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How did a grass reach Antarctica? The Patagonian connection of *Deschampsia antarctica* (Poaceae)

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Deschampsia antarctica is the only grass naturally occurring in Antarctica, and it is also indigenous to southern South America. We aimed to evaluate patterns of within-population genetic diversity and between the focal areas Patagonia and Antarctica by using 144 sequences of nuclear internal transcribed spacer and non-coding plastid regions. We analysed phylogenetic relationships between these two main areas and performed demographic and landscape analysis. To test the divergence time between Antarctic and Patagonian populations we used approximate Bayesian computation. We found 17 nuclear and eight plastid haplotypes. For both molecular markers, Patagonia was the most genetically variable area in the range of *D. antarctica*. The divergence time between populations from Antarctica and Patagonia was dated to the mid to late Pleistocene. The large number of private haplotypes found in Patagonia and the great genetic variability support the hypothesis of a South American origin of the Antarctic populations of *D. antarctica*. Finally, we suggest that *D. antarctica* probably survived the Last Glacial Maximum and possibly earlier glaciations in ice-free refugia in Patagonia and Antarctica. Dispersal to Antarctica possibly occurred in the mid to late Pleistocene through bird-aided long-distance transport from South America.

ADDITIONAL KEYWORDS: Antarctic hair grass – chloroplast DNA – DIYABC – ITS – long-distance dispersal – Patagonia – Pleistocene.

INTRODUCTION

Long-distance dispersal (LDD) is an unpredictable but common event explaining the existence of conspecific populations in remote regions (Cain, Milligan & Strand, 2000; Givnish & Renner, 2004; de Queiroz, 2005; Gillespie *et al.*, 2012). Grasses count among the plant groups with the most LDD events, as inferred from the existence of the same genera on different continents (Linder & Barker, 2014), for example *Arundo* L. (Hardion *et al.*, 2014), *Festuca* L. (Inda *et al.*, 2008) and *Hordeum* L. (Blattner, 2006). In the Southern Hemisphere, Antarctica is particularly isolated from other landmasses by the Antarctic Circumpolar Current (ACC), the largest ocean current on earth (Barker & Thomas, 2004). The *c.* 1000 km of the Drake Passage separating southern South America from Antarctica poses a formidable barrier to dispersal; however, the transport of spores and pollen from South America to Antarctica (Marshall, 1996) and the existence of some common taxa, mainly mosses and lichens (Marshall & Convey, 1997; Convey *et al.*, 2000), suggest that dispersal is common.

Only two flowering plants [*Deschampsia antarctica* É.Desv. and *Colobanthus quitensis* (Kunth) Bartl.] inhabit Antarctica, and these suggest some basic questions regarding patterns of phylogeographic history concerning, for example, the relatedness of populations and whether the demographic parameters reflect changes in population size or divergence between the

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two areas (Patagonia and Antarctica). *Deschampsia antarctica* is the only grass occurring naturally in Antarctica; the genus belongs to the cool-season grasses lineage (Saarela *et al.*, 2015) and comprises *c.* 30 species distributed in cold-temperate regions of both hemispheres (Chiapella & Zuloaga, 2010). The species has a disjunct distribution in southern South America, from northern Patagonia (*c.* 38°S) to Tierra del Fuego (*c.* 55°S), and in Antarctica. The influence of the circumpolar current moderates the climate of the west coast of the Antarctic Peninsula (Lewis Smith, 1984); the Antarctic hair grass is found in many spots along this coast and adjacent islands (Komárková, Poncet & Poncet, 1985, 1990) from *c.* 61°S to its southernmost known locality in Lazarev Bay (Alexander Island, 69°22.0′S, 71°50.7′W; Convey *et al.*, 2011). Population genetic studies conducted so far on *D. antarctica* have been restricted to the Antarctic and sub-Antarctic islands, revealing overall a low genetic diversity and a discrete genetic diversity gradient from a maximum value in the Falkland Islands to a minimum in the Antarctic Peninsula (Holderegger *et al.*, 2003; Chwedorzewska, Bednarek & Puchalski, 2004; Chwedorzewska, 2006; Chwedorzewska & Bednarek, 2008; Van de Wouw, Van Dijk & Huiskes, 2008). Other studies including sequences from Tierra del Fuego (Andreev *et al.*, 2010: one sequence; Volkov *et al.*, 2010: two sequences) were inconclusive about the genetic structure and history of the species.

Phylogeographic studies in Antarctica have revealed variable patterns: springtails (Collembola) survived in Pleistocene refugia (McGaughran *et al.*, 2010); limpets (*Nacella*) showed a low genetic variability, with a few haplotypes and a demographic expansion related to glacial–interglacial cycles (González-Wevar, David & Poulin, 2011); and the moss *Pyrrhobryum* Mitten experienced an ancient Gondwanan vicariance event with a later expansion in South America and Australasia (McDaniel & Shaw, 2003). Most of the surface of the Antarctic continent has been razed by successive glaciations, a fact that implies that most of the current flora elements have reached the continent by dispersal after glaciations (Convey & Stevens, 2007). Regarding Patagonia, Sérsic *et al.* (2011) reviewed phylogeographic patterns of plants and terrestrial vertebrates, suggesting that the interactions between Quaternary and even pre-Quaternary climatic oscillations and tectonic events were the forces modelling evolutionary histories of the Patagonian region.

Studies on phylogeographic patterns of organisms with distribution ranges spanning two or more continents in the Southern Hemisphere are rare (Beheregaray, 2008; Runquist, Forister & Shapiro, 2012), and no study has evaluated related plant populations in South America and Antarctica. Thus, this is the first study including population of the species from austral South America. The disjunct distribution of *D. antarctica* between Patagonia and Antarctica offers a unique model with which to examine the relative contribution of the two factors driving evolutionary history in plants, that is the interaction between historical patterns of dispersal and/or isolation by vicariance of actual populations that have shaped its genetic structure. In order to explore relationships of populations between the two areas, we compared the distribution of genetic polymorphisms between and within regions across its range, by means of nuclear and plastid DNA sequences. Taking into account the low variability found in Antarctic populations by previous studies, we tested two main hypotheses: (1) *D. antarctica* migrated from Patagonia to Antarctica and (2) Antarctic populations will be genetically less diverse than Patagonian populations due to bottlenecks that probably occur during founding events.

