

Two independent dispersals to the Southern Hemisphere to become the most widespread bipolar *Carex* species: biogeography of *C. canescens* (Cyperaceae)

TAMARA VILLAVERDE^{1*}, MARCIAL ESCUDERO², SANTIAGO MARTÍN-BRAVO¹ and MODESTO LUCEÑO¹

¹Department of Molecular Biology and Biochemical Engineering, Pablo de Olavide University, 41013 Seville, Spain

²Department of Plant Biology and Ecology, University of Seville, 41012 Seville, Spain

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About 30 plant species occur at high latitudes in both hemispheres, thus achieving a so-called bipolar distribution. Six of these species belong to *Carex*, of which just one, *Carex canescens*, occurs on two different landmasses in the Southern Hemisphere (South America and Oceania). The goals of this study are (1) to test the various hypotheses accounting for the bipolar disjunction of *C. canescens* and (2) to elucidate if *C. canescens* migrated twice from the Northern Hemisphere to the Southern Hemisphere or if it dispersed from South America to Oceania (or vice versa). We obtained and analysed DNA sequences from the nuclear internal and external transcribed spacers (ITS and ETS) and from the plastid 5' *trnK* and *rps16* introns from 57 populations of *C. canescens* spanning its bipolar range. We characterized the species distribution climatically by adding 1995 presence data points from the Global Biodiversity Information Facility. Our results suggest a Northern Hemisphere origin of *C. canescens* during the Pleistocene and two independent long distance-dispersal events to South America and Australia, by either direct dispersal or mountain-hopping. Long-distance dispersal appears to be the most widespread process resulting in the bipolar distribution of *Carex* spp.

ADDITIONAL KEYWORDS: Australia – climatic niche – disjunction – divergence time estimation – *Glareosae* – long-distance dispersal – South America.

INTRODUCTION

Interest in establishing the relationships between floras in the Southern Hemisphere has been fostered by their similarities with floras of the Northern Hemisphere (e.g. Raven, 1963, 1972; Wen & Ickert-Bond, 2009; Leslie *et al.*, 2012). Endemic Plant families between hemispheres are unusual, and c. 75–85% of families present in Tasmania and southern South America (south of c. 40° S) also occur in the Northern Hemisphere. Endemic genera in plants are more common; c. 20–27% are shared between New Zealand–South America and the Northern Hemisphere (Moore, 1972). Plant disjunctions between hemispheres are formidable when species reach high latitudes on both sides of the Equator, regardless of their occurrence at intermediate latitudes, thus achieving

the so-called bipolar distribution (Moore & Chater, 1971). About 30 vascular plant species are known to have such a distribution and are mainly restricted to Alpine and Arctic regions (Moore & Chater, 1971). Bipolar disjunctions have historically been explained by four hypotheses: (1) vicariance (Du Rietz, 1940), which implies a fragmentation of a continuous distribution during the Mesozoic Era (Scotese, Gahagan & Larson, 1988); (2) convergent or parallel evolution of the disjunct populations (Hofsten, 1916; Scotland, 2011); (3) stepwise long-distance dispersal across the Equator via mountain ranges ('mountain-hopping'; Raven, 1963; Moore & Chater, 1971; Ball, 1990; Vollan *et al.*, 2006); and (4) direct long-distance seed dispersal by birds or wind and/or ocean currents (Cruden, 1966; Muñoz *et al.*, 2004; Nathan *et al.*, 2008; Gillespie *et al.*, 2012).

Carex L. (Cyperaceae), which consists of c. 2000 species (Govaerts *et al.* 2014; Global *Carex* Group, 2015),

*Corresponding author. E-mail: tvilhid@gmail.com

has the greatest number of bipolar taxa (six); these generally have a circumboreal distribution and are limited to austral latitudes in South America ($>52^{\circ}$). An exception is *C. canescens* L. (section *Glareosae* G. Don), the single bipolar *Carex* sp. that reaches not only the southernmost region of South America (Tierra del Fuego and Falkland Islands) but also Oceania (including Australia, Tasmania and New Guinea; Fig. 1 and Supporting Information S1; see Supplemental Data with the online version of this article), occurring in five biogeographical regions (Nearctic, Palearctic, Andean, Neoguinean and Australotemperate; Morrone, 2002). *Carex canescens* is not only the bipolar member of *Carex* with the widest distribution, but it is probably also the most widespread species in the genus.

The great morphological variability in *C. canescens* across its wide distribution has motivated the description of >40 infraspecific taxa, of which only *C. canescens* subsp. *disjuncta* (Fernald) Toivonen (in eastern North America) and *C. canescens* var. *robustior* Blytt ex Andersson (in Patagonia and the Falkland Islands) are currently accepted (Govaerts *et al.*, 2014). A morphological study of *C. canescens* covering its total range found slight differences between Northern and Southern Hemisphere populations, which only

deserved varietal recognition (Moore & Chater, 1971). In general, Southern Hemisphere plants tend to be larger than their Northern Hemisphere counterparts for various parts (e.g. stem diameter, leaf size and utricle width), although there is some overlap (Moore & Chater, 1971). Moore (1972) interpreted these morphological differences between hemispheres as possibly suggesting a transtropical migration in the Americas and subsequent circum-Antarctic dispersal. Nelmes (1951) proposed that *C. canescens* populations from Malaysia are intermediate between Australian and European forms based on the number of conspicuously (or not conspicuously) nerved utricles and suggested a southward migration followed by adaptation of southern populations (Moore, 1972). In *C. canescens*, and in other temperate sedges, leaf elongation has been proved to increase with temperature (Heide, 1997, 2002) and thus might not have importance as a taxonomic character. Maguilla *et al.* (2015) conducted a molecular phylogenetic analysis of *Carex* section *Glareosae* and suggested that the only distinct infraspecific taxon of *C. canescens* was subsp. *disjuncta*, whereas var. *robustior* appeared intermingled among other *C. canescens* samples. Vollan *et al.* (2006) analysed samples of *C. canescens* from Europe (only Norway), South

