Niche shifts after long-distance dispersal events in bipolar sedges (*Carex*, Cyperaceae)[1]

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PREMISE OF THE STUDY: Bipolar species represent the greatest biogeographical disjunction on Earth, raising many questions about the colonization and adaptive processes behind such striking distribution. We investigated climatic niche differences of five *Carex* bipolar species in North and South America to assess niche shifts between these two regions. Moreover, we assessed potential distribution changes with future climate change.

METHODS: We used 1202 presence data points from herbarium specimens and 19 bioclimatic variables to assess climatic niche differences and potential distributions among the five species using ordination methods and Maxent.

KEY RESULTS: The niche overlap analyses showed low levels of niche filling and high climatic niche expansion between North and South America. *Carex macloviana* and *C. maritima* showed the greatest niche expansion (60% and 96%, respectively), followed by *C. magellanica* (45%) and *C. microglochin* (39%). Only *C. canescens* did not colonize new environments (niche expansion = 0.2%). In contrast, all species but *C. magellanica* had niche filling that was <40%; hence, they are absent in the south from many environments they inhabit in North America. Climate change will push all species toward higher latitudes and elevation, reducing the availability of suitable environments.

CONCLUSIONS: The colonization of South America seems to have involved frequent climatic niche shifts. Most species have colonized new environments from those occupied in the North. Observed niche shifts appear congruent with time since colonization and with current genetic structure within species. In these cold-dwelling species, climate change will most likely decrease their suitable environments in the future.

KEY WORDS biodiversity loss; climate change; climatic niche; colonization; distribution modeling; extinction; niche overlap

Species distributions are shaped by the interplay of dispersal and biotic and abiotic factors that determine positive population growth (Peterson et al., 2011). Dispersal is a key process, not only enabling colonization of new areas, but also explaining species absence from suitable places (Gaston, 2003). When dispersal is not limiting, abiotic conditions or new biotic interactions may limit species' establishment beyond their current range boundaries. If species are unable to adapt to new environmental conditions (i.e., niche conservatism), species may only expand their range by reaching areas with environmental characteristics similar to those in their native range (Pulliam, 2000). In contrast, species' ability to exploit new environmental conditions (i.e., niche shifts), would enable the colonization of new habitats and climatic regimes, as well as persistence in changing environments (Pearman et al., 2008; Koecke et al., 2013). These niche shifts, or changes in the range of environments exploited by a species, may be due to phenotypic plasticity, biotic interactions, changes in the availability of different environments, and/or adaptive evolution of their environmental tolerance (Guisan et al., 2014). For instance, niche shifts can arise following dispersal to previously unoccupied environments, which become accessible due to enemy release (e.g., Fitzpatrick et al., 2007), lack of competitors (Schluter, 2000), increased genetic variation (Lavergne and Molofsky, 2007), or adaptive evolution (e.g., Henery et al., 2010). Some niche shifts imply colonization of new environments (niche expansion), but in other cases new colonizers are missing from environments matching those of their native ranges (niche unfilling) (Guisan et al., 2014).

In the face of global climate change and biodiversity loss, exploring the range of niche conservatism or niche shift responses for taxa confronted with new environments can be very informative to anticipate biodiversity responses. There are abundant published examples of both niche conservatism (e.g., Peterson et al., 1999; Wiens and Graham, 2005; Palaoro et al., 2013; Callen and Miller, 2015) and niche shifts (e.g., Broennimann et al., 2007; Mukherjee et al., 2012; Wüest et al., 2015) across species ranges. But a synthesis or generalization of what degree of niche conservatism or niche shift to expect from a group of taxa is still elusive. For example, a study involving two sister families (Burseraceae and Anacardiaceae) with similar number of species and similar age of diversification (Weeks et al., 2014) found that, whereas lineages within Burseraceae have diverged mainly within a similar climatic niche experiencing very few climatic shifts, lineages of Anacardiaceae have shifted climatic niches very frequently. Patterns of niche dynamics, even at microevolutionary levels, can be complex. For instance, in *Alloteropsis semialata* (R.Br.) Hitchc. (Poaceae), the only known species with both C_4 and non-C_4 genotypes, non-C_4 individuals are confined to a limited geographic area and restricted ecological conditions, whereas C_4 individuals (which can achieve higher productivity in warm and arid conditions) spread across multiple continents and environments (Lundgren et al., 2015).

Species present at high latitudes in both hemispheres, that is, having a bipolar distribution (Moore and Chater, 1971; Villaverde et al., 2017a, this issue), represent the greatest biogeographical disjunction on Earth, raising many questions about the colonization and adaptive processes behind such striking distribution. For the niche conservatism hypothesis, we would expect populations from northern and southern hemispheres to occupy similar climatic niches. In contrast, disjunct populations might have different climatic niches in both extremes, which may be due to phenotypic plasticity, biotic interactions, changes in the availability of different environments, and/or adaptive evolution of their environmental tolerance (Guisan et al., 2014). Thus, the characterization of climatic niches between disjunct populations in the same species, such as bipolar distributions, could be particularly informative about species ability to adapt and colonize new environmental conditions. This scenario is similar to what we found in a very well-documented case of invasive species introduced to new ranges (i.e., *Oxalis pes-caprae* L.; González-Moreno et al., 2015) but involving a natural, and much longer, process of colonization. In our study species, the long times elapsed since the colonization of the southern hemisphere (Villaverde et al., 2017a, this issue) would increase the probability of evolutionary differentiation compared to invasive species of very recent human introduction.