MATERIAL AND METHODS

Plant material

Samples were collected during the austral summer seasons of 2012–2015 from six locations in Antarctica and 17 locations in Patagonia (Argentina), covering a large part of its natural distribution (*c.* 2500 km from north to south). We also included two internal transcribed spacer (ITS) sequences from Tierra del Fuego that represent an intermediate location between Antarctica and Patagonia, which were previously analysed by one of the co-authors of this paper (Chiapella, 2007). We collected three to 50 individuals randomly selected from each population (Table 1). Vouchers were included in the collection of the herbarium of the Botanical Museum of Córdoba (CORD; *Chiapella, J. 2771–2783* from Antarctica and *Urdampilleta, J.D. 841–880* from Patagonia).

DNA extraction, amplification and sequencing

DNA was extracted from the collected samples from *c.* 50 mg of partially dried tissue following a modified cetyltrimethylammonium bromide (CTAB) method (Doyle & Doyle, 1987) using alkyltrimethylammonium bromide and dichloromethane instead of CTAB and chloroform. We tested four non-coding regions of the plastid genome [*trnL-trnF* and *trnT-trnL* (Taberlet *et al.*, 1991), *rps16-trnK* and *ndhC-trnVr* (Shaw *et al.*, 2007)], but only the last two regions (Shaw *et al.*, 2007) were polymorphic. From nuclear genome, we amplified the ITS regions 1 and 2 and 5.8s (using primers ITS5 and ITS4; White *et al.*, 1990). The polymerase chain reaction (PCR) mix contained 1 µL template DNA (10 ng), 0.5 U Taq DNA polymerase (Invitrogen), 2.5 µL 5× Taq buffer (Invitrogen), 0.25 mM each deoxyribonucleotide triphosphates and 0.3

Table 1. Geographical location of sampled populations of *Deschampsia antarctica*, chromosome counts (González *et al.* 2016) and number of samples analysed for each population (*N*) and molecular marker (*N* ITS and *N* plastid)

Region		Location	Latitude (°S)	Longitude (°W)	Elevation (msnm)	2*n*	*N*	*N* ITS	*N* plastid
Patagonia	1	Languiñeo, Chubut	–43.834	–71.469	992	26	5	5 (2)	5 (2)
	2	Lago Winter, Chubut	–43.918	–71.430	924	52†	3	3 (1)	3 (1)
	3	Tehuelches, Chubut	–44.578	–71.064	953		5	3 (3)	4 (2)
	4	Rio Senger_1, Chubut	–44.924	–71.484	928		5	5 (1)	4 (2)
	5	Rio Senger_2, Chubut	–45.523	–69.704	400		5	5 (2)	5 (1)
	6	Rio Senger_3, Chubut	–45.904	–71.666	758		5	5 (3)	5 (2)
	7	Rio Senger_4, Chubut	–45.950	–71.727	566–707		10	6 (3)	6 (1)
	8	Rio Senger_5, Chubut	–46.044	–70.594	655	26	5	5 (3)	5 (1)
	9	Rio Chico_1, Santa Cruz	–47.587	–71.489	424	26	5	5 (2)	5 (1)
	10	Rio Chico_2, Santa Cruz	–47.909	–71.965	886		10	10 (4)	10 (2)
	11	Rio Chico_3, Santa Cruz	–49.343	–71.326	569		5	4 (3)	5 (1)
	12	Lago Argentino_1, Santa Cruz	–49.189	–72.487	270		5	3 (2)	5 (2)
	13	Lago Argentino_2, Santa Cruz	–50.004	–72.608	636		5	4 (3)	5 (1)
	14	Lago Argentino_3, Santa Cruz	–50.401	–72.456	195		5	5 (1)	5 (2)
	15	Güer Aike, Santa Cruz	–51.767	–71.778	214		5	5 (2)	4 (2)
	16	Rio Turbio, Santa Cruz	–52.016	–71.216	133		3	3 (2)	3 (2)
	17	Tierra del Fuego*	–54.367	–67.250	149		2	2 (2)	–
Antarctica	18	Isla 25 de Mayo	–62.227	–58.768	< 50	26	50	30 (1)	30 (3)
	19	Isla Nelson	–62.309	–58.849	< 50	26	10	10 (1)	10 (1)
	20	Islote Barrientos	–62.409	–59.758	< 50	26	5	5 (1)	5 (2)
	21	Isla Media Luna	–62.600	–59.907	< 50	26	8	8 (1)	8 (2)
	22	Base Primavera	–64.154	–60.941	< 50	26	10	9 (1)	8 (2)
	23	Base Brown	–64.899	–62.866	< 50	26	5	4 (1)	4 (2)

Numbers of haplotypes for each marker/population are in parentheses. ITS, internal transcribed spacer.
*Populations with ITS GenBank sequences.
†Tetraploid population.

μM each primer in a total volume of 25 μL. Thermal cycling for PCR consisted of 35 cycles, each with 1 min denaturation at 94 °C, 1 min annealing 48–52 °C (depending on the primer pair used), 1 min extension at 72 °C and a final extension of 10 min. Amplification products were separated by electrophoresis on a 1% agarose gel, stained with Syber Safe (Invitrogen, Eugene, OR, USA) and visualized with a UV transilluminator. PCR products were cleaned with Exonuclease I (Fermentas, Burlington, ON, Canada) and Shrimp Alkaline Phosphatase (USB, Cleveland, OH, USA). Cycle sequencing was performed using Big Dye terminator chemistry (Applied Biosystems).

Automated sequencing was conducted at the Laboratorio Ecotono, Universidad Nacional del Comahue (Argentina) and at Macrogen (South Korea). Sequencing data were aligned manually using BioEdit (Hall, 1999), and the plastid *rps16-trnK* and *ndhC-trnVr* sequences were concatenated manually into a single combined data set for analyses. All haplotypes were deposited in GenBank (MF422657–MF422680).

Demographic and phylogenetic analysis

We calculated diversity and demographic parameters including the number of haplotypes (*H*), haplotype (*h*) and nucleotide (π) diversity, Tajima's *D* (Tajima, 1989), Fu and Li's *F* (Fu & Li, 1993) and mismatch distribution using DnaSP v5 (Librado & Rozas, 2009). A median-joining network (Bandelt, Forster & Röhl, 1999) was computed in Network v4.6.1.3 (http://www.fluxus-engineering.com). All the analyses were performed separately for nuclear DNA and plastid DNA markers. For the nuclear DNA analysis, we included two sequences from populations on Tierra del Fuego from GenBank (AM041214 and AM041215; Chiapella, 2007).