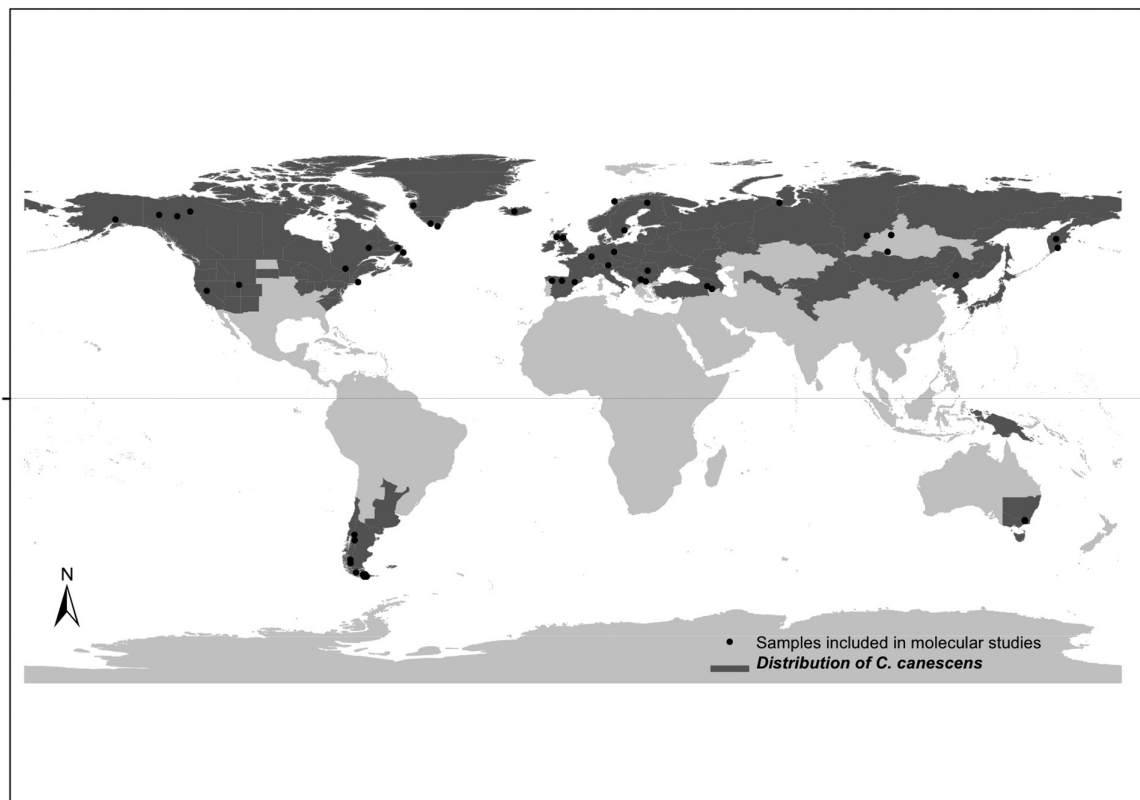


Figure 1. Distribution map of the sampled populations of *Carex canescens*. The shaded region denotes the distribution of *C. canescens* obtained from the World Checklist of Cyperaceae (Govaerts *et al.*, 2014).

America (Chile) and Oceania (Australia) using amplified fragment length polymorphisms (AFLPs) and found genetic differentiation between Northern and Southern Hemisphere populations. They hypothesized a Northern Hemisphere origin and a single colonization of the Southern Hemisphere, followed by secondary dispersal from Australia to South America or vice versa. Escudero *et al.* (2010a) found that the genetic distance between populations of *C. canescens* from North and South America was lower than between some populations from the Northern Hemisphere, which could indicate a more recent connection between North America and Patagonia than among some areas of the Northern Hemisphere. However, sampling was limited in both of these studies, including only six or seven populations and lacking samples from North America (Vollan *et al.*, 2006) or Australia (Escudero *et al.*, 2010a). For bipolar *Carex* spp., the vicariance hypothesis (Du Rietz, 1940) is rejected, as the origin of Cyperaceae (82.6 Ma, 95% highest posterior density: 75.9–85.6 Ma; Escudero & Hipp, 2013) is placed during the Cretaceous, which is well after the fragmentation of the trans-tropical highland bridges that occurred during the Mesozoic (195 Ma; Scotese *et al.*, 1988).

Here we aimed (1) to test the various hypotheses accounting for the bipolar disjunction of *C. canescens* and (2) to determine whether *C. canescens* migrated twice to the Southern Hemisphere or was dispersed from South America to Australia or vice versa.

MATERIAL AND METHODS

STUDY SPECIES AND SAMPLING

Carex canescens is distributed in the temperate areas of both hemispheres, with a circumpolar range in the Northern Hemisphere, whereas its range is limited to Patagonia and south-eastern Australia in the Southern Hemisphere (Fig. 1). *Carex canescens* is a wind-pollinated, herbaceous hemicryptophyte that usually grows in persistently wet, base-poor sites (e.g. sphagnum bogs), moist coniferous forests, woodlands, meadows, lakeshores, rivers and other freshwater bodies. We obtained plant material representing the entire range of *C. canescens* subsp. *canescens* (56 populations) as circumscribed by Egorova (1999) and Toivonen (2002). We also included one population each of *C. canescens* subsp. *disjuncta*, *C. lachenalii* Schkuhr, *C. glareosa* Schkuhr ex Wahlenb., *C. furva* Webb and *C. arcta* Boott from section *Glareosae*. We use *C. macloviana* d'Urv., *C. maritima* Gunn., *C. paniculata* subsp. *Paniculata* and *C. remota* L. as outgroup (Waterway, Hoshino & Masaki, 2009). For all species, one individual per population was sampled. Samples used for the molecular study were obtained from silica-dried leaf material collected in the field and from herbarium

specimens (Supporting Information S1). Vouchers for new collections are deposited in the herbaria CAN, SI and UPOS (abbreviation following *Index Herbariorum*; Thiers, 2016).

