

Original article

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RRH: Bipolar disjunction in *Carex arctogena*

**Direct long-distance dispersal best explains the bipolar distribution of *Carex arctogena*
(*Carex* sect. *Capituligerae*, Cyperaceae)**

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ABSTRACT

Aim The bipolar disjunction, a biogeographical pattern defined by taxa with a distribution at very high latitudes in both hemispheres (> 61° N; > 54° S), is only known

to occur in about 30 vascular plant species. Our aim was to use the bipolar species *Carex arctogena* to test the four classic hypotheses proposed to explain this exceptional disjunction: convergent evolution, vicariance, mountain-hopping and direct long-distance dispersal.

Location Arctic/boreal and temperate latitudes of both hemispheres.

Methods A combination of molecular and bioclimatic data was used to test phylogeographical hypotheses in *C. arctogena*. Three chloroplast markers (*atpF-atpH*, *matK* and *rps16*) and the nuclear ITS region were sequenced for all species in *Carex* sections *Capituligerae* and *Longespicatae*; *Carex rupestris*, *C. obtusata* and *Uncinia triquetra* were used as outgroups. Phylogenetic relationships, divergence-time estimates and biogeographical patterns were inferred using maximum likelihood, statistical parsimony and Bayesian inference.

Results *Carex* sections *Capituligerae* and *Longespicatae* formed a monophyletic group that diverged during the late Miocene. Two main lineages of *C. arctogena* were inferred. Southern Hemisphere populations of *C. arctogena* shared the same haplotype as a widespread circumboreal lineage. Bioclimatic data shows that Southern and Northern Hemisphere populations currently differ in their ecological regimes.

Main conclusions Two of the four hypotheses accounting for bipolar disjunctions may be rejected. Our results suggest that direct long-distance dispersal, probably southwards and mediated by birds, best explains the bipolar distribution of *C. arctogena*.

Keywords

Biogeography, bipolar distribution, *Capituligerae*, *Carex*, climatic niche, Cyperaceae, divergence-time estimation, long-distance dispersal.

INTRODUCTION

Arctic taxa are often widely distributed, their distributions usually fitting into one of three patterns: circumpolar, amphi-Atlantic or amphi-Beringian. When Arctic taxa also occur at very high latitudes in the Southern Hemisphere ($> 54^{\circ}$ S), they achieve what is known as a bipolar distribution (Moore & Chater, 1971). This remarkable biogeographical pattern provides some of the greatest biological disjunctions known and it has inspired authors in biogeography since the 19th century (e.g. Darwin, 1859). However, resolving the biogeographical and evolutionary origins of bipolar taxa has been challenging due to the scale of their distributions. Four main mechanisms have been proposed to account for bipolar taxa: (1) vicariance (Du Rietz, 1940), implying fragmentation of a continuous distribution that would date back to the trans-tropical highland bridges of the Mesozoic (c. 195 million years ago, Ma; Scotese *et al.*, 1988); (2) convergent or parallel evolution of disjunct populations that have independent origins but similar phenotypes through adaptation to comparable environmental pressures (Scotland, 2011); (3) stepwise long-distance dispersal across the equator via mountain ranges ('mountain-hopping', Moore & Chater, 1971; Heide, 2002; Vollan *et al.*, 2006) during the last cold periods of the Pliocene and Pleistocene that extended the polar regions of both hemispheres (Raven, 1963); and (4) direct long-distance seed dispersal by birds, wind or ocean currents (Nathan *et al.*, 2008, and references therein). These hypotheses can now be tested objectively by examining the distribution of haplotypes and by dating molecular phylogenies to better assess the possible evolutionary, climatic and geological changes at the origin of biogeographical patterns (Crisp *et al.*, 2011).

Most recent studies addressing the origin of bipolar plants have focused on supraspecific groups (e.g. *Euphrasia*, Gussarova *et al.*, 2008; *Empetrum*, Popp *et al.*, 2011) and used molecular data only. Nonetheless, these studies estimated that the

divergence of bipolar lineages occurred a maximum of 10 million years ago, and concluded that the best explanation for bipolar distributions was long-distance dispersal. Of the approximately 30 bipolar angiosperm species that are known (Moore & Chater, 1971), six are found in *Carex* L., a diverse genus (> 2000 species) that is most common in the cold and temperate regions of the Northern Hemisphere (Reznicek, 1990). Because most *Carex* species, and especially the bipolar species, live under long-day conditions, Heide (2002) tested whether the plants could reproduce under the short-day conditions seen in the tropics, in an attempt to refute the hypothesis of trans-equatorial mountain-hopping. Heide's results showed that, at least for *Carex canescens* L. and *Carex magellanica* Lam., cool, short-day conditions are sufficient to induce flowering. The few molecular studies that have focused on bipolar *Carex* are consistent with Heide's (2002) results. Both Vollan *et al.* (2006) and Escudero *et al.* (2010) found low levels of genetic differentiation in five of the six known bipolar species of *Carex*, suggesting that either mountain-hopping or direct long-distance dispersal was the best explanation for the species' current distributions. However, neither Vollan *et al.* (2006) nor Escudero *et al.* (2010) could determine definitively which hypothesis best explained the distributions of bipolar species. The only remaining bipolar *Carex* not to have been studied using molecular markers is *Carex arctogena* Harry Sm. (in *Carex* sect. *Capituligeræ* Kük.), a species that reaches both the Canadian Arctic Archipelago in the Northern Hemisphere and the southernmost region of South America, Tierra del Fuego (Fig. 1). *Carex* sect. *Capituligeræ* includes two other species, the alpine *Carex oreophila* C. A. Mey, a species confined to the mountains of south-western Asia, and the circumboreal *Carex capitata* L. (Egorova, 1999).

Although morphological, ecological and molecular data clearly separate *C. arctogena* from its sister species, *C. capitata*, in northern Europe (Reinhammar *et al.*,

1999; Reinhammar & Bele, 2001), these differences are less clear in North America, where these species are considered to form a complex (Murray, 2002). Ecological factors could be influencing the geographical distribution of *C. arctogena* and *C. capitata* and may therefore constitute a key element in determining their distributional patterns. The integration of phylogeographical inferences from DNA sequences with bioclimatic data could thus be valuable in clarifying the evolutionary history of this bipolar species.

The goal of this study was to determine which of the four classic hypotheses used to account for bipolar taxa could best explain the distribution of *C. arctogena*. By evaluating the combined evidence provided by phylogenetic reconstructions, molecular dating and bioclimatic data, we will be able to test biogeographical hypotheses and to improve our understanding of the historical events that promoted the formation of the bipolar disjunction seen in *C. arctogena*.

MATERIALS AND METHODS

Sampling

Carex arctogena has a circumboreal distribution, with its range limited to Patagonia in the Southern Hemisphere (Fig. 1). It is a wind-pollinated herbaceous hemicryptophyte that generally occurs in arctic–alpine habitats and wind-exposed heaths where the soil water content is low. We obtained plant material representing the entire range of *C. arctogena* (55 populations), as circumscribed by Egorova (1999). We also included 36 populations of *C. capitata* and one population of *C. oreophila*. Two East African species from *Carex* sect. *Longespicatae* Kük., *Carex runssoroensis* K. Schum. and *Carex monostachya* A. Rich., were also sampled (one and two populations, respectively; Fig. 1, and see Appendix S1 in Supporting Information), because molecular studies suggest that *C. sect. Longespicatae* is sister to *C. sect. Capituligerae* (e.g. Starr & Ford, 2009).

Finally, we used *Carex obtusata* Lili., *Carex rupestris* All. and *Uncinia triquetra* Kük. as outgroups (Starr & Ford, 2009). For all species, one individual per population was sampled, except for five populations of *C. arctogena* that consisted of two individuals each (Appendix S1). Samples used for the molecular study were obtained from silica-dried leaf material collected in the field and from herbarium specimens (Appendix S1). Vouchers for new collections have been deposited in the herbaria CAN, SI and UPOS.

PCR amplification and sequencing

All regions were amplified by polymerase chain reaction (PCR) from total genomic DNA extracted as described by Starr *et al.* (2009). We amplified the nuclear ITS region (using the primers ITSA and ITS4; White *et al.*, 1990; Blattner, 1999) and three chloroplast DNA (cpDNA) regions: the *atpF*–*atpH* spacer, using primers *atpF* and *atpH* (Fazekas *et al.*, 2008); a portion of the *matK* gene, using primers *matK* 2.1f_J and *matK* 5r_J (Plant Working Group, Royal Botanical Gardens Kew, <http://www.kew.org/barcoding/protocols.html> modified by Chouinard, 2010), and the *rps16* intron, using primers *rps16F* and *rps16R* (Shaw *et al.*, 2005). The ITS region has been one of the most useful markers for inferring plant phylogenies at low taxonomic levels, but concerted evolution within this multicopy gene family is known to blur signals of migration and isolation (Schaal & Olsen, 2000). Consequently, this region was used for phylogenetic purposes alone and was only amplified for a subset of samples.

Nuclear and plastid regions were amplified and sequenced following the conditions described by Escudero *et al.* (2008) and Starr *et al.* (2009), respectively. Minor adjustments (e.g. reagent concentrations or annealing temperature) were sometimes necessary in order to obtain suitable amplification products. Sequence data were assembled and edited using SEQUENCHER 4.10 (Gene Codes, Ann Arbor, MI, USA)

and subsequently submitted to GenBank (Appendix S1). Sequences were automatically aligned with MUSCLE (Edgar, 2004) and manually adjusted using GENEIOUS 6.1.7 (Biomatters, Auckland, New Zealand).

Genetic variation, neutrality and selection tests

Nucleotide diversity (π ; Nei, 1987) and haplotype diversity (H_d ; Nei & Tajima, 1983) were calculated for the amplified chloroplast regions of *C. arctogena* and *C. capitata* in DNASP 5.10 (Librado & Rozas, 2009). DNASP was also used to test for molecular selection in *matK* with Tajima's D (Tajima, 1989) and Fu and Li's D^* and F^* (Fu & Li, 1993) neutrality tests. Selective pressure on *matK* was evaluated using the codon-based Z test (Nei & Gojobori, 1986). To test the null hypothesis of neutral selection, the number of synonymous substitutions per synonymous site (d_S), the number of non-synonymous substitutions per non-synonymous site (d_N), and their variances (estimated by bootstrap over 10,000 pseudoreplicates) were calculated for each pair of sequences in MEGA 4 (Tamura *et al.*, 2007). Gaps or missing data were deleted in the pairwise distance estimation. Because they showed incongruence due to positive selection, we removed the *matK* sequences of *C. monostachya* and *C. runssoroensis* from subsequent phylogenetic analyses (see Results), mirroring the removal by Gehrke *et al.* (2010) of ITS sequences that showed incongruence between samples.

Phylogenetic analyses

We obtained a total of 19 sequences of ITS, 87 of *atpF-atpH*, 85 of *matK* and 49 of *rps16* (Appendix S1). The ITS region was only analysed in combination with the plastid regions due to the low number of sequences obtained. The three plastid loci were analysed independently and in combination using maximum likelihood (ML) and

Bayesian inference (BI). The combined nuclear and plastid matrix consisted of 107 sequences with 2835 sites (see Appendix S1). Maximum-likelihood analyses were performed using RAxML 7.2.6 (Stamatakis, 2006), with a GTRGAMMA model of sequence evolution and node support assessed via 1000 bootstrap (BS) pseudoreplicates. Bayesian analyses were executed in MRBAYES 3.2 (Ronquist *et al.*, 2012) using the most appropriate nucleotide substitution model for each partition as chosen by jMODELTEST (Posada, 2008) under the Akaike information criterion (AIC). The selected nucleotide substitution models were HKY for *atpF-atpH*, HKY+I for *matK*, GTR for *rps16*, HKY+I for ITS1, JC for ITS 5.8S and GTR for ITS2 (Appendix S1). The Markov chain Monte Carlo (MCMC) search was run for five million generations with one tree sampled every 1000 generations and two simultaneous analyses ('Nruns = 2') each of four Markov chains ('Nchains = 4') started from different random trees. The first 20% of trees were discarded from each run as burn-in. A Bayesian majority-rule consensus tree was calculated in MRBAYES with posterior probability (PP) values as a measure of clade support. Trees were edited using FIGTREE 1.3.1 (<http://tree.bio.ed.ac.uk/software/figtree/>).

Haplotype network

We obtained the genealogical relationships among all three cpDNA haplotypes using the plastid matrix and statistical parsimony as implemented in TCS 1.21 (Clement *et al.*, 2000). The maximum number of differences resulting from single substitutions among haplotypes was calculated with 95% confidence limits. The only informative indel (*atpF-atpH* region) was coded as a presence/absence character for analysis. Gaps due to mononucleotide repeat units (poly-T and poly-A) are considered to be highly homoplastic (Kelchner, 2000) and were therefore treated as missing data.

Divergence-time estimation

Dated phylogenies were estimated for the nuclear and plastid matrix in BEAST 1.7.5 (Drummond *et al.*, 2012). All *matK* sequences were excluded because run convergence was hampered by incongruence in *matK*, which showed a significant departure from neutrality (Appendix S1). The analysed matrix therefore consisted of 94 ITS, *atpF-atpH* and *rps16* sequences with an aligned length of 2089 sites. All phylogenies were estimated using an uncorrelated log-normal relaxed clock model. A normal age prior with a mean of 13.1982 Ma \pm 2.5 Myr was applied to the crown node, based on the previous estimate for the divergence of *Carex* sections *Capituligerae* and *Longespicatae* from the outgroups in the analysis of Escudero & Hipp (2013). Analyses were conducted using two independent MCMC runs of 40 million generations each, assuming a birth-death tree prior with a mean substitution rate set at 1.0. Run convergence and burn-in were assessed in TRACER 1.5 (Rambaut & Drummond, 2009). Maximum-clade-credibility (MCC) trees were calculated with TREEANNOTATOR 1.7.2 (Drummond & Rambaut, 2007) using a posterior probability limit of 0.9 and the mean heights option.

