

INVITED PAPER

For the Special Issue: Patterns and Processes of American Amphitropical Plant Disjunctions: New Insights

Bipolar distributions in vascular plants: A review¹

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Bipolar disjunct distributions are a fascinating biogeographic pattern exhibited by about 30 vascular plants, whose populations reach very high latitudes in the northern and southern hemispheres. In this review, we first propose a new framework for the definition of bipolar disjunctions and then reformulate a list of guiding principles to consider how to study bipolar species. Vicariance and convergent evolution hypotheses have been argued to explain the origin of this fragmented distribution pattern, but we show here that they can be rejected for all bipolar species, except for *Carex microglochis*. Instead, human introduction and dispersal (either direct or by mountain-hopping)—facilitated by standard and nonstandard vectors—are the most likely explanations for the origin of bipolar plant disjunctions. Successful establishment after dispersal is key for colonization of the disjunct areas and appear to be related to both intrinsic (e.g., self-compatibility) and extrinsic (mutualistic and antagonistic interactions) characteristics. Most studies on plant bipolar disjunctions have been conducted in *Carex* (Cyperaceae), the genus of vascular plants with the largest number of bipolar species. We found a predominant north-to-south direction of dispersal, with an estimated time of diversification in agreement with major cooling events during the Pliocene and Pleistocene. Bipolar *Carex* species do not seem to depend on specialized traits for long-distance dispersal and could have dispersed through one or multiple stochastic events, with birds as the most likely dispersal vector.

KEY WORDS amphitropical; Antarctic; biogeographic patterns; boreal; dispersal vectors; New Zealand; polar regions; South America

One of the most fascinating plant distribution patterns concerning the southern hemisphere is the bipolar disjunction, which is mostly a special case of the American amphitropical disjunction (see Simpson et al., 2017, in this issue). Bipolarity represents the most extreme possible case of geographic disjunction on Earth, in which a species is distributed in polar regions of both hemispheres (Arctic and Antarctic). Before the advancement of phylogenetics, the study of bipolar species was fundamentally based on floristics and taxonomic studies (e.g., Du Reitz, 1940; Raven, 1963; Ball, 1990; Reinhammar and Bele, 2001). Modern bipolar biogeography relies not only on the description of relationships among taxa, but also in the estimation of divergence dates that allow testing different hypotheses to explain the origin of such disjunction (e.g., Popp et al., 2011).

Most recent studies of bipolar vascular plants (Escudero et al., 2010a; Villaverde et al., 2015a, b, 2017a; Márquez-Corro et al., 2017) have followed Moore and Chater's (1971) definition of bipolar distributions: species having populations distributed at very high latitudes in both hemispheres (>55°N and >52°S). This stringent geographic criterion limits the distribution of bipolar species in the southern hemisphere to the southernmost tip of South America (Tierra del Fuego), excluding other regions with similar climatic conditions (e.g., New Zealand).

In this review, we summarize current knowledge and progress in the study of bipolar distributions in vascular plants, with special emphasis on the western hemisphere and the genus *Carex*. Specifically, we suggest a new framework for the definition of bipolar distributions and discuss the evolutionary origins of bipolar species in light of recent phylogenetic studies, as well as dispersal syndromes and other factors that might have promoted establishment in the colonized regions.

BIPOLAR DISTRIBUTION

Moore and Chater's (1971) criterion to define a bipolar distribution was based only on latitude (i.e., species living over 55°N and 52°S), which simply circumscribes the geographic limits but does not account for ecological criteria. Here, we suggest a new framework

¹ Manuscript received 30 April 2017; revision accepted 3 October 2017.

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for the definition of a bipolar distribution using a biogeographic-ecological criterion. Specifically, we consider the most geographically distant but ecologically very similar floral regions as defined by Huggett (2004) (based in turn on Good, 1974)—the Arctic and Subarctic subregions of the Boreal Region in the northern hemisphere and the Patagonian and/or New Zealand subregions in the Antarctic Region in the southern hemisphere.

Here, bipolar distribution is defined as the distribution of a species whose populations are distributed within the Huggett regions listed above (see Fig. 1), irrespective of the presence of additional populations in highlands at lower latitudes (i.e., temperate and tropical regions). This new framework for bipolar distributions corrects Moore and Chater's (1971) geographic bias and makes climate and latitude-mediated requirements equivalent between the northern and southern hemispheres. In other words, we use climatic requirements to establish minimum latitudes for a species to have a bipolar distribution. Following this new definition, we list 24 bipolar species, belonging to 18 genera and 10 families (Table 1). Poaceae and Cyperaceae are the families with the highest number of bipolar species (ca. 30%). *Carex* (Cyperaceae) is the genus with the highest number of bipolar species.

PRINCIPLES FOR THE STUDY OF DISJUNCT (BIPOLAR) SPECIES

In his review of disjunct distributions in seed plants, Thorne (1972) suggested several principles to aid in the classification of major seed plant disjunctions. Here, we describe how we adopt (and extend) these general principles into studies of native bipolar species:

(1) The smaller the rank of a taxon, the more informative its disjunct range is. Bipolar disjunctions can be present within a species, between sister species, within sections, tribes, genera, or families. However, the smaller the taxonomic rank exhibiting the disjunction, the more accurate the reconstruction of its true biogeographic history is because as we move back in time, a weaker signal of shared evolutionary history may be reconstructed due to extinctions or genetic saturation (multiple DNA changes at the same site, Ho et al., 2005). In this review, we considered only species-level disjunctions, that is, disjunct populations within a species in the defined regions (see previous section, "Bipolar Distribution"). Bipolar species whose origin has been described as introduced are not regarded in this study because we are interested in the natural patterns that characterize native bipolar species.