PCR AMPLIFICATION AND SEQUENCING

Total DNA was extracted using DNeasy Plant Mini Kit (Qiagen, CA, USA). Forward, and reverse primers were used for amplification of the internal transcribed spacer region (ITS: ITS-A, ITS-4; White *et al.*, 1990; Blattner, 1999), external transcribed spacer regions (ETS: ETS-1f, 18S-R; Starr, Harris & Simpson, 2003), the 5' *trnK* intron (5'*trnK*CarexF, 5'*trnK*CarexR; Escudero & Luceño, 2009) and the *rps16* intron (*rps16F-rps16R*; Shaw *et al.*, 2005). Amplification was carried out using a Perkin Elmer PCR-system 9700 (California) under the conditions specified by Escudero *et al.* (2010a) for ITS and *rps16*, Starr *et al.* (2003) for ETS and Escudero & Luceño (2009) for the 5' *trnK* intron. Polymerase chain reaction (PCR) products were cleaned and sequenced following Escudero *et al.* (2008). Sequences were edited, automatically aligned with MUSCLE (Edgar, 2004), and manually adjusted using GENEIOUS v6.1.7 (Biomatters, Auckland, New Zealand). We coded three informative indels for the 5' *trnK* region following the simple gap coding method of Simmons & Ochoterena (2000).

PHYLOGENETIC ANALYSES

We obtained 56 sequences of ITS (six from NCBI GenBank), 41 of ETS (four from NCBI GenBank), 43 of *rps16* (two from NCBI GenBank) and 47 of 5' *trnK* (one from NCBI GenBank; Supporting Information S1). Each of the four loci was analysed independently and in combination using maximum likelihood (ML) and Bayesian inference (BI). The combined nuclear and plastid matrix consisted of 64 combined sequences with 2635 sites (see Supporting Information S1). ML and Bayesian analyses were performed as described by Villaverde *et al.* (2015a). Selected nucleotide substitution models under the Akaike information criterion (AIC) in jModeltest (Posada, 2008) were GTR+G for ITS1 and ITS2, HKY for ITS 5.8s; GTR for *rps16* and HKY+I for 5' *trnK* (Supporting Information S1).

HAPLOTYPE NETWORK AND DIVERGENCE TIME ESTIMATION

We obtained the genealogical relationships among plastid DNA haplotypes using a plastid matrix that included only samples that had the two amplified plastid regions (34) and statistical parsimony as implemented in TCS v1.21 (Clement, Posada & Crandall, 2000) and described in Villaverde *et al.* (2015a).

Dated phylogenies were estimated for the nuclear and plastid matrices in BEAST v1.7.5 (Drummond *et al.*, 2012). All phylogenies were estimated using an uncorrelated log-normal relaxed clock model. A normal age prior with a mean of 14.82 million years ago (Ma) \pm 2.5 million years (Myr) was applied to the root of the tree based on previous estimates (Escudero & Hipp, 2013). Analyses were conducted using two independent MCMC runs of 40 million generations each, assuming the birth–death tree prior with a mean substitution rate set at 1.0. Run convergence and burn-in were assessed in TRACER v1.5 (Rambaut & Drummond, 2009). Maximum clade credibility (MCC) trees were calculated with TREEANNOTATOR v1.7.2 (Drummond & Rambaut, 2007) using a posterior probability limit of 0.7 and the mean heights option.

CLIMATIC ENVIRONMENT

We obtained values for 19 bioclimatic variables (Supporting Information S1) as described by Escudero, Maguilla & Luceño (2013) for each sampled population of *C. canescens*, except for one population from the USA (Wisconsin) lacking precise geographical coordinates. This data set was completed by adding (1) five additional populations from Australia for which we failed to amplify any loci (see Supporting Information S1); and (2) 1992 species occurrence records originated from herbarium specimens, collected between 1950 and 2014 and downloaded from the Global Biodiversity Information Facility data portal (<http://www.gbif.org/>, downloaded 12 February 2015). This data set was refined by removing probably incorrectly identified (e.g. occurrences outside the distribution range defined by Monocot checklist; Govaerts *et al.*, 2014) or incorrectly georeferenced populations (e.g. occurrences in oceans) and duplicate records from the same locality to reduce the effects of spatial autocorrelation. Our final data set included 2057 populations (Supporting Information S2; see Supplemental Data with the online version of this article). To characterize the climatic niche space of the species, we performed a principal component analysis (PCA) of the climatic data set using the prcomp function (SD, rotation, centre and scale options were set as TRUE) in R (R Core Team, 2014).

