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A tale of worldwide success: behind the scenes of *Carex* (Cyperaceae) biogeography and diversification

Running title: Global biogeography of *Carex*

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ABSTRACT

The megadiverse genus *Carex* (c. 2 000 species, Cyperaceae) has a nearly cosmopolitan distribution, displaying an inverted latitudinal richness gradient with higher species diversity in cold-temperate areas of the Northern Hemisphere. Despite great progress in its phylogenetic knowledge and many molecular studies focusing on the biogeography of particular groups during the last decades, a global approach to *Carex* biogeography and

diversification is still lacking. For this purpose, we built the hitherto most comprehensive *Carex* dated phylogeny based on three markers (ETS–ITS–*matK*), using a previous phylogenomic Hyb-Seq framework, and a sampling of two-thirds of its species and all recognized sections. Ancestral area reconstruction, Biogeographic Stochastic Mapping and diversification rate analyses were conducted to elucidate macro-evolutionary biogeographic and diversification patterns. Our results reveal that *Carex* originated in the late Eocene in E Asia, where it probably remained until the synchronous diversification of its main subgeneric lineages during the late Oligocene. E Asia is supported as the cradle of *Carex* diversification, as well as a "museum" of extant species diversity. Subsequent “out-of-Asia” colonization patterns feature multiple asymmetric dispersals clustered towards present times among Northern Hemisphere regions, acting both as source and sink (especially Asia and North America) as well as several independent colonization events of the Southern Hemisphere. We detected 13 diversification rate shifts during the last 10 My, including remarkable radiations in North America and New Zealand that occurred concurrently with the Late Neogene global cooling, which suggests that diversification involved the colonization of new areas and expansion into novel niche spaces.

Keywords: Ancestral Area Reconstruction, Biogeographic Stochastic Mapping, boreo-temperate, dispersal, diversification rates, hyperdiverse, phylogeny

1. INTRODUCTION

The sedge genus *Carex* L. (Cyperaceae), with nearly 2 000 species, is among the five largest Angiosperm genera in the world (POWO, 2019; WCSP, 2019). Remarkably, it has undergone few taxonomic rearrangements since its formal description by Linnaeus in

1753. Beyond a few minor satellite genera recently subsumed into *Carex* (c. 150 spp.; *Cymophyllus* Mack., *Kobresia* Willd., *Schoenoxiphium* Nees, and *Uncinia* Pers.; Global *Carex* Group -GCG-, 2015), the morphological homogeneity for the diagnostic characters of *Carex* (unisexual flowers, with the pistillate ones enclosed in a bract-derived structure called perigynium or utricle; Kükenthal, 1909, Egorova, 1999, see also Jiménez-Mejías et al., 2016a) has reinforced the integrity of the genus and prevented its decomposition into a number of smaller genera. *Carex* represents a remarkable success as an evolutionary model, maintaining morphological coherence as a genus while diversifying ecologically and taxonomically.

Carex as currently circumscribed (GCG, 2015) is a nearly cosmopolitan genus. It is most diverse in the Northern Hemisphere boreo-temperate zone and, to a lesser extent, the Southern Hemisphere temperate zone. As such, it exhibits an inverted latitudinal species richness gradient, with higher diversity in cold-temperate areas and tropical regions harboring few species (Kindlmann et al., 2007; Escudero et al., 2012; see Fig. 1). Approximately 20 years of phylogenetic studies at multiple sampling scales, from species complexes to the genus as a whole (Starr et al., 1999; Roalson et al., 2001; Hendrichs et al., 2004a, b; Starr et al., 2004; Waterway & Starr, 2007; Derieg et al., 2008; Starr et al., 2008; Dragon & Barrington, 2009; Escudero & Luceño, 2009; Gehrke & Linder, 2009; Waterway et al., 2009; Gehrke et al., 2010; Ford et al., 2012; Jiménez-Mejías et al., 2012a; Martín-Bravo et al., 2013; Gebauer et al. 2014; Yano et al., 2014; Gebauer et al., 2015; Maguilla et al., 2015; Starr et al., 2015; Villaverde et al., 2015a, b, 2017b,c in review; GCG, 2016a, b; Míguez et al., 2017), have predominantly focused on investigating systematic relationships, morphological evolution, and biogeography at fine

phylogenetic scales. These studies have demonstrated that while historical sectional classification units were often geographically delimited, shallow clades within the genus may sometimes be found distributed on multiple continents. This, together with the frequent homoplasy observed for certain characters, led to the creation of artificial sections grouping apparently similar species that displayed more or less congruent distributions and/or ecologies. As a direct consequence of this, historical sectional classifications are largely incongruent with what we know today about the phylogenetic relationships in *Carex* (see GCG, 2016a).

Biogeography appears to have played a critical role in the diversification of *Carex*. The origin and worldwide diversification of *Carex* has been discussed in relation to chromosome evolution and adaptation to colder climates (Escudero et al., 2012; Gebauer et al. 2014; Hoffmann et al., 2017), as well as fine-scale partitioning of niche and distributional ranges of individual species within continents (Waterway et al. 2009; Gebauer et al., 2014; Pender, 2016; Spalink et al., 2016 a,b, 2018; Benítez-Benítez et al., 2018). While Cyperaceae have been inferred to have arisen in South America at the late Cretaceous, it was the migration of the ancestors of *Carex* to the Northern Hemisphere that was the catalyst for the major diversification of this lineage (Léveillé-Bourret et al., 2014, 2015, 2018a, b; Spalink et al., 2016b). Recent phylogenetic studies have discovered that several early-diverged lineages of *Carex* and its closest living relatives are Southeast Asian (Starr & Ford, 2009; Waterway et al., 2009; Starr et al., 2015; Léveillé-Bourret et al., 2018c), supporting the long-held view that the genus originated in SE Asia (Nelmes, 1951; Raymond, 1955, 1959; Koyama, 1957; Ball, 1990). A diversification shift has been documented when considering the base of the genus tree (Escudero et al., 2012; Spalink

et al., 2016b; Márquez-Corro et al., 2019), which is possibly associated with its transition into cooler climates and a shift to fissions and fusions as the dominant mode of chromosome evolution (Hipp et al., 2009; Escudero et al., 2012; Márquez-Corro et al., 2019). However, this origin story, which has become well understood over the past decade, does not explain the astonishing biogeographic diversity of the genus. *Carex* displays many of the large-scale diversity patterns observed in angiosperms, with different groups showing various diversity gradients, centers of endemism, and diversity hotspots. Despite the polyphyly of many *Carex* sections (GCG, 2016a), species relationships across geographic areas have in many cases been predicted fairly accurately by morphological taxonomy before the development and popularization of molecular systematic techniques (see Reznicek, 1990; Egorova, 1999; Ball & Reznicek, 2002). Having a striking capacity for long-distance dispersal (Villaverde et al., 2017a), *Carex* has colonized the Southern Hemisphere several times from different source areas (Spalink et al., 2016b). Gehrke & Linder (2009), for example, showed that all northern continents were probably involved in the colonization of sub-Saharan Africa. Escudero et al. (2009) demonstrated dispersal within sect. *Spirostachyae* from Europe to tropical Africa and South America, Míguez et al. (2017) demonstrated transitions in sect. *Rhynchocystis* between Europe and Tropical Africa and Jiménez-Mejías et al. (2012a) between the Northern Hemisphere, South America, South Africa and New Zealand in sect. *Ceratocystis*. Bipolar distributions at the species level have also been particularly well-documented in *Carex* and explained mostly by direct long-distance dispersal from the Northern Hemisphere to high latitudes of the Southern Hemisphere in South America and New Zealand (Villaverde et al., 2015a, b, 2017b, c; Márquez-Corro et al., 2017;

Maguilla et al., 2018). The genus also exhibits circumpolar (Gebauer et al., 2014, Hoffmann et al., 2017; Maguilla et al., 2018), Beringian (Schönswetter et al., 2008; King & Roalson, 2009; Maguilla et al., 2018), Amphi-Atlantic (Schönswetter et al., 2008; Jiménez-Mejías et al., 2012a; Westergaard et al., 2019), Arctic-Alpine (Schönswetter et al., 2006, 2008; Jiménez-Mejías et al., 2012b; Gebauer et al., 2014; Hoffmann et al., 2017), Pan-Himalayan (Uzma et al., 2019), Europe-Central Asia (Schönswetter et al., 2006), East-West Europe/Mediterranean (Escudero et al., 2009, 2010; Jiménez-Mejías et al., 2011, 2012b; Míguez et al., 2017; Benítez-Benítez et al., 2017, 2018), and Eastern-Western North America (Roalson & Friar, 2004a,b; Hipp et al., 2006; Hipp, 2008; Dragon & Barrington, 2009) distribution patterns, all illuminated using phylogenetic approaches. Colonization of isolated oceanic archipelagos from mainland sources has also been documented by several authors; these include: Hawaii (Dragon & Barrington, 2009), Macaronesia (Escudero et al., 2009; Jiménez-Mejías et al., 2012a; Míguez et al., 2017), Mascarenes and Tristan da Cunha (Escudero et al., 2009), and Juan Fernández (Ridley & Jiménez-Mejías, in prep.). The genus is a real treasure trove of biogeographic scenarios. Yet, many striking disjunctions identified by previous authors and apparently supported by the most recent phylogenies (e.g. GCG, 2016a) are not well understood, such as the Gondwanan, Circumantarctic, pantropical, Trans-Pacific, Madrean-Tethyan, Trans-Caribbean, or Western-Eastern Eurasian distributions found in several *Carex* species groups and clades. The recent inference of a phylogeny comprising about 50% of all the accepted species (GCG, 2016a) and a specimen-level aggregation of the vast majority of the previously published sequences available in NCBI GenBank comprising about 800 taxa (GCG, 2016b) provides the opportunity to explore these biogeographic

scenarios more broadly. At the same time, development of novel phylogenomic tools has given us a robust understanding of the framework phylogenetic structure of the genus (Villaverde et al., in review). While most relationships between deep nodes remain poorly resolved, with significant conflict among studies (see Villaverde et al., in review), the new available data resulted in a robust phylogenetic framework that provides a significant clarification of the relationships among the main *Carex* lineages, also serving as the base for a revised subgeneric classification (Villaverde et al., in review).

In this study, we increase the sampling of the global phylogeny of the GCG (2016a, b) by more than 300 species and constrain the backbone of the phylogeny using this phylogenomic framework (Villaverde et al., in review) to study broad-scale patterns of historical biogeography and diversification. The result is the most comprehensively sampled time-calibrated phylogenetic hypothesis of the world's *Carex*, which we expect to serve as the basis for subsequent more detailed and hypothesis-testing analyses.

