

Assembly of the Arctic flora: Highly parallel and recurrent patterns in sedges (*Carex*)¹

Matthias H. Hoffmann², Sebastian Gebauer, and Torsten von Rozycki

PREMISE OF THE STUDY: Understanding the origin of ecosystems and their changes through time is important. Two mutually contrasting types of grasslands existed in the Arctic: dry- and cold-adapted grasslands of the Pleistocene dominated by Poaceae species, and presently dominating graminoid grasslands composed of sedges and rushes. We studied the taxon recruitment of the Arctic flora for *Carex*, the most species-rich and widespread genus of the Arctic. In this study we explore the possible geographical and altitudinal origins of the species, their ecological provenance in terms of soil moisture and light requirements, and salt tolerance.

METHODS: We addressed these questions in a phylogenetic context using the latest megaphylogeny of *Carex* comprising almost all Arctic species and about half of the genus' total species diversity. Ecological data were extracted from the literature and analyzed for each clade comprising Arctic species.

KEY RESULTS: Arctic *Carex* species were observed in 48 independent lineages. Almost all areas north of the meridional zone of the Northern Hemisphere may have served as sources of Arctic lineages. Source areas are unrelated to the distribution within the Arctic. Arctic species evolved in lowland and high mountain clades; mostly in wet, rarely in dry adapted clades that occur principally in open conditions. Salt tolerant Arctic species occur in five clades.

CONCLUSIONS: Many independent lineages of different geographical areas and ecological backgrounds provided species for the northernmost ecosystem; clear main sources were not discernible. *Carex* shows the whole dynamic of ecosystem assembly from a seemingly simple immigration of preadapted species, evolution in geographical distant areas, to species radiations in the North.

KEY WORDS Arctic; *Carex*; Cyperaceae; ecosystem assembly; ecological origin; grasslands; molecular phylogeny; parallel evolution; wetlands

Understanding the history and origin of ecosystems as well as comprehending their structural and compositional changes through time are important research fields in natural sciences; these fields are at the intersection of biogeography, ecology, phylogenetics, and evolution (e.g., Pennington et al., 2004; Crisp, 2006). Studies on the past and present vegetation indicated that two mutually contrasting types of grasslands existed in the Arctic: dry- and cold-adapted (cryo-xerophilous) grasslands of the Pleistocene dominated by members of the family Poaceae (true grasslands, tundra-steppe), and presently dominating graminoid grasslands composed of sedges and rushes in which true grasses play a minor role (e.g., Yurtsev, 1962, 2001; Alfimov and Berman, 2001; Guthrie, 2001; Blinnikov et al., 2011). Some authors considered that the true cryo-xerophilous grasslands, in which the now extinct megaherbivores (i.e., herbivorous megafaunal mammals) dwelled, have no recent analogs and argue that most

similar vegetation types are confined to rather dry, southerly exposed slopes and bluffs, mainly of the Amphi-Beringian region (Yurtsev, 2001; Blinnikov et al., 2011). In contrast, the graminoid grassland is presently widespread across the Arctic. Particularly, *Carex* species are dominant and abundant for many of these different Arctic plant communities covering vast areas (CAVM Team, 2003; Kade et al., 2005; Reynolds et al., 2005). Some species of *Carex* and other members of the graminoid grassland were addressed in several phylogeographic studies, which revealed considerable migrations, the existence of a number of refugia across the Arctic, as well as isolation and gene flow among Arctic and non-Arctic populations of these species (e.g., Stenström et al., 2001; Schönschwetter et al., 2006, 2008; Volkova et al., 2008; Westergaard et al., 2011). However, these phylogeographic studies cover only the last tens of thousands of years of vegetation development of the Arctic, where these species were already present in the northernmost ecosystem. By contrast, the evolutionary origin of the arctic species of *Carex* is still largely unknown (Abbott and Brochmann, 2003; Blinnikov et al., 2011, but see Dragon and Barrington, 2009; Gebauer et al., 2014). The aim of this study is to fill this gap of knowledge. In particular, we want to reveal putative

¹ Manuscript received 2 April 2017; revision accepted 3 August 2017.

Martin Luther University Halle-Wittenberg, Institute of Biology, Geobotany and Botanical Garden, Am Kirchtor 3 06108 Halle, Germany

² Author for correspondence (e-mail: matthias.hoffmann@botanik.uni-halle.de)
<https://doi.org/10.3732/ajb.1700133>

areas of origin and the ecological background in terms of altitude, soil moisture, and light requirements from which the arctic species may have been recruited.

The arctic flora comprises about 2800 species (Elven et al., 2011). *Carex* (sedges) is the most species-rich genus in the Arctic, having 165 taxa of 136 species growing in the northernmost ecosystem and are here termed the Arctic *Carex* species, irrespective of endemism to the Arctic or frequency of occurrences in the Arctic (e.g., Hoffmann and Röser, 2009; Elven et al., 2011). Furthermore, *Carex* belongs to one of the most species-rich genera of the world. In the latest treatment of *Carex*, about 2000 species were estimated to belong to the genus, including those species from the segregate genera *Cymophyllus*, *Kobresia*, *Schoenoxiphium*, and *Uncinia* (Global *Carex* Group, 2015, we follow this broad circumscription of the genus here and include *Kobresia* in *Carex*). *Carex* is a rather difficult genus taxonomically. Early monographers of the genus—Kükenthal (1909), Kreczetowicz (1935), or Mackenzie (1931–1935)—realized that many morphological characters are seemingly highly homoplastic, therefore preventing a comprehensive and rather unambiguous subdivision of this large genus into smaller manageable units such as subgenera or sections. In the meantime, a considerable number of molecular phylogenetic studies have become available (reviewed in Gebauer et al., 2015 and Global *Carex* Group, 2016) culminating in the largest molecular phylogeny available of the Global *Carex* Group (2016), which included 2146 individuals from 996 species covering about half of the genus' species richness. The molecular studies revealed that many morphology-based classifications of *Carex* were paraphyletic, albeit generally the majority of species were properly placed according to their relationship. However, the studies also revealed that many species were molecularly not strongly differentiated, and thus seemingly paraphyletic and probably of very recent origin (e.g., Dragon and Barrington, 2009; Gebauer et al., 2014; Maguilla et al., 2015; Villaverde et al., 2015a; Massatti et al., 2016).

In terms of distribution, *Carex* seems to grow abundantly almost everywhere, with the exception of tropical rain forests and deserts, where the genus is represented by only a few species (Kükenthal, 1909; Reznicek, 1990). A rather high number of species occupies large temperate-to-boreal circumpolar distribution ranges (e.g., *C. canescens* L., *C. rostrata* Stokes) and some species even have bipolar distributions (e.g., Escudero et al., 2010; Villaverde et al., 2012, 2015a, b; *C. maritima* Gunn., *C. magellanica* Lam.). These species contrast with many species occupying very small and restricted distribution ranges. A comparable pattern may be observed for the abundances of the species, as well as their ecological tolerances. For example, *C. aquatilis* Wahlenb., which has many millions of individuals, dominates many plant communities in wet conditions across the Arctic (Kade et al., 2005), whereas *C. heleonastes* L.f. has a similarly large distribution range but is rare throughout its range (Hoffmann and Welk, 1999). Some species have very wide ecological tolerances and may grow in bogs as well as dry meadows (e.g., *C. flacca* Schreb.). Others are restricted with respect to soil and moisture conditions (e.g., *C. fimbriata* Schkuhr on serpentine soils and *C. specuicola* Howell in hanging gardens, Reznicek and Murray, 2013). Some *Carex* species grow almost exclusively in forests, others only in open conditions, and still others may occupy both sunny and shady habitats. Many species are restricted to the alpine belt, others to lowland areas, and still others grow from lowlands to high mountain areas. Some studies have shown considerable niche conservatism in the genus (Waterway et al., 2009, 2016; Gehrke and Linder, 2011; Gebauer et al., 2014), but also parallel differentiation and shifts in soil moisture and other

microhabitat requirements were reported (Waterway et al., 2009, 2016; Massatti and Knowles, 2014).