Climatic environment – ecological niche

Carex arctogena and *C. capitata* are known to have different ecological preferences in Scandinavia (Reinhammar & Bele, 2001). Because the range limits of species and lineages can be influenced by spatial variation in ecological factors (Wiens, 2011), we obtained values for 19 bioclimatic variables (Appendix S1) as described by Escudero *et al.* (2013) for each sampled population of species in *Carex* sections *Capituligerae* and *Longespicatae*. To characterize the climatic niche space occupied by each species, we performed a principal components analysis (PCA) of the climatic dataset using the

'prcomp' function (sdev, rotation, centre and scale options were set as TRUE) and a phylogenetic PCA using the 'phyl_pca' function in the PHYTOOLS package (assuming Brownian motion and covariance matrix option; Revell, 2009) in R (R Development Core Team, 2011). A phylogenetic size-correction was performed in our dataset for non-independence among the observations for lineages. We represented the data associated with the most important bioclimatic variables retained in the PCA for *C. arctogena* in boxplots.

RESULTS

Haplotype diversity and neutrality tests

The number of cpDNA haplotypes and haplotype diversity were highest in *matK* (Nh, 6; Hd, 0.746; nucleotide diversity, π , 0.00397), whereas nucleotide diversity was highest in *atpF-atpH* (Nh, 5; Hd, 0.725; π , 0.00442; Appendix S1). The number of segregating sites was eight in both *matK* and *atpF-atpH*, twice that in *rps16*. A significant departure from neutrality was found in *matK* sequences (F^* -test, $P < 0.05$; Appendix S1). Estimates of the average within-group nucleotide substitution rates for *matK* revealed significant positive selection ($dN > dS$) in *C. monostachya* and *C. runssoroensis*. The *matK* sequences for these species were therefore eliminated from the subsequent analyses as they could affect the results of phylogenetic reconstructions. Selective pressure has also been detected on *matK* in other plant groups (e.g. McNeal *et al.*, 2009) and in other chloroplast regions (e.g. Kapralov & Filatov, 2007).

Phylogenetic reconstruction

Bayesian-inference (BI) and ML analyses revealed strong support (97% BS / 1.00 PP, Fig. 2) for a clade including both sections. *Carex monostachya* was poorly supported as

sister to a large polytomy composed of *C. runssoroensis* plus *C. sect. Capituligerae*. *Carex sect. Capituligerae* was retrieved as an unresolved group with four main lineages (see below). Neither *C. arctogena* nor *C. capitata* was resolved as a monophyletic taxon; instead, two different geographically defined lineages were detected for each species: (1) *C. arctogena* lineage A (90% BS / 0.71 PP) includes samples from Europe and North and South America; (2) *C. arctogena* lineage B (91% BS / 0.90 PP) only includes samples from western North America; (3) *C. capitata* A lineage (88% BS / 0.78 PP) includes samples from Russia; and (4) *C. capitata* B (97 BS / 0.92 PP) comprises samples from North America, Europe and Russia.

Haplotype network

The cpDNA haplotype network (Fig. 3) revealed 10 haplotypes and five missing haplotypes. Geographical structure was detected in most lineages, similar to that found in the phylogenetic reconstruction. We found one unique haplotype in *C. arctogena* lineage A, four in *C. arctogena* lineage B, one in *C. capitata* lineage A and two in *C. capitata* lineage B. There is a haplotype shared by eight samples of *C. arctogena* A, *C. oreophila*, *C. monostachya* and one individual of *C. capitata*. *Carex runssoroensis* occupied a central position in the network. The 10 *C. arctogena* samples from the Southern Hemisphere shared the same haplotype as the 10 Northern Hemisphere samples of *C. arctogena* A.

Estimation of divergence times

The dating analyses produced a partly incongruent topology with respect to the BI and ML analyses presented above (Fig. 4, Table 1). The divergence time of the clade comprising *Carex* sections *Capituligerae* and *Longespicatae* was 6.76 Ma (95% highest

posterior density interval, HPD, 3.05–11.29 Ma), which falls in the late Miocene to early Pliocene. The diversification of the clade consisting of *C. arctogena*, *C. capitata*, *C. oreophila* and *C. runssoroensis* is estimated to have begun 5.0 Ma (95% HPD 2.10–8.03 Ma). The crown nodes of the main lineages obtained in the phylogeny were placed in the late Pleistocene (*C. monostachya*: 0.13 Ma, 95% HPD 0–0.51 Ma; *C. capitata* A plus *C. oreophila*: 0.37 Ma, 95% HPD 0.01–1.17 Ma; *C. capitata* B: 0.68 Ma, 95% HPD 0.14–1.39 Ma; *C. arctogena* B: 0.81 Ma, 95% HPD 0.19–1.66 Ma, Table 1). The grouping of *Carex arctogena* A with *C. runssoroensis* did not receive statistical support in the MCC tree above 0.9.

Climatic environment

The PCA of the climatic dataset from 94 total populations consisting of *C. arctogena* (53 individuals; two populations had missing data in the WorldClim database), *C. capitata* (35), *C. oreophila* (3), *C. monostachya* (2) and *C. runssoroensis* (1) showed that principal component 1 (PC1) explained 98.99% of variance and PC2 explained 0.78% (Fig. 5). The variables with the highest loadings on PC1 were temperature seasonality (BIO4), the mean temperature of the coldest quarter (BIO11), the minimum temperature of the warmest month (BIO6) and isothermality (BIO3; Appendix S1). Maxima and minima for each lineage are shown in Table 2. Similar results were obtained when the analysis was not corrected for the phylogeny (results not shown). Northern and Southern Hemisphere samples of *C. arctogena* A were clearly separated into two groups. The boxplots of the variables with the highest loadings revealed that northern populations of *C. arctogena* A tolerate greater temperature oscillations through the year and a wider range of minimum temperatures during the coldest month than populations from the Southern Hemisphere (Table 2, Fig. 6a,b).

DISCUSSION

Origin of the bipolar distribution of *C. arctogena*

Our study provides strong evidence for a recent origin of the bipolar disjunction in *C. arctogena* lineage A. The divergence time for the clade comprising *Carex* sections *Capituligerae* and *Longespicatae* (crown node: 6.76 Ma, 95% HPD 3.05–11.29 Ma; Fig. 4, Table 1) is far younger than the trans-tropical highland bridges (c. 195 Ma; Scotese *et al.*, 1988) and we therefore reject the vicariance hypothesis for the bipolar disjunction of *C. arctogena* (Du Rietz, 1940). If convergent evolution could explain the bipolar distribution of *C. arctogena*, northern and southern populations of the species would not share an immediate common ancestor. In contrast, our phylogenetic results place all *C. arctogena* A samples in a single clade (Fig. 2) and our haplotype data demonstrate that populations from both hemispheres share identical cpDNA haplotypes over the 2207 bp of three chloroplast markers (Fig. 3). This clearly suggests that *C. arctogena* A is a bipolar monophyletic clade, so we reject a hypothesis of convergent evolution (Stern, 2013).

The bipolar disjunction is best explained by long-distance dispersal, which may have been either by mountain-hopping ('stepping stones') or by a direct event (a 'giant leap'). This could have occurred during some of the last cold periods at the end of the Pliocene or in the Pleistocene, which expanded the polar regions in both hemispheres (Raven, 1963; Ball, 1990), or even at present times. Given that all other taxa in *Carex* section *Capituligerae* and all but one haplotype are found in the Northern Hemisphere, our data suggest that this dispersal occurred from the Northern to the Southern Hemisphere.

The remaining question is: which mechanism better explains the bipolar

disjunction – mountain-hopping or direct long-distance dispersal? The mountain-hopping hypothesis (Ball, 1990) proposes a stepwise long-distance migration by mountain peaks as stepping-stones for polar and temperate taxa to cross the ecological barrier presented by the tropics. A route connecting North and South America through the American Cordillera has been in place since the late Miocene (Smith, 1986). For species of *Carex*, no ecophysiological adaptations to crossing the short-day conditions of the tropical alpine environment seem to be necessary (Heide, 2002), but we are not aware of any published fossil records or any other evidence for the occurrence of *C. arctogena* in areas between northern North America and southern South America. If *C. arctogena* had migrated to South America by the slow and gradual means predicted by mountain-hopping, we would expect that such a process would leave a trace of genetic differences in the plastid loci of populations from both hemispheres (Brochmann *et al.*, 2003; Scotland, 2011), as has been shown for other bipolar species (Vollan *et al.*, 2006; Escudero *et al.*, 2010). Although we cannot completely reject the mountain-hopping hypothesis, the absence of genetic variability between populations of *C. arctogena* A from both hemispheres fits better with a recent and direct long-distance dispersal. Direct long-distance dispersal has been shown to be remarkably frequent in some other species of Cyperaceae (e.g. Viljoen *et al.*, 2013).

The utricle surrounding *Carex* fruit can show some features for wind dispersal, as seen in *Carex physodes* (Egorova, 1999) or for animal dispersal as seen in *Carex microglochin* (Savile, 1972). However, with the exception of the bladder-like utricle, fruits of *Carex* generally lack any obvious morphological features for dispersal by abiotic or biotic forces. The perigynia of *Carex arctogena* do not have any apparent mechanism for dispersal; even the aculeolate teeth on the margin of the perigynia are variable in number, sometimes being entirely absent. We suggest that relatively unspecialized

structures for dispersal might play a role in the distribution of *C. arctogena*. We regard the hypothesis of nonstandard vector-mediated dispersal, either by abiotic or biotic forces, as a possible explanation of the bipolar disjunction of *C. arctogena*.

It is possible that populations of *C. arctogena* in the Southern Hemisphere may have been the result of an accidental anthropogenic introduction. In this scenario, adaptation to local environmental conditions, biotic interactions and demographic processes of this species would all have established relatively quickly (Theoharides & Dukes, 2007). Populations of *C. arctogena* in Patagonia occur in well-conserved habitats and most are only accessible on foot. Specimens of *C. arctogena* from Patagonia are few in the South American herbaria BA, BAA, BAB, BCRU, HIP and SI, with some dating to the late 1880s, when the human influence in the southernmost parts of South America was very limited. Although we cannot rule out an anthropogenic introduction of this species to South America, it seems unlikely.

Bird-mediated direct long-distance dispersal from North America has already been used to explain a bipolar disjunction in crowberries (*Empetrum*; Popp *et al.*, 2011). Most migratory birds that disperse seeds live in temperate and boreal regions (Wheelwright, 1988). For birds to act as vectors for seed dispersal by endo- or ectozoochory, the seeds must have morphological features for association with these animals, and must be able to maintain their viability after intestinal transit to allow for establishment in new environments (Gillespie *et al.*, 2012). Although *Carex* fruits lack obvious morphological features for zoochorous dispersal, other structures or features that are not directly related with dispersal syndromes may be involved, including anatomical features such as deposits of silica in the pericarp that harden seeds (Graven *et al.*, 1996; Prychid *et al.*, 2004). These silica deposits could protect seeds when passing through birds' alimentary tracts (Graven *et al.*, 1996) but could also make the seeds as

hard as pebbles and useful for grinding other organic material in bird gizzards. *Carex* fruits could therefore be doubly preferred by birds – both as nourishment and as gastroliths (Alexander *et al.*, 1996).

Some birds from North America, such as the pectoral sandpiper, *Calidris melanotos* (Holmes & Pitelka, 1998), and the lesser yellowlegs, *Tringa flavipes* (Tibbitts & Moskoff, 1999), are known to feed in sedge meadows before migrating southwards to their wintering grounds in South America. Their breeding ranges closely match the current distribution of *C. arctogena* A in both hemispheres (Fig. 1). Although current bird migratory patterns do not necessarily coincide with past migrations, these observations suggest that the bipolar disjunction in *C. arctogena* may have originated via bird-mediated long-distance dispersal. Additionally, dispersal may occur through accidental displacement – vagrant birds or migrants, such as those flying to Australia or New Zealand, deviating widely from their normal route (Battley *et al.*, 2012). With satellite telemetry, Gill *et al.* (2009) recorded transoceanic flights of bar-tailed godwits (*Limosa lapponica baueri*) from Alaska to New Zealand and showed that they can fly 10,153 km (± 1043 SD) non-stop in 7.8 days (± 1.3 SD). This extraordinary flight, combined with species that can be preferentially chosen for fuel, could help species such as *C. arctogena* to achieve a bipolar distribution by means of direct long-distance dispersal.

Climatic regime differentiation

Theoretically, *C. arctogena* A is most likely to become established at the high latitudes and elevations in the Southern Hemisphere that have similar climatic conditions to those of northern populations (Carlquist, 1966). Although our results from the bioclimatic data show that Southern Hemisphere populations currently differ from

Northern Hemisphere populations of *C. arctogena* A in their climatic niches (Fig. 6), differences in community assembly, which suggest differences in competitive interactions, may explain how *C. arctogena* A was able to establish itself in South America after one or more initial dispersal events (Waters, 2011). Such differences could have allowed *C. arctogena* to shift into new habitats and climate zones (Broennimann *et al.*, 2007). Alternatively, establishment could have taken place at a time when both areas had similar climatic conditions.

CONCLUSIONS

Evidence from multiple analytical approaches was used to infer the possible mechanisms underlying the distribution of a bipolar species. Bioclimatic data, phylogenetic and phylogeographical analyses and divergence-time estimates have been integrated to test hypotheses that are traditionally used to account for the origin of bipolar distributions at the species level. Our study highlights the importance of long-distance dispersal in explaining this extraordinary pattern of plant distribution, although further comparative studies using multiple bipolar species are necessary to test for the same explanation in other phylogenetically independent cases.