2. MATERIALS AND METHODS

2.1. Study group nomenclature

We follow the most recent subgeneric rearrangement proposed by Villaverde et al. (in review), that consider each of the six main *Carex* clades as different subgenera: subg. *Siderosticta* Waterway, subg. *Carex*, subg. *Euthyceras* Peterm., subg. *Psyllophora* (Degl.) Peterm., subg. *Uncinia* (Pers.) Peterm., and subg. *Vignea* (P. Beauv. ex T. Lestib.) Heer. Accordingly we will refer to these main clades directly using the names of the subgenera.

Species groups are named using *Carex* sectional names according to the sectional partition provided in Data S1, which is a modified version of the one presented in GCG

(2016). Given the intricate nomenclature of *Carex* sections and for the sake of clarity, the use of sectional authorities is avoided, as there is no intention to settle new nomenclatural rearrangements. Since a number of sections are polyphyletic, and in order to simplify the text, whenever a clade contains the vast majority of the species belonging to a single section, we will refer to the clade as that section. When further explanation is needed to specify what subset of species we are talking about, we will resort to commonly used terms for systematic grouping: "alliances" for monophyletic groups of intermingled sections, "core" for the clade containing the type species of a non-monophyletic section, or geographic references (e.g. "North American clade of section x").

2.2.Sampling

We built a comprehensive *Carex* phylogeny based on the DNA barcoding nrDNA ITS and ETS and ptDNA *matK*, using the dataset published by GCG (2016a) as the starting point. This initial matrix consisted of 2150 concatenated *Carex* sequences, representing 996 of the currently 1992 accepted species (50%; Govaerts et al., 2019+) from 110 of the 126 recognized sections (92.06%; see GCG, 2016a). We expanded this dataset by adding: 2402 concatenated sequences available in GenBank for these DNA regions up to mid-2014 as compiled in GCG (2016b); 522 new concatenated sequences (see Data S2) obtained for this study from materials on loan from A, BISH, E, K, MO, NY, and TUS (Thiers, 2019), following the lab protocols described in GCG (2016a); and 448 concatenated sequences available in GenBank for these DNA regions (ITS, ETS, *matK*) and published in recent phylogenetic studies (Léveillé-Bourret et al., 2014, 2018a, b; Gebauer et al., 2015; Molina et al., 2015; Starr et al., 2015; Villaverde et al., 2015a, b, 2017c; Elliott et al., 2016; Benítez-Benítez et al., 2017; Márquez-Corro et al., 2017;

Míguez et al., 2017; see Data S2). The outgroup was composed of seven samples, representing tribe Scirpeae (*Eriophorum vaginatum*, *Scirpus polystachyus*), and the recently described tribes Trichophoreae (*Trichophorum alpinum*, *T. cespitosum*) and Sumatrosirpeae (*Sumatrosirpus paniculatocorymbosus*, *S. rupestris*), which are successive sister clades to *Carex* (Léveillé-Bourret et al., 2018a, b; Léveillé-Bourret & Starr, 2019; Semmouri et al., 2019). This sequence compilation yielded a raw multi-accession matrix (hereafter the “multiple tips matrix”) of 5529 individuals comprising one or more concatenated ETS, ITS, and *matK* sequences each.

Due to the huge size of the matrix, this was subjected to several rounds of curation to detect conflicting phylogenetic placements due to contamination, mislabeling, duplication, misidentification, and misconcatenation. We also removed those accessions whose placement in the trees was odd and poorly supported due to low phylogenetic signal (usually when *matK* was the only sequence available). Accessions from the former tribe Cariceae genera (*Cymophyllus*, *Kobresia*, *Schoenoxiphium*, and *Uncinia*) were renamed to conform to current *Carex* taxonomy (GCG, 2015). Through this process, we selected a single accession for each taxon (species, subspecies or variety), prioritizing individuals with the longest and highest number of sequences. The resulting one-tip-per-taxon matrix (hereafter, the “singletons matrix”) was subsequently used for the biogeographic and diversification analyses. The final, curated multiple tips matrix was composed of 4467 concatenated sequences, of which 1392 were retained in the singletons matrix, representing 1386 *Carex* taxa (six accessions corresponded to the outgroup) and 1312 *Carex* species belonging to 126 sections. This dataset comprises the first complete sampling of sections for any *Carex* phylogenetic analysis and a 32% increase in species

sampling from the GCG (2016a) dataset, reaching 66% of the total number of accepted *Carex* species (Govaerts et al., 2019+). The sampling proportion significantly varied between the different regions considered in the biogeographic analyses (see results).

2.3.Alignment

Owing to the large nucleotide variability across the multiple tips matrix, especially among the sequences of the nrDNA regions (ETS and ITS), and the consequent difficulty of aligning homologous positions, two different alignment approaches were conducted. Each DNA region (ETS, ITS and *matK*) was aligned separately by means of: (1) a default alignment using MUSCLE v.3.8.31 (Edgar, 2004); and (2) following the approach taken in GCG (2016a), that consisted on a profile-to-profile approach in which each gene region was separated in three submatrices corresponding to the major clades found in previous works, aligned with MUSCLE, then aligned to one another using profile-to-profile alignment in MUSCLE, retaining alignments within groups but inserting gaps to align between groups. The matrices and phylogenetic reconstructions (see below) resulting from each of these approaches were visually examined and compared, clearly revealing that the default MUSCLE alignment, our first approach, produced a better resolved topology (profile-to-profile alignment results not shown).

To build the singletons matrix the selected sequences were realigned from scratch using the default MUSCLE alignment. The lower missing data of the singletons matrix compared to the multiple tips matrix considerably reduced the ambiguity of the alignment and improved topology resolution in the phylogenetic analyses (see below).

2.4. Phylogenetic analyses

The aligned multiple tips matrix (3006 bp) contained a high amount of missing data (60.08%), since one or two of the three selected DNA regions were frequently missing, either because we failed in the amplification from herbarium specimens or because the selected GenBank accessions only represented one or two of the selected regions. This produced poorly resolved topologies when the matrix was directly analyzed (results not shown). Therefore, we resorted to two different scaffolding approaches (Hinchliff & Roalson, 2013; GCG, 2016a).

For the first, we followed the GCG (2016a) scaffolding approach in which we first selected only those accessions of the multiple tips matrix represented for ITS–ETS (regardless of their having *matK* or not), to build an nrDNA-complete matrix (2394 accessions, 3006 aligned bp) with a reduced amount of missing data (46.17%). This multiple tips nrDNA-complete matrix was subsequently used to build a backbone tree (“reference tree”) with Maximum Likelihood (ML), as implemented in RAxML v. 8.2.10 (Stamatakis, 2014), through the CIPRES Science Gateway (Miller et al., 2010). Then, the phylogenetic placement of all excluded sequences –those present in the complete multiple tips matrix, but not in the multiple tips nrDNA-complete matrix, was obtained building a “query tree” based on the reference tree, by using the evolutionary placement algorithm (Berger et al., 2011) as implemented in RAxML. Finally, the SH-aLRT value (nonparametric Shimodaira-Hasegawa implementation of the approximate likelihood-ratio test; Anisimova & Gascuel, 2006; Anisimova et al., 2011) was used to evaluate query tree branch support with RAxML. This analytical procedure was performed to build two query trees, one from the multiple tips matrix (multiple tips query tree) and

another from the singletons matrix (singletons query tree). The singletons matrix (2797 aligned bp) had 41% missing data, while this percentage decreased to 33.38% in the singletons nrDNA-complete matrix (1109 concatenated sequences, 2797 aligned bp).

For the second approach, we constrained ML analyses in RAxML using a backbone topology for the genus *Carex* obtained using a phylogenomic approach (Hyb-Seq; Villaverde et al., in review). This phylogeny has uncovered a novel and strongly supported backbone topology for *Carex*, demonstrating subg. *Uncinia* to be sister to subg. *Vignea* instead of being nested within subg. *Euthyceras*, as has been suggested by most Sanger-based phylogenies. After constraining the singletons nrDNA-complete matrix using the Hyb-Seq tree, we then used in turn the resulting constrained singletons tree as a constraint for the complete singletons matrix to obtain the final constrained singletons tree. Clade bootstrap support and search for the best-scoring ML tree were jointly obtained through 100 replicates in the same single run. Throughout the remainder of the paper, “constrained singletons tree” refers to this twice-constrained singletons tree.

2.5. Dating and diversification analyses

We fossil-calibrated the singletons query tree and the constrained singletons tree (1386 *Carex* taxa, 1312 species) using the recently reassessed *Carex* fossil record (Jiménez-Mejías et al., 2016b) to establish calibration points. Ten fossil constraints were applied (Table 1), with ages ranging from the Eocene for the crown node of *Carex* (*C. colwellensis*), to the Pliocene for sections *Ammoglochin* and *Ovales* (*C. ungeri* and *C. klarae*, respectively). Three fossils were used to calibrate deep nodes (crown node of genus *Carex*, subg. *Carex* and subg. *Vignea*), and seven for shallower nodes (Table 1). The taxonomic identity of these fossils has been recently evaluated (Jiménez-Mejías &

Martinetto, 2013; Jiménez-Mejías et al., 2016b). They consist mostly of fossil nutlets, though some preserved utricles were utilized as well (i.e. *C. hartauensis* and *C. flagellata*).

The joint use of fossils at both deep and shallow nodes may produce interaction among the calibrations because the node ages in a tree are not mutually independent (Ho & Phillips, 2009). To assess sensitivity of our inferences to this potential interaction, we analyzed the trees by using (a) all ten fossils, and (b) only the three oldest fossils that constrain the deepest nodes (i.e. *C. colwellensis*, *C. marchica*, *C. hartauensis*; Table 1).

Preliminary analyses using Bayesian MCMC in BEAST v. 1.8.4 (Drummond & Rambaut, 2007; Drummond et al., 2012) yielded problems with mixing of chains and low ESS values. Consequently, the analyses presented here utilize the penalized likelihood approach (Sanderson, 2002) as implemented in TreePL (Smith & O'Meara, 2012), which was designed for large phylogenies. The rate smoothing parameter was set on the basis of cross-validation and the χ -square test in TreePL. Nine smoothing values between 1e-5 and 1e3 were compared.

