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Source: Systematic Botany, 41(3) : 558-579

Published By: The American Society of Plant Taxonomists

URL: https://doi.org/10.1600/036364416X692514

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Systematic Botany (2016), 41(3): pp. 558–579
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DOI 10.1600/036364416X692514
Date of publication August 26, 2016

Ecological and Evolutionary Diversification within the Genus *Carex* (Cyperaceae): Consequences for Community Assembly in Subarctic Fens

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Communicating Editor: James Smith

Abstract—The concept of limiting similarity predicts that closely related taxa are less likely to co-occur than expected by chance. The degree to which the phylogenetic relatedness in plant communities is in accord with limiting similarity has been little tested at the scale where the consequences of adaptive differentiation during speciation should be most evident: the scale of neighboring, congeneric plants within a community. To quantify species co-occurrence patterns in relation to environment, we sampled sedge species, their rooting level relative to the water table, and the water pH in 2,124 0.25 m^2 quadrats distributed across 29 subarctic fens in the central Labrador Peninsula. We estimated phylogenetic relationships using four DNA regions (ETS, ITS, *matK*, *trnL-trnF*) for all species of *Carex* (42), *Eriophorum* (6), and *Trichophorum* (2) in the region, of which 21, four, and two, respectively, occurred in the sampled fens. We demonstrate that closely related species of *Carex* are less likely to co-occur than expected by chance using 1) a probabilistic method to test the significance of pairwise co-occurrence patterns of species, and 2) linear mixed modeling to relate these patterns to phylogenetic relationships and ecological tolerances along gradients of substrate pH and rooting level in relation to the water table. The results also indicate that suites of species with significant mutual pairwise co-occurrence belong to distant lineages within the Cariceae-Dulichieae-Scirpeae clade of Cyperaceae and have stabilizing niche differences. We suggest that niche differentiation during the evolution and diversification of a clade of wetland *Carex* species over the past few million years, especially during the dynamic glacial cycles of the Pleistocene, has resulted in diverse sedge communities that share space and resources in harsh northern peatland habitats.

Keywords—Coexistence theory, community phylogenetics, ecological speciation, ecophylogenetics, limiting similarity, niche differentiation.

Contemporary perspectives on the processes of plant community assembly (Mittelbach and Schemske 2015) are firmly rooted in Gleason's (1926, 1939) individualistic concept, which emphasizes that the presence and relative abundance of species in a plant community are predicated on individuals of a species having first dispersed to a site and then having successfully colonized and persisted at the site. The role of dispersal in this Gleasonian view of community assembly is currently expressed in discussions of the species pool (Ricklefs and Jenkins 2011), propagule pressure (Simberloff 2009), and neutral theory (Hubbell 2001, 2005), and the role of successful establishment in a community in the concept of environmental filtering (Götzenberger et al. 2012; Kraft et al. 2015), niche theory (Chase 2011), coexistence theory (Chesson 2000; HilleRisLambers et al. 2012), and trait-based approaches to community assembly (McGill et al. 2006; Shipley 2010). A decidedly bottom-up, Gleasonian perspective organizes all these lines of contemporary research on plant community assembly, which typically is concerned with the functional diversity within and among the species in a region that allows a subset of those species to co-occur in a particular plant community associated with certain characteristic environmental conditions.

An allied field of research, variously characterized as community phylogenetics or ecophylogenetics (Mouquet et al. 2012; Ndiribe et al. 2013; Pearse et al. 2014), has become prominent since the publication of an influential paper by Webb et al. (2002) and the increasing availability of DNA sequence data. This research respects the elements of Gleason's individualistic concept, but adopts a more top-down approach to assessing the nature of community assembly. The approach combines data on community composition and the traits of species in the community with a phylogenetic hypothesis for evolutionary relationships among those species to infer the relative importance of phylogenetic and functional constraints on community assembly (Cadotte et al. 2013). The line of inference that underpins this approach depends on the assumption that phylogenetic similarity is a good proxy for functional similarity, an assumption that has been widely applied at taxonomic levels above the genus and at large spatial scales (Vamosi et al. 2009) but that recently has come into question (reviewed in Gerhold et al. 2015). For plant communities, the community phylogenetic approach has scarcely been applied at all in what Vamosi et al. (2009) refer to as the Darwin-Hutchinson zone, the realm of direct interactions among closely related species. There are only a few studies of ecophylogenetic constraints on community assembly among species within a genus of vascular plants. The most notable are in herbaceous species of *Tetraria* (Slingsby and Verboom 2006) and among woody species in the genera *Quercus* (Cavender-Bares et al. 2004a; Cavender-Bares et al. 2004b), *Pinus*, *Ilex* (Cavender-Bares et al. 2006), and *Salix* (Savage and Cavender-Bares 2012). However, the spatial scale at which these studies have been done is larger than the scale at which biotic interactions most often occur, that is, at the neighborhood spatial scale (Stoll and Weiner 2000), where the consequences of adaptive differentiation during past speciation events should be most evident during community assembly.

Herbaceous species in *Carex* and allied genera such as *Eriophorum* and *Trichophorum* in the family Cyperaceae provide an opportunity to extend tests of evolutionary and ecological theory related to assembly of plant communities down to the scale of interactions among neighboring individuals (Elliott et al. 2016) using plots on the order of 1 m^2 or less. In this paper we employ sampling and analytic protocols congruent with the phylogenetic, spatial, and environmental scales at which the processes of community assembly actually occur in plant communities. First, we work at a spatial scale in which individual plants interact, considering

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the patterns of co-occurrence among immediate neighbors within 0.25 m^2 quadrats in subarctic fens, a well-defined and well-studied habitat that has a high level of fine-scale environmental heterogeneity within sites (Bubier 1995; Payette and Rochefort 2001; Gignac et al. 2004; Dabros and Waterway 2008; Rochefort et al. 2012). Second, we work at the phylogenetic scale of a single clade within the large and diverse family Cyperaceae, comparing a set of species from the Cariceae-Dulicheae-Scirpeae clade (Muasya et al. 2009; Léveillé-Bourret et al. 2014; Global *Carex* Group 2015) within a single geographic region, the central Labrador Peninsula in eastern Canada. Third, we assess phylogenetic relationships among the sedges using a molecular data matrix with only a single missing cell across four gene regions that include the nuclear ribosomal spacers ETS and ITS, plus both a coding gene (*matK*) and non-coding regions (*trnL* intron, *trnL-trnF* intergenic spacer) from the plastid genome, to derive a nearly completely resolved phylogenetic hypothesis for the species of interest. Fourth, we quantify water pH in the root zone of the sampled individuals and their rooting position in relation to the water table, two environmental variables known to affect the distribution of the studied sedges (Gignac et al. 2004; Dabros and Waterway 2008). Combining data on phylogeny, co-occurrence, and environmental factors affecting their distribution allows a direct test of the contribution of phylogenetic constraints during community assembly, including the means to segregate environmental and phylogenetic factors influencing species co-occurrence. We focus in particular on testing the longstanding expectation, based on the concept of limiting similarity, that the more closely related species are, the less likely they are to occur together (Violle et al. 2011). We also consider the nature of stabilizing niche differences (Chesson 2000) that allow sets of more distantly related sedges to co-occur at the neighborhood scale.

Materials and Methods

***Study Area and Sampling Strategy*—** We conducted this study in the central Labrador Peninsula near the iron-mining town of Schefferville, Quebec. This is a geologically and topographically complex region known as the Labrador Trough (Fig. 1; Conliffe 2015), from which the Wisconsinan ice retreated only about 6500 yr ago (Jansson 2003; Dyke 2004). The regional vegetation is a mosaic of plant communities ranging from dry tundra on low, windswept ridges to lichen woodland and spruce-moss forests interspersed with numerous lakes, ponds, streams, and peatlands in the intervening valleys (Waterway et al. 1984). Glacial deposits and landforms combined with heterogeneous bedrock geology create a landscape especially rich in fens, minerotrophic peatlands that grade continuously from nutrient-poor fens in more acidic areas associated with runoff from shales to relatively rich fens associated with runoff from dolomitic rocks (Payette and Rochefort 2001; Vitt 2002; Hajek et al. 2006; Rochefort et al. 2012). These numerous, topographically discrete fens with their high diversity of sedges (Cyperaceae) provide an excellent study system to explore the impact of evolutionary history on the assembly of plant communities.

The ecological data set is an expansion of the one analyzed by Dabros and Waterway (2008) to demonstrate the environmental affinities of sedges in the fens of the Schefferville region. The data matrix analyzed here includes the 21 fens sampled for that study plus an additional eight fens sampled in the following year to bring the total number of quadrats sampled to 2,124. Fen names, locations, estimated sizes, sedge species richness, the total number of quadrats sampled in each fen, along with environmental data, are given in Table 1, and the distribution of the fens on the landscape is shown in Fig. 1. The sampled fens varied in size from less than 1 hectare (10 fens) to more than 10 hectares (seven fens), with the largest being 19.6 hectares. Since environmental heterogeneity is high within these fens, we stratified fine-scale (0.25 m^2) quadrat sampling across and within the 29 fens. We sampled a series of five transects placed across the short axis of each fen, with each transect randomly located in one of five equal-sized segments spaced along the long axis. For the three smallest fens, only three transects were sampled. Deep, open pools within the fens were not considered eligible for sampling because no vascular plants were growing in them. Percent cover of each sedge species was estimated within the 0.25 m^2 quadrats, which were randomly placed within each 5 m segment along each transect using the 'ignorant man' technique (Ward 1974). The number of quadrats per transect was thus proportional to the width of the fen, resulting in more quadrats in large fens than in smaller ones. Abundance was estimated as percent cover using a modified Braun-Blanquet scale (Mueller-Dombois and Ellenberg 1974): 0 (not present), 1 (< 5%), 2 (5–25%), 3 (26–75%) and 4 (>75%). Voucher specimens to verify and document identifications were deposited in the McGill University Herbarium (MTMG). Position of the water table relative to the shoot bases of the plants (hereafter referred to as rooting level) and the pH of the water in the root zone (hereafter referred to as water pH or simply as pH) were measured in each quadrat using a calibrated pole and a portable Sentron 10489 pH meter (Welling Inc., Van der Waalspark, Netherlands), respectively. All field data were collected during midsummer (July to early August) when the water levels in the fens were stable except during and immediately after heavy rain events, when we did not do field sampling. Data on species occurrence, water pH, and rooting level are given for each of the 2,124 sampled quadrats in Supplemental Table 1, available from the Dryad Digital Repository at http://dx.doi.org/10.5061/dryad.q810f.

***DNA Extraction, Amplification, and Sequencing*—** To estimate the phylogenetic relationships among the 42 *Carex*, six *Eriophorum*, and two *Trichophorum* species in the regional species pool, we used sequences from four DNA regions: internal and external transcribed spacers of the nuclear ribosomal genes (ITS and ETS), a portion of the plastid coding gene maturase K (*matK*) often used for barcoding (Hollingsworth et al. 2009), and the plastid *trnL-trnF* region including the *trnL* intron and the *trnL-trnF* intergenic spacer (Taberlet et al. 1991). DNA was extracted from fresh samples using a modified CTAB protocol (Doyle and Doyle 1987) or from silica-dried samples of each species using a semi-automated Autogen 850 DNA extractor (Autogen, Holliston, Massachussetts) following the manufacturer's recommended protocol for plants as described in Smith and Waterway (2008). ETS, ITS and *trnL-trnF* were amplified and sequenced as described in Waterway and Starr (2007). The *matK* region was amplified and sequenced using matK-2.1 forward and matK-5 reverse primers and PCR conditions as listed in Hollingsworth (2009, appendices 2 and 3). For this study, we used 146 sequences we had previously deposited in GenBank, six additional sequences from GenBank, and we added 71 new sequences that we also deposited in GenBank (Appendix 1). For 75% of the species, all four gene regions were represented by sequences from the same individual.

***Phylogenetic Analysis*—** The DNA matrix for the regional species pool was augmented with sequences from *Dulichium arundinaceum* to serve as an outgroup. Tribe Dulicheae, represented here by the monotypic genus *Dulichium*, is sister to the rest of the Cariceae-Dulicheae-Scirpeae (CDS) clade, a major lineage of Cyperaceae that includes all three genera found in the studied fens (Muasya et al. 2009; Léveillé-Bourret et al. 2014). Three species in the *Siderostictae* clade and *C. gibba* were also added to allow us to estimate clade divergence times. The *Siderostictae* clade has been shown to be sister to all other species of *Carex* (Waterway et al. 2009; Starr et al. 2015) and the divergence date between *Siderostictae* and non-*Siderostictae* species of *Carex* was estimated by Escudero et al. (2012) based on fossil evidence. *Carex gibba* is sister to all other species of *Carex* subg. *Vignea* in all published analyses, so it was included to help establish the crown age of the *Vignea* clade.

DNA sequences were edited in ChromasPro v1.7.6 (Technelysium Pty. Ltd, Brisbane, Australia), aligned with ClustalW v2 (Larkin et al. 2007) and the alignment manually refined using Mesquite v3.02 (Maddison and Maddison 2008). The concatenated alignment file is deposited in the Dryad Digital Repository (http://dx.doi.org/10.5061/dryad.q810f). The best-fit models of molecular evolution were chosen based on the Akaike information criterion (AIC) implemented in jModelTest2 v2.1.6 using seven nucleotide substitution schemes (Guindon and Gascuel 2003; Darriba et al. 2012; Table 2).

All phylogenetic analyses were performed using the CIPRES Science Gateway v3.3 platform (Miller et al. 2010) and the cluster located in Andalusian Scientific Information Technology Center (CICA, Spain). The first phylogenetic analysis involved Bayesian phylogenetic inference as implemented in MrBayes 3.2.6 (Ronquist and Huelsenbeck 2003) consisting of two independent runs of 10 million generations of a data set partitioned by the four genes with appropriate models applied

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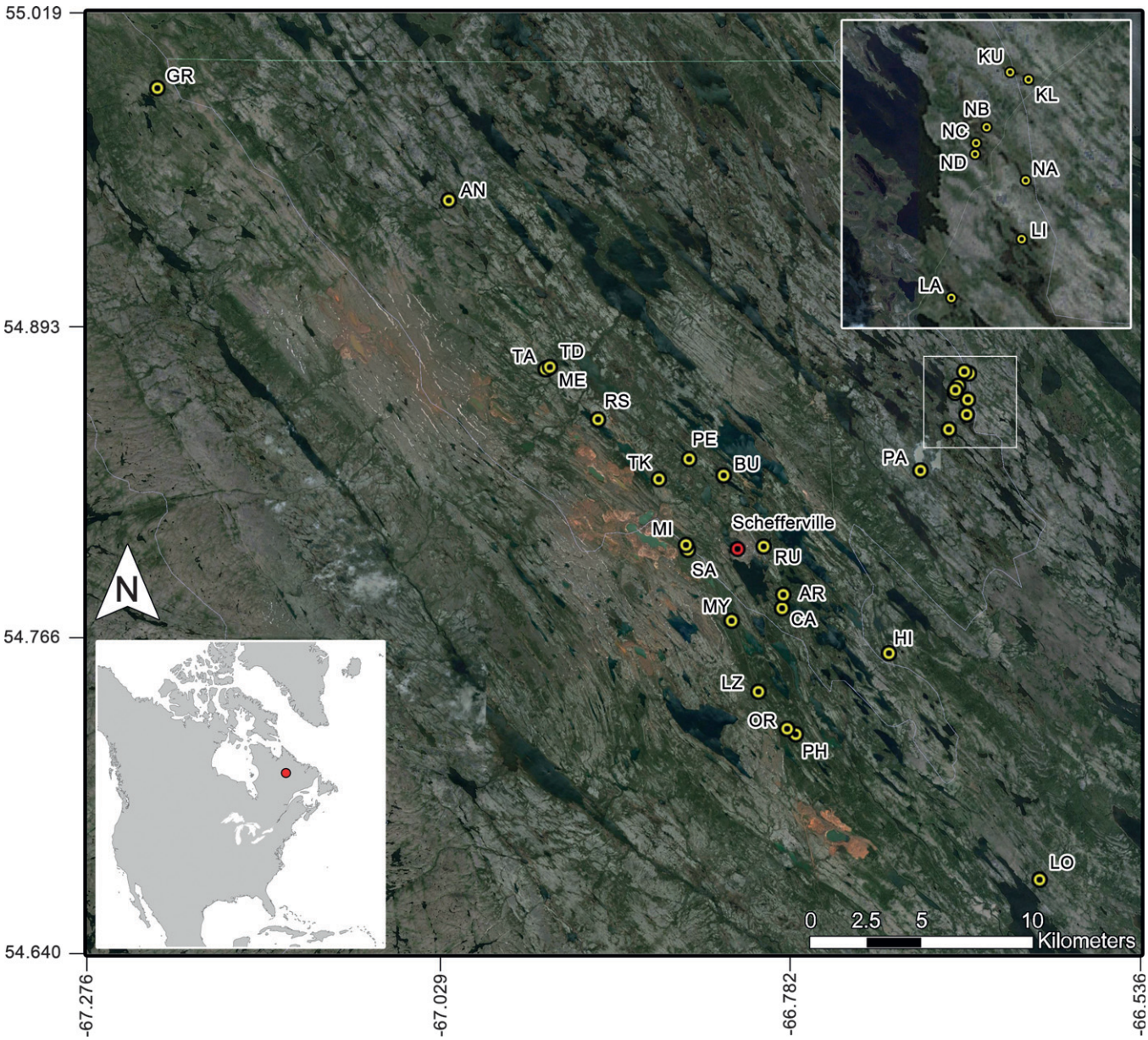


