Taxon recruitment of the arctic flora: an analysis of phylogenies

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Summary

• The Arctic is the endpoint of many climatic gradients and is presently occupied by *c*. 2200 vascular plant species. Glaciation started in the Middle Eocene but a significant expansion of the Greenland ice shield occurred only *c*. 3.2 million yr ago, leading to the expansion of the treeless circumpolar arctic tundra.
• Available molecular phylogenetic studies were evaluated for 148 of 374 genera occurring in the Arctic to determine the relative roles of their independent origins and their diversification in the development of the contemporary arctic flora.
• The number of arctic species paralleled the total number of species in a genus. Multiple arctic species within a genus originated mostly independently of each other and from different lineages. Minor radiations occurred in only a few genera and major radiations were absent.
• Mostly parallel evolution of arctic taxa from nonarctic ancestors, supposedly of different ages of origin, scarcity of radiations and rarity of endemics are main features of the arctic flora.

Introduction

Throughout much of the Tertiary, most of the Arctic, which is now cold and treeless, was covered with deciduous and coniferous forests (Murray, 1995; McIver & Basinger, 1999). Global temperatures began to decrease in the Middle Eocene (*c*. 45 million yr ago (mya)) when temporary ice sheets formed (Moran *et al.*, 2006). The more recent expansion of the Greenland ice shield *c*. 3.2 mya corresponds with the emergence of patches of the Arctic tundra ecosystem (Matthews, 1979; Matthews & Ovenden, 1990), whose extensions varied largely during late Pliocene and Pleistocene (Svendsen *et al.*, 2004). Rapid cooling during the late Tertiary created unprecedented open ecological space for organisms that were already adapted to low temperatures and short growing periods. Thus, the mountain florae of America and Eurasia have been considered major sources of arctic species (Hultén, 1958; Tolmachev, 1960; Hedberg, 1992; Abbott *et al.*, 2000). This is supported, first, by the distribution of many species in both the Arctic and the high mountains of southern Eurasia and North America (Tolmachev, 1960; Tkach *et al.*, 2008c) and, second, by many molecular phylogeographic studies, which have revealed Pleistocene survival in southern refugia and migration of populations to higher latitudes after the retreat of the ice sheets (Hewitt, 1996, 2000; Abbott *et al.*, 2000; Abbott & Brochmann, 2003).

During the glacial periods arctic plants may also have temporarily survived in the vicinity of glaciers to where they migrated with the expanding or retreating ice. Recent molecular phylogenetic studies have contributed substantially to elucidating the origin of such taxa. For example, if arctic taxa are nested within an entirely nonarctic lineage it is likely that they colonized the Arctic only secondarily and did not originate in this region (e.g. *Elymus*; Liu *et al.*, 2006).

In situ origin of arctic plants in the tundra and a later colonization of high southern mountains or other habitats is the alternative hypothesis. In a phylogenetic framework such taxa would be nested within arctic clades as found in our study on arctic *Artemisia* for *A. punctigera* Krasch. ex Poljak. from dune habitats of Sakhalin (Tkach *et al.*, 2008b). However, this species is very closely related to the arctic *Artemisia arctica* Less. and may be conspecific. *Artemisia* is one of the most species-rich genera of the Arctic and its arctic species evolved from time to time in the phylogeny of the genus, independently within different lineages. There were no major radiations of the type starting with a single or few ancestors that invaded the Arctic and subsequently split into different species. Moreover, a clear principal source of origin of arctic taxa has not been discernable in this genus, since arctic species had southern sister taxa in quite different vegetation types. In addition the southern high mountains, steppes of the northern hemisphere have served as

an important provenance for the recruitment of arctic taxa (Tkach *et al.*, 2008b).

To determine whether the pattern seen in *Artemisia* is accidental or generally representative of the taxon recruitment of the contemporary arctic flora we explored a large number of phylogenetic studies conducted on seed plants, ferns and fern-allies occurring in this region. We also examined whether speciation by the radiation of single lineages (Baldwin & Sanderson, 1998; Richardson *et al.*, 2001; Linder & Hardy, 2004; Barraclough, 2006) was common in the Arctic. Specifically, we posed the following questions: Is the number of arctic species in a genus correlated with the total number of species (in those genera that contain arctic species)? In other words, do large genera of the northern hemisphere possess more arctic species than smaller genera? Do the arctic species originate from a few evolutionary splits or do they occur repeatedly and in parallel in the phylogeny of the genera? Are the numbers of evolutionary transitions generating arctic species related to the number of arctic species?