ECOLOGICAL NICHE MODEL

A species distribution modelling was performed to reconstruct the potential ranges of *C. canescens* under present climate with MAXENT v3.3.3k (Phillips, Anderson & Schapire, 2006). We performed a correlation analysis with the variance inflation factor (VIF) using the vif function in the usdm package in R (R Core Team, 2014) and a correlation threshold of

0.7 (Dormann *et al.*, 2013). Only three variables were uncorrelated and consequently included in the analyses: bio1 (annual mean temperature), bio6 (minimum temperature of the warmest month) and bio12 (annual precipitation). Replicate runs (500) were performed using the bootstrap run type. Analyses were performed for all populations of *C. canescens* and separately for Northern and Southern Hemisphere populations and populations of *C. canescens* from South America and Australia. We partitioned all the locality data into training and testing data sets (75% vs. 25%, respectively) in order to build niche models and to evaluate the quality of the model. We also ran the analyses without excluding any of the climatic variables and we obtained similar results (not shown).

RESULTS

PHYLOGENETIC RECONSTRUCTION

Carex section *Glareosae* was monophyletic in all analyses with strong support (94% BS / 1 PP, Supporting Information S2). The monophyly of *C. canescens* was strongly supported (97% BS / 1 PP), with the single sampled population of *C. canescens* subsp. *disjuncta* retrieved as sister to the remainder of *C. canescens* subsp. *canescens*. The internal phylogenetic resolution of the species was poor and populations from different hemispheres or continents did not form clades. Most populations were embedded in a polytomy, independently of their geographical origin, with the exception of two samples from South America, which formed a weakly supported clade (61% BS / 0.84 PP, Supporting Information S2).

HAPLOTYPE NETWORK

The obtained plastid DNA(5' *trnK-rps16*) haplotype network revealed seven different haplotypes (H1–H7), of which five corresponded to *C. canescens* and ten missing haplotypes (Fig. 3). Haplotype 1 (H1) is shared by 18 samples of *C. canescens* subsp. *canescens* from Australia, Eurasia and North America, and haplotype 2 (H2), separated by one mutation from H1, is shared by 11 samples of *C. canescens* subsp. *canescens* from Eurasia and North and South America. There are three haplotypes exclusive to single populations of *C. canescens*: one of subsp. *canescens* from western North America (California; H3), one of subsp. *canescens* from South America (Argentina, Santa Cruz; H4) and one of subsp. *disjuncta* from north-eastern North America (Massachusetts; H5). No more than one mutation is needed to connect these singletons with H1 or H2 (Fig. 3). Four of the five haplotypes (H1, H2, H3 and H5) were found in North America, two in Eurasia (H1, H2) and South

America (H2, H3) and only one in Australia (H1). Samples from Australia and South America did not share any haplotype.

DIVERGENCE TIME ESTIMATION

The dating analyses produced a congruent topology with respect to the BI and ML analyses presented above (Fig. 2; Table 1). The divergence time of the clade comprising section *Glareosae* was 6.55 Ma (95% highest posterior density, HPD, 2.56–10.99 Ma), which falls in the Late Miocene-Pliocene. The diversification of *C. canescens* could have occurred during the Pleistocene (1.17 Ma; 95% HPD 0.34–2.17 Ma).

CLIMATIC ENVIRONMENT

The PCA of the climatic data set showed that PC1 explained 48.1% of the variance and PC2 and PC3 explained 15.7 and 14.5%, respectively (Supporting Information S1). The variables with the highest loadings in PC1 were annual precipitation (bio12), temperature seasonality (bio4) and precipitation of coldest quarter (bio19; Supporting Information S1). The scatter plot of the three first components (Fig. 4) is coloured by geographical groups corresponding to: *C. canescens* samples from north-east (Eurasia), north-west (North America), south-east (Australasia) and south-west (South America) quadrants of the Earth. Separation between the Northern and Southern

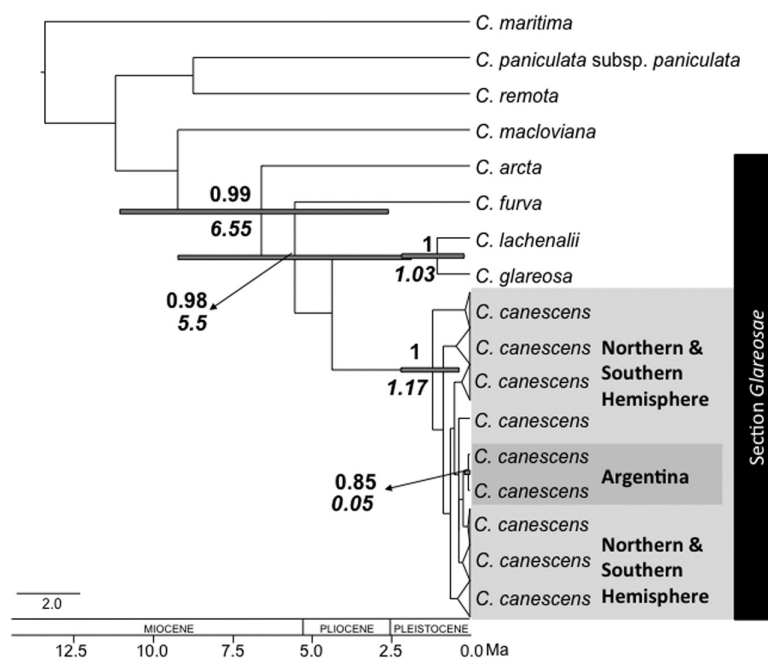


Figure 2. Maximum credibility clade phylogenetic tree from the Bayesian divergence time analysis for *Carex canescens*, other related species of *Carex* section *Glareosae* and outgroup using a combined matrix of nuclear (ITS and ETS) and plastid (5' *trnK* and *rps16*) sequences. Node bars represent the 95% highest posterior density intervals of the divergence time estimates linked to nodes with posterior probabilities >0.85 (values above branches) with mean ages inferred for clades in million years (below branches). Light grey rectangle depicts *C. canescens* populations; dark grey rectangle depicts two populations of *C. canescens* from Argentina.