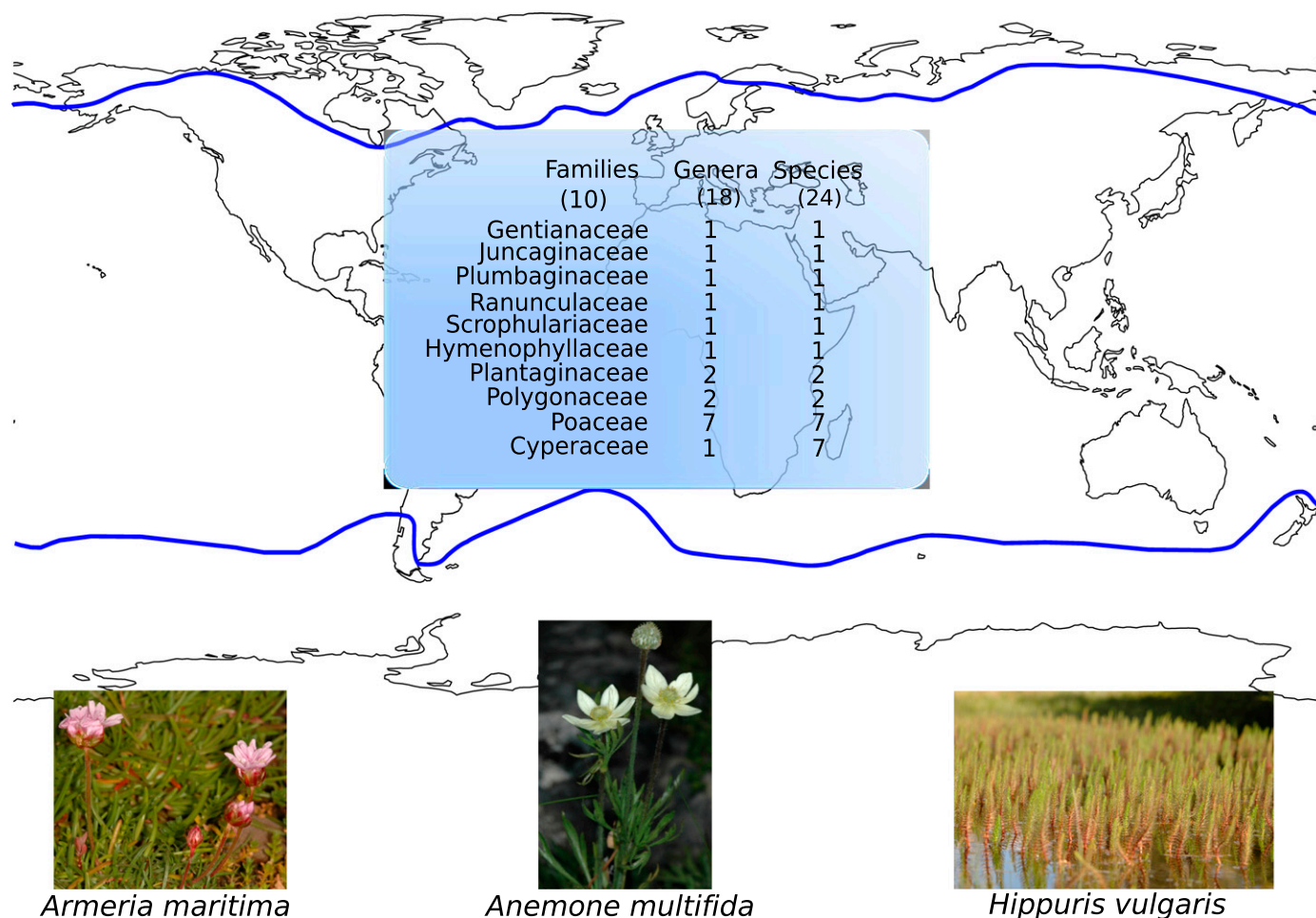


FIGURE 1 Bipolar distribution delimited by blue lines. The table inserted corresponds to the accepted number of species from Table 2. Photographs of bipolar species: Photos of *Hippuris vulgaris* from Tierra de Fuego (Argentina); *Anemone multifida* from Patagonia (Chile) and *Armeria maritima* from United Kingdom (Dumbar) by M. Luceño.

TABLE 1. List of the 24 bipolar species from 18 genera and 10 different families accepted in this review. From these, only *Carex lachenalii* does not conform to the concept of American amphitropical disjunction, since it is present in the southern hemisphere exclusively in New Zealand.

Family	Species
Hymenophyllaceae	<i>Hymenophyllum peltatum</i> (Poir.) Desv.
Polygonaceae	<i>Koenigia islandica</i> L. <i>Polygonum maritimum</i> L.
Ranunculaceae	<i>Anemone multifida</i> Poir.
Plantaginaceae	<i>Plantago maritima</i> L. <i>Hippuris vulgaris</i> L.
Plumbaginaceae	<i>Armeria maritima</i> (Mill.) Willd.
Gentianaceae	<i>Gentiana prostrata</i> Haenke
Scrophulariaceae	<i>Limosella australis</i> R. Br.
Juncaginaceae	<i>Triglochin palustris</i> L.
Poaceae	<i>Alopecurus magellanicus</i> Lam. <i>Avenella flexuosa</i> (L.) Drejer <i>Catabrosa aquatica</i> (L.) P. Beauv. <i>Trisetum spicatum</i> (L.) Richt. <i>Vahlodea atropurpurea</i> (Wahlenb.) Fr. ex Hartm. <i>Calamagrostis stricta</i> (Timm.) Koeler <i>Phleum alpinum</i> L.
Cyperaceae	<i>Carex arctogena</i> L. <i>C. canescens</i> L. <i>C. macloviana</i> D'Urv. <i>C. magellanica</i> Lam. <i>C. maritima</i> Gunnerus <i>C. microglochin</i> Wahlenb. <i>C. lachenalii</i> Schkuhr

(2) Only species that have been subject to thorough taxonomic revision should be considered. A taxonomic revision of the species, or at least of the populations at the two extremes of the disjunction, as well as phylogenetic analyses, should be conducted before defining a species as bipolar. For instance, Moore and Chater (1971) included *Huperzia selago* (L.) Bernh. ex Schrank & Mart. (Lycopodiaceae) in their list of bipolar species, but a systematic study has revealed that the southern hemisphere populations are indeed two morphologically similar species, *Huperzia saururoides* (Bory & d'Urv. ex Baker) Rothm. and *H. fuegiana* (Roiv.) Holub (Arana and Øllgaard, 2012). Similarly, *Botrychium lunaria* (L.) Swartz (Ophioglossaceae) or *Hymenophyllum tunbrigense* (L.) Sm. (Hymenophyllaceae), have traditionally been described as examples of bipolar disjunction, but Stensvold (2007) and Larsen et al. (2017) showed that southern hemisphere populations of these two species form distinct taxonomic units. Conducting an accurate taxonomic reassessment as well as phylogenetic studies of bipolar species are particularly important because of the risk of parallel or convergent evolution in morphological traits, as an adaptation or evolutionary response to a harsh (extreme) environment (see below *Hypotheses accounting for the bipolar distribution* and *Hypothesis testing of bipolar Carex*). Thus, special attention should be taken when considering species with taxonomic hurdles and/or phylogenetic uncertainty.

(3) Accurate distributional data should be used in constructing distribution maps. Because of the risk of erroneous taxonomic identification or inaccurate geographic collection data, occurrences downloaded from noncurated online databases, such as the Global Biodiversity Information Facility portal (www.gbif.org), should be carefully inspected before including them into the analysis. Instead, curated public repositories of species occurrences (e.g., Anthos, www.anthos.es), published floras (e.g., *Flora of North America*

North of Mexico; Flora of North America Editorial Committee, 1993), continuously updated checklists (e.g., "World Checklist of Selected Plants Families"; WCSP, 2017; Flora del Cono Sur, 2017) and herbarium collections should be preferred but, notwithstanding, checked also for accuracy. This step, although obvious, is crucial as previous studies have shown how a careful data curation may be critical in terms of inferred results and conclusions (Cardoso et al., 2017).

(4) Bipolar species must have a discontinuous range between northern and southern hemispheres according to our redefined geographic criterion. Only species with disjunct populations occurring in northern and southern boreal and polar regions, respectively, as defined above, should be considered as bipolar. In other words, all bipolar species considered here are absent from low-altitude areas in the tropics, even though their distribution might extend into the highlands of low latitude regions (Fig. 1).

(5) The current distribution of a species may not indicate its past distribution. Because species evolve over hundreds of thousands or millions of years, historic populations might have been subject to different evolutionary and climatic conditions than the present ones, and their geographic ranges might have changed accordingly (Meseguer et al., 2015). Phylogeographic reconstructions might be helpful in this case to infer the distribution of ancestral genotypes and link the evolution of geographic ranges to past and current distributions (Avice, 2009; Gavin et al., 2014; Mairal et al., 2015).

(6) Not all bipolar species follow necessarily the same dispersal history. Although bipolar species share a similar disjunct distribution, phylogeographic histories should be reconstructed for each individual species before assuming shared history, such as vicariance or concordant dispersal (e.g., Sanmartín et al., 2010; Vargas et al., 2013). Different explanations on how a species achieved its bipolar distribution highlight the existence of contrasting dispersal and colonization strategies behind this extraordinary biogeographic pattern.

CHECKLIST OF BIPOLAR SPECIES

Phylogeographic analyses are missing for the majority of bipolar species (see Appendix S1 in the Supplemental Data with this article), whereas biogeographical studies that include bipolar species often do not directly address the origin of this disjunction. Some studies include at least one population from each of the two extremes of the disjunction: *Anemone multifida* (Ranunculaceae; Ehrendorfer et al., 2009; Mlinarec et al., 2012), *Triglochin palustris* (Juncaginaceae; von Mering, 2013), *Avenella flexuosa* (Poaceae; Chiapella, 2007) and *Phleum alpinum* (Poaceae; Boudko, 2014; see Appendix S1). The main exception to this is genus *Carex*, where several recent phylogeographic studies have focused specifically on disentangling the evolutionary origins of these extreme distributions, often using a population-level approach (Villaverde et al., 2015a, b, 2017a; Márquez-Corro et al., 2017; L. P. Bruederle, 2017, personal communication).