Landscape analysis

A hierarchical analysis of molecular variance was performed at different levels: between geographical regions (Antarctica and Patagonia), among populations within regions and within populations using GenAlEx 6.5 (Peakall & Smouse, 2012) with 10 000 random permutations. To test for isolation-by-distance, the genetic distance (F_{ST}) was correlated to geographical distance (Km) using the Mantel test implemented in GenAlEx 6.5 (Peakall & Smouse, 2012) and was evaluated separately for nuclear DNA and plastid DNA. Correlated matrices were pairwise between-population linearized F_{ST} values $[F_{ST}/(1 - F_{ST})]$ and log-transformed geographical distances. The significance of the correlation between genetic and geographical distances for each marker was tested with the Mantel test. Multiple regression models were used to investigate the combined effect of independent variables as latitude, longitude and elevation on measures of genetic diversity as explanatory ones as haplotype richness, nucleotide and haplotype diversity.

Divergence analysis

To test the divergence time between Antarctic and Patagonian populations, we used approximate Bayesian computation as implemented in DIYABC 2.0 (Cornuet *et al.*, 2014). Approximate Bayesian Computation (ABC) analyses were conducted on sequence data from nuclear and plastid DNA simulating a demographic historical model of population divergence between those two regions. We tested two possible hypothetical evolutionary scenarios: the first (scenario 1) considered two populations of size N1 (Antarctica) and N2 (Patagonia) that have diverged at *t* generations in the past from an ancestral population of size N1 + N2; the second (scenario 2) considered a bottleneck scenario, also two population sizes (N1 and N2) that diverged at *t* generations in the past from an ancestral population size Na including a reduction in population size in the Antarctic population (N1) at a bottleneck time (*td*) (Fig. 1). Prior distributions of demographic parameters were defined after several preliminary simulations (which considered different combinations of values ranging from one to 60 000 000) as follows: the effective population sizes of N1, N2, Na, *t* and *td* were set to have a uniform distribution. We used a substitution rate of 3.81×10^{-9} for nuclear ITS (Poaceae, Kay, Whittall & Hodges, 2006) and of 5×10^{-10} for plastid DNA (Zhong *et al.*, 2011). The values of the posterior probabilities of N1, N2, Na, *t* and *td* were then estimated based on 1 000 000 simulated data sets. Posterior model checking was performed using a local linear regression on 1% of the simulated data sets closest to our real data. All summary statistics were used for model checking. We compared the scenarios and evaluated their goodness-of-fit. The coalescence time (*t1*) and *td* were determined by multiplying the median posterior distribution by the generation time. Harsh environmental conditions (i.e. low temperatures, short summers, lack of water etc.) may shorten favourable periods for plant growth and development (Wagner *et al.*, 2012), but species with an extended distribution range may adapt to

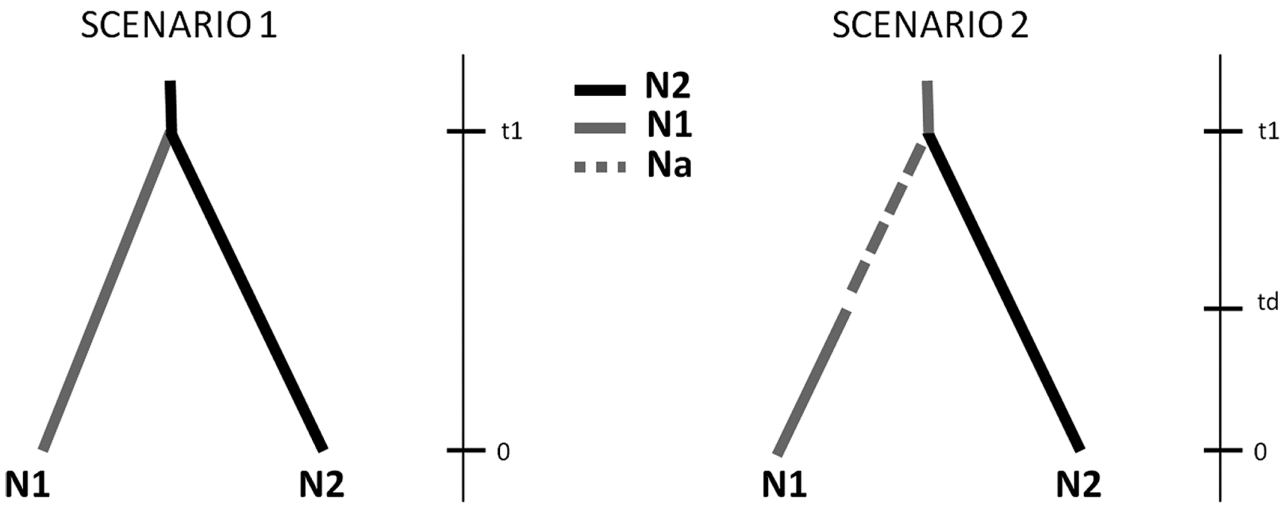

Figure 1. Evolutionary scenarios to test the divergence time between Antarctic and Patagonian populations. Scenario 1 (without bottleneck) considered two populations of size N1 (Antarctica) and N2 (Patagonia) that have diverged at t1 generations in the past from an ancestral population. Scenario 2 considered a bottleneck scenario, also two population sizes (N1 and N2) that have diverged at *t1* generations in the past from an ancestral population size Na including a reduction in population size in the Antarctic population (N1) at and a bottleneck time (*td*). Time is not at scale. See text of Material and Methods for details regarding prior distributions of sequence markers.

local conditions and exhibit differential responses to day length (Heide, 2005). In consequence, we set two different generation times, a minimum of 2 years for the Patagonian populations and a maximum of 5 years for those from Antarctica.

Finally, in order to estimate population size and migration parameters, sequence data were analysed using the programme MIGRATE-N v3.6.8 (Beerli, 2002). We inferred the population parameters, migration rates among regions and associated thetas using a Bayesian approach. To estimate parameters, MIGRATE-N was run using the Bayesian mode with a Metropolis-coupled heating scheme, using one cold and three heated chains; each of four chains was run after burn-in 50 000 steps, for a total of five million steps. MIGRATE-N estimates the mutation-scaled effective population size $\Theta = 4 N_e \mu$, where N_e is the effective population size and μ is the mutation rate per generation per locus [$\mu = 3.81 \times 10^{-9}$ for nuclear DNA (Kay *et al.*, 2006) and 5×10^{-10} for plastid DNA (Zhong *et al.*, 2011)], and the mutation-scaled migration rate $M = m/\mu$, where m is the inmigration rate per generation among regions.