Considering the relatively high number of *Carex* species in the Arctic, the available phylogenetic tree of the genus (i.e., Global *Carex* Group, 2016) and occurrences in almost all environmental conditions in southern adjacent areas to the Arctic make *Carex* a suitable genus for the study of a biome assembly (i.e., the origins of important components of an ecosystem). Additionally, the Arctic is particularly suitable for studies of this kind because it is a relatively young and new type of ecosystem in Earth's history, dating to about 3 million years before present (e.g., Zachos et al., 2001). Important places of origin for the arctic flora inferred previously include wetlands (*Ranunculus*, Hoffmann et al., 2010; *Carex* sect. *Vesicariae* and allies, *Carex* sect. *Phacocystis*, Gebauer et al., 2014; Hoffmann and Gebauer, 2016), high mountains (*Pedicularis*, Tkach et al., 2014), and steppes (*Artemisia*, Tkach et al., 2008a, b). In *Carex* sections *Vesicariae* and *Phacocystis*, a replicate pattern of origin and diversification of Arctic clades were observed (Gebauer et al., 2014; Hoffmann and Gebauer, 2016). Given the large number of Arctic *Carex*, it seems likely that the above-mentioned sources served multiple times for the origin of arctic species and lineages. Thus, the aim of this study is to infer the origins of the Arctic *Carex* species within the framework of the phylogenetic tree of the Global *Carex* Group (2016).

The ideal background to perform such analyses would be to have a fully resolved and almost complete phylogenetic hypothesis (Waterway et al., 2009), well-structured distribution ranges, and an equally well-known ecology of the species. For the large and worldwide distributed genus *Carex*, these data are not yet available. The phylogenetic tree possesses many polytomies and some clades were only moderately supported. However, with the exception of five species, the phylogenetic tree comprises all *Carex* species reported for the Arctic and is thus suitable to address our objectives. Considering the more than 2000 species in total, or the approximately 1000 species of the phylogenetic tree, the mapped distribution ranges on the basis of 369 TDWG level 3 areas (TDWG—Taxonomic Database Working Group; Brummitt, 2001; Govaerts et al., 2016) form a continuum with respect to range size and location of the ranges (personal observation). For easier comprehension, it might be possible to reduce these detailed maps into a few categories, but this would introduce an undesirable amount of subjectivity and loss of information. The available information on the species ecology diverges greatly, ranging from detailed information on soil, moisture, light requirements, and altitudinal distribution, to very scarce data noting only that the species, for example, grows in 'mountains'. Usually, for widespread species of the colder regions, more information is available than for narrow endemics of southern areas. In spite of some data limitations, the species' ecological amplitudes along the soil moisture gradient (dry to boggy), the altitudinal gradient (plains to nival), and the light requirements (deep forest to open steppe or tundra conditions) may be recorded. Given the large number of *Carex* species, their very unequal distribution ranges, and ecological requirements, it cannot a priori be expected that a clear-cut picture on the provenance of the arctic species will emerge. Instead, it is to be expected that the different clades consisting of arctic species may show some common ground, but also some differences, forming a continuum of possibilities from which arctic species may have recruited.

MATERIALS AND METHODS

Phylogenetic tree—We used a tree comprising 2146 individuals of 996 *Carex* species plus four outgroup taxa (reference tree, supplemental

material 5 of Global *Carex* Group, 2016). The application of the whole tree instead of an aggregated tree that comprises one individual per species has the advantage of indicating which clades may be weakly supported because of infraspecific sequence divergence. The disadvantage is that some clades comprising many sequences from a single species, like that of *Carex* sect. *Glareosae*, will be visually overrepresented in the figures.

Selecting appropriate clades for analyzing the origin of the Arctic *Carex* species is difficult and admittedly sometimes arbitrary. The phylogenetic tree of that size has very different branching patterns, ranging from well-resolved and statistically well-supported clades, to large nested polytomies (i.e., polytomies that are situated in other polytomies). Therefore, three approaches for an objective selection of clades were assessed. (1) Theoretically, a character mapping of the states “Arctic” vs. “non-Arctic” on the tree may guide clade selection for further analysis. However, multiple individuals in some branches affect the stochastic character optimization as calculated in the R statistical package (R Core Team, 2014) using the ‘phytools’ package (Revell, 2012, 100 simulations, symmetric model). These multiple individuals force a different likelihood of being ‘Arctic’ onto internal nodes than in cases where only a single individual was available for analysis. The continuous range of likelihood values provides no unambiguous criterion for group selection and they are also ‘blind’ with respect to the support values of the nodes. (2) The bootstrap support alone likewise provides no unambiguous criterion for clade selection, particularly, if multiple individuals were included in the analysis. (3) An approach using every possible clade of the tree for calculations is not yet feasible, because a number of species are still absent from the tree.

Because these criteria cannot accommodate all branching patterns encountered in the tree, the selection of Arctic clades for further analyses was performed manually using the following principles: The clade has at least one Arctic and one non-Arctic taxon. If there were multiple individuals from a species, the clades were defined to include all individuals of a species. Lower nodes consisting of further non-Arctic species were included for analysis if these species belong to that evolutionary lineage, as revealed by other studies dealing with these particular groups of *Carex* (as reviewed in Global *Carex* Group, 2015 and Gebauer et al., 2015). If such studies were not available, current sectional affiliation and morphological similarities were used for the decision to include or exclude non-Arctic sister groups. If there were no clear sister relationships among two or more Arctic species of a clade, they were assigned to one clade and subsequently counted as one independent Arctic lineage. Species nested in polytomies were treated as one clade wherever possible. Clades in polytomies were considered separately if joining the clades would strongly inflate the number of species to be considered for calculations, or if it would include obviously divergent lineages in this group. Thus, the total count of independent lineages possessing Arctic species represents a minimum estimate; the number may increase as more species are added to the tree or a better resolution is achieved. This approach is slightly different than in Hoffmann and Röser (2009) where the focus was on counting independent Arctic lineages. In this study, we want to count not only the number of lineages that provided Arctic species, we also want to select clades for additional analyses with respect to their putative areas of origin and their preferred ecological conditions. The inclusion of many non-Arctic sisters to the clades was useful for such calculations.

The naming of the clades comprising Arctic taxa follows these premises: (1) If the clade consists completely or overwhelmingly of

species from a traditionally defined section of *Carex*, then the current sectional name is used. (2) If a clade contains only a part of a section, then a specific name is added to the sectional name. (3) If specific clades were named and addressed in previous publications, that name is retained. In some cases the specific name of an Arctic species or combinations of Arctic species names were used for identification.

Distribution data—We used the World Checklist of selected plant families of Cyperaceae to study the distribution of *Carex* (Govaerts et al., 2016). This database records the occurrences of all species in the specified TDWG (Brummitt, 2001) level 3 areas, consisting worldwide of a total of 369 areas.

Ecological data—Ecological data were usually reported in floristic works and are suitable to characterize the species’ ecological requirements. Because we are focusing on the Arctic species, it was not necessary to collect data for every species included in the phylogenetic tree, only for the clades comprising Arctic species. We used the following main sources: Flora of North America (Flora of North America Editorial Committee, 2002), Flora Sibiri (Krasnoborov et al., 1990), Flora of the Russian Far East (Charkevich, 1988), Hoshino and Masaki (2011), Flora of China (Flora of China Editorial Committee, 2010), Flora of Pakistan (2016), Flora of New Zealand (Moore and Edgar, 1970), and Flora of Switzerland (Info Flora, 2016). These publications provide data for 769 taxa. Data for an additional 93 species were manually collected in the literature using a wide array of sources such as local floristic treatments, ecological studies, older standard treatments (e.g., Kükenenthal, 1909), or data from herbarium labels for rare and endemic species.

In this study, we focus on the species’ soil moisture requirements and altitudinal distribution, as well as their growth in forests or under open conditions. Furthermore, we study which clades may have evolved salt tolerance. Soil moisture, altitudinal distribution, and shade tolerance each form a gradient. In the data set collected from the above-mentioned literature, the gradients were semantically divided into various categories describing the species’ preferences unless numeric ranges were indicated, e.g., the altitudinal distribution. The latter is unfortunate for this purpose, because the numbers or spans are difficult to translate into altitudinal belts because of their latitudinal dependence. Regardless of the original language used in the literature (cited above), the extreme categories can easily be extracted. In contrast, the different terms used across the texts for the intermediate conditions of the gradients were difficult to align and may best be merged. Therefore, for each environmental gradient, three categories can be derived. For soil moisture it is dry, moist, and wet—including boggy and swampy conditions. The altitudinal gradient can be described by alpine (including nival and subalpine), mountainous (colline to montane), and lowlands. There are also three categories for shade tolerances: open conditions, forest occurrences, and an intermediate category consisting of occurrences in shrub formations or the margins of forests.