The taxonomic circumscription of some bipolar species is still poorly understood, and some of the species listed in Appendix S1 might turn out to be non-monophyletic after careful systematic revision, whereas some new species might be added as we get a better taxonomic knowledge on the polar floras of the two hemispheres (e.g., *Huperzia selago*, Arana and Øllgaard, 2012). With the framework

suggested here for the definition of what constitutes a bipolar species, at least two new species from New Zealand have been included in the bipolar checklist with respect to Moore and Chater's (1971) list (see Appendix S1): *Alopecurus magellanicus* Lam. (Poaceae; Moore, 1983; Boudko, 2014) and *Carex lachenalii* Schkuhr (Cyperaceae; Vollan et al., 2006; Maguilla et al., 2015).

EVOLUTIONARY HYPOTHESES TO EXPLAIN BIPOLAR DISJUNCTIONS

In this section, we discuss hypotheses traditionally considered to explain bipolar distributions.

Vicariance—The splitting of the continuous geographical range of a taxon into two or more parts by the development of one or multiple (e.g., geographic or climatic) barriers to dispersal and gene flow is defined as vicariance (de Queiroz, 2005). The fossil record or molecular estimates of divergence times are often used to evaluate vicariance hypotheses vs. independent events of lineage dispersal. The following criteria are often used: (1) If the phylogenetic node or speciation event associated with the geographic disjunction is estimated to be as old as or older than the barrier that caused the geographical range fragmentation, then a vicariant explanation may be assumed. (2) If the speciation node is estimated to be younger than the fragmentation event, then a dispersal event across the geographical barrier is assumed. Because phylogenetic estimates of divergence times are often not very exact, i.e., the fossil might represent only a younger derived lineage or there might be considerable uncertainty in the molecular age, this criterion is not as clear-cut as stated. Moreover, the formation of a barrier (e.g., mountain uplift or the opening of an ocean basin) is not an instant event in geological time. Therefore, biogeographers need to be careful in discriminating between both hypotheses, for example, using temporal ranges instead of point events. In other words, the divergence between disjunct lineages must be *considerably* more recent than the age of the barrier to accept the dispersal hypothesis (Sanmartín, 2014).

For bipolar species, tectonic-mediated vicariance, or the geographic fragmentation of a potential continuous distribution across the polar regions, could only be argued if the age of the taxon dates back to the transtropical highland bridges of the Mesozoic Era (Early Jurassic, 195–200 Ma; Scotese et al., 1988). During this time, taxa could have had a continuous distribution from the high latitudes in the northern hemisphere to the high latitudes in the southern hemisphere.

Tectonic-mediated vicariance that can be rejected for all bipolar species listed here, because the estimated crown age, or the initial diversification event within their respective families, has been dated as considerably younger than the transtropical land bridges that connected northern and southern hemispheres in the Mesozoic Era (see Appendix S2).

Convergent evolution—Convergent and parallel evolution is another explanation for the existence of bipolar taxa. Here, we consider convergence and parallel evolution as the same phenomenon, i.e., synonymous hypotheses as suggested by Stern (2013). If phylogenetic inference demonstrates that a given bipolar species is monophyletic across the two extremes of its distribution, convergent or parallel evolution can be rejected. If a

species is recovered as non-monophyletic then, a taxonomic revision of the disjunct populations must be carried out before accepting bipolarity.

Dispersal—Dispersal, whether by direct jump or stepwise range expansion, is an alternative explanation for the origin of bipolar distributions. Long-distance dispersal (LDD) by direct jump is defined as the rapid movement of individual organisms over large distances, often across inhospitable habitats; this jump must occur within an individual's life span (Huggett, 2004). Such dispersal events might be rather occasional and imply the use of hazardous routes or the involvement of accidental mechanisms to cross over the major barriers involved. Accordingly, these events have been termed sweepstakes dispersal (Ali and Huber, 2010). In other cases, dispersal might involve the gradual spread along mountain chains or (stepwise) mountain-hopping (Ball, 1990) followed by extinction of the populations occurring in the intermediate areas, leaving the surviving disjunct populations on the two extremes of the distribution. As defined above, the main difference between LDD and stepwise dispersal or mountain-hopping in plants is the number of stops or "way stations" made before reaching the end of the dispersal process. In bipolar disjunctions, direct LDD implies that the taxa have been carried from one side of the disjunction to the other, without any stop between source and sink areas. Conversely, the mountain-hopping hypothesis proposes relatively short-distance migrations of taxa, using mountain peaks as stepping-stones to cross the tropical regions. The same means of dispersal used in direct LDD events could have been used in the mountain-hopping dispersal hypothesis.

Climate change—We summarize below several major climatic and geological events that might have favored dispersal in bipolar species in the late Cenozoic.

Starting in the late Cenozoic, particularly in the Miocene (ca. 23 Ma), the Earth underwent major temperature changes related to various causes, including continental displacement due to plate tectonics and changes in astronomical parameters, e.g., eccentricity of the Earth's orbit, obliquity of the planetary axis and equinoctial precession (Rabassa et al., 2005). All these events led to climatic cycles of cold and warm periods and the development of planetary ice ages from the Miocene onwards (Zachos et al., 2001; Rabassa et al., 2005; Rabassa and Coronato, 2009). These climatic variations were accompanied by major changes in plant distributions with expansion and retraction of different vegetation belts, including wax-and-wane patterns for the distribution of bipolar species, in which plant distributions grew alternatively larger and smaller.

The large mountain chains running north to south along the Americas might have helped bipolar species to migrate between hemispheres. In South America, the uplift of the central Andean plateau had probably started by the Early Miocene, ca. 20 Ma (McQuarrie et al., 2005; Hoorn et al., 2010). From this time onward, and especially after the closing of the Panama Isthmus, an extensive migration occurred (known as the Great American Biotic Interchange, GABI) from North America to South America and vice versa (Hoorn et al., 2010). New mountainous habitats in the Andean region might have facilitated dispersal of bipolar species between the northern and southern New World landmasses. Some bipolar species show also a disjunct distribution across the eastern hemisphere (e.g., involving New Zealand).

Vicariance vs. dispersal: Two competing hypotheses?—Traditionally in biogeography, dispersal hypotheses were considered difficult to falsify, i.e., any pattern of distribution could be explained by LDD simply by invoking a sufficient number of events (Sanmartín, 2014). The introduction of molecular estimates of divergence times allowed the rejection of vicariance and indicated a greater role for LDD in shaping current species distributions than previously thought (de Queiroz, 2005; Michalak et al., 2010). Even the distribution of paradigmatic examples of vicariant taxa, such as *Araucaria* (Kershaw and Wagstaff, 2001) or *Nothofagus* (Swenson et al., 2001; Cook and Crisp, 2005; but see Heads, 2006), seems to have been formed, at least partially, by LDD events. Comparative studies across taxa with disjunct distributions have also rejected the vicariance hypothesis and argued instead LDD explanations, e.g., in South Africa (Galley and Linder, 2006), New Zealand (Winkworth et al., 2005; Waters and Craw, 2006), or Madagascar (Yoder and Nowak, 2006). In other cases, however, vicariance and extinction driven by climate change have been convincingly demonstrated using molecular and climatic data (Crisp and Cook, 2007; Pokorný et al., 2015; Mairal et al., 2017). It is important to note that vicariance and dispersal do not necessarily compete. In the case of bipolar distributions, tectonic vicariance might be rejected by molecular age estimates (i.e., the group's origin largely postdates the Mesozoic), but still the group might have had a wider distribution in the past, when the climatic conditions in one of the hemispheres allowed bipolar species to occur closer to the Equator (e.g., Poaceae, Bouchenak-Khelladi et al., 2010). The past distribution of a species may have not necessarily covered the two poles and could have been achieved by gradual stepwise or short-range dispersal over mountain chains between both hemispheres, with subsequent climatic-driven extinction reducing it to the extreme disjunction observed today. For example, ecological vicariance and extinction driven by aridification have been suggested in the case of the continental Rand Flora disjunction, connecting the eastern and western margins of Africa (e.g., Mairal et al., 2015; Pokorný et al., 2015).

