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Research Article

The spatial structure of phylogenetic and functional diversity in the United States and Canada: An example using the sedge family (Cyperaceae)

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Abstract Systematically quantifying diversity across landscapes is necessary to understand how clade history and ecological heterogeneity contribute to the origin, distribution, and maintenance of biodiversity. Here, we chart the spatial structure of diversity among all species in the sedge family (Cyperaceae) throughout the USA and Canada. We first identify areas of remarkable species richness, phylogenetic diversity, and functional trait diversity, and highlight regions of conservation priority. We then test predictions about the spatial structure of this diversity based on the historical biogeography of the family. Incorporating a phylogeny, over 400 000 herbarium records, and a database of functional traits mined from online floras, we find that species richness and functional trait diversity peak in the Northeastern USA, while phylogenetic diversity peaks along the Gulf of Mexico. Floristic turnover among assemblages increases significantly with distance, but phylogenetic turnover is twice as rapid along latitudinal gradients as along longitudinal gradients. These patterns reflect the expected distribution of Cyperaceae, which originated in the tropics but radiated in temperate regions. We identify assemblages with an abundance of rare, range-restricted lineages, and assemblages composed of species generally lacking from diverse regions. We argue that both of these metrics are useful for developing targeted conservation strategies. We use the data generated here to establish future research priorities, including the testing of a series of hypotheses regarding the distribution of chromosome numbers, photosynthetic pathways, and resource partitioning in sedges.

Key words: beta-diversity, biogeography, C_4 photosynthesis, CANAPE, chromosome number, functional diversity, herbarium data, phylogenetic bet-diversity, phylogenetic diversity.

1 Introduction

Diversity is unevenly distributed around the world (Chown & Gaston, 2000; Ricklefs, 2004). This is, in part, because landscapes are climatically and geologically heterogeneous, and dispersal limitations notwithstanding (Eiserhardt et al., 2013), species have different niches that affect their success across these landscapes (Aguirre-Gutiérrez et al., 2014; Boucher et al., 2014). Uneven distribution of diversity also arises because different clades have different histories. The time, rate, location, and drivers of their diversification determine the ecological variation and number of distinct lineages that comprise them (Ricklefs & Renner, 1994; Mittelbach et al., 2007; Escudero & Hipp, 2013). Systematically quantifying diversity is important for identifying areas or lineages of conservation concern (Orme et al., 2005), testing or generating hypotheses about observed patterns of diversity (Jablonski et al., 2006), and establishing a baseline for quantifying or predicting future changes to these patterns (Dawson et al., 2011).

With ~844 species in 22 genera (Govaerts et al., 2017), Cyperaceae (Poales) is the third largest family in the flora of the USA and Canada. Sedges (here used collectively to refer to all species in the family) comprise a major component of all types of wetlands across this region (Ball et al., 2003), where

they are often dominant or co-dominant (Ball et al., 2003; Pender, 2016). They are also present in forest understories, prairies, grasslands, rocky outcrops, savannas, tundra, and to a much lesser extent, deserts (Ball et al., 2003). Many sedges are considered to be indicators of high quality habitats (Herman et al., 1997; Andreas et al., 2004; Jog et al., 2006), and reflecting their ecological dominance, many communities are classified according to the sedges contained within them (Curtis, 1959; Vince & Snow, 1984; Henry & Svoboda, 1986; Lord & Lee, 2001; Werner & Zedler, 2002; Gebauer et al., 2014). Sedges are also a significant source of food and refuge for many insects, birds, and grazers (Chamberlain, 1959; Strong, 1979; Catling et al., 1994; Dennis & Eales, 1997). Given the importance of Cyperaceae throughout the USA and Canada, understanding the roles of environmental heterogeneity, clade history, and species ecological variation in the assembly of the sedge flora should provide a useful baseline for preserving this diversity in the future.

The timing, tempo, and location of sedge diversification should influence spatial variations in diversity across the USA and Canada. The Cyperaceae originated as a tropical lineage in the late-Cretaceous (Spalink et al., 2016b) and since then has diversified globally into more than 5500 species and ~90 genera (Govaerts et al., 2017). At least two independent rapid radiations have occurred in temperate regions of the Northern Hemisphere (Bremer, 2002; Escudero & Hipp, 2013; Spalink et al., 2016b). As a result of the tropical origin and temperate radiation of the family, there is a clear phylogenetic pattern associated with the distribution and diversity of sedge genera around the globe, and this is evident in North America as well. The genera of the USA and Canada that have tropical or otherwise southern hemispheric origins collectively represent only about 1/3 of the total diversity in the flora (~318 species; Spalink et al., 2016a; Govaerts et al., 2017). By contrast, the remaining eight genera, which form a clade nested within the tropical genera, are the product of a major temperate Northern Hemisphere radiation (Spalink et al., 2016a). The single most diverse of these, *Carex*, comprises more than 57% of the entire sedge flora in North America (~487 species; Govaerts et al., 2017). Sedges are also the most species-rich family in the Arctic (Gebauer et al., 2014; Hoffmann & Gebauer, 2016; Spalink et al., 2016b; Hoffmann et al., 2017), but relatively few lineages have achieved the necessary adaptations to survive north of 57°N, and these are almost entirely limited to the genera *Carex* L., *Trichophorum* Pers., and *Eriophorum* L.

Given this context, phylogenetic diversity and species richness should exhibit different spatial patterns (Cavender-Bares et al., 2009; Devictor et al., 2010; Mishler et al., 2014). Phylogenetic diversity should peak where most lineages intersect (i.e., where long-branch tropical lineages meet their northern limits and short-branch temperate lineages meet their southern limits), whereas species richness should peak in the climate where most species originated. Patterns of phylogenetic turnover (phylogenetic beta-diversity) should similarly be different from patterns of species turnover (floristic beta-diversity). Because temperatures decrease with increased distance from the tropics, we would expect environmental filtering to limit the distribution of whole clades (as opposed to individual species) along latitudinal gradients (Losos, 2008). Thus, phylogenetic dissimilarity among assemblages should increase most strongly with latitudinal distance. By contrast, the floristic composition of assemblages should vary along both latitudinal and longitudinal gradients, as individual species niches and biogeographic histories should influence species distributions across climatically and geologically heterogeneous landscapes. Therefore, while floristic turnover should be a function of distance, we expect a stronger phylogenetic bias across temperature (i.e., latitudinal) gradients.

The functional correlates of sedge evolution, as they relate to ecological tolerances, should also influence patterns of sedge diversity. For example, the C_4 photosynthetic pathway has at least six independent origins in the family (Li et al., 1999; Bruhl & Wilson, 2007; Besnard et al., 2009; Roalson et al., 2010; Larridon et al., 2013). C_4 photosynthesis offers competitive advantages in hot environments, during times of reduced atmospheric CO_2, when water is limiting, and in low-nutrient substrates (Sage et al., 2012; Christin & Osborne, 2014). We expect that temperature or possibly potential evapotranspiration (PET) may be better predictors than precipitation of the geographic structure of C_4 sedges in North America, as these would better reflect water stress than precipitation alone (Ehleringer et al., 1997).

The holocentric chromosomes in the genus *Carex* are another trait that may affect the distribution of sedges in the USA and Canada. This is a rare syndrome where centromeres are diffusely distributed across the length of the chromosomes. In the genus *Carex*, genome sizes and chromosome numbers evolve independently (Hipp et al., 2007; Chung et al., 2010, 2012; Lipnerova et al., 2012; Escudero et al., 2015), as these diffuse centromeres allow small chromosomal fragments to be inherited through meiosis (Hipp et al., 2009). High chromosome numbers in *Carex* resulting from this process (agmatoploidy), are linked to elevated rates of recombination (Escudero et al., 2012a, 2012b; Escudero et al., 2013), which could have implications for the geographic structure of chromosome numbers in *Carex* species of the USA and Canada. Low recombination rates could be advantageous, for example, in climatically unstable communities where competition is low, and where maximizing fecundity by reducing potentially maladaptive genotypes would be more important than maximizing occupancy of niche space through evolutionary innovation (Escudero et al., 2013). By contrast, the risks of high recombination rates may be outweighed in climatically more stable, highly competitive environments where evolutionary innovation through novel allelic combinations could result in overall improved fitness (Escudero et al., 2013). If this is the case, we might expect to see lower chromosome numbers in climatically unstable regions where competition is low, for example in insolated habitats with dry soils that exhibit high seasonality, low temperatures, and low precipitation (Bell, 1982; Burt, 2000; Escudero et al., 2012a, 2012b; Escudero et al., 2013).