Calculations—An objective of this study was to infer the ecological preferences of the different clades along the altitudinal, moisture, and light gradients. For this purpose we tested ‘cladewise’ if significant agglomerations of ecological preferences occur (prop.test of the R statistical package, R Core Team, 2014). If there were data available for every species of a clade, the calculation would be straightforward, but for some species, only incomplete data were available, for example, the

altitudinal distribution is known, but not the soil moisture requirements. The test of differences for proportions may still be calculated for that clade, using a randomization of ecological preferences for the species with missing data. Species with missing data were assigned randomly to one of the seven possible ecological combinations: occurrence in one of the three categories, to occurrences in two categories, and finally, having a very broad ecological constitution occurring in all of the three categories. The randomization was run 1000 times and the percentage of significant differences ($p < 0.05$) was calculated, similarly as in bootstrap analyses. The percentage of significant differences shows how stable the observed differences of proportions are and if the proportions may change upon availability of ecological data for the species with currently unknown ecological preferences.

RESULTS

Arctic species in the phylogeny—The Panarctic Flora Checklist (Elven et al., 2011) lists 165 taxa of *Carex* occurring in the Arctic: 136 species plus 29 infraspecific taxa (treated as varieties or subspecies). The phylogenetic tree of the Global *Carex* Group (2016) comprises all but five Arctic species, i.e., 96% of the Arctic species were included. Missing are *C. recta* Boott and *C. rufina* Drejer from *Carex* sect. *Phacocystis* (Northern radiation), *C. minuta* Franch. [sometimes treated as *C. cespitosa* L. var. *minuta* (Franch.) Kük. or placed under synonymy of *C. cespitosa*] also from *Carex* sect. *Phacocystis* [*C. nigra* (L.) Reichard clade], and *C. arctogena* Harry Sm. from *Carex* section *Capituligeræ* (the clade of *C. capitata* Sol.). The affiliation of *C. concinna* R.Br. with one of the clades of the tree cannot currently be established.

The Arctic species belong to 48 different clades, which were nested within otherwise non-Arctic lineages (Appendix S1, see Supplemental Data with this article). Four additional Arctic taxa were situated in polytomies and may represent additional independent lineages, but may also belong to 1 of the 48 clades. Thus, the 48 clades represent the minimum number of independent Arctic lineages evolved in the genus *Carex*. These lineages comprise either a single Arctic species or even 22 Arctic species as in *Carex* sect.

Glareosae (mean three Arctic species and median two Arctic species per lineage, respectively).

Distribution of the Arctic species—The highest species numbers of *Carex* in the Arctic were observed in Alaska and adjacent areas (Fig. 1). Less species-rich were Chukotka, the regions east and west of the Polar Ural mountains and the amphi-Atlantic region. The most continental parts of Arctic Eurasia and America and the Arctic islands possess a lower number of *Carex* species than the oceanic areas. Twenty-eight out of the 165 taxa were confined to the Arctic and immediately adjacent areas, and might have evolved in the Arctic. There is only one taxon almost completely restricted to the Arctic—*C. marina* Dewey subsp. *pseudolagopina* (T. J. Sørensen) Böcher, and perhaps some taxa of questionable taxonomic value. Most diverse of these nearly endemic species are the *Glareosae* (six taxa), and to a lesser extent, the northern radiations of the *Phacocystis* (three taxa), and *Vesicariæ* (two taxa), but also the *Racemosae-Buxbaumii* group (two taxa). Other clades have only a single or no species confined to the Arctic.

For 46 clades, the centers of highest species number were assessed (Table 1). Fifteen clades were centered in North America, 6 in Europe, 13 in Asia, 1 in the amphi-Atlantic region, 2 in the northern circumpolar region, and for 10 clades, a clear geographic distribution center was not discernible. Figures 2–4 indicate approximately where the area of highest species number is situated. Many of the clades have diversified in the eastern or western parts of North America, but also in the more north-central part of the continent. The *Ceratocystis* clade has an amphi-Atlantic distribution with roughly the same number of species in eastern North America and Europe. The European clades partly have an affiliation with either mountain areas (e.g., *Microglochin*) or lowlands (*Ammoglochin*). Many Asian clades are centered along the Tian Shan-Himalayan mountain chains; some have their center in Central Asia (*Racemosae-Sabulosa* clade, *Petricosa* clade). For Asia it is interesting that no clade shows a clear center of diversity in Japan and adjacent China, nor in the Russian Far East. Of the widespread northern centered clades, the *Glareosae* and the northern radiation of the *Vesicariæ* have no clear diversity center, whereas the *Limosae* have a weak center in North America and the *Chlorostachyæ* in Northern Asia, but have a

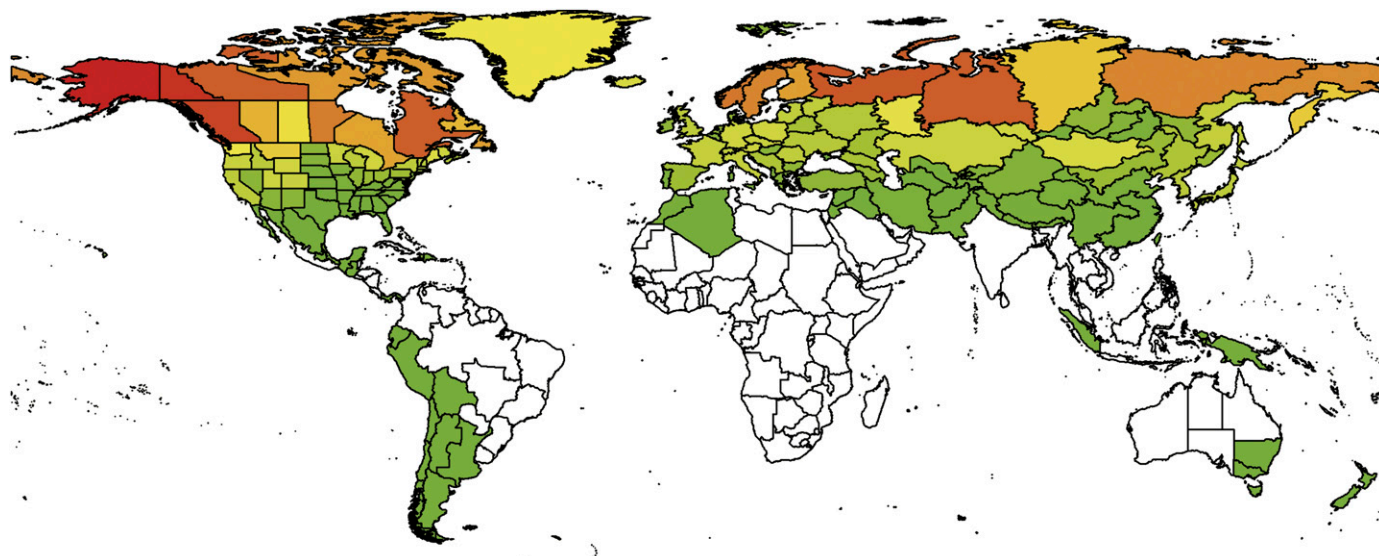


FIGURE 1 Map of the joint distribution of the 165 taxa of 136 *Carex* species reported to grow in the Arctic in the 369 TDWG level 3 areas (see text). The color codes are from green—one species to red—97 taxa in Alaska.

TABLE 1. Number of species in the studied clades, their support in the phylogenetic tree, their diversity centers, distribution in the Arctic, and number of missing data for the calculations of ecological preferences, *p* values of the tests of proportions and, where applicable, the bootstrap values (BS) of these calculations. The ecological preferences were shown in Figs. 2–4. Abbreviations used for the diversity centers and the distribution in the Arctic were the abbreviations for the directions and M—Middle, C—Central, NAM—North America, EUR—Europe, AS—Asia. Brackets indicate a weak center or, if applicable, the occurrence of only one to a few species. If a cell is empty, a clear center was not discernible.