Transitions in lineage diversification rates were estimated on the constrained singletons tree calibrated with 10 fossils using the speciation-extinction model implemented in Bayesian Analysis of Macroevolutionary Mixtures (BAMM; Rabosky, 2014). The method models transitions in net diversification rates by allowing changes in the numbers and locations of nodes at which speciation and extinction rates shift, averaging over models and parameters using reversible-jump Markov chain Monte Carlo (rjMCMC; Green, 1995). The R package 'BAMMtools' (Rabosky et al., 2014) was used for configuration and analysis of MCMC. All priors were set as recommended using the

setBAMMpriors function on the 10-fossils tree, with the exception that analyses were conducted using a prior of one shift in diversification rates and a prior of 50 shifts, to see whether model-averaged rates were affected. Analyses were conducted assuming a global sampling fraction of 0.693 to account for missing taxa. Missing taxa were assumed missing at random from the tree, which may bias toward lower estimates of diversification of predominantly E Asian and Neotropical clades, which are relatively undersampled. However, given the difficulty of assigning missing taxa to particular clades in our study, and the fact that biogeographic transitions are very common in *Carex* (see results), it was not practical to estimate clade-level sampling partitions. Additionally, it has been found that even in cases where the random sampling assumption is dramatically violated (Hipp et al., 2019) and taxon sampling is near 60%, global sampling partitions can yield results not significantly different from clade-specific sampling partitions. The rjMCMC was run using Metropolis-coupling with four chains, each run for 20,000,000 generations, saving trees every 20,000 generations for analysis. The rjMCMC results were investigated using effective sample size for log-likelihood and number of model shifts in the R package ‘coda’ (Plummer et al., 2006).

2.6. Biogeographic analyses

Ancestral area reconstruction (AAR) was conducted using the R package ‘BioGeoBEARS’ (Matzke, 2013, 2014a). Due to the nearly cosmopolitan distribution and wide diversity of biogeographic patterns in *Carex*, coding of areas for the biogeographic analyses to accurately represent the spatial distribution and endemism of the genus was problematic. An initial coding with 10 areas (Nearctic, W Palearctic, E Palearctic, Afrotropic, Tropical Asia, Polynesia, Neotropic, Australia, New Zealand, and

Subantarctic Islands) was computationally too demanding. Therefore, we merged them resulting in six areas: Nearctic, W Palearctic, E Asia (including E Palearctic and Tropical Asia), Afrotropic, Neotropic (including Central America and the Caribbean), and Pacific (including Australia, New Zealand and Polynesia). For the most part, these areas correspond to classic biogeographic realms (Takhtajan, 1986), except for the treatment of E Asia and Pacific regions. They also correspond with major diversity patterns in *Carex*: Australia and New Zealand share many species groups, and a taxonomic turnover in Eurasia is observed between the W and the E Palearctic (see species listed in Chater, 1980; Egorova, 1999 and Dai et al., 2010). We did not consider any adjacency coding given the ability of *Carex* to disperse long-distances, involving numerous trans-oceanic dispersals and sometimes between not-adjacent landmasses (as reviewed in the Introduction). All of the sampled taxa were coded as present or absent in these areas (Data S1), based on distributions in Govaerts et al. (2019+). We analyzed our dataset under the DIVA-like (Dispersal-Vicariance Analysis; Ronquist, 1997) and DEC models (Dispersal-Extinction-Cladogenesis; Ree et al., 2005; Ree & Smith, 2008) as well as in combination with the “jump dispersal” or founder (j) parameter (models: DEC, DEC+J, DIVALIKE, DIVALIKE+J; Matzke, 2014b). The estimated likelihood of models DEC and DIVALIKE were not compared with estimated likelihood of models DEC+J and DIVALIKE+J, as their likelihoods are not directly comparable based on the way that the J and C parameters enter into the model (Ree & Sanmartín, 2018). In addition, results from models considering the parameter J will be interpreted cautiously as they have greater tendency towards explaining the data entirely by cladogenetic events and inferring, in some cases, anagenetic rates of 0 (Ree & Sanmartín, 2018). Following these

analyses, we performed Biogeographic stochastic mapping (BSM) based on the DEC and DEC+J model parameters (Dupin et al., 2016; Matzke, 2016) to estimate the frequency, timing, and locations of anagenetic and cladogenetic events. For each model, we simulated 100 possible histories, given the phylogeny and model parameters, under the constraint that these histories result in the same distributions that we input for the tips of the phylogeny. From these stochastic maps, we calculated the relative frequency of anagenetic and cladogenetic dispersal, sympatry, and vicariance events at 1 million-year intervals. We also calculated the frequency of biogeographic regions that were either the source or destination of anagenetic and cladogenetic dispersal events through time.

3. RESULTS

The results presented here are based on a dataset including sequences for 65.8% of all recognized *Carex* species, which is to date the largest dataset compiled for the genus. Though 34.2% of the species remain to be sampled (mainly Neotropical and E Asian taxa), this dataset includes taxa belonging to all accepted sections, implying that the phylogenetic and morphological diversity of the genus is relatively well covered. Although we cannot rule out the possibility that the addition of more taxa may reveal lineages that could be sister to one or several of the six currently known subgeneric lineages, we expect that such new lineages would not significantly alter currently established patterns of relationship.

3.1. Phylogenetic and divergence-time analyses

The multiple tips query tree built from the multiple tips matrix (Data S3) and the singletons query tree (Data S4) built using the GCG (2016a) scaffolding approach revealed topologies broadly concordant with the GCG (2016a) tree with respect to the

strongly supported monophyly of *Carex* and the five major lineages found to comprise the genus in previous Sanger-based phylogenies (matching subg. *Carex*, *Euthyceras* (with *Uncinia* nested within), *Psyllophora*, *Siderosticta*, and *Vignea*). Species groupings, shallow clades and unresolved relationships among the five major clades (except for the well-known sister relationship of subg. *Siderosticta* to the rest of *Carex*) were also mostly congruent with GCG (2016a). On the other hand, the constrained singletons tree (Fig. 2A; Data S5) recovered all except three of 1312 sampled species placed within each of the six main subgeneric clades retrieved by Villaverde's et al. (in review) tree, even though that the phylogenomic tree was built using only 88 *Carex* species. The only exceptions were the orphan species *C. bostrychostigma*, *C. dissitiflora*, and *C. satsumensis* which remained unresolved. These species arose from deep nodes in the constrained singletons tree, not forming part of any of the subgeneric lineages (Fig. 2A; Data S5), whereas they appeared at the base of the subg. *Carex* clade in the query trees, but with low support (Data S3–S4). At the shallowest levels, the query trees tended to be better resolved than the constrained singletons tree, although those groups recovered in the constrained singletons tree were also shared with the query trees and made taxonomic sense.

Inferred diversification times were more influenced by the calibration strategy employed in the dating analyses (10 vs 3 fossils; Table 1) than by the topology of the dated tree (singletons query tree vs constrained singletons tree). Thus, the ages recovered under each strategy on each of the two different dated trees were mostly similar, except for differences attributable to the species composition of the dated lineage (Table 2; Data S6–S9). Ages obtained by calibrating the tree using all ten fossils were considerably older than those obtained using only three fossils at deeper nodes in the phylogeny.

For the remainder of this paper, we will report results based on the most informative dataset we considered: the ten-fossil calibration of the twice-constrained singletons tree (Fig. 2A; Data S6), which takes advantage of both phylogenomic data (Villaverde et al., in review) and a thorough review of the fossil record (Jiménez-Mejías et al., 2016b). In this analysis, the crown node of *Carex* was placed at the late Eocene (Priabonian, 37.17 Mya). Remarkably, the crown nodes of the six major subgeneric lineages within *Carex* were all dated to the late Oligocene (Chattian)-Early Miocene (Aquitanian), with a mean age 22.91–25.18 Mya. These ages are generally older than those obtained in previous studies dating *Carex* (see Table 2).

3.2. Biogeographic analyses

Ancestral area reconstruction with DEC (Figs. 2A, S1), DEC+J (Fig. S2), DIVA-like (Fig. S3) and DIVA-like+J (Fig. S4) models produced broadly congruent estimations, though multiple areas were inferred as ancestral more commonly under DIVA-like models than under the DEC models. No significant differences in the most likely estimated area were found among nodes of interest. DEC models had a better fit (DEC, DEC+J: LnL = -2271.46, -2177.61; AIC= 4546.92, 4361.24; respectively) than DIVA-like models (DIVA-like, DIVA-like+J: LnL = -2363.74, -2255.76; AIC= 4731.48, 4517.52; respectively) so we will hereafter report the results from DEC analyses.

The origin of *Carex* is placed in E Asia, as are the ancestral nodes of subg. *Carex*, *Euthyceras*, *Siderosticta*, and *Vignea* clades (Figs. 2A, S1–S2). E Asia is also maintained as the ancestral area through a number of lineages along all the major clades. Indeed, only subg. *Psyllophora* and the vast majority of species in subg. *Uncinia* are currently

absent from that area. The ancestral distribution of subg. *Uncinia* is inferred to be the Americas by DEC (Figs. 2A, S1), with the most probable area being both the Nearctic–Neotropic and the second most probable area the Neotropic. On the contrary, DEC+J inferred the Neotropic as the most probable ancestral area (Fig. S2). Subgenus *Psyllophora* is inferred to have arisen in the W Palearctic (Figs. 2A, S1–S2). A number of large radiations (> 15–20 species) have taken place within the last 10 Mya, mostly involving a single geographical area. These areas include E Asia (core sect. *Clandestinae*, core sect. *Mitratae*, core *Kobresia*), the Nearctic (e.g. American sect. *Acrocystis*, sects. *Griseae-Granulares-Careyanae* alliance, sects. *Porocystis-Hymenochlaenae-Longicaules* alliance, sect. *Ovales*), and to a lesser extent the Pacific (specifically two synchronic radiations in New Zealand: sects. *Echinochlaenae* and *Uncinia*) and the Afrotropic (sect. *Indicae* p.p., sect. *Schoenoxiphium*). Such large radiations seem to be conspicuously absent from the W Palearctic and the Neotropic (Figs. S1–S2).

Results from the BSM analyses under the DEC (Table 3) and DEC+J (Table S1) models were similar in terms of the number of inferred biogeographic events (1812 and 1714, respectively), the proportion of events cladogenetic rather than anagenetic (81.15/18.84% and 76.76/23.23%, respectively), and the relative importance of the areas as source/sink of dispersal events. In addition, DEC+J inferred 119.5 founder events, a parameter (J) not included in the DEC model.