Carex L. is the genus with the largest number of bipolar species (Moore and Chater, 1971; Villaverde et al., 2017a, this issue). Most of these species, with the exception of *C. arctogena* Harry Sm. (Villaverde et al., 2015b), probably diverged in the Pliocene/Pleistocene (Villaverde et al., 2017a, this issue), a time of geological and climatic changes (Audley-Charles, 1991; Rabassa et al., 2005; Rabassa and Coronato, 2009; Hoorn et al., 2010) that might have helped these species to disperse across hemispheres. Most or all of the southern hemisphere populations of bipolar *Carex* species are the result of long-distance dispersal from the northern hemisphere (Vollan et al., 2006; Escudero et al., 2010a; Villaverde et al., 2015a, b, 2017b; L. P. Bruederle, 2017, personal communication). Species that have acquired their distribution by means of long-distance dispersal tend to be more genetically isolated through time, favoring

local adaptation and hence fostering niche differentiation (Wasof et al., 2015). It has also been suggested that colonization of new habitats can select for increased plasticity (Richards et al., 2006). Those species that dispersed more recently to South America, such as *C. canescens* L., are expected to occupy a narrower climatic niche (higher niche unfilling) than those that dispersed earlier (i.e., during Mid or Late Pleistocene) such as *C. magellanica* Lam. (lower niche unfilling).

Although previous analyses detected that populations of *C. arctogena*, *C. maritima* Mack., and *C. canescens* from the northern and southern hemisphere occupy different climatic spaces (Villaverde et al., 2015a, b, 2017b), it is still unclear how frequent and strong niche shifts are among bipolar *Carex* species. In this study, we focus on five *Carex* bipolar species—*C. canescens*, *C. macloviana* d'Urv., *C. magellanica*, *C. maritima*, and *C. microglochin* Wahlenb. aiming to answer the following questions: (1) Do climatic niches of *Carex* bipolar species differ between North and South America populations, and to what extent does their climatic niche overlap between these two regions? (2) Is there a trend toward a wider or narrower climatic niche in the South America? (3) What are the consequences of niche shift or conservatism for long-distance dispersal and the colonization process? (4) Is there an association between niche shift or conservatism and genetic differentiation? (5) What range shifts are expected for these species under current scenarios of climate change?

MATERIALS AND METHODS

Occurrence data sets—Species occurrence data were downloaded from the Global Biodiversity Information Facility data portal (http://www.gbif.org/; Appendix S1, see Supplemental Data with this article) after pruning for likely incorrect identification or georeferencing (e.g., occurrences in oceans). Additional localities of *C. canescens* and *C. maritima* were obtained from Villaverde et al. (2017b), and Villaverde et al. (2015a), respectively. We used a grid resolution of 30 arc-min to remove duplicate records (i.e., only one occurrence record per 50 km), reducing clustering (spatial bias). In the end, we obtained 1202 presence data points from preserved specimens of *C. canescens* (662), *C. macloviana* (106), *C. magellanica* (172), *C. maritima* (179), and *C. microglochin* (83).

Environmental variables—We used the 19 bioclimatic variables obtained from WorldClim climate database at 30 arc-min spatial resolution (~50 km; Hijmans et al., 2005). We define the environmental range in North and South America according to the biogeographic regions defined by Morrone (2002) for the Nearctic and Andean regions (Fig. 1).

Measuring niche shifts—We investigated whether the climatic niche of five bipolar *Carex* species differs between North and South America. These niche comparisons were used to describe possible climatic niche shifts between these two areas. We assumed that these species originated in the northern hemisphere and dispersed from North America to South America, as suggested for *C. maritima*, *C. canescens*, *C. magellanica*, and possibly *C. macloviana* (Villaverde et al., 2015a, b, 2017b; L. P. Bruederle, 2017, personal communication; Márquez-Corro et al., 2017). *Carex microglochin* was studied by Escudero et al. (2010a), but its direction of dispersal was equivocal.