MECHANISMS OF DISPERSAL

Next we discuss different dispersal mechanisms that could have facilitated LDD in bipolar vascular plant species.

Wind and ocean currents—Wind currents that characterize the Intertropical Convergence Zone have been in place since the late Miocene (Hyeong et al., 2005), whereas ocean currents would have been modified in association with glacial cycles (Khélifi and Frank, 2014). Even if ocean paleocurrents were faster than today (0.7–2.7 km/h; Gillespie et al., 2012) and had different directions, the ability of an organism to disperse by ocean water would still depend on its buoyancy mechanisms, its tolerance to transportation on seawater over different climatic conditions between the northern and southern hemisphere, and its ability to survive in areas close to the seashore. Though they have been suggested in other examples of intercontinental plant migration within hemispheres (e.g., Brooker et al., 2001; Brochmann et al., 2003; Renner, 2004; Alsos et al., 2009; Gillespie et al., 2012; Christenhusz and Chase, 2013), wind and ocean currents seem unlikely dispersal drivers for bipolar distributions in vascular plants. These currents

run in opposite directions when approaching the Equator from each hemisphere (Hyeong et al., 2005), which would force propagules to make a stop at low latitudes before being transported into the other hemisphere. Nonetheless, we cannot discard exceptional, rare events (Nathan, 2006), which could have facilitated LDD in some of these species.

Birds—Three of the eight flyways of migratory birds (Kirby et al., 2008; BirdLife International, 2010) that travel through the high latitudes of North America, also cross southern Patagonia to Tierra del Fuego. A number of birds of the order Charadriiformes make the migration journey between the northern and southern hemispheres in days or weeks. Among those known to fly between high latitudes of North and South America are the Hudsonian godwit (*Limosa haemastica*, Elphick and Klima, 2002), the red knot (*Calidris canutus*, Harrington, 2001), the white-rumped sandpiper (*C. fuscicollis*, Parmelee, 1992), the Baird's sandpiper (*C. bairdii*, Moskoff and Montgomerie, 2002), the sanderling (*C. alba*, MacWhirter et al., 2002), the pectoral sandpiper (*C. melanotos*, Holmes and Pitelka, 1998), the lesser yellowlegs (*Tringa flavipes*, Tibbitts and Moskoff, 1999), and the semipalmated plover (*Charadrius semipalmatus*, Nol and Blanken, 1999). However, only a few of these species regularly occur where bipolar species grow at both northern and southern high latitudes. Remarkably, some of these migratory Charadriiformes, such as semipalmated sandpipers (*Calidris pusilla*), American goldenplover (*Pluvialis dominica*), or red phalaropes (*Phalaropus fulicarius*), which were observed carrying bryophyte diaspores (Lewis et al., 2014a), could also be claimed as bird species promoting bipolarity in vascular plants. Also, there are at least 18 Charadriiformes species making regular migration events between high latitudes of the northern hemisphere and New Zealand. This migration occurs either straight from Alaska through the Pacific in a single direct 12,000 km flight (bar-tailed godwits (*Limosa lapponica*), Riegen, 1999; Minton et al., 2001) or through different flyways from Siberia through eastern Asia and Australasia (Williams et al., 2006). Additionally, dispersal may have occurred through accidental displacement, such as vagrant birds or migrants deviating widely from their normal route, some reaching Australia or New Zealand from North America (e.g., Battley et al., 2012).

It is difficult to find direct evidence supporting avian dispersal of propagules, externally or internally, between austral and boreal regions as done by Lewis et al. (2014b). Viana et al. (2016) directly observed and quantified LDD of plant species by sampling birds caught by falcons while in migratory flight. Although a similar sampling (i.e., retrieving seeds of bipolar species from birds on flight) would prove LDD for bipolarity, the small number of propagules that might be transported by birds between hemispheres severely decreases the probability of sampling such an event. In addition, birds that could have transported seeds in the past may have changed migratory patterns or are extinct today. Unless seeds are directly sampled in bird species in flight during trans-hemispherical migration, experimental evidence of LDD of bipolar species mediated by birds will remain elusive.

Long-distance dispersal in plants has also been linked to seed morphology or diaspore syndrome (morphological trait sets of the diaspores associated with dispersal; Vargas et al., 2014), though the actual mechanisms are still unknown and rare stochastic events have also been proposed (Nathan et al., 2008; Heleno and Vargas, 2015). The presence of fruits and seeds with specialized structures such as hairs or wings, has generally been associated with a specific

dispersal vector, termed haplochory (i.e., dispersal mediated by a single standard dispersal vector; Nathan et al., 2008), although in some cases a specialized character might be associated with more than one vector (see Vargas et al., 2015). Despite the apparent disadvantage of lacking specialized morphological traits for LDD, unspecialized plants can also be successful long-distance dispersers (e.g., Vargas et al., 2014, 2015). Moreover, the presence of a particular LDD syndrome does not necessarily imply that it was responsible for the actual arrival of the propagules (Higgins et al., 2003; Thomson et al., 2010). Heleno and Vargas (2015) showed that the distribution of plants within the Azores archipelago was largely independent of specializations related to LDD. Thus, a specialized LDD syndrome may promote dispersal but it is not a necessary condition.

Human introductions—Dispersal facilitated by human action might be behind some bipolar species disjunctions observed today. For example, *Poa pratensis* L. was originally introduced in Cierva Point of the Antarctic Peninsula, during the 1954–1955 season (Perterra et al., 2013). Six of the 30 bipolar species listed by Moore and Chater (1971) are either probable or confirmed human introductions in the southern hemisphere (see Appendix S1). The anthropogenic origin of these species might be confirmed by a combination of phylogeographical tools, dating approaches and historical records. The hypothesis of a human introduction for bipolar species could be rejected if the divergence of the disjunct populations pre-dates humans or human activities in the area. Many of the species listed by Moore and Chater (1971) have been poorly studied using molecular data (e.g., some studies included only a population from the southern hemisphere) or not studied at all (see Appendix S1).

HYPOTHESES FOR ESTABLISHMENT AFTER DISPERSAL

To generate a disjunct distribution, an LDD dispersal event needs to be followed by the establishment of a permanent population in the newly colonized area. In many cases, establishment might be more difficult to achieve than LDD, since establishment depends on the abiotic and biotic conditions of the host community (Mitchell et al., 2006). Therefore, it is not only the opportunity for dispersal but also establishment that is critical for a species to expand its geographical range.

A niche reflects how an individual, species, or population interacts with and exploits its environment, which involves adaptation to the existing abiotic conditions. Yet, different populations may occupy the same (niche conservatism) or different niches (niche evolution) in different geographical regions, as seen in some bipolar species of *Carex* (see Villaverde et al., 2017b for a deeper discussion regarding niche conservatism and niche shift in bipolar species). A species' past and present ecological and climatic tolerance strongly influences its actual and potential geographical range, and species with wide ecological tolerances are usually the most widespread. However, even in the case of large population sizes, a species does not necessarily occupy all favorable habitats within its geographical range. There might be climatic areas, inside and outside its geographical range, where suitable climatic conditions exist but that the species was unable to colonize due to other abiotic factors (e.g., soil chemistry) or because of biotic interactions (e.g., presence of competitors).