Table 1. Divergence dates of clades in *Carex* section *Glareosae* presented as the posterior probability followed by the mean time to the most recent common ancestor in million years ago (Ma) and the 95% HPD interval obtained from the divergence time analysis of the combined nuclear (ITS and ETS) and plastid (5' *trnK* intron and *rps16*) regions

Clade	Posterior probability	Mean (Ma)	Min (Ma)	Max (Ma)
Section <i>Glareosae</i>	0.99	6.55	2.56	10.99
<i>C. furva</i> + <i>C. lachenalii</i> + <i>C. glareosa</i> + <i>C. canescens</i>	0.98	5.5	1.84	9.17
<i>C. lachenalii</i> + <i>C. glareosa</i>	1	1.03	0.18	2.14
<i>C. canescens</i>	1	1.17	0.34	2.17
<i>C. canescens</i> from South America (two populations)	0.85	0.05	0	0.17

Hemisphere samples of *C. canescens* or between different landmasses in the same hemisphere was not observed (Fig. 4).

PRESENT DISTRIBUTION UNDER CLIMATIC CHANGE SCENARIOS

Our results show that the modelled ecological niche of *C. canescens*, including the Northern and Southern Hemisphere samples, predicts suitable areas in both hemispheres. Special caution should be taken in northern Siberia and Mongolia, as these areas were underrepresented in our sampling; the projected area may increase in this region if more samples are included. The environmental variable that contributed most to explain the MAXENT models under WorldClim database layers and the most important environmental variable when used alone, according to the jackknife test, was annual mean temperature (bio1). The modelled ecological niche of *C. canescens* including only the Northern Hemisphere populations also predicts suitable habitats in the Southern Hemisphere (Supporting Information S2). Values for the area under the curve (AUC) were all >0.89, indicating a good fit of the models. The average AUC for each group and the most important environmental

variables detected in each analysis are reported in Supporting Information S1.

DISCUSSION

Our results show that *C. canescens* is monophyletic, in agreement with what was found by Escudero *et al.* (2010b). However, Maguilla *et al.* (2015) in a detailed study of *Carex* section *Glareosae* found that *C. arctiformis* Mack. was monophyletic species but embedded in *C. canescens*, making the latter paraphyletic. The molecular similarity of these two species which are morphologically distinctive merits a more profound study. The nonpolyphyly of *C. canescens* allows us to reject strongly the convergent evolution hypotheses for the origin of the bipolar disjunction (Hofsten, 1916; Scotland, 2011), since we would expect two or more lineages of *C. canescens* with different common ancestors under these hypotheses. *Carex canescens* diverged 1.17 Ma (95% HPD: 0.34–2.17) and the clade formed by only two samples from South America is of recent origin (Fig. 3). Therefore, the only remaining alternative hypothesis to explain the distribution of *C. canescens* is long-distance dispersal. This hypothesis best explains the distribution of all bipolar

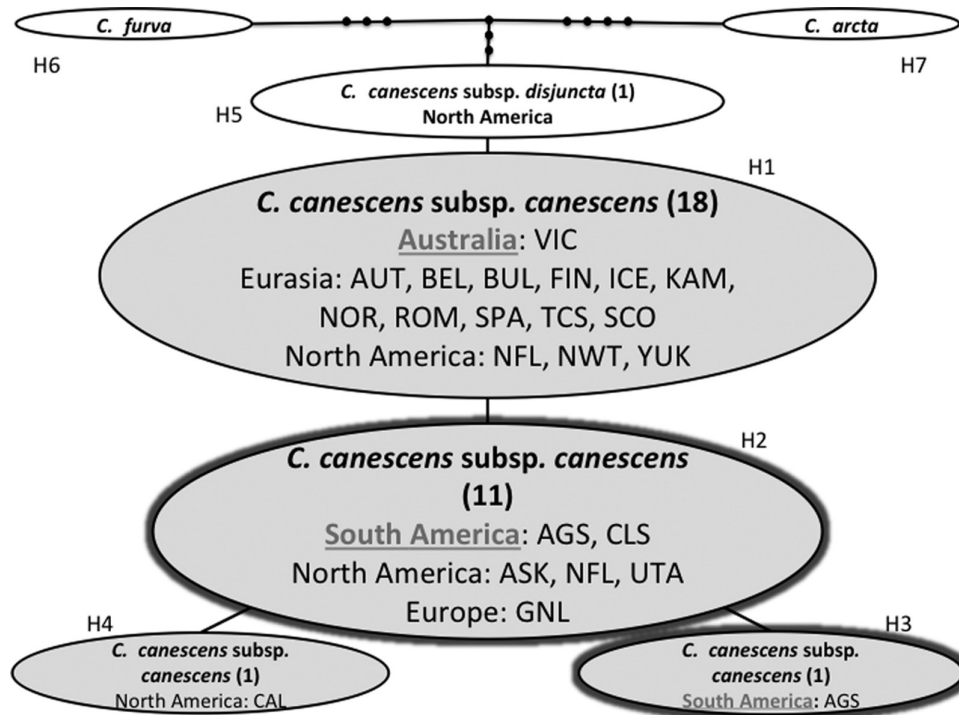


Figure 3. Haplotype network of concatenated plastid DNA sequences of *Carex canescens* subsp. *canescens*, *C. canescens* subsp. *disjuncta*, *C. furva* and *C. arcta*. Circles represent the five haplotypes found (H1–H7), lines represent single mutational steps, and small black circles missing haplotypes. Number of samples per haplotype is indicated in parentheses and abbreviations after the names correspond to the geographical regions of the world (Brummitt, 2001).