We built a PCA based on all the 19 bioclimatic variables within the environmental range defined for the study area (see above) and
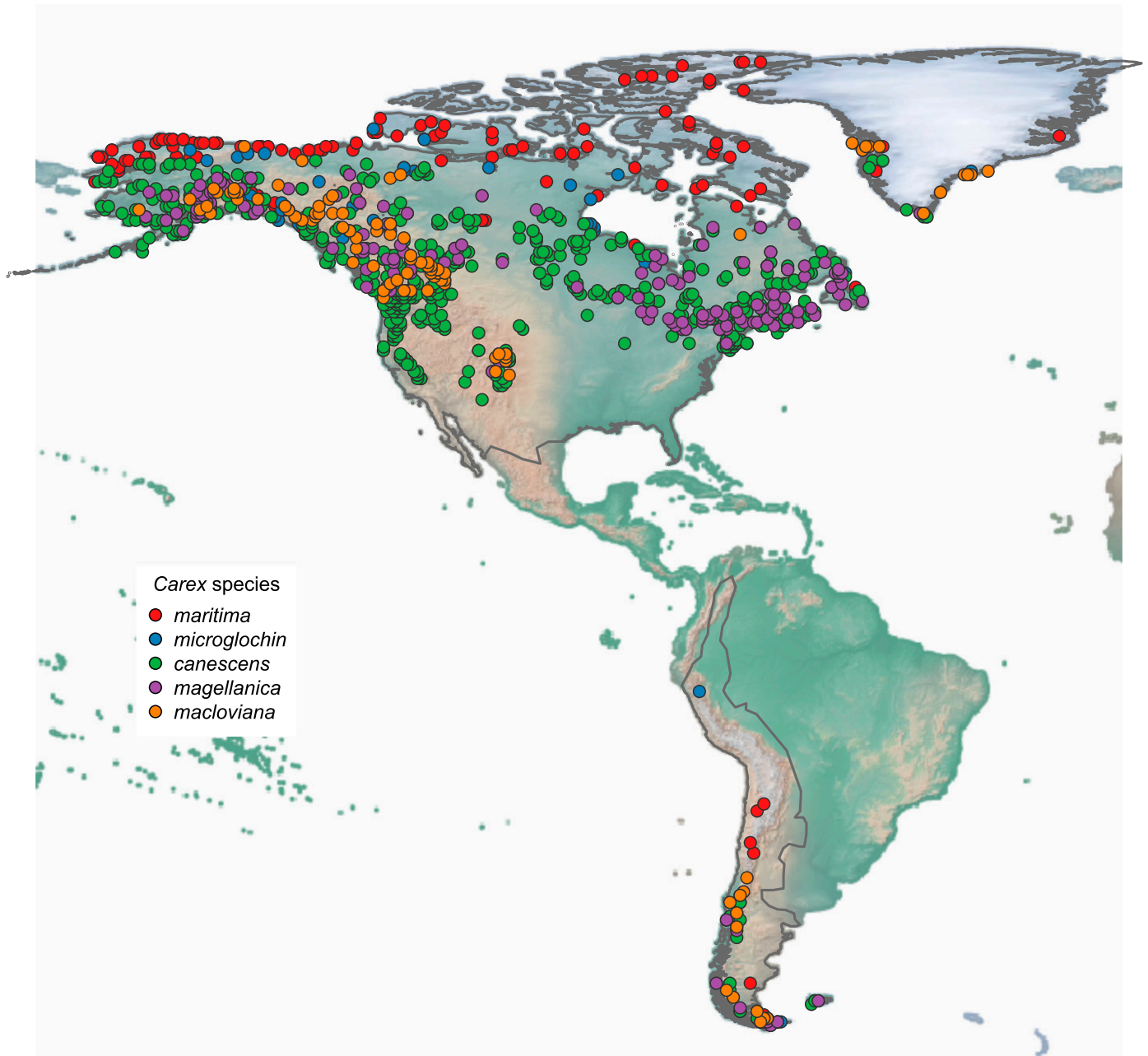
FIGURE 1 Map of the occurrences of the five bipolar *Carex* species studied. Gray polygons enclose the Andean and Nearctic biogeographic regions where these species occur.

used its first two axes to characterize the environmental space within which we could compare the northern and southern populations for each species. We then divided this environmental space into a grid of 100×100 cells, as in Broennimann et al. (2012). We measured the frequency of species occurrences for each combination of environmental conditions in each grid cell of the environmental space using a kernel smoother function to correct for sampling bias and environmental availability and to ensure that the results were independent of the grid resolution (ecospat.grid.clim.dyn function of the ecospat package (Di Cola et al., 2017) in R v3.3.1 R Core Team, 2015).

For each of the five species, we calculated the differences in occurrence densities between the two areas (ecospat.niche.overlap function) and used the Schoener *D* metric to calculate the degree of overlap (from no overlap to complete overlap, i.e., from 0 to 1). A test of niche equivalency (Warren et al., 2008; Broennimann et al., 2012) was performed to assess the equivalency of the two niches through 100 random permutations of occurrences between North and South America (ecospat.niche.equivalency.test function). A test of niche similarity was performed to assess whether the two niches are more or less similar than expected by chance through 100 random shifts of the niches within the available conditions in North and South

America (ecospat.niche.similarity.test function). In both analyses, we tested for niche conservatism and niche divergence (i.e., alternative "greater" and "lower"). Histograms of the observed and randomly simulated overlaps, with *p* values of the equivalency or similarity tests, were plotted. Finally, we also calculated niche expansion and unfilling (Petitpierre et al., 2012) using the ecospat.niche.dyn.index function. Unfilling is defined as the proportion of the densities in the native range (i.e., North America) located in different conditions from the colonized range (i.e., South America), expansion is the proportion of the densities in the colonized range located in different conditions from the native range, and stability is the proportion of the densities in the colonized range that overlaps with the native range (1-expansion). We calculated each index using the 90th percentile of the available environmental conditions common to both ranges (Di Cola et al., 2017). This approach removes the marginal environments and avoids bias due to artifacts of the density function (Petitpierre et al., 2012). We also calculated the median of the distribution density and the median of the available climatic space in both ranges to assess the overall direction of the shifts. Finally, we calculated the multivariate environmental similarity surface (MESS) index for each bioclimatic variable and the two first axis of its PCA to indicate analogous climates between ranges (Appendix S2). The index shows good overlap in the climatic conditions with most of the climatic space of South America also occurring in North America.