In this study, we provide a systematic overview of sedge diversity across the USA and Canada. Our objectives are threefold. First, we highlight areas of remarkable species richness, phylogenetic and functional diversity, and of conservation concern. Second, we test the following predictions about the spatial structure of this diversity based on the background provided above: (i) Given that most sedge species occur in wetlands and that Arctic habitats are generally species

depauperate, species richness should increase with both temperature and precipitation; (ii) Phylogenetic diversity should peak in the subtropical USA, where the merger of temperate and tropical lineages is likely to be most concentrated; (iii) Phylogenetic turnover should increase more strongly with distance along latitudinal than longitudinal gradients, but floristic turnover should increase approximately equally along both gradients; (iv) Occurrences of C_4 photosynthesis should be higher in regions with high potential evapotranspiration; (v) Chromosome numbers in *Carex* should be lower in regions with low temperature and precipitation and high seasonality. Finally, given the patterns we observe through the integration of phylogenetic, functional, and distribution data, we develop a series of future research priorities pertaining to the diversification and assembly of sedges across the USA and Canada.

2 Material and Methods

2.1 Geographic context

The USA and Canada collectively cover over 19 million km^2 of the North American continent, and as such, they exhibit large temperature and precipitation gradients that may be expected to influence patterns of sedge assembly. Mean annual temperatures across this region range from −25 °C to 25 °C, and with the exception of the southern Alaskan coast, all areas north of ~57°N have mean annual temperatures below 0 °C. (Figs. S1A, S1B; Fick & Hijmans, 2017). Spatial variation in mean annual precipitation is more complex, with the northwestern coast receiving over 5400 mm per year and the southwestern US deserts receiving as little as 40 mm per year (Fig. S1C; Fick & Hijmans, 2017). In integrating measures of precipitation and potential evapotranspiration, the Pacific Northwest and eastern half of the USA and Canada are generally classified as having a surplus of water, while the remainder of the region is generally classified as dry (Fig. S1D; Willmott & Feddema, 1992; Title & Bemmels, 2017).

2.2 Phylogenetic data

We combined two previously published datasets for phylogenetic analysis. First, we used the supermatrix dataset from Spalink et al. (2016a), which contained about 74% of the native sedges of the USA and Canada. This supermatrix was based on a core dataset of four chloroplast DNA gene regions (*matK, ndhF, rbcL*, and *trnLF*) and two nuclear ribosomal regions (ITS and ETS). Here, we added to this dataset new *Carex* sequences published by the Global *Carex* Group (2016), which included the gene regions *matK*, ITS, and ETS for over 98% of the native North American *Carex*. After removing duplicate sequences and non-native taxa, the dataset contained 697 taxa and was aligned using MUSCLE (Edgar, 2004). In cases where we had two sequences of the same gene for the same taxon, we retained the sequences from the Global *Carex* Group, whose specimen identifications have been more recently vetted. After alignment, we replicated the methods of Spalink et al. (2016b) for gene partitioning, phylogenetic analysis, and calibrating branch lengths to time. Briefly, we used PartitionFinder2 (Lanfear et al., 2017) to identify the best-fitting models of molecular evolution, RAxML v8.0 (Stamatakis, 2014) to construct the phylogeny, and treePL (Smith & O'Meara, 2012) to transform the phylogeny to ultrametric. To identify additional calibration points, we reviewed a recently published list of *Carex* fossils (Jiménez-Mejías et al., 2016). However, we were unable to place additional fossils in this analysis due to uncertainty in the taxonomy (Jiménez-Mejías, pers. comm.), the ages of most of these fossils, and the floristic bias in the sampling used in our datasets.

2.3 Species distribution data

We downloaded species occurrence data from several online repositories. These included all records with geographic coordinates and no documented geospatial issues from Global Biodiversity Information Facility (GBIF; gbif.org), all "research-grade" records from iNaturalist (iNaturalist.org), and all records from iDigBio (idigbio.org/portal). To supplement these datasets, we searched for additional online databases and retrieved records from a number of herbaria (see SI Materials and Methods for details). We performed a series of filtering steps to remove erroneous or questionable records following Spalink et al. (2016a, 2016b; see SI Materials and Methods for details).

2.4 Functional trait data

In order to quantify the spatial structure of functional diversity throughout the USA and Canada, we scored each species for three continuous and four categorical traits: achene length, achene width, culm height, photosynthesis type, wetness tolerance, shade tolerance, and growth form. These traits were chosen based on data availability and their potential to influence the distribution of species across heterogeneous landscapes (Pender, 2016). We are particularly interested in the utility of data gleaned from online floras and databases for measuring functional diversity. Because such resources lack a common editorship, we emphasize that some caution is needed in interpreting the results. The traits selected for these analyses, however, have large coverage across taxa, suggesting that they are important for the identification or ecology of species and that there is agreement amongst authors about their definitions. We were able to code most of these traits by parsing species descriptions from the online Flora of North America (FNA; Ball et al., 2003). For achene size and culm height, we took the midpoint of size ranges provided in the text. For shade tolerance, we coded species as intolerant (occurring only in open areas), shade obligate (occurring only in forest understories), or partially shade tolerant (occurring along forest edges, or present in both closed and open canopy habitats).

We parsed growth form into three categories: (i) densely cespitose or tussock-forming; (ii) rhizomatous using a "phalanx" strategy, where species produce short rhizomes and individuals occupy a relatively closed space, allowing them to capitalize on nutrient-rich areas; and (iii) rhizomatous using a "guerrilla" strategy, where species produce rhizomes that spread out widely and capture nutrients from different localities (Ye et al., 2006). In some cases, distinguishing between the latter two categories is challenging, and in some species the trait is situationally labile (Chen et al., 2011). In these cases, we categorized species according to their most common growth form based on our field experience. We also used a second, simpler classification system for this trait, categorizing species as either cespitose or rhizomatous.

We performed a literature survey to classify species as either C_3 or C_4 (Ueno & Takeda, 1992; Li et al., 1999; Stock et al., 2004; Bruhl & Wilson, 2007; Besnard et al., 2009; Larridon et al., 2013).

We used the USDA PLANTS database (plants.usda.gov) to parse species into five ordinal wetness categories: obligate wetland (5; nearly always in wetlands), facultative wetland (4; usually in wetlands), facultative (3; equally in wetlands or other habitats), facultative upland (2; usually not in wetlands), and obligate upland (1; almost never in wetlands). As unique wetness values are assigned to species in each of the USDA Region and Subregion categories, we averaged the numerical scores to summarize the wetness preferences of species across their entire ranges.

We used both the FNA (Ball et al., 2003) and the Chromosome Counts Database v1.45 (ccdb.tau.ac.il; Rice et al., 2015) to identify the number of chromosomes in each species of *Carex*. We took midpoint values in instances where more than one value was reported for a species. We omitted outliers from the Chromosome Counts Database when these records were not associated with a voucher specimen. We also omitted all records published by Löve and Löve, as the integrity of these records have been questioned in some cases (Elven et al., 2011).

2.5 Bioclimatic data

To relate species richness, phylogenetic diversity, and functional diversity to geographic patterns of climate, we downloaded climate raster data from WorldClim version 2 (Hijmans et al., 2005; Fick & Hijmans, 2017) and the Environmental Rasters for Ecological Modeling dataset (ENVIREM, envirem.github.io; Title & Bemmels, 2017). From these datasets, we downloaded the six rasters that were most closely related to the stated hypotheses. From WorldClim, these included mean annual temperature (BIO1), temperature seasonality (BIO4), mean annual precipitation (BIO12), and precipitation seasonality (BIO15). From ENVIREM, we downloaded potential evapotranspiration (PET) and PET seasonality. All rasters were downloaded at 2.5 min resolution.

2.6 Defining assemblages

We arranged a grid of $2^\circ \times 2^\circ$ cells over a shapefile of the USA and Canada and quantified diversity within each cell. The position of the cells is arbitrary, and not defined by any political or natural borders. We explored the use of smaller and larger cells, but found $2^\circ \times 2^\circ$ to be large enough to account for missing data and collection biases, but small enough to continue to depict meaningful spatial patterns that would be lost at a coarser resolution. We use the term "assemblage" to simply refer to the species pool present within the cells, not to refer to species that are necessarily co-occurring within a more traditionally defined community. Accordingly, we make no claims about the ecological dynamics of the species within the assemblages and only analyze the structure of diversity among assemblages. To avoid underestimating diversity in "sliver" polygons, which were formed when the $2^\circ \times 2^\circ$ cells only partially overlaid land, we removed assemblages that were less than 20% of the average assemblage size. We characterized the climate in each of these assemblages by overlaying climate rasters onto the $2^\circ \times 2^\circ$ matrix. For each climate variable, we calculated the mean of all raster cells that were contained within each of the assemblages.

2.7 Species richness

To calculate species richness, we overlaid the species distribution data onto the assemblages and scored the number of species present within each. Because cell sizes become smaller with increased distance from the equator, we weighted the observed species richness by the size of the cell relative to the average cell size. We tested whether observed patterns of species richness were a spatial artifact (e.g., reflecting the mid-domain effect; Colwell et al., 2004) or varied from what would be expected if there were no ecological constraints on species distributions. We performed a simulation of distributions by first assigning a species to a random cell and maintaining range cohesion, randomly selecting neighboring cells until the simulated range size matched the observed range size of that species. The average species richness value for each cell was then calculated from 10 000 simulated datasets. We then tested whether the observed species richness was greater or lower than random. Species distributions were simulated using the "rangemod.2d" function from the R package rangemodelR (Marathe et al., 2016).