Fig. 1. Locations of fens sampled along the western edge of the Labrador Trough near the town of Schefferville, QC, in the central Labrador Peninsula. Note the many elongated and interconnected water bodies organized by the strong NW-SE orientation of the ridges and valleys. See Table 1 for full names and other detailed information about the individual fens.

independently to each partition (Table 2). A second phylogenetic analysis to estimate divergence times was performed using BEAST 2.3.0 (Drummond et al. 2012; Bouckaert et al. 2014) with an uncorrelated log-normal model of molecular evolution and a calibrated Yule model as the tree prior for 1.5×10^8 generations (Heled and Drummond 2015). Two independent calibration points with normal distribution were used to estimate the divergence times of the *Carex* phylogeny following Escudero et al. (2012): 42.2 million years ($\sigma = 6.5$) for the crown age of the genus *Carex* and 30.8 million years ($\sigma = 5$) for the crown age of the non-*Siderosticta Carex*. We assessed convergence and stationarity under Bayesian inference using the graphical analyses implemented in Tracer v1.4 (Rambaut and Drummond 2007); a total of 9,000 and 8,501 post-burn-in trees were pooled and used to generate a 50% majority-rule tree and a maximum clade credibility tree for MrBayes and BEAST results, respectively. We also tested two alternatives for calibrating the tree in BEAST, one using secondary calibration points based on the analysis of Escudero and Hipp (2013) for the root of the tree (43.6 million years, $\sigma = 4$) and for the crown age of *Carex* (32.6 million years, $\sigma = 2.9$), and another using the same secondary calibration point for the root, but using a late Eocene fossilized perigynium from *C. colwellensis* Chandler (33.9–41.3 million years), considered to be the oldest unequivocal fossil perigynium as reviewed in Smith et al. (2010) and Jiménez-Mejías and Martinetto (2013), to calibrate the crown age of *Carex* using a log-normal prior distribution with the mean of 32.7 million years placed at the origin of the crown node and the probability distribution accounting for the uncertainty.

***Phylogenetic Distance Between Species Pairs*—** All statistical analyses described here and subsequently were conducted using R version 3.2.0 (R Core Team 2015). We computed the cophenetic distances (Paradis et al. 2004) for species pairs assessed in the co-occurrence analysis in two ways: one using branch lengths calibrated in number of changes/site/time on the 50% majority-rule tree described above from the MrBayes analysis as a measure of sequence divergence (hereafter referred to as dBayes), and the other using branch lengths calibrated in years on the ultrametric tree from the BEAST analyses (hereafter referred to as dBEAST) as a measure of phylogenetic distance in years. The cophenetic metric uses branch lengths of a given phylogenetic tree to measure the distance between species pairs. Following the suggestion of Letten and Cornwell (2015), we used a square-root transformation for the dBEAST distances to avoid overweighting deep time relative to recent time. The

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TABLE 1. Location, approximate area, sample sizes, and means and standard deviations for water pH and rooting level values for fens in which quadrats were sampled. Note that # of species is an underestimate of species richness in each fen because only those found in the random quadrats are included in the total. The codes are used to show the location of each fen on Fig. 1.

Code	Fen name	# of species sampled	# of quadrats sampled	Approximate area (hectares)	Centroid of each fen Latitude (N), Longitude (W)	pH Mean	pH Std. Dev.	Rooting level (cm) Mean	Rooting level (cm) Std. Dev.
AN	Anabel	19	180	19.60	54.944226°, −67.020925°	5.85	0.906	4.2	7.36
AR	Aries	18	147	7.21	54.785088°, −66.786124°	5.68	0.736	10.4	6.82
BU	Butcher	21	137	6.42	54.833272°, −66.827832°	5.85	0.918	2.4	10.88
CA	Capricorn	22	134	11.40	54.779599°, −66.786982°	4.85	0.655	7.0	10.16
GR	Greenbush	24	106	14.91	54.988979°, −67.225699°	5.82	0.694	1.0	9.55
HI	Hilltop	11	33	0.80	54.761380°, −66.712250°	4.56	0.560	5.4	7.91
KL	Klucha	15	80	1.90	54.874294°, −66.655658°	3.99	0.436	1.8	17.31
KU	Kluska	7	58	1.67	54.875078°, −66.658948°	3.48	0.178	3.8	10.97
LA	Large	10	67	3.00	54.851714°, −66.669823°	3.40	0.155	3.6	7.09
LI	Livida	10	46	2.08	54.857691°, −66.657280°	4.74	0.536	0.1	5.36
LO	Leo	20	93	12.16	54.669671°, −66.607333°	6.74	0.734	3.6	8.64
LZ	Lazy	6	28	0.94	54.745916°, −66.803574°	5.52	0.724	8.5	7.66
ME	Menyanthes	4	15	0.33	54.876995°, −66.949716°	3.47	0.187	0.7	19.92
MI	MiniSatellite	11	17	0.25	54.805203°, −66.854224°	5.37	0.718	−17.3	30.75
MY	Myszka	15	51	1.16	54.774572°, −66.822334°	5.29	0.671	11.6	11.00
NA	Nasa 1	14	104	10.84	54.863743°, −66.656407°	5.23	0.377	1.5	9.34
NB	Nasa 2	12	93	6.93	54.869308°, −66.663273°	4.90	0.542	0.4	7.03
NC	Nasa 3	10	83	2.39	54.867652°, −66.665191°	4.74	0.534	0.8	6.11
ND	Nasa 4	10	95	5.16	54.866498°, −66.665398°	5.09	0.566	−2.6	4.58
OR	Orchid	17	98	13.10	54.730925°, −66.783522°	6.59	0.871	6.2	11.17
PA	Paupercula	11	49	0.80	54.835136°, −66.689922°	4.60	0.383	0.9	8.07
PE	Pelletier	17	77	3.84	54.839888°, −66.852012°	4.44	0.410	8.5	10.54
PH	Philemon	7	32	0.85	54.728692°, −66.777485°	4.50	0.421	−0.5	7.01
RS	Rusty	6	17	0.33	54.855843°, −66.915871°	4.15	0.285	5.2	10.77
RU	Runway	20	167	11.58	54.804554°, −66.799841°	4.63	0.537	5.4	8.08
SA	Satellite	18	52	2.52	54.803260°, −66.852906°	4.55	0.556	4.0	18.23
TA	Tadpole 1	11	20	0.65	54.876125°, −66.952644°	4.95	0.928	−1.1	16.88
TD	Tadpole 2	10	21	0.30	54.876396°, −66.951766°	3.92	0.730	1.9	10.94
TK	Teeka	8	30	0.67	54.831758°, −66.873220°	5.20	0.400	0.8	7.21

dBayes distances range between zero and one because time is incorporated in the unit of measure and can approach infinity, so transformation was not necessary.

Definition of Clade Divergence Levels—Considering the phylogenetic trees obtained for the regional species pool of Cyperaceae (Figs. 2, 3), we defined different levels of clade divergence in order to test the effect of clade divergence level (CDL) on the patterns of pairwise co-occurrence of species in the fens (see below). Pairwise comparisons between species from different genera (*Carex*, *Eriophorum*, and *Trichophorum*) in the Cariceae-Dulichieae-Scirpeae (CDS) clade of Cyperaceae were defined as level A to reflect the highest level of divergence among major sedge lineages found in the fens. These generic clades are each strongly supported as monophyletic and are easily distinguished by morphology. Levels of divergence within *Eriophorum* and within *Trichophorum* (both tribe Scirpeae) were together treated as a separate category (defined as level S to emphasize the change in lineage) from those within *Carex* because of their different levels of species diversity and hence, divergence rates among the genera. *Carex*, in its current broad sense (Global *Carex* Group 2015), has diversified into approximately 2000 extant species while *Eriophorum* and *Trichophorum* comprise only 15 and 12 species, respectively (Govaerts et al. 2015).

Carex has had many more branching events than the two allied genera in tribe Scirpeae, so we used three hierarchical levels to characterize this more complex pattern of diversification: level B, between species from different major clades within non-*Siderostictae Carex*; level C, between species from different strongly supported subclades within each major clade; and finally level D, between species within the strongly supported subclades in our analyses (Figs. 2, 3). The three major clades, Core *Carex*, *Vignea* and Caricoid, classed as level B divergences are strongly supported not only by the matrix analyzed here (Fig. 2), but they also receive at least moderate support in published analyses (Waterway and Starr 2007; Starr and Ford 2009; Waterway et al. 2009; Gehrke et al. 2010; Hinchliff and Roalson 2013), and in a recent set of analyses using nine DNA regions and 250 species that represent a wide variety of *Carex* sections from six continents (Waterway et al. 2015).

Level B divergences among the Core *Carex*, Caricoid, and *Vignea* clades date to 28–31 (plus or minus 7) million years ago in our analysis while the Level C divergences within these major clades are more recent and vary from approximately 18–5 million years ago (Fig. 3). The criteria for recognition as a subclade for this analysis were as follows: 1) the clade had to have a posterior probability of at least 0.93, indicating strong support (Zander 2004); and 2) the clade had to have morphological integrity. Within the Core *Carex* clade, the fen species were represented in five multi-species subclades representing sections *Limosae*, *Vesicariae*, *Phacocystis*, *Chlorostachyae*, and *Paniceae*, the last three of which

TABLE 2. Alignment length, number of characters, and models of evolution for each DNA region used in the phylogenetic analyses. The numbers in parenthesis for the *matK* gene refer to the codon position for the models of evolution.

DNA region:	ETS	ITS	*trnL-trnF*	*matK* (1)	*matK* (2)	*matK* (3)
Alignment length	682	694	1,218	820		
No. of informative characters	274	188	159	80		
No. of excluded characters	0	16	155	0		
Model of evolution AIC	GTR + I + G	GTR + I + G	TPM1uf + I + G	TVM + G	TPM1uf + G	TVM + G
Model of evolution BIC	GTR + I + G	GTR + I + G	TPM1uf + I + G	TPM1uf + G	TPM1uf + G	TVM + G
Model specified for *MrBayes*	GTR + I + G	GTR + I + G	GTR + I + G	GTR + G	GTR + G	GTR + G

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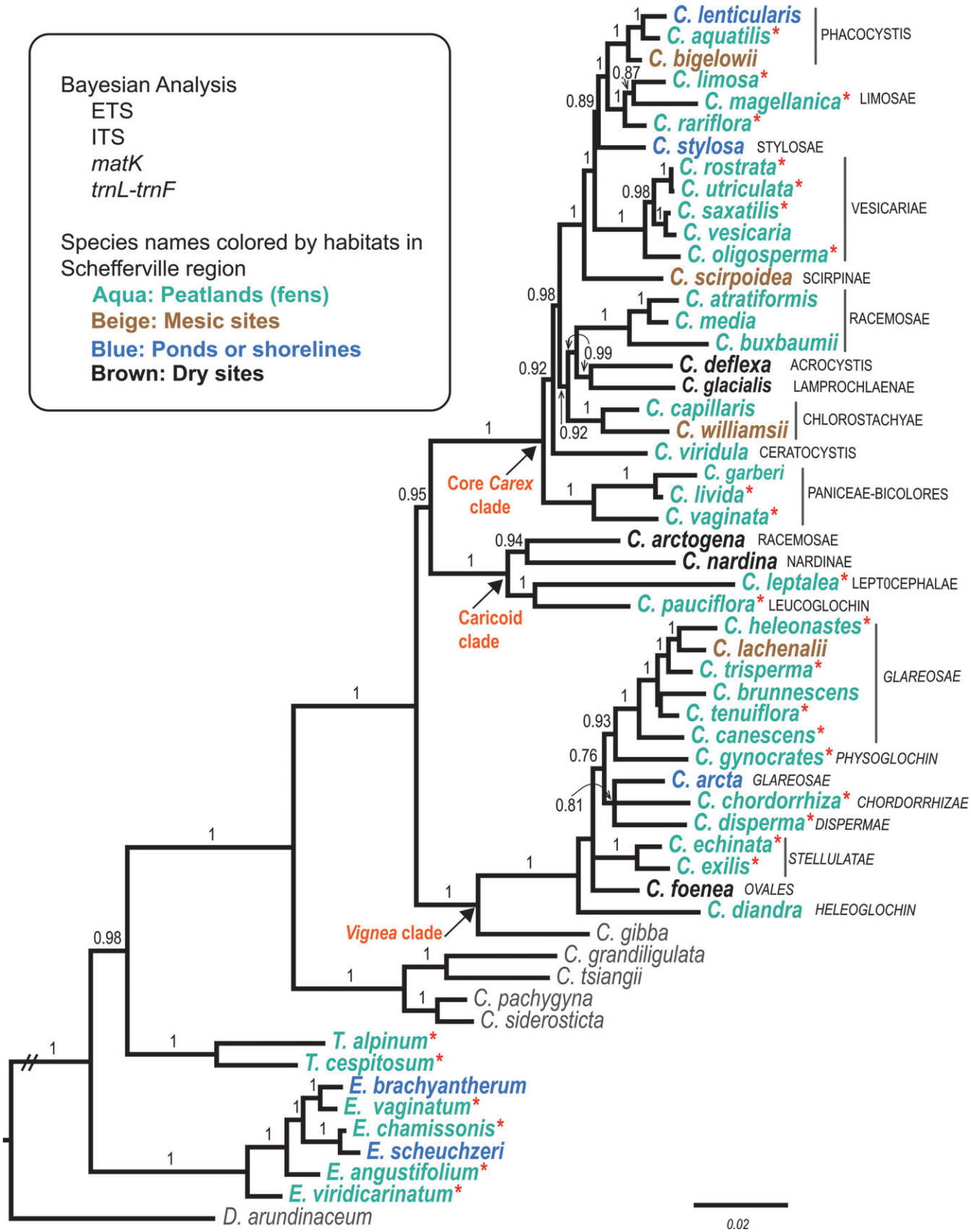


FIG. 2. Phylogram based on Bayesian analysis using *MrBayes* for sedge species in the Schefferville region plus selected Asian species added for rooting and dating the tree. Branch lengths are proportional to the number of nucleotide changes/site/time. Posterior probabilities > 0.7 are shown above the branches. Sectional placements are given for *Carex* species in the region, and habitat categories are based on Cayouette (2008) and Ball et al. (2002) and coded by color. Species sampled for co-occurrence are followed by an asterisk. Species not in the Schefferville regional species pool are shown in gray.