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SUPPORTING INFORMATION

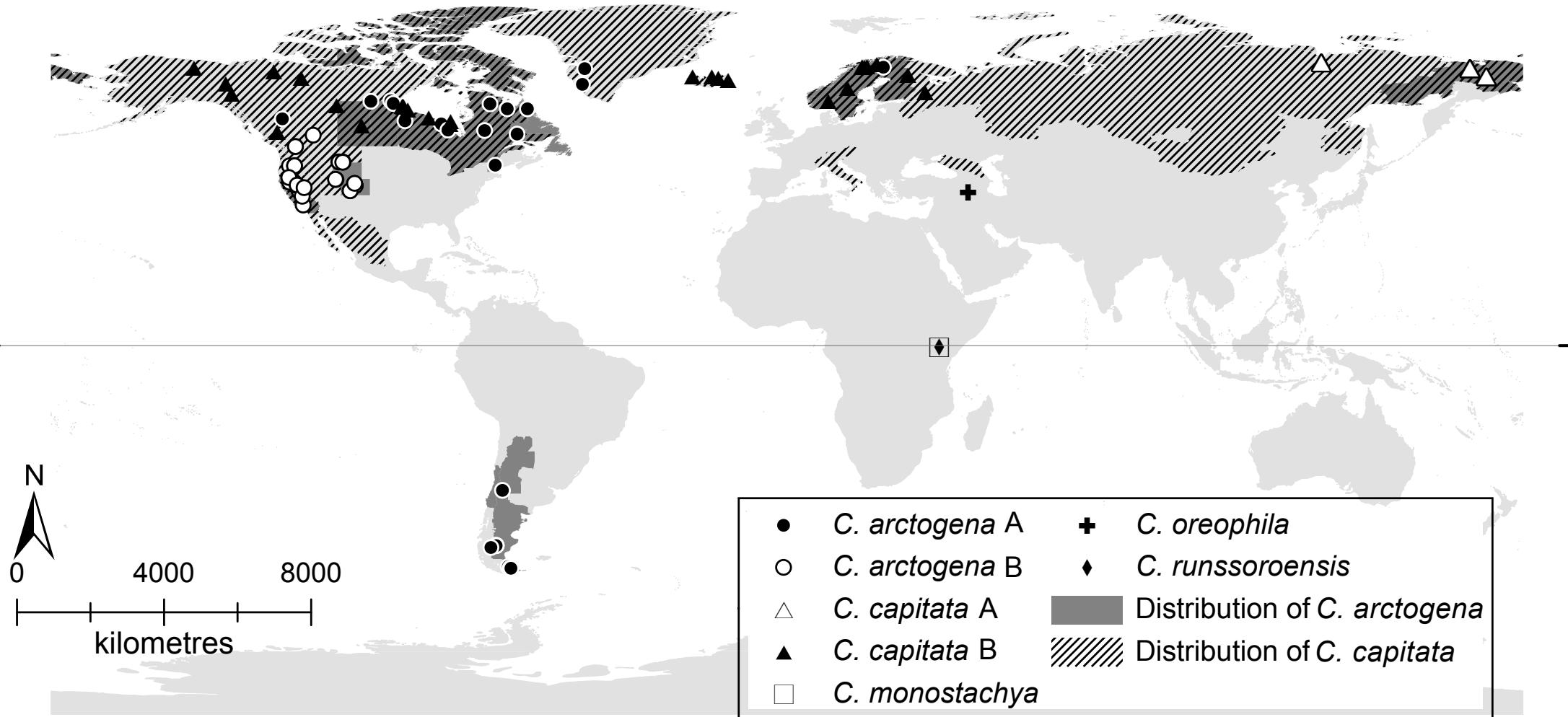
Additional Supporting Information may be found in the online version of this article: **Appendix S1** Studied material, molecular characteristics of the amplified regions, and results from the principal components analysis of 19 bioclimatic variables from the WorldClim database, both corrected for phylogeny and uncorrected.

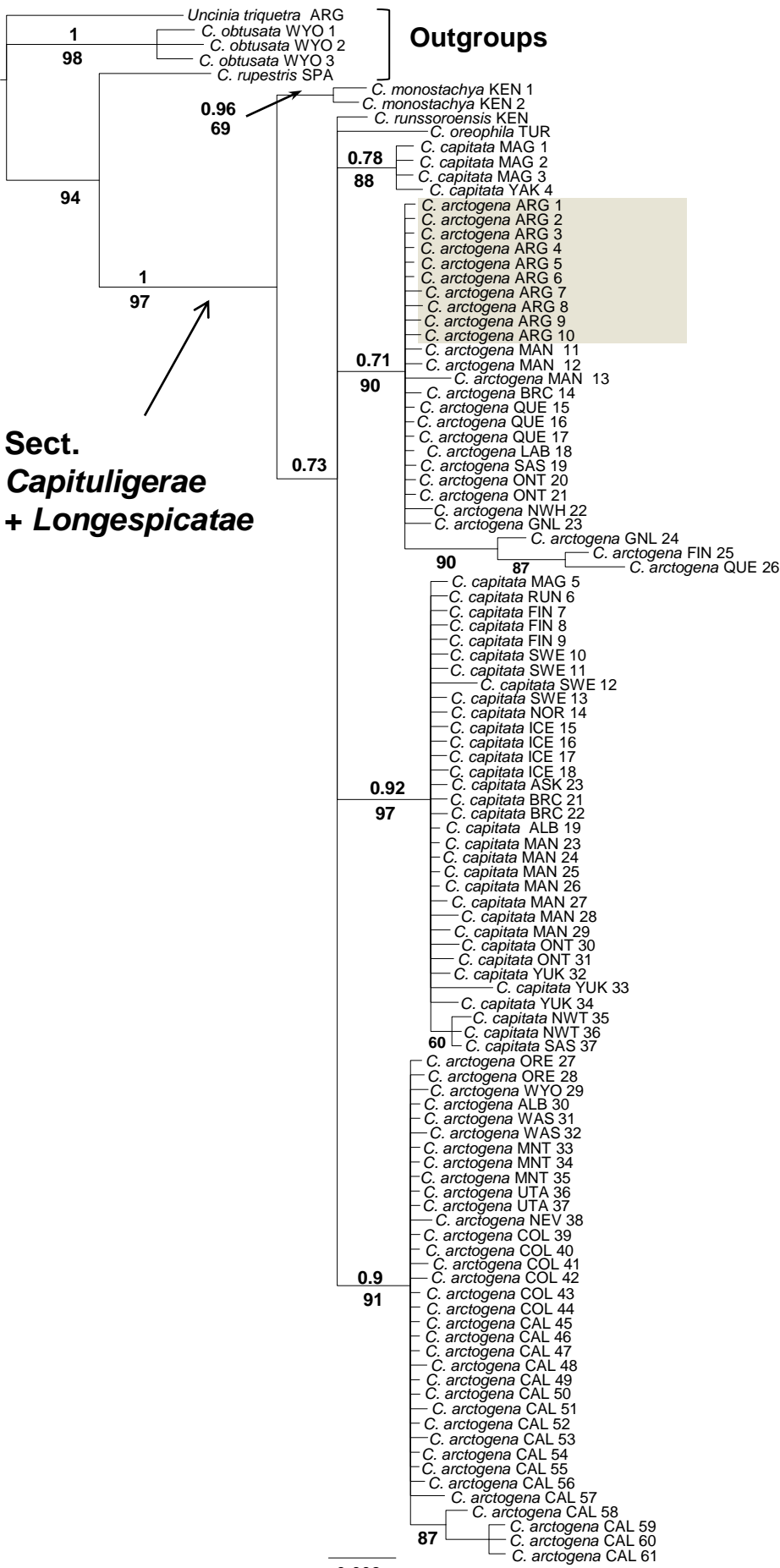
BIOSKETCH

Tamara Villaverde is a PhD student at Pablo de Olavide University, Seville (Spain). Her research is focused on the evolution and phylogeography of angiosperms, with special interest in the biogeography and systematics of the genus *Carex* (Cyperaceae).

Authors contributions: M.E., M.L. and J.R.S. conceived the idea; T.V., S.M.-B., L.P.B. M.L., J.R.S. collected the plant material; T.V., M.E. and S.M.-B., carried out the lab work and analysed the data; T.V., M.E. and S.M.-B. led the writing and drafted the manuscript, and all authors contributed to its preparation.