Under both models, the great majority of dispersal events were inferred to have taken place between Northern Hemisphere regions (Nearctic, E Asia, and W Palearctic), both as sources (c. 91%) and sinks (c. 71%) of dispersals events (Fig. 2B; Tables 3A, S1A). Southern Hemisphere landmasses play a minor role as source of dispersals (c. 9%,

half of which correspond to dispersal from the Neotropic to the Nearctic), but are more relevant as sinks for dispersals (c. 28%; Fig. 2B; Tables 3A, S1A). In addition, when the type of dispersal is considered in the DEC+J model (anagenetic dispersal or range expansion vs. cladogenetic dispersal or founder event), the Southern Hemisphere gains importance as sink of cladogenetic dispersal events (39.4%; Table S1A). Prevailing dispersal routes (Fig. 2B) are between any of the Northern Hemisphere areas and, to a much lesser extent, between any of these as source and a Southern Hemisphere area as sink (except for the dispersal connection between the Nearctic and the Afrotropic, which is negligible). An additional significant connection was inferred from the Neotropic to the Nearctic. The relative contribution of dispersal connections among Southern Hemisphere areas is negligible when compared to the rest of the world. The areas that were inferred to be the most important sources of dispersal were the Nearctic and E Asia, with c. 38% and c. 35% (considering both DEC and DEC+J models) of the total number of dispersal events inferred to have taken place from each of these areas (Tables 3, S1A). The most important sink for dispersal was the W Palearctic, at 27% of dispersals inferred to have colonized this area. E Asia and the Nearctic act as source for dispersals more frequently than as sink. Thus, more than 70% of the total dispersal events were inferred to have taken place from these two areas (see above), whereas less than a half of dispersals were inferred to have colonized these areas (c. 20% and c. 23%, respectively). In contrast, the remaining areas act less frequently as source than sink, which is especially evident for the Neotropic (c. 4% vs c. 15%) and, to a lesser extent, the W Palearctic (c. 20% vs c. 27%), the Afrotropic (c. 1 vs c. 6%), and the Pacific (c. 3% vs c. 8%). Finally, the majority of biogeographical events inferred by BSM correspond to cladogenetic events (77%, 81% in

DEC and DEC+J, respectively), of which speciation within an area appears as the most frequent event (69%, 71%), whereas cladogenetic dispersal (7%, only in DEC+J model) and vicariance (3%, 8%) had a relatively minor contribution (Tables 3B, S1D). In summarizing the timing and frequency of biogeographic events, the BSMs indicate some uncertainty in the models, particularly at the basal nodes of the tree where all cladogenetic and anagenetic event types were estimated with equal frequency (Fig. S5). Over the past 25 million years, BSM analyses suggests that while sympatric speciation is most common, dispersal and vicariance events collectively accounted for 25–60% of all biogeographical events. The frequency of sympatric speciation plummeted while the frequency of anagenetic dispersal rises dramatically (Fig. S5). These anagenetic events largely reflect the exchange of lineages amongst the Nearctic, the W Palearctic, and E Asia (Fig. 2B).

3.3. Diversification

Net diversification rates across the 10-fossils tree range from 0.138–1.041, a 7.5-fold range, under a prior of 1 shift, and from 0.107–1.090, a 10.2-fold range, under a prior of 50 shifts. The estimated number of shifts also differs significantly, from 17.49 +/- 3.33 (s.d.) under a shift prior of 1 to 27.68 +/- 4.50 under a prior of 50 shifts. However, these differences do not manifest in significant differences in the model-averaged net diversification rates as estimated on the tree, which correlate strongly (for net diversification rate, branchwise Pearson product-moment (r) = 0.989, $p < 1 \times 10^{-16}$), so we will restrict our discussion to the single-shift prior (Fig. 3). Moreover, as there are many possible shifts to discuss, we focus on the 13 shifts to net diversification rates above 0.5 species·My⁻¹, which were distributed across the tree (Table 4; Fig. 3A). In the

Northern Hemisphere, shifts largely comprised on one hand mainly Nearctic radiations (five shifts), and on the other largely Circumboreal groups (four shifts). The mean age of the crown node of the clades involved in most shifts affecting Nearctic radiations took place in a window of about 2 My flanking the Mio-Pliocene boundary (5.3 Mya), except for the American sect. *Acrocystis*, which happened around 2.6 Mya at the end of the Pliocene. For the Circumboreal groups the shift happened 7–5.4 Mya at the end of the Miocene. Two additional shifts happened in groups from E Asia during the Miocene (8 Mya; core *Kobresia*) and Pliocene (4.1 Mya; *Clandestinae* clade). In the Southern Hemisphere there are two other additional shifts: sect. *Uncinia* (former genus *Uncinia* s.s.; starting in South America and involving New Zealand, 10.9 Mya, Middle Miocene), and sect. *Echinochlaenae* (centered in New Zealand, 4.5 Mya, early Pliocene).

4. DISCUSSION

4.1. Towards a unified interpretation of *Carex* phylogeny: robustness of the inferences under different approaches

The phylogenies presented in this study represent by far the most comprehensive sampling to date in the two decades of phylogenetic studies of the megadiverse genus *Carex* with 100% of sections and almost 66% of accepted species included. However, it should be noted that our species sampling is not uniformly distributed geographically: while there are nearly completely sampled geographic areas, such as the Nearctic and the W Palearctic (>97% species), other areas have a high proportion of non-sampled species, particularly E Asia and the Neotropic (c. 51% and 57% respectively; Data S1; Govaerts et al., 2019+). Given the great richness of species in E Asia (more than 1000 species; Fig. 1B), this region appears to be the critical sampling gap that requires filling in future

phylogenetic studies. Nonetheless, our complete sampling of sections likely ensures a good coverage of the phylogenetic diversity of the genus.

The multiple tips query tree with 4470 accessions (Data S3) is the largest *Carex* phylogeny hitherto built to date. Our curation procedure, which resulted in the exclusion of almost 20% of all initially gathered accessions (>1000 concatenated ETS–ITS–*matK* sequences), underlines the need for carefully checking the phylogenetic placement of *Carex* sequences, both newly obtained and downloaded from GenBank, to discard possible contaminations or misidentifications/mislabelings. Our analytical approaches for phylogenetic reconstruction, namely the scaffolding approach (GCG, 2016a) and twofold constraint procedure starting with a phylogenomic (Hyb-Seq) backbone tree (Villaverde et al., in review), proved successful in overcoming the problems posed by the large amount of missing data in our dataset (60% and 41% in the multiple tips and singletons matrices, respectively) and yielded relationships largely in agreement with previous studies (e.g. GCG, 2016a) for our greatly expanded species sampling. While three gene regions are certainly insufficient to resolve many of the relationships in the genus, our twice-constrained approach ensures that the deeper relationships are driven by the HybSeq nuclear topology, while the species relationships towards the tips are primarily given by the three barcode DNA regions (ETS, ITS, and *matK*), where they provide the best resolution. While the large amount of missing data in our matrices may imply that we could be misrepresenting some of the shallowest species-level phylogenetic relationships, remarkably we were able to retrieve a mostly highly supported topology based on only three DNA regions (ETS, ITS, and *matK*), with clade supports above 80%BS and 90%SH for most internal nodes in both, the singleton trees (Data S4–S5) and

the multiple tips query tree (Data S3). That said, broader sampling of loci will be necessary to recover a better-supported species tree that accounts for among-gene incongruence that we cannot resolve with only the aforementioned nrDNA and cpDNA loci.

Our dating strategy took advantage of the recent assessment of the rich *Carex* fossil record (Table 1; Jiménez-Mejías et al., 2016b) and compared various analytical approaches to explore the sensitivity of our age estimates to alternative topologies and calibration schemes. Estimated ages using ten fossils as calibration points were considerably older than using only three fossils (Table 2). This agrees with other studies exploring the effect of the number, quality and age of calibration points on divergence estimates (Tripp & McDade, 2014; Sauquet et al., 2012; Saladin et al., 2017) and advocates for the use of as many reliable fossil calibrations as possible (Hug & Roger, 2007), especially on deeper nodes (Mello & Schrago, 2014). Estimated divergence times are generally older than those obtained in previous studies dating *Carex* (Escudero et al., 2012; Spalink et al., 2016b; Lévillé-Bourret et al., 2018; Márquez-Corro et al., 2019; Uzma et al., 2019), which relied on a limited sampling of the genus and/or used few reliable primary calibration points (Table 2). As an exception, the use of a controversial *Carex* fossil from the Early Paleocene (*C. tsagajonica* Krassilov) to constrain the stem node of *Carex* yielded a slightly older *Carex* crown age (mean 42.19 Mya) in Escudero et al. (2012) relative to our estimates. However, significant questions regarding the identity of this fossil have been raised by Jiménez-Mejías et al. (2016b), so we discarded it and used *C. colwellensis* (Table 1) from the Late Eocene as the oldest reliable *Carex* fossil available to constrain the crown node of *Carex*.

4.2. The early biogeographic history of *Carex*

All biogeographic reconstructions clearly inferred E Asia as the unambiguous ancestral area not only for the whole genus but also for most of its main lineages. Exceptions include subg. *Psyllophora* and subg. *Uncinia*, which arose in the W Palearctic and America respectively (Fig. 2A). The E Asian origin of *Carex* has been proposed since the discovery that subg. *Siderosticta*, formed exclusively of E Asian species, is sister to the rest of the genus (Waterway et al., 2009; Starr et al., 2015). The subsequent discovery of tribe Sumatrosclirpeae, another SE Asian lineage, as sister to *Carex* (Léveillé-Bourret et al., 2018a, b; Semmouri et al., 2019), reinforced this hypothesis. However, the early biogeographic history of *Carex* has only been tested with a limited sampling and within a broader study focused on all Cyperaceae (Spalink et al., 2016b). Our study lends extensive support to the general “out-of-Asia” biogeographic pattern previously suggested for *Carex*. Given that our main sampling gaps in *Carex* also corresponds to E Asian species (see above), an increased sampling in E Asia will probably reinforce both the diversification origin area and main species diversity center of the genus. Additional sampling in E Asia may of course also reveal additional reversions to Asia from other regions. Thus, E Asia could be considered not only the “cradle” of the early diversified lineages, but also a “museum” (Moreau & Bell, 2013) of *Carex* species, as inferred in other important plant groups with high diversity of extant species (Dupin et al., 2016; Echeverría-Londoño et al., 2018; Huang et al., 2019).

However, our results should still be interpreted carefully given that ancestral area estimation can be strongly biased in the presence of variation in extinction rates between different geographic areas. When this occurs, areas with the lowest extinction rate are

often mistakenly inferred as ancestral even when they are not (Sanmartín & Meseguer, 2016). Eastern Asia is the region of the Northern Hemisphere that has been least impacted by both Pleistocene glaciations and previous Cenozoic climatic changes (Milne & Abbott, 2002; Manchester et al., 2009). It is thus likely that extinction rates have been lower in Eastern Asia compared to other Northern hemisphere areas over most of the evolutionary history of *Carex*, and this could bias ancestral area estimation in a way that cannot be solved with additional taxonomic sampling. Future studies will need to examine the potential role that unequal extinction rates could have played in the diversification and geographic partitioning of *Carex* diversity across the Northern Hemisphere.