Materials and Methods

According to most phytogeographical delineations (Takhtajan, 1986; Yurtsev, 1994; Elvebakk *et al.*, 1999) the Arctic is considered to be the area north of the boreal tree line and comprises three subzones: the arctic desert normally found at highest latitudes, the moss and lichen tundra and the southern forest tundra with scattered occurrences of trees and shrub species, many of which also have large boreal ranges. Of the Eurasian arctic flora less than 5% of species are endemic to the Arctic (Tkach *et al.*, 2008c). The present study deals with the entire arctic flora (in the following 'arctic plants' is defined as plants occurring in the Arctic). It thus includes not only the arctic endemics but all species present in the Arctic even if they have partial ranges or even their widest ranges outside the Arctic. Nevertheless, many of them are important constituents of the arctic flora dominating arctic landscapes and occur in all subzones (cf. examples studied by Alsos *et al.*, 2007).

The arctic species inventory analysed in this study is compiled from the 'Arctic Flora of the former Soviet Union' (Tolmachev, 1960–1987) and the 'Panarctic Flora Project' (PAF; Nordal & Razzhivin, 1999, online http://www.binran.ru/infsys/paflist/taxon/taxonomy.htm). The genera *Taraxacum* and *Hieracium* were excluded from analysis because of the absence of a comprehensive systematic treatment of their species, which reproduce mainly by agamospermy as genetic clones.

We searched the ISI Web of Knowledge (http://www.isiwebofknowledge.com/) for molecular phylogenetic studies conducted to date on the vascular plants of the Arctic. Genera revealed the most suitable taxonomic entities for our investigation because this taxonomic unit was addressed in most molecular phylogenetic studies and frequently turned out to be monophyletic. If there was a completely resolved phylogeny of the vascular plants, major clades could be used instead of genera to infer their species' diversity and the number of splits leading
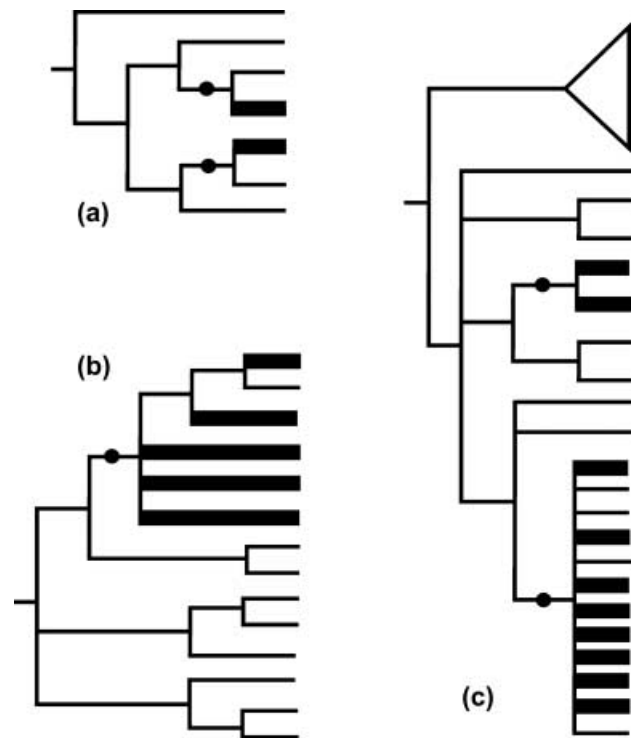