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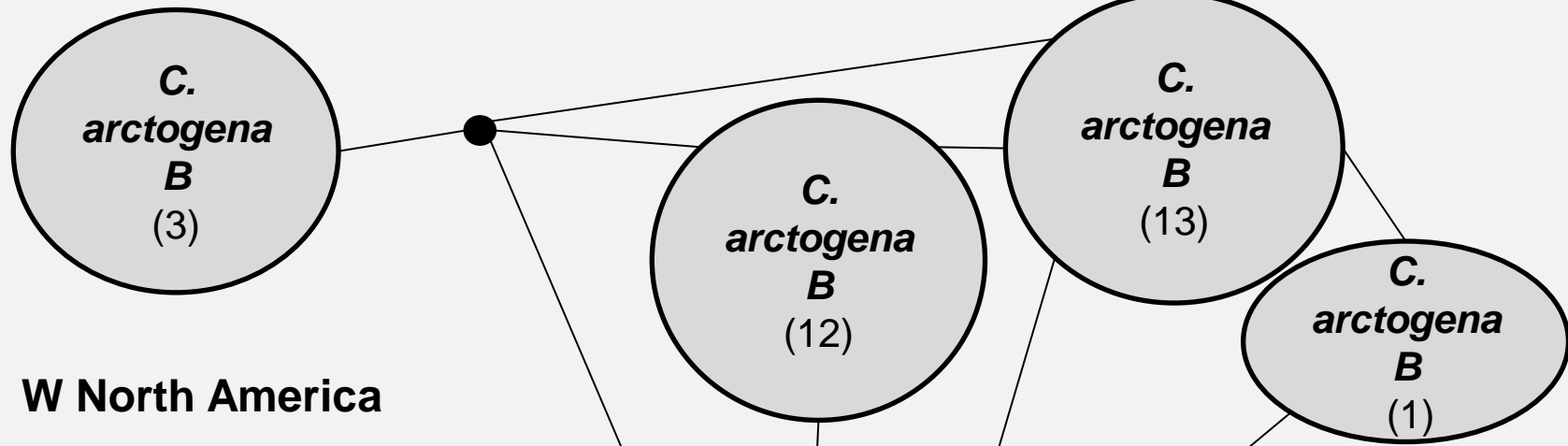
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C. arctogena A
Northern &
Southern
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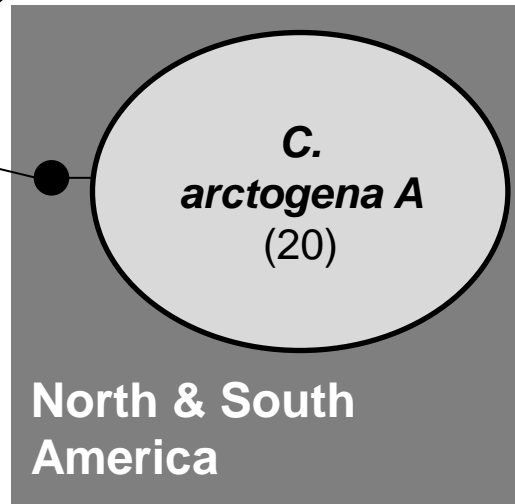
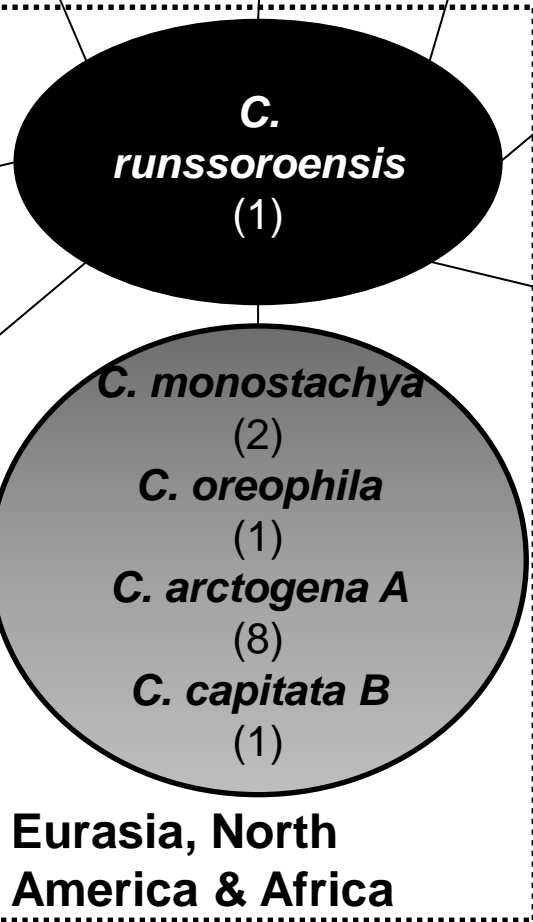
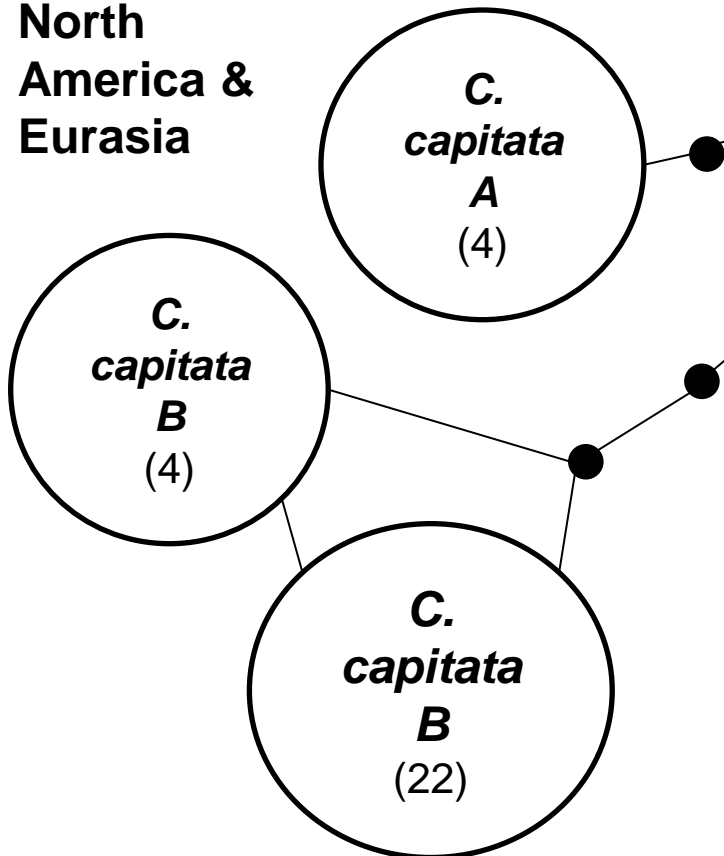
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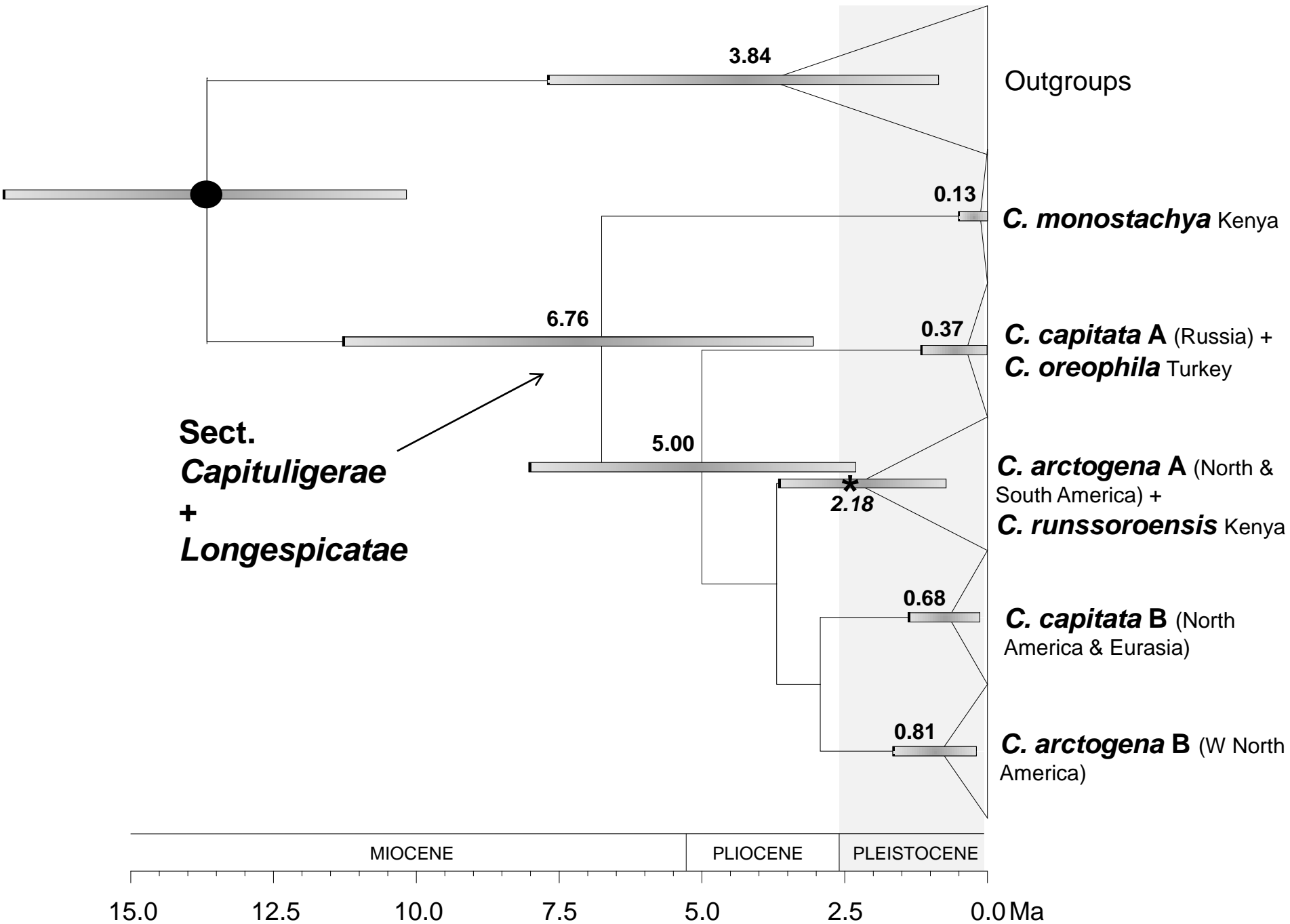
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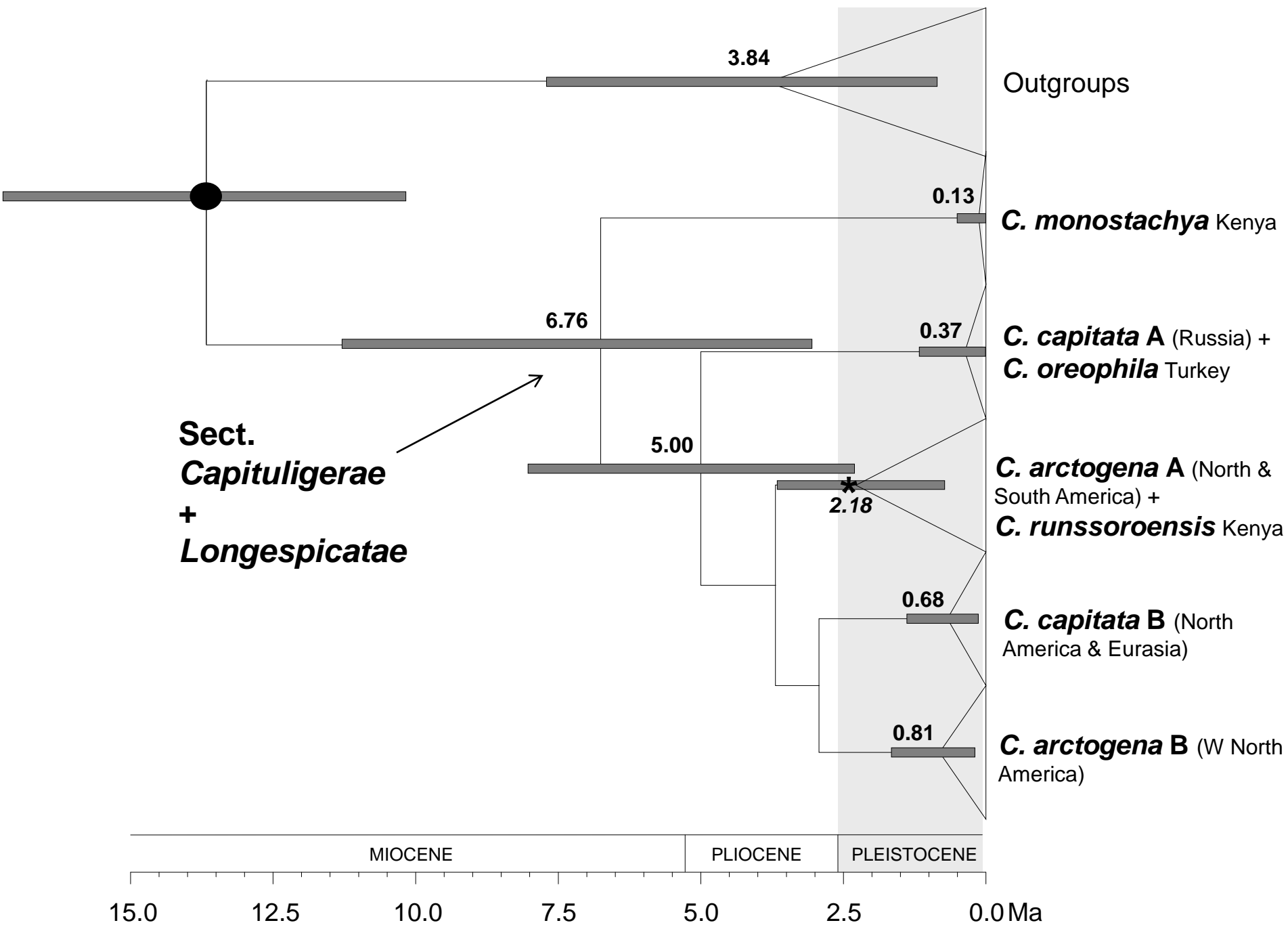
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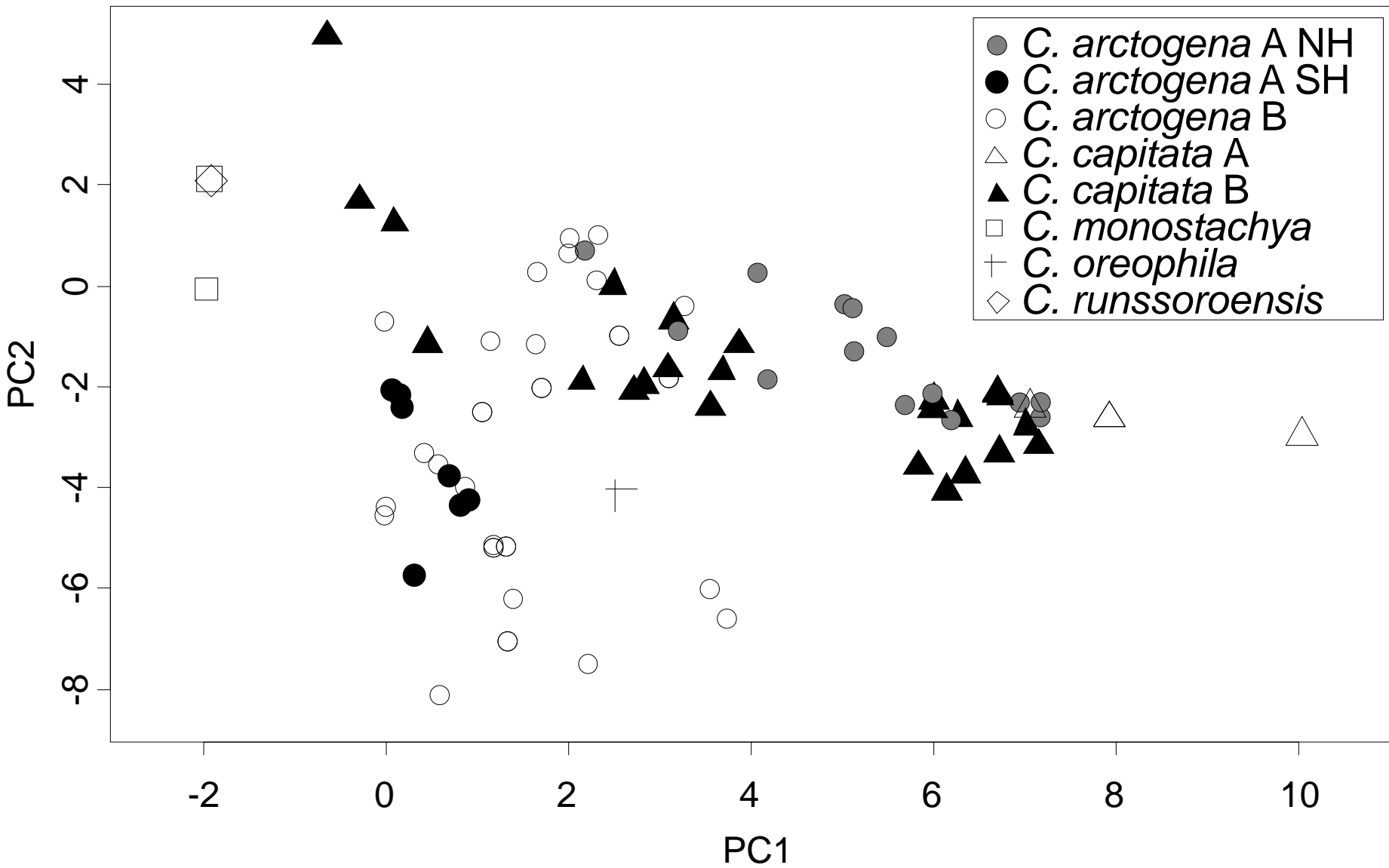