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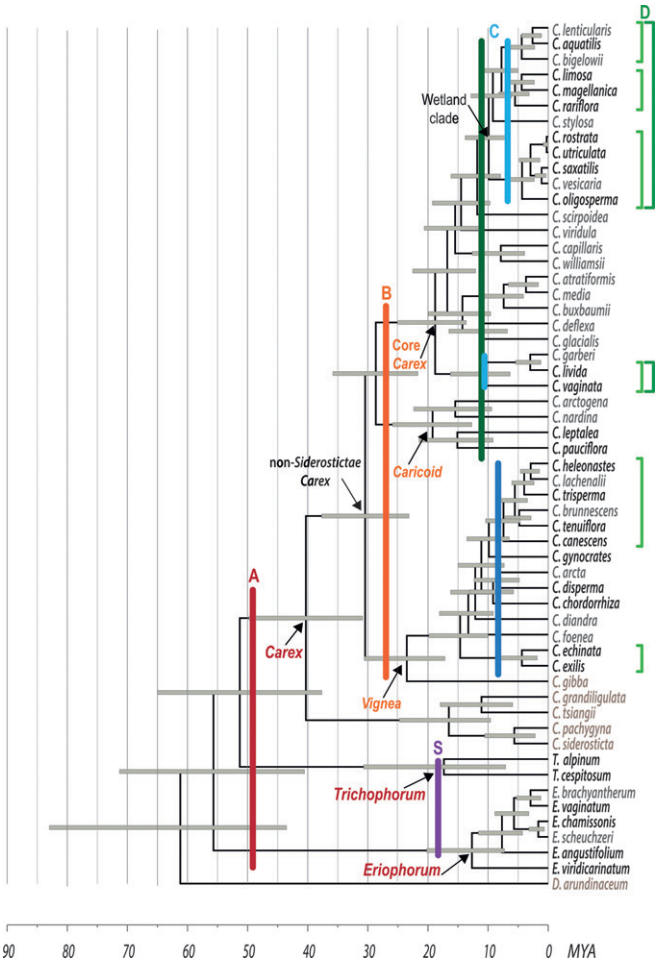


FIG. 3. Chronogram based on Bayesian analysis in BEAST for sedge species in the Schefferville region plus selected Asian species added for rooting and dating the tree. Error bars on the node divergence time estimates are shown as horizontal gray bars. Colored vertical bars indicate the clade divergence level classifications used in linear modeling. Species pairs in which species connect to the left of the red A line belong to different genera, those that connect to the left of the orange B line belong to different major clades of *Carex*, and those that connect to the left of the blue C lines belong to different subclades within the major clades of *Carex*. Species pairs that can be connected without crossing the blue C lines belong to the same subclades within major clades of *Carex*, and species pairs that can be connected without crossing the purple S lines are congeners within the small genera, *Trichophorum* or *Eriophorum*. Subclades are indicated as green brackets for the two alternate D classification levels, which differ only in the treatment of the Wetland clade within Core *Carex*. Light green D brackets correspond to subclades marked by the blue C line. The alternate C line is shown in dark green and the revised D subclade, which includes all species in the Wetland clade, is shown with a dark green bracket. Species names in black are those included in the co-occurrence matrix, those in gray are species in the Schefferville regional species pool that were not found in the sampling of fens, and those in pale brown are species added for rooting or dating the tree.

also included a single non-fen species. Similarly, within the *Vignea* clade, fen species occupied multi-species subclades representing sections *Glareosae* and *Stellulatae* as well as two lineages represented by single species and a poorly supported polytomy of dissimilar species. The Caricoid clade had four different single-species lineages, two of which occurred in fens. We divided the level C divergences into two categories (Cc for those within the Core *Carex* or Caricoid clades and Cv for those within the *Vignea* clade) based on another study of *Carex* in the Schefferville region, which showed that Core *Carex* tended to demonstrate clustered phylogenetic community structure while the *Vignea* clade tended toward overdispersion (Elliott et al. 2016).

The most recent divergence level, the one between species within subclades, was defined as level D and included comparisons at this level from within both the Core *Carex* and the *Vignea* clades. For the fen species, comparisons at this level were those within clades representing sections *Limosae*, *Vesicariae*, and *Paniceae* in the Core *Carex* clade, and sections *Glareosae* and *Stellulatae* in the *Vignea* clade. All of these clades were strongly supported by the molecular data as well as by morphological synapomorphies. Level D1 mostly represented divergences within the last 5 million years with some being much younger (e.g. *C. rostrata* and *C. utriculata* estimated to have diverged only 200,000 yr ago, Fig. 3). We also tested an alternate definition of level D (D2) that differed only in how we treated the clades representing sections *Limosae*, *Vesicariae*, and *Phacocystis*. These three subclades form a larger "Wetland" clade within Core *Carex* (Figs. 2, 3; Waterway et al. 2009) which also has a posterior probability of 1.0 in our analyses and is comparable in age to the *Paniceae* subclade (~11 MYA). In that alternative analysis we transferred all pairs in which the two species were from different subclades within the Wetland clade from the C level to the D level. These two different definitions for level D are the only difference between what we term Clade Divergence Level 1 (CDL1) and Clade Divergence Level 2 (CDL2) in the analyses described below in which we test which factors best predict significant pairwise species co-occurrence.

Quantifying Co-occurrence—Using the R package co-occur (Veech 2013; Veech 2014; Griffith et al. 2016) we analyzed the pairwise associations between sedge species in fens of the Schefferville region at the boreal-subarctic transition in northern Quebec. This co-occurrence algorithm classifies species pairs as positively, negatively, or randomly associated by calculating observed and expected frequencies of co-occurrence between each pair of species and returning probabilities that a more extreme (either high or low) value of co-occurrence could have been obtained by chance (Veech 2013; Griffith et al. 2016). The effect size of co-occurrence, that is to say the strength of the association between a given species pair, is expressed as the difference between observed and expected frequencies (Griffith et al. 2016). The effect size quantifies the strength of species attraction (more positive values) or aversion (more negative values). We use 'attraction' and 'aversion' here and in the following discussion only as terms to indicate that the probability of pairwise co-occurrence is greater or less than expected by chance, with no implication of specific mechanisms to attract or avoid. This probabilistic model of species co-occurrence does not rely on data randomization and thus has the desirable properties of a low Type 1 error rate as well as the power of a low Type II error rate (Veech 2013). Following Veech (cf. Griffith et al. 2016), we dropped from subsequent analyses all species pairs that occurred in so few quadrats that their expected frequencies were less than one.

We conducted the initial co-occurrence analyses in two modes: 1) in a regional analysis pooling all the data without regard to the fen in which a quadrat occurred; and 2) in separate analyses for each of the 29 sampled fens. In the first mode the quadrats were considered as stratified random samples of the fen habitat in the Schefferville region. Note that in this mode of analysis fewer pairwise comparisons are discarded due to expected values falling below one, but on the other hand, any filtering effects due to environmental or size variation among fens will not be detected. The analyses in the second mode respect the possible effects of environmental differences along the gradient from poor to rich fens known to occur in the region (Bubier 1995; Dabros and Waterway 2008) but the dimensionality of the data matrices varied with the number of quadrats sampled in each fen and the number of sedge species observed. We standardized effect sizes (SES) calculated for each species pair by dividing them by the total number of quadrats sampled in a given fen to enable cross-fen comparisons. Although the fens retain their individual identity, sample size effects led to discarding more pairings with expected values below one than in the pooled data set. We report and compare the patterns of species association detected in both modes of analysis. In subsequent linear mixed modeling analyses relating species association to the degree of relatedness between species and differences in their environmental affinities, we used only the second, more conservative co-occurrence results, having combined SES values from each fen into a single table consisting of 1,278 fen by species-pair records (Supplemental Table 2, available from the Dryad Data Repository at http://dx.doi.org/10.5061/dryad.q810f).

Predicting Co-occurrence—We used linear mixed modeling (R package lme4; Bates et al. 2015) to predict these fen by species-pair SES records as a function of the phylogenetic distance between species pairs (dBayes or dBEAST), the mean difference in the environmental affinities of each species pair (water pH and rooting level), and the two previously described factors coding for different definitions of clade divergence

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levels (CDL1 and CDL2). We first developed four model sets in order to 1) distinguish the relative importance of clade versus distance-based assessments of phylogeny, 2) assess the significance of either of two valid ways of defining clade levels (CDL1 vs CDL2) and phylogenetic distances (dBayes vs. dBeast), and 3) test the importance of these six variables while avoiding collinearity between fixed effects since the two phylogenetic distance metrics were very similar to each other ($r > 0.6$) as were the CDL variables. The four models all included differences in the environmental affinities of each species pair with regard to water pH and rooting level, but differed in whether they used dBayes or dBEAST distances and whether they used the CDL1 or CDL2 clade divergence levels. The four models thus represent all possible combinations of the two phylogenetic distance metrics with the two CDL schemes; however, no model included both types of distance metric and no model included both sets of CDL variables. We used standard diagnostic tests (Zuur et al. 2009) separately for each model set to select the best model in each case. Tests included verifying the significance of fixed effects using likelihood ratio tests, examining model residuals for heterogeneity and violations of normality and, finally, comparing model fit using the AIC. We then compared the best models from each model set to identify the single best model across all model sets. In all these models, we used two separate factors as crossed random effects after having verified their significance using likelihood ratio tests: 1) the fen in which the observations were made; and 2) the species pair being assessed. The overall intercept of our models thus reflects a weighted average over fens and species pairs. These analyses were repeated using the dBEAST values from the alternative dating calibrations described above to test their effect on the conclusions.

Mean Pairwise Differences in Environmental Affinities—We calculated mean differences in environmental affinities for water pH and rooting level for each species pair that was assessed in each fen for the co-occurrence analysis (see below). We first calculated the weighted means of both pH and rooting level for a given species across all quadrats in which it occurred in a given fen. Values were weighted by the midpoints of the abundance classes of that species where it occurred in the fen. In this way we estimated multiple fen- and species-specific weighted mean values as opposed to a single value for each species across all fens. We then calculated the absolute difference in the weighted mean water pH (mean delta pH) and rooting level (mean delta rooting level) for each species pair at each fen.

For species pairs in the level D clade divergence category (both variants) that were significantly less likely to occur than expected by chance in the fen-by-fen co-occurrence analysis, we used Tukey's honestly significant difference test (HSD) for significant differences in water pH and rooting level between the two species in each pair based only on quadrats in which one or the other of the two species in the pair occurred, but not those where they co-occurred. We compared environmental variables for these species pairs both at the regional level using appropriate quadrats from all fens and on a fen-by-fen basis.

Ordination of Quadrat Data on Sedge Community Composition—We used a detrended correspondence analysis (DCA), calculated using the R package vegan (Oksanen et al. 2015), to illustrate patterns of sedge species covariance across all fens and to see how the ordination reflected underlying pH and rooting level gradients. Specifically, we analyzed the entire 2,124 quadrat by 27 sedge species matrix using DCA with abundance estimates for each species on a 0–4 scale, as described above. We then fit vectors with measures of pH and rooting level at each quadrat onto the resulting ordination. To draw comparisons with results from the linear mixed model analysis, we color-coded the labels for species vectors according to their subclade membership (D1 divergence level), which also corresponded to their sectional affiliations.

Results

Species Distribution and Abundance—Sedges are so widespread and frequent in fens of the Schefferville region that only one of the 2,124 randomly sampled quadrats across the 29 fens lacked sedge species. The sedges varied in frequency with the most frequent being found in about a third (*Carex aquatilis*, *T. cespitosum*) to nearly half (*C. limosa*) of the 2,124 sampled quadrats, and the least frequent, *C. saxatilis* and *E. vaginatum*, found in only 10 and four quadrats, respectively (Table 3). *Carex saxatilis* and *E. vaginatum* were each found in only two fens, whereas *C. magellanica* and *E. chamissonis* were the two most widespread species, found in 27 and 26 of the 29 fens, respectively. In addition to the 27 sedge species found in the quadrats, four *Carex* species were infrequently observed in the fens but not sampled in any of the random quadrats: *C. brunnescens*, *C. capillaris*, *C. diandra*, and *C. vesicaria*. The number of sedge species per 0.25 m^2 quadrat varied from one to eight, with a mean of 2.8 and a median of three. A total of 328 (15%) of the quadrats had only one sedge species and thus provided information on environmental tolerances but could not be used in the analysis of pairwise co-occurrence.

Phylogenetic Distance—Based on the ultrametric BEAST tree (Fig. 3), phylogenetic distances (dBEAST) measured in millions of years between species pairs of *Carex* in the ecological data set from the fens varied from 0.5–62 while phylogenetic distances between species pairs representing different genera in the CDS clade varied from 102–111 million years. The square roots of these distances are strongly correlated with mean phylogenetic distances based directly on levels of sequence divergence that were calculated from a set of 9000 trees in the clade credibility set from Mr. Bayes (dBayes; $r = 0.96$). The DNA data matrix is complete for these species, so no bias has been introduced by incomplete gene sampling in some parts of the tree compared to others, and as a result, the high correlation is not surprising. This also suggests that although the estimated divergence times have a high variance and depend on limited fossil evidence, the relative divergence times across the phylogenetic tree are likely to be robust.

We also used two alternative calibrations based on dates from Escudero and Hipp's (2013) paper on Cyperaceae phylogeny. That paper used a younger (Eocene) fossil (*C. colwellensis*) to calibrate the crown node of *Carex* rather than the older (Paleocene) putative fossil (*C. tsagajanica* Krassilov) to calibrate the stem node of *Carex*. These two alternative calibrations resulted in smaller phylogenetic distances (as low as 0.5–47 million years for species pairs of *Carex* and as low as 77–84 million years for species pairs representing different genera in the CDS clade (Supplemental Figs. 1, 2, available from the Dryad Data Repository at http://dx.doi.org/10.5061/dryad.q810f). Crown ages for the three largest *Carex* clades (Core *Carex*, Caricoid, and *Vignea*) in these two alternative analyses ranged from 19–14 million years, similar to the 15–16 million year crown ages found by Spalink et al. (2016). Despite these differences, the crown ages for the three largest *Carex* clades in our original analysis ranged from 23–19 million years, similar to the crown ages of approximately 20 million years found for these clades in a recent analysis of Poales using 9 fossils for calibration (Bouchenak-Khelladi et al. 2014) and in line with the fact that *Carex* fossil diversity was already established in the Oligocene, that is, prior to 23.7 million years ago. We therefore present our original BEAST analysis here (Fig. 3), with the caveat that estimating divergence times in *Carex* will remain an inexact science at least until additional fossils can be reliably determined. Although the absolute distances differed among analyses, the relative branch lengths were maintained across all three calibration methods, and all three gave the same results in our subsequent analyses.

Patterns of Pairwise Co-occurrence—When pooling data from all fens into a single regional analysis, we were unable to test 44 of the 351 possible species pairs because the expected probability of their co-occurrence was less than one

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TABLE 3. Classification, sample sizes, and environmental data for the sampled sedge species from the Schefferville region in the central Labrador Peninsula. Number of fens (of 29 total) and number of quadrats (of 2,124 total) indicate the number of fens and quadrats in which each species was recorded during the random quadrat sampling. Means and standard deviations (Std. Dev.) weighted by % cover in the quadrats, and ranges from maximum (Max) to minimum (Min) are given for rooting level relative to the water table (cm) and water pH for the quadrats in which each species occurred. Habitats from Cayouette (2008) are given for *Carex* species using the following abbreviations: mb = mud boils; s = shores; w = wetlands, including peatlands; sb = snowbanks. Habitats for *Eriophorum* and *Trichophorum* are based on Ball et al. (2002) and defined as follows: s = shores; w = wetlands, including peatlands; wf = wet forest; wt = tundra. Acronyms used in the figures are given in the column labeled Code.