Clade	Node support	Nr. Arctic taxa	Nr. non-Arctic taxa	Diversity center	Distribution in the Arctic	Soil missing data	Soil <i>p</i> value	Soil BS	Altitude missing data	Altitude <i>p</i> value	Altitude BS	Light missing data	Light <i>p</i> value	Light BS
Phacocystis Northern Radiation	85	8	7	NAM	Circumarctic	3	<0.001	100	4	0.012	70	6	<0.001	96
Phacocystis Bigelowii	78	2	5		Circumarctic	0	0.032		4	0.734	3	0	<0.001	
Phacocystis Nigra	76	7	9	EUR	EURAS - (Amphi-Atlantic)	2	0.002	100	11	0.35	14	5	0.04	65
Phacocystis Scitae	85	4	2	W-NAM	Amphiberlingian	1	0.012	73	1	0.024	59	0	0.001	
Limosae	87	6	2	(NAM)	Circumarctic	0	<0.001		5	0.777	3	0	0.001	
Stylosae	91	2	1		Amphiberlingian- Amphi-Atlantic	0	0.076		2	0.526	14	0	0.011	
Scirpoidea	93	2	2	W-NAM	NAM-E-AS	2	0.264	18	3	0.549	8	3	0.549	9
Gloularis	90	1	50	E-NAM	EURAS	16	0.702	1	39	0.225	11	16	<0.001	100
Atherodes	97	1	9		Circumarctic	0	0.044		4	0.475	2	1	0.054	57
Lasiocarpa	98	1	8	E-NAM	NAM-EUR	0	0.03		4	0.145	20	2	0.06	54
Vesicariae	92	6	6	Circumpolar North	Circumarctic	1	<0.001	100	4	0.877	18	1	0.027	85
Ceratocystis	99	5	12	Amphiatlantic	Amphiatlantic - (disjunct)	5	<0.001	100	7	0.177	18	2	<0.001	100
Chlorostachya	100	4	1	Siberia	Circumarctic	0	0.343		1	0.435		0	0.287	
Racomosae Atrosquama	77	1	7	W-NAM	WNAM	1	0.006	100	6	0.319	13	2	<0.001	98
Racomosae Sabulosa	91	1	5	C-AS	disjunct	1	0.799		1	0.105	42	0	0.105	
Racomosae Gmelinii	84	1	2	E-AS	Amphiberlingian	0	0.223		0	0.638		0	0.043	
Racomosae Atrata	78	3	5		Circumarctic	1	0.504		2	0.005	93	1	0.03	72
Racomosae Buxbaumii	100	3	1		Circumarctic	0	0.072		0	0.254		0	0.012	
Bicolores Paniceae	99	6	29		Circumarctic	3	0.005	100	27	0.323	9	1	<0.001	100
Melanocarpa	89	2	3	EUR	EURAS	2	0.435	7	1	0.153	27	1	0.153	31
Fulgiosa	100	1	2	M-AS-(Himalaya)	Circumarctic	0	0.011		1	0.223	30	0	0.011	
Atrifusca	100	1	3	Himalaya	Circumarctic	1	0.254	14	1	0.254	14	1	0.687	
Acrocystis Umbellata	99	1	5	E-NAM	Greenland	0	0.004		5	0.347	6	0	0.002	
Acrocystis Deflexa	86	1	6	W-NAM	NAM-Greenland	0	0.817		3	0.159	20	0	0.032	
Petricosa	98	1	6	Tianshan-Himalaya	AS-NAM	1	0.263		2	0.122	22	0	0.424	
Glacialis	97	3	5	EUR	Circumarctic	1	0.118	28	2	0.817		0	0.002	
Clandestinae	93	5	5	E Himalayan-Tibetan-SW Chinese	EURAS	4	0.013	48	2	0.005	93	0	0.303	
Albae	100	2	3	E-AS	disjunct	1	0.036	73	2	0.092	36	0	0.036	
Glareosae	100	22	7	Arctic	Circumarctic	2	<0.001	100	8	0.014	73	2	<0.001	100
Armmoglochin	77	1	4	EUR	WEURAS	1	0.031	72	3	0.562	4	2	0.435	9
Physoglochin	100	3	1	(NW)-EURAS	Circumarctic	0	0.71		0	0.072		0	0.018	
Divisae	100	1	2	C-AS	Amphiberlingian	0	0.325		1	0.223	30	0		
Chordorrhiza Glareosae	93	4	2		Circumarctic	0	<0.001		5	0.347	7	0	0.05	
Dispermae														
Stellulatae	93	4	6	E-NAM	NAM-EUR	0	0.001		7	0.383	10	0	0.001	
Ovales	99	4	80	NAM	NAM-(Amphi-Atlantic)	11	0.008	97	46	0.005	55	10	<0.001	100
Heleoglochin	96	1	2	(W)-NAM	Circumarctic	0	0.076		1	0.638		0	0.043	
Accrescens	100	1	9		E-AS	1	0.054	57	7	1	2	0	0.001	
Foetidae Maritima	99	1	3		Circumarctic	0	0.71		0	0.05		0	0.012	
Dornera Leucoglochin	90	3	5		(Amphiberlingian) - NAM - (Amphi-Atlantic)	1	0.202	14	2	0.005	93	0	0.002	

continued

TABLE 1, continued

Clade	Node support	Nr. Arctic taxa	Nr. non-Arctic taxa	Diversity center	Distribution in the Arctic	Soil missing data	Soil p value	Soil BS	Altitude missing data	Altitude p value	Altitude BS	Light missing data	Light p value	Light BS
Anthoxantha	86	1	4	W-NAM	Amphiberingian	0	0.435		3	0.099	20	1	0.004	85
Nardinae	98	3	11	W-NAM—Mexico	(Amphiberingian) - NAM - (Amphi-Atlantic)	10	0.052	20	12	0.592	5	9	0.003	44
Capitulgerae	84	3	6	(mountains of Eurasia)	Circumarctic	1	0.136	28	4	0.099	33	2	0.145	31
Simpliciuscula	99	2	4	Himalayan-Tibetan	Circumarctic	0	0.393		3	0.027	33	0	0.207	
Microglochin	93	2	4	EUR	WEURAS-AM	3	0.792	4	1	0.014	70	1	0.012	70
Myosuroides	100	2	20	E Himalayan-Tibetan-SW Chinese	Circumarctic	1	0.004	100	5	<0.001	100	1	<0.001	100
Psyllophora	94	1	6	EUR	EUR	3	0.497	3	3	0.159	17	0	0.017	

continuous circumarctic distribution. The geographical positions of diversity centers of the clades were not related to the distribution of the species in the Arctic. In some of the clades having centers in western and eastern North America, Europe, or Eastern Asia, widespread and almost circumarctic species may have evolved. In contrast, other clades having these centers of diversity possess Arctic taxa that were more or less restricted to Arctic regions close to their center of diversity. Thus, a general pattern is not obvious.

Altitudinal distribution—origin of Arctic *Carex* in lowlands and high mountains (Fig. 2, Table 1)—A high mountain origin may be the case for the arctic species of the *C. atrata* L. clade of *Carex* sect. *Racemosae*, *C. atrofusca* Schkuhr, and *C. fuliginosa* Schkuhr of the *Atrofusca* clade (*Carex* sect. *Aulocystis*), as well as the *Myosuroides* clade (formerly *Kobresia myosuroides*). Less statistically supported were a high mountain origin of the *Maritima*, *Dornera-Leucoglochin*, *Microglochin*, and *Simpliciuscula* clades. The western North American *Anthoxantha* and *Phacocystis-Scitae* clade may also be of high mountain origin, but could not readily be included in the analysis because of the availability of numeric altitudinal data. Of lowland origin may be the species of the northern radiation of *Carex* sect. *Phacocystis*, and the *Lasiocarpa* and *Carex* sect. *Glareosae* clades. The altitudinal center of diversity in middle elevations may be observed in, e.g., the *Clandestinae* clade. It may be possible that some clades of eastern North America also belong to this group.

Soil moisture conditions (Fig. 3, Table 1)—Many of the clades comprising arctic species have a preference for wet soil conditions, particularly swamps and bogs. Important examples were the *Limosae*, the northern radiations of *Carex* sections *Phacocystis* and *Vesicariae*, or the *Stellulatae* clade. Arctic species from clades of rather dry soils were only rarely observed, e.g., the *Clandestinae*, *Ammoglochin*, and *Acrocystis-Umbellata* clades are examples of lineages diversified in dry soils. More prominent, albeit not significant caused by large amounts of missing data, is the *Nardinae* clade with species that are predominantly confined to drier soil conditions. Other clades occur mostly in moist conditions and rarely appear to occupy the extremes.

Shade tolerance (Fig. 4, Table 1)—The Arctic rarely provides shaded places for the growth of plants. Nevertheless, the *Bicolores-Paniceae*, *Acrocystis-Umbellata*, and *Albae* clades may be examples of clades that are centered in forests and in which arctic species have also evolved.