2.8 Phylogenetic diversity

We calculated phylogenetic diversity (PD) using two metrics. We used Faith's phylogenetic diversity (FPD; Faith, 1994), which is simply the sum of the branch lengths connecting all species in an assemblage, and the mean phylogenetic distance (MPD) of those species. FPD and MPD are two of many useful measures of alpha diversity, and these were chosen specifically for their ability to capture different dimensions of the phylogenetic structure of this diversity (Webb et al., 2002; Tucker & Cadotte, 2013; Mishler et al., 2014; Tucker et al., 2016). FPD is the phylogenetic equivalent of species richness, and is sensitive to both the number and position of the species on the phylogeny (Tucker et al., 2016). MPD, however, more directly measures the phylogenetic divergence of diversity present within an assemblage. FPD can be high either because many closely related species co-occur (i.e., many short branches), or because distantly related species co-occur (i.e., several long branches). MPD on the other hand, is more sensitive to the phylogenetic breadth of the species present in an assemblage than to the number of species. Using these metrics in concert, then, is useful for characterizing the extent and phylogenetic structure of diversity at this taxonomic and geographic scale.

In addition to calculating raw FPD and MPD, we also calculated the standardized effect size (SES) of these metrics to test whether assemblages exhibited more or less PD than would be expected by chance (Webb et al., 2002; Tucker et al., 2016). For each metric, we generated a null distribution of 10 000 randomizations by shuffling the taxon labels on the phylogeny while maintaining the species richness in each cell and the range sizes of each species (Gotelli, 2000; Webb et al., 2002). We categorized assemblages as phylogenetically overdispersed when values were significantly higher than the randomized values, and phylogenetically conserved when observed values were significantly lower than randomized values at the 1% confidence level. Measures of FPD and MPD and associated randomization tests were conducted using the

"ses.pd" and "ses.mpd" functions with the "independentswap" option from the picante package (Kembel et al., 2010) in R. Definitions of "overdispersed" and "clustered" vary slightly when analyzing FPD and MPD. In the case of FPD, these terms mean that a greater or lesser total branch length was observed than expected by chance, whereas with MPD, they mean that species within assemblages are more distantly or more closely related to each other than expected by chance. In most cases, these two metrics should be related, as both total branch lengths and distances should increase with the addition of more taxa.

2.9 Functional diversity

We measured functional diversity using the functional dispersion metric of Laliberté & Legendre (2010). Functional dispersion is the average Gower distance in ordinated trait space between individual species in an assemblage and the ordination centroid (Laliberté & Legendre, 2010). Advantages of using this approach include the weighting of species by their relative abundance across all assemblages and the insensitivity to the relative species richness within assemblages (Laliberté & Legendre, 2010). We used the entire trait database to measure functional diversity, except for chromosome number, as these traits reflect both competition for resources and the partitioning of these resources across the ecologically heterogeneous landscape of the USA and Canada. We scaled all continuous traits prior to calculating functional dispersion, which was conducted using the FD package (Laliberté & Legendre, 2010) in R.

2.10 Correlates of alpha diversity

We tested for correlations among species richness, FPD, MPD, and functional diversity to determine if these metrics capture similar spatial patterns. We also tested how these measures of alpha diversity correspond to climatic heterogeneity across the USA and Canada. Thus, for every assemblage, we compared diversity to the mean annual temperature, precipitation, and seasonality of temperature and precipitation observed within the assemblage. For these comparisons, we used a modified t-test approach, based on a reduction of the degrees of freedom using Moran's index to account for spatial autocorrelation among the assemblages (Clifford et al., 1989; Dutilleul et al., 1993). The modified t-test was conducted using the "modified.ttest" function in the R package SpatialPack (Osorio & Vallejos, 2014).

2.11 Beta diversity

We calculated both floristic and phylogenetic beta diversity among assemblages. We used the Bray-Curtis dissimilarity among assemblages as our metric for floristic turnover, which is the sum of species shared among assemblages divided by the total number of species in both assemblages (Oksanen et al., 2017). For phylogenetic beta diversity (PBD), we calculated the total branch length shared among any two assemblages. We tested whether floristic and phylogenetic turnover increases with geographic distance using Mantel tests. To test the hypothesis that phylogenetic turnover should increase more sharply along latitudinal than longitudinal gradients, we separately binned assemblages according to their centroid latitudes and longitudes. We then combined the latitudinal bins and tested for correlated distances, and repeated the process for the longitudinal bins. In this way, we compared distances among assemblages with identical longitudes or latitudes, but conducted no comparisons among assemblages that differed both in their latitude and longitude. Phylogenetic beta diversity was measured using the "phylosor" function in the picante package (Kembel et al., 2010), physical distance was measured using the "spDists" function in the sp package (Bivend & Lewin-Kof, 2014), floristic beta diversity was measured using the "vegdist" function in the package vegan (Oksanen et al., 2017), and Mantel tests were conducted using the "mantel.rtest" function in the package ade4 (Dray & Dufour, 2007).

2.12 Identifying conservation priorities

We used two approaches to identify potential conservation priorities. First, we identified assemblages that have an abundance of rare lineages using the categorical analysis of neo- and paleo-endemism (CANAPE) method of Mishler et al. (2014). CANAPE involves first calculating Rosauer's phylogenetic endemism (PE; Rosauer et al., 2009) for each assemblage. PE is the sum of branch lengths in the phylogeny that occur in an assemblage, with each branch divided by the number of assemblages in which it occurs. PE values will thus be positively influenced by phylogenetic diversity and geographic uniqueness of branches. Stated another way, PE identifies assemblages that contain an abundance of geographically limited portions of the tree (Mishler et al., 2014). CANAPE then involves identifying areas where PE is higher than expected, based on a randomization where range sizes and assemblage richness are held constant. Assemblages that are identified as exhibiting an excess of rare lineages are then parsed into areas of areas of neo-endemism (i.e., overabundance of rare, short branches) and paleo-endemism (i.e., overabundance of rare, long branches). This final step is based on a randomization of relative phylogenetic endemism, or the ratio of observed PE to PE as calculated using a null phylogeny where all branch lengths are equal. Areas of neo-endemism are identified as assemblages where this ratio is significantly high, and areas of paleo-endemism are identified as assemblages where this ratio is significantly low. We also identified areas of mixed endemism (where both PE and relative PE are significantly high, but the ratio is not) and areas of super-endemism (areas of mixed endemism that were highly significant, i.e., $p < 0.01$). CANAPE was conducted using Biodiverse v1.99.007 (Laffan et al., 2010).

Aside from identifying areas with exceptional diversity and areas with an abundance of rare lineages, we also identified areas that have an abundance of species that are generally lacking from diverse sites. These species could be widespread, for example, but only occurring in areas where sedges are uncommon relative to the diversity hotspots (i.e., in Arctic habitats). These species may become vulnerable if they are not already rare, as the low diversity areas in which they occur may not be typically targeted as areas for conservation priority (Naidoo et al., 2008; Summers et al., 2012). For each species, we calculated the average FPD and species richness among the assemblages in which that species occurs. Then for each assemblage, we tabulated the number of species present that occur, on average, in assemblages where the FPD or species richness is less than the average among all assemblages.

2.13 Identifying spatial patterns of trait diversity

To examine the spatial structure of functional traits, we summarized the diversity of traits present in each assemblage. For continuous traits, we calculated the mean value of the species present within each assemblage. We parsed categorical variables according to the number of character states, and then computed the percentage of species in each assemblage that exhibited that state. For example, we calculated the percentage of shade tolerant, shade intolerant, and partially shade tolerant species in each assemblage. We mapped these traits onto the assemblages using QGIS v2.18.7 (QGIS Team, 2017). We performed modified t-tests, accounting for spatial autocorrelation, to determine whether the average culm heights and achene sizes in assemblages vary along climatic or latitudinal gradients.

We tested the hypothesis that annual PET should exert a strong influence on the distribution of C_4 species throughout the US and Canada. We tested this hypothesis from both a geographic and a species perspective. For the geographic perspective, in each assemblage we calculated the percentage of all species present that exhibit the C_4 photosynthetic pathway. We then used the modified t-test approach to test whether the proportion of C_4 species increases with annual PET and temperature, and with decreased precipitation. From the species perspective, we conducted an analysis of variance (ANOVA) to test whether C_3 and C_4 species differ in their climatic niche. For this test, we used the average climate value among all records for each species as a simple representation of species niche. To test whether differences in niche were an artifact of phylogenetic relatedness (i.e., C_4 are more ecologically similar to each other because they have a shared history), we used Garland's phylogenetic ANOVA (Garland et al., 1993), using the "phylANOVA" function in the R package phytools (Revell, 2012).