Species	Code	*Carex* Section	No. of fens	Number of quadrats	Rooting depth				Water pH				Habitats
					Mean	Std. Dev.	Min	Max	Mean	Std. Dev.	Min	Max	
Carex aquatilis Wahlenb.	Caqu	*Phacocystis* Dumort.	17	686	6.3	5.5	−30	48	5.4	0.9	3.4	8.3	w, s, mb
Carex canescens L.	Ccan	*Glareosae* G. Don	15	86	8.0	8.3	−30	25	5.4	1.0	3.9	8.3	s
Carex chordorrhiza L. f.	Ccho	*Chordorrhizae* (Heuff.) Meinsh.	10	153	7.0	7.2	−18	23	5.4	1.1	3.3	7.3	w, s
Carex disperma Dewey	Cdis	*Dispermae* Ohwi	5	31	9.8	5.5	−4	27	5.3	1.0	3.7	7.8	w
Carex echinata Murray	Cech	*Stellulatae* Kunth	14	88	7.7	7.5	−30	25	5.2	0.9	3.7	7.6	w, s
Carex exilis Dewey	Cexi	*Stellulatae* Kunth	11	66	5.6	11.0	−18	36	5.1	1.1	3.8	7.5	w
Carex gynocrates Wormsk.	Cgyn	*Physoglochin* Neck. ex Dumort.	14	182	13.4	12.1	−20	36	5.5	0.9	2.9	8.3	w, s, mb
Carex heleonastes L.f.	Chel	*Glareosae* G. Don	5	36	4.8	4.7	−16	19	6.2	0.7	4.5	7.4	w
Carex leptalea Wahlenb.	Clep	*Leptocephalae* L. H. Bailey	13	139	11.4	6.8	−13	48	5.8	0.9	3.5	8.3	w, s
Carex limosa L.	Clim	*Limosae* (Heuff.) Meinsh.	25	1016	0.3	3.8	−62	32	4.9	0.9	3	8	w
Carex livida (Wahlenb.) Willd.	Cliv	*Paniceae* G. Don	16	292	−2.7	3.3	−18	21	5.5	0.9	3.4	8	w
Carex magellanica Lam.	Cmag	*Limosae* (Heuff.) Meinsh.	27	387	6.5	8.4	−16	40	4.5	0.7	2.9	7.2	w, s
Carex oligosperma Michx.	Coli	*Vesicariae* (Heuff.) J. Carey	15	224	2.9	7.3	−19	35	4.5	1.0	3	6.7	w, s
Carex pauciflora Lightf.	Cpau	*Leucoglochin* Dumort.	22	217	12.5	7.1	−4	40	4.3	0.7	2.9	6.6	w
Carex rariflora (Wahlenb.) J.E. Smith	Crar	*Limosae* (Heuff.) Meinsh.	13	148	11.5	7.0	−12	33	5.2	1.0	3.4	7.7	w, s, sb
Carex rostrata Stokes	Cros	*Vesicariae* (Heuff.) J. Carey	23	434	−6.1	13.7	−65	30	5.1	0.7	3.1	7.2	s
Carex saxatilis L.	Csax	*Vesicariae* (Heuff.) J. Carey	2	10	−32.0	43.2	−65	15	6.0	0.5	4.7	6.7	w, s
Carex tenuiflora Wahlenb.	Cten	*Glareosae* G. Don	11	45	12.4	10.8	−7	43	4.9	1.0	2.9	6.9	w, s
Carex trisperma Dewey	Ctri	*Glareosae* G. Don	18	121	17.7	9.0	−16	50	4.3	0.7	3	6.4	w
Carex utriculata F. Boott	Cutr	*Vesicariae* (Heuff.) J. Carey	11	87	−1.8	16.1	−35	30	5.0	0.7	3.6	6.7	s
Carex vaginata Tausch.	Cvag	*Paniceae* G. Don	17	191	16.0	6.8	−3	50	4.8	0.9	3.3	7.9	w, s, sb
Trichophorum alpinum (L.) Pers.	Talp		10	194	8.9	8.0	−4	30	5.8	1.1	3.5	8.0	w, s, wt
Trichophorum cespitosum (L.) Hartm.	Tces		22	721	2.8	3.3	−18	34	5.1	1.0	3.0	8.0	w, s
Eriophorum angustifolium Honck.	Eang		11	54	−0.4	3.5	−15	23	5.1	0.7	3.9	7.0	w, s
Eriophorum chamissonis C.A. Mey.	Echa		26	325	−1.9	3.2	−17	35	4.9	0.9	3.0	7.0	w, wf
Eriophorum vaginatum L.	Evag		2	4	13.7	11.7	−2	22	3.7	0.4	3.4	4.0	w, wt
Eriophorum viridicarinatum (Engelm.) Fernald	Evir		9	68	7.3	6.0	−6	25	5.9	1.1	3.5	8.0	w, wf

due to the rarity of a few species, particularly *E. vaginatum* and *C. saxatilis*. Of the 307 testable species pairs, 120 (39%) demonstrated significant levels of aversion and 72 (23%) showed significant levels of attraction (Fig. 4A; Table 4). These findings were comparable to those in which we assessed each fen separately. In the fen-by-fen analysis, an additional 44 pairwise combinations were removed due to expected probabilities of co-occurrence less than one, and species pairs were classified into predominantly aversive or predominantly attractive by subtracting the total number of significant positive associations across fens from the total number of negative associations. Of the remaining 263 species pairs, 83 (32%) pairings were predominantly aversive and 63 (24%) were predominantly attractive (Fig. 4B; Table 4). In this fen-by-fen analysis, 90% of the species pairs were consistently aversive or consistently attractive across the sets of fens in which they co-occurred (Supplemental Table 2, available from the Dryad Data Repository at http://dx.doi.org/10.5061/dryad.q810f).

This general tendency for more species pairs to show aversion than attraction varied depending on the clade divergence level of the pairs and on the particular clade (Fig. 4; Table 4). In the regional analysis, comparisons between species of different genera (A-level) and those between species from different major clades within *Carex* (B-level), as well as those between different subclades within the large Core *Carex* clade (Cc- and Cv-levels) all showed higher levels of aversion than attraction, substantially higher for the C levels (Fig. 4A; Table 4). Comparisons within subclades (D-level) differed markedly between the Core *Carex* clade and the *Vignea* clade. Six (67%) of the D1-level pairwise comparisons in Core *Carex* showed aversion while the rest were neutral. In contrast, one species pair (17%) in the *Vignea* clade showed significant attraction while the remainder were neutral. D2-level comparisons, in which the D-level for the Core *Carex* clade was expanded to include all pairwise comparisons for the Wetland clade (see Fig. 3), still had 16 (55%) aversive pairs and only 10% attractive pairs, the others being neutral. The pattern was similar in the fen-by-fen analysis (Fig. 4B; Table 4). Overall, within *Carex* the number of pairwise comparisons demonstrating aversion increased as the phylogenetic relationship between the species pairs became closer, with the exception of the *Vignea* clade in which pairwise co-occurrence was neutral, or in one pair, significantly attractive. The infrageneric pattern was different for the smaller genera: the two species of *Trichophorum* showed strong attraction in both regional and fen-by-fen analyses, as did one pair of *Eriophorum* species. Another *Eriophorum* pair showed significant aversion in the regional analysis, but no significant pattern in the fen-by-fen analysis.

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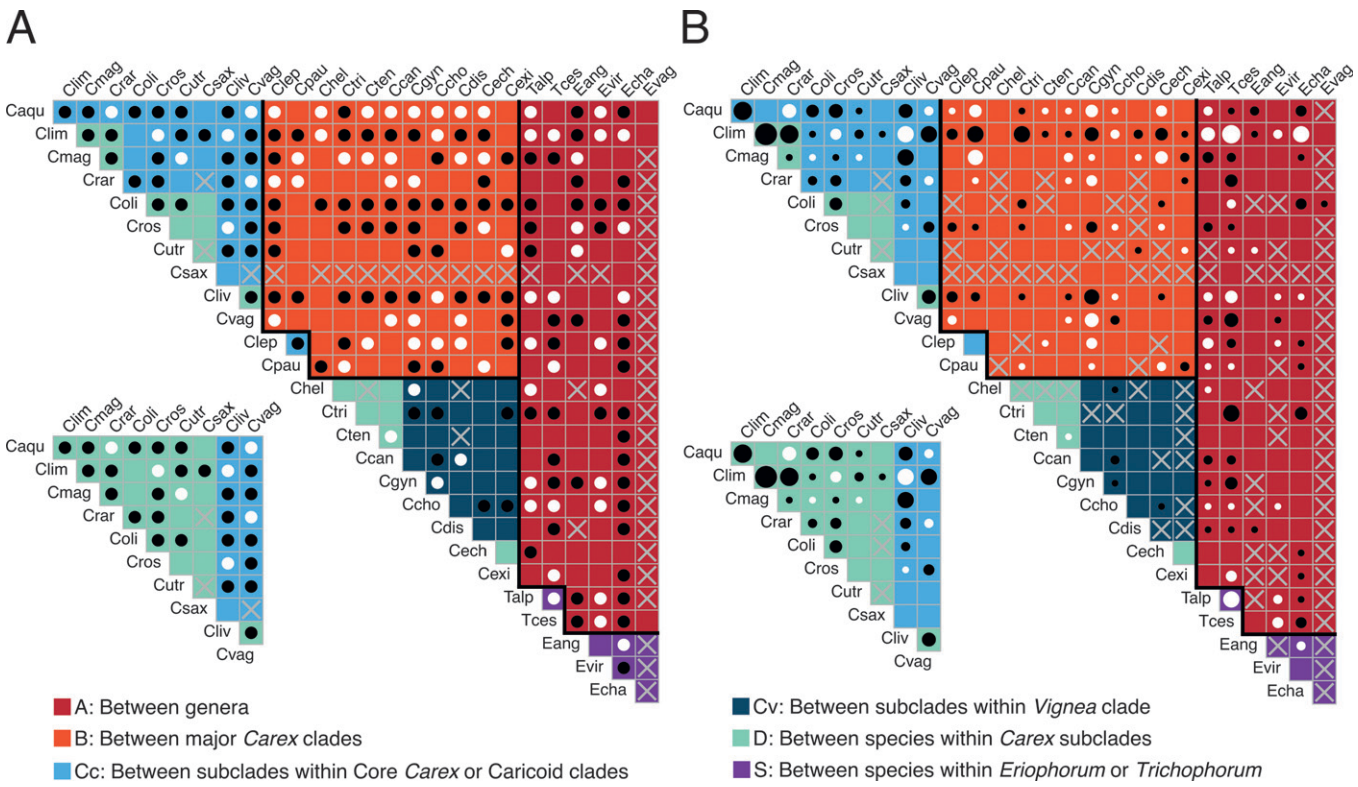


FIG. 4. Half-matrices showing the results of pairwise co-occurrence analyses (cf. Veech 2013, Griffith et al. 2016); species acronyms follow Table 3 and are color-coded to show which species pairs belong to each clade divergence level (CDL) shown in Fig. 3. The large matrices in each panel show the CDL1 classification scheme for clade divergence level. Only species pairs in the Core *Carex* clade change classification for the CDL2 scheme; the small inset matrices in each panel are color-coded to show the CDL2 classification for Core *Carex* pairs. In all matrices, black circles indicate that the species in the pair are less likely to occur together in a 0.25 m^2 quadrat than expected by chance (significant aversion) while white circles indicate that they are more likely to co-occur (significant attraction). Empty boxes indicate species pairs with no significant aversion or attraction. Species pairs marked with X were removed from the analyses because their expected co-occurrences were less than one, i.e. there was insufficient data to reliably evaluate their aversion or attraction. A. Results of the regional analysis where all quadrats were considered random samples of fen habitat in the region. B. Results of analyzing the same data matrix but on a fen-by-fen basis. Circles are scaled to indicate the proportion of the 29 sampled fens in which a pairwise attraction or aversion was significant; the smaller a circle, the fewer fens support the result.

Predicted Co-occurrence using Linear Mixed Modeling—A likelihood ratio test comparing models with and without the specified random effect structure showed that the model with the random effect structure was a better fit than the one without for all model sets (Table 5). Specifying the appropriate random effect structure, we then sequentially dropped non-significant fixed effects. The models not including the phylogenetic distance metrics (either dBayes or dBEAST) were better fit than the ones with these variables for all model sets (Table 5), i.e. cladistic structure was more informative than cophenetic distance per se. Once these distance metrics were removed, all remaining fixed effects were significant or had factor levels that were significant (Table 6). Both the mean delta pH and mean delta rooting level were Box-Cox transformed to reduce heterogeneity in the residuals. We compared the best models from all model sets, all of which included mean delta pH and mean delta rooting level as fixed effects but differed in whether cladistic relationships between species pairs were coded using CDL1 or CDL2 (i.e. the alternative clade structures previously described). Using either of these two cladistics variables as fixed effects made no difference in terms of overall model fit (ΔAIC = 1.1; $\chi 2$ (df = 0) = 0; p = 1). In all of the best models, SES decreased with increasing mean delta rooting level and mean delta pH (Table 6; Fig. 5), indicating, not surprisingly, that the greater the difference in environmental affinities, the less likely two species are to co-occur at the scale of 0.25 m^2 quadrats. In models with either CDL1 or CDL2, the level coding for the most closely related species pairs (D1 and D2, respectively) had, on average, significantly low values of SES, indicating they are unlikely to co-occur. Values of SES for D1 were slightly more negative and variable than for D2. The clade divergence level S had significantly high values for both CDL1 and CDL2 indicating that, in contrast to species pairs within *Carex*, species pairs within *Eriophorum* and *Trichophorum* are likely to co-occur. Mean values of SES for all other divergence levels (A, B, Cc and Cv) were not significantly different from each other (Table 6) in either CDL1 or CDL2 and were all negative.

Repeating the linear mixed modeling using dBEAST distances based on the alternative calibrations demonstrated that the results described above were robust with respect to the calibration methods used to estimate divergence times; values were nearly identical and all results remained the same.

Fen Community Structure and Environmental Conditions—The number of sedge species in each fen varied from 3–24 with a positive correlation between species richness and fen size (r^2 = 0.569, p < 0.001). The fens also varied in the range of rooting levels and especially of water pH values that we recorded from the quadrats (Table 1; Fig. 6). In four fens,

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TABLE 4. Tabular summary of co-occurrence results, giving the number of attractive, aversive and neutral pairs in each of the regional and fen-by-fen analyses for each of the two clade divergence level definitions (CDL1 and CDL2). Clade divergence levels are lettered as in Fig. 3: A refers to divergence between species that belong to different genera of the Cariceae-Dulicheae-Scirpeae clade; B to species that belong to different major clades within *Carex*; Cc to species that belong to different subclades within the Core *Carex* clade; Cv to species that belong to different subclades within the *Vignea* clade; and D to species that belong to the same subclade within either the Core *Carex* or *Vignea* clades. The total number of testable pairs pertains to those species pairs per CDL whose expected co-occurrence was greater than one for any given analysis.

Clade Divergence Level:		A	B	Cc1 | Cc2	Cv	D1 | D2	S	Total
CDL 1								
Regional	Attractive Pairs	26 (23.9%)	33 (28.0%)	7 (20.6%)	3 (11.1%)	1 (6.7%)	2 (50.0%)	72 (23.5%)
	Aversive Pairs	39 (35.8%)	47 (39.8%)	21 (61.8%)	6 (22.2%)	6 (40.0%)	1 (25.0%)	120 (39.1%)
	Neutral Pairs	44 (40.4%)	38 (32.2%)	6 (17.6%)	18 (66.7%)	8 (53.3%)	1 (25.0%)	115 (37.5%)
	Total Testable	109	118	34	27	15	4	307
Fen by Fen	Attractive Pairs	23 (24.5%)	29 (28.7%)	8 (22.9%)	0 (0.0%)	1 (8.3%)	2 (66.7%)	63 (24.0%)
	Aversive Pairs	31 (33.0%)	27 (26.7%)	16 (45.7%)	4 (22.2%)	5 (41.7%)	0 (0.0%)	83 (31.6%)
	Neutral Pairs	40 (42.6%)	45 (44.6%)	11 (31.4%)	14 (77.8%)	6 (50.0%)	1 (33.3%)	117 (44.5%)
	Total Testable	94	101	35	18	12	3	263
CDL2								
Regional	Attractive Pairs	26 (23.9%)	33 (28.0%)	4 (25.0%)	3 (11.1%)	4 (12.1%)	2 (50.0%)	72 (23.5%)
	Aversive Pairs	39 (35.8%)	47 (39.8%)	11 (68.8%)	6 (22.2%)	16 (48.5%)	1 (25.0%)	120 (39.1%)
	Neutral Pairs	44 (40.4%)	38 (32.2%)	1 (6.2%)	18 (66.7%)	13 (39.4%)	1 (25.0%)	115 (37.5%)
	Total Testable	109	118	16	27	33	4	307
Fen by Fen	Attractive Pairs	23 (24.5%)	29 (28.7%)	4 (23.5%)	0 (0.0%)	5 (16.7%)	2 (66.7%)	63 (24.0%)
	Aversive Pairs	31 (33.0%)	27 (26.7%)	6 (35.3%)	4 (22.2%)	15 (50.0%)	0 (0.0%)	83 (31.6%)
	Neutral Pairs	40 (42.6%)	45 (44.6%)	7 (41.2%)	14 (77.8%)	10 (33.3%)	1 (33.3%)	117 (44.5%)
	Total Testable	94	101	17	18	30	3	263
Total Possible Pairs		134	128	36 | 17	29	17 | 36	7	351

mean rooting levels were below the water table and in seven fens, the means were above the water table, with the remainder having mean rooting levels more or less at the water table. Water pH values for the fens varied from 3.4–7. The range of values within each fen was also highly variable, with ranges spanning as little as 0.3–0.5 pH units, mostly at the acidic end of the gradient, to fens with pH ranges spanning up to 4 pH units, mostly in fens with mean pH values above 5 (Table 1; Fig. 6). The two environmental variables were very weakly correlated ($r^2 = 0.0322$, $p < 0.001$).