**North
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Eurasia**









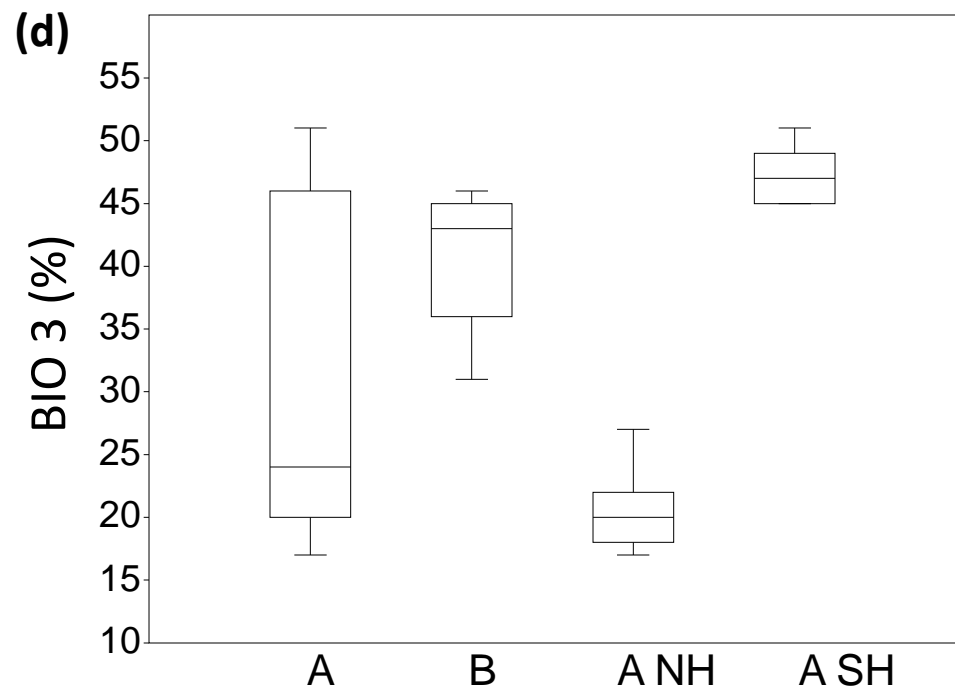
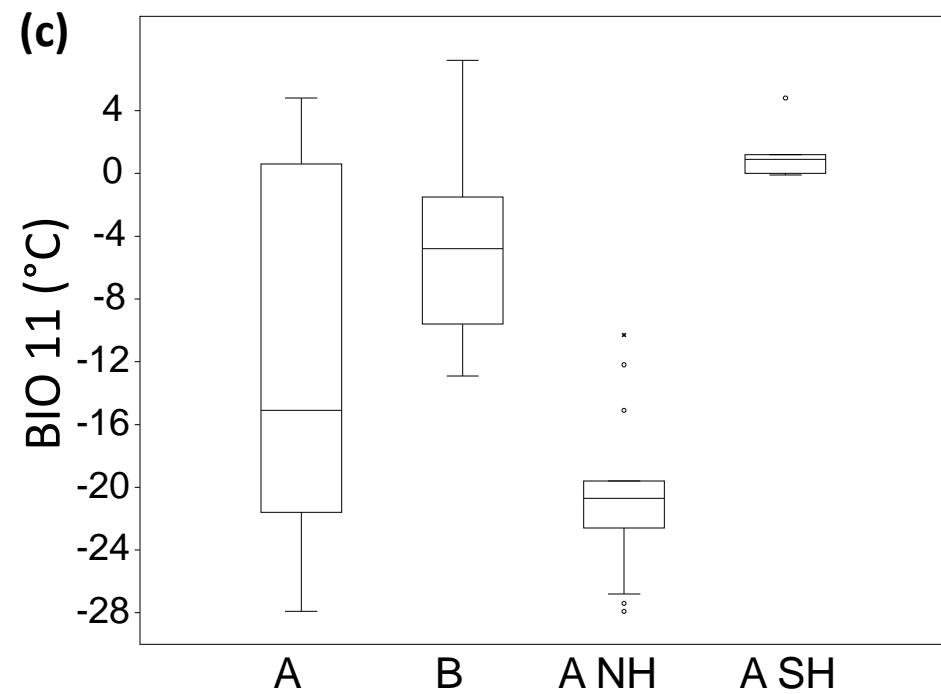
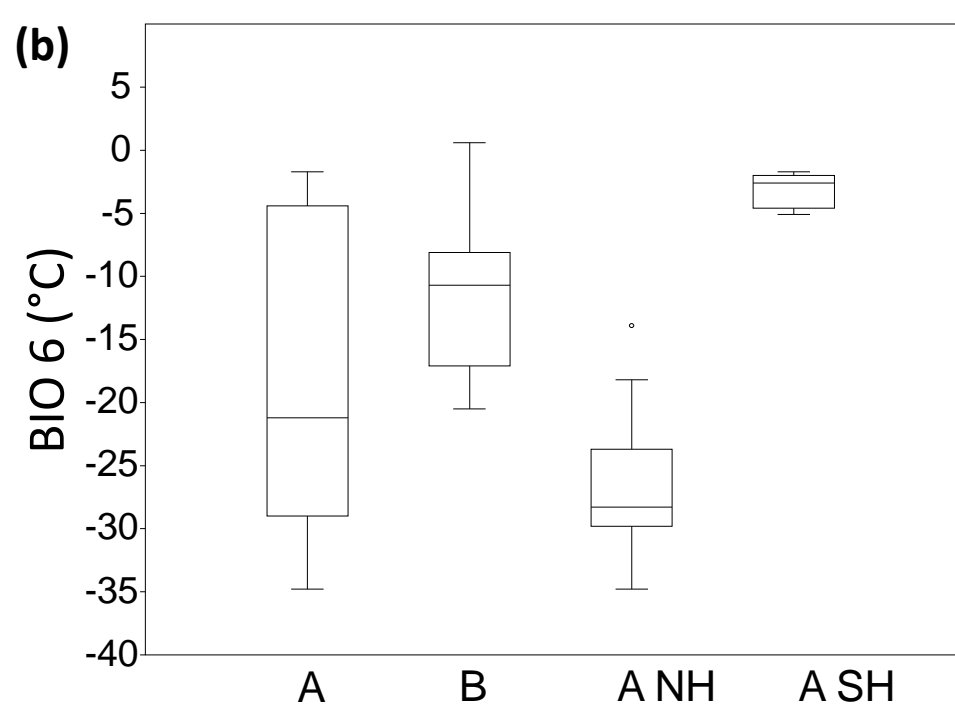
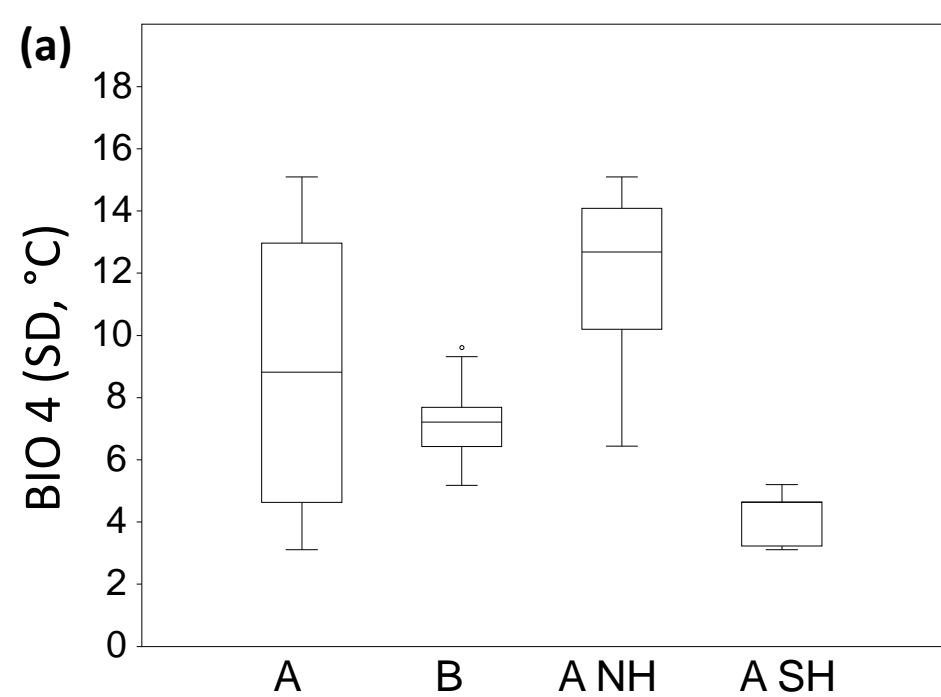


Table S3 Locus information for the regions amplified in the study including samples sizes, summary statistics. Nh, number of haplotypes (gaps were excluded); Hd, haplotype diversity; *S*, segregating sites; π , nucleotide diversity.

Locus	Nh	Hd	<i>S</i>	π	Tajima's <i>D</i>	Fu & Li's <i>D</i> *	Fu & Li's <i>F</i> *
<i>atpF-atpH</i>	5	0.725	8	0.00442	1.27151 ^{n.s.}	1.27758 ^{n.s.}	1.50645 ^{n.s.}
<i>rps16</i>	4	0.729	4	0.00245	1.63220 ^{n.s.}	1.01718 ^{n.s.}	1.40374 ^{n.s.}
<i>matK</i>	6	0.746	8	0.00397	1.85050 ^{n.s.}	1.28088 ^{n.s.}	1.73597*

**P* < 0.05; n.s., not significant.

Table S4 Average within-group nucleotide substitution estimates for the *matK* gene of the complete dataset.

Species	Selection hypothesis tested					
	Neutrality		Positive		Purifying	
	Probability	(dS - dN)	Probability	(dS - dN)	Probability	(dS - dN)
Outgroups	0.508 ^{n.s.}	-0.664	1.000 ^{n.s.}	-0.667	0.252 ^{n.s.}	0.670
<i>C. monostachya</i> and <i>C. runssoroensis</i>	0.040*	2.081	0.019*	2.106	1.000 ^{n.s.}	-2.093
<i>C. capitata</i> A	1.000 ^{n.s.}	0.000	1.000 ^{n.s.}	0.000	1.000 ^{n.s.}	0.000
<i>C. capitata</i> B	0.304 ^{n.s.}	1.031	0.154 ^{n.s.}	1.022	1.000 ^{n.s.}	-1.038
<i>C. arctogena</i> A	1.000 ^{n.s.}	0.000	1.000 ^{n.s.}	0.000	1.000 ^{n.s.}	0.000
<i>C. arctogena</i> B	0.297 ^{n.s.}	-1.048	0.150 ^{n.s.}	1.039	1.000 ^{n.s.}	-1.030

**P* < 0.05; n.s., not significant.

dS: Numbers of synonymous sites

dN: Numbers of non-synonymous sites

Table S5 Loadings matrix obtained by the principal components analysis not corrected by phylogeny of 19 bioclimatic variables on *Carex* sections *Capituligerae* and *Longespicatae*.

Variable	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10	PC11	PC12	PC13	PC14	PC15	PC16	PC17	PC18	PC19
bio1	-0.286	-0.219	-0.069	0.217	-0.052	-0.145	-0.091	-0.191	-0.105	-0.110	0.286	-0.531	0.062	-0.029	0.377	-0.019	0.464	0.033	0.000
bio2	-0.110	-0.294	0.187	-0.037	0.570	0.339	0.330	0.076	-0.062	-0.378	0.008	-0.058	0.045	0.145	-0.316	-0.053	0.185	0.009	0.000
bio3	-0.308	-0.093	-0.027	0.093	0.053	0.601	0.083	-0.061	-0.136	0.652	0.150	0.023	-0.124	-0.080	0.105	0.000	-0.112	-0.019	0.000
bio4	0.328	0.009	0.209	-0.018	0.113	-0.112	-0.059	0.035	0.071	0.394	0.064	0.058	-0.007	0.021	-0.162	-0.051	0.447	0.650	0.000
bio5	-0.069	-0.375	0.209	0.157	0.273	-0.194	-0.101	-0.072	-0.007	0.008	-0.354	0.395	-0.113	-0.327	0.379	0.100	0.021	-0.017	-0.323
bio6	-0.322	-0.105	-0.173	0.083	-0.163	-0.054	-0.053	0.014	-0.106	-0.043	-0.207	0.400	-0.057	-0.084	-0.160	-0.029	0.331	-0.011	0.674
bio7	0.293	-0.075	0.277	-0.008	0.297	-0.039	0.004	-0.049	0.104	0.048	0.038	-0.214	0.003	-0.073	0.347	0.078	-0.326	0.003	0.665
bio8	0.152	0.008	0.125	0.658	-0.286	-0.033	0.580	0.317	0.029	0.007	-0.065	-0.020	0.018	-0.025	0.044	-0.001	-0.004	-0.003	0.000
bio9	-0.298	-0.190	-0.097	-0.121	0.031	-0.063	-0.062	0.499	0.754	0.103	0.048	-0.091	0.028	-0.045	0.007	-0.001	-0.005	-0.002	0.000
bio10	-0.064	-0.364	0.150	0.308	0.072	-0.401	-0.229	-0.103	-0.070	0.274	0.180	-0.027	0.033	0.282	-0.452	-0.081	-0.236	-0.239	0.000
bio11	-0.323	-0.132	-0.139	0.107	-0.080	-0.025	-0.015	-0.047	-0.099	-0.222	-0.037	-0.026	0.045	0.080	-0.006	0.072	-0.497	0.718	0.000
bio12	-0.244	0.252	0.265	-0.009	0.028	-0.104	0.069	-0.112	-0.002	0.058	0.017	-0.152	0.359	-0.568	-0.337	0.430	-0.013	-0.018	0.000
bio13	-0.231	0.178	0.378	0.005	-0.117	0.064	-0.028	-0.166	0.164	0.062	-0.414	-0.104	-0.090	0.575	0.083	0.391	0.115	-0.022	0.000
bio14	-0.150	0.351	-0.101	0.101	0.340	-0.210	-0.115	0.405	-0.290	0.053	-0.136	-0.262	-0.558	-0.072	-0.071	0.044	-0.013	0.006	0.000
bio15	0.014	-0.161	0.496	-0.095	-0.334	0.230	-0.403	0.501	-0.309	-0.159	0.112	0.001	0.063	-0.046	0.035	-0.003	-0.001	-0.003	0.000
bio16	-0.231	0.172	0.384	-0.046	-0.107	-0.025	0.056	-0.219	0.137	-0.021	-0.211	-0.143	-0.117	-0.176	-0.056	-0.752	-0.071	0.032	0.000
bio17	-0.182	0.344	-0.034	0.120	0.318	-0.093	-0.082	0.231	-0.156	0.118	-0.040	0.174	0.646	0.236	0.253	-0.235	0.006	-0.016	0.000
bio18	-0.046	0.346	0.141	0.420	0.127	0.179	-0.285	-0.156	0.298	-0.273	0.463	0.323	-0.207	-0.004	0.008	0.042	0.018	0.025	0.000
bio19	-0.254	0.048	0.244	-0.381	-0.050	-0.360	0.441	0.044	-0.127	0.039	0.467	0.286	-0.181	0.124	0.176	0.054	-0.022	0.000	0.000
% of variance	41.900%	26.940%	14.340%	7.699%	4.640%	2.338%	0.915%	0.511%	0.312%	0.213%	0.063%	0.053%	0.031%	0.017%	0.015%	0.010%	0.003%	0.001%	0.000%

Table S7 Bioclimatic variables used. Units of bioclimatic variables are °C × 10 for temperature (excluding bio 4, which was calculated based on K × 10 to deal with negative temperatures) and mm for precipitation.