Subsequent to its split from its sister group *Sumatrosclirpus*, the earliest lineages of *Carex* persisted exclusively in E Asia for more than 10 million years, before diversification in the Late Eocene (*Carex* stem and crown nodes: 37.2-39.8 Mya; Fig. 2A; Table 2) and the mostly simultaneous diversification of the main lineages in the Late Oligocene (crown nodes: 22.9–25.2 Mya; Table 2). However, the use of the *C. colwellensis* fossil constraint seems to pose a conflict with respect to our dated biogeographic inferences, since it is reported from the late Eocene (38.0–33.9 Mya) in England (Chandler, 1963). Its age would therefore predate any of our inferred colonization events to the W Palearctic which did not take place at least until the origin of subg. *Psyllophora* in the late Oligocene (24.4 Mya). This could either indicate migration out of E Asia of ancient *Carex* lineages that are now extinct, or that E Asian endemic lineages were formerly more widespread in Eurasia, and have now become extinct in the W Palearctic but survived in E Asia. Such an inference would mirror the history of other

Cyperaceae groups present in the fossil record of Europe but now entirely absent from the continent (e.g. Mapanioideae, Smith et al., 2009; *Dulichium* Pers., May & Walther, 1998), and also argues for a careful interpretation of our inferred biogeographic history. Another hypothesis that must be considered with caution is that the age of *Carex* may be much older than *C. colwellensis*, and in that case, we would be underestimating the age of the genus. This idea is plausible given that Asia, the inferred origin of *Carex*, has less fossil records in general because of the smaller number of palaeobiological studies focused in this area (see Jiménez-Mejías et al., 2016b).

One of the most interesting discoveries of this work is the near-simultaneous diversification detected in the main *Carex* lineages (i.e. subg. *Carex*, *Euthyceras*, *Siderosticta*, and *Vignea*; crown nodes: 23.1–25.2 Mya; Table 2) in E Asia during the late Oligocene (Chattian; 28.1–23.03 Mya) and their subsequent expansion (Figs. S1–S2), which constitute a remarkable example of biogeographic congruence for extant species groups (shared geographic and temporal scenario; Vargas et al., 2014). While this near-simultaneous diversification of the clades that gave rise to the world's *Carex* diversity has not previously been noted, this major diversification of *Carex* has been attributed both to global cooling from the late Eocene to the Miocene, as well as a shift in the mode of chromosome evolution (Escudero et al., 2012; Márquez-Corro et al., 2019). Such combinations of abiotic and biotic drivers are increasingly found implicated in key angiosperm diversifications (Bouchenak-Khelladi et al., 2015; Fernández-Mazuecos et al., 2018; Otero et al., 2019).

Two contrasting patterns are detected in the largely Southern Hemisphere radiations of subg. *Psyllophora* and subg. *Uncinia*. On one hand, the South American origin of sect. *Uncinia* (Figs. S1-S2) and its increased diversification rate (Fig 3A; Table 4) suggest a joint effect of the colonization of the Neotropic via long-distance dispersal (LDD; Uribe-Convers & Tank, 2015) together with a potential key innovation, the presence of a hooked rachilla, one of the only two unequivocal epizoochoric syndrome known in the genus (see Villaverde et al., 2017a; the other being the hooked utricle beaks of *C. collinsii*, Reznicek, pers. obs.). On the other hand, subgenus *Psyllophora* has been found to be of W Palearctic origin (Fig. 2A) with a subsequent Early Miocene (17.2 Mya) dispersal to the Southern Hemisphere (Data S6; Figs. S1-S2). The long branches and deep nodes of subg. *Psyllophora* suggest either differential extinction or low diversification rates in that group (Fig 2A; Data S6). Species of that clade lack any clear epizoochorous trait (except perhaps the short-protruding rachilla of *C. camptoglochin*). Nonetheless, this clade shows a remarkable distribution that includes disjunctions between and within Northern and Southern Hemispheres that are congruent with both Rand Flora (Mairal et al., 2017; Pokorny et al., 2015) and Gondwanan patterns (Givnish & Renner, 2004; Sanmartín & Ronquist 2004).

Congruent with the different number and diversity of species that have been reported from the different landmasses (Fig. 1B), BSM revealed a strong asymmetry in the number of inferred dispersal events between the Northern and Southern Hemispheres (Fig. 2B). The three Northern Hemisphere landmasses (E Asia, Nearctic and, to a lesser extent, W Palearctic) clearly emerge as the most important sources and destinations of colonization (Fig. 2B; Tables 3A, S1A). On the other hand, primarily Southern

Hemisphere regions (Neotropic, Afrotropic and Pacific region) are retrieved as colonization sinks (although with a much reduced numbers of colonizations inferred than for Northern Hemisphere regions), while their role as colonization sources is almost negligible (exceptions including a few colonizations inferred from the Neotropic to the Nearctic; Fig. 2B; Tables 3A, S1A). Asymmetric patterns of dispersal between different continents have been previously reported from other groups (e.g. Sanmartín et al., 2007; Dupin et al., 2016; Zuloaga et al., 2018). While animal and plant migration from the Late Miocene (c. 7 Mya) onwards is considered about 30% more frequent from South America to North America (Bacon et al., 2015), our results inferred a 5-7 times as many dispersals in the opposite direction (Fig. 2B; Tables 3A, S1A), which is congruent with the general pattern of the amphitropical American disjunctions (Simpson et al., 2017). The positive relationship between species richness in each region (Govaerts et al., 2019+; Fig. 1B) and the number of inferred dispersal events (Fig. 2B; Tables 3A, S1A) should be taken into account as it regards this asymmetric dispersal pattern (Dupin et al., 2016). In any case, the well-known faunistic turnover in South America due to the Great American Biotic Interchange (Stehli & Webb, 1985) contrasts with the relative stability of the Neotropical flora, which even migrated northwards into Central and North America as climatic conditions changed and migrations routes opened (Willis et al., 2014; Willis & Davis 2015). The colonization of boreotemperate elements into the Tropics, such as the one shown by *Carex*, has only been reported in few cases (e.g. in the Afrotropic, Escudero et al., 2009; Gehrke & Linder, 2009; Míguez et al., 2017; or the Neotropic, Uribe-Convers & Tank, 2015, Simpson et al., 2017).

The inferred timing of biogeographic events (Fig. S5) strongly suggests that multiple, recurrent LDD events better explain *Carex* biogeographic patterns than tectonic vicariance or Northern Hemisphere land-bridge hypotheses, perhaps with the exception of some relatively recent Beringian lineages (see Maguilla et al., 2018). The occurrence of dispersal events is clearly biased towards more recent times, especially to the last 10 My corresponding to the most recent 25% of the age of the genus. LDD has often been invoked to explain widely disjunct ranges in *Carex* and Cyperaceae as a whole (e.g. Escudero et al., 2009; Viljoen et al., 2013; Gebauer et al., 2015; Spalink et al., 2016b; Míguez et al., 2017; Villaverde et al., 2017a). A skewed distribution of dispersal events towards present times has also been observed in other groups in which LDD is regarded as a critical process shaping their biogeographic patterns (Tripp & McDade, 2014; Dupin et al., 2016; Ruhfel et al., 2016; Rose et al., 2018; Huang et al., 2019). With respect to the dispersal source, recurrent dispersal from E Asia is inferred not to have started until the late Oligocene-early Miocene (c. 25-20 Mya; Figs. 2A, S1-S2; Data S6), consistent with a temporal lag between the origin of the group and the diversification of its main lineages. This has been also found in other groups (Dupin et al., 2016; Zuloaga et al., 2018; Huang et al., 2019), although extinct lineages may have dispersed earlier from E Asia as noted above.

In situ cladogenetic diversification is inferred as the most important biogeographic event, accounting for about 70% of the total events inferred under both the DEC and DEC+J models (Tables 3B, S1D). This is explained by the large size of the areas coded for the biogeographical analyses (Fig. 2B) and the presence of large clades endemic to an area (Figs. 2A, S1–S2). As in other studies (Dupin et al., 2016; Berger et al., 2016;

Spalink et al., 2016a, b; Zuloaga et al., 2018), the real importance of allopatric speciation can be masked by these facts, and thus caution should be taken in interpreting our results as suggesting sympatric speciation in the strict sense is predominant in *Carex*. Biogeographic analyses focusing on particular clades and implementing a fine-scale geographic division within the wide areas considered here would probably unveil a greater role of allopatric speciation processes (i.e. founder events; Spalink et al., 2016a; Johnson et al., 2017).

4.3. Biogeographic diversity at shallow evolutionary scales

As mentioned previously, the enormous diversity in *Carex* and its worldwide distribution make it possible for the group to display almost every distribution pattern known in angiosperms (Raymond, 1951). This fact, combined with its ecological importance and ubiquity, make biogeographic insights in *Carex* relevant beyond the limits of the genus. In this epigraph, we comment on some of the most striking and less-explored aspects of *Carex* biogeography and discuss possible drivers of the observed geographical ranges. Remarkably, all of the biogeographic events discussed here transpired in the late Miocene-Pliocene, a geological epoch of marked global cooling (Gradstein et al., 2004) that probably contributed to the geographical expansion of the involved lineages.

While many shallow clades (sectional level and below) are restricted to a single area, a number are widespread (Figs. S1–S2), with members native to up to five or even all six coded areas. It is noteworthy that these widespread groups mostly belong to subg. *Carex* (e.g. *C. pseudocyperus* and allies, sects. *Ceratocystis*, *Spirostachyae* — including

Echinochlaenae — and *Phacocystis*) and, to a lesser degree subg. *Vignea* (sect. *Glareosae*) and subg. *Euthyceras* (sect. *Capituligerae*). While this may just be ascertainment bias — the probability of detecting any significant clade-level effects increases in larger clades, and subg. *Carex* and *Vignea* are by far the largest — it may also suggest a dispersal and colonization ability unique to these groups, as discussed in previous studies (Escudero et al., 2009; Jiménez-Mejías et al., 2012a; Villaverde et al., 2015b, 2017b; Maguilla et al., 2018). However, none of them display clear anemochorous or epizoochorous traits (though the bent utricle beaks in some sect. *Ceratocystis* species and the spreading utricle beak teeth in *C. pseudocyperus* and allies may play a role in animal dispersal). Such large distributions are particularly remarkable in light of the putatively non-specialized diaspore in most *Carex* groups. Different hypotheses have been proposed to explain the dispersal ability of *Carex*. One of the most widely accepted is the possible endozoochorous dispersal of the seeds by birds, but epizoochory of diaspores carried on birds' feet cannot be definitely ruled out (see discussion in Villaverde et al., 2017a). In both cases, the two kinds of animal dispersal would be facilitated by the small size of most *Carex* fruits and the wetland habitat of a majority of the species (including the six widespread groups mentioned above).