We tested the hypothesis that chromosome numbers in *Carex* should be lower in species adapted to highly seasonal habitats with low temperature, precipitation, moisture, and sunlight. Again, we tested this from geographic and species perspectives. For the geographic perspective, we calculated the mean chromosome count for all species present in each assemblage. We then used modified t-tests to assess whether assemblages in more ecologically harsh areas (i.e., colder temperatures, less precipitation, more seasonality) are composed of species with more chromosomes, on average. From the species perspective, we used a phylogenetic generalized least squares (PGLS) model to test for correlations between chromosome numbers and the temperature, precipitation, and seasonality of the species centroids. We used the "pgls" function in the R package caper (Orme et al., 2013) for these analyses, in which branch lengths were optimized under a maximum likelihood framework to account for phylogenetic signal in the traits (Freckleton et al., 2002). We used phylogenetic ANOVA to test whether chromosome numbers vary according to the shade tolerance and wetness requirements of species.

3 Results

3.1 Phylogenetic analysis

The combined datasets from Spalink et al. (2016b) and the Global Carex Group (2016) contained a total of 697 species, or about 83% of all native Cyperaceae species of the USA and Canada (Figs. 1, S2; Data S1). Missing species were generally evenly spread throughout the phylogeny, except for the genera *Cyperus* and *Rhynchospora*, which were missing 33% and 44.5% of species, respectively. The topology was largely consistent with both Spalink et al. (2016b) and the Global Carex Group (2016), with incongruences limited to nodes that were weakly supported in either analysis.

3.2 Species distribution data

We downloaded a total of 470 404 unique species occurrence records, which were filtered down to 411 159 records (Fig. S3A; Data S1). Record density was not normally distributed along either latitudinal or longitudinal gradients (Figs. S3B, S3C), with relatively few specimens collected north of 55°N (about halfway through British Colombia, Alberta, Saskatchewan, Manitoba and Quebec, and just skimming the northern edge of Ontario south of the Hudson Bay), west of 125°W (western coast of the continental USA), and between 102°W and 108°W (the Great Plains). Reduced record density in these areas largely reflects expected patterns of species richness and abundance, but may also be indicative of reduced sampling efforts in some cases. Species distribution maps are presented in Fig. S4.

3.3 Species richness

Species richness among assemblages ranged from 2 to 265 species (Fig. 2A). Four assemblages were omitted from analyses because they contained no specimen records. Two of these assemblages overlaid a contiguous section of northern Ontario, and the remaining two overlaid separate regions of Nunavut. The most diverse assemblage overlaid Long Island, NY and southern Connecticut. Overall, species diversity was highest in the northeast and northern Midwestern USA, with secondary areas of richness in the Southeast USA, California, Pacific Northwest, and the intermountain region. Areas of low species richness occurred in the desert regions of Nevada, Utah, Arizona, and Texas as well as throughout the Great Plains and throughout northern Canada. Nearly all assemblages exhibited either more or less species richness than expected by chance (Fig. 3A). Most assemblages overlaying the desert regions of Texas and Nevada, the Great Plains, and most of the high latitude regions exhibited less than random species richness. Nearly all other assemblages exhibited more species richness than random, including those in southern Alaska. Several assemblages did not differ from the null model in their species richness, and these usually geographically occurred between assemblages that exhibited more and less diversity than random.

3.4 Phylogenetic diversity

The two phylogenetic measures revealed contrasting geographic patterns of diversity. FPD ranged from 88 million years (MY) to 2427 MY (Fig. 2B). FPD closely mirrored patterns of species richness, though the highest FPD occurred in assemblages along the Gulf Coast of Alabama rather than Long Island and Connecticut. MPD ranged from 15.3 to 127 MY (Fig. 2C). Highest MPD occurred along the entire southern border of the USA, and lowest MPD occurred in Arctic assemblages.

Despite contrasting patterns of raw FPD and MPD, comparisons of observed diversity to the standardized effect

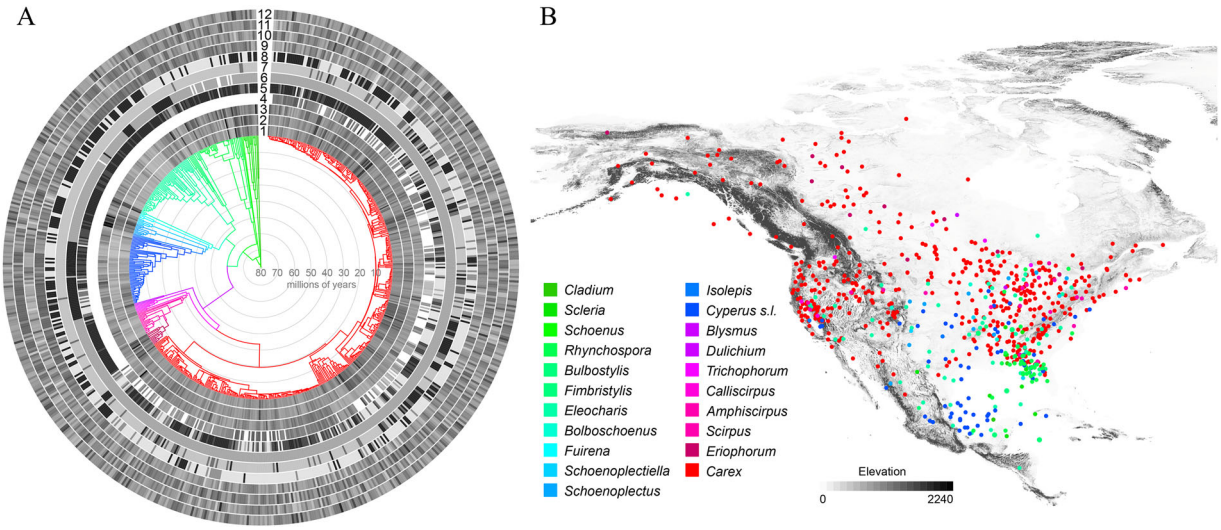

Fig. 1. Phylogeny, functional traits, and distribution of the sedge flora of the USA and Canada. **A,** Time-calibrated phylogeny, with branches color coded according to the legend. Inset time-scale is in millions of years. The twelve tracks surrounding the phylogeny indicate scaled values for functional and ecological traits. Tracks 1–4: Continuous functional traits, with increasing color intensity indicating higher values. Track 1: Achene length. Track 2: Achene width. Track 3: Culm height. Track 4: Chromosome number (*Carex* only). Track 5: Wetness tolerance. White = obligate upland; light gray = facultative upland; medium gray = facultative; dark gray = facultative wetland; black = obligate upland. Track 6: Photosynthetic pathway. White = missing data; gray = C_3; black = C_4. Track 7: Shade tolerance. Light gray = obligate open; medium gray = partially shade tolerant; black = obligate shade. Track 8: Growth form. White = densely cespitose or tussock-forming; gray = phalanx strategy; black = guerilla strategy. Track 9–12: Climatic niche characteristics, with increasing color intensity indicating higher values. Track 9: Mean annual temperature. Track 10: Mean annual precipitation. Track 11: Temperature seasonality. Track 12: Precipitation seasonality. Note that the full phylogeny, with all tips labeled, is presented as Fig. S2 and the unscaled trait values are presented in SI Table 1. **B,** Topographical map of North America depicting the centroid locations of all sedges of the USA and Canada. Dot colors correspond to genera colors in the legend. Dots in shades of green and blue, representing genera with centers of diversity in the tropics, have more southerly distributions than purple and red dots, which represent genera with temperate origins.

size of these metrics revealed a very similar spatial structure to phylogenetic clustering and overdispersion (Figs. 3B, 3C). Both metrics indicated that areas of significant phylogenetic overdispersion were geographically restricted to the southern states. With FPD, phylogenetic overdispersion occurred exclusively in cells bordering Mexico or the Gulf or Atlantic coasts (Fig. 3B), whereas overdispersion also occurred in slightly more inland regions with MPD (Fig. 3C). By contrast, phylogenetically clustered regions were far more abundant throughout the northern US and Canada. In both analyses, large portions of the northeastern and western portions of the continent exhibited phylogenetic clustering. A swath of assemblages that did not vary significantly from the null model separated the southern overdispersed assemblages from the northern clustered areas, and the eastern clustered areas from those in the west.

3.5 Functional diversity

We compiled a nearly complete functional trait dataset using primarily online resources (Figs. 1, S2; Table S1), with missing data only in the categories of photosynthetic pathway (~2.6% missing) and chromosome numbers (~43% missing from *Carex*). Functional diversity peaks in the eastern half of the USA, particularly between 35° and 40° N (Fig. 2D). The western half of the USA generally exhibits much lower functional diversity, with the deserts of New Mexico having the lowest functional diversity of the continental USA. High latitude regions of Canada and Alaska had low functional diversity. Only high latitude, low diversity assemblages had significantly high functional diversity (Fig. 3D).