Ordination of the 2,124 quadrats showed broad spread on both synthetic axes; not surprisingly given the large data matrix, the first DCA axis explained only 7.5% of the variance and the second 6.4% (Fig. 7). When fit onto the ordination space, the squared correlation coefficients for mean delta pH and mean delta rooting level with the first two DCA axes were 0.38 ($p < 0.001$) and 0.37 ($p < 0.001$), respectively. Species vectors on the ordination plot suggested that most of the species tended to segregate from their closest relatives on the pH gradient, the rooting level gradient, or both.

Ecological Tolerances of the Species—Abundance-weighted means, standard deviations, and ranges across all fens for rooting level in relation to the water table and water pH are given in Table 3. *Carex saxatilis*, *C. rostrata*, *C. utriculata*, *C. livida*, *E. chamissonis*, and *E. angustifolium* all tended to root below the water table and frequently occurred in quadrats alone or with only one or a few other sedges, often without other competing plant species. In contrast, *C. trisperma*, *C. vaginata*, *C. gynocrates*, *C. pauciflora*, *C. leptalea*, *C. rariflora*, and *C. tenuiflora* all had mean rooting levels more than 10 cm above the water table, and grew on low to high hummocks that were richer in species, including ericaceous shrubs and non-graminoid herbaceous plants. Many species tended to grow at or just above the water table so quadrats at this level frequently had 3–7 sedge species. *Carex pauciflora*, *C. trisperma*, *C. oligosperma*, *C. magellanica*, and *E. vaginatum* had mean water pH values below 4.8, while *C. gynocrates*, *C. leptalea*, *C. heleonastes*, *C. livida*, *E. viridicarinatum*, and *T. alpinum* occupied the opposite end of the pH gradient with mean values of 5.5. Many of the species showed a remarkable range of tolerance along the pH gradient, in some cases with individuals occupying quadrats from pH 3 to pH 8 (e.g. *C. limosa*, *C. aquatilis*, *T. cespitosum*). Not only was the spread among individual points large, but the means within fens for these species varied nearly as much (Fig. 8). The range of tolerance for different water

TABLE 5. χ^2 values from likelihood ratio tests comparing models with and without variables listed in the "Variable Tested" column. Random effects pertain to crossed factors coding for the fen in which the observations were made and the species pair being assessed. Asterisks are printed beside χ^2 values to signify significance levels, with *** for $p < 0.001$.

Variable Tested	Test Statistic	Model Set 1	Model Set 2	Model Set 3	Model Set 4
Random Effects	χ^2 (df=3)	143.51***	155.06***	155.07***	143.49***
dBayes	χ^2 (df=1)	0.395	-	0.471	-
dBEAST	χ^2 (df=1)	-	0.382	-	0.537

TABLE 6. Values for the coefficients, standard errors and t-values for each fixed effect in the best linear mixed model (LMM). T-values represent the ratios between coefficient estimates and their standard errors. Cladistic associations are coded using CDL1. Asterisks are printed beside t-values to signify significance levels, with ** for $p < 0.01$ and *** for $p < 0.001$.

Fixed Effect	Coefficient Estimate	Standard Error	t-Value
Mean delta rooting level	−0.006654	0.000623	−10.685***
Mean delta pH	−0.003702	0.001428	−2.592**
CDL B	0.004872	0.003160	1.542
CDL Cc	−0.005986	0.004189	−1.429
CDL Cv	−0.003715	0.006859	−0.542
CDL D1	−0.020870	0.006963	−2.998**
CDL S	0.044620	0.013050	3.420***

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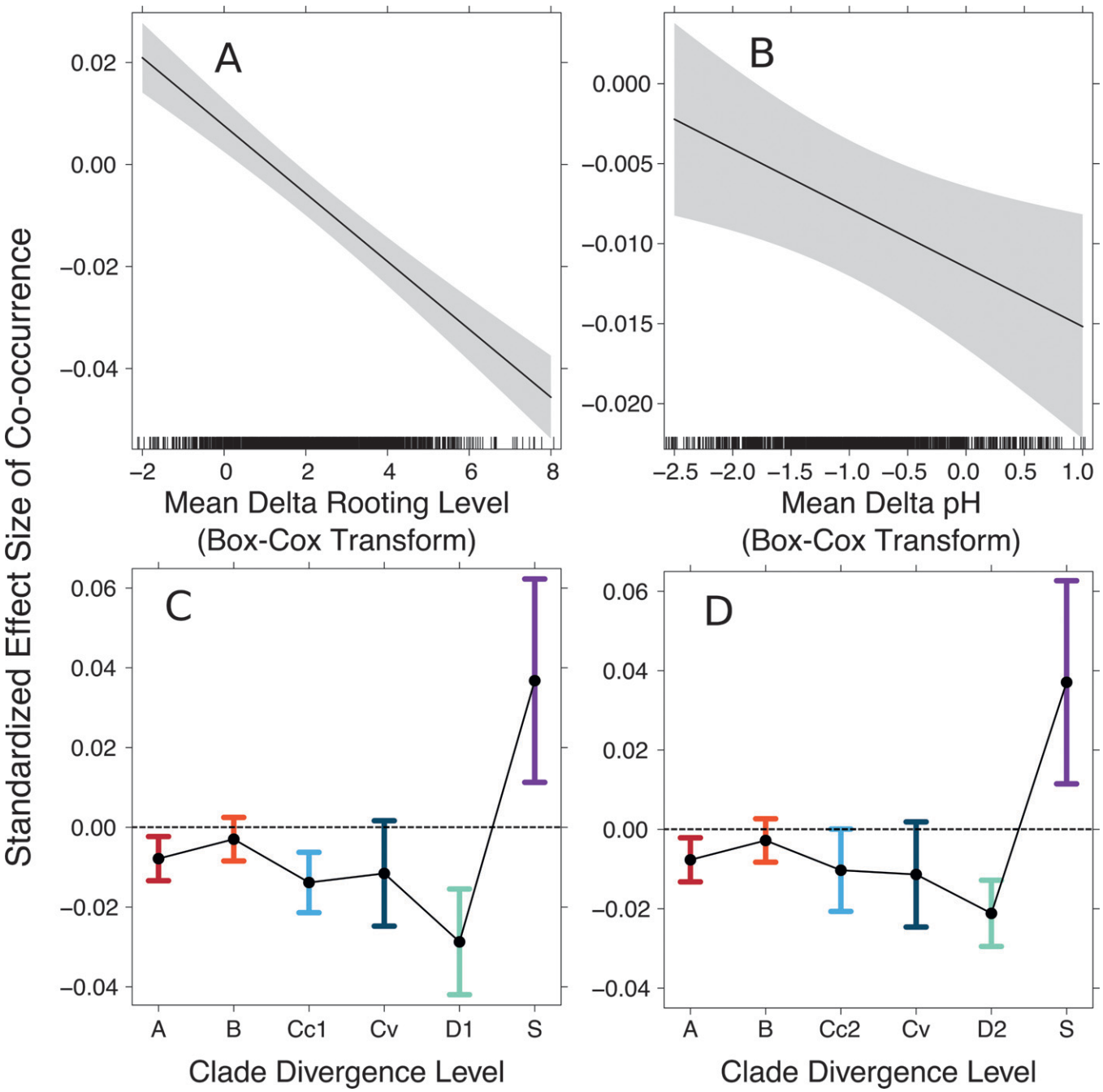


FIG. 5. Graphs showing the results of the linear mixed model (LMM) analysis. A–C. Partial effect graphs for the single best LMM identified through model selection, with the standardized effect size of co-occurrence (SES) taken as a function of mean delta rooting level, mean delta pH and clade divergence level (CDL). Both mean delta rooting level and mean delta pH have been Box-Cox transformed. D. Partial effect graph from an alternate model with the same fixed and random effects except that clade divergence level D1 has been defined as D2. The partial effect graphs for mean delta rooting level and mean delta pH of this second model were identical to those presented in panels A and B, respectively. Dotted lines have been added to panels C and D when SES is equal to zero to distinguish between aversive (negative SES) and attractive (positive SES) patterns of co-occurrence. Error bars and confidence envelopes represent 95% confidence limits. The colors of the bars correspond to the clade divergence levels defined in Fig. 3 and used in the half-matrices in Fig. 4.

levels was also quite broad but 78% of the species had mean and median rooting depths between 0 and 15 cm, and the three species mentioned above with broad water pH ranges all had rooting level means within a narrow range at or above the water table.

With one exception, pairs of closely related species (D-level) that showed significant aversion in the co-occurrence analyses were all significantly different along both water pH and rooting level gradients based on the Tukey HSD test using data pooled across all fens (Table 7). *Carex limosa* and *C. utriculata* did not differ significantly from each other along either gradient. Within individual fens, the differentiation among species along the environmental gradients was not as obvious because sample sizes were smaller and often unbalanced. The relative relationship of the means for rooting level within fens was the same as the regional

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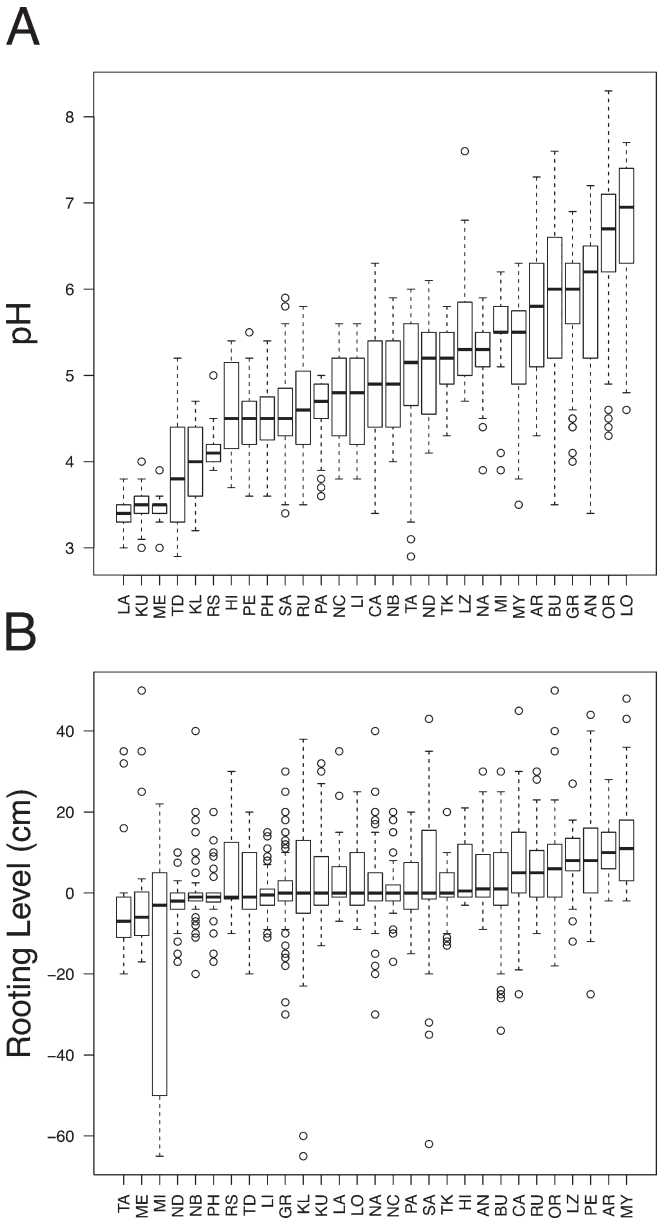


FIG. 6. Box plots for the 29 fens showing variation among the sampled quadrats in each fen for A: rooting level (cm) and B: water pH. Fens are ordered in terms of their median values on each panel; the acronyms refer to fen names in Table 1.

relationship for a high proportion of the species pairs. Among the species with significant differences at the regional level, the only exceptions to this trend were the *C. oligosperma–C. aquatilis* and *C. utriculata–C. aquatilis* pairs, in both of which the within-fen relationships between the means matched the regional relationship only about half the time (Table 7). The concordance between the regional relationship and the within-fen relationships was much less consistent along the water pH gradient. The relative difference between the species in a pair was consistent with the regional relationship in less than 60% of the fens for five pairs, more than 85% of the fens for five pairs, and between these two values for the remaining five pairs (Table 7).

The positions of species vectors on the ordination plot (Fig. 7) are consistent with the pairwise tests of environmental tolerances between species. Most closely related species segregate on the axis that is strongly correlated with rooting level, or the axis that is strongly correlated with water pH, or both. Although there is high variance along one or both of these gradients for many species and 95% confidence ellipses for species in the same D1 level subclade overlap (Fig. 8), the central tendency, shown by the species names at the end points of the species vectors, differs for all species pairs except the most recently diverged pair, *C. rostrata–C. utriculata*.

DISCUSSION

By focusing on sedges growing in subarctic fens on the central Labrador Peninsula, we have circumscribed a study system well suited to testing hypotheses about the evolutionary ecology of closely related species able to coexist as immediate neighbors within the same habitat. First, since fens are extensively distributed on this recently deglaciated landscape (Fig. 1), dispersal is unlikely to limit the colonization of individual fens by species in the regional species pool. There is good evidence for rapid and wide dispersal within this region during deglaciation (Alsos et al. 2015; Gajewski 2015). Second, cool climates, long harsh winters, low nutrient levels, frequently anoxic substrates, and the often extreme pH conditions that make nutrient uptake difficult all impose a strong environmental filter on species in the fen habitat. The sedge species occurring in an individual fen will have been subjected to habitat filtering in the sense this term is used in ecophylogenetics (Mouquet et al. 2012; Mittelbach and Schemske 2015), allowing us to focus on the biotic interactions among species within the fen habitat during the process of community assembly. Third, since successful colonization of this inherently harsh habitat requires an unusual suite of adaptations, the sedge community is dominated by relatively few species in the Cariceae-Dulichieae-Scirpeae (CDS) clade of Cyperaceae. The number of sedge species involved is tractable, yet has sufficient functional and phylogenetic diversity to allow testing of theoretical expectations.