Bipolar species are usually chill-resistant (or frost-resilient) plants, which can survive at temperatures below -10°C . Some of

them are considered frost-tolerant plants, possessing physiological changes that enable them to survive temperatures as low as -40°C . Frost-tolerant plants are capable during freezing of moving cellular water from their protoplast to the intercellular spaces by withdrawing water from their cells; thus, they can prevent ice forming (Thomashow, 1999; Beck et al., 2007). Adaptation to cold involves other important molecular changes, such as membrane lipid desaturation (Senser and Beck, 1982), or transition from the common starch-dominated carbohydrate metabolism to an oligosaccharide-dominated metabolism, using sucrose and its galactosides as cryoprotectants (Hansen et al., 1996). In some species, cold tolerance can vary between seasons. For instance, willow twigs (*Salix* sp.) collected in winter can survive freezing temperatures below -150°C , but a temperature of -5°C kills the same twigs in the summer (Sakai, 1970). Timing is important in cold resistance, while absolute resistance to temperature can be modified.

STUDY CASES IN SEDGES

Carex, the genus with the highest number of bipolar species, has also been the center of much of the research in bipolar distributions. In this section, we summarize what these studies can teach us regarding the evolutionary origins of this disjunction, as well as to guide us on future research.

Bipolar *Carex* species—Bipolar *Carex* species do not form a monophyletic entity but are included in different lineages within the genus (Fig. 2; see the phylogeny of the Global *Carex* Group, 2016). Indeed, this extraordinary geographic disjunction seems to have been independently achieved at least seven times during the evolutionary history of *Carex*, from species of at least three different main lineages (Fig. 2).

Bipolar *Carex* species inhabit the lowlands of high latitudes at both hemispheres, but they are also found in arctic-alpine habitats at lower latitudes; for example, *C. maritima* is found at sea level in Tierra del Fuego but over 4000 m a.s.l. in the Andes in northern Argentina. *Carex canescens* and *C. lachenalii* (sect. *Glareosae*) are two bipolar species that reach Oceania—*C. canescens* occurs in Australia, Tasmania, and New Guinea, whereas *C. lachenalii* occurs exclusively in New Zealand—but only *C. canescens* is found in the southernmost region of South America (Tierra del Fuego and Falkland Islands), extending over five biogeographical regions: Nearctic, Palearctic, Andean, Neoguinean, and Australotemperate (Morrone, 2002). *Carex canescens* is therefore the bipolar *Carex* species with the widest distribution, followed by *C. maritima*, which has a circumboreal distribution including the Moroccan Atlas, European Alps, and the Himalayas in the northern hemisphere, and extending from Ecuador to Patagonia in the southern hemisphere (Govaerts et al., 2017).

Hypothesis testing in bipolar *Carex*—*Parallel evolution*—*Carex microglochis* has traditionally been considered a widespread species in northern areas of the northern hemisphere, occurring also in a few localities in southernmost South America. Wheeler and Guaglianone (2003) carried out a morphological study of *C. microglochis* in South America and concluded that the species comprised two morphologically similar, yet taxonomically and ecologically different species, *C. microglochis* and *C. camptoglochis* V.I.Krecz. Starr and colleagues (2008) studied two populations of what they

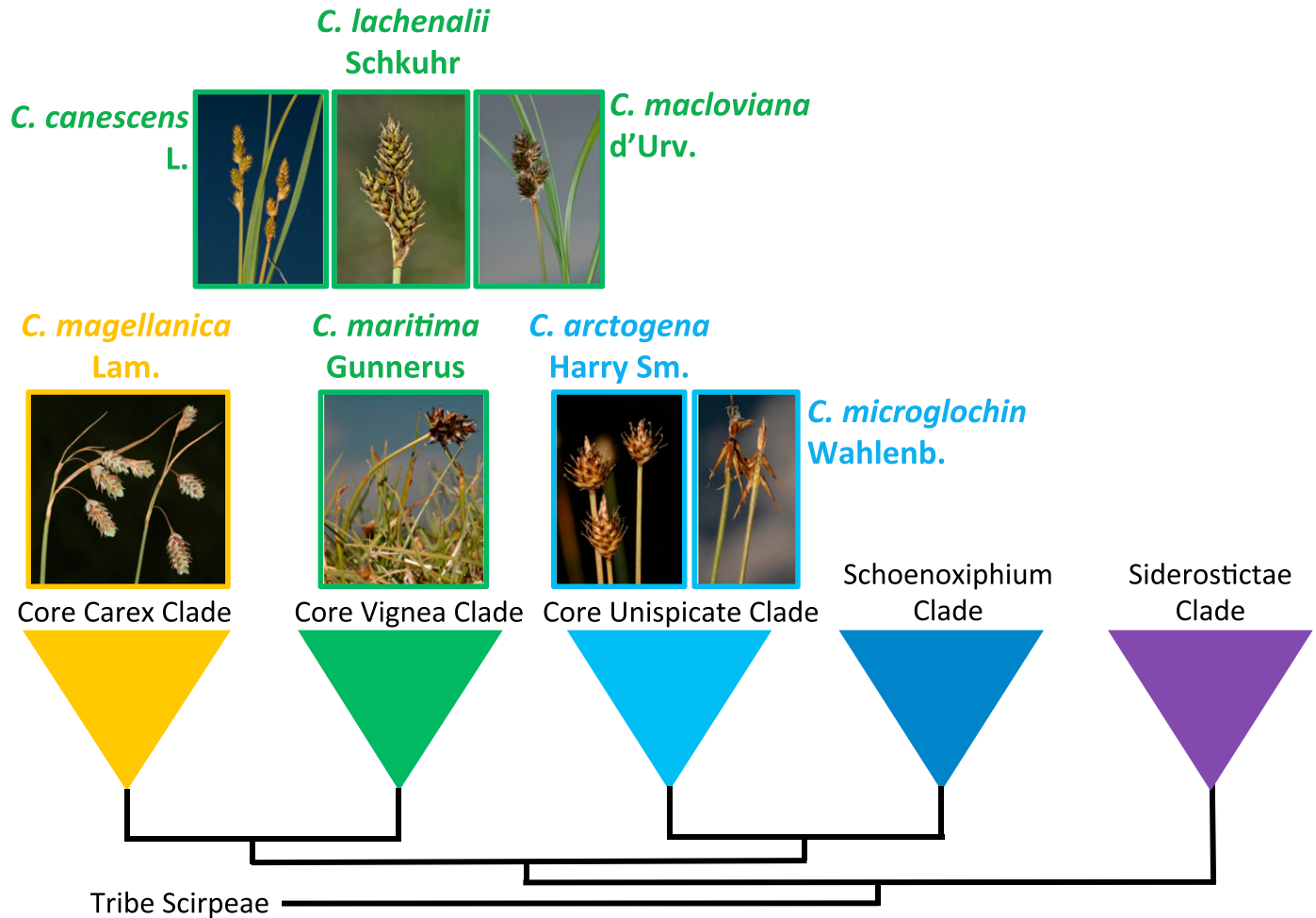


FIGURE 2 Phylogenetic position of the bipolar *Carex* species: *C. canescens*, *C. maritima* and *C. microglochin* from Tierra de Fuego (Argentina); *C. lachenalii* from Lérida (Spain); *C. macloviana* from Patagonia (Chile); *C. magellanica* subsp. *irrigua* from Pöntsö (Finland); *C. arctogena* from Tugtutoq Island (Greenland). Some relationships between the main clades in *Carex* are still unresolved (see Global *Carex* Group, 2015, 2016). Photographs: M. Luceño.