RESULTS

Molecular Diversity

We analysed 144 individuals from 22 populations for plastid DNA and 144 individuals from 23 populations for ITS. The length of the ITS marker (ITS1–5.8s–ITS2) was 592 bp, which included 19 variable sites (gaps were not considered) that yielded 17 nuclear DNA haplotypes (Table 2). The length of the aligned plastid DNA sequences was 494 and 679 bp for the *ndhC-trnVr* and *rps16-trnK* regions, respectively. Both regions were concatenated totalling a matrix of 1173 characters with six variable sites that yielded eight plastid DNA haplotypes (Table 2). Neutrality tests (Tajima's *D*, and Fu and Li's *F*) yielded no significant results for plastid DNA ($D = -0.47$, $P > 0.10$; $F = 0.66$, $P > 0.10$) and ITS ($D = -0.58$, $P > 0.10$; $F = -0.83$, $P > 0.10$). The mismatch distribution analysis showed a unimodal distribution for both molecular markers. When we analysed regions separately (Patagonia and Antarctica) for each molecular marker, the mismatch distribution showed the same pattern (unimodal for plastid and ITS).

Geographical distribution of genetic variation

Patagonia was the most genetically variable area in the range of *D. antarctica*, with 17 nuclear DNA and six plastid DNA haplotypes; Antarctica had one nuclear DNA and four plastid DNA haplotypes (Table 2; Figs 2, 3). Also, Patagonia had the highest number of private haplotypes: 16 for ITS and four for plastid DNA, whereas Antarctica had only two for plastid DNA. For both markers, shared haplotypes (HAP 1 for ITS and HAP 1 and HAP 5 for plastid) are widespread from Patagonia to Antarctica; six of 16 haplotypes are unique to single populations (Figs 2, 3).

Landscape analysis

Hierarchical analysis of population structure by *F* statistics yielded significantly high values between Patagonia and Antarctica (nuclear DNA $F_{ST} = 0.823$, $P < 0.001$; plastid DNA $F_{ST} = 0.518$, $P < 0.001$). Significant F_{ST} values were also found among populations within each area. For both molecular markers, Patagonian populations showed greater among-population divergence values ($F_{ST} = 0.720$, $P < 0.001$ for ITS and $F_{ST} = 0.571$, $P = 0.001$ for plastid DNA) than those in Antarctica ($F_{ST} = 0.430$, $P = 0.001$ for plastid DNA). Divergence in Antarctica for ITS was not calculated since there is only one haplotype.

Table 2. Molecular diversity in *Deschampsia antarctica* calculated for plastid and nuclear markers for Antarctica and Patagonia

	Plastid ($N = 144$)		Nuclear ($N = 144$)	
	Antarctica ($N = 65$)	Patagonia ($N = 79$)	Antarctica ($N = 66$)	Patagonia ($N = 78$)
H	4	6	1	18
h	0.648 (0.001)	0.596 (0.002)		0.913 (0.001)
π	0.001 (< 0.001)	0.001 (< 0.001)		0.007 (< 0.001)
Unique haplotypes	2	4	0	16
Shared haplotypes	2		1	
Hd	0.637 (0.001)		0.683 (0.002)	

Number of individuals (*N*), number of haplotypes (*H*), haplotype (*h*) and nucleotide (π) diversity. Unique and shared haplotypes and haplotype diverstity (Hd) for each marker are shown. SE are in parentheses.