We observed 31 species from this CDS clade in the fens of the Schefferville region, including 25 *Carex*, four *Eriophorum* and two *Trichophorum*; all but four were common enough to have been found in our random sampling of 2,124 quadrats across 29 fens. Three predominantly northern circumboreal lineages, *Limosae* (three species), *Vesicariae* (four species), and *Glareosae* (four species), account for 11 of the 21 *Carex* species in our quadrats. The remaining 10 species, with the exception of *C. leptalea* (North America and extending south to Mexico and the West Indies) and *C. exilis* (temperate to boreal Eastern North America) all belong to circumboreal lineages (including some that are also bipolar) or to northern clades within more broadly distributed groups (e.g. *C. aquatilis* in section *Phacocystis* (Dragon and Barrington 2008) and several species in section *Vesicariae* (Gebauer et al. 2014)). From three to 24 of these species in the CDS clade co-occurred in the same fen, and up to eight species (median 3) were found in the same 0.25 m^2 quadrat. The frequent co-occurrence of so many closely related species of *Carex* and allied genera as immediate neighbors in the studied fens affords an opportunity to test existing theory for community assembly and co-existence. We focus primarily on testing the expectation that the more closely species are related, the less likely they

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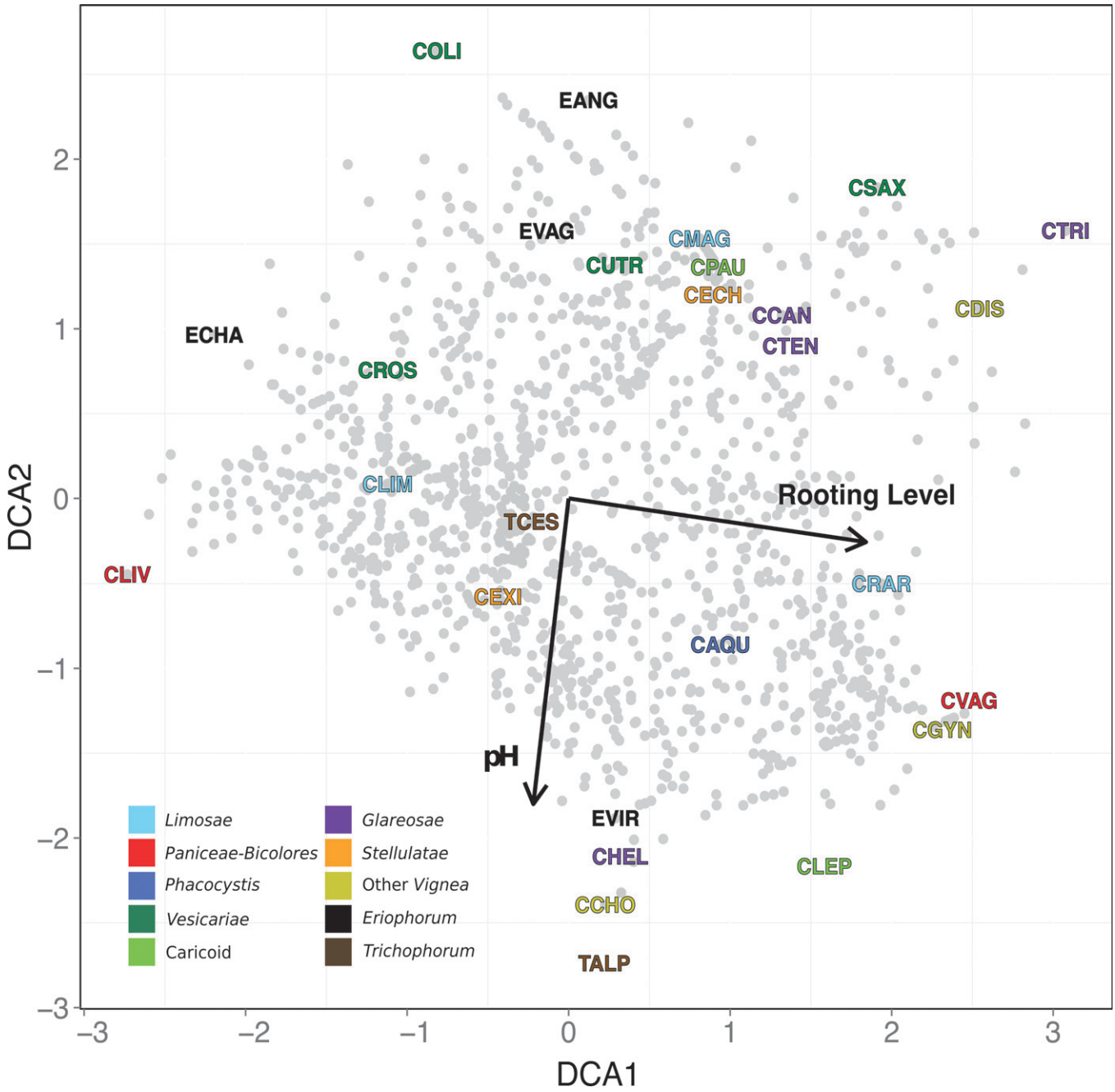


FIG. 7. Detrended Correspondence Analysis (DCA) ordination plot of the Schefferville fen data. Grey dots are used to represent the 2,124 quadrats, many of which overlap, and labels for the end points of species vectors are color-coded according to genus or sectional membership of the species. Vectors for rooting level and pH were added to the ordination diagram, depicted by black arrows, pointing in the direction of increasing values.

will be to occur together (cf. Violle et al. 2011 on testing the "phylogenetic limiting similarity hypothesis"). We discuss both the tendency for species in the same subclade to be neighbors less often than expected by chance and the tendency for suites of species that commonly occur together in particular microhabitats to be only distantly related within the CDS clade of Cyperaceae. We also comment on the importance of considering spatial and phylogenetic scale in interpreting the observed patterns.

Testing Phylogenetic Limiting Similarity—This line of inquiry arises from a longstanding expectation expressed by Darwin (1859) that the more closely related two species are, the stronger will be their struggle for existence, and by implication, the lower will be their likelihood of co-occurring as immediate neighbors. This expectation, rooted ecologically in the concepts of limiting similarity (Abrams 1983) and evolutionarily in its obverse, ecological character displacement (Stuart and Losos 2013), is deeply embedded in niche theory (Chase 2011). The relevant expectations from neutral theory (Hubbell 2001), which assumes no functional differences among species and focuses solely on dispersal limitation, are unlikely to apply in our study system except as a null model. A strong test of the phylogenetic limiting similarity hypothesis in our study system necessarily lies at the interface between the evolved characteristics of the sedge species in the regional pool and the ecological processes that

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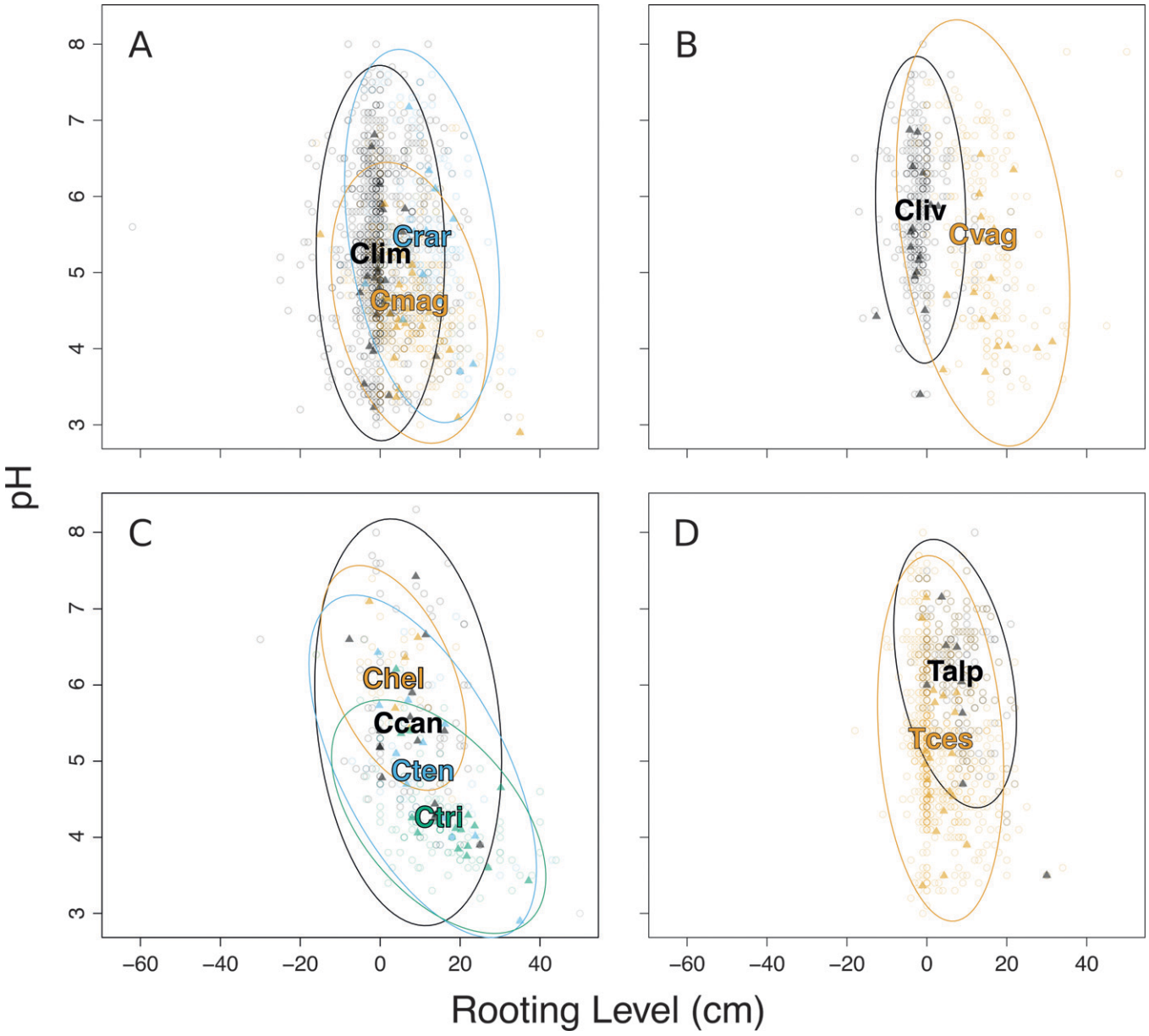


FIG. 8 Graphs of pH vs. rooting level (cm) for species within subclades showing symbols to represent quadrats where they occur (open circles), the abundance weighted means within fens (triangles) and 95% confidence ellipses for each species in different colors. A. section *Limosae* subclade. B. *Paniceae–Bicolores* subclade. C. section *Glareosae* subclade. D. *Trichophorum* subclade.

govern both community assembly and the co-occurrence of neighboring individuals within the fen habitat. The different adaptations of species in the regional pool that allow their successful colonization of the fen have arisen over time through adaptive evolution and are essentially fixed in terms of present day community assembly, although genotypic diversity within species may play some role (Violle et al. 2012; Siefert 2014). Hence, it is primarily Chesson's coexistence theory (Chesson 2000; HilleRisLambers et al. 2012) that bears most directly on the question of co-occurrence of the various species at the neighborhood scale (Stoll and Weiner 2000) within a given fen.

Chesson's analysis is framed in terms of the population dynamics of species in a community, which arise in the aggregate influence of interactions among neighboring plants. Coexistence theory predicts that co-occurrence can result from stabilizing niche differences, relative fitness differences, or a combination of these two effects. Stabilizing niche differences are attributable to traits that lead to spatiotemporal segregation among neighboring species, e.g. differences in rooting depth or timing of peak seasonal growth. Relative fitness differences in contrast originate in quantitative differences in traits that mediate competitive interactions, e.g. differences in the photosynthetic capacity or nutrient uptake rates. Using our data on the phylogenetic relatedness between neighboring plants, the distribution of sedge species along pH gradients, the levels at which the species root, and any ancillary information on the functional traits that may be available for the species, we first test the hypothesis that the likelihood of two sedge species co-occurring as immediate neighbors is inversely related to their phylogenetic relatedness against a null hypothesis of random co-occurrence.

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TABLE 7. Summary of environmental affinities for significantly aversive species pairs, giving the means of water pH and rooting level (cm) at the quadrats where the first species in the pair occurs but not the second, and vice versa. Means were calculated across all fens. Delta mean refers to the untransformed difference in these means for a given environmental parameter. Differences were tested for their significance using Tukey HSD tests ($p < 0.001$ ***, $p < 0.01$ **, $p < 0.05$ *). The table also gives the number of fens in which both species of a pair were found (# of Fens) and the percentage of those fens in which the relative relationship of the means was the same as the regional relationship for that pair (Concordance pH and Rooting Level).

	pH			Rooting Level (cm)					
	Species 1 Mean	Species 2 Mean	Delta Mean	Species 1 Mean	Species 2 Mean	Delta Mean	# of Fens	Concordance pH	Concordance Rooting Level
C. limosa-C. aquatilis	5.02	5.58	−0.56***	−1.11	9.6	−10.71***	13	46%	92%
C. magellanica-C. limosa	4.59	5.29	−0.71***	8.06	−0.15	8.21***	25	88%	96%
C. oligosperma-C. aquatilis	4.06	5.75	−1.69***	2.87	7.79	−4.92***	7	86%	43%
C. oligosperma-C. limosa	4.14	5.41	−1.27***	5.22	0.05	5.17***	14	71%	79%
C. rariflora-C. limosa	5.5	5.26	0.24*	10.93	0.03	10.91***	11	45%	100%
C. rariflora-C. magellanica	5.51	4.6	0.91***	10.51	7.25	3.26**	12	67%	83%
C. rariflora-C. oligosperma	5.48	4.07	1.41***	10.47	2.85	7.62***	7	57%	86%
C. rostrata-C. aquatilis	5.15	5.76	−0.61***	−2.8	7.97	−10.77***	11	55%	100%
C. rostrata-C. magellanica	5.25	4.6	0.65***	−3.92	7.24	−11.16***	21	86%	100%
C. rostrata-C. oligosperma	5.17	4.06	1.12***	−2.45	2.82	−5.26***	14	79%	79%
C. rostrata-C. rariflora	5.17	5.5	−0.33**	−2.43	10.74	−13.17***	11	36%	100%
C. saxatilis-C. limosa	6.15	5.26	0.89*	−14.1	0.07	−14.17***	1	100%	100%
C. utriculata-C. aquatilis	5.13	5.74	−0.61***	0.2	7.83	−7.63***	7	71%	57%
C. utriculata-C. limosa	5.1	5.25	−0.15	0.19	0.09	0.1	8	38%	62%
C. vaginata-C. livida	5.47	5.82	−0.36***	14.04	−1.63	15.67***	10	90%	100%

Second, we test whether neighboring sedge species differ significantly in ecological tolerances along two environmental gradients: water pH and rooting level in relation to the water table, both known to be important in the distribution of sedges (Gignac et al. 2004; Dabros and Waterway 2008). This uses character displacement (Stuart and Losos 2013) along environmental gradients within and across fens as an indirect test of expectations from the phylogenetic limiting similarity hypothesis. In discussing the results, we use selected examples of specific species pairs to illustrate the nature of the functional differences affecting the likelihood that sedge species in these subarctic fens do or do not occur as immediate neighbors. We then turn from the results of these general tests to discussion of selected examples of specific species pairs to illustrate the nature of the functional differences that characterize patterns of ecological speciation affecting present processes of sedge community assembly in these subarctic fens.

Species Aversion—The pairwise co-occurrence results show that nearly all of the most closely related species in the large Core *Carex* clade, especially those in the Wetland clade, show significant aversion both across fens and within them (Fig. 4). In the regional analysis, which considers the quadrats as random samples of fen habitat in the region (Fig. 4A), nine of the 10 pairwise comparisons within subclades representing sections *Limosae*, *Vesicariae*, and *Paniceae* in Core *Carex* (clade divergence level D1, which represents sister pairs or sets of very closely related species) have sample sizes large enough to test significance. Six of these show significant aversion, that is, the two species in the pair co-occur in the 0.25 m^2 quadrats much less often than expected by chance, while the others are neutral. In the analysis considering pairings within fens (Fig. 4B), five of the six pairs that show aversion in the regional analysis also occur significantly less often than expected by chance within the fens, the remaining pair being neutral. These results are consistent with expectations under phylogenetic limiting similarity.

There is, however, one apparent exception: *C. oligosperma* and *C. utriculata* show no significant aversion or attraction within fens, but the regional analysis shows their significant aversion. This is a good example of niche segregation expressed more strongly among than within the regional fens, which range from more acidic poor fens to more alkaline-rich fens (Table 1; Fig. 6). These two species are known to segregate on this pH gradient, with *C. oligosperma* favoring more acidic fens than *C. utriculata* (Gignac et al. 2004; Dabros and Waterway 2008; Table 3). Several of the acidic fens have relatively narrow pH ranges, as do several of the fens with pH means above 6 (Fig. 6), making it likely that the strong pattern of aversion shown in 21 of the 25 possible species pairs that involve *C. oligosperma* result from filtering on the gradient in pH among regional fens that precludes *C. oligosperma* colonizing the full range of fen habitats. *Carex oligosperma* also shows a predominant pattern of significant aversion with other species within fens, but the number of pairings with *C. oligosperma* that show such aversion within fens is reduced from 21 to only nine, with most of its other pairings neutral within fens. Hence this species pair is also consistent with the expectations from limiting similarity, or more appropriately from the obverse perspective of ecological character displacement (Stuart and Losos 2013) expressed in their differing pH tolerances. The two species tend to occur at different extremes along the pH gradient among the fens in the region; in the infrequent cases where they both occur in an intermediate fen along the gradient, they occupy different pH microenvironments within that fen. Similarly, in a study of co-occurrence of two sister species in *Carex* section *Racemosae* that both occur in high elevation alpine tundra in the Rocky Mountains, Massatti and Knowles (2014) found microhabitat differentiation and thus pairwise aversion between these two closely related species based on different ecological tolerances along gradients in the frequency of water-saturated soils.