Salt tolerance—Salt tolerance has rarely evolved in the genus *Carex*. In at least five unrelated clades out of the 46 more closely studied clades, salt tolerant species were recorded, i.e., particularly in the northern radiation of *Carex* sect. *Phacocystis*, but also in the *Atherodes*, *Glareosae*, *Divisae*, and *Racemosae-Gmelinii* clades. Geographically, this salt tolerance may have evolved in well-separated regions: for the *Phacocystis* Northern radiation predominantly in North America, for the *Divisae* clade in Central Asia, and for the *Carex* sect. *Glareosae* in the North. For the *Atherodes* clade, whose species are mainly distributed in North America or Eastern Asia, a center of diversity could not be inferred.

Out of the Arctic—The dynamic nature of *Carex* may raise the question whether species have evolved in the Arctic but occur currently outside this ecosystem (Hou et al., 2016). This could be inferred if non-arctic species were nested within otherwise Arctic clades. With the

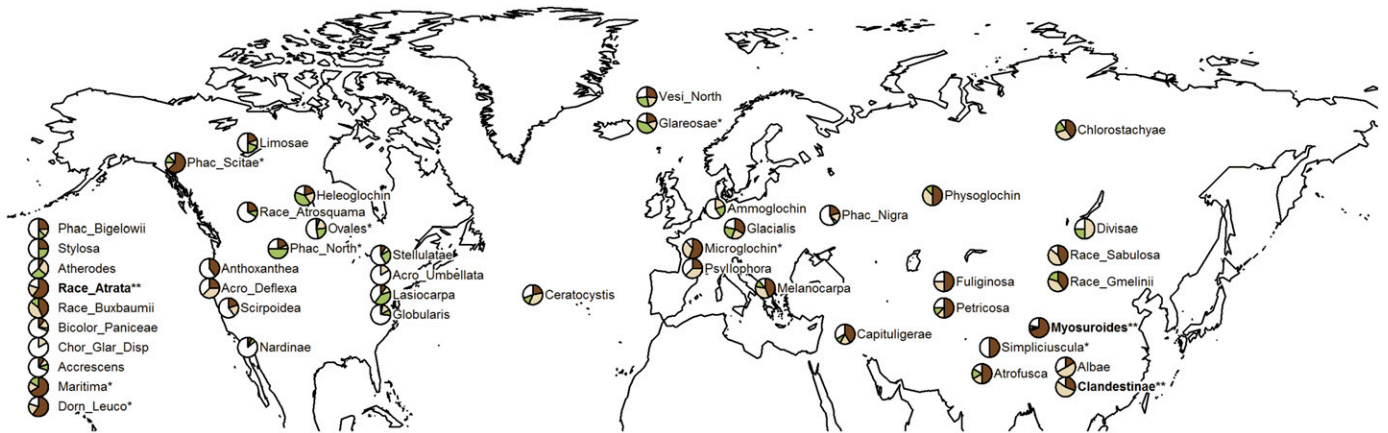


FIGURE 2 Altitudinal distribution of the species of the Arctic clades. The clades were arranged according to their diversity centers. Clades for which the center was not clearly discernible were placed at the left side of the figure. *Ceratocystis* has an amph-Atlantic distribution, thus the chart is placed in between the centers. The northern radiations of the *Vesicariae* and the *Glareosae* have a northern distribution. They were deliberately placed in the North Atlantic. Color codes of the pie charts and names: dark brown—alpine, light brown—mountains, green—plains, white—no data available. Significances of the test of proportions and bootstrap values (BS) as described in Material and Methods were indicated as bold letters and two asterisks: $p < 0.01$ and $BS > 80$; one asterisk: $p < 0.05$ and $BS > 70$ or $p < 0.01$ and $BS > 50$; labels without an asterisk: $p > 0.05$, $BS < 50$. Abbreviations: *Acro_Deflexa*—*Acrocystis Deflexa*, *Acro_Umbellata*—*Acrocystis Umbellata*, *Chor_Glar_Dis*—*Chordorrhiza Glareosae* pp *Dispermae*, *Dorn_Leuco*—*Dornera Leucoglochin*, *Maritima*—*Foetidae Maritima*, *Phac_Bigelowii*—*Phacocystis Bigelowii*, *Phac_Nigra*—*Phacocystis Nigra*, *Phac_North*—*Phacocystis* northern radiation, *Phac_Scirtae*—*Phacocystis Scirtae*, *Race_Atrata*—*Racemosae Atrata*, *Race_Atrosquama*—*Racemosae Atrosquama*, *Race_Buxbaumii*—*Racemosae Buxbaumii*, *Race_Gmelinii*—*Racemosae Gmelinii*, *Race_Sabulosa*—*Racemosae Sabulosa*, *Ves_North*—*Vesicariae* northern radiation.

phylogenetic tree at hand, it is difficult to ascertain this pattern with confidence because putative taxa were mostly nested in polytomies. Candidates for this pattern may be species of *Carex* sections *Phacocystis* and *Vesicariae*, the non-Arctic *C. delicata* C. B. Clarke of *Carex* sect. *Chlorostachyae*, and *C. filipes* Franch. and Sav. of the *Panicaceae*.

DISCUSSION

In a geological timescale, the Arctic regions provide a very young ecosystem that has apparently no analog in earlier times because of the unprecedented climatic cooling in the Cenozoic. The first sea ice was recorded about 45 mya (Moran et al., 2006), temporal ice sheets about 8 mya, and permanent ice sheets in the Northern Hemisphere less than 4 mya (Zachos et al., 2001). These data may set the time

frame in which the present flora of the large Arctic tundra ecosystem has assembled and evolved. From previous work, some origins of the arctic flora could already be inferred: Southern high mountains, wetlands, boreal forests, more rarely steppes, and in situ evolution of new species (e.g., Tkach et al., 2008a, b, 2014; Dragon and Barrington, 2009; Hoffmann et al., 2010; Gebauer et al., 2014).

Here we studied the geographical and ecological sources of Arctic *Carex*, the most diverse and abundant genus of arctic flora. Interestingly, the species diversity of *Carex* within the Arctic follows general diversity patterns of vascular plants in the Arctic with higher species richness in oceanic areas and lower species number in continental areas (Tkach et al., 2008c). The phylogenetic tree revealed that arctic species were situated in at least 48 clades, thus minimally from 48 independent lineages arctic species were recruited. Because these lineages were widespread across the whole phylogenetic tree, with the

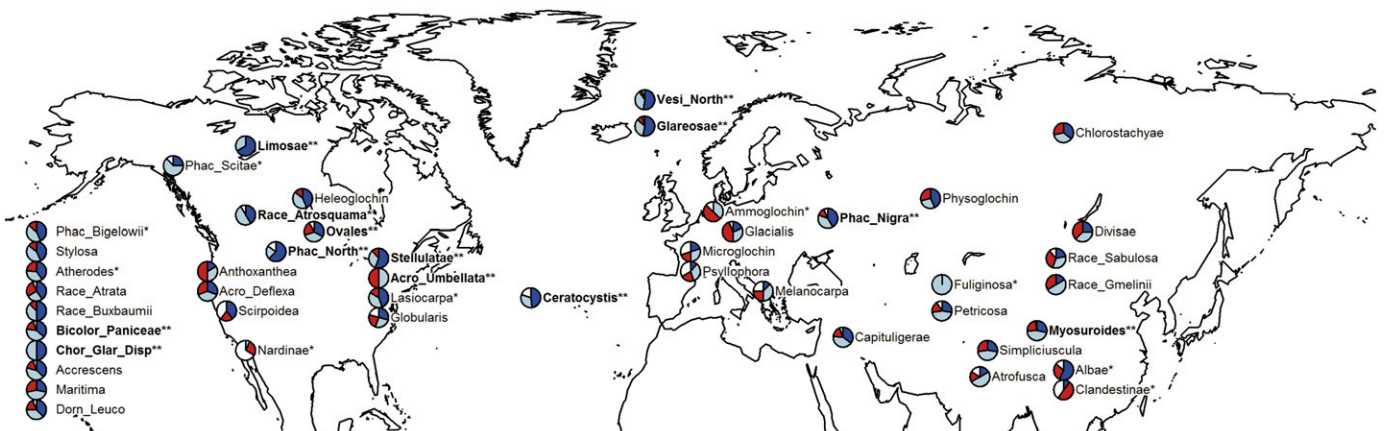


FIGURE 3 Soil moisture preferences of the species of the Arctic clades. Color codes for the pie charts are blue—wet, light blue—moist, red—dry, white—no data available. For the arrangement of the pie charts, asterisks, and abbreviations, see the caption of Fig. 2.