Bioclimatic variable	Description
BIO 1	annual mean temperature
BIO 2	mean diurnal temperature range [mean of monthly (maximum temperature – minimum temperature)]
BIO 3	isothermality (BIO2 / BIO7 × 100)
BIO 4	temperature seasonality (standard deviation of monthly temperature)
BIO 5	maximum temperature of the coldest month
BIO 6	minimum temperature of the warmest month
BIO 7	temperature range (BIO6 – BIO5)
BIO 8	mean temperature of the wettest quarter
BIO 9	mean temperature of the driest quarter
BIO 10	mean temperature of the warmest quarter
BIO 11	mean temperature of the coldest quarter
BIO 12	annual precipitation
BIO 13	precipitation of the wettest month
BIO 14	precipitation of the driest month
BIO 15	precipitation seasonality (coefficient of variation of monthly precipitation)
BIO 16	precipitation of the wettest quarter
BIO 17	precipitation of the driest quarter
BIO 18	precipitation of the warmest quarter
BIO 19	precipitation of the coldest quarter

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SUPPORTING INFORMATION

Direct long-distance dispersal best explains the bipolar distribution of *Carex arctogena* (*Carex* sect. *Capituligerae*, Cyperaceae)

Tamara Villaverde, Marcial Escudero, Santiago Martín-Bravo, Leo P. Bruederle, Modesto. Luceño and Julian R. Starr

Appendix S1 Studied material, molecular characteristics of the amplified regions and results from the principal components analysis of 19 bioclimatic variables from the WorldClim database, uncorrected and corrected for phylogeny.

Table S1 List of material studied.

Table S2 Characteristics of the DNA regions sequenced.

Table S3 Locus information for the regions amplified in the study.

Table S4 Average within-group nucleotide substitution estimates for the *matK* gene of the complete dataset.

Table S5 Loadings matrix obtained by the principal components analysis not corrected by phylogeny of 19 bioclimatic variables on *Carex* sections *Capituligerae* and *Longespicatae*.

Table S6 Loadings matrix obtained by the principal components analysis corrected by phylogeny of 19 bioclimatic variables on *Carex* sections *Capituligerae* and *Longespicatae*.

Table S7 Bioclimatic variables used.

Table S1 List of material studied of *Carex arctogena*, *C. capitata*, *C. monostachya*, *C. oreophila*, *C. runssoroensis*, *C. rupestris*, *C. obtusata* and *Uncinia triquetra* including population code, coordinates, voucher information, corresponding clade and GenBank accessions for markers used for molecular studies. Population codes correspond to geographical regions of the world (Brummitt, 2001) and population number.

Species	Pop. code	Latitude	Longitude	Voucher	Clade	GenBank accession (ITS/atp/mat k/rps16)
<i>C. arctogena</i>	BRC 14	55.61667	-122.65000	Canada, British Columbia, Pine Pass. G. W. Argus 8831. 12/7/1973. (CAN-372267)	arctogena A NH	- / KP996286 / KP996374 / -
<i>C. arctogena</i>	FIN 25	68.22200	23.62700	Finland, Enontekiö. H. Väre 17177. 17/7/2006. (H-809948)	arctogena A NH	KP984469 / - / - / -
<i>C. arctogena</i>	GNL 23	67.90000	-49.41667	Greenland, Arfersoprflk. B. Fredskild & V. Dalgaard s.n. 19/8/1987. (COLO-456814)	arctogena A NH	- / KP996285 / KP996372 / -
<i>C. arctogena</i>	GNL 24	64.05000	-49.95000	Greenland, Pingorssuaq kitdleq. S. Hanfgam 83-175. 11/7/1983. (C-17/2009N3)	arctogena A NH	KP984471 / - / - / -
<i>C. arctogena</i>	LAB 18	51.88333	-65.95000	Canada, Labrador, Esker area. Y. Mäkinen & E. Kankainen s.n. 21/7/1967. (CAN-314758)	arctogena A NH	- / KP996287 / KP996375 / KP996451
<i>C. arctogena</i>	MAN 11	60.00000	-96.83333	Canada, Manitoba, Baralzon Lake. H. J. Scoggan 22434 & W. K. W. Baldwin. 18/7/1950. (WIN, 22434)	arctogena A NH	- / KP996284 / KP996371 / -
<i>C. arctogena</i>	MAN 12	58.06000	-68.39900	Canada, Québec, Fort Chimo. A. Legault 6782. 22/7/1963. (COLO-491481)	arctogena A NH	- / KP996281 / KP996368 / -
<i>C. arctogena</i>	MAN 13	59.36667	-96.23333	Canada, Manitoba, Hudsons Bay Co., Duck Lake. H. J. Scoggan 8288 & W. K. W. Baldwin. 19/8/1950. (CAN-201506)	arctogena A NH	- / KP996289 / KP996377 / KP996453

Species	Pop. code	Latitude	Longitude	Voucher	Clade	GenBank accession (ITS/atp/mat k/rps16)
<i>C. arctogena</i>	ONT 20	54.36280	-84.47950	Canada, Ontario, Kenora District, Patricia Portion. J. L. Riley 11856. 12/8/1980. (CAN-462937)	arctogena A NH	- / KP996354 / - / -
<i>C. arctogena</i>	ONT 21	55.11160	-93.35590	Canada, Ontario, Hudson Bay Lowlands. A. E. Porsild <i>et al.</i> 19898. 4/7/1957. (CAN-278707)	arctogena A NH	- / KP996282 / KP996369 / -
<i>C. arctogena</i>	QUE 15	59.26667	-72.58333	Canada, Quebec, Lac Payne. A. Legault A7849. 2/8/1965. (CCO-23398)	arctogena A NH	- / KP996280 / KP996367 / -
<i>C. arctogena</i>	QUE 16	52.87400	-82.83700	Canada, Quebec, Boatswain Bay. W. K. W. Baldwin 406 <i>et al.</i> 8/7/1947. (CAN-17333)	arctogena A NH	- / KP996283 / KP996370 / -
<i>C. arctogena</i>	QUE 17	52.75000	-73.88333	Canada, Québec, Lac Jaucourt Region, Lichteneger Lake. G. W. Argus 9221. 16/7/1974. (CAN-3779977)	arctogena A NH	- / KP996288 / KP996376 / KP996452
<i>C. arctogena</i>	QUE 26	58.15000	-68.41000	Canada, Quebec, Fort Chimo. T. Sorensen 293. 17/7/1959. (C15/2009N4)	arctogena A NH	KP984474 / - / - / -
<i>C. arctogena</i>	SAS 19	59.91667	-101.66667	Canada, Saskatchewan, Vicinity of Patterson Lake. G. W. Argus s.n. 20/7/1963. (CAN-282691)	arctogena A NH	- / KP996290 / KP996378 / KP996454
<i>C. arctogena</i>	ARG 1	-54.33320	-67.44960	Argentina, Tierra del Fuego, Tolhuin. S. Martín-Bravo <i>et al.</i> 40SMB10(1). 14/1/2010. (UPOS-4271)	arctogena A SH	KP984465 / - / KP996361 / KP996445
<i>C. arctogena</i>	ARG 2	-54.35160	-67.65000	Argentina, Tierra del Fuego, Tolhuin. S. Martín-Bravo <i>et al.</i> 35SMB10(1). 12/1/2010. (UPOS-4272)	arctogena A SH	KP984466 / - / KP996362 / KP996446

Species	Pop. code	Latitude	Longitude	Voucher	Clade	GenBank accession (ITS/atp/mat k/rps16)
<i>C. arctogena</i>	ARG 3	-53.93000	-68.08800	Argentina, Tierra del Fuego, Río Grande. J. Starr 10015 & T. Villaverde. 13/1/2010. (CAN)	arctogena A SH	- / KP996276 / KP996362 / KP996447
<i>C. arctogena</i>	ARG 4	-48.71056	-71.05081	Argentina, Santa Cruz, Los Glaciares National Park. J. Starr 10020 & T. Villaverde. 21/1/2010. (CAN)	arctogena A SH	- / KP996277 / KP996364 / KP996448
<i>C. arctogena</i>	ARG 5	-48.71056	-71.05081	Argentina, Santa Cruz, Los Glaciares National Park. J. Starr 10020 & T. Villaverde. 21/1/2010. (CAN)	arctogena A SH	- / KP996278 / KP996365 / KP996449
<i>C. arctogena</i>	ARG 6	-48.82136	-71.05250	Argentina, Santa Cruz, Los Glaciares National Park. J. Starr 10023 & T. Villaverde. 22/1/2010. (CAN)	arctogena A SH	- / KP996279 / KP996366 / KP996450
<i>C. arctogena</i>	ARG 7	-53.93230	-68.08870	Argentina, Tierra del Fuego, Río Grande. J. Starr 10015 & T. Villaverde. 13/1/2010. (CAN)	arctogena A SH	- / KP996348 / - / KP996483
<i>C. arctogena</i>	ARG 8	-48.82136	-71.05250	Argentina, Santa Cruz, Los Glaciares National Park. J. Starr 10023 & T. Villaverde. 22/1/2010. (CAN)	arctogena A SH	- / KP996349 / - / KP996484
<i>C. arctogena</i>	ARG 9	-49.26667	-71.66667	Argentina, Santa Cruz, Sierra Baguales, M. K. Arroyo 85201. 16/1/1985. (HIP-10500)	arctogena A SH	- / KP996350 / - / KP996485
<i>C. arctogena</i>	ARG 10	-35.28333	-69.53333	Argentina, Neuquén, Chos Mala. O. Boeckle <i>et al.</i> s.n. 30/1/1964. (BAA-11368)	arctogena A SH	- / KP996353 / - / -
<i>C. arctogena</i>	CAL 36	41.24700	-121.75500	USA, California, Siskiyou Co. J. D. Jokerst 1823. 5/7/1983. (CHICO-38999)	arctogena B	KP984467/- / - / KP996482

Species	Pop. code	Latitude	Longitude	Voucher	Clade	GenBank accession (ITS/atp/mat k/rps16)
<i>C. arctogena</i>	ALB 30	51.61000	-115.82100	Canada, Alberta, Snow Creek Pass, A. E. Porsild 22673. 29/7/1960. (CAN-266077)	arctogena B	- / KP996347 / KP996436 / KP996481
<i>C. arctogena</i>	CAL 45	40.10253	-120.49992	USA, California, Butte Co., J. Starr 10S-054 & T. Villaverde. 6/8/2010. (CAN)	arctogena B	- / KP996323 / KP996412 / KP996465
<i>C. arctogena</i>	CAL 46	40.10222	-120.49917	USA, California, Butte Co., J. Starr 06018 & J. Thibeault. 3/8/2006. (CAN)	arctogena B	- / KP996319 / KP996408 / KP996462
<i>C. arctogena</i>	CAL 47	40.12739	-120.50903	USA, California, Tehama Co., Yellow Pine Forest. L. Ahart 94326. 19/7/2006. (CHSC-94326)	arctogena B	- / KP996320 / KP996409 / KP996463
<i>C. arctogena</i>	CAL 48	39.47800	-120.29200	USA, California, Sierra Co., Anderson Mdw. R.K. Gierischerisch 3493 & D. Esplin. 25/6/1969. (COLO-246761)	arctogena B	- / KP996333 / KP996422 / -
<i>C. arctogena</i>	CAL 49	40.10400	-121.50200	USA, California, Butte Co. J. Starr 10S-054 & T. Villaverde. 6/8/2010. (CAN)	arctogena B	- / KP996322 / KP996411 / KP996464
<i>C. arctogena</i>	CAL 51	39.50191	-120.18325	USA, California, Sierra Nevada Co. W.A. Nisbet 45. 20/7/1957. (CAN-272091)	arctogena B	- / KP996343 / KP996432 / -
<i>C. arctogena</i>	CAL 52	39.49500	-120.41100	USA, California, Sierra Co. H. Oswald 8221 & L. Ahart. 19/8/1996. (CHSC-66824)	arctogena B	- / KP996329 / KP996418 / KP996468

Species	Pop. code	Latitude	Longitude	Voucher	Clade	GenBank accession (ITS/atp/mat k/rps16)
<i>C. arctogena</i>	CAL 53	39.42472	-120.25667	USA, California, Nevada Co. R. Naczi 11420. 3/8/2006. (US-3534689)	arctogena B	KP984464 / - / KP996359 / -
<i>C. arctogena</i>	CAL 54	39.41917	-119.74333	USA, California, Nevada Co. R. Naczi 11420. 3/8/2006. (CHICO-99406)	arctogena B	- / - / KP996358 / KP996443
<i>C. arctogena</i>	CAL 55	40.07700	-121.55000	USA, California, Butte Co. L. P. Janeway 3111. 29/7/1988. (CHICO-44118)	arctogena B	KP984463 / - / KP996357 / KP996442
<i>C. arctogena</i>	CAL 57	38.79167	-118.04167	USA, California, El Dorado Co. J. Pykäla <i>et al.</i> s.n. 23/7/1987. (H-15/2009N6)	arctogena B	KP984468 / - / - / -
<i>C. arctogena</i>	CAL 58	36.65800	-118.47300	USA, California, Tulare Co. S. Brush & J. Oliphant 155. 24/8/1991. (CAS-857890)	arctogena B	- / - / KP996360 / KP996444
<i>C. arctogena</i>	CAL 59	37.92100	-119.21400	USA, California, Mono Co., Mt. Dana Plateau. D. Taylor 7550. 25/7/1979. (COLO-330874)	arctogena B	- / KP996326 / KP996415 / -
<i>C. arctogena</i>	CAL 60	37.92200	-119.21400	USA, California, Mono County, Mt. Dana Plateau. D. Taylor 7550, 25/7/1979. (COLO-330874)	arctogena B	- / KP996327 / KP996416 / -
<i>C. arctogena</i>	CAL 61	34.49900	-118.24800	USA, California, Tulare Co., Sierra Nevada. J. T. Howell s.n. 5/8/1949. (DAO-257423)	arctogena B	- / KP996328 / KP996417 / -
<i>C. arctogena</i>	COL 39	39.83400	-105.67800	USA, Colorado, Clear Creek Co. W. A. Weber <i>et al.</i> s.n. 8/8/1972. (CAN-374041)	arctogena B	- / KP996346 / KP996435 / KP996480