Modeling potential distributions—We used the program Maxent v.3.3.3k (Phillips et al., 2006) to model the potential distribution of each *Carex* species, both at present and for the middle of this century (around 2050). We used the same occurrence data and the 19 bioclimatic variables as in the niche overlap analyses, randomly selecting 10,000 grid cells within the Nearctic and Andes bioregions as background points. We used ENMeval R package v. 0.2.2 (Muscarella et al., 2014) to test different model configurations for regularization values (0.5, 1, 1.5, and 2) and feature types (linear, quadratic and hinge, i.e., excluding threshold and product features that may lead to overfitting; Phillips et al., 2017). The final models included only linear and quadratic features, except for *C. canescens* where the Akaike Information criterion (AICc) supported the inclusion of hinge features. The best models for *C. magellanica* and *C. microglochin* had regularization values of 1 (the default in Maxent), while *C. macloviana* and *C. maritima* had optimal regularization of 1.5, and *C. canescens* of 2 (i.e., imposing more smooth response curves). For future projections, we used five climate models from the Coupled Model Intercomparison Project Phase 5 (CCSM4, GFDL-CM3, GISS-E2-R, HadGEM2-ES, and MIROC5), as provided by World Clim v. 1.4 (www.worldclim.org). We used two climate change scenarios, one intermediate (RCP4.5) and another more extreme (RCP8.5), the latter in which radiative forcing is higher (8.5 W/m^2 compared to preindustrial values) due to increased emission of greenhouse gases (Collins et al., 2013). These analyses were performed using the R package dismo v. 1.1-4 (Hijmans et al., 2017). The full code and data to reproduce these analyses is available online (Rodríguez-Sánchez, 2017).

RESULTS

Niche shifts—The niche overlap analyses showed low climatic niche expansion between North and South America for *C. canescens* (0.2% niche expansion), but high for *C. microglochin* (39%), *C. magellanica* (45%), *C. macloviana* (60%), and *C. maritima* (96%;

Table 1). While southern populations of *C. canescens* completely matched climates of the northern hemisphere, the other species occupied increasingly dissimilar climates in South America compared to their northern populations (Fig. 2). Niche unfilling also indicated that all species in South America, with the exception of *C. magellanica*, are not yet filling their whole climatic niche as inferred from their northern counterparts (Table 1; Fig. 2).

Overall, there was low overlap of climatic niches between North and South American populations within species (Schoener's *D* < 0.42; Table 1; Fig. 2). *Carex magellanica* had the highest niche overlap (Schoener's *D* = 0.41) and showed evidence of high niche conservatism (Table 1; Fig. 2). *Carex canescens* (60% niche unfilling) and *C. macloviana* (ca. 61% niche unfilling) had very similar niche overlap (Schoener's *D* = 0.17 and 0.21, respectively). But, while *C. macloviana* has colonized new climates in the South, *C. canescens* is occupying the same environments in both hemispheres (60% and 0.2% niche expansion, respectively). Finally, *C. maritima* and *C. microglochin* presented very low niche overlap (Schoener's *D* = 0.001 and 0.12, respectively). Equivalency and similarity tests (Table 1) indicate that *C. magellanica* populations in South America occupy niches more equivalent and similar to those in the North America than expected by chance, whereas *C. macloviana* populations in South America occupy niches more similar than expected by chance.

The first two principal components (PCs) explained 78.3% of the variation (54.4% and 24.9%, respectively). The variables that contributed the most to PC1 were minimum temperature of the coldest month (bio6) and mean temperature of the coldest quarter (bio11), whereas mean diurnal range (bio2) and precipitation in the driest month (bio14) contributed the most to PC2.

Potential distributions—Maxent models based on the bioclimatic variables were able to reproduce the current distribution of all species (Fig. 3; mean AUC = 0.88, range 0.86–0.93). In the northern hemisphere, some species (*C. canescens*, *C. magellanica*) are abundant on both sides of North America, whereas *C. macloviana* appears more restricted to the western side (Figs. 1, 3). *Carex maritima* had the most northern distribution. Species distributions also differed in the southern hemisphere. Whereas *C. canescens* and *C. magellanica* were restricted to more southern latitudes, the remaining species could potentially spread further north following the Andes cordillera (Fig. 3). These results match those of the niche overlap analyses (Fig. 2; Table 1) in suggesting that these species

TABLE 1. Niche expansion and unfilling of the studied species in South America and results of niche overlap (*D*), niche conservatism, and niche similarity tests for North and South America ranges of five bipolar *Carex* species. Measures of niche expansion and unfilling are based on the 90th percentiles of the common environment between ranges. Niche overlap (Schoener's *D*) values of North American populations are compared with 100 simulated data sets; *p* < 0.05 indicates that niches are more conserved or similar than expected by chance and are denoted by an asterisk.