Carex spp. (Escudero *et al.*, 2010b; Villaverde *et al.*, 2015a, b; Bruederle *et al.*, unpublished data). Human introduction is a hypothesis that can be rejected here for South America as we have found a private haplotype on this landmass. However, molecular data cannot help to reject this hypothesis for Australia where we found a single haplotype which is shared with the Northern Hemisphere. Nevertheless, taking into account that *C. canescens* occurs in well-conserved habitats in Australia and with little influence by humans until recently makes this hypothesis improbable.

The six bipolar *Carex* spp. are unique in their distribution pattern in comparison to the distribution of their counterparts. In section *Glareosae*, 11 out of 23 species are distributed in both Eurasia and North America; only two of those (*C. canescens* and *C. lachenalii* Schkuhr) reach Australia and only *C. canescens* is found also in South America. The remaining 12 species are found only in Eurasia (eight) or are endemic to North America (four). Similar situations occur in other sections with bipolar *Carex* spp., for example section *Limosae* (Heuff.) Meinsh. (six species; only *C. magellanica* Lam. reaches South America), section *Capituligerae* Kük. (three species; only *C. arctogena* Harry Sm. reaches South America) and section *Foetidae* (Tuck. ex L.H.Bailey) Kük. (only *C. maritima* out of the 11 species distributed in the Northern Hemisphere is also in South America). Bipolar species distribution resembles the wide distribution of typical species that disperse easily by long-distance dispersal and cover many, if not all, continents and biomes (e.g. birds; Proches & Ramdhani, 2013; bryophytes, Lewis, Rozzi & Goffinet, 2014).

DIRECTION OF DISPERSAL

Based on our haplotype network (Fig. 2) and patterns of species diversity and distribution in *Carex* section *Glareosae*, we infer that the most plausible direction of dispersal is north-to-south. The haplotype with the highest number of mutational connections (three), considered the ancestral haplotype under the coalescent theory (Posada & Crandall, 2001), comprises populations from Eurasia and North and South America (H2). Nevertheless, haplotype H1 could also be an ancestral, as it is also widely distributed (Eurasia, North America and Australia) and has only one connection less than H2. All 23–25 species of *Carex* section *Glareosae* (Maguilla *et al.*, 2015), with the exception of *C. canescens* and *C. lachenalii*, are exclusively distributed in the Northern Hemisphere, supporting the hypothesis of a northern origin of the species and a subsequent north-to-south direction of dispersal. The same hypothesis is supported by the widespread distribution of *C. canescens*

in the Northern Hemisphere relative to its much more restricted distribution in the Southern Hemisphere (Fig. 1). Other works on bipolar taxa (including three examples of bipolar *Carex* spp.) have also shown a predominantly southwards colonization route (Gussarova *et al.*, 2008; Popp, Mirré & Brochmann, 2011; Piñeiro *et al.*, 2012; Villaverde *et al.*, 2015a, b; Bruederle *et al.*, unpublished data). Therefore, we suggest that the distribution of *C. canescens* is a result of long-distance dispersal from the Northern Hemisphere to the Southern Hemisphere.

NOT ONCE BUT TWICE: THE DOUBLE COLONIZATION OF THE SOUTHERN HEMISPHERE BY *C. CANESCENS*

None of the haplotypes of *C. canescens* was shared by samples from Australia and South America (Fig. 3). This geographical structure suggests that two different colonization events are needed to explain the presence of *C. canescens* in South America and Oceania. These dispersals might have been from north-to-south, one to each of these two southern landmasses. Multiple independent dispersals from the Northern to the Southern Hemisphere have also been reported to occur in other species of Northern Hemisphere origin and distributed in two southern landmasses (e.g. Yokoyama *et al.*, 2000; Escudero *et al.*, 2009; Schaefer, Heibl & Renner, 2009; Emadzade *et al.* 2011; Banasiak *et al.*, 2013). In contrast, other species first colonized one of the landmasses and then dispersed within the hemisphere (e.g. Schuettelpelz & Hoot, 2004; Gussarova *et al.*, 2008; Inda *et al.*, 2008; Nie *et al.*, 2012).

Two different mountain ranges connect the Northern and Southern Hemispheres, allowing migration of cold-adapted plant species by mountain-hopping. The mountain uplift in Malaysia in the Miocene-Pliocene (10 Ma; Sanmartín & Ronquist, 2004) and the gradually cooler climate in both hemispheres at that time (Scotese, 2002) could have facilitated the dispersal of cold-adapted species into the Southern Hemisphere from Eurasia (Smith, 1981). Similarly, the American cordillera has connected North and South America since the Late Miocene (Smith, 1986; Hoorn *et al.*, 2010b) and has acted as a corridor for the dispersal of different organisms (e.g. Moreno *et al.*, 1994; Antonelli & Sanmartín, 2011). However, the absence of genetic differentiation between the Southern and the Northern Hemisphere and its diversification time suggest a much more recent dispersal of *C. canescens* to the Southern Hemisphere. The same pattern of genetic similarity between hemispheres was found in another bipolar *Carex* sp. (*C. arctogena*; Villaverde *et al.*, 2015b), for which direct long-distance dispersal best explains the bipolar disjunction. A different genetic pattern was, however, found for *C. maritima* (Villaverde *et al.*,

2015a) and *C. magellanica* (Bruederle *et al.*, unpublished data), populations of which from the Southern Hemisphere are genetically distinct from those from the Northern Hemisphere. However, results for *C. maritima* or *C. magellanica* did not favour direct long-distance dispersal over mountain hopping or vice versa. Likewise, we consider that the current study is not conclusive enough to be able to distinguish between mountain-hopping or direct long-distance dispersal as an explanation of disjunction in *C. canescens*. Although further studies at the population level would keep the direction and the timing of the dispersal, it would be needed to reject one of these two possibilities of long-distance dispersals and to give further detail about the means and pathways of dispersals.