A similar situation prevails when using the alternative definition of D level clade divergence (D2), in which the entire Wetland clade is considered to be closely related. This increases the number of possible D2 pairings in Core *Carex* to 29, 26 of which have sample sizes large enough to potentially show significance. Sixteen and 15 of these 26 pairings show significant aversion in the regional and fen-by-fen

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analyses, respectively, and all but three or four of the remaining pairings are neutral (Fig. 4A; Table 4). The *C. aquatilis* – *C. magellanica* pairing is significant in the regional analysis but not in the analysis within fens, probably for the same reason noted above; *C. magellanica*, like *C. oligosperma*, grows more commonly in fens with more acidic pH ranges that lack many of the other species. On the other hand, *C. limosa* is significantly less likely to occur in the same quadrat as *C. oligosperma* within fens, but not in the regional analysis pooling data from all the fens. Overall, it is apparent from the co-occurrence analyses that closely related species in the Core *Carex* clade, following either the D1 or D2 definition of clade divergence level, are not very likely to co-occur as immediate neighbors in fens of the Schefferville region. At the same time, the level of fine-scale heterogeneity in water pH and rooting level within fens is high enough that species in these pairs can both grow within many of the same fens (cf. Figure 8), although not often as immediate neighbors.

In contrast to the pattern in Core *Carex*, D-level species pairs in the *Vignea* clade (that is, within subclades representing sections *Glareosae* and *Stellulatae*) show neither significant attraction nor significant aversion in either the regional analysis or the analysis within fens, with the exception of *C. canescens* and *C. tenuiflora*, which tend to occur more often than expected by chance in both types of analysis. *Carex canescens* and *C. tenuiflora* are not sister species, but we still consider them closely related because they belong to sister clades of six and eleven species, respectively, within the larger *Glareosae* clade, a group in which all of the species are quite similar in morphology and branch lengths are short (Maguilla et al. 2015). This pairwise attraction between two species in the group is contrary to expectations from the phylogenetic limiting similarity hypothesis but akin to the finding of different patterns of co-occurrence between the Core *Carex* clade and the Core *Vignea* clade in another community phylogenetic study of sedge species in the Schefferville region (Elliott et al. 2016). However, in that study, Core *Carex* tended to exhibit clustering while the *Vignea* clade tended toward overdispersion. That study sampled a broader spectrum of habitats, including ponds, lake and river shores, dry ridges, tundra, and wet to dry forests, so the outcome of the community phylogenetic analysis may have been driven by abiotic filtering effects. In any case, it is clear from both studies that the two major clades differ in the degree to which their species can co-occur, but further research is needed to understand the exact nature and functional basis for this phylogenetic contrast.

In summary, the results of the co-occurrence analyses reject the null hypothesis that closely related species co-occur at random and agree with the expectation that closely related species in the same habitat will have diverged enough in their ecological tolerances that they are unlikely to co-occur as immediate neighbors. Results from the linear modeling also support this expectation. The best model to predict pairwise co-occurrence included the level of clade divergence, as well as both pH and rooting level in relation to the water table (Fig. 5; Table 4). Significant aversion was predicted by the model for pairings of the most closely related species (D-level divergence) and p values for divergence between subclades (C-level divergence) were 0.15 and 0.63 for the CLD1 and CLD2 analyses, respectively, suggesting that character displacement is limited to closely related species. The fact that both environmental factors were also significant further supports the idea that lineage diversification within the Wetland clade and the *Paniceae* clade has involved ecological speciation events. The BEAST analysis suggests that diversification in these flood-tolerant lineages started as early as the late Miocene and continued during the cooler and drier Pliocene and the glacial cycles of the Pleistocene; be that as it may, the species that colonized the Schefferville region in the 6,500 yr since the retreat of the Wisconsinan ice (Jansson 2003; Dyke 2004) have undoubtedly been subject to repeated cycles of glaciation throughout the Quaternary. The repeated alternation between periods of isolation in glacial refugia associated with different parent materials and recolonization of the sodden landscapes that accompanied the glacial retreats (Alsos et al. 2015; Gajewski 2015) would have provided ample opportunities for adaptive evolution and functional diversification relevant to present patterns of co-occurrence in cool wetland and peatland habitats.

Species Attraction—Expectations for significant attraction of species pairs in relation to their phylogenetic relationships are less clear. The phylogenetic limiting similarity hypothesis leaves open the question of a threshold at which relatedness no longer influences the likelihood of co-occurrence. Certainly there could be a threshold beyond which there is no longer aversion to co-occurrence, but conversely no necessity that more distantly related sedge species should have evolved characteristics that increase their chances of co-occurrence. Nevertheless, from coexistence theory (Chesson 2000; HilleRisLambers et al. 2012) we can expect that immediately neighboring individuals of different species should exploit resources in different ways, thus avoiding competition. Because of the high degree of horizontal and vertical heterogeneity in the fen environment (Rochefort et al. 2012; Macrae et al. 2013; Ulanowski and Branfireun 2013), there is ample opportunity for such functional segregation even between immediately neighboring plants. For example, the availability of N and P as the water table fluctuates seasonally is lower for plants rooted on a hummock as opposed to in an adjacent hollow (Rochefort et al. 2012; Macrae et al. 2013), but so is the risk of exposure to anaerobic conditions when water levels are high (Visser et al. 2000). Competitive interactions even for neighboring plants rooted at the same level can also be reduced by functional differences; e.g. *Eriophorum vaginatum* and *Carex aquatilis* take up nitrogen in different forms, a stabilizing niche difference (Chapin et al. 1993; Jonasson and Shaver 1999). Species from different lineages might be more likely to co-occur because they have evolved such differences or species may co-occur if one facilitates the growth of another in some way.

In this study, the most frequent set of species pairs that exhibit significant attraction root at or below the water table in areas with moderate to high pH. These species include *Carex limosa*, *C. livida*, *C. chordorrhiza*, *T. cespitosum*, *T. alpinum*, *E. chamissonis*, and *E. viridicarinatum*, all of which exhibit mutual pairwise attraction except the *C. chordorrhiza* – *E. chamissonis* pair (Fig. 4). Consistent with expectations for significant attraction, these seven species represent diverse lineages within the CDS clade: two Core *Carex* species are from distantly related subclades, one species from the *Vignea* clade, and two from each of the other genera. The two *Trichophorum* species each represent one of the two major clades within that genus (Dhooge 2005), and the two *Eriophorum* are from different subclades, both in our

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phylogenetic tree and in a larger study of the CDS clade (Léveillé-Bourret et al. 2014).

In line with the general expectations about functional diversity described above, this set of species that frequently co-occur at fine scales shows clear differences in morphology that are likely to reflect different nutrient acquisition and space-filling strategies. For example, the three midsize species have a spreading habit but differ in how they spread as well as in their root structure and position relative to the water table. Both *C. limosa* and *C. chordorrhiza* spread by laying down their aerial stems at the end of each season and sending up new aerial stems from the nodes in the following year. The roots are relatively short and near the surface of the peat in both species, but *C. limosa* has abundant matted root hairs while *C. chordorrhiza* has smoother roots likely to differ in nutrient uptake capacity (Gerke 2015). The strategy of *C. livida* is the most different of the three; it has deep, long-spreading narrow rhizomes, and white, smooth, extremely long roots that extend several cm below the water surface. *Carex livida* is also capable of forming dauciform roots, a type of cluster root that facilitates phosphorus uptake and is induced by low phosphorus levels (Gerke 2015), while *C. chordorrhiza* is not (Bérubé, Waterway and Lechowicz, unpublished data).

The *Trichophorum* and *Eriophorum* species also exhibit disparate functional traits that may facilitate their co-existence in this network of co-occurring pairs. For example, *Trichophorum* species are also mid-sized, but in contrast to the *Carex* species in this network, which spread out radially, they grow in cespitose clumps: smaller looser clumps in *T. alpinum*, and very large dense clumps in *T. cespitosum.* Not much is known about either of their nutrient acquisition strategies, but there are examples of other cespitose sedge species that can recycle nutrients within the clump or release phosphorus to the zone of active roots (Jonasson and Chapin 1991). C*arex limosa* and *C. chordorrhiza* may even facilitate the establishment of the *Trichophorum* species; mosses colonize the horizontal stems and create floating mats on which *Trichophorum* species are frequently found. The two *Eriophorum* species in this network of co-occurring pairs are both larger in stature and spread with long, relatively narrow rhizomes that connect single culms or small clumps. They tend to spread quickly with widely spaced culms so individual genets can conceivably occupy a large area for nutrient capture. C*arex rostrata,* which is also large in stature and spreads by both short and rapidly growing, long, thick rhizomes that can grow quite deep due to their high proportion of aerenchyma for oxygen transport (Visser et al. 2000), is found with the other species in the network only when the two *Eriophorum* species, which are of similar size and growth form, are absent.

Similarly, hummock microhabitats are also characterized by the co-occurrence of species representing distantly related lineages within the CDS clade of Cyperaceae, although the patterns of mutual pairwise attraction are not as strong as those described above for the wetter microhabitats like flarks and pools. Hummocks vary in pH depending on the water pH where they are found and the particular assemblages of bryophyte species that form the hummock; those richer in species of Amblystegiaceae (brown mosses) tend to be found at higher pH than those dominated by *Sphagnum* species. Sedges that prefer rooting above the water level and are generalists with regard to water pH show positive co-occurrence relationships to specialist sedge species that occur at both ends of the pH gradient, but these specialists do not co-occur with each other. For example, the generalists *C. aquatilis* (Core *Carex*) and *C. gynocrates* (*Vignea*) show significant attraction to *C. pauciflora* (Caricoid) and *C. echinata* (*Vignea*) at the lower end of the pH gradient and with *C. vaginata* (Core *Carex*), *C. leptalea* (Caricoid), and *T. alpinum* at the higher end, but the two species from the Caricoid clade have different pH preferences and show significant aversion, and most of the other pairwise comparisons between hummock species with different pH preferences are neutral (Fig. 4). Many of the species that grow mostly or exclusively on hummocks are relatively short in stature, and the rhizomes of hummock species vary from threadlike in *C. leptalea*, *C. gynocrates*, and *C. pauciflora*, to much more robust in larger species like *C. aquatilis*, in which single individuals can spread across hummocks and hollows, or cross between the strings and flarks in patterned fens.

Effects of Scale—A key consideration in this discussion has been the effect of spatial and phylogenetic scale in studies of community assembly. We have argued that ecophylogenetic insights into the process of community assembly are strengthened by assessing interactions among congeners at the neighborhood scale (Stoll and Weiner 2000), and in particular through the consideration of pairwise comparisons between immediate neighbors that can help elucidate the functional basis for their coexistence. Defining the spatial scaling of a neighborhood relevant to pairwise tests of coexistence, however, is not entirely straightforward. Sessile organisms such as plants invite the use of either focal sampling centered on a specific individual (Ricotta et al. 2015; Elliott et al. 2016) or the use of suitably small, randomly placed quadrats as in this study. Such fine-scale sampling designed to discern interactions between individual plants is in contrast to traditional approaches in plant community ecology and community phylogenetics, which emphasize the use of quadrats sufficiently large to provide a "representative sample" of the community per se. We are aware of only one previous study (Slingsby and Verboom 2006) that has used a pairwise analysis characterized as 'fine-scale' to study community assembly in congeneric plant species.

Slingsby and Verboom (2006) analyzed the patterns of co-occurrence among species of *Tetraria*, another genus with high local diversity (Slingsby et al. 2014), and four co-distributed allied genera in tribe Schoeneae (Cyperaceae). They drew on vegetation data from 921 50 m^2 plots representing different plant community types at 11 sites from across the Cape Floristic Region (cf. McDonald 1993a, b); plots contained from two to 11 (median 5) *Tetraria* species and from three to 17 (median 10) schoenoid sedges in total (cf. Supplemental Table A2 in Slingsby and Verboom 2006). They considered these 50 m^2 plots to be a suitable scale at which to evaluate co-occurrence because at this scale there was a "visually assessed homogeneity of vegetation structure and habitat" (Werger et al. 1972), although they acknowledge that this spatial scale does not directly capture interactions among neighboring individual plants. In an analysis of pairwise co-occurrence in these 50 m^2 plots, they detected evidence of significant pairwise aversion among the 15 species in the reticulate-sheathed *Tetraria* clade, but not at a broader phylogenetic scale that included other species of *Tetraria* and allied genera. Given the considerable diversity of plant community types sampled (McDonald 1993a, b)

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as well as the likely environmental heterogeneity within the 50 m^2 plots, these results may well have arisen primarily through habitat filtering rather than biotic interactions. It would be informative to carry out a study of community assembly in the fynbos region using a focal sampling approach at a neighborhood spatial scale.

Conversely, we can easily collapse our neighborhood scale data to the level of individual fens as discrete samples of a habitat type on the regional landscape. We have reanalyzed our data to consider co-occurrence at the fen level rather than the quadrat level, that is, to consider what Silvertown et al. (2006) called the β-niche or habitat niche. Because subarctic fens are discrete habitats with easily defined boundaries and environmental conditions quite different from their surroundings as well as being inhospitable to most plant species, it is therefore not surprising that in this analysis, in which each of the 29 fens was considered as a single observation of sedge species co-occurrence, most species pairs were either attractive (56 pairs) or randomly associated (293 pairs) while only two pairs were aversive (unpublished results). Both aversive pairs were also aversive in our quadrat level analyses, but most other pairs that were aversive in the quadrat level analyses showed no significantly aversive or attractive tendencies at the fen level. Two species pairs (*C. limosa* – *C. magellanica* and *C. limosa* – *C. oligosperma*), showed significant attraction at the fen level, indicating that they were frequently found in the same fens, although they only rarely co-occurred at the quadrat level. These results underscore how critical it is to consider spatial scale in evaluating patterns of co-occurrence.

The common coexistence of many sedge species in the Schefferville region in the same fens (cf. Table 3) supports habitat filtering in the regional species pool, yet at the same time, most of the closely related species that occupy these fen habitats have diverged on one or more of the important environmental gradients that structure fen communities, and as a result, they do not co-occur at a fine scale within the fens. This suggests that niche differentiation has accompanied the process of lineage divergence, which is consistent with the expectation of Silvertown et al. (2006) that β niches are more conservative than α niches and that traits that allow plants to exploit particular habitats, such as subarctic fens, trace to earlier branching events in the phylogenetic tree. The Wetland clade in Core *Carex* appears to have diverged between 7.5 (plus or minus 2.5) and 12 (plus or minus 3) million years ago, depending on the calibration used (Fig. 3; Supplemental Figs. 1, 2, available from the Dryad Data Repository at http://dx.doi.org/10.5061/dryad.q810f). Nearly all species in that clade, worldwide, grow in wetland habitats that require some degree of flooding tolerance suggesting β-niche conservatism. Evolution of adaptations to acquire nutrients at different water levels and at different water pH levels appears to have occurred frequently in the Wetland clade, with diversification in actual rooting levels and pH tolerances varying at the tips of the phylogenetic tree and allowing coexistence of species with these different α-niches within a given fen.