Species	Expansion (%)	Unfilling (%)	*D*	Niche conservatism (*p*)	Niche similarity (*p*)
C. canescens	0.2	60.1	0.17	0.58	0.06
C. microglochin	39.1	74.8	0.12	0.56	0.09
C. magellanica	45.4	0.7	0.41	0.01*	0.04*
C. macloviana	59.8	60.6	0.21	0.77	0.02*
C. maritima	96.1	98.7	0.001	0.57	0.10
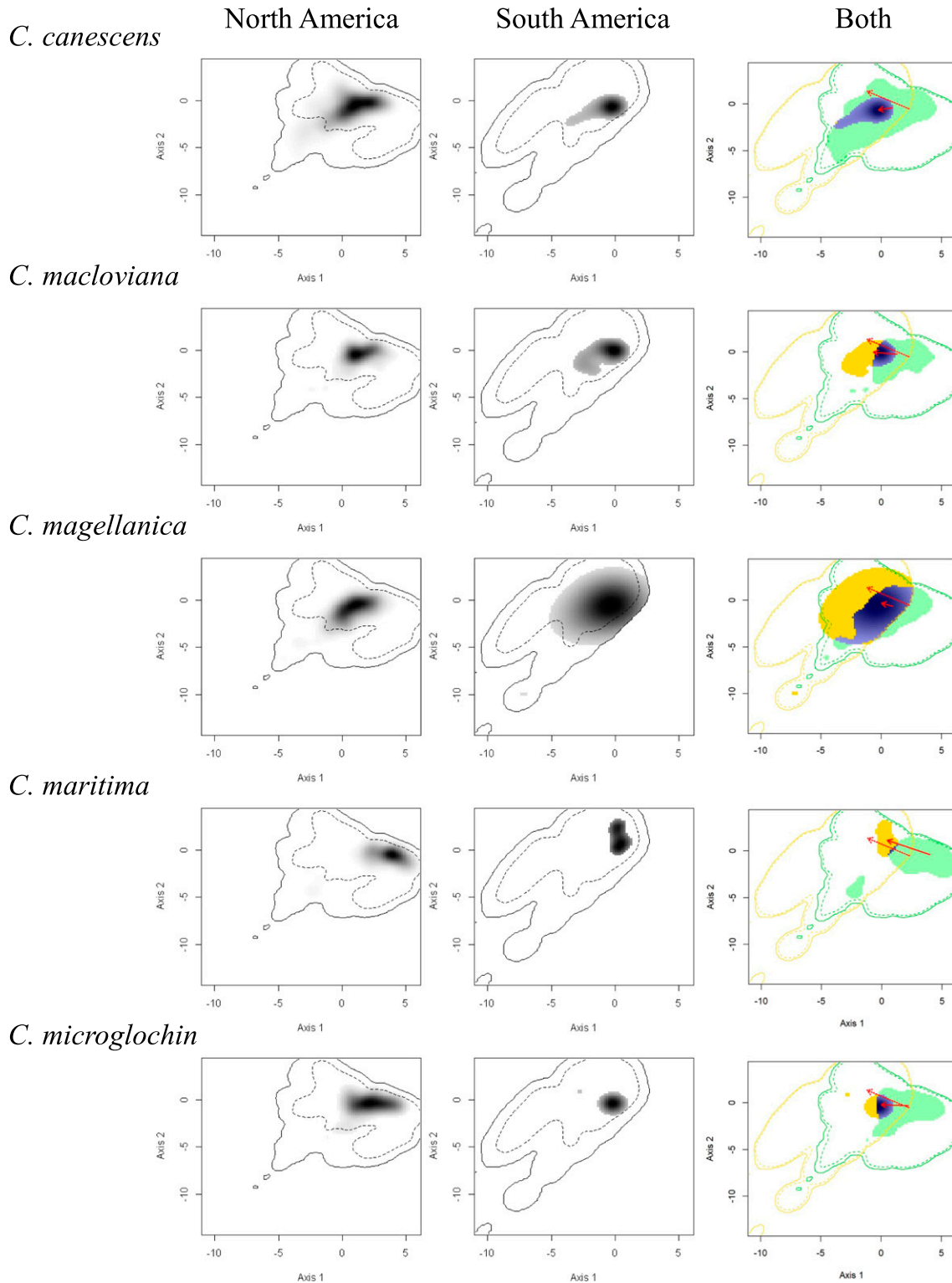
FIGURE 2 Comparison of climatic niches of five bipolar *Carex* species in North America (left column), South America (middle column), and niche shifts between both ranges (right column). Colors indicate niche expansion (yellow), stability (blue), and unfilling (green). Darker shading indicates higher density of species occurrences in South America; solid contour lines enclose all available environments for each range; dashed contour lines, 90th percentile of the background environment for both ranges. In the right column, yellow contour lines correspond to South America and green line to North America. The continuous arrow shows the environmental distance between the median of the distribution density for each range. The dashed arrow shows the environmental distance between the median of the available climatic space in each range.
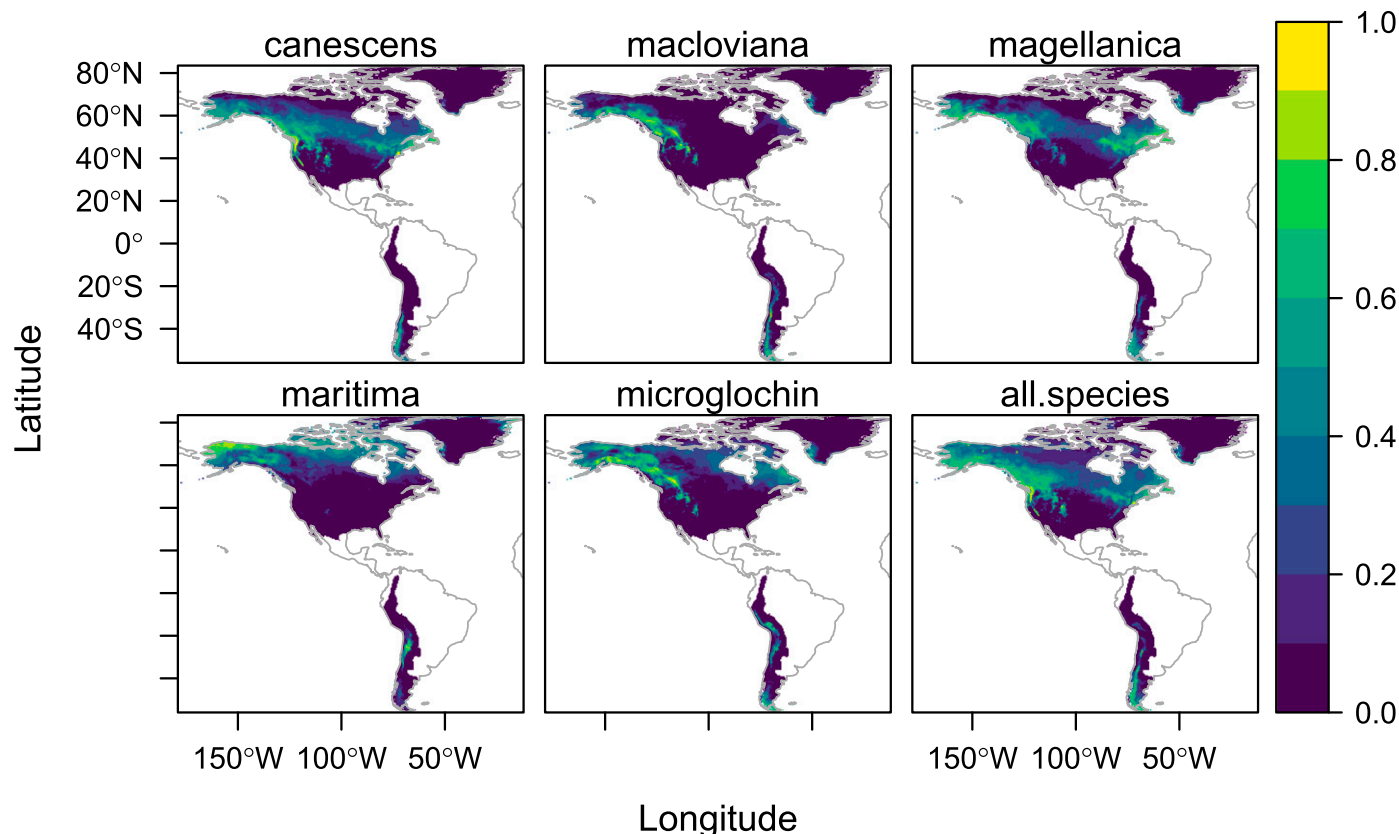
FIGURE 3 Potential distribution (climatic suitability) of each *Carex* species at present, as inferred from Maxent. Also included is the climatic suitability of all species considered together (bottom right panel).