3.6 Correlates of alpha diversity

Among all assemblages, modified t-tests accounting for spatial autocorrelation indicated that species richness, phylogenetic diversity, and functional diversity were all strongly correlated (Table 1). Species richness exhibited nearly identical patterns to FPD ($R = 0.97$, $p < 0.01$), and was 56% correlated to functional diversity ($p < 0.01$) and 49% correlated to MPD ($p < 0.01$; Table 1). These measures of alpha diversity were also significantly correlated to climatic variation throughout the USA and Canada. Regardless of the metric, alpha diversity increased significantly with increased temperature and precipitation and with decreased seasonality in temperature and precipitation (Table 1). Mean annual temperature was the strongest predictor of diversity, while precipitation and precipitation seasonality were the weakest (Table 1).

3.7 Beta diversity

Floristic and phylogenetic turnover increased significantly with geographic distance, though the relationship was stronger with floristic beta diversity ($r = 0.59$, $p < 0.01$) than with phylogenetic beta diversity ($r = 0.49$, $p < 0.01$). Along

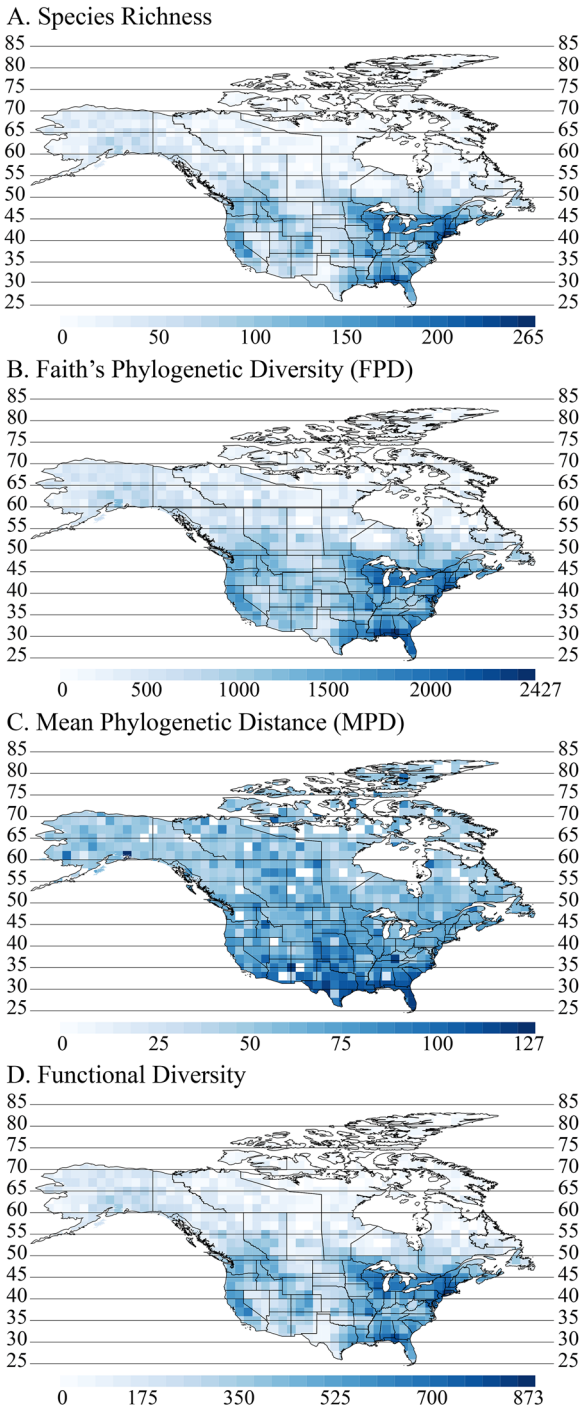

Fig. 2. Alpha diversity among assemblages throughout USA and Canada. All metrics except for mean phylogenetic distance (C) show diversity peaking in the northeastern and southeastern USA. **A,** Species richness ranged from 2 to 265 species. **B,** Faith's phylogenetic diversity, or the sum of branch lengths connecting all species contained within an assemblage. Units are in millions of years. **C,** Mean phylogenetic distance among all species contained within an assemblage. Units are in millions of years. **D,** Functional diversity.

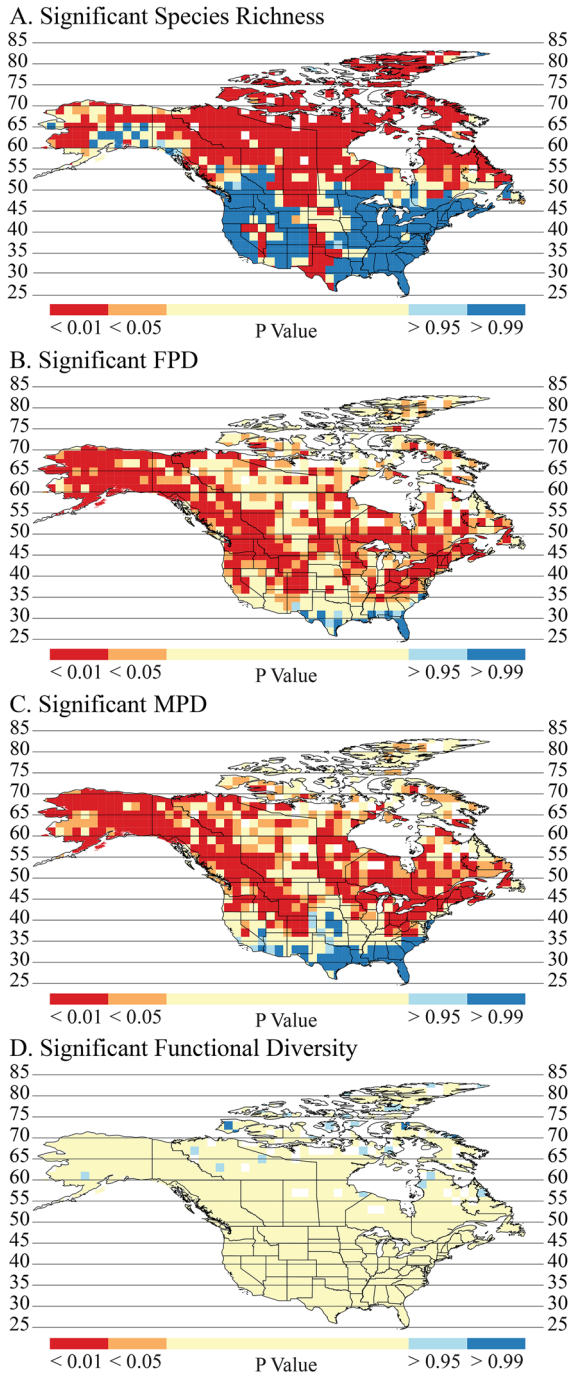

Fig. 3. Tests of significant departures from expectations of null models. **A,** Significantly high *p*-values (blue colors) indicate that greater species richness was observed than expected by chance, while significantly low *p*-values (red colors) suggest that lower species richness was observed than expected by chance. Nearly all assemblages exhibited more or less diversity than expected, indicating that the distribution of species richness is nonrandom. **B, C,** High *p*-values indicate that communities are phylogenetically overdispersed, and low *p*-values indicate that communities are phylogenetically clustered. **D,** High *p*-values indicate more functional diversity than expected by chance. FPD = Faith's phylogenetic diversity. MPD = mean phylogenetic distance.

Table 1 Results of modified *t*-tests, which include a reduction of the degrees of freedom to account for autocorrelation among spatial processes