THE HIGH DISPERSAL CAPACITY AND COMPETITIVENESS OF *C. CANESCENS*

Carex canescens is the only one of the six bipolar species in the genus that occurs in two landmasses in the Southern Hemisphere (South America and Oceania; including the Falkland Islands, New Guinea and Tasmania). The colonization of such remote areas emphasizes the high dispersal capability of *C. canescens*, ranked as the bipolar *Carex* sp. with the greatest distribution and with two different disjunctions. With the exception of *C. microglochin* Wahlenb., none of the bipolar *Carex* species displays standard morphological syndromes for long-distance dispersal (as described by Higgins, Nathan & Cain, 2003). The only apparent character that might be helping *Carex* spp. to achieve bipolar distribution is the small size of their fruits. Different dispersal agents might have been involved in the distribution of *C. canescens*, such as birds, ocean or wind currents (Nathan *et al.*, 2008; Gillespie *et al.*, 2012). Rare processes or unusual behaviour of vectors have been inferred to disperse seeds over long distances (Higgins & Richardson, 1999; Nathan *et al.*, 2002; Higgins, Nathan & Cain, 2003; Nathan *et al.*, 2008). In fact, long-distance dispersal is claimed as a widespread phenomenon in many plant species without standard morphological syndromes for long-distance dispersal (Carlquist, 1967; Cain, Milligan & Strand, 2000; Higgins, Nathan & Cain, 2003; Alsos *et al.*, 2007; Martín-Bravo, Vargas & Luceño, 2009). The fact that all bipolar *Carex* spp. occur in the same areas in the Northern Hemisphere and South America (e.g. all bipolar *Carex* spp. are found in Patagonia and in northern Europe and North America), together with their early divergence (most of them from the Late Pliocene to Early Pleistocene; e.g. *C. maritima*; Villaverde *et al.*, 2015a) and the low genetic variability between disjunct populations, could indicate some similarities between their means of dispersal. In the case of *C. arctogena*, the lack of any genetic variability between Northern

and Southern Hemisphere populations pointed to a recent dispersal, probably mediated by birds. There are eight global flyways for all fully migratory bird species (BirdLife International, 2010); as described by Kirby *et al.* (2008), three of them cross the Americas and only one connects Eurasia with Australasia. Typically, birds breed in the temperate, boreal or Arctic biomes of the Northern Hemisphere during the northern summer and then fly southwards to spend the nonbreeding season in the warmer biomes of the Tropics (Kirby *et al.*, 2008). Few species undertake trans-equatorial migrations to reach the temperate zones of the Southern Hemisphere during the southern summer. However, the twice-yearly redistribution of billions of individual birds through these flyways highlights the significant proportion of birds that might transport seeds across the Earth. In fact, Viana *et al.* (2016) demonstrated that migratory birds mediate regular seed dispersal, on the order of millions of seeds, over the ocean between Europe and Africa and into the Canary Islands.

In the case of *C. canescens*, birds could also be good candidates for promoting or facilitating its dispersal, as postulated for other bipolar disjunctions (e.g. in *Empetrum* L.; Popp, Mirré & Brochmann, 2011; *Tetraplodon* Bruch & Schimp.; Lewis *et al.*, 2014; *Sphagnum* L.; Kyrkjeeide *et al.*, 2016). Birds could transport *Carex* seeds either externally or internally. For instance, Hohensee & Frey (2001) found a large number of utricles of *C. bohemica* Schreb. on the feathers and mud attached to body and legs of mallards (*Anas platyrhynchos*), especially when birds did not have access to water (i.e. as might happen during migration). Furthermore, it has been recently shown that even for some species of *Cuscuta* L. (Convolvulaceae) that lack morphological syndromes for long-distance dispersal, endozoochory by waterbirds may explain their current subcosmopolitan distribution (Costea *et al.*, 2016). Thus, ecto- and endozoochory could be overlooked as effective long-distance dispersal mechanisms for *Carex* spp.

Establishment of plants following long-distance dispersal is determined by the environment and biotic conditions of the host community and by the colonization capacity and competitiveness of the new-hosted species. Our results show that *C. canescens* occupies a more restricted climatic niche in the Southern than in the Northern Hemisphere (Fig. 4; Supporting Information S2), but falling within the general ecological conditions tolerated by the species, which is wide (Fig. 4). Our sampling is underrepresented in northern Siberia and Mongolia, but we would expect to see the climatic conditions of these localities falling within the climatic space of the Northern Hemisphere and possibly expanding the niche occupied by the northern populations. Similar ecological differentiation was found in *C. arctogena* and *C. maritima* (Villaverde *et*