called *C. microglochin* from the northern and the southern hemisphere and concluded that the observed remarkable phylogenetic divergence might be a result of hybridization, the sequencing of pseudogenes, or other factors. Subsequently, Escudero et al. (2010a) found that South American populations classified as *C. microglochin* did not form a monophyletic clade: two samples from Chile grouped together with *C. pulicaris* L. (distributed in Europe) and *C. macrostyla* Lapeyr. (distributed through the Pyrenees to northwestern Spain) in a strongly supported clade, phylogenetically distant from the remaining samples of *C. microglochin* from Iceland, Norway, Greenland, and Argentina, which grouped with *C. lechleriana* (Steud.) J.R.Starr (= *Uncinia lechleriana*), *C. pauciflora* Lightf., and *C. curvula* All. These molecular phylogenetic studies confirmed Wheeler and Guaglianone's (2003) observations that *C. microglochin* comprised two distantly related species in South America: *C. microglochin* (truly bipolar and growing in snow beds and other damp meadows) and *C. camptoglochin* (restricted to *Sphagnum magellanicum* bogs in Patagonia and Andean America). Therefore, *C. microglochin* and *C. camptoglochin*, with a stunningly similar morphology (Fig. 3), constitute a remarkable example of a convergent phenotype (parallel evolution), which has evolved in distantly related lineages.

Mountain-hopping vs direct LDD—Long-distant dispersal of bipolar *Carex* species may have been achieved by either mountain-hopping (“stepping-stone” dispersal) or a direct LDD event (a “giant leap”). These LDD event(s) could have occurred during some of the last cold periods during the Pliocene (5.3–2.6 Ma) or in the Pleistocene (2.6–0.01 Ma; see Fig. 4), when the polar regions of both hemispheres recurrently expanded (Raven, 1963; Ball, 1990), or even at present times. Molecular age estimates for the crown node of the *Carex* bipolar species fall within recorded periods of major climatic changes, in which polar and alpine regions in the two hemispheres extended their geographic cover (Zachos et al., 2001; see Fig. 4). For southern hemisphere populations, crown age estimates fall within the Pleistocene (Fig. 4). Throughout the evolutionary diversification of bipolar *Carex* species, mountain ranges were available to facilitate the connection between northern Eurasia-North America and the southern hemisphere continents (see earlier section *Hypotheses considered to explain bipolar disjunctions*).

Heide (2002) demonstrated that the floral traits of some bipolar species (i.e., absence of obligatory long-day floral induction) could have facilitated or been a prerequisite for transequatorial migration by mountain-hopping. Some bipolar *Carex* species have populations

*Carex microglochis* Wahlenb.*Carex camptoglochis* V.I.Krecz

FIGURE 3 *Carex microglochis* (Sudurland, Iceland) and *C. camptoglochis* (Patagonia, Chile) inflorescences. Their stunningly similar morphology constitutes an example of a convergent phenotype (parallel evolution) evolved in distantly related lineages. Consequently, *C. microglochis* is still considered a bipolar species, since some populations of the southern hemisphere are shown to be *C. microglochis* s.s., while *C. camptoglochis* is only found in the southern hemisphere. Photographs: M. Luceño.

in northern South America that would support the mountain-hopping hypothesis (i.e., *C. maritima*, *C. macloviana*, *C. magellanica*, *C. microglochis*). Some putative hybrid populations of *C. canescens* have also been detected in New Guinea, which could also support a mountain-hopping hypothesis from Asia to Australia, and merit further study (T. Villaverde, personal observation).

If any of the bipolar *Carex* species migrated to South America and/or Australasia, or vice versa, by the slow and gradual means predicted by mountain-hopping, we would expect that such processes would leave a trace of genetic differences in the nuclear and/or plastid loci of populations from both hemispheres (Brochmann et al., 2003; Scotland, 2011). We would expect intermediate populations to be phylogenetically closer than the populations on the extreme ends of their disjunction. In contrast, for recent, direct LDD, we would expect low genetic differentiation between the populations on the two extremes.

Although we cannot completely reject the mountain-hopping hypothesis, the absence of genetic variability between disjunct populations of the bipolar species *C. arctogena* and *C. canescens* and the young estimates for the age of divergence (Villaverde et al., 2015a, 2017a), better fit a hypothesis of recent and direct LDD than slow dispersal through mountain ranges. Direct LDD has been shown to be remarkably frequent in some other genera of Cyperaceae (e.g., Viljoen et al., 2013).

In the case of *C. macloviana*, *C. maritima*, and *C. magellanica*, their genetic structure between northern and southern hemisphere populations does not provide conclusive evidence to support either direct LDD or mountain-hopping because there is some genetic differentiation between disjunct (northern vs. southern hemisphere) populations, but there is no correlation between

phylogenetic and geographic patterns, i.e., populations in southern North America are not phylogenetically closer to populations in northern South America than to populations in southern South America, as expected from the mountain-hopping hypothesis. One possibility is that the extinction of intermediate populations might have produced such a genetic pattern or that these populations colonized first South America and diversified there, with a subsequent northward and southward colonization along the Andes.

North-to-south dispersal—Patterns of genetic diversity described for *Carex* bipolar species suggests north-to-south movement as the prevalent direction in bipolar LDD events between the two hemispheres, as also suggested in other nonbipolar species of *Carex* (Escudero et al., 2009; Gehrke and Linder, 2009; Jiménez-Mejías et al., 2012a; Míguez et al., 2017). The most widely distributed haplotypes were consistently found in the northern hemisphere (except for some northern hemisphere populations of *C. canescens* and *C. macloviana*, which shared their haplotype with southern hemisphere populations, see Table 2); these northern haplotypes also shared the highest number of haplotype connections with other haplotypes, which in coalescent theory is interpreted as representing the ancestral haplotypes (Posada and Crandall, 2001). Moreover, the generic sections to which these bipolar species are ascribed (see Table 2) have the majority of their species distributed in the northern hemisphere, a fact that supports a northern origin and subsequent north-to-south LDD for these species. Among bipolar *Carex* species, *C. macloviana* is the only one that displays a genetic pattern that could suggest a south-to-north migration, but this hypothesis needs further research (Márquez-Corro et al., 2017) including a much broader taxonomic sampling.

North-to-south LDD is a very frequent pattern of dispersal in plants (e.g., Vargas et al., 1998; Vijverberg et al., 1999; Yokoyama et al., 2000; Clayton et al., 2009; Escudero et al., 2009; Schaefer et al., 2009; Wen and Ickert-Bond, 2009; Emadzade et al., 2011; Popp et al., 2011; Banasiak et al., 2013; Lewis et al., 2014a) and found in other bipolar living organisms such as the lichen *Cetraria aculeata* (Fernández-Mendoza and Printzen, 2013). One explanation is that the southern hemisphere harbors a smaller geographic area with suitable climatic conditions for arctic-alpine species in comparison with the northern hemisphere (e.g., Villaverde et al., 2017b, this issue). Yet, some plant genera support the opposite direction of dispersal (e.g., *Larrea* [Zygophyllaceae], Lia et al., 2001; *Hoffmannseggia glauca* [Fabaceae], Simpson et al., 2005; *Munroa* [Poaceae], Amarilla et al., 2015; see Simpson et al., 2017, this issue), so other factors might be involved.