		F	*DF*	*R*	*P*-value
Species Richness	FPD	255	17	0.97	0
Species Richness	Functional Diversity	13.6	29	0.56	0
Species Richness	MPD	241	771	0.49	0
Species Richness	Temperature	8.34	13	0.63	0.012
Species Richness	Temperature Seasonality	5.82	17	−0.51	0.027
Species Richness	Precipitation	6.27	27	0.43	0.019
Species Richness	Precipitation Seasonality	6.9	22	−0.49	0.015
FPD	Temperature	11.9	10	0.73	0.006
FPD	Temperature Seasonality	7.4	14	−0.58	0.016
FPD	Precipitation	7.4	24	0.48	0.012
FPD	Precipitation Seasonality	5.9	19.2	−0.49	0.025
MPD	Temperature	1224.4	770	0.78	0
MPD	Temperature Seasonality	428.7	768	−0.598	0
MPD	Precipitation	117.9	769	0.36	0
MPD	Precipitation Seasonality	45.3	771	−0.24	0
Functional Diversity	Temperature	8.5	17	0.58	0.01
Functional Diversity	Temperature Seasonality	3.9	24	−0.37	0.06
Functional Diversity	Precipitation	4.9	41	0.33	0.032
Functional Diversity	Precipitation Seasonality	4.1	31.6	−0.34	0.05
% C4	PET	1131	601	0.81	0
% C4	Temperature	845.7	600	0.76	0
% C4	Temperature Seasonality	213	616	−0.51	0
% C4	Precipitation	24	617	0.19	0
% C4	Precipitation Seasonality	0.89	607	0.03	0.376
# Chromosomes	PET	23.5	541	−0.2	0
# Chromosomes	Temperature	34.2	546	−0.24	0
# Chromosomes	Temperature Seasonality	1.2	547	0.05	0.27
# Chromosomes	Precipitation	75.6	561	−0.34	0
# Chromosomes	Precipitation Seasonality	26	558	0.21	0
Culm Height	Temperature	223.8	603	0.52	0
Culm Height	Temperature Seasonality	47.7	614	−0.27	0
Culm Height	Precipitation	125	619	0.41	0
Culm Height	Precipitation Seasonality	86	611	0.35	0
Culm Height	Latitude	249	600	−0.54	0
Achene Length	Temperature	70	615	−0.32	0
Achene Length	Temperature Seasonality	66	615	0.31	0
Achene Length	Precipitation	0.57	617	0.03	0.45
Achene Length	Precipitation Seasonality	11	611	−0.133	0
Achene Length	Latitude	44.5	618	0.26	0
Achene Width	Temperature	208.75	615	−0.5	0
Achene Width	Temperature Seasonality	153	614	0.45	0
Achene Width	Precipitation	4.4	624	−0.08	0.04
Achene Width	Precipitation Seasonality	0.24	610	−0.02	0.63
Achene Width	Latitude	137	617	0.43	0

The first two columns indicate the processes being compared. *F* = *F*-statistic. *DF* = reduced number of degrees of freedom, where the default value (no spatial autocorrelation) is 808. *R* = strength of correlation. FPD = Faith's phylogenetic diversity; MPD = mean phylogenetic distance; PET = potential evapotranspiration.

both latitudinal and longitudinal gradients, the relationship between floristic turnover and geographic distance was equally strong ($r = 0.68$, $p < 0.01$). However, the correlation with phylogenetic turnover was nearly twice as strong along latitudinal gradients ($r = 0.68$, $p < 0.01$) than along longitudinal gradients ($r = 0.35$, $p < 0.01$). Together, these results suggest that while the floristic composition of assemblages changes at equal rates in all directions, there is a much stronger phylogenetic bias in species turnover from the Tropic of Cancer to the Arctic than from coast to coast.

3.8 Identifying areas of potential conservation priority

In addition to highlighting assemblages with remarkable diversity as sites of conservation priority, we also identified assemblages with an overabundance of narrowly endemic lineages and species-poor assemblages that were floristically

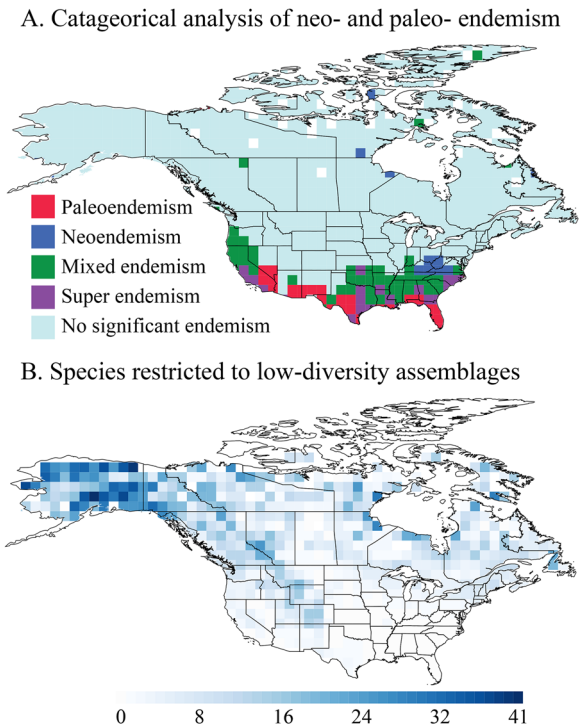

Fig. 4. Identification of areas of conservation concern. **A,** CANAPE (categorical analysis of neo- and paleo-endemism) analysis. Areas of paleo-endemism contain more, rare long-branches than expected by chance, and areas of neo-endemism contain more, rare short-branches than expected by chance. Areas of mixed endemism and super-endemism contain a both an abundance of rare long and short branches and are differentiated by significance scores ($p < 0.05$ and $p < 0.01$, respectively). **B,** The number of species in each assemblage that preferentially occur in low-diversity communities. Most of Alaska, the Rocky Mountains, and assemblages surrounding the Hudson Bay contain an abundance of these floristically unique species.

unique. Assemblages that contained more narrowly endemic lineages than expected by chance were largely restricted to the southern USA (Fig. 4A). While several assemblages scattered throughout Canada were recovered as areas of significant phylogenetic endemism, these all had very low species richness (usually only 1 or 2 species, and fewer than 10 in all cases), suggesting that their significance was likely an artifact of low diversity. Areas of paleo-endemism occurred in Florida, southern Alabama, and the desert regions of the southwestern USA. Areas of neo-endemism occurred only in the Appalachian region, from the northern half of Tennessee and North Carolina to the northern end of West Virginia, and areas of very low diversity in the Arctic. Areas of mixed endemism and super-endemism (differentiated by significance scores of 0.05 and 0.01, respectively) occurred throughout California, western Oregon, and the southeastern USA.

We identified a total of 62 species that occur most commonly in assemblages with lower than average diversity (Table S2). We used these species to identify assemblages that were floristically unique, containing species that were generally lacking from more diverse assemblages. These were most heavily concentrated in assemblages in Alaska, which contained as many as 41 of these species (Fig. 4B). Many assemblages along the Rocky Mountain range and surrounding the Hudson Bay contained 10 or more of these species. These indicator species were entirely lacking from the Southeastern US and most of the Great Plains.

3.9 Spatial patterns of functional traits

From a geographic perspective, assemblages varied according to their composition of functional traits (Fig. S5). Achenes tended to be longest in the East and North (Fig. S5A) and widest in the North (Fig. S5B). Average culm height tended to be higher in Florida and the Great Plains, and lower in the intermountain and Arctic regions (Fig. S5C). *Carex* chromosome numbers were highest in plains, deserts, the mountainous western USA, and the Arctic, and lowest in the Southeast (Fig. S5D). C_4 photosynthesis was completely lacking in assemblages north of 53°N but formed the largest proportion of the species composition in the desert, Great Plains, and southeastern regions of the US (Fig. S5E). While all assemblages had more wetland than upland species, assemblages in the North and Great Plains tended to have the highest percentage of wetland species and those in the Appalachian region had higher percentages of obligate upland species (Fig. S5F). Obligate understory species were heavily concentrated in the Midwest and Appalachian USA, with assemblages being composed of as many as 26% of species requiring shade in these regions (Fig. S5G). Partially shade-tolerant species were more evenly distributed (Fig. S5H), while shade intolerant species comprised the largest proportion of species in desert, coastal, Great Plains, and arctic assemblages (Fig. S5I). Species exhibiting a densely cespitose growth form were most abundant in the eastern USA and least abundant in deserts (Fig. S5J); species exhibiting the phalanx rhizome strategy were most abundant in the North (Fig. S5K); species exhibiting the guerrilla rhizome strategy were most abundant in the deserts and dry plains and least abundant in the eastern USA (Fig. S5L); species that were simply classified as rhizomatous (either phalanx or guerrilla) exhibited similar patterns (Fig. S5M).

On average, culm height in assemblages decreased significantly with increasing latitude and temperature seasonality and with decreasing temperature, precipitation, and precipitation seasonality ($p < 0.01$ in all cases; Table 1). Achene lengths and widths both increased with decreasing temperature and increasing temperature seasonality and latitude ($p < 0.01$ in all cases; Table 1).

The distribution of species with C_4 photosynthesis appears to be climatically constrained. Mean annual PET, temperature, temperature seasonality, and precipitation were all significant predictors of the proportion of species in assemblages that exhibit the C_4 photosynthetic pathway, based on modified t-tests (Table 1). Among these, the proportion of C_4 species in assemblages increased most strongly with annual PET ($r = 0.81$, $p < 0.01$) and temperature ($r = 0.76$, $p < 0.01$). C_4 photosynthesis was lacking entirely from assemblages with mean annual temperatures below −1.3 °C and with PET below 560 mm. While the proportion of C_4 species increased significantly with precipitation, this correlation was much weaker ($r = 0.19$, $p < 0.01$). From a species perspective, C_4 species occupy niches with significantly greater annual PET,

temperature, precipitation, and significantly less temperature and precipitation seasonality based on ANOVA ($p < 0.01$ in all cases). However, these relationships were not significant when accounting for phylogenetic relatedness ($p > 0.4$ in all cases), indicating that C_4 photosynthesis and climatic niche are phylogenetically autocorrelated.