still have not colonized all the suitable environments in the southern hemisphere.

Future climate change will most likely reduce the availability of suitable environments for these species, especially in low latitudes and elevations (Fig. 4; Appendix S3).

DISCUSSION

The bipolar pattern: Niche shift or niche conservatism?—The patterns of niche dynamics documented here suggest that shifts in climatic niches are frequent in bipolar *Carex* species. All of the studied species showed low niche overlap between North and South America (Schoener's *D* always lower than 0.42), and our results demonstrate a change in the density of occurrences (shift in centroid position) between North and South America caused by niche unfilling and expansion. Unfilling indicates that the species have not colonized all climates in South America mirroring those occupied by source populations in North America. All species but *C. magellanica* had high levels of unfilling, suggesting (data limitations apart) new biotic interactions or dispersal–establishment limitation processes.

On the other hand, niche expansion reveals that South American populations have colonized novel climates that are analogs (i.e., available but unoccupied in the North American range). *Carex canescens* had the lowest value of expansion (0.2%), indicating that climate at their southern range matches that of North American

populations. Coincidentally, this species seems to be the most recent to have colonized South America (Villaverde et al., 2017a, this issue). In contrast, *C. maritima*, whose estimated age of diversification of the southern populations falls within the late Pleistocene (Villaverde et al., 2015a), had the highest value of niche expansion (96%). Genetic differentiation or adaptive evolution (Lavergne and Molofsky, 2007) might have a role in the niche expansion observed for *C. maritima*, *C. magellanica* (45% expansion), and *C. macloviana* (60%), whose estimated age of divergence of the South American populations falls within the Mid to Late Pleistocene (L. P. Bruederle, 2017, personal communication; Márquez-Corro et al., 2017). These findings are in line with previous results shown by Villaverde et al. (2015a, 2017a, this issue), that indicated clear climatic niche differences for *C. maritima* but less-clear differences for *C. canescens*.

These large expansion rates, even considering only analogous climates, largely exceed the values shown for invasive species in similar studies (Petitpierre et al., 2012; González-Moreno et al., 2015), in which up to 85% of the species showed <10% expansion. Despite rapid evolution could occur in invasive species, the disparity of rates between bipolar and invasive plant species could be largely influenced by the time since divergence (>10,000 yr vs. centuries).

