSTRUCTURE result with an optimal K = 8 is shown in bold.

northernmost systems and dispersal across it may thus be more frequent than further north. However, for most populations that we see today, these large river valleys represent geographical barriers that limit gene flow between the "Tillandsiales" in all three geographical clusters. These physical barriers may act in combination with scarcity of suitable environmental conditions for establishment across the barrier, reducing the probability of successful colonization. While fog and topography are certainly important factors (Hesse, 2012; Rundel and Dillon, 1998), little is known about the exact combination of environmental conditions required for the establishment of "Tillandsiales".

Furthermore, in a scenario of fragmentation of a formerly continuous metapopulation one would expect to find a more balanced number of distinct ancient genetic lineages between geographical clusters than observed in our data. Additionally, genetic distance would tend to be lower within geographical clusters than between them. While this is indeed the case for most of the investigated populations, it did not apply to two of them (Pop 18 and Pop 21). The F_{ST} values of Pop 18 (Vitor, northern genetic group) are equally high between Pop 18 and other populations from the northern group, and between Pop 18 and populations from the central group. A similar situation is found with population Pop 21 (Río Lluta), another highly clonal population (see also Fig. 5). With the apparent limitation to gene flow between

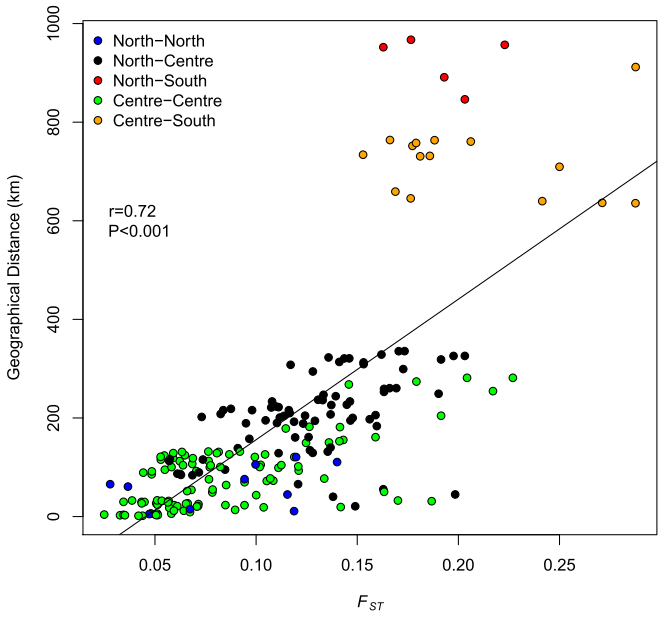

Fig. 4. Plot of genetic distance (F_{ST}) and geographic distance (km) between every population pair. The correlation is $r = 0.72$. The line is the best fitting linear model. Color codes represent the comparisons between and within geographical clusters. Mantel test significance $P < .001$.

geographical clusters, the question arises what led to the establishment of the geographically outlying populations. An explanation may be founder effects, a particular type of genetic bottleneck in which the founder(s) of a new population carry only a small subset of the genetic diversity of the source population (Freeland, 2007; Hewitt, 1996). The central genetic group, displaying the highest levels of admixture and the largest numbers of genetically distinct lineages, would represent the source population from which few founder individuals could have spread to the north and south, carrying only a fraction of the genetic diversity of their source. Founding individuals may have dispersed through a "stepping stone" dispersal process. The Caldera population (Pop 1) in particular appears to be the result of very few founding individuals, perhaps originating from a dispersal event. While it has the largest number of shared heterozygous SNPs pointing to almost exclusive clonal reproduction, it has very few distinct genetic lineages, which excludes the possibility of a single founding plant. The northern region may have been repeatedly colonized by individuals from the central cluster. At least two independent colonization events would be required to explain the genetic diversity and among-population differentiation found within the northern cluster. The isolated population Pop 18 and the populations of the Azapa/Lluta area, Pop 20 and Pop 21 represent two distinct genetic groups (Fig. 3), the latter two showing very low genetic differentiation with the Camarones population Pop 17 (Fig. 5), the southernmost population of the northern cluster.

The Chilean "Tillandsiales" are protected by the Chilean protected areas in only around 1% of their total area (Luebert and Pliscoff, 2017). Our results suggest that new protected areas would more effectively be located in the central cluster, because they concentrate the largest proportion of the genetic diversity of the species.