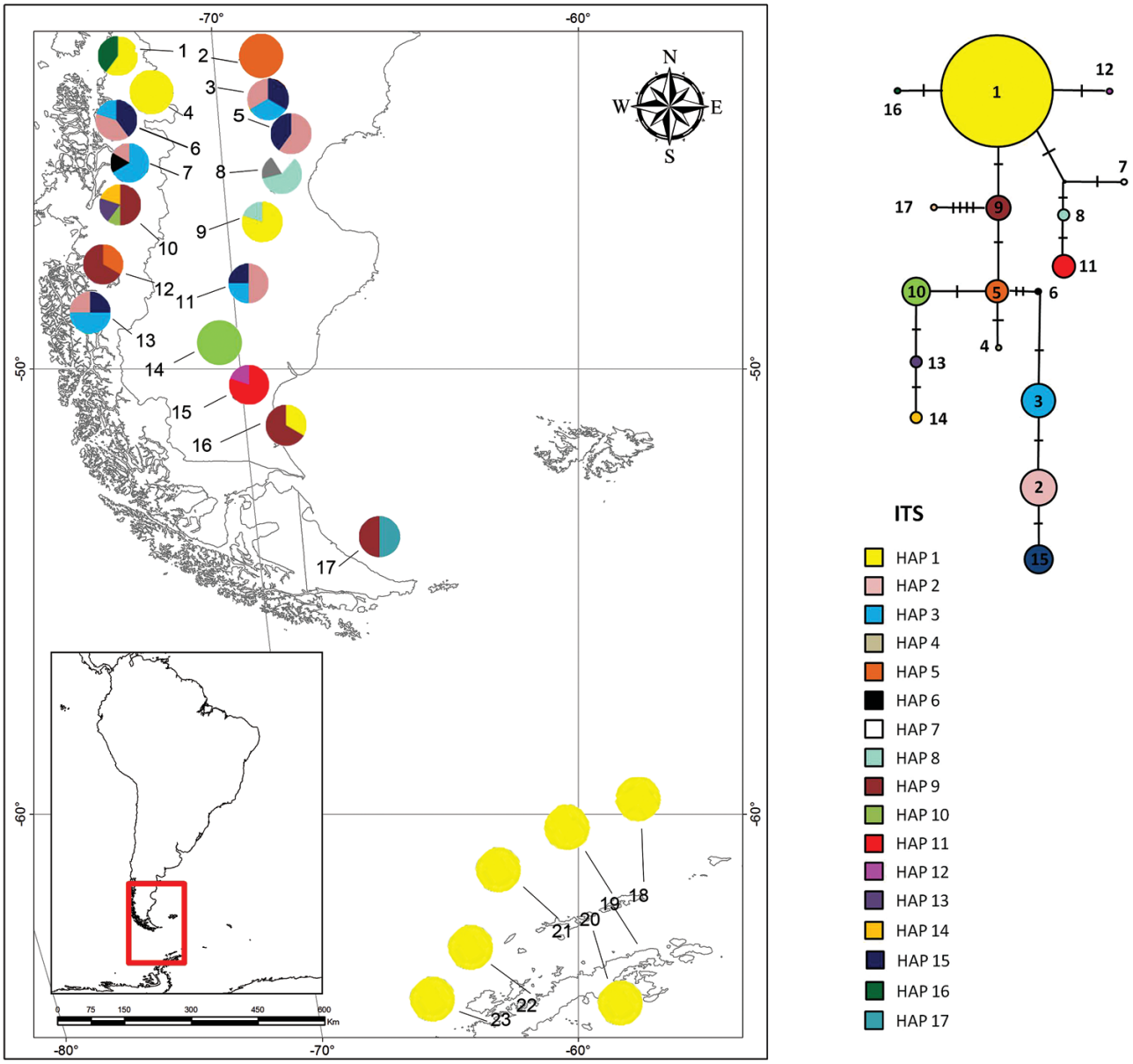

Figure 2. Map of the southern South America and Antarctic Peninsula showing the distribution of 17 internal transcribed spacer (ITS) haplotypes for 23 populations of *Deschampsia antarctica*. To the right, median-joining network showing the relationships among 17 nDNA haplotypes of *D. antarctica*. Circle size is proportional to the haplotype frequency.

We found no significant correlation of genetic and geographical distances for the plastid DNA (Mantel test, $R = 0.004$, $P = 0.463$); however, the ITS yielded a significant and positive correlation (Mantel test, $R = 0.252$, $P = 0.004$) revealing an influence of the Drake Strait barrier. No significant effect of independent variables, latitude, longitude and elevation, was found on variation patterns of haplotype richness or haplotype (h) and nucleotide (π) diversity for the ITS and plastid DNA by means of multiple regression.

DIVERGENCE ANALYSIS, EFFECTIVE POPULATION SIZE AND MIGRATION

Posterior estimates for population sizes, time of divergence and time of bottleneck (median and quartiles) calculated by DIYABC for each scenario showed that scenario 1 was more suitable for both molecular markers. So, for ITS, the product of the coalescent time ($t_{MRCA} = 0.060$ Mya) with both generation times (2 and 5 years) resulted in 120 200–300 500 years (mid to late Pleistocene) as estimates of divergence between populations from Antarctica and

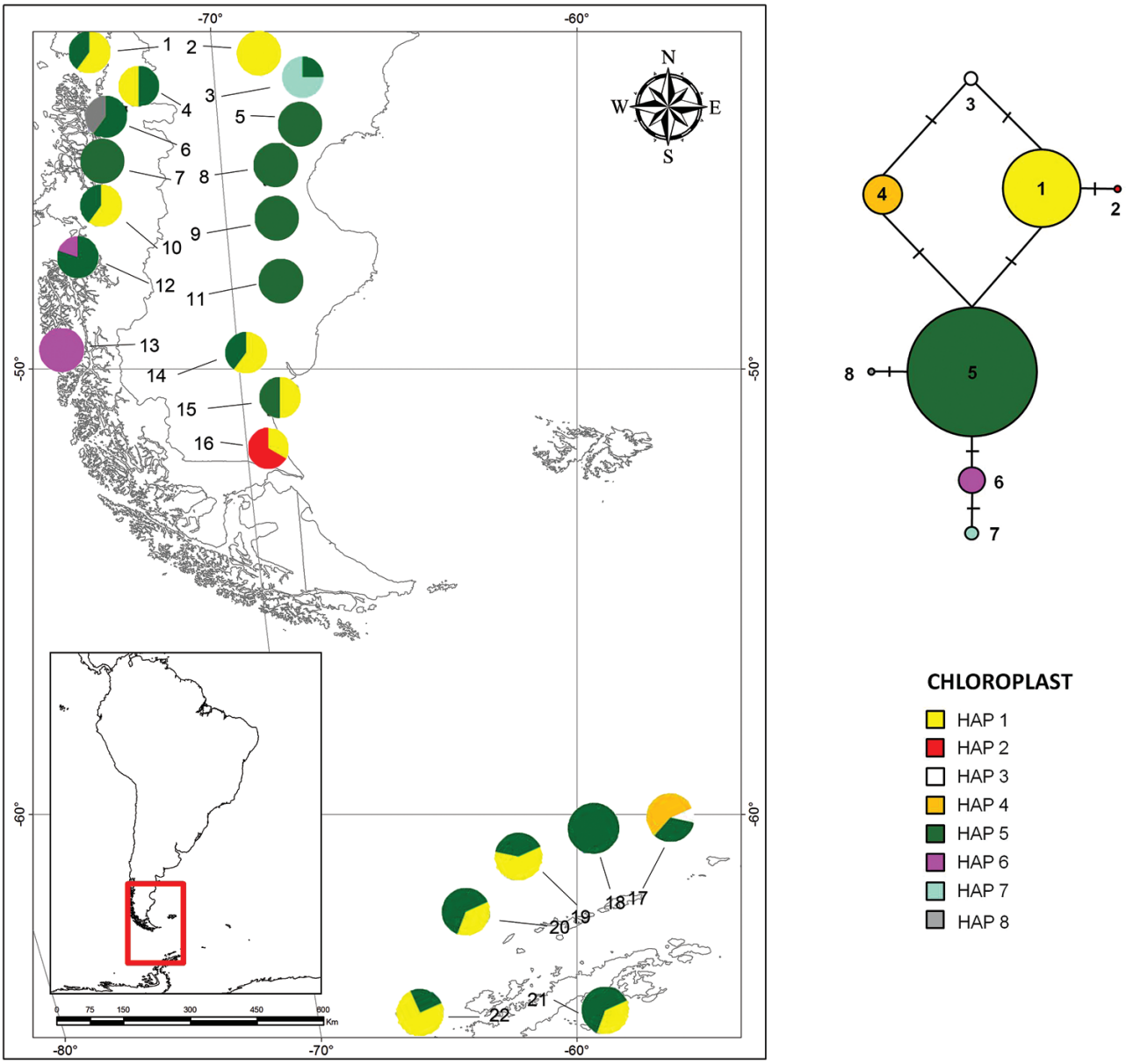

Figure 3. Map of the southern South America and Antarctic Peninsula showing the distribution of eight plastid DNA haplotypes based on the combined sequences of *ndhC-trnVr* and *rps16-trnK* for 22 populations of *Deschampsia antarctica*. To the right, median-joining network showing the relationships among eight plastid DNA haplotypes of *D. antarctica*. Circle size is proportional to the haplotype frequency.