In summary, working at fine spatial and phylogenetic scales, we have detected pairwise co-occurrence patterns suggesting that ecological speciation events at the tips of the phylogenetic tree allow coexistence of several species in the species-rich CDS clade of Cyperaceae within subarctic fens. We suggest that such coexistence within these harsh habitats, characterized by fine scale environmental heterogeneity, results from niche differentiation among closely related species along ecological gradients of rooting level in relation to the water table and water pH such that closely related species are significantly less likely to co-occur in the same microhabitats within the fens. We have also shown that mutually co-occurring species that show significant pairwise attraction also exhibit diverse strategies for acquiring nutrients and colonizing wetter microhabitats within the fen, thus allowing stable coexistence. Ecological tolerances within species along the pH gradient ranged from moderate to broad, but all species showed high levels of flexibility evidenced by wide variance among means across the 29 sampled fens. Ranges of rooting level were much narrower. Studies on mechanisms of nutrient capture in these species, and more detailed exploration of the evolution of traits that allow coexistence at the fen scale as well as co-occurrence at the fine scale are needed to further characterize these stabilizing niche differences. Finally, working with clade divergence levels rather than phylogenetic distances allowed us to evaluate co-occurrence patterns at different levels of the phylogenetic tree and to uncover contrasting patterns between the *Vignea* and Core *Carex* clades at the same level of divergence. It is notable that linear modeling consistently showed that clade divergence level was significant in predicting co-occurrence whereas phylogenetic distance was not, even when it was the only measure of phylogenetic relationship in the model. A likely explanation for this result is that phylogenetic distance metrics inappropriately treat all branches as if they have equal support whereas only clades with significant levels of support were used to determine clade divergence level. As phylogenetic hypotheses for *Carex* become more complete and well-resolved, there will be many opportunities to assess the generality of the results described here by comparing different lineages within and between habitats at broader geographic scales.

Acknowledgments. We thank Rachel Anderson Toews, Nadia Cavallin, and Chantal Duval for field assistance; Oksana Choulik for logistic support at the McGill Subarctic Research Station in Schefferville; Christina Cho, Yaroslava Chtompel, Sofia Fuga, Anita Rogic, and Nadia Surdek, for assistance with DNA extraction and amplification, the McGill University & Genome Quebec Innovation Centre for DNA sequencing, Marcial Escudero for assistance with the BEAST analyses and advice about fossil calibration, Vahid Gazestani and Elijah Perez for help with data management, A.I. Luz for preparing Fig. 1, and Will Pearse for helpful discussions about the ecophylogenetic literature. We also thank Andrew Hipp for organizing the symposium, "Ecological diversification and niche evolution in the temperate zone's largest genus: *Carex*," in which the work in this paper was originally presented at Botany 2015, the American Society of Plant Taxonomists for funding the symposium, James Smith for managing publication of the symposium papers, and two anonymous reviewers for useful suggestions that improved the manuscript. The research was funded by an NSERC fellowship to AD, NSERC Discovery Grants to MJL and MJW, and Northern Scientific Training grants from the Department of Indian and Northern Development to AD and her field assistants.

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Appendix 1. Voucher information and GenBank accession numbers for sequence data used in this study. Taxa are ordered by genus, major clade within the genus, sectional classification, and then alphabetically by species. Each entry is in the following order: Taxon name, collection locality, collector, collection number, voucher location with herbarium acronyms following *Index Herbariorum*, and Genbank accession numbers for ETS, ITS, *matK*, and *trnL-trnF* gene regions. Missing sequences within each accession are noted by —.

Carex* L.—Core *Carex* Clade**: Section *Acrocystis* Dumort., ***C. deflexa Hornem. CANADA: Quebec, Schefferville region, *Waterway 2001.107* (MTMG), KR902928, KP980468, KP980093, KR902940. Section *Bicolores* (Tuck. Ex L. H. Bailey) Rouy, ***C. garberi*** Fernald. USA: Alaska, Nome, *Waterway 2006.233* (MTMG), KR902929, KU496603, KU496573, KR902941. Section *Ceratocystis* Dumort., ***C. viridula*** Michx. CANADA: Quebec, Bristol, *Waterway 99.082* (MTMG), AY757658, AY757597, KU496593, AY757524. Section *Chlorostachyae* Tuck. ex Meinsh., ***C. capillaris*** L. CANADA: Quebec, Schefferville region, *Waterway 97.075* (MTMG), DQ998852, DQ998905, KU496569, DQ998958; ***C. williamsii*** Britton. CANADA: Yukon, Klondike, *Waterway 96.Y46* (MTMG), KR902935, KR902920, KU496594, KU496624. Section *Lamprochlaenae* (Drejer) L. H. Bailey, ***C. glacialis*** (Drejer) L.H. Bailey. CANADA: Quebec, 25 km N of Schefferville, *Waterway 2001.114* (MTMG), AY757685, AY757625, KU496574, AY757553. Section *Limosae* (Heuff.) Meinsh., ***C. limosa*** L. CANADA: Quebec, Chisasibi, *C. Novo 1.15* (MTMG), AY757656, AY757595, KU496577, AY757522; ***C. magellanica*** Lam subsp. ***irrigua*** (Wahlenb.) Hiitonen. (1) CANADA: Quebec, Schefferville region, *Waterway 97.90* (MTMG), AY757655, AY757594, —, AY757521; (2) Finland: Lappland, *Waterway 2012.190.7* (MTMG), —, —, KU496579, —; ***C. rariflora*** (Wahlenb.) J.E.Smith. CANADA: Yukon, Klondike, *Waterway 96.Y5-24* (MTMG) KR902930, KU496608, KU496584, KR902943. Section *Paniceae* G. Don, ***C. livida*** (Wahlenb.) Willd. USA: New Jersey, Burlington Co., *Waterway 98.078* (MTMG), AY757688, AY757628, KU496578, AY757556; ***C. vaginata*** Tausch. CANADA: Labrador, ca. 12 km E of Schefferville, *Waterway 97.085* (MTMG), AY757689, AY757629, KU496591, AY757557. Section *Phacocystis* Dumort., ***C. aquatilis*** Wahlenb.USA: Alaska, Nome, *Waterway 2006.239* (MTMG), AY757651, AY757590, KU496566, AY757517. ***C. bigelowii*** Torr. ex Schwein. (1) USA: Vermont, *J. Dragon 03-91* (VT), GQ223498, AY770469, —, —, (2) CANADA: Quebec, Schefferville region, *Waterway 2006.139* (MTMG) —, —, KU496568, —; (3) GQ244699. ***C. lenticularis*** Michx. (1) CANADA: Quebec, Schefferville region, *Waterway 2006.126* (MTMG), KU377553, KU496605, —, —; (2) USA: Washington, *Waterway 97.055* (MTMG), —, —, KR902911, KR902942. Section *Racemosae* G. Don, ***C. atratiformis*** Britton, CANADA: Quebec, Schefferville, *Waterway 97.097* (MTMG), KR902926, KR902921, KR902908, KR902939. ***C. buxbaumii*** Wahlenb. (1) USA: Washington, Kittitas Co., *Waterway 97.070* (MTMG), KR902927, KU496601, —, KU496615; (2) USA: Alaska, Kenai Peninsula, *Waterway 2006.302* (MTMG) —, —, KR902907, —; ***C. media*** R. Br. CANADA: Quebec, 20 km S of Schefferville, *Waterway 2001.102* (MTMG), KU377554, KU496606, KU496580, KU496619. Section *Scirpinae* (Tuck.) Kük., ***C. scirpoidea*** Michx. CANADA: Quebec, 25 km N of Schefferville, *Waterway 2001.113* (MTMG), EF014489, AY757582, KU496587, AY757509. Section *Stylosae* (T. V. Egorova) S. Gebauer & M. H. Hoffm., ***C. stylosa*** C. A. Mey. (1) CANADA: Newfoundland & Labrador, Schefferville region, *Waterway 97.095* (MTMG), AY757652, AY757591,—, AY757518; (2) USA: Alaska, Sitka, *Waterway 2006.166* (MTMG) —, —, KU496589, —. Section *Vesicariae* (Heuff.) J. Carey, ***C. oligosperma*** Michx., CANADA: Quebec, Schefferville region, *Waterway 2002.091* (MTMG), AY757640, AY757578, KR902910, AY757505; ***C. rostrata*** Stokes, CANADA: Quebec, Schefferville region, *Waterway 2001.116* (MTMG), KR902931, KU496609, —, KU496621; (2) CANADA: Quebec, Schefferville region, *Waterway 97.083* (MTMG), —, —, KU496585, —; ***C. saxatilis*** L. CANADA: Quebec, Schefferville region, *Y. Bérubé 98.000.02* (MTMG) KR902932, KR902919, KU496586, KU496622; ***C. utriculata*** Boott, (1) CANADA: Quebec, Brome-Missisquoi MRC, *M. Mercure ALDU1* (MTMG), KR9029833, KR902918, —, KR902944; (2) CANADA: Manitoba, Churchill, York Factory, *D. Punter 09PROBE-05795*, —, —, JN966210,—; ***C. vesicaria*** L. CANADA: Quebec, Schefferville region, *M. Mercure TADV4* (MTMG), KR902934, KU496611, KU496592, KR902945.

Caricoid Clade: Section *Capituligerae* Kük., ***C. arctogena*** Harry Sm. CANADA: Quebec, 25 km N of Schefferville, *Waterway 2003.033* (MTMG), KU377551, KU496600, KU496567, KU500896 Section *Leptocephalae* L. H. Bailey, ***C. leptalea*** Wahlenb. USA: Maine, Oxford Co., *Waterway 2001.099* (MTMG), AY757690, AY757630, KR902913, AY757559. Section *Leucoglochin* Dumort., ***C. pauciflora*** Lightf. CANADA: Quebec, 20 km N of Schefferville, *Waterway 2002.098* (MTMG), AY757691, AY757631, KU496583, AY75756. Section *Nardinae* Fries, ***C. nardina*** Fries. USA: Alaska, Juneau, *Waterway 2006.185* (MTMG), KU377555, KU496607, KU496581, KU496620.

Vignea* Clade:** Section *Chordorrhizae* (Heuff.) Meinsh., ***C. chordorrhiza L.f. CANADA: Quebec, Schefferrville region, *Waterway 2001.107* (MTMG), AY757389, AY757409, —, AY757485 (2) CANADA: Manitoba, 24 km E of Churchill, *M. Kuzmina 09PROBE-05550*, —, —, JN966176, —. Section *Dispermae* Ohwi, ***C. disperma*** Dewey. (1) USA: Colorado, Clear Creek Co., *Waterway 2008.034* (MTMG), KP980279, KP980468, KP980093, —; (2) CANADA: Quebec, *A. Bond s.n.* (MTMG), —, —, —, AY757489. Section *Gibbae* Kük., ***C. gibba*** Wahlenb. JAPAN: Honshu, Kyoto Pref., Kyoto Univ. Campus, *Waterway 2004.259* (MTMG), DQ998864, DQ998917, KU500897, DQ998970. Section *Glareosae* G. Don, ***C. arcta*** Boott, CANADA: Quebec, 15 km N of Schefferville, *Waterway 2006.148* (MTMG), KU377550, KP980424, KP979877, —. ***C. brunnescens*** (Pers.) Poir. (1) USA: Alaska, Kenai Peninsula, *Waterway 2006.304* (MTMG), KP980279, —, KP980078, —; (2) CANADA: Labrador, Schefferville region, *Waterway 2006.129* (MTMG), —, KP980422, —, KU496614; ***C. canescens*** L. CANADA: Quebec, Laurentides MRC, Mont Tremblant, *A. Bond s.n.* (MTMG), AY757384, AY757406, KP980141, AY757480). ***C. heleonastes*** L.f. CANADA: Quebec, Schefferville region, *Waterway 97.078* (MTMG), AY757388, AY757418, KP980092, AY757484. ***C. lachenalii*** Schkuhr (1) USA: Alaska, Juneau, *Waterway 2006.188* (MTMG), KP980255, KP980442, —,—; (2) USA: Alaska, Valdez-Cordova, *Waterway 2006.261* (MTMG) —,—, KP980075, —; (3) USA: Alaska, Nome, *Waterway 2006.237* (MTMG), —,—, —, KU496618; ***C. tenuiflora*** Wahlenb. CANADA:

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Newfoundland &Labrador, Schefferville region, *Waterway 97.079* (MTMG) AY757386, AY757427, KP980009, AY757482; ***C. trisperma*** Dewey, CANADA: Quebec, Duhamel near Lac Doré, *Y. Bérubé 99.032* (MTMG), AY757387, AY757429, KP980079, AY757483. Section *Heleoglochin* Dumort., ***C. diandra*** Schrank, (1) JAPAN: Hokkaido, Kushiro Mire, *Waterway 4009* (MTMG), AY757377, AY757413, —, AY757473; (2) NEW ZEALAND: Auckland, *Waterway 2004.PDLGH9*, —,—, KU496570, —. Section *Ovales* Kunth, ***C. foenea*** Willd. (1) USA: Maine, *Reznicek 10928* (WIS), DQ460975, —, —, —; (2) CANADA: Quebec, Mont St. Hilaire, *B. Gilbert 53.1.4.1* (MTMG), —,KU496602, KU496572, KU496616. Section *Physoglochin* Neck. ex Dumort., ***C. gynocrates*** Wormsk. CANADA: Quebec, Schefferville region, *A. Dabros s.n.* (MTMG), AY757383, AY757417, KU496576, AY757479. Section *Stellulatae* Kunth, ***C. echinata*** Murr., USA: Maine, Oxford Co., *Waterway 2001.*101 (MTMG), AY757381, AY757415, KU496571, AY757477; ***C. exilis*** Dewey, CANADA: Newfoundland & Labrador, Schefferville region, *Waterway 2001.103* (MTMG), AY757382, AY757416, KR902912, AY757478.

Siderostictae* Clade**: Section *Siderostictae* Franch. ex Ohwi, ***C. grandiligulata Kük. (1) China: Shaanxi province, *Wenli Ji 2008.2-018* (MTMG), KU377552, KU496604, KU496575, —; (2) China: Shaanxi province, Wenli Ji 2008.2-004 (MTMG), —, —, —, KU496617; ***C. pachygyna*** Franch. & Sav. JAPAN: Honshu, Okayama Pref., Okayama-shi, Kakehata, *Waterway 2004.225* (MTMG), DQ998882, DQ998936, KU496582, DQ998989; ***C. siderosticta*** Hance, JAPAN: Honshu, Gunma Pref., Usui-gun, Matsuida-cho, *Waterway 2004.268* (MTMG), DQ998892, DQ998946, KU496588, DQ998999. Section *Surculosae* Raymond, ***C. tsiangii*** F. T. Wang & Tang. CHINA, Zhejiang, Hangzhou Normal University greenhouse, *Waterway 2012.092* (MTMG), KU377556, KU496610, KU496590, KU496623.

Eriophorum L.—***E. angustifolium*** Honck. CANADA: Quebec, Squaw Lake, Schefferville, *Waterway 2001.118* (MTMG), DQ998896, DQ998950, KU496596, DQ999003. ***E. brachyantherum*** Trautv.& C. A. Mey. CANADA: Quebec, Schefferville region, *Waterway 2006.125* (MTMG), KR902936, KR902924, KR902916, KU496625; ***E. chamissonis*** C. A. Mey. CANADA: Quebec, Schefferville region, *Waterway 2002.087* (MTMG), KR902937, KR902923, KR902914, KR902946; ***E. scheuchzeri*** Hoppe, CANADA: Quebec, Schefferville region, *Waterway 2001.105* (MTMG), KU377557, KU496612, KU496597, KU496626; ***E. vaginatum*** L. CANADA: Quebec, Schefferville region, *Waterway 2002.094*, (MTMG), KU377558, KU496613, KU496598, AY757692**.** ***E. viridicarinatum*** (Engelm.) Fernald, CANADA: Quebec, Schefferville region, *Waterway 2001.115* (MTMG), KR902938, KR902925, KR902915, KR902947.

Trichophorum L.—***T. alpinum*** (L.) Pers. CANADA: Quebec, Schefferville region, *Waterway 2001.110* (MTMG), AY757400, AY757432, KR902917, AY757496. ***T. cespitosum*** (L.) Hartm. CANADA: Quebec, Schefferville, *Dabros s.n.* (MTMG), DQ998897, DQ998951, KU496599, DQ999004.

Outgroup—*Dulichium arundinaceum* L. CANADA: Ontario, Glengarry Co., Cooper Marsh, *Waterway 2003.052* (MTMG), DQ998895, DQ998949, KU496595, DQ999002.

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