While the predominant dispersal routes between the landmasses along the Atlantic mainly involve the well-known (North) ampho-Atlantic pattern (Nearctic-W Palearctic; Hultén, 1958) and North-South relationships (Nearctic-Neotropic, and W Palearctic-Afrotropic; Fig. 2B), there is a striking crossed pattern in certain groups of species, involving dispersals between the W Palearctic and the Neotropic (e.g. sects. *Abditispicae-Pellucidae*, *C. punctata* and *C. extensa* groups in sect. *Spirostachyae*; Figs. S1–S2; Table

3A), and, almost incidentally, between the Nearctic and the Afrotropic (*C. conferta* group, perhaps also *C. pseudocyperus*; Figs. S1–S2). Phylogenetic reconstructions (i.e. Data S5) strongly support the nested position of these Neotropical and Afrotropical groups within predominantly W Palearctic and Nearctic lineages, respectively. Of these, the oldest disjunction is the one involving sects. *Abditispicae-Pellucidae*, dating back to the late Miocene (8.4 Mya), while the others are entirely placed in the Pleistocene (1.9–1.7 Mya) (Figs S1–S2). Escudero et al. (2009) previously discussed the European origin of sect. *Spirostachyae* and subsequent colonization of SE South America and the Southern Atlantic archipelago of Tristan da Cunha involving LDD. Without any known bird flyway among the involved landmasses, it seems to point to non-standard stochastic dispersal processes (Nogales et al., 2012) as the origin of these LDDs between non-adjacent landmasses. In this sense, palaeo-paths of the trade winds may help explaining this striking crossed pattern (see McGee et al., 2018).

While the vast majority of *Carex* species have a preference for cold-temperate climates, shifting to high elevations in the Tropics, a few species-rich groups dwell in tropical montane forests (e.g. sect. *Fecundae*, most species of subg. *Siderosticta*, or the Tropical African clade of sect. *Spirostachyae*). Of them, the Asian-African-American sect. *Indicae* (hereafter the ‘AAA clade’), is the only one that exhibits a pantropical distribution. In addition, the AAA clade is the most successful in terms of species diversity (c. 80) and dispersal/colonization ability. Originating in tropical E Asia, the species comprising the AAA clade dispersed to the Afrotropics at the end of the Miocene (5.64 Mya) and from there dispersed across the Atlantic to tropical America, apparently in a single Pliocene (2.65 Mya) LDD (Figs. S1–S2; Data S6).

4.4. Diversification rate shifts in the light of biogeography

The starkly different pattern of species richness and extent of distribution between the near cosmopolitan *Carex* with 2000 species and its sister group *Sumatrosclirpus* with three species that are restricted to SE Asia (Léveillé-Bourret et al., 2018a) is congruent with a positive area-richness correlation pattern and suggests that colonization out of E Asia may have facilitated the diversification in *Carex* through the occupation of novel ecological niches (Spalink et al., 2016b). A similar scenario is found within *Carex*, with the subg. *Siderosticta* being comprised by only c. 28 E Asian species, while its sister group, the rest of the genus, comprising almost 99% of all *Carex* species (>1950 spp) and subcosmopolitan. In fact, when compared to the rest of Cyperaceae, a diversification rate shift in *Carex* has been previously detected involving all the non-*Siderosticta* clade (Escudero et al., 2012; Spalink et al., 2016b). As this transition also entails a shift in the mode of chromosome evolution from predominantly polyploid (genome duplications) to predominantly agmatoploid (chromosome fission and fusion) (Escudero et al., 2012; Hipp et al., 2009), teasing apart the relative effect of chromosome evolution and ecological diversification on sedge diversity may prove difficult. That said, our analyses suggest that the success of *Carex* globally may have depended on colonization of novel geographic areas, where over and over alternative axes of niche space were available for diversification (Wellborn & Langerhans 2015).

The particular groups where diversification shifts have been detected (Table 4) seem to share certain features of sympatry and synchrony (see below) correlated with geoclimatic cooling phenomena during the Late Neogene (Late Miocene-Pliocene), as

previously found at smaller taxonomic and geographical scales (Gebauer et al., 2014; Hoffmann & Gebauer, 2016; Hoffmann et al., 2017). This could have been favored by the intrinsic cold-adapted nature of *Carex*, as suggested previously by Escudero et al. (2012). In the Northern Hemisphere, for example, diversification shifts involved primarily two kinds of radiations: predominantly Nearctic, and predominantly Circumboreal (five and four radiations respectively; Table 4; Fig. 3A). The diversification boost promoted by global cooling at the Late Miocene-Pliocene likely had greater impact on Northern Hemisphere clades simply because of the historically higher northern *Carex* diversity compared to the Southern Hemisphere.

The contrasting diversification pattern on both sides of the Atlantic, with five shifts (Table 4) located in the Nearctic, but only one centered exclusively in the W Palearctic (core sect. *Phacocystis*), demands further reasons involving historical climatic differences between the North Atlantic landmasses. These contrasting climatic patterns could date back to the closure of isthmus of Panama, which initiated with the onset of the Pleistocene glaciations (e.g. Bartoli et al., 2005). The conjoined effect of this climatic transformation, together with the mass Pleistocene extinctions in Europe (favored by the E-W orientation of mountain ranges and the Mediterranean sea, and by disappearance of temperate forest; Svenning, 2003) could help to explain not only the contrasting diversification patterns but also the remarkably different diversity levels (c. 562 species in the Nearctic vs c. 244 in the W Palearctic; Fig. 1B) between landmasses on opposite sides of the North Atlantic.

Also striking are the few diversification shifts detected in E Asia when compared to the Nearctic, despite its almost two-fold species diversity (c. 1000 species; Fig. 1B). While this may reflect the sampling bias in our study, the role of this area as a cradle for the genus, characterized by the early diversification and long-term persistence of the main *Carex* lineages (see above), may also be instrumental in this pattern. Under this scenario, the accumulation of lineages in E Asia would have progressively filled available niche spaces, preventing by competitive exclusion diversification by emerging groups (Abrams, 1983). The only two E Asian groups that experienced diversification shifts are centered in the Himalayas (core *Kobresia* and core sect. *Clandestinae*; see Dai et al., 2010), each at a different geological time (Table 4). The former genus *Kobresia* as a whole is believed to have entered the Himalayas about 20.6 Mya (Uzma et al., 2019), which agrees with the mean crown ages retrieved by our dating analyses (21.5 Mya; Data S6). That colonization predates by about 12 Mya the detected diversification shift at the Late Miocene (c. 8 Mya), a period where a major uplift of the Himalaya and neighboring mountains has been reported (Zhisheng et al., 2001) together with cooling on the Qinghai-Tibetan Plateau (Favre et al., 2015). This uplift could have created new ecological opportunities enabling the diversification of the already existing *Kobresia* lineages. Indeed, at a finer geographical scale, *Kobresia* species could have prevented the diversification of most of the numerous groups that inhabit the Himalayas by the aforementioned competitive exclusion (Uzma et al., 2019). Only core sect. *Clandestinae* species would have diversified in the Himalayas at the Plio-Pleistocene boundary, perhaps promoted by Pleistocene glaciations. In any case, given the sampling gap of E Asian species, additional diversification shifts may be detected in other Asian groups.

In the Southern Hemisphere, there are two additional shifts (Table 4) in two distantly related lineages: sect. *Uncinia*, starting in South America at the Late Miocene (10.9 Mya), later dispersing into the southeastern Pacific; and sect. *Echinochlaenae*, starting in the Pliocene (4.5 Mya) and entirely centered in New Zealand (Figs. 3A, S1-S2; Data S6). Diversification of sect. *Uncinia* in South America can be linked with the widening of the Drake and Tasmanian Passages, reinforcement of the Circumantarctic current, and the freezing of Antarctica (Cantril & Poole, 2012). There is a qualitative change around the Middle Miocene with the consolidation of the Antarctic ice sheet and disappearance of the last tundra remains there (Lewis et al., 2008), coupled with the climate cooling and changes in biota composition in the surrounding lands (Mildenhall, 1980; Iglesias et al., 2011, Pole, 2014) that might have facilitated the establishment and diversification of new cold-temperate lineages. Later, the colonization and radiation of both groups within the SE Pacific has been dated by our biogeographic reconstructions as synchronous, happening during the Late Miocene (crown nodes c. 7.5 Mya; Data S6). In the case of sect. *Uncinia*, dispersal was likely from South America whereas in sect. *Echinochlaenae*, remarkably, it has been recovered to happen from the W Palearctic (Figs. S1–S2), although the possibility of an extinct or unsampled ancestor present in an adjacent area cannot be completely excluded. These lineages could represent two remarkable evolutionary radiations (Simões et al., 2016) in New Zealand, with sect. *Echinochlaenae* (with 40 endemic species) and sect. *Uncinia* (34 endemic species; Ford, 2007; Schönberger et al., 2017) accounting for about 65% of native *Carex* species there. *Carex* is the second most species-rich angiosperm genus in New Zealand, where it also displays an extraordinary endemism rate (c. 86%; Schönberger et al., 2017). This is

especially interesting from an evolutionary and biogeographical point of view, taking into account its location in the relatively *Carex*-poor Southern Hemisphere, its insular condition and its prolonged geographic isolation for more than 50 million years (Veevers et al., 1991; Schellart et al., 2006).

4.5. Final remarks: *Carex* as a case study in how to colonize (almost) the entire planet

Our study contributes significantly to a better understanding of the worldwide macroevolutionary success of *Carex*, which should inform subsequent research on the evolution, biogeography, and ecology of this megadiverse genus. If there are a discrete suite of take-away messages from our study, we consider them to be:

- 1. East Asia is the cradle of the genus: *Carex* originated there, and its major clades diversified there synchronously.** Early diversification of subgeneric lineages took place from the Late Eocene to the Late Oligocene, although fossil evidence seems to point to an earlier expansion of now extinct lineages. Synchronous diversification of most main lineages in E Asia constitutes a remarkable example of biogeographic congruence that needs further research.
- 2. Modern distribution of *Carex* is primarily a product of recent diversification on northern landmasses.** While crown diversification transpired early in the evolution of the genus, recent speciation events produced most of the species we observe today: diversification rate shifts observed in our study (Fig. 3) affect mostly shallow lineages and are clustered around the late Miocene-Pliocene, possibly promoted by different large-scale climate cooling events that happened during the late Neogene. East Asia, the Nearctic and, to a lesser extent, the W Palearctic, predominate both as dispersal

sources and sinks, while landmasses of the Southern Hemisphere act mostly as the destination of colonizations.