Chromosome numbers in *Carex* similarly exhibit variation according to climate. Assemblages with lower annual PET ($r = 0.2$), colder temperatures ($r = 0.24$), less precipitation ($r = 0.34$), and more precipitation seasonality ($r = 0.21$) are composed of species with higher chromosome counts on average than those that are warmer, wetter, and less seasonal ($p < 0.01$ in all cases; Table 1). From a species perspective, however, chromosome numbers in *Carex* did not vary significantly with climatic niche when using species centroids as a proxy for temperature and precipitation preferences. All PGLS models showed insignificant correlations between chromosome number, annual temperature and precipitation, and seasonality of temperature and precipitation. However, phylogenetic ANOVA indicated that shade-requiring or shade-tolerant species have fewer chromosomes than those that are shade intolerant ($p < 0.05$; Fig. S6A). Similarly, obligate upland species have significantly fewer chromosomes than obligate wetland species ($p < 0.05$; Fig. S6B).

4 Discussion

The historical biogeography and ecological diversification of Cyperaceae is evident in the distribution of sedge diversity across the climatically heterogeneous USA and Canada. In incorporating hundreds of thousands of herbarium species and data gleaned from online databases and floras, we document the structure of diversity across this large spatial scale for the first time. Consistent with our hypotheses, we found that species richness increases with temperature and precipitation, phylogenetic diversity peaks in the southern USA, phylogenetic turnover increases most strongly along latitudinal gradients, occurrence of C_4 photosynthesis increases with PET, and chromosome numbers vary with climate.

4.1 Different measures of diversity reveal contrasting spatial patterns

Species richness among assemblages varied by over two orders of magnitude (Fig. 2A), and this diversity was not randomly distributed. High diversity is significantly linked to high annual temperature and precipitation and low seasonality in temperature and precipitation (Table 1). The relatively high moisture availability in the eastern and northwestern USA and Canada as well as in the western ranges coincides with areas of high species richness (Figs. 2, S1). Given that 67% of the species in our dataset are classified as obligate or facultative wetland organisms (Fig. S2; Table S1), it is not surprising that species richness would be low in assemblages where water is scarce. The low precipitation in deserts, and dry western plains, combined with low temperature and high seasonality in the high latitudes, therefore seem to be meaningful predictors of Cyperaceae species richness across the USA and Canada.

Patterns of species richness are strongly congruent with FPD and functional diversity ($r = 0.97$ and 0.56, respectively; Figs. 2B, 2D; Table 1). This suggests that, in most cases, areas that harbor many species also harbor many distinct lineages and are composed of species exhibiting a wide array of functional traits. These results have two implications. First, any of these metrics should be equally useful for identifying regions in North America with exceptional sedge diversity, whether the purpose is to target many species, lineages, or functional types. Second, areas considered to be more ecologically extreme, e.g., deserts and tundra, apply both phylogenetic and functional filters on the species that can become established within them. Relatively few lineages have evolved the specific functional strategies necessary to survive in these areas.

In contrast to species richness, FPD, and functional diversity, MPD is highest in the subtropical USA and decreases with increased latitude, indicating that species become more closely related to each other on average towards the Arctic (Fig. 2C). MPD can decrease either because long branch connections among species are lost (i.e., fewer distantly related species), or because the number of short branches increases (i.e., more closely related species). In the case of Cyperaceae, both of these patterns are evident. For example, 62% of the species from the genera *Cladium*, *Scleria*, *Schoenus*, and *Rhynchospora,* which collectively form a grade sister to the rest of the family (i.e., long-branch connections; Figs. 1, S2), are present in northwest Florida. However, northwest Florida contains only about 3% of *Carex* species. In comparison, Long Island, NY and southern Connecticut host only 19% of *Cladium*, *Scleria*, *Schoenus*, and *Rhynchospora,* but 36% of *Carex*. Our finding is precisely what we would expect if environmental filtering limits the distribution of these primarily tropical lineages (Webb et al., 2002) along a latitudinal gradient, particularly as it relates to decreases in temperature towards the Arctic (Table 1).

4.2 Influence of historical biogeography on spatial structure of diversity

Though FPD and MPD reveal distinct patterns regarding the distribution of lineages throughout North America (Figs. 2C, 2D), comparisons of these metrics to null models indicate that southern assemblages contain more phylogenetic diversity than expected by chance and that northern lineages contain less phylogenetic diversity than expected by chance (Figs. 3B, 3C). We have also shown that the correlation between phylogenetic turnover and latitudinal distance is nearly twice as strong as the relationship between phylogenetic turnover and longitudinal distance (Table 1), and that species richness, FPD, and functional diversity all increase with increased temperature and precipitation (Table 1). By contrast, species turnover occurs equally across both latitudinal and longitudinal gradients. These results suggest that, while the individual species composition among assemblages is constantly changing due to a combination of interacting climatic, geologic, and ecological dynamics, the environmental filtering of clades occurs primarily with increasing distance from the equator.

Previous analyses have demonstrated tropical Central and South America to be the "museum" of early Cyperaceae diversification (Spalink et al., 2016b), with migrations of individual lineages into the northern hemisphere not occurring until the Eocene (~55 mya), and the temperate radiation of *Carex* not occurring until the late Oligocene to early

Miocene (~25–20 mya) (Escudero & Hipp, 2013; Spalink et al., 2016b). By these estimates, the invasion and diversification of Cyperaceae in the temperate north is a relatively recent phenomenon. This would imply that the southernmost regions of the USA, which are classified as phylogenetically overdispersed (Figs. 3B, 3C) and show the closest climatic affinity to the tropics, should harbor the greatest diversity of lineages with centers of distribution in the tropics (Fig. 1). By comparison, the functional adaptations necessary to diversify, or invade and become established, in temperate climates have primarily been achieved only in more recent clades, and of these, relatively few have become successful in the boreal and arctic regions (Fig. 1). Glacial history also likely plays a role here, as colonization of these high latitude habitats would have been precluded until as recently as the Holocene. Our dataset indicates that 32 species have distribution centroids north of 60°N (the northern border of British Colombia, Alberta, Manitoba, and Ontario; Fig. 1). A clear phylogenetic filter is evident in these species, as they are comprised entirely of the closely related genera *Carex* and *Eriophorum*. Functional trait filters appear to be evident as well, as these species all use the C_3 photosynthetic pathway, are all shade intolerant, and are in the lowest 20th percentile of culm height and upper 37th percentile of achene size (Figs. 1, S2, S5A, S5B, S5C, S5E; Table S1). While the temperate diversification of *Carex* drives the high species richness in the mid-latitudes of North America (Fig. 2A), the short branches connecting these species (Figs. 1, S2) collectively contribute relatively little to the overall phylogenetic diversity of these regions. This historical biogeographical perspective therefore allows meaningful insight into the contrasting patterns between species richness and phylogenetic diversity and their contrasting patterns of latitudinal and longitudinal turnover.

4.3 Conservation implications

Each measure of diversity used here provides useful insight for establishing conservation priorities among sedge assemblages in North America (Cavender-Bares et al., 2009). Species richness, phylogenetic diversity, and functional diversity all vary considerably among assemblages. We have identified assemblages where each of these measures peaks (Fig. 2), that contain a significant abundance of rare lineages (Fig. 4A), and that contain an abundance of species that are generally lacking from diverse sites (Fig. 4B). Assemblages with high species richness, phylogenetic diversity, functional diversity, and lineage rarity are all clustered in the eastern and southern USA, suggesting that these regions should be a high priority for conservation efforts. To refine these results, we emphasize that areas of neo-endemism, mixed endemism, and super-endemism should perhaps take the highest priority. As mentioned, the abundance of rare, long branches in the southern areas of paleo-endemism is likely driven by the presence of a few, largely tropical genera that reach their northern limits in these regions. From a global perspective, these lineages are not rare. By comparison, areas where short branches are rare tend to contain recently diversified clades with species that are globally restricted in distribution. Given the geographic and taxonomic scope of our sampling, then, areas where rare short-branches are abundant are likely to be more globally unique than areas of paleo-endemism.

Focusing conservation efforts only on high diversity sites or sites with an abundance of rare lineages, however, would ignore 62 species (~7% of the sedge flora) that preferentially occur in low diversity regions. These species are clustered in high latitude assemblages as well as high elevation assemblages throughout the Rocky Mountains (Fig. 4B). While these assemblages are not classified as diverse by any of our metrics (Fig. 2), nor are the species that they contain narrowly distributed, we must consider the projected effects of recent and ongoing climate change on their long-term survival. Southern lineages may continue to invade more northern territories as climates continue to change (Ash et al., 2017), just as low latitude species continue to encroach into higher elevations (Odland et al., 2010). As a result, competition dynamics may become altered (Sturm et al., 2001; Pearson, 2013) and available habitat for these northern or montane lineages may become more restricted (Engler et al., 2011; Dullinger et al., 2012; Gottfried et al., 2012). Furthermore, if migration is necessary for these species to remain competitive under changing climates, high elevation and high latitude species may ultimately be at greater risk of losing potentially habitable areas altogether (Steinbauer et al., 2018).