Species	Pop. code	Latitude	Longitude	Voucher	Clade	GenBank accession (ITS/atp/mat k/rps16)
<i>C. arctogena</i>	COL 40	39.80700	-105.71000	USA, Colorado, Clear Creek Co., Bill Moore Lake. N. Lederer s.n. 31/8/1993. (COLO-00263731)	arctogena B	- / KP996330 / KP996419 / KP996469
<i>C. arctogena</i>	COL 41	38.02547	-106.75992	USA, Colorado, Hinsdale Co., Gunnison National Forest. J. Starr 10S-033 & T. Villaverde. 26/7/2010. (CAN)	arctogena B	- / KP996338 / KP996427 / KP996475
<i>C. arctogena</i>	COL 42	38.02547	-106.75992	USA, Colorado, Hinsdale Co., Gunnison National Forest. J. Starr 10S-033 & T. Villaverde. 26/7/2010. (CAN)	arctogena B	- / KP996337 / KP996426 / KP996474
<i>C. arctogena</i>	COL 43	39.26528	-105.52067	USA, Colorado, Lake Co., San Isabel National Forest. J. Starr 10S-030 & T. Villaverde. 25/7/2010. (CAN)	arctogena B	- / KP996335 / KP996424 / KP996472
<i>C. arctogena</i>	COL 44	39.26528	-105.52067	USA, Colorado, Lake Co., San Isabel National Forest. J. Starr 10S-030 & T. Villaverde. 25/7/2010. (CAN)	arctogena B	- / KP996336 / KP996425 / KP996473
<i>C. arctogena</i>	MNT 33	45.05800	-109.47600	USA, Montana, Carbon Co. H. Lackshewitz 7790. 11/8/1977. (WTU-288770)	arctogena B	- / KP996334 / KP996423 / -
<i>C. arctogena</i>	MNT 34	45.03203	-108.51497	USA, Montana, Carbon Co., Custer National Forest J. Starr 10S-047A & T. Villaverde. 31/7/2010. (CAN)	arctogena B	- / KP996339 / KP996428 / KP996476
<i>C. arctogena</i>	MNT 35	44.97142	-108.57928	USA, Wyoming, Park Co. J. Starr 10S-047B & T. Villaverde. 31/7/2010. (CAN)	arctogena B	- / KP996340 / KP996429 / -
<i>C. arctogena</i>	NEV 38	40.81100	-110.33100	USA, Utah, Duchesne Co., Uinta Mountains. E. Lewis 512. 15/8/1955. (CAN-515168)	arctogena B	- / KP996344 / KP996433 / KP996479

Species	Pop. code	Latitude	Longitude	Voucher	Clade	GenBank accession (ITS/atp/mat k/rps16)
<i>C. arctogena</i>	ORE 27	44.11467	-120.37594	USA, Oregon, Deschutes Co., Dechustes National Forest. J. Starr 10S-057 & T. Villaverde. 9/8/2010. (CAN)	arctogena B	-/KP996325 /KP996414/ KP996467
<i>C. arctogena</i>	ORE 28	44.11400	-121.62200	USA, Oregon, Deschutes Co. C. Halpern 159046 & T. Magee. 30/8/1982. (OSC-159046)	arctogena B	- / KP996321 / KP996410 / -
<i>C. arctogena</i>	ORE 50	44.11467	-120.37594	USA, Oregon, Deschutes Co., Dechustes National Forest. J. Starr 10S-057 & T. Villaverde. 9/8/2010. (CAN)	arctogena B	- / KP996324 / KP996413 / KP996466
<i>C. arctogena</i>	UTA 36	40.77800	-110.23700	USA, Utah, Duchesnes Co., Gilbert Creek. A. Huber 440 & S. Goodrich. 25/8/1993. (BRY-368578)	arctogena B	- / KP996331 / KP996420 / KP996470
<i>C. arctogena</i>	NEV 37	39.38800	-119.79200	USA, Nevada, Washoe Co. M.E. Lewis 448. 17/7/1955. (CAN-550536)	arctogena B	- / KP996345 / KP996434 / -
<i>C. arctogena</i>	NWH 22	42.27083	-71.30550	USA, New Hampshire, Alpine Garden, Mt. Washington. W. W. Eggleston 1681. 29/7/1989. (RM-23379)	arctogena B	- / - / KP996373 / -
<i>C. arctogena</i>	WAS 31	48.84233	-120.14225	USA, Washington, Whatcom Co. J. Starr 10S-061 & T. Villaverde. 11/8/2010. (CAN)	arctogena B	- / KP996342 / KP996431 / KP996478
<i>C. arctogena</i>	WAS 32	48.84233	-120.14225	USA, Washington, Whatcom Co. J. Starr 10S-061 & T. Villaverde. 11/8/2010. (CAN)	arctogena B	- / KP996341 / KP996430 / KP996477
<i>C. arctogena</i>	WYO 29	45.05200	-109.57400	USA, Wyoming, Park Co., Beartooth Plateau. B. Neely s.n. 18/8/1984. (COLO-399492)	arctogena B	- / KP996332 / KP996421 / KP996471

Species	Pop. code	Latitude	Longitude	Voucher	Clade	GenBank accession (ITS/atp/mat k/rps16)
<i>C. capitata</i>	MAG 1	66.00000	171.00000	Russia, Chukotski Peninsula. U. P. Kozhevnikov <i>et al.</i> s.n. 27/7/1970. (DAO-139887)	capitata A	- / KP996304 / KP996393 / -
<i>C. capitata</i>	MAG 2	68.00000	167.00000	Russia, Chukotka, Anui upland region. E.V. Zimarskaja <i>et al.</i> s.n. 12/7/1967. (DAO-139880)	capitata A	- / KP996308 / KP996397 / -
<i>C. capitata</i>	MAG 3	68.00000	167.00000	Russia, Western Chukotka. E. V. Zimarskaja <i>et al.</i> s.n. 12/7/1967. (BRY-122530)	capitata A	- / KP996310 / KP996399 / -
<i>C. capitata</i>	YAK 4	69.41667	130.66667	Russia, Sakha Republic, Bulnsk region. B. Yurtsev s.n. 25/6/1960. (DAO-257437)	capitata A	- / KP996352 / - / -
<i>C. capitata</i>	ALB 19	58.98333	-110.16667	Canada, Alberta, Ft. Fitzgerald. W. J. Cody 4533 & C. C. Loan. 19/7/1950. (RM-228683)	capitata B	- / KP996300 / KP996389 / -
<i>C. capitata</i>	ASK 23	68.06300	-145.09300	USA, Alaska, Old John Lake Area. K. Holmen 61-1227. 13/7/1961. (CAN-271116)	capitata B	- / KP996312 / KP996401 / KP996456
<i>C. capitata</i>	BRC 21	52.46667	-124.68333	Canada, British Columbia, Anahim Lake. J. Calder 18578 <i>et al.</i> s.n. 9/7/1956. (COLO-158463)	capitata B	- / KP996301 / KP996390 / -
<i>C. capitata</i>	BRC 22	52.46667	-124.68333	Canada, British Columbia, Anahim Lake. J. Calder 18578. J. A. Parmelee & R. L. Taylor s.n. 9/7/1956. (WTU-197744)	capitata B	- / KP996307 / KP996396 / -
<i>C. capitata</i>	FIN 7	69.08800	21.92800	Finland, Enontekiö lapland. H. Väre 11515. 29/7/2001. (H-737814)	capitata B	KP984470 / - / - / -
<i>C. capitata</i>	FIN 8	66.36700	29.53300	Finland, Kuusamo, Liikasenvaara. T. Ulvinen s.n. 9/8/1962. (CAN-276804)	capitata B	- / KP996316 / KP996405 / KP996460

Species	Pop. code	Latitude	Longitude	Voucher	Clade	GenBank accession (ITS/atp/mat k/rps16)
<i>C. capitata</i>	FIN 9	66.36700	29.53300	Finland,Kuusamo, Liikasenvaara. T. Ulvinen s.n. 9/8/1962. (CAN-276804)	capitata B	- / KP996305 / KP996394 / -
<i>C. capitata</i>	ICE 15	65.14400	-14.39400	Iceland, Hallormsstadhur. H. F. Gotzsche HFG81-37. 22/7/1981. (C-15/2009)	capitata B	KP984472 / - / - / -
<i>C. capitata</i>	ICE 16	66.05000	-23.13300	Iceland, Lagarfoss, Hróarstungu, Lagarfljótsrannsóknir s.n. 26/6/1976. (ICEL-04081)	capitata B	- / KP996306 / KP996395 / -
<i>C. capitata</i>	ICE 17	66.00000	-18.38300	Iceland, Hrísey, Eyjafirði. A. Garðarsson s.n. 12/8/1967. (ICEL-04078)	capitata B	- / KP996298 / KP996386 / -
<i>C. capitata</i>	ICE 18	65.65700	-16.81500	Iceland, Dalfjall, Mývatnssvei. E. Einarsson s.n. 21/8/1974. (ICEL-04073)	capitata B	- / KP996299 / KP996388 / -
<i>C. capitata</i>	MAG 5	62.20000	33.78333	Russia, Magadan region, North Even area. A.P. Hohrjakov s.n. 2/8/1976. (CAN- 455497)	capitata B	- / KP996314 / KP996403 / KP996458
<i>C. capitata</i>	MAN 23	58.63500	-94.13000	Canada, Manitoba, Churchill, south of Fort. K. Johnson J73-402. 26/8/1973. (WIN-33557)	capitata B	- / - / KP996387 / -
<i>C. capitata</i>	MAN 24	58.74700	-94.16500	Canada, Manitoba, Fort Churchill. J. Shay 83-60. 11/7/1983. (WIN-40808)	capitata B	- / KP996292 / KP996380 / -
<i>C. capitata</i>	MAN 25	58.75500	-94.07800	Canada, Manitoba, Fort Churchill. J. Ritchie 2104. 5/8/1956. (WIN-22433)	capitata B	- / KP996294 / KP996382 / -

Species	Pop. code	Latitude	Longitude	Voucher	Clade	GenBank accession (ITS/atp/mat k/rps16)
<i>C. capitata</i>	MAN 26	57.83000	-92.80430	Canada, Manitoba, Wapusk National Park. E. Punter 03-509 & M. Piercey-Normore. 19/7/2003. (WIN-71429)	capitata B	- / KP996296 / KP996384 / -
<i>C. capitata</i>	MAN 27	58.63700	-93.82700	Canada, Manitoba, Twin Lakes. A. Ford 02379 <i>et al.</i> 25/7/2002. (WIN-71024)	capitata B	- / KP996297 / KP996385 / -
<i>C. capitata</i>	MAN 29	58.75500	-94.07800	Canada, Manitoba, Fort Churchill. J. Ritchie 2104. 5/8/1956. (CAN-248387)	capitata B	- / KP996313 / KP996402 / KP996457
<i>C. capitata</i>	MAN 30	58.76667	-93.83333	Canada, Manitoba, Vicinity of Churchill. W. Schofield 6862 & H. Crum. 21/7/1956. (CAN-247332)	capitata B	- / KP996315 / KP996404 / KP996459
<i>C. capitata</i>	NOR 14	60.07900	10.03300	Norway, Folldal Gammelsetran. M. Vileid s.n. 18/8/1998. (O-235091)	capitata B	KP984473 / - / - / -
<i>C. capitata</i>	NWT 35	65.71700	-118.83300	Canada, Northwest Territories, Sawmill Bay. H. T. Shacklette 2970. 13/7/1948. (CAN-199991)	capitata B	- / KP996291 / KP996379 / -
<i>C. capitata</i>	NWT 36	67.33333	-125.58333	Canada, Northwest Territories, Aubry Lake. R. Riewe 225 & M. G. Marsh. 17/7/1976. (CAN-433230)	capitata B	- / KP996318 / KP996407 / KP996461
<i>C. capitata</i>	ONT 30	55.13420	-82.31280	Canada, Ontario, Kenora District. J. L. Riley 5848. 23/8/1976. (CAN-409561)	capitata B	- / KP996302 / KP996391 / -
<i>C. capitata</i>	ONT 31	55.98000	-87.64400	Canada, Ontario, Fort Severn. I. Hustich 1296. 13/7/1956. (CAN-242845)	capitata B	- / KP996351 / - / -
<i>C. capitata</i>	RUN 6	62.20000	33.78333	Russia, Karelia Republic. Ruuhijävi 40-02. 9/7/2002. (H-744530)	capitata B	- / KP996309 / KP996398 / -