Also, the low number of populations recorded in the south may have increased the role of stochasticity on the distribution of colonized climates. The potential distribution models show that all species can still spread farther in the south, suggesting lags in the colonization process. Alternatively, existing populations (particularly
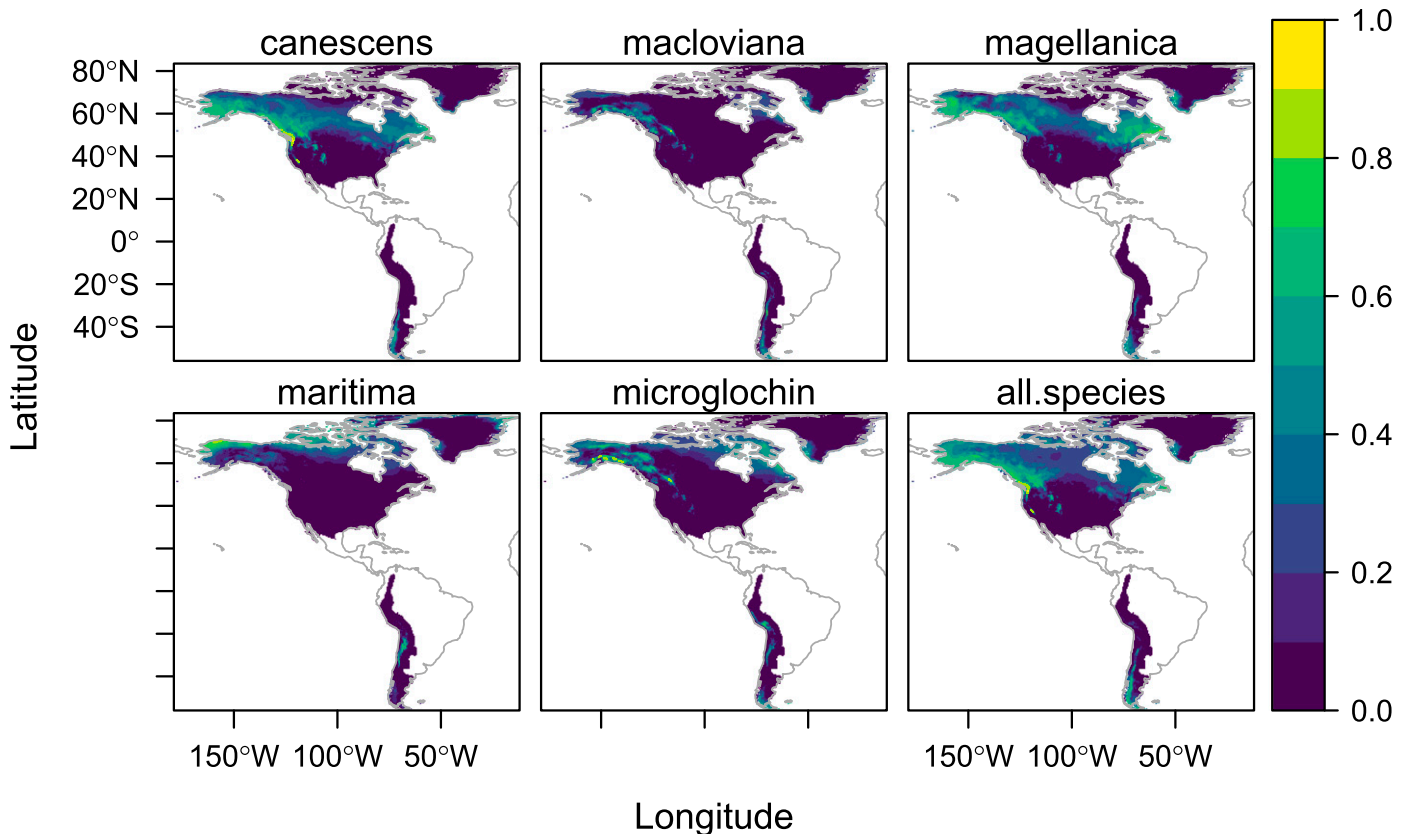
FIGURE 4 Potential distribution of each *Carex* species for the middle of 21st century (2050), as inferred from Maxent using an ensemble of five climate models and an intermediate emissions scenario (RCP4.5). Maps represent the average suitability as predicted by each climate model (see Appendix S3 for further results, including an RCP8.5 climate change scenario). Also included is the projected climatic suitability of all species considered together (bottom right panel).

in the Andes cordillera) might still be unreported. In any case, niche differences are not due to the size of the landmass available in both ranges. Although North America comprises a much greater extension of territory than South America, the environmental range available in both areas is similar (see Fig. 2). The inspection of variables related with temperature (see Appendix S4a, b) showed that southern hemisphere populations occur within the climatic range present in North America, but the median of the distribution densities in the South is toward higher temperature values.

Niche shift and genetic differentiation—Niche dynamics analyses can help us understand colonization processes, and different studies have found evidence of niche conservatism (e.g., Peterson et al., 1999; Wiens and Graham, 2005; Palaoro et al., 2013; Callen and Miller, 2015) and niche shifts (Broennimann et al., 2007; Mukherjee et al., 2012; Wüest et al., 2015). Partially overlapping niches could increase the probability of establishment of these bipolar species, without the necessity of evolutionary responses to colonize novel environments in the new areas. In fact, although some of these bipolar *Carex* species are genetically structured (e.g., *C. maritima*; Villaverde et al., 2015a), none of their southern populations have received formal taxonomic recognition (with the exception of *C. magellanica* whose southern populations correspond to *C. magellanica* subsp. *magellanica*).

Bipolar *Carex* species display a great diversity of genetic patterns, from low overall genetic differentiation (*C. canescens*, Villaverde

et al., 2017a, this issue) to higher genetic differentiation but not associated with northern or southern hemispheres (*C. actogena* complex, Villaverde et al., 2015b; *C. microglochin*, Starr et al., 2011; and *C. macloviana*, Márquez-Corro et al., 2017), and to genetic differentiation associated with northern vs. southern hemisphere (*C. maritima*, Villaverde et al., 2015a; and *C. magellanica*, L. P. Bruederle, 2017, personal communication). Importantly, observed niche shifts appear congruent with the genetic structure within species. First, *C. canescens*, with the lowest levels of niche expansion (0.2%), shows low genetic differentiation in South America. Second, *C. macloviana* (niche expansion 60% and Schoener's $D = 0.21$) and *C. microglochin* (niche expansion 39% and $D = 0.12$) have some genetic differentiation but are not completely congruent with a genetic separation between North and South America. And third, *C. maritima* (with highest niche expansion 96% and lowest niche overlap) and *C. magellanica* (with highest overlapping $D = 0.41$ and lowest unfilling; see Table 1), have high levels of niche shift and genetic differentiation, with a clear genetic differentiation between North and South American lineages.