Fig. 1 Different types of evolutionary splits between nonarctic (thin branches) and arctic species or lineages (bold branches). Arctic branches separated from each other by branches of nonarctic taxa originated most likely independently (black dots). If there is a polytomy comprising arctic and nonarctic taxa (marked node in (b) and lower node in (c)), only one split is counted as the most parsimonious estimate. (b) and (c) also show likely radiations of arctic clades. The phylogenetic trees in (b) and (c) may have different interpretations taking the unresolved clades into account. The most parsimonious interpretation of (b) is one transition, resulting in five arctic taxa, but with one reversal. If the basal polytomy in (b) is a ladder, then there could be a maximum of five transitions to arctic taxa, with one species derived from each. If the basal three taxa form a clade, then there could be three transitions, one resulting in three arctic taxa and the other two in one arctic taxon each. The polytomy of (c), depending on how it is resolved, could have anywhere from one to eight transitions to arctic taxa with zero to four reversals. The triangle in (c) represents an entirely nonarctic clade. Simplified and redrawn from studies of (a) Albach *et al.* (2004), (b) Schneeweiss *et al.* (2004) and (c) Scheen *et al.* (2004).

to arctic taxa. For each of the 181 studies identified (see the Supporting Information, Table S1), we recorded the number of evolutionary splits between the species/lineages that were entirely nonarctic and those that were arctic or contained arctic taxa (see Fig. 1). In addition to recording the minimum number of splits as the most parsimonious interpretation of the trees, the possible maximum number of transitions to arctic species/lineages were also counted. The latter takes into account uncertainties that arise from polytomies in the phylogenetic trees. Possible reversals (i.e. the evolution of nonarctic taxa from arctic progenitors) were also counted (Table S1) but we have

an a priori belief that they are not very likely given the short time the clades have been able to colonize and to diversify in the Arctic. The depth of the phylogeny at which arctic sister lineages were identified varied among the studies and also depended on their taxon sampling. The different levels of the phylogeny, at which independent splits were defined, corresponded to different ages of arctic taxa (Tkach *et al.*, 2008a) and thus should not affect the conclusions about the number of evolutionary splits leading to arctic species.

Reticulation via hybridization and allopolyploidy occurs in some genera of the Arctic (Brochmann & Brysting, 2008; Jordon-Thaden & Koch, 2008), whereas others show no signs of reticulation (e.g. *Artemisia*, Tkach *et al.*, 2008b). Our study deals exclusively with the nodes in molecular phylogenetic studies that first gave rise to clades encompassing arctic species. If reticulation patterns had already played a role in the relatively basal nodes but had been overlooked by the original research, this error would inevitably have been carried over to our study. Allopolyploid speciation and occurrences of cryptic species (such as in *Draba*) may underestimate radiations in some genera but probably do not affect the general conclusions of taxon recruitment of the Arctic.

To reflect the different statistical support of tree topologies two categories were used (Figs 3, 4): first, nodes with > 85% in maximum parsimony bootstrap and maximum likelihood or > 0.95 in Bayesian posterior probability and, second, nodes with lower support or trees without support values. Numbers of arctic, nonarctic and entire species number per genus were taken from the original studies. If no total species number was recorded, we followed Mabberley (1997). The relationships between arctic and total species number, the number of evolutionary splits and the arctic species numbers of the genera were studied by correlation analyses using the software SPSS (SPSS Inc., 1999). Linear regression was applied to answer the question of whether large genera could produce more arctic species per split than smaller genera.

Results

A total of 2185 species and subspecies from 374 genera and 90 families present in the Arctic were counted. The total species number of a genus was a good predictor of the number of its arctic species (*Pearson correlation coefficient* $r = 0.533$, $n = 374$, $P < 0.0001$; Fig. 2). Genera that are species-rich elsewhere in the northern hemisphere are also represented by more species in the Arctic. In some genera all species occupy at least parts of the Arctic (e.g. *Andromeda*, *Beckmannia*, *Eriophorum* and *Hippuris*), whereas other species-rich genera comprise only a relatively low number of species growing in arctic conditions (e.g. *Astragalus*, *Carex*, *Senecio* and *Vaccinium*).