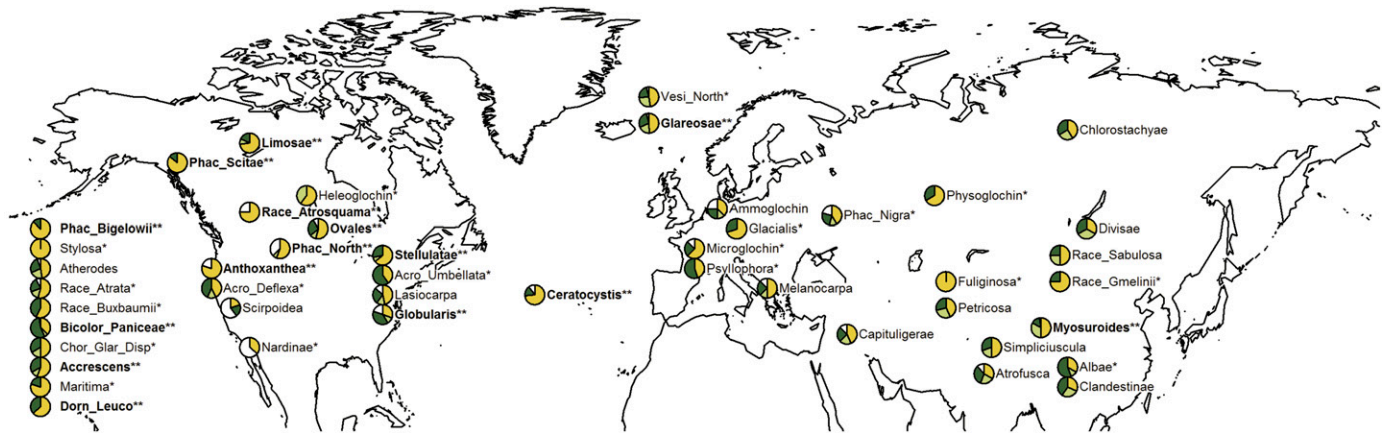


FIGURE 4 Light preferences of the species of the Arctic clades. Color codes for the pie charts are green—forest, yellow—open, light green—intermediate, white—no data available. For the arrangement of the pie charts, asterisks, and abbreviations, see the caption of Fig. 2.

exception of predominantly Southern Hemisphere clades like the *Uncinia* and *Schoenoxiphium* clades, it is likely that this number will hardly decrease if more taxa are added to the phylogeny in the future. On the contrary, it seems possible that the number of Arctic lineages would increase if polytomies and the phylogenetic positions of the four Arctic taxa that are currently of uncertain position were resolved (see above) and the still-missing species were included in phylogenetic analyses. Because of the high species number, the genus *Carex* may provide a rewarding framework for analyzing adaptive traits in sister clades. However, because roughly half of the total species diversity is missing from the tree, a differential analysis of sister clades may not provide tangible results.

Although not completely unexpected from a classical taxonomic view of the genus (e.g., Kükenthal, 1909; Egorova, 1999), as well as from the studies of the above-mentioned other genera, the number of 48 independent lineages contributing to the present Arctic flora is astonishing. At first glance, it might raise the impression that virtually every lineage may reach the Arctic, provided it is geographically close. For some northern lineages having sufficiently wide ecological and climatic amplitudes to cope with at least southern Arctic conditions, this may indeed be the main avenue to grow in the northernmost ecosystem and to become Arctic per definition (e.g., as in the *Chlorostachyae*, *Ceratocystis*, and *Limosae* clades). Moreover, this simple immigration of preadapted species may be an important and common mode of ecosystem assembly (e.g., Pennington et al., 2004; Crisp, 2006; Lancaster and Kay, 2013), particularly in the transition zones between typical expressions of both adjacent ecosystems (Tolmachev, 1960). However, this mode of taxon recruitment from adjacent zones is not achieved by every widespread species, i.e., widespread boreal *Carex* species that do not occur in the Arctic, such as *C. appropinquata* Schumach., *C. disticha* Huds., and *C. schmidtii* Meish.

Some lineages provided single-to-few species to the arctic flora, whereas others underwent considerable diversification in the North such as the two parallel northern radiations in the traditionally circumscribed *Carex* sections *Phacocystis* and *Vesicariae* (Dragon and Barrington, 2009; Gebauer et al., 2014; Hoffmann and Gebauer, 2016). To the list of northern radiations, one in particular may be added: *Carex* sect. *Glareosae* (Maguilla et al., 2015). The high evolutionary variations in *Carex* in the North exceed those of other Arctic genera as previously reported (Hoffmann and Röser, 2009) and may place it in line with the famous Southern Hemisphere radiations of the Andes, New Zealand,

and Southern Africa (reviewed in Linder, 2008; Valente et al., 2010). The time frame in which Arctic species may have evolved was addressed for some clades and revealed a young age for the species (Dragon and Barrington, 2009; Gebauer et al., 2014); it is similar to divergence time estimates for some non-Arctic clades (Escudero et al., 2009; Villaverde et al., 2015a, b). Some species of *Carex* sect. *Glareosae* are weakly differentiated at the morphological and molecular level and may also be of rather recent origin (Maguilla et al., 2015). Based on the estimated root age of the tribe *Cariceae* of about 32 mya around the Eocene/Oligocene boundary (e.g., Escudero et al., 2012; Escudero and Hipp, 2013; Bouchenak-Khelladi et al., 2014; Spalink et al., 2016), it may be assumed that the origin of the majority of Arctic *Carex* species do not date very far back in time.

Besides the *in situ* evolution of many *Carex* species, other species may have their origins outside the Arctic and have migrated to the North (e.g., *C. atrofusca*; Schönswetter et al., 2006). The sources of these Arctic lineages are as diverse as the genus itself. It appears that in almost all regions and ecosystems of the temperate Northern Hemisphere, species have evolved that can deal with the environmental conditions of the Arctic (see above). In terms of geography, these are the high mountain regions of the Northern Hemisphere, perhaps with the exception of the Caucasus and the mountains of Eastern and Northeastern Asia. However, many species may have their origin in clades that are most diverse in lowlands and lower mountain ranges, e.g., the Appalachians in eastern North America. In terms of ecology, arctic species may have their origin in bogs, swamps, meadows, high mountain tundra, saline coastal marshes, steppes, and also, albeit more rarely, temperate to boreal forests (see above). Missing in this enumeration seems to be deserts or semideserts, as well as aquatic ecosystems, where the genus is generally rare or almost absent. It also seems likely that, from Arctic predecessors, species evolved that are of a non-Arctic distribution (Hou et al., 2016). However, the resolution of the phylogenetic tree is not yet sufficient to infer this pattern with confidence.

The extraordinarily diverse sources for the Arctic *Carex* flora might give the impression that simple chance determines which species or lineage may become Arctic, and that origin plays no role. However, the repeated and seemingly parallel geographical and ecological evolution of Arctic lineages shows that origin matters and dispersal is not random in the Arctic (Hoffmann, 2012). Furthermore, a large number of clades comprise no Arctic lineages, although their species are distributed in the Northern Hemisphere, revealing that not every lineage has

the ability to tolerate Arctic conditions. The reason may include considerable niche conservatism that precludes growth in Arctic conditions. However, it might also be that some species have not yet dispersed to the Arctic because dispersal barriers prevented immigration into the Arctic ecosystem (e.g., Hoffmann, 2012).

Arctic grasslands experienced considerable changes in species compositions during its past temporal development, probably because they are largely dependent on precipitation and available soil moisture. The current study revealed that the *Carex* species of the present arctic flora is overwhelmingly recruited from wetland clades, although some dry-adapted lineages were also present in some habitats. The spatial co-occurrence of these disparate ecological and evolutionary groups in the Arctic may provide a look of an interesting interplay between them and the mechanisms of vegetation changes. It might be possible that the dry-adapted lineages (e.g., *C. duriuscula* C. A. Mey., *C. obtusata* Lilj., and *C. rupestris* All.) represent relicts of the widespread cryoxerophilous true grasslands of the Pleistocene in which the now widespread species of the graminoid grasslands probably played a subordinate role in the vegetation (e.g., Yurtsev, 2001; Willerslev et al., 2014). In spite of their low abundance, the dry-adapted species may have considerable resistance against extinction because they occupy small-scale, patchy, suitable habitats in an otherwise adverse environment (for a comparable pattern, see Hochheimer and Hoffmann, 2016). If this hypothesis is true, then the spatial coexistence of the ecological groups point to mechanisms in which the Arctic vegetation may rapidly react to changing environmental conditions by changing abundances of either vegetation type that are already present in the vegetation. In addition, the many different and distantly related lineages co-occurring in the vegetation suggest a highly redundant recruitment of the species, as studied in details for *Carex* sect. *Phacocystis* and *Carex* sect. *Vesicariae* and allies (Gebauer et al., 2014). The coexistence and redundancy may provide another key for a deeper understanding of the evolution and assembly of the northernmost ecosystem.