Species	Pop. code	Latitude	Longitude	Voucher	Clade	GenBank accession (ITS/atp/mat k/rps16)
<i>C. capitata</i>	SAS 37	54.06667	-104.05944	Canada, Saskatchewan, Waskesim. J. Hudson 5063. 31/7/1992. (CAN-565528)	capitata B	- / KP996311 / KP996400 / KP996455
<i>C. capitata</i>	SWE 10	68.32700	18.83800	Sweden, Torne, Gemeinde Kiruna. H. Hertel 22918. 8/8/1980. (M-0151931)	capitata B	KP984477 / - / - / -
<i>C. capitata</i>	SWE 11	63.18100	14.75100	Sweden, Jämtland, Paroecia Frösö. E. Asplund s.n. 2/6/1925. (C15-2009N2)	capitata B	KP984476 / - / - / -
<i>C. capitata</i>	SWE 12	68.56667	19.50000	Sweden, Soland, Torne. C. G. Alm s.n. 9/8/1958. (V-539346)	capitata B	KP984475 / - / - / -
<i>C. capitata</i>	SWE 13	68.56667	18.34167	Sweden, Torne Lappmark, Abisko. G. Alm s.n. 6/8/1958. (H-1226056)	capitata B	- / KP996303 / KP996392 / -
<i>C. capitata</i>	YUK 32	64.36700	-137.26700	Canada, Yukon Territory, Dempster Highway. R. Porsild 1593. 17/7/1968. (CAN-318505)	capitata B	- / KP996293 / KP996381 / -
<i>C. capitata</i>	YUK 33	64.36700	-137.26700	Canada, Yukon, Ogilvie Mountains. A. E. Porsild 1462 & R. Porsild. 28/6/1968. (CAN-318349)	capitata B	- / KP996317 / KP996406 / -
<i>C. capitata</i>	YUK 34	61.86667	-135.88333	Canada, Yukon, Dawson. J. Calder 25796 & J. Gillett. 22/6/1960. (ALA-43436)	capitata B	- / KP996295 / KP996383 / -
<i>C. monostachya</i>	KEN 1	-0.16256	37.20828	Kenya, Mt. Kenya National Park. Naro Moru route. M.L. Buide 114UPO-K. 28/7/2007. (UPOS3304-111)	monostachya	- / KP996274 / - / - / -
<i>C. monostachya</i>	KEN 2	-0.16561	37.24197	Kenya, Mt. Kenya National Park, Naro Moru route. M.L. Buide 114UPO-K. 28/7/2007. (UPOS3306-462)	monostachya	- / KP996273 / - / - / -

Species	Pop. code	Latitude	Longitude	Voucher	Clade	GenBank accession (ITS/atp/mat k/rps16)
<i>C. oreophila</i>	TUR	37.75100	44.31600	Turkey. Hakkari Province, Kara Dag. Davis & Polunim 24438. 16/8/1954. (E00353688)	oreophila	KP984462 / - / - / KP996441
<i>C. obtusata</i>	WYO 1	44.98930	-110.7667	USA, Wyoming, Park Co., Yellowstone National Park. E. F. Evert 38901. 9/7/2001. (MOR0060897-164295)	Outgroup	KP984459 / KP996270 / - / KP996437
<i>C. obtusata</i>	WYO 2	43.81930	-109.0633	USA, Wyoming, Hot Springs Co., Shoshone Natl. Forest. E. Evert 39259. 2/7/2002. (MOR-0060899-162917)	Outgroup	KP984460 / KP996271 / - / KP996438
<i>C. obtusata</i>	WYO 3	43.77250	-109.19850	USA, Wyoming, Hot Springs Co., Absaroka Mtns. E. Evert 38141. 29/6/2000. (MOR-0060898-161081)	Outgroup	KP984461 / KP996272 / - / KP996439
<i>C. rupestris</i>	SPA	42.68350	0.07240	Spain, Huesca, Parque Natural de Ordeasa y Monte Perdido. M. Buide 57MBR04 & J. M. Marín. 30/7/2004. (UPOS-168)	Outgroup	- / KP996269 / KP996356 / -
<i>C. runssoroensis</i>	KEN	-0.13369	37.23439	Kenya, Mt. Kenya National Park, Naro Moru route. M.L. Buide <i>et al.</i> 113UPO-K. 28/7/2007.(UPOS3305-461)	runssoroensis	- / KP996275 / - / -
<i>Uncinia triquetra</i>	ARG	-53.15950	-71.17610	Chile, Punta Arenas, Reserva forestal de Magallanes. M. Luceño 185ML05 & R. Álvarez. 28/12/2005. (UPOS-1803)	Outgroup	- / KP996268 / KP996355 / -

Table S2 Characteristics of the DNA regions sequenced for complete datasets including all species in *Carex* sections *Capituligerae* and *Longespicatae* and outgroups

Primers	ITS-4 / ITS-A	<i>atpF</i> / <i>atpH</i>	matk 2.1f_J / matk 5r_J	<i>rps16F</i> / <i>rps16R</i>
Description of regions	Internal transcribed spacers 1 and 2 and 5.8S ribosomal RNA	Intergenic spacer of chloroplast region	Chloroplast gene of a maturase protein	Intergenic spacer of chloroplast region
References	White (1990) and Blattner (1999)	Fazekas <i>et al.</i> (2008)	Plant Working Group, Royal Botanical Gardens Kew, http://www.kew.org/barcoding/protocols.html , modified by Chouinard (2010)	Shaw <i>et al.</i> (2005)
Total number of sequences in the alignment	19	87	89	49
Aligned length (bp)	628	605	746	856
Ungapped length range	616–624	516–601	693–746	643–856
Identical sites	571 (91.8%)	579 (97.7%)	722 (96.8%)	833 (97.3%)
Pairwise identity	64.50%	99.30%	99.50%	99.50%
Variable characters	51	17	21	34
Parsimony-informative characters	36	14	12	14
Number of informative indels	13	1	0	0
Mean G+C content	47.90%	27.90%	28.90%	27.10%
Substitution model	HKY+I / JC / GTR	HKY	HKY+I	GTR

Table S3 Locus information for the regions amplified in the study including samples sizes, summary statistics. Nh, number of haplotypes (gaps were excluded); Hd, haplotype diversity; *S*, segregating sites; π , nucleotide diversity.

Locus	Nh	Hd	<i>S</i>	π	Tajima's <i>D</i>	Fu & Li's <i>D</i> *	Fu & Li's <i>F</i> *
<i>atpF-atpH</i>	5	0.725	8	0.00442	1.27151 ^{n.s.}	1.27758 ^{n.s.}	1.50645 ^{n.s.}
<i>rps16</i>	4	0.729	4	0.00245	1.63220 ^{n.s.}	1.01718 ^{n.s.}	1.40374 ^{n.s.}
<i>matK</i>	6	0.746	8	0.00397	1.85050 ^{n.s.}	1.28088 ^{n.s.}	1.73597*

**P* < 0.05; n.s., not significant.

Table S4 Average within-group nucleotide substitution estimates for the *matK* gene of the complete dataset.

Species	Selection hypothesis tested					
	Neutrality		Positive		Purifying	
	Probability	(dS - dN)	Probability	(dS - dN)	Probability	(dS - dN)
Outgroups	0.508 ^{n.s.}	-0.664	1.000 ^{n.s.}	-0.667	0.252 ^{n.s.}	0.670
<i>C. monostachya</i> and <i>C. runssoroensis</i>	0.040*	2.081	0.019*	2.106	1.000 ^{n.s.}	-2.093
<i>C. capitata</i> A	1.000 ^{n.s.}	0.000	1.000 ^{n.s.}	0.000	1.000 ^{n.s.}	0.000
<i>C. capitata</i> B	0.304 ^{n.s.}	1.031	0.154 ^{n.s.}	1.022	1.000 ^{n.s.}	-1.038
<i>C. arctogena</i> A	1.000 ^{n.s.}	0.000	1.000 ^{n.s.}	0.000	1.000 ^{n.s.}	0.000
<i>C. arctogena</i> B	0.297 ^{n.s.}	-1.048	0.150 ^{n.s.}	1.039	1.000 ^{n.s.}	-1.030

**P* < 0.05; n.s., not significant.

dS: Numbers of synonymous sites

dN: Numbers of non-synonymous sites

Table S5 Loadings matrix obtained by the principal components analysis not corrected by phylogeny of 19 bioclimatic variables on *Carex* sections *Capituligerae* and *Longespicatae*.

Variable	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10	PC11	PC12	PC13	PC14	PC15	PC16	PC17	PC18	PC19
bio1	-0.286	-0.219	-0.069	0.217	-0.052	-0.145	-0.091	-0.191	-0.105	-0.110	0.286	-0.531	0.062	-0.029	0.377	-0.019	0.464	0.033	0.000
bio2	-0.110	-0.294	0.187	-0.037	0.570	0.339	0.330	0.076	-0.062	-0.378	0.008	-0.058	0.045	0.145	-0.316	-0.053	0.185	0.009	0.000
bio3	-0.308	-0.093	-0.027	0.093	0.053	0.601	0.083	-0.061	-0.136	0.652	0.150	0.023	-0.124	-0.080	0.105	0.000	-0.112	-0.019	0.000
bio4	0.328	0.009	0.209	-0.018	0.113	-0.112	-0.059	0.035	0.071	0.394	0.064	0.058	-0.007	0.021	-0.162	-0.051	0.447	0.650	0.000
bio5	-0.069	-0.375	0.209	0.157	0.273	-0.194	-0.101	-0.072	-0.007	0.008	-0.354	0.395	-0.113	-0.327	0.379	0.100	0.021	-0.017	-0.323
bio6	-0.322	-0.105	-0.173	0.083	-0.163	-0.054	-0.053	0.014	-0.106	-0.043	-0.207	0.400	-0.057	-0.084	-0.160	-0.029	0.331	-0.011	0.674
bio7	0.293	-0.075	0.277	-0.008	0.297	-0.039	0.004	-0.049	0.104	0.048	0.038	-0.214	0.003	-0.073	0.347	0.078	-0.326	0.003	0.665
bio8	0.152	0.008	0.125	0.658	-0.286	-0.033	0.580	0.317	0.029	0.007	-0.065	-0.020	0.018	-0.025	0.044	-0.001	-0.004	-0.003	0.000
bio9	-0.298	-0.190	-0.097	-0.121	0.031	-0.063	-0.062	0.499	0.754	0.103	0.048	-0.091	0.028	-0.045	0.007	-0.001	-0.005	-0.002	0.000
bio10	-0.064	-0.364	0.150	0.308	0.072	-0.401	-0.229	-0.103	-0.070	0.274	0.180	-0.027	0.033	0.282	-0.452	-0.081	-0.236	-0.239	0.000
bio11	-0.323	-0.132	-0.139	0.107	-0.080	-0.025	-0.015	-0.047	-0.099	-0.222	-0.037	-0.026	0.045	0.080	-0.006	0.072	-0.497	0.718	0.000
bio12	-0.244	0.252	0.265	-0.009	0.028	-0.104	0.069	-0.112	-0.002	0.058	0.017	-0.152	0.359	-0.568	-0.337	0.430	-0.013	-0.018	0.000
bio13	-0.231	0.178	0.378	0.005	-0.117	0.064	-0.028	-0.166	0.164	0.062	-0.414	-0.104	-0.090	0.575	0.083	0.391	0.115	-0.022	0.000
bio14	-0.150	0.351	-0.101	0.101	0.340	-0.210	-0.115	0.405	-0.290	0.053	-0.136	-0.262	-0.558	-0.072	-0.071	0.044	-0.013	0.006	0.000
bio15	0.014	-0.161	0.496	-0.095	-0.334	0.230	-0.403	0.501	-0.309	-0.159	0.112	0.001	0.063	-0.046	0.035	-0.003	-0.001	-0.003	0.000
bio16	-0.231	0.172	0.384	-0.046	-0.107	-0.025	0.056	-0.219	0.137	-0.021	-0.211	-0.143	-0.117	-0.176	-0.056	-0.752	-0.071	0.032	0.000
bio17	-0.182	0.344	-0.034	0.120	0.318	-0.093	-0.082	0.231	-0.156	0.118	-0.040	0.174	0.646	0.236	0.253	-0.235	0.006	-0.016	0.000
bio18	-0.046	0.346	0.141	0.420	0.127	0.179	-0.285	-0.156	0.298	-0.273	0.463	0.323	-0.207	-0.004	0.008	0.042	0.018	0.025	0.000
bio19	-0.254	0.048	0.244	-0.381	-0.050	-0.360	0.441	0.044	-0.127	0.039	0.467	0.286	-0.181	0.124	0.176	0.054	-0.022	0.000	0.000
% of variance	41.900%	26.940%	14.340%	7.699%	4.640%	2.338%	0.915%	0.511%	0.312%	0.213%	0.063%	0.053%	0.031%	0.017%	0.015%	0.010%	0.003%	0.001%	0.000%

Table S7 Bioclimatic variables used. Units of bioclimatic variables are °C × 10 for temperature (excluding bio 4, which was calculated based on K × 10 to deal with negative temperatures) and mm for precipitation.

Bioclimatic variable	Description
BIO 1	annual mean temperature
BIO 2	mean diurnal temperature range [mean of monthly (maximum temperature – minimum temperature)]
BIO 3	isothermality (BIO2 / BIO7 × 100)
BIO 4	temperature seasonality (standard deviation of monthly temperature)
BIO 5	maximum temperature of the coldest month
BIO 6	minimum temperature of the warmest month
BIO 7	temperature range (BIO6 – BIO5)
BIO 8	mean temperature of the wettest quarter
BIO 9	mean temperature of the driest quarter
BIO 10	mean temperature of the warmest quarter
BIO 11	mean temperature of the coldest quarter
BIO 12	annual precipitation
BIO 13	precipitation of the wettest month
BIO 14	precipitation of the driest month
BIO 15	precipitation seasonality (coefficient of variation of monthly precipitation)
BIO 16	precipitation of the wettest quarter
BIO 17	precipitation of the driest quarter
BIO 18	precipitation of the warmest quarter
BIO 19	precipitation of the coldest quarter

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