Patagonia. The divergence time estimates for plastid (t_{MRCA} = 0.034 Mya) were in 68 600–171 500 years, also in the mid to late Pleistocene (Table 3; Supporting Information, Table S1). Effective population sizes and migration rates differ among regions, but both were greater in Patagonian populations (Table 3). Nonetheless, for scenario 2, divergence time yielded similar estimates of 1.3 Mya for both markers, and the time of divergence of ITS due to a bottleneck was concordant with that estimated under scenario 1. In contrast, the time of the bottleneck calculated for the plastid occurs during the Holocene (Supporting Information, Table S1).

DISCUSSION

GENETIC VARIATION IN THE ANTARCTIC HAIR GRASS

Our study showed that populations of *D. antarctica* in Patagonia are genetically more variable than those

Table 3. Median and quantiles of posterior distribution for parameters estimated in DIYABC and estimates of effective population sizes and migration rates (median and quantiles) estimated from Migrate for scenario 1 for nuclear ITS and plastid molecular markers in *Deschampsia antarctica*

	ITS			Plastid		
	Median	$Q_{0.05}$	$Q_{0.95}$	Median	$Q_{0.05}$	$Q_{0.95}$
Divergence time	60 100	23 500	97 400	34 300	8320	92 800
N_e Antarctica	656 824	0	2 230 971	58 875 000	17 665 000	144 000 000
N_e Patagonia	26 721 128	12 554 461	25 568 897	16 533 0000	29 000 000	370 665 000
$M_{A\rightarrow P}$	16.1	0	33.2	25.7	0	74.1
$M_{P\rightarrow A}$	49.1	0	160.3	34.8	0	85.7

ITS, internal transcribed spacer.

from Antarctica, 17 ITS and six plastid DNA haplotypes were found in the former compared to one ITS and four plastid DNA haplotypes in the latter. We also found a significant genetic divergence between Patagonia and Antarctica. The low genetic diversity found within Antarctic populations and the high genetic divergence between Patagonia and Antarctica reflects the isolation of the Antarctic populations.

High genetic diversity of Patagonian populations suggests that they have either persisted *in situ* for periods long enough for the maintenance of high genetic variation or that the inhabited area was recolonized by a number of genetically distinct lineages from multiple refugia, as suggested by Premoli, Kitzberger & Veblen (2000) and Sérsic *et al*. (2011) for other plant groups. The presence of private haplotypes allowed distinguishing between these alternatives because areas with low or null levels of within-population genetic diversity but with private haplotypes suggest the existence of long-lasting fragmented refugial areas probably as small populations. In Patagonia, we found four private haplotypes for plastid DNA and 16 for ITS. Of four plastid DNA haplotypes, only one is shared between two sites and the other three are single-site exclusive (HAP 2, HAP 7 and HAP 8; Fig. 3). For ITS, six out of 16 Patagonian haplotypes are unique to single populations (Fig. 2). The high haplotype diversity and the finding of a tetraploid population ($2n = 52$) (González *et al.*, 2016) are congruent with the possible existence of refugia in central-eastern Patagonia, as outlined by Sérsic *et al*. (2011). On the other hand, this area has already been considered as a geographical barrier that prompted lineage divergence in Nothofagaceae, due to an ancient marine ingression (Premoli *et al.*, 2012). Possible origin of polyploid populations could be explained by hybridization of relatively distinct genomes of *D. antarctica* or with other related species (González *et al.*, 2016). Regarding reproductive biology, flowers in Patagonia are cleistogamous and chasmogamous (Chiapella & Zuloaga, 2010), so cross-pollination could occur. The high haplotype diversity in Patagonia, the presence of a single ITS haplotype (Hap 1, Fig. 2) in Antarctica (which is also present in central and southern Patagonia) and the higher migration rates from Patagonia to Antarctica (Table 3) support the hypothesis of dispersal from a South American origin to Antarctica, as hinted at by Van de Wouw *et al.* (2008). The single Antarctic ITS haplotype is also in agreement with previous studies depicting a low genetic diversity in Antarctic populations (Holderegger *et al.*, 2003; Chwedorzewska *et al.*, 2008; Andreev *et al.*, 2010; Volkov *et al.*, 2010). The lower number of haplotypes for both markers (one nuclear and four plastid) found in Antarctica supports the formation of the gene pool from a small number of initial genotypes (i.e. founder effect). Currently, plants in the Antarctic populations commonly have cleistogamous spikelets (Chiapella & Zuloaga, 2010), a fact that leaves local expansion of populations only to vegetative propagation, producing single, dense, contiguous tufts of variable area (Parnikoza, Kozeretska & Kunakh, 2011).

Divergence time between Patagonian and Antarctic populations

One of the longest standing paradigms in ecology has been how populations survived through Pleistocene glaciations when whole regions (e.g. Patagonia and Antarctica) were covered by ice (Stewart & Lister, 1991; Pointing, Bollard-Breen & Gillman, 2014).

It is known that severe climatic oscillations that occurred during the Pleistocene produced major changes in the distribution of species and consequently in their genetic structures (Ramos-Fregonezi *et al.*, 2015). Our data suggest that *D. antarctica* probably survived the Last Glacial Maximum (LGM) and possibly earlier glaciations in ice-free areas, that is refugia in Patagonia, and later dispersed to Antarctica. Although grass pollen is hardly differentiable and the oldest

pollen records of Poaceae in Antarctica are from the LGM (Van der Putten *et al.*, 2012), its detection in deep cores could help to confirm the existence of a grass in Antarctica since the early Pleistocene. Reconstructions of previous glacial extent on this continent support the existence of ice-free biological refuges at least from 1.8 million to 10 000 years ago. Also, evidence preserved from volcanic eruptions below the ice allows for possibility of low-elevation ice-free localities even at glacial maxima (Convey & Stevens, 2007).

Previous studies have estimated the origin of Antarctic populations of *D. antarctica* in the Oligocene–Pliocene, before the onset of the Antarctic Circumpolar Current, in a period when the Antarctic Peninsula climate was milder (Parnikoza, Maidanuk & Kozeretska, 2007). Other estimations set a Holocene time (Lewis Smith, 1984, 2003) or late Pleistocene-Holocene time (Mosyakin, Bezusko & Mosyakin, 2007). Our estimation based on current distribution of genetic variability of populations in Patagonia and Antarctica supports a Pleistocene LDD event from Patagonia to Antarctica, specifically in the mid to late Pleistocene (< 300 000 years ago).