4.4 Future research priorities

Given the remarkable diversity and ecological importance of Cyperaceae, we highlight other patterns that were uncovered in this research that merit additional study. First, the distribution of C_4 sedges in the USA and Canada is strongly correlated to temperature and PET and only weakly correlated to variations in precipitation (Table 1). This leads to a strong geographic signal (Fig. S5), where no assemblages north of 53°N contains any C_4 species and every assemblage south of 39°N has at least one C_4 species. C_4 species are also restricted to open habitats (except for *Cyperus lancastriensis* Porter, which occasionally occurs in partly shaded areas), though they occur across the entire wetness spectrum (Figs. 1, S2; Table S1).

Ehleringer et al. (1997) suggested that variations in light-use efficiency among C_3 and C_4 grasses along temperature gradients is the best explanation for the distribution of these species across North America, and that a band between 43° and 45°N latitude should be where the competitive advantage among the two photosynthetic pathways crosses over. This narrow band is consistent with the observed pattern in North American C_4 sedges, which shift from always-present to always-absent between 39° and 53° N. These ecological correlates are somewhat inconsistent with those observed among C_4 sedges in South African communities, where seasonal variations in precipitation were important predictors of C_4 abundance (Stock et al., 2004). A finer-scale partitioning of geographical and ecological space is necessary to fully examine these patterns. For example, the drivers of C_4 photosynthesis evolution in sedges may vary depending on the habitats to which the species are adapted (Christin & Osborne, 2014), as fast growth rates resulting from efficient light usage could be advantageous for species in fertile wetlands, efficient nutrient use could be advantageous in infertile wetlands, and efficient water usage could be advantageous in dry or seasonally dry habitats (Christin & Osborne, 2014).

The ecological correlates of chromosome number variation in *Carex* remain a central issue in understanding how

the genus *Carex* has accumulated over 2000 species in just over 20 million years (Spalink et al., 2016b). Chromosome numbers in *Carex* are strongly linked to recombination rates (Burt, 2000), speciation rates (Chung et al., 2012; Escudero et al., 2012a), gene flow rates (Hipp et al., 2010), and the fitness of species across landscapes (Bell, 1982; Escudero et al., 2012a, 2013). Bell (1982) found support for the hypothesis that chromosome numbers in *Carex* should be low in unstable and low competition environments, such as montane and high latitude habitats that are highly seasonal, dry, and insolated. Here, we found support for the opposite pattern: chromosome numbers were highest in assemblages with low precipitation ($r = 0.34$), low temperature ($r = 0.24$), and high precipitation seasonality ($r = 0.21$; Table 1). Further contrary to expectations (Escudero et al., 2013), chromosome numbers were significantly higher in species adapted to insolated habitats than shady habitats (Fig. S6A). Given that *Sumatroscirpus* Oteng-Yeb., the genus sister to *Carex* (Léveillé-Bourret et al., 2018), and *Carex* sect. *Siderostictae,* which is sister to all remaining *Carex* (Yano et al., 2013; Global Carex Group, 2015), occur in forests of southeastern Asia, it could be the case that elevated rates of recombination resulting from higher chromosome numbers contributed to the evolution of the novel traits necessary for survival in more extreme habitats. Also given that most sedges occur in wetlands, which tend to be insolated, the relationship between chromosome number and shade tolerance could be an artifact. These hypotheses clearly require further study, and we suggest that more nuanced investigations should occur at the species or population level and at a much higher spatial resolution (e.g., Escudero et al., 2013).

Shade tolerance has evolved in some species of *Cyperus, Scirpus, Rhynchospora, Scleria*, and *Carex*, but only *Carex* has exclusively shade-requiring species (Table S1). While most shade-tolerant species are classified as either facultative or obligate wetland species, the great majority of obligate shade species occur in dry to mesic temperate, deciduous forests (Table S1; Ball et al., 2003). This invasion of forest understories, apparently associated with low chromosome numbers (Fig. S6A), represents a significant ecological shift in *Carex* and has likely evolved multiple times. Indeed, species in *Carex* sect. *Siderostictae*, an endemic Asian clade sister to the remainder of *Carex*, occur exclusively in forest understories (Yano et al., 2013). The geographic dominance of this trait in eastern North America is not surprising, as this is the only North American region where temperate deciduous forests dominate. What remains uncertain is when, where, and how many times shade tolerance was gained and lost during the evolution of *Carex*, and whether regions such as eastern North America are areas of diversification for obligate shade lineages or represent the geographic and ecological convergence of more distantly related species.

We found that culm sizes decrease and achene sizes tend to increase with increased latitude (Table 1; Figs. S5A–S5C), with particular shifts associated with occurrence in high latitudes. Adaptation to the arctic biome appears to be a recent phenomenon in many plant lineages (Abbott & Brochmann, 2003; Liu et al., 2014), and the lineages that inhabit these areas tend to exhibit phylogenetic niche conservatism (Hawkins et al., 2013; Gebauer et al., 2014; Tkach et al., 2014). Nevertheless, a large number of sedge lineages have acquired the necessary adaptations to survive in Arctic climates, including at least 48 different *Carex* clades (Hoffmann et al., 2017) and the genera *Eriophorum* and *Trichophorum*. Decreased culm height and increased achene size may be two of these adaptations. The relationship between latitude and plant height is a well-established phenomenon across all plant families, with an average 29-fold decrease in plant height along a latitudinal gradient from the tropics to the arctic (Moles et al., 2009). Decreases in both temperature and precipitation are associated with the decline in culm height of sedges in higher latitudes ($r = 0.52$ and 0.41, respectively; $p < 0.01$; Table 1). We expect that this decrease in plant stature is likely also related to diurnal and seasonal variations in solar radiation, shorter growing and decomposition seasons leading to poorer soils and permafrost, high winds, and possibly an increased partitioning of energy resources to reproduction in some species. Within widespread species, the extent to which culm height is labile along latitudinal or climatic gradients requires investigation and could offer insight into the ability of these species to exhibit phenotypic plasticity in response to climate change.

Similarly, we found that achene size varies with latitude, with achene length and width both increasing with increased latitude ($r = 0.26$ and 0.43, respectively; $p < 0.01$; Table 1). This pattern is stronger when comparing clades containing both northern and southern species. For example, the genus *Scirpus* has a mean North American latitude of 40.5°N and a mean achene area (achene length × achene width) of 0.66 mm^2. By comparison, the genus *Eriophorum*, which forms a clade nested within *Scirpus* (Fig. S2; Léveillé-Bourret et al., 2014), has a mean latitude of 55°N and achene area of 5.26 mm^2. We hypothesize that a tradeoff between energy investment into individual seeds and the probability that they will become established on nutrient poor soils (Kidson & Westoby, 2000) is the likely explanation for this trend, not only in *Scirpus* and *Eriophorum*, but among all Cyperaceae. The extent to which seed sizes vary in relation to latitudinal or nutrient gradients within widespread species remains untested in Cyperaceae.

Finally, we found that northern and high-elevation assemblages have the highest proportion of species classified as mat-forming or turf-forming, and assemblages in the East have the highest proportion of densely cespitose and tussock forming species (Figs. S5J, S5K). Mat formation, comparable to the cushion growth form of many alpine and arctic plants (Billings, 1973), may be important for both for microclimate regulation (Cavieres et al., 2007) and for efficient nutrient capture in poor soils (Waterway et al., 2008, 2016; Hoffmann et al., 2017). By comparison, our data indicate that the cespitose habit is the most common growth form in North American sedges and occurs in open or closed-canopy habitats and in either wet or dry conditions. While the formation of tussocks may be advantageous for nutrient recycling (Waterway et al., 2008, 2016) and stability throughout varying hydroperiods (Lawrence & Zedler, 2011), the geographical signal associated with this trait may simply be incidental, i.e., the most common growth form occurring where sedges are most species rich.

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Supplementary Material

The following supplementary material is available online for this article at http://onlinelibrary.wiley.com/doi/10.1111/jse.12423/suppinfo:

Fig. S1. Heterogeneity of climate, moisture, and elevation throughout North America.

Fig. S2. Time-calibrated phylogeny of the sedge flora of the US and Canada.

Fig. S3. Distribution of herbarium records used in this study.

Fig. S4. Maps of species distributions based on herbarium records.

Fig. S5. Spatial distribution of functional traits.

Fig. S6. Boxplots showing the number of chromosomes in species of Carex according to shade and wetness preferences.

Table S1. Functional traits, centroid location, and mean climatic tolerance of sedges (Cyperaceae) of the US and Canada.

Table S2. Average species richness, phylogenetic diversity (PD), and mean phylogenetic distance (MPD) of assemblages in which each species occurs.

Data S1. Specimen coordinates of all species analyzed in this study, and phylogeny of the North American Cyperaceae. Available from the Dryad Digital Repository: http://doi.org/doi:10.5061/dryad.3d8332h.