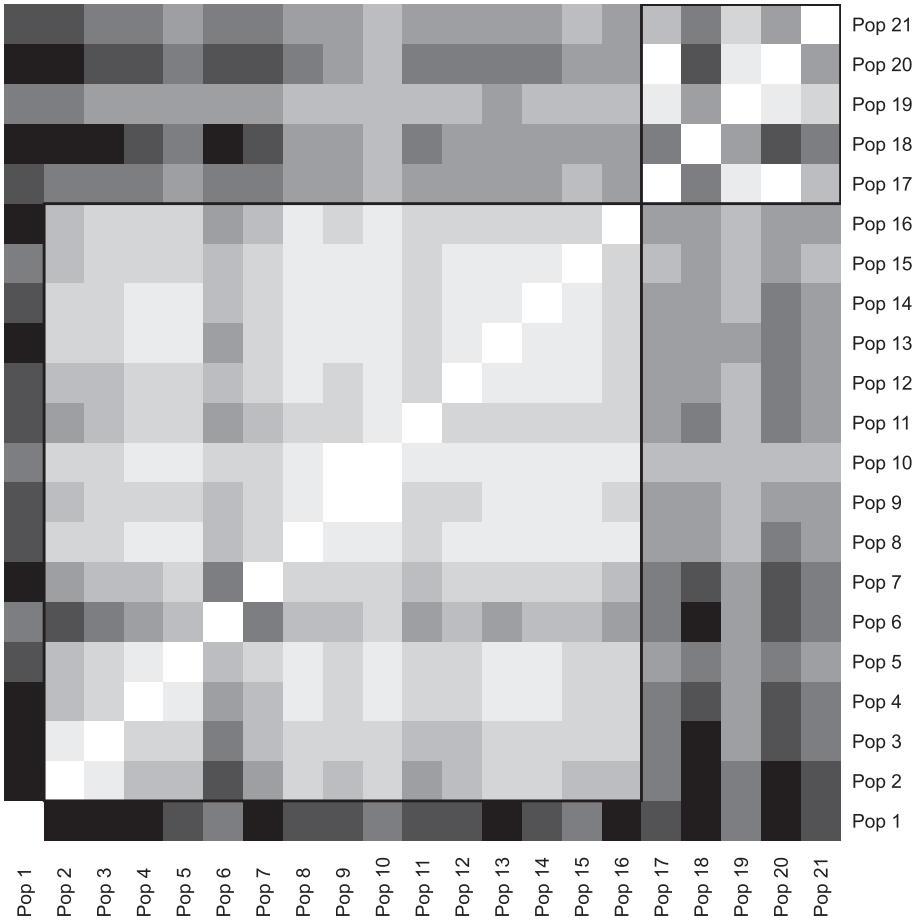

Fig. 5. Heat map of F_{ST} pairwise comparisons between populations. White cells are low F_{ST} values, darker cells are increasingly higher F_{ST}. The upper right (smaller) square represents the northern genetic group, including Pop 18 and the central (larger) square represents the central genetic group.

5. Conclusions

Twenty-one of the > 30 populations of *T. landbeckii* reported by Pinto et al. (2006) were sampled in this study. The sampling size of over 300 individuals and the subsequent analyses of historical genetic connectivity based on GBS data represent a hitherto unprecedented population-based study of any plant group in the core Atacama Desert of northern Chile. Our results show three main findings: (1) In addition to sexual reproduction, asexual (clonal) reproduction seems to be an important mechanism by which this species maintains its populations, particularly at the southern and northern range limits of the Chilean distribution of *T. landbeckii*. (2) In most cases, genetic differentiation increases with geographical distance between the populations as shown by our results of F_{ST} and Mantel test indicating signatures of past migration and ancient gene flow. Present-day geographical barriers appear to play an important role to preserve these genetic patterns, in particular between the northern and central clusters, so shaping current distribution patterns and colonization success of this species, resulting in an overall picture of unbalanced genetic diversity. (3) There is considerable genetic diversity within populations of *Tillandsia* belonging to the central geographical cluster, pointing to sexually reproducing individuals, which probably represent the most ancient populations in the Atacama Desert of Chile. Low genetic connectivity between geographical clusters probably resulted from few founding individuals and subsequent isolation. The northern and southern geographical clusters were probably colonized at least twice by long distance dispersal events from the center to the north, one from the center to the south as well as additional short distance colonization events within the central cluster. Maintaining a mixed-mating strategy, combined with varying degrees of clonal reproduction, as well as producing wind dispersed seeds with a pseudo-pappus enables this species to disperse over considerable distances, and facilitates the establishment of "Tillandsiales". Further studies including populations of *Tillandsia* from Peru, a more explicit temporal framework and modeling of past and present climate may shed further light onto the population dynamics of this species.

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Declaration of Competing Interest

The authors declare that all research was conducted independently of any commercial or financial relationships that could be interpreted as a conflict of interest.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gloplacha.2019.103076.

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