Vectors of dispersal in bipolar *Carex* species—The true fruit of *Carex* (a nutlet) is unspecialized, but it is enclosed in a prophyll-derived structure called a utricle (see Jiménez-Mejías et al., 2016 for

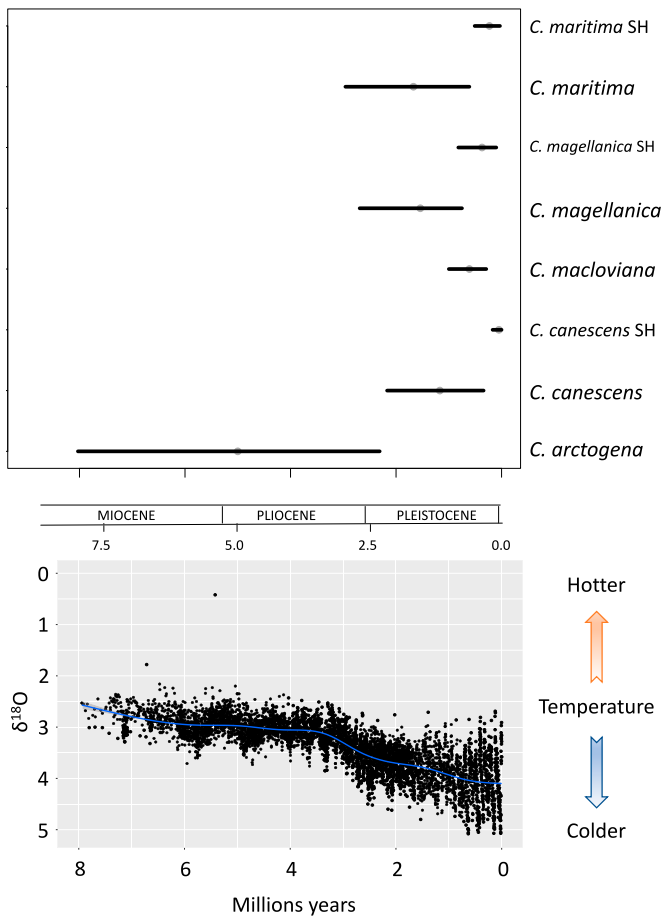


FIGURE 4 Estimated time of divergence for the studied bipolar *Carex* species (as cited in the text). Bars represent 95% high probability density credibility intervals for the age of initial diversification event (crown age) of bipolar *Carex* species (or lineages). Crosses indicate the mean age estimated of the crown age. Below, multiple records of the isotope oxygen -18 ($\delta^{18}O$, a measure of the ratio of stable isotopes ^{18}O and ^{16}O ; black dots; Lisiecki and Raymo, 2005) and geometric mean (blue line), as a proxy for global climate are presented against the geological time scale. *Abbreviation:* SH, southern hemisphere populations.

terminology), which in some species may play a role in facilitating dispersal (Table 3). Yet, bipolar species of *Carex* do not show any suite of diaspore traits in the utricle or the nutlet associated with dispersal syndromes (but see Table 3).

Most migratory birds that disperse seeds over long distances live in temperate and boreal regions (Wheelwright, 1988). For birds to act as vectors for seed dispersal by ectozoochory or endozoochory, the plant species should, respectively, have morphological features for attaching to these animals or be able to maintain their viability after intestinal transit to allow for establishment in new environments (Gillespie et al., 2012). Yet, *Carex* species seem to be transported by birds even in the absence of such morphological features for zoochorous dispersal (Alessio Leck and Schütz, 2005; Soons et al., 2008; Green et al., 2016). There might be other structures or features involved that are not so obviously linked to dispersal syndromes, for example, anatomical features such as deposits of silica in the pericarp which help harden the seeds (Graven et al., 1996; Prychid

TABLE 2. Comparison of the different haplotype networks calculated for studied bipolar *Carex* species.

Species	No. of NH / # SH / and shared haplotypes	Most common haplotype	Ancestral haplotype for SH?	Connections of ancestral haplotype	Connection of outgroup	Section / Total no. of spp. / Species in SH	Direction of dispersal	Ref.
<i>C. arctogena</i>	8/-/1	NH	No	8	NH, NH-SH	<i>Capituligeraceae</i> / 3 / 1	N-S	1
<i>C. canescens</i>	2/1/2	NH-SH	No	3	NH	<i>Glareosae</i> / 23 - 25 / 2	N-S	2
<i>C. macloviana</i>	2/2/-	NH-SH	NH-SH	3 / 3	SH	<i>Ovales</i> / 90 / c. 15?	N-S or S-N	3
<i>C. magellanica</i>	-/1/1	NH-SH	Yes	3 / 3	NH-SH	<i>Limosae</i> / 6 / 1	N-S	4
<i>C. maritima</i>	2/3/-	NH	No	3	NH	<i>Foetidae</i> / 10 - 15 / 3	N-S	5
	4/1/-	NH	No	4	NH			

Notes: NH, northern hemisphere; SH, southern hemisphere. Reference 1, Villaverde et al., 2015a; 2, Villaverde et al., 2017a; 3, Márquez-Corro et al., 2017; 4, L. P. Bruederle, 2017, personal communication; 5, Villaverde et al., 2015b.

TABLE 3. Dispersal vectors for bipolar *Carex* species.

Dispersal vector	Syndrome	Examples
Standard dispersal		
Sea currents	Thalasochoy	<i>C. canescens</i> utricles are reported to float over 12 months (Ridley, 1930).
Wind currents	Anemochory	<i>C. macloviana</i> has winged utricles that could facilitate dispersal by wind.
External animal transportation	Epizoochory	<i>C. microglochis</i> has a very fine rachilla protruding through the utricule tip (Savile, 1972). Other nonbipolar <i>Carex</i> species have a hook-like rachilla that facilitates the detachment of the fruit and successful clinging to hair or fur (Fig. 5).
Internal animal transportation	Endozoochory	Some <i>Carex</i> fruits remain intact and viable after internal transport by birds (Mueller and van der Valk, 2002). Arrivals to newly formed islands reported when seeds were eaten and carried inside by birds (Alessio Leck and Schütz, 2005; Green et al., 2016). Recovered from bird's excrements (Schmid, 1984). Achene external silicon layers of Cyperaceae may play a defensive role against digestive acids and be used for grinding (as pebbles) in bird's gizzards (Lye, 2016), helping the seed to remain viable after certain residence time inside the digestive system of the animal. Increase in germination rates after bird gut passage reported for other Cyperaceae (Brochet et al., 2010).
Nonstandard vectors for dispersal		
Human introductions		Not confirmed for any bipolar <i>Carex</i> species

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, as both nourishment and gastroliths (Alexander et al., 1996).

Some birds, such as the pectoral sandpiper, *Calidris melanotos* (Holmes and Pitelka, 1998), and the lesser yellowlegs, *Tringa flavipes* (Tibbitts and Moskoff, 1999), are known to feed in sedge meadows in North America before migrating southward to their wintering grounds in South America. Their breeding ranges closely match the current distribution of *Carex* bipolar species in North and South America. Although current migratory bird patterns do not necessarily match those of past migrations, these observations suggest that the bipolar disjunction of *Carex* species may have originated via bird-mediated LDD. Other bird species such as ducks are known to disperse seeds of *Carex* species (e.g., *C. canescens* and *C. magellanica*; Green et al., 2016).

Nonstandard vectors for dispersal—In any flora, a large percentage of species (even >50%) succeeded in colonizing distantly separated landmasses despite a lack of traits related to LDD (see Heleno and Vargas, 2015). For instance, *C. maritima* colonized the Surtsey Island (Iceland) without any apparent morphological adaptations to LDD (Magnússon et al., 2014).

Moreover, when the dispersal vectors involved are unrelated to specific diaspore traits, they are considered as nonstandard means of dispersal (Higgins et al., 2003). Such could also be the case in dispersal of *Carex* by birds (Green et al., 2016; Soons et al., 2008) because despite apparent success in colonizing the polar regions, no clear diaspore specializations related to LDD have been reported (except for the few cases cited above). In fact, LDD is claimed as a widespread phenomenon in many plant species without standard morphological syndromes for LDD (Cain et al., 2000; Higgins et al., 2003; Alsos et al., 2007; Dixon et al., 2009; Vargas et al., 2014, 2015). In any case, unspecific dispersal does not pose a conflict with the endozoochorous dispersal possibilities evaluated above.