3. Ecological opportunity may have played a large role in *Carex* diversification.

Asymmetric patterns of diversification among regions suggest that the availability of novel niche space after successful colonization of new territories may facilitate *Carex* diversification, as happened in the Nearctic; on the contrary, the accumulation of lineages filling the available niche spaces could have prevented emerging groups from undergoing diversification by competitive exclusion, as inferred in E Asia.

4. Long distance dispersals have played a large role in *Carex* distribution. This is particularly surprising in light of the lack of obvious LDD syndromes in the genus, except for sect. *Uncinia* and *C. collinsii*.

We have yet to understand the elusive question of why *Carex* diversity is apportioned as it is across the globe. Our work, however, provides a foundation needed for understanding patterns of biogeography and diversification in the genus, and lay a groundwork for future studies aimed at understanding what has shaped the disparate patterns of diversity we observe in *Carex*.

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7. TABLES

Table 1. Fossil calibrations used in the dating analysis. Fossil ages according to Jiménez-Mejías et al. (2016b). Placement is described according to the topology of the constrained singletons tree (Fig. 2A, Data S5). Asterisks indicate the fossil constraining deep nodes in the alternative dating approach using only three fossils.

Fossil	Age (Mya)	Placement
<i>Carex colwellensis</i> Chandler*	Eocene (Priabonian; 38.0–33.9)	Crown node of genus <i>Carex</i>
<i>Carex marchica</i> Mai*	Early Miocene (23.0–16.0)	Crown node of subg. <i>Vignea</i>
<i>Carex ungeri</i> Mai & H. Walther	Pliocene (5.3–2.6)	Crown node of sect. <i>Ammoglochin</i> (including <i>C. arenaria</i> and excluding <i>C. remota</i>)
<i>Carex klarae</i> Mai	Pliocene (5.3–2.6)	Stem node of sect. <i>Ovales</i> (excluding its sister clade containing <i>C. bonplandii</i>)
<i>Carex hartauensis</i> Mai*	Late Oligocene (Chattian, 28.1–23.0)	Crown node of subg. <i>Carex</i> (not considering the position of <i>C. bostrychostigma</i> and <i>C. dissitiflora</i>)
<i>Carex praehirta</i> Mai & Walther	Late Miocene (Messinian, 7.3–5.3)	Stem node of sect. <i>Paniceae</i> (excluding its sister clade containing <i>C. pilosa</i> and <i>C. auriculata</i>)
<i>Carex klettvicensis</i> Mai	Early Miocene (23.0–16.0)	Crown node of sect. <i>Phacocystis</i> (excluding its sister clade containing sects. <i>Fecundae</i> and <i>Limosae</i>)

<i>Carex</i> sect. <i>Rhomboidales</i>	Late Miocene (Tortonian, 11.6–7.2)	Crown node of the clade containing the vast majority of sects. <i>Rhomboidales</i> and <i>Mitratae</i>
<i>Carex plicata</i> Łańcucka- Środoniowa	Late early Miocene (Burdigalian, 20.4– 16.0)	Crown node of sect. <i>Rhynchocystis</i>
<i>Carex</i> <i>flagellata</i> C.Reid & E.M.Reid	Early Miocene (23.0– 16.0)	Crown node of sect. <i>Vesicariae-Paludosae</i> alliance clade (including <i>C. grayi</i> and <i>C. lasiocarpa</i>)

Note: Mya = Million years ago

Table 2. Crown node mean ages obtained with treePL for the main *Carex* lineages. Results from the four dating analytical approaches are shown, whether constraining or not the topology with the Hyb-Seq tree (Villaverde et al., in review), and enforcing ten vs. three fossils priors (see Table 1) as primary calibrations points. Age estimates from previous studies dating *Carex* are also given for comparison. ^aOne *Carex* (*C. tsagajanica*) fossil calibration. ^bSix Cyperaceae (1 *Carex*) fossil calibrations. ^cThree *Carex* + seven other Cyperaceae + six other Poales fossil calibrations. ^dEight Cyperaceae secondary + 3 *Carex* fossil calibrations. ^eOne *Carex* (*C. colwellensis*) fossil calibration. ^gsubg. *Uncinia* members nested within subg. *Euthyceras*.

Lineage	Crown node mean ages (Mya)								
	Constrained singlet topology – 10 fossils	Constrained singlet topology – 3 fossils	Singlet query unconstrained tree – 10 fossils	Singlet query unconstrained tree – 3 fossils	Escudérot et al. (2012) ^a	Spalinski et al. (2016) ^b	Lévesque Bourret et al. (2018) ^c	Márquez Corro et al. (2019) ^d	Uzma et al. (2019) ^e
<i>Carex</i>	37.17	34.17	37.21	34.64	42.19	33.9	31.33	34.52	-
subg. <i>Siderosticta</i>	24.64	14.86	24.79	16.81	5.8	10.8	22.10	15.45	17.2
subg. <i>Psyllophora</i>	24.41	21.17	24.91	17.37	10.36	-	18.80	14.76	19.4

subg. <i>Euthyceras</i>	23.06	17.41	29.10 ^e	19.85 ^e	-	-	18.5 5	16.6 8	24. 0
"Caricoid clade" (<i>Psyllophora</i> + <i>Euthyceras</i>)	24.50	21.17	-	-	23.0 7	14.5 7	23.6 7	21.5 5	-
subg. <i>Uncinia</i>	22.91	15.50	22.91 ^f	15.64 ^f	7.85 ^e	-	3.73 ^f	-	-
subg. <i>Vignea</i>	23.29	18.64	22.28	22.98	24.0 5	12.2 7	20.1 7	20.1 0	23. 8
subg. <i>Carex</i>	25.18	23.21	32.01	30.16	21.1 4	16.1	23.1 2	22.3 7	22. 9

Table 3. A. Summary of the number of dispersal events (and standard deviations) between the different considered regions (sources of dispersal in rows and sinks of dispersals in columns) inferred by the BSM analysis under the DEC model. Cell color indicates the range of the number of inferred dispersal events: blue, 0-5; green, 5-10; yellow, 10-30; orange, 30-50; red, >50. Note: All events correspond to anagenetic dispersal (range expansion) events. For the events inferred under the DEC+J model, see Table S1. B. Summary of the type of biogeographical events inferred with BSM under the DEC model.

A

To \ From	Nearctic	W Palearctic	E Asia	Afrotropic	Neotropic	Pacific	Total (%)
Nearctic	-	44.06 (4.15)	55.83 (5.17)	4.43 (1.18)	46.46 (2.62)	8.71 (1.71)	159.49 (37.86)
W	26.59	-	32.43	10.31	6.41	5.39	81.13

Palearctic	(3.69)		(4.13)	(1.55)	(1.84)	(1.61)	(19.26)
E Asia	49.26 (5.12)	66.97 (4.62)	-	8.37 (1.45)	5.72 (1.92)	13.93 (1.71)	144.25 (34.24)
Afrotropic	1.52 (0.67)	1.36 (0.98)	1.48 (0.85)	-	1.04 (0.83)	0.73 (0.76)	6.13 (1.46)
Neotropic	6.81 (2)	2.2 (1.45)	2.07 (1.39)	2.14 (0.89)	-	4.34 (1.3)	17.56 (4.17)
Pacific	1.58 (1.21)	1.77 (1.14)	3.81 (1.42)	1.93 (0.98)	3.64 (1.29)	-	12.73 (3.02)
Total (%)	85.76 (20.36)	116.36 (27.62)	95.62 (22.70)	27.18 (6.45)	63.27 (15.02)	33.1 (7.86)	421.29 (100)

B

Mode	Type of event	Cladogenetic/Anagenetic event	Mean (SD)	Percentage
Speciation within area	Narrow sympatry	Cladogenetic	1057 (9.21)	58.33
	Speciation subset	Cladogenetic	191.3 (10.12)	10.55
Dispersal	Founder events	Cladogenetic	0	0
	Range expansions	Anagenetic	421.3 (3.46)	23.25
Vicariance	Vicariance	Cladogenetic	142.6 (3.86)	7.87

Total		Cladogenetic	1391	76.76
		Anagenetic	421	23.23
			1812	100

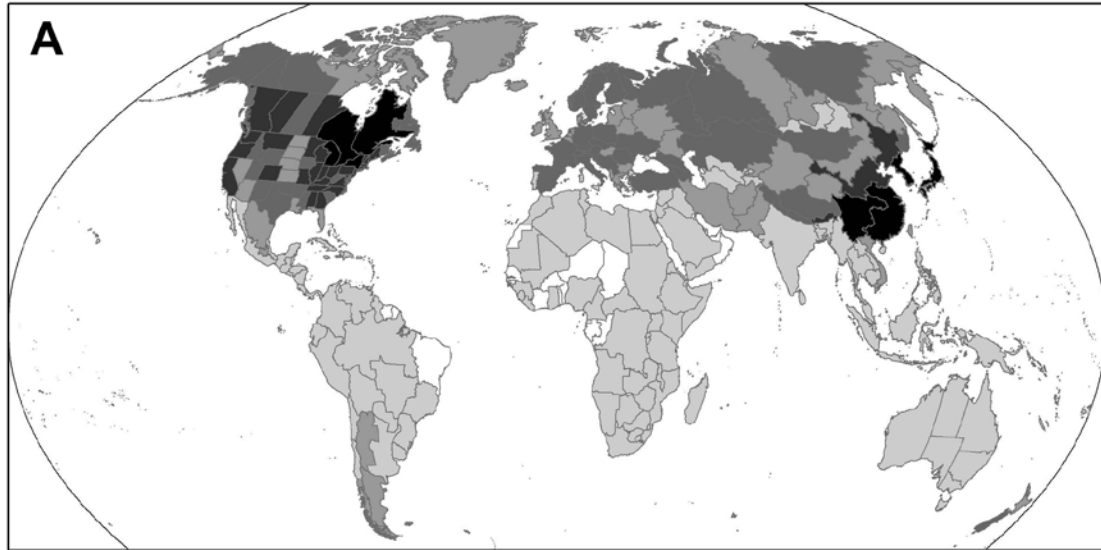
Table 4. Clades involved in the diversification shifts detected by BAMM analysis, with their distribution, and mean age of crown node according to the constrained singletons tree calibrated with the 10 available fossils (Data S6). Clades are presented in clock-wise order from the tree root according to Fig. 3A.