Attempts to test the hypothesis of Patagonia→Antarctica migration, using MIGRATE Bayesian models, resulted in lower effective population sizes for Antarctica ($N_{e(\text{nuclear DNA})}$ = 0.6 million; $N_{e(\text{plastid DNA})}$ = 58 million) than for Patagonian populations ($N_{e(\text{nuclear DNA})}$ = 26 million; $N_{e(\text{plastid DNA})}$ = 165 million). More importantly, migration rates from Patagonia to Antarctica were larger ($M_{P\rightarrow A(\text{nuclear DNA})}$ = 49.1; $M_{P\rightarrow A(\text{plastid DNA})}$ = 34.8) than in the reverse direction ($M_{A\rightarrow P(\text{nuclear DNA})}$ = 16.1; $M_{A\rightarrow P(\text{plastid DNA})}$ = 25.7); also, genetic variability in Patagonia was higher than in Antarctica, reinforcing the idea that Patagonia was the source and Antarctica the sink (Table 3).

The thickness of ice cover in the Antarctic Peninsula during the LGM was variable (Bentley *et al.*, 2006), consisting of 'small glacial systems' (Anderson *et al.*, 2002), as opposed to larger ice shields of East and West Antarctica. Furthermore, the existence of nunataks along the west side of the Antarctic Peninsula (Bentley *et al.*, 2006: 1151; Bergstrom, Hodgson & Convey, 2006: 21) might have offered potential 'safe' places in maritime environments for the arrival of propagules or diaspores, which in turn might have resulted in successful establishment of plants (Parnikoza *et al.*, 2007; Van der Putten *et al.*, 2010). In southern Patagonia, some cold-tolerant species survived in local refugia in glaciated regions, but many cold-sensitive taxa retreated to non-glaciated areas (Fraser *et al.*, 2012). Some other taxa exhibit phylogeographic patterns consistent with survival in large populations in periglacial refugia east of the Andes (Cosacov *et al.*, 2010 and references therein).

Studies providing evidence of deeply divergent lineages unique to Antarctica suggested glacial survival in fragmented habitats followed by post-glacial expansion and pointed to long-term persistence of terrestrial taxa such as arthropods (Convey *et al.*, 2008) and flowering plants (Van der Putten *et al.*, 2010). Hills, Stevens & Gemmill (2010) found a lower genetic variability in Antarctic populations of *Bryum argenteum* Hedw. as compared to others from lower latitudes, thus suggesting a probable persistence in refugia at least since the Holocene or even since the Pleistocene. This result can be partly explained due to a lack of sexual reproduction of these mosses in the Antarctic environment in conjunction with isolation in refugia (Hills *et al.*, 2010). This is similar to the genetic breaks identified for other Antarctic organisms [e.g. the Antarctic springtail, *Cryptopygus antarcticus*, McGaughran *et al.* (2010)] and which have been used to infer the presence of long-standing (Holocene–Pleistocene) glacial refugia. The prevalence of vegetative reproduction in *D. antarctica* and the persistence in refugia since early Pleistocene could also be the reason for the lower genetic variability in Antarctic populations detected in our study (as compared to Patagonian populations). The genetic bottleneck, and the genetically equivalent founder effect, observed for the ITS (scenario 2 which in turn is concordant with scenario 1 for both markers; Supporting Information, Table S1) may suggest that overall warmer interglacial conditions (Holloway *et al.*, 2016) may have prompted population dispersal. Although some degree of imprecision may result from model choice using approximate Bayesian computation (Robert *et al.*, 2011), estimates of the bottleneck by means of the plastid yielded at least an order of magnitude lower divergence time than that of the ITS (Supporting Information, Table S1). This probably relates to the fact that the original genetic structure was conserved over time in the former marker mainly due to vegetative spread. We can speculate that the bottleneck yielded by the plastid is showing a recent population establishment (< 10 Ky) under warmer trends (Convey *et al.*, 2011).

Reaching Antarctica: a difficult migration

Bryophytes are known to be early colonizers, favouring the establishment of vascular plants (Convey *et al.*, 2000). *Bryum argenteum* has had multiple colonization events into Antarctica during Pliocene and Pleistocene (Pisa *et al.*, 2014), and bryophytes were present in Antarctica earlier than *D. antarctica* and probably facilitated the establishment of the grass. In addition, humans have probably recently introduced changes in two important aspects in the establishment of viable populations in Antarctica: first, by directly aiding

transport (this will increase the number and range of taxa arriving in Antarctica) and second, indirectly through the anthropogenic processes that have led to the rapid regional warming (this will most probably increase the probability of establishment and survival of species). Indeed, the response to recent regional climate warming along the Antarctic Peninsula and the maritime Antarctic archipelagos has been a considerable increase in the local ranges and population sizes of the two native vascular plants (Convey, 2003). Although studies show other vascular plant species becoming naturalized in sub-Antarctic islands and even in the Antarctic Peninsula (Frenot *et al.*, 2005; Lewis Smith & Richardson, 2011), *D. antarctica* and *C. quitensis* remain as the only native flowering plants thriving in the Antarctic flora. This emphasizes the uniqueness of these plant species; despite having similar physiological mechanisms providing cold tolerance, no other taxa of the southern cold-temperate regions have naturally colonized sub-Antarctic/Antarctic areas since the LGM.