Human introductions—Age estimates for lineage divergence of southern hemisphere populations of *C. maritima* and *C. magellan-*

ica have been shown to predate human presence in the Americas (c. 30,000 yr ago; Goebel et al., 2008; see Fig. 4). For *C. arctogena*, *C. macloviana*, and *C. canescens*, lack of a clear phylogenetic differentiation among southern hemisphere populations does not allow us to reject the hypothesis of human introduction. If so, species adaptation to the local environmental conditions, biotic interactions, and demographic processes involved in the establishment would necessarily have occurred relatively quickly (Theoharides and Dukes, 2007), given the low genetic differentiation among populations. Moreover, most populations of *C. arctogena*, *C. macloviana*, and *C. canescens* in southern South America occur in well-preserved habitats, many of them only accessible by foot. Although most introduced species are generalist and become widespread in disturbed habitats (Liston et al., 1989), this is not the case for bipolar *Carex* species. Therefore, although we cannot definitely rule out an anthropogenic introduction, this possibility seems very unlikely for bipolar species of *Carex* in South America.



FIGURE 5 Hundreds of *Carex* species utricles (from the former genus *Utricularia*; see Global *Carex* Group, 2015) attached to a kiwi species (*Apteryx* sp.). These utricles have a hook-like rachilla that facilitates the detachment of the fruit and successful clinging to hair or fur. Photograph: Mike Thorsen.

Establishment after dispersal—Abundance of *Carex* species in specific habitats shared by the two polar environments may have been crucial for successful establishment of the bipolar species. Populations of bipolar *Carex* species in the northern hemisphere generally occupy large geographic ranges and have large populations, whereas in the southern hemisphere, populations are smaller and geographically narrow. *Carex* bipolar species generally occupy a more restricted climatic niche in South America than in North America, and the overlap between their respective niches is small (Villaverde et al., 2017b, this issue). The environmental space available for bipolar *Carex* populations in South America are often included within the environmental suitability range of North American populations. The only exception is a small niche expansion in Patagonian *C. magellanica*, with some populations occupying new climatic conditions not available in North America. This ecological plasticity of the species could have been key for its successful establishment after dispersal (Villaverde et al., 2017b, this issue). The small overlap between the realized (actual) climatic niche in North and South America could be found in processes related to community assembly or differences in competitive interaction among the disjunct areas (Waters, 2011), which could have excluded species otherwise adapted to those climatic conditions. Such community interactions could have allowed them to shift into new habitats and climate zones (Broennimann et al., 2007) in the southern hemisphere. In addition, regions with suitable climatic conditions for bipolar species (i.e., arctic-alpine habitats) occupy larger extensions of land in the northern hemisphere than in the southern hemisphere. Thus, the differences found between northern and southern populations in terms of climate niche breadth could simply be explained by land availability. Alternatively, establishment could have taken place at a time when both hemispheres had similar climatic conditions.

Intrinsic conditions favoring colonization—Some species traits intrinsic to *Carex* might have favored colonization. Many *Carex* species are perennial with elongated rhizomes and form extensive clones (e.g., Stemström et al., 2001; Jiménez-Mejías et al., 2012b). Asexual reproduction is a strategy that has been shown to favor the successful establishment of plant species in early stages of colonization (e.g., Thomas et al., 2012), allowing populations to perpetuate without the aid of sexual reproduction (Klimes et al., 1997). Other species traits such as self-fertilization along with bisexuality might have favored colonization of new regions because, in that case, a single propagule of a self-compatible individual would be sufficient to start a sexually reproducing colony (Baker, 1955). *Carex* species are predominantly monoecious and in general highly self-pollinated (Friedman and Barrett, 2009), as evidenced by studies using hand pollination experiments and microsatellite markers (e.g., Ohkawa et al., 2000; Friedman and Barrett, 2009; Escudero et al., 2010b, 2013). This characteristic could also contribute to a relatively high rate of establishment (successful colonization) after a LDD event in *Carex* species (Moore and Chater, 1971; Ball, 1990; Escudero et al., 2009). In addition, chromosome number variation—associated with variation in recombination rates—has been shown to be correlated with phenotypic differences and increased fitness in different habitat types (Escudero et al., 2012, 2013). The high chromosome number variation in some bipolar *Carex* species (*C. canescens*, $2n = 52-54, 56-58, 60, 62$; *C. macloviana*, $2n = 82, 82-86, 86$; *C. magellanica*, $2n = 58, ca. 60$; reviewed by Roalson, 2008) might also be a result of the difference in climatic environments between different

latitudes and distant regions. *Carex arctogena* ($2n = 50$) and *C. maritima* ($2n = 60$) have not been reported to display chromosome number variation (Roalson, 2008), although there is a paucity of chromosome counts available for these species considering their wide distribution, and none of the reported ones (except for one count of *C. canescens* from South America, $2n = 56$ Moore, 1967) are from the southern hemisphere.

Finally, climatic flowering requirements might also be important for bipolar species when migrating by stepping-stones across the equator. Many plants use the signal of short days in autumn as an early warning system. Short days trigger metabolic changes that stop plant growth and produce resistance to cold. In the case of some species of *Carex*, Heide (2002) demonstrated that no change or adaptation in the flowering requirements was necessary for these cold-tolerant species to have migrated over the tropics. For example, in *C. canescens*, Norwegian and Chilean populations had different responses to high and low temperatures, with the Chilean populations having more extended flowering and also requiring longer exposure to short days (low temperature for full flowering) than the Norwegian populations (Heide, 2002). Surprisingly, two Australian populations of *C. canescens* had primary induction requirements similar to lowland populations from southern Norway. Other studied species, such as *C. lachenalii* and *C. echinata*, responded similarly (Heide, 2002). This evidence suggests that populations adapted to the short growing seasons of the arctic-alpine environment are less photoperiodic and initiate floral primordia more freely in long-day conditions than those adapted to the longer growing seasons of the low latitudes (Heide, 2002).

COMMON PATTERNS IN BIPOLAR CAREX SPECIES

In conclusion, we can highlight the following common patterns in bipolar *Carex* species:

- (1) The studied bipolar species seem to have acquired their disjunct distribution by means of LDD, rather than tectonic vicariance, either by a direct jump or mountain-hopping.
- (2) Dispersal of bipolar species does not depend on specialized traits for LDD and could have been achieved through one, several, and/or stochastic events. Bird-mediated dispersal seems to be the most plausible mean of dispersal.
- (3) Estimated ages for the studied bipolar species generally fall within the Pliocene/Pleistocene periods.
- (4) Establishment of bipolar species could have been facilitated by intrinsic characteristics such as vegetative reproduction via rhizomes and self-compatibility.

CONCLUSIONS

In this review, we have summarized the current knowledge and progress in the study of bipolar distributions of vascular plants in the last decade. We list 24 bipolar species from 18 genera and 10 families. Most phylogenetic studies on this disjunction to date have focused on the genus *Carex* (Cyperaceae), so studies across other plant families are needed to shed light into the evolutionary origins of the bipolar biogeographic distribution. The increasing availability of molecular (genomic) data—generated by next-generation sequencing techniques—may help discriminate between different competing hypotheses (i.e., direct long-distance dispersal or mountain-hopping).

ACKNOWLEDGEMENTS

The authors thank Michael Simpson, Matt Williams, Leigh Johnson, and Justen Whittall for organizing the “Patterns and Processes of American Amphotropical Plant Disjunctions: New Insights” symposium at the Botanical Society of America annual meeting during 30 July–3 August 2016 in Savannah, Georgia (USA). We also thank Marcelo Arana and Weston Testo for their help with *Huperzia* and Isaac Garrido Benavent and two anonymous reviewers for their comments on the manuscript. This research was supported by the Spanish Ministry of Economy and Competitiveness (projects CGL2012-3874 and CGL2016-77401-P).

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