Recent studies have also found congruent patterns between niche shift and genetic differentiation. Kolář et al. (2016a) suggested that niche differentiation along altitude-related bioclimatic gradients was related to the genetic structure in *Arabidopsis arenosa* (L.) Lawalrée (Brassicaceae). Kolář et al. (2016b) also suggested that niche shifts and range expansions in the Andes seem to have driven diversification in *Loricaria* Wedd. (Asteraceae). The results from an

interesting case study of a clade of 12 diploid *Hordeum* L. (Poaceae) species from the New World suggest that, while population stability was associated with niche conservatism, niche shifts were inferred after population bottlenecks (Jakob et al., 2010). Finally, a study for the whole Cyperaceae in North America showed that diversification was highly associated with range and niche evolution. Specifically, speciation was more rapid on an east–west transect and along precipitation and soil gradients (Spalink et al., 2016).

Long-distance dispersal and establishment (LDDE) in the context of niche shift—In recent years, studies of bipolar species have focused on biogeographical hypotheses to explain such remarkable disjunctions, concluding that long-distance dispersal (from North to South) has been the common process that explains the bipolar distribution (Vollan et al., 2006; Escudero et al., 2010a; Starr et al., 2011; Villaverde et al., 2015a, b, 2017a [this issue], b; Márquez-Corro et al., 2017). While several of these studies have discussed at great detail the syndromes and vectors that could explain such remarkable long-distance dispersal events, little has been said about the process of establishment after arrival (Villaverde et al., 2017a, this issue). The establishment process could be even more important than the probability of arrival since species with high capacity for dispersal will have a small distribution if they have low capacity for establishment.

Although *Carex* species lack syndromes for long-distance dispersal (e.g., Allessio Leck and Schutz, 2005; Villaverde et al., 2017a, this issue), they have been able to spread globally (Escudero et al., 2009; Schönswetter et al., 2008). Several recent studies (e.g., Villaverde et al., 2015a, b, 2017a [this issue], b; Soons et al., 2008; Green et al., 2016) seem to agree that nonspecialized syndromes can also be associated with high-dispersal capacity. In addition to dispersal, other factors could explain high establishment success in *Carex*: herbaceous habit, usually short to medium perennial cycle, autocompatibility, and frequent self-pollination (Whitkus, 1988; Ohkawa et al., 2000; Arens et al., 2005; Friedman and Barrett, 2009; Escudero et al., 2010b, 2013). All this evidence suggests that *Carex* has a great capacity for LDDE, which helps to explain the bipolar distribution in these five species.

Distribution shifts with climate change—As expected, future climate change scenarios will not favor these cold-dwelling species. Climate change will most likely push all them toward higher latitudes and elevations, reducing the availability of suitable environments (Fig. 4; Appendix S3a–e). Detrimental effects are, as expected, stronger with the RCP8.5 scenario (Appendix S3c–e). *Carex macloviana*, *C. maritima*, and *C. microglochin* may see their potential distributions particularly reduced (Fig. 4). In conclusion, our projections of potential distributions for the middle of this century (around year 2050) indicate that climate change may cause severe range contractions of these bipolar species, with likely local extinctions in low latitudes and/or low altitudes in both hemispheres (Fig. 4). Future climatic conditions will favor polewards range shifts, less so in species mostly distributed along the Rocky Mountains (like *Carex macloviana*), where they may suffer severe range loss. Notwithstanding these results, phenotypic plasticity, microrefugia, or rapid adaptation could ameliorate the impact of climate change (Bellard et al., 2012). For example, in an experimental study comparing native and nonnative ranges of *Anolis cristatellus*, Kolbe et al. (2012) inferred a rapid acquisition of thermal plasticity, which may have been advantageous for range expansion. They concluded that in this case the assumption of niche conservatism and no trait variation could lead to erroneous conclusions.

Will the bipolar species be able to shift their niches and/or distributions at the required pace under the fast human-mediated climate change that characterize the Anthropocene? We have reported here that these species have been able to colonize since the Pleistocene new climatic conditions in the southern hemisphere, different from those in their source ranges in the northern hemisphere. The pace of niche and range shifts required to deal with current climate change will, however, be higher than that required for past Pliocene and Pleistocene climate oscillations. Although the apparently high dispersal and colonization capacity of these species invite optimism about their future fate, global warming will certainly not benefit cold-dwelling species like these.

CONCLUSIONS

Our results show that climatic niche shifts are frequent in bipolar *Carex* species. All the studied bipolar species have colonized new analog climatic conditions in South America, following long-distance dispersal from source populations in North America. Although there are still unoccupied sites in the south potentially suitable for establishment, the detrimental effects of future climate change may slow, or even reverse, further spread in the region. Finally, although some species show genetic structure in South America, which might be associated with evolutionary responses to novel environments, further common garden experiments should confirm this hypothesis.

ACKNOWLEDGEMENTS

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