ACKNOWLEDGEMENTS

The authors thank the members of the Global *Carex* Group for discussions on this topic, and the editor and reviewers for helpful suggestions. This work was supported by grants from the German Science Foundation (DFG, project numbers HO2213/3-1 and HO2213/3-2).

LITERATURE CITED

- Abbott, R. I., and C. Brochmann. 2003. History and evolution of the arctic flora: in the footsteps of Eric Hultén. *Molecular Ecology* 12: 299–313.
- Alfimov, A. V., and D. I. Berman. 2001. Beringian climate during the Late Pleistocene and Holocene. *Quaternary Science Reviews* 20: 127–134.
- Blinnikov, M. S., B. V. Gaglioti, D. A. Walker, M. J. Wooller, and G. D. Zazula. 2011. Pleistocene graminoid-dominated ecosystems in the Arctic. *Quaternary Science Reviews* 30: 2906–2929.
- Bouchenak-Khelladi, Y., A. M. Muasya, and H. P. Linder. 2014. A revised evolutionary history of Poales: origins and diversification. *Botanical Journal of the Linnean Society* 175: 4–16.
- Brummitt, R. K. 2001. World geographical scheme for recording plant distributions. Edition 2. Plant Taxonomic Database Standards No. 2 [online]. Website <http://www.tdwg.org> [accessed 15 December 2016].
- CAVM Team. 2003. Circumpolar Arctic Vegetation Map. Scale 1:7,500,000. Conservation of Arctic Flora and Fauna (CAFF) Map No. 1. U.S. Fish and Wildlife Service, Anchorage, Alaska [online]. Website <http://www.geobotany.uaf.edu>, <http://www.caff.is> [accessed 02 February 2011].
- Charkevich, S. S. [ed.]. 1988. Sosudistye rastenija sovetskogo dalnego vostoka (Flora of the Soviet Far East). Vol. 4. Nauka, Leningrad, USSR.
- Crisp, M. 2006. Biome assembly: what we know and what we need to know. *Journal of Biogeography* 33: 1332–1333.
- Dragon, J. A., and D. S. Barrington. 2009. Systematics of the *Carex aquatilis* and *C. lenticularis* lineages: Geographically and ecologically divergent sister clades of *Carex* section *Phacocystis* (Cyperaceae). *American Journal of Botany* 96: 1896–1906.
- Egorova, T. V. 1999. The sedges (*Carex* L.) of Russia and adjacent states (within the limits of the former USSR). St. Petersburg State Chemical-Pharmaceutical Academy, St. Petersburg, USSR and Missouri Botanical Garden Press, St. Louis, Missouri, USA.
- Elven, R., D. F. Murray, V. Y. Razzhivin, and B. A. Yurtsev. [eds.] 2011. Annotated Checklist of the Panarctic Flora (PAF) Vascular plants version 1.0 [online]. Website <http://nhm2.uio.no/paf>. [accessed 17 April 2010].
- Escudero, M., and A. Hipp. 2013. Shifts in diversification rates and clade ages explain species richness in higher-level sedge taxa (Cyperaceae). *American Journal of Botany* 100: 2403–2411.
- Escudero, M., A. L. Hipp, M. J. Waterway, and L. M. Valente. 2012. Diversification rates and chromosome evolution in the most diverse angiosperm genus of the temperate zone (*Carex*, Cyperaceae). *Molecular Phylogenetics and Evolution* 63: 650–655.
- Escudero, M., V. Valcárcel, P. Vargas, and M. Luceno. 2009. Significance of ecological vicariance and long distance dispersal in the diversification of *Carex* sect. *Spirostachyae* (Cyperaceae). *American Journal of Botany* 96: 2100–2114.
- Escudero, M., V. Valcárcel, P. Vargas, and M. Luceno. 2010. Bipolar disjunctions in *Carex*: Long-distance dispersal, vicariance, or parallel evolution? *Flora* 205: 118–127.
- Flora of China Editorial Committee. 2010. Flora of China, Vol. 23, Acoraceae through Cyperaceae: Cyperaceae. Missouri Botanical Garden Press, St. Louis, Missouri, USA.
- Flora of North America Editorial Committee. 2002. Flora of North America, north of Mexico, Vol. 23, Magnoliophyta: Commelinidae (in part). Cyperaceae. Oxford University Press, New York, New York, USA.
- Flora of Pakistan. 2016. Tropicos.org. Missouri Botanical Garden [online]. Website <http://www.tropicos.org>. [accessed 12 January 2017].
- Gebauer, S., M. Röser, and M. H. Hoffmann. 2015. Molecular phylogeny of the species-rich *Carex* sect. *Racemosae* (Cyperaceae) based on four nuclear and chloroplast markers. *Systematic Botany* 40: 433–447.
- Gebauer, S., J. R. Starr, and M. H. Hoffmann. 2014. Parallel and convergent diversification in two northern hemispheric species-rich *Carex* lineages (Cyperaceae). *Organisms, Diversity & Evolution* 14: 247–258.
- Gehrke, B., and H. P. Linder. 2011. Time, space and ecology: why some clades have more species than others. *Journal of Biogeography* 38: 1948–1962.
- Global *Carex* Group. 2015. Making *Carex* monophyletic (Cyperaceae, tribe Cariceae): a new broader circumscription. *Botanical Journal of the Linnean Society* 179: 1–42.
- Global *Carex* Group. 2016. Megaphylogenetic specimen-level approaches to the *Carex* (Cyperaceae) phylogeny using ITS, ETS, and matK sequences: Implications for classification. *Systematic Botany* 41: 500–518.
- Govaerts, R., P. Jimenez-Mejias, J. Koopman, D. Simpson, P. Goetghebeur, K. Wilson, T. Egorova, and J. Bruhl. 2016. *World Checklist of Cyperaceae*. Royal Botanic Gardens, Kew. [online]. Website <http://apps.kew.org/wcsp/> [accessed 21 January 2016].
- Guthrie, D. R. 2001. Origin and causes of the mammoth steppe: a story of cloud cover, woolly mammal tooth pits, buckles, and inside-out Beringia. *Quaternary Science Reviews* 20: 549–574.
- Hochheimer, J., and M. H. Hoffmann. 2016. Footprints of the Last Glacial: Past competition may have shaped strongly disjunct distribution ranges in *Artemisia rupestris* and *A. laciniata*. *Flora* 224: 203–210.
- Hoffmann, M. H. 2012. Not across the North Pole: Plant migration in the Arctic. *New Phytologist* 193: 474–480.
- Hoffmann, M. H., and S. Gebauer. 2016. Quantitative morphological and molecular divergence in replicated and parallel radiations in *Carex* (Cyperaceae) using symbolic data analysis. *Systematic Botany* 41: 552–557.