Clade	Distribution
Subg. <i>Euthyceras</i> Core <i>Kobresia</i>	E Asia (Himalayas)
Subg. <i>Uncinia</i> sect. <i>Uncinia</i> (excl. <i>C. kingii</i>)	Primarily South American and New Zealand
Subg. <i>Vignea</i> Sect. <i>Holarrhenae</i> + <i>C. maritima</i> alliance (excl. sect. <i>Chordorrhizae</i>) Sect. <i>Ovales</i> (incl. <i>C. bonplandii</i> clade) Sect. <i>Multiflorae</i> + American sects. <i>Phaestoglochin-Divisae</i> alliance	Primarily Circumboreal Almost entirely North American Primarily North American
Subg. <i>Carex</i> Core sect. <i>Clandestinae</i> American sect. <i>Acrocystis</i> clade (excl. <i>C. pilulifera</i>) Sects. <i>Paniceae-Laxiflorae-Bicolores</i> alliance (excl. <i>C.</i>	E Asia (Himalayas) Almost entirely North American Almost entirely North American

<i>olbiensis</i>)	
Sects. <i>Vesicariae-Paludosae</i> alliance (excl. <i>C. aureolensis</i> clade)	Primarily circumboreal
Sect. <i>Ceratocystis</i>	Primarily circumboreal
Sect. <i>Echinochlaenae</i> (excl. <i>C. blakei</i> clade)	New Zealand
Sect. <i>Porocystis-Hymenochlaenae-Longicaules</i> alliance (excl. <i>C. sartwelliana</i> clade)	Primarily North American
Sect. <i>Phacocystis</i> (sister to <i>C. podocarpa</i> clade)	Circumboreal, with a nested diversification rate increase in a primarily W Palearctic clade

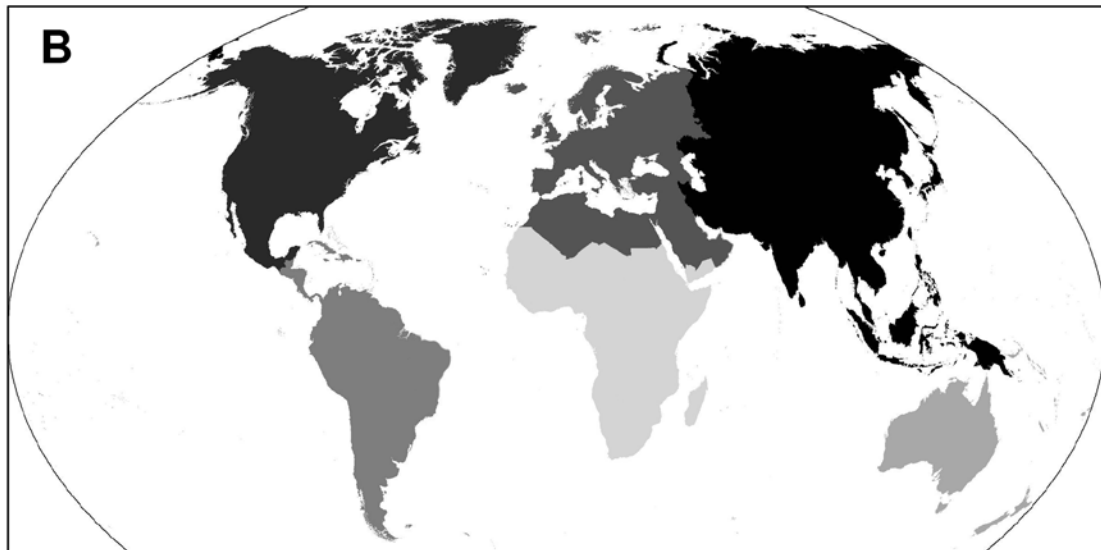
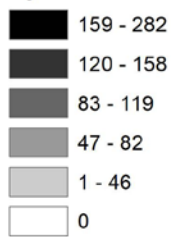
8. FIGURE LEGENDS

Fig. 1. Global diversity of *Carex* species represented according to: A. TDWG level 3 regions (“botanical countries”; Brummitt, 2001); and B. Biogeographical regions as coded in the present work. Note in Fig. 1A the much higher species diversity in cold-temperate zones of both Hemispheres (especially the Northern Hemisphere) and the much lower diversity of tropical areas.



Carex Species Count by TDWG Level 3 Region

Species Count



Carex Species Count by Biogeographical Region

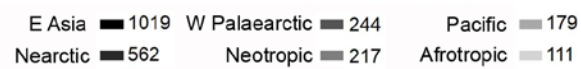


Fig. 2. A. Chronogram based on the ML constrained singletons phylogenetic tree of the genus *Carex* calibrated with 10 fossils (Data S6). Geological time scale is displayed at the top of the figure. Subgenera are presented on the vertical black bar at the right. Colored squares at nodes represent the ancestral areas as inferred by DEC model showing the most probable area or combination of areas on each node (Fig. S1; colors according to map in Fig. 2B). For branch support see Data S5. B. Map displaying the regions coded for the biogeographic analyses in different colors (dark blue: Nearctic; light blue: W Palearctic; green: E Asia; yellow: Afrotropic; red: Neotropic; lilac: Pacific). Arrows represent the dispersal events among the different regions as inferred by the BSM analyses. Arrow thickness is proportional to the number of inferred dispersal events, as shown in the legend. Connections between regions with less than five inferred dispersal events are not illustrated for clarity.

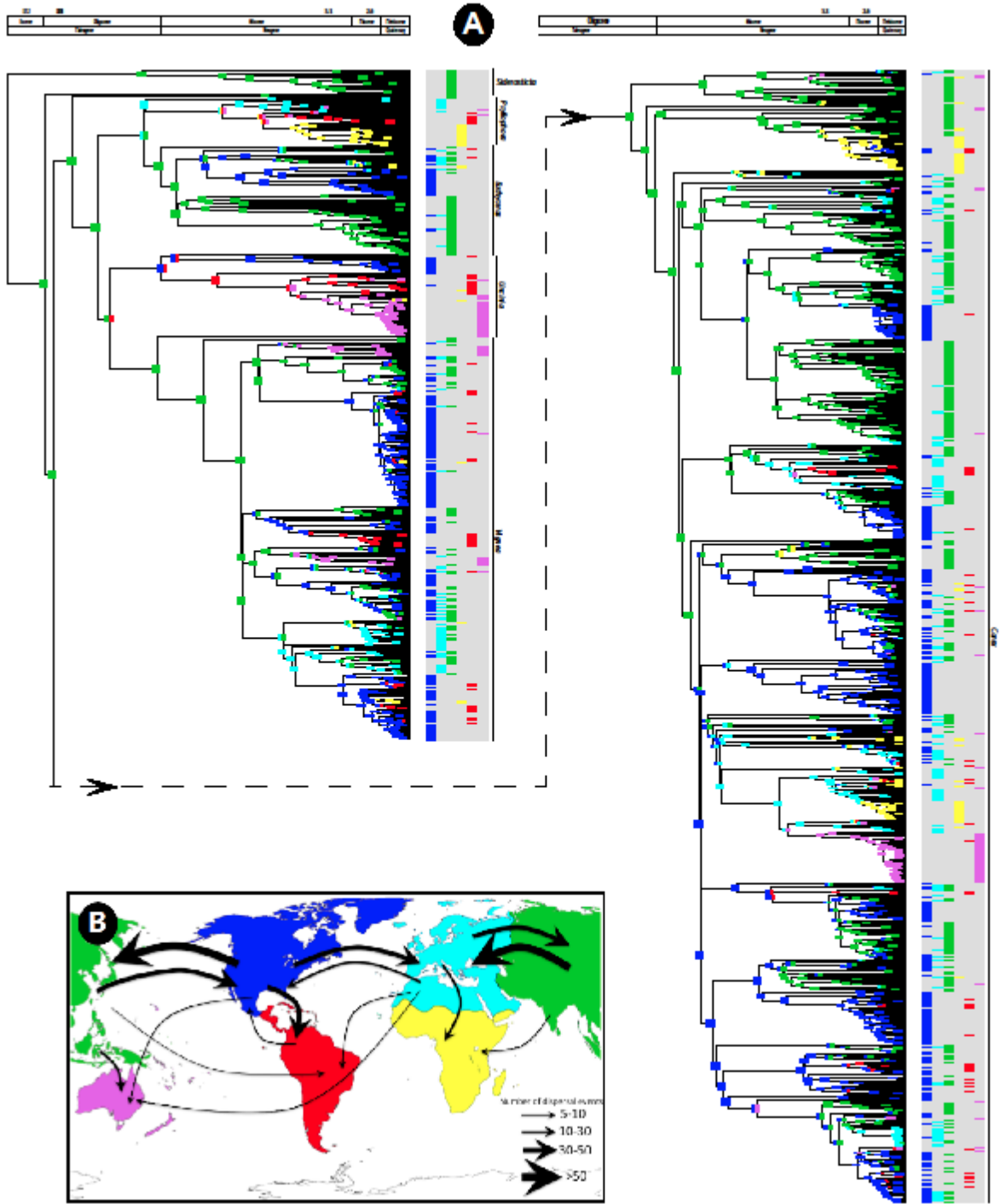


Fig. 3. A. Phylorate plot obtained from the analysis of diversification rate in *Carex* with BAMM and based on the ML constrained singletons chronogram calibrated with 10 fossils (Data S6). Tree branch color scale from dark blue (low) to dark red (high) indicates the relative net diversification rates (species per Million year; spp/My) along the branches. Thirteen diversification rate shifts to rates above 0.5 spp/My are marked in the figure using red circles. Black circles indicate fossil calibrations used in the dating analysis (Table 1): *C. colwellensis* (Col), *C. marchica* (Mar), *C. ungeri* (Ung), *C. klarae* (Kla), *C. hartauensis* (Har), *C. praehirta* (Pra), *C. klettvicensis* (Kle), *C. sect. Rhomboidales* (Rho), *C. plicata* (Pli), and *C. flagellata* (Fla). Encircling text and lines depict (from inside to outside): distribution of species at the tips (colored dots according to legend and Fig. 2B), subgenera (black arcs), and clades involved in the diversification rate shifts detected (according to Table 4). B. Net diversification rate through time plot for *Carex*. The thick red line marks mean net diversification rate, and the shaded range indicates its variance.