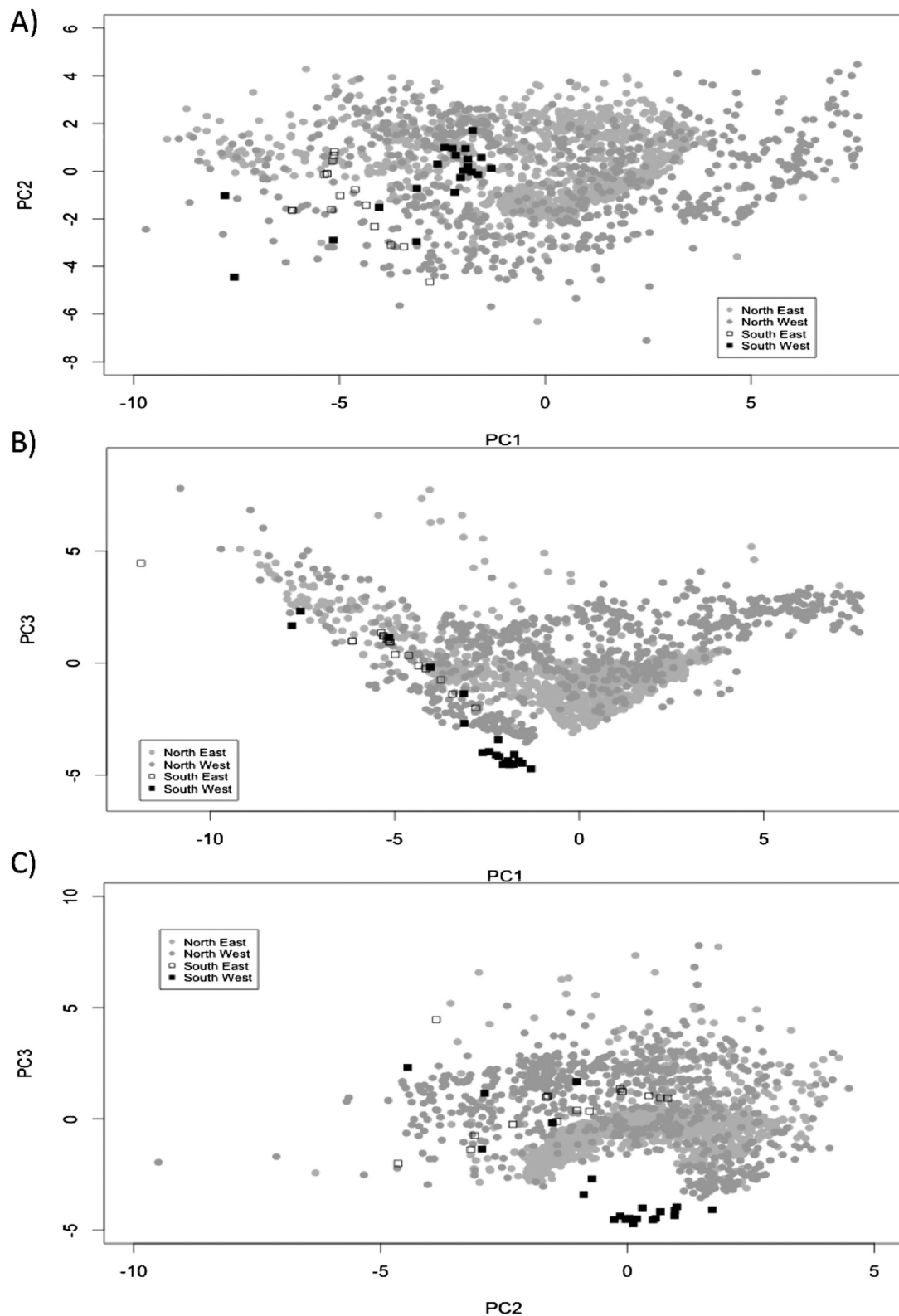


Figure 4. Scatter plots of the first three components of the principal component analysis depicting the position in a climate-niche space of the sampled populations of *Carex canescens* geographically grouped by quadrants of the Earth (north-east, grey dots; north-west, dark grey dots; south-east, open black squares; south-west, black squares).

al., 2015a, b) and in *C. magellanica*, *C. macloviana* and *C. microglochin* (Villaverde *et al.*, unpublished data). These ecological disparities would merit further exploration to understand if these particular niches are solely found in one hemisphere or in both.

Carex spp. are generally highly self-pollinated (Whitkus, 1988; Ohkawa, Yokota & Hoshino, 2000; Arens *et al.*, 2005; Friedman & Barrett, 2009; Escudero *et al.*, 2010b; Escudero, Maguilla & Luceño, 2013), which could also explain, at least in part, successful establishment after dispersal (Baker, 1955; Carlquist, 1983). In addition, chromosome rearrangements were shown to be correlated with phenotypic differences and are thought to enhance fitness in different habitats (Coghlan *et al.*, 2005). Specifically, high chromosome number evolution within the same species could be the result of (1) selection by climatic regime and ecological strategies and (2) neutral processes such as phylogenetic inertia or migration processes (Escudero *et al.*, 2012, 2013). The high chromosome number variation in *C. canescens* ($2n = 52-54, 56-58, 60, 62$; reviewed in Roalson, 2008) might also be a result of the influence of the different climatic environments at different latitudes and distant regions. However, chromosome counts have never been obtained for Southern Hemisphere populations of any of the bipolar *Carex* spp. Testing for chromosome differences between Northern and Southern Hemisphere populations would help to get more insights regarding establishment of these species on different climatic niches.

CONCLUSIONS

Our results suggest that *C. canescens* diversified during the Pleistocene and that its disjunction could be explained by long-distance dispersal from the Northern to the Southern Hemisphere. *Carex canescens* could have dispersed at least twice to the Southern Hemisphere, once to Australia and once to South America, either by mountain-hopping through the Andes cordillera and Malaysian mountains, by direct jump or by a combination of both.

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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:

Supporting Information S1. Studied material of *Carex canescens*, related species and outgroups; molecular characteristics of the amplified regions; results from the principal components analysis of 19 bioclimatic variables from the WorldClim database; description of bioclimatic variables; and AUC values from MAXENT analyses.

Supporting Information S2. Distribution map of *Carex canescens*, phylogenetic tree for *C. canescens*, boxplots of the most important variables from bioclimatic principal component analyses and ecological niche models of *C. canescens*.