- Hoffmann, M. H., and M. Röser. 2009. Taxon recruitment of the arctic flora: an analysis of phylogenies. *New Phytologist* 182: 774–780.
- Hoffmann, M. H., and E. Welk. 1999. A method for the estimation of the global population sizes of plant species—the Area-abundance-index. *Global Ecology and Biogeography* 8: 39–46.
- Hoffmann, M. H., K. B. von Hagen, E. Hörandl, M. Röser, and N. V. Tkach. 2010. Sources of the arctic flora: Origins of arctic species in *Ranunculus* and related genera. *International Journal of Plant Sciences* 171: 90–106.
- Hoshino, T., and T. Masaki. 2011. Illustrated sedges of Japan. Heibonsha, Tokyo, Japan.
- Hou, Y., C. S. Bjora, H. Ikeda, C. Brochmann, and M. Popp. 2016. From the north into the Himalayan–Hengduan Mountains: fossil-calibrated phylogenetic and biogeographical inference in the arctic-alpine genus *Diapensia* (Diapensiaceae). *Journal of Biogeography* 43: 1502–1513.
- Info Flora. 2016. Das nationale Daten- und Informationszentrum der Schweizer Flora. [online]. Website <http://www.infocflora.ch> [accessed 30 May 2016].
- Kade, A., D. A. Walker, and M. K. Raynolds. 2005. Plant communities and soils in cryoturbated tundra along a bioclimate gradient in the Low Arctic, Alaska. *Phytocoenologia* 35: 761–820.
- Krasnoborov, I. M., L. I. Malyshev, G. A. Peschkova, A. V. Polozhij, A. K. Skvortsov, and B. A. Yurtsev. 1990. Flora Sibiri: Cyperaceae. Vol. 3. Nauka, Novosibirsk, SSSR.
- Kreczetovicz, V. I. 1935. *Carex* L. In V. L. Komarov [ed.], Flora URSS, Vol. 3, 114–464. Academy Science, Leningrad, USSR.
- Kükenthal, G. 1909. Cyperaceae–Caricoideae. In A. Engler [ed.], Das Pflanzenreich, IV. 20 Heft 38, 1–824. W. Engelmann, Leipzig, Germany.
- Lancaster, L. T., and K. M. Kay. 2013. Origin and diversification of the California flora: Re-examining classic hypotheses with molecular phylogenies. *Evolution* 67: 1041–1054.
- Linder, H. P. 2008. Plant species radiations: where, when, why? *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 363: 3097–3105.
- Mackenzie, K. K. 1931–1935. Cyperaceae–Cariceae. *North American Flora* 18 (parts 1–7): 1–478. New York Botanical Garden, New York, New York, USA.
- Maguilla, E., M. Escudero, M. J. Waterway, A. L. Hipp, and M. Luceño. 2015. Phylogeny, systematics, and trait evolution of *Carex* section *Glareosae*. *American Journal of Botany* 102: 1128–1144.
- Massatti, R., and L. L. Knowles. 2014. Microhabitat differences impact phylogeographic concordance of codistributed species: Genomic evidence in montane sedges (*Carex* L.) from the Rocky Mountains. *Evolution* 68: 2833–2846.
- Massatti, R., A. A. Reznicek, and L. L. Knowles. 2016. Utilizing RADseq data for phylogenetic analysis of challenging taxonomic groups: A case study in *Carex* sect. *Racemosae*. *American Journal of Botany* 103: 337–347.
- Moore, L. B., and E. Edgar. 1970. Flora of New Zealand. Volume II. Indigenous Tracheophyta. Monocotyledones except Gramineae. Shearer, Wellington, New Zealand.
- Moran, K., J. Backman, H. Brinkhuis, S. C. Clemens, T. Cronin, G. R. Dickens, F. Eynaud, et al. 2006. The Cenozoic palaeoenvironment of the Arctic Ocean. *Nature* 441: 601–605.
- Pennington, R. T., Q. C. B. Cronk, and J. A. Richardson. 2004. Introduction and synthesis: plant phylogeny and the origin of major biomes. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 359: 1455–1464.
- R Core Team. 2014. R: A language and environment for statistical computing, version 3.1.0, Website: www.r-project.org [accessed 16 June 2014].
- Raynolds, M. K., D. A. Walker, and H. A. Maier. 2005. Plant community-level mapping of arctic Alaska based on the Circumpolar Arctic Vegetation Map. *Phytocoenologia* 35: 821–848.
- Revell, L. J. 2012. phytools: An R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution* 3: 217–223.
- Reznicek, A. A. 1990. Evolution in sedges (*Carex*, Cyperaceae). *Canadian Journal of Botany* 68: 1409–1432.
- Reznicek, A. A., and D. F. Murray. 2013. A re-evaluation of *Carex specuicola* and the *Carex parryana* complex (Cyperaceae). *Journal of the Botanical Research Institute of Texas* 7: 37–51.
- Schönswetter, P., R. Elven, and C. Brochmann. 2008. Trans-Atlantic dispersal and large-scale lack of genetic structure in the circumpolar, arctic-alpine sedge *Carex bigelowii* s. l. (Cyperaceae). *American Journal of Botany* 95: 1006–1014.
- Schönswetter, P., M. Popp, and C. Brochmann. 2006. Central Asian origin of and strong genetic differentiation among populations of the rare and disjunct *Carex atrofusca* (Cyperaceae) in the Alps. *Journal of Biogeography* 33: 948–956.
- Spalink, D., B. T. Drew, M. C. Pace, J. G. Zaborsky, J. R. Starr, K. M. Cameron, T. J. Givnish, and K. J. Sytsma. 2016. Biogeography of the cosmopolitan sedges (Cyperaceae) and the area-richness correlation in plants. *Journal of Biogeography* 43: 1893–1904.
- Stenström, A., B. O. Jonsson, I. S. Jonsdottir, T. Fagerström, and M. Augner. 2001. Genetic variation and clonal diversity in four clonal sedges (*Carex*) along the Arctic coast of Eurasia. *Molecular Ecology* 10: 497–513.
- Tkach, N., M. H. Hoffmann, M. Röser, A. A. Korobkov, and K. B. von Hagen. 2008a. Parallel evolutionary patterns in multiple lineages of arctic *Artemisia* L. (Asteraceae). *Evolution* 62: 184–198.
- Tkach, N. V., M. H. Hoffmann, M. Röser, and K. B. von Hagen. 2008b. Temporal patterns of evolution in the Arctic explored in *Artemisia* L. (Asteraceae) lineages of different age. *Plant Ecology & Diversity* 1: 161–169.
- Tkach, N. V., M. Röser, and M. H. Hoffmann. 2008c. Ranges and range size variation in the vascular plant flora of the Eurasian Arctic. *Organisms, Diversity & Evolution* 8: 251–266.
- Tkach, N., R. H. Ree, P. Kuss, M. Röser, and M. H. Hoffmann. 2014. High mountain origin, phylogenetics, evolution, and niche conservatism of arctic lineages in the hemiparasitic genus *Pedicularis* (Orobanchaceae). *Molecular Phylogenetics and Evolution* 76: 75–92.
- Tolmachev, A. I. 1960. Der autochthone Grundstock der arktischen Flora und ihre Beziehungen zu den Hochgebirgslflore Nord- und Zentralasiens. *Botanisk Tidsskrift* 55: 269–276.
- Valente, L. M., V. Savolainen, and P. Vargas. 2010. Unparalleled rates of species diversification in Europe. *Proceedings of the Royal Society, B, Biological Sciences* 277: 1489–1496.
- Villaverde, T., M. Escudero, M. Luceño, and S. Martín-Bravo. 2015b. Long-distance dispersal during the middle-late Pleistocene explains the bipolar distribution of *Carex maritima* (Cyperaceae). *Journal of Biogeography* 42: 1820–1831.
- Villaverde, T., M. Escudero, S. Martín-Bravo, L. P. Bruederle, M. Luceño, and J. R. Starr. 2015a. Direct long-distance dispersal best explains the bipolar distribution of *Carex arctogena* (*Carex* sect. *Capituligeriae*, Cyperaceae). *Journal of Biogeography* 42: 1514–1525.
- Villaverde, T., S. Martín-Bravo, and M. Escudero. 2012. Extreme phylogeography in *Carex* (Cyperaceae). *Informatore Botanico Italiano* 44: 58–61.
- Volkova, P. A., A. B. Shipunov, R. Elven, and C. Brochmann. 2008. The sea-shore sedges of the Russian Kola Peninsula: How many species? *Flora* 203: 523–533.
- Waterway, M. J., T. Hoshino, and T. Masaki. 2009. Phylogeny, species richness, and ecological specialization in Cyperaceae Tribe Cariceae. *Botanical Review* 75: 138–159.
- Waterway, M. J., K. T. Martins, A. Dabros, A. Prado, and M. J. Lechowicz. 2016. Ecological and evolutionary diversification within the genus *Carex* (Cyperaceae): Consequences for community assembly in subarctic fens. *Systematic Botany* 41: 558–579.
- Westergaard, K. B., I. G. Alsos, T. Engelskjoen, K. I. Flatberg, and C. Brochmann. 2011. Trans-Atlantic genetic uniformity in the rare snowbed sedge *Carex rufoa*. *Conservation Genetics* 12: 1367–1371.
- Willerslev, E., J. Davison, M. Moora, M. Zobel, E. Coissac, M. E. Edwards, E. D. Lorenzen, et al. 2014. Fifty thousand years of Arctic vegetation and megafaunal diet. *Nature* 506: 47–51.
- Yurtsev, B. A. 1962. The floristic relations between the steppes of Siberia and the prairies of North America. (in Russian) *Botanicheskii Zhurnal* 47: 317–336.
- Yurtsev, B. A. 2001. The Pleistocene “Tundra-Steppe” and the productivity paradox: the landscape approach. *Quaternary Science Reviews* 20: 165–174.
- Zachos, J., M. Pagani, L. Sloan, E. Thomas, and K. Billups. 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* 292: 686–693.