The results of the analysis of divergence time and the direction of migration, as inferred by the greater genetic diversity in Patagonia, support migration from there to Antarctica in the mid to late Pleistocene, although there was also some migration in the opposite direction at a much smaller scale. Nowadays, F_{ST} values (for both markers) show that Patagonian

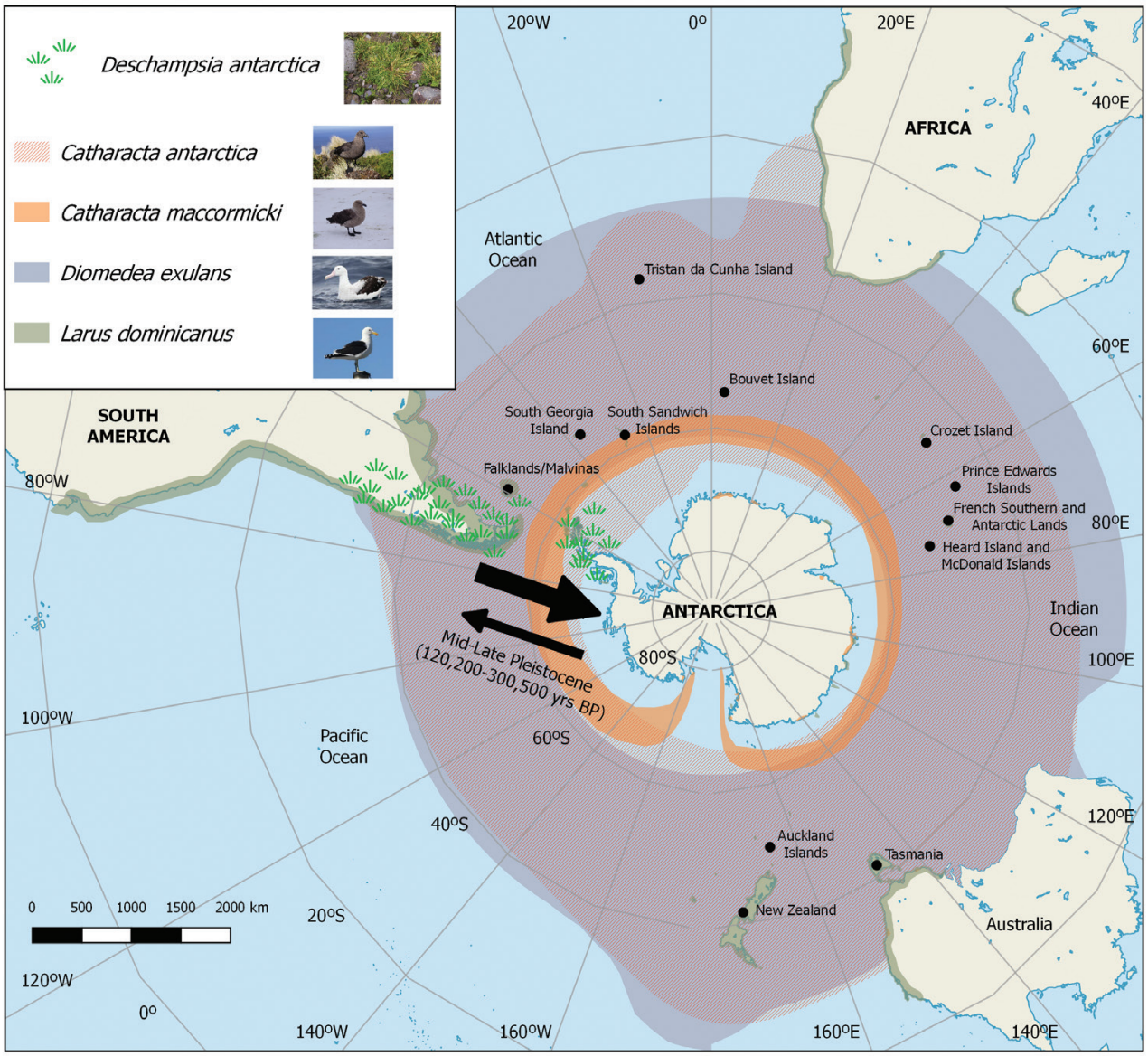

Figure 4. Distribution of the grass *Deschampsia antarctica* (in South America and Antarctica) and of the three seabirds species that might be related to the dispersal of the former from Patagonia to Antarctica.

and Antarctic populations are isolated from each other, and according to the lower variability found in Antarctica, gene flow between the regions is low (or absent).

DESCHAMPSIA IN THE SOUTHERN SEAS: DISPERSAL, BIRDS AND ISLANDS

The evidence presented here deals with the relationships among populations of *D. antarctica* in southern South America, the Antarctic Peninsula and nearby islands (King George, Nelson, Half Moon); however, the Antarctic hair grass is also found in other islands in the South Atlantic (South Georgia, Sandwich Islands, Bouvet) and in the southern Indian Ocean (Kerguélen, Crozet, Prince Edward, Heard). Therefore, a complete view of the evolutionary history of the species will only be achieved through a comprehensive population sampling from all islands.

Deschampsia antarctica seeds do not have structures enhancing aerial dispersal over long distance, so the arrival of the species to Antarctica occurred most possibly by seabirds. Additionally, low genetic variation among localities in Antarctica suggests predominant vegetative reproduction due to climatic constraints.

As to potential dispersal vectors with extended Southern Hemisphere distribution, the kelp gull (*Larus dominicanus*, Baker *et al.*, 2007), the south polar skua and brown skua (*Catharacta antarctica* and *C. maccormicki*, Ritz *et al.*, 2008) and albatrosses (*Diomedea* spp., Burg & Croxall, 2004) stand out as the most likely candidates (Fig. 4). Tillers, roots and seeds of *D. antarctica* have been found near and inside the nests of skuas and kelp gulls (Van de Wouw *et al.*, 2008; Parnikoza *et al.*, 2012); these are generalists in breeding habitat requirements and are also common in Patagonia (García Borboroglu & Yorio, 2004; Roesler *et al.*, 2012). Winds could have had an indirect favourable effect, by creating low-cost 'wind-highways' linking breeding and wintering areas (Felicísimo, Muñoz & González-Solis, 2008); the Southern Hemisphere westerlies wind system (Wyrwoll, Dong & Valdes, 2000) has blown pollen and small propagules from southern South America into the Antarctic maritime (e.g. King George Island) and as far as Wilkes Land (Kappen & Straka, 1988).

Aside from *D. antarctica*, other species of the genus are found in islands in the southern islands and lands, for example the near-cosmopolitan *D. cespitosa* (L.) P.Beauv. in Patagonia, Tasmania and New Zealand; two endemics (*D. chapmanii* Petrie and *D. gracillima* Kirk.) in the Auckland Islands and four endemics (*D. christophersenii* C.E.Hubb., *D. mejlandii* C.E.Hubb., *D. robusta* C.E.Hubb., *D. wacei* C.E.Hubb.) in the Tristan da Cunha archipelago. The distribution of these species suggests an evolutionary history shaped by several LDD events through enormous stretches of ocean.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. Median and quantiles of posterior distribution for parameters yielded by DIYABC and effective population sizes (median and quantiles) estimated from Migrate for scenarios 1 and 2 for nuclear ITS and plastid molecular markers in *Deschampsia antarctica*.