The 181 molecular phylogenetic investigations evaluated in this study encompassed 148 of 374 arctic plant genera (*c.* 40%) and 649 arctic species (*c.* 30%) from many different families (Table S1). Investigations ranged from species-poor genera (e.g.
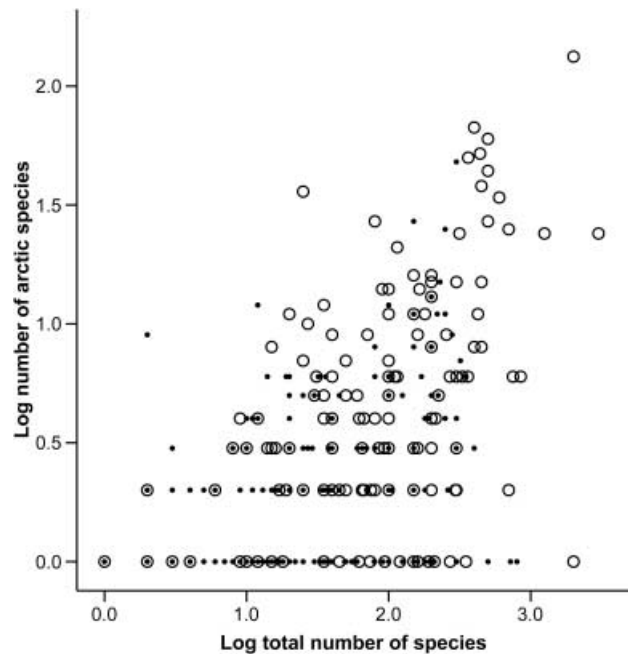

Fig. 2 Total numbers of species and numbers of arctic species in the 374 genera recorded for the Arctic (Pearson correlation coefficient $r = 0.533$, $n = 374$, $P < 0.0001$). Circles denote genera with available species-level molecular phylogenetic studies (see the Supporting Information, Table S1) and dots denote genera not studied molecularly. The two points above the line of equality refer to *Dryas* and *Puccinellia*, in which the number of species within the Arctic (Nordal & Razzhivin, 1999) exceeds the total number of species per genus recorded by Mabberley (1997).

Scheuchzeria) to species-rich genera. *Carex*, the largest genus in the Arctic, was investigated by no less than five studies. Arctic species were mostly better sampled than nonarctic species (Fig. S1).

The number of evolutionary splits in a genus leading to clades comprising arctic species strongly correlates with the number of arctic species per genus included in the molecular phylogenetic studies (Pearson correlation coefficient $r = 0.603$, $n = 181$, $P < 0.001$). The observed number of splits also correlates with the species richness of the genera (Pearson correlation coefficient $r = 0.384$, $n = 181$, $P < 0.001$). The number of arctic species per evolutionary split is on average less than two (Fig. 3). This evidence is slightly more pronounced considering the possible maximum number of transitions to arctic species/lineages (Fig. S2). This indicates that arctic species within a genus evolved mainly independently of each other and not by major rapid radiation. Only a few arctic species of some species-rich genera evolved from minor radiations (*Draba*, *Saxifraga* and *Androsace* subg. *Douglasia* in Fig. 1b, and *Cerastium* in Fig. 1c). With improved taxon sampling the position of some genera in Fig. 3 may change slightly, for example that of *Carex* because many of its arctic species have not been molecularly studied to date.

Plotting the relation between the observed numbers of splits and of arctic species on logarithmic axes recognizes the fact that species number increases exponentially assuming constant

Fig. 3 Number of arctic species originated per evolutionary split (most parsimonious interpretation of the phylogenies) in comparison with the taxon sampling density of the molecular phylogenetic studies evaluated. The x-axis shows the ratio of arctic species included in the molecular study to the total number of arctic species per genus, thus indicating the completeness of arctic taxon sampling. The further right the study the more complete is the sampling. The y-axis shows the numbers of arctic species that originated after a split between nonarctic and arctic lineages. Studies with statistically supported nodes are denoted by circles, those without are denoted by triangles (see the Materials and Methods section). Symbol sizes indicate the number of arctic species per genus not sampled in the respective studies. The studies on *Poa* are biased because of their focus on arctic taxa (see the Supporting Information, Table S1). There is no significant correlation between taxon sampling density and the number of arctic taxa originating per split (Pearson correlation coefficient = −0.065, n = 181, P = 0.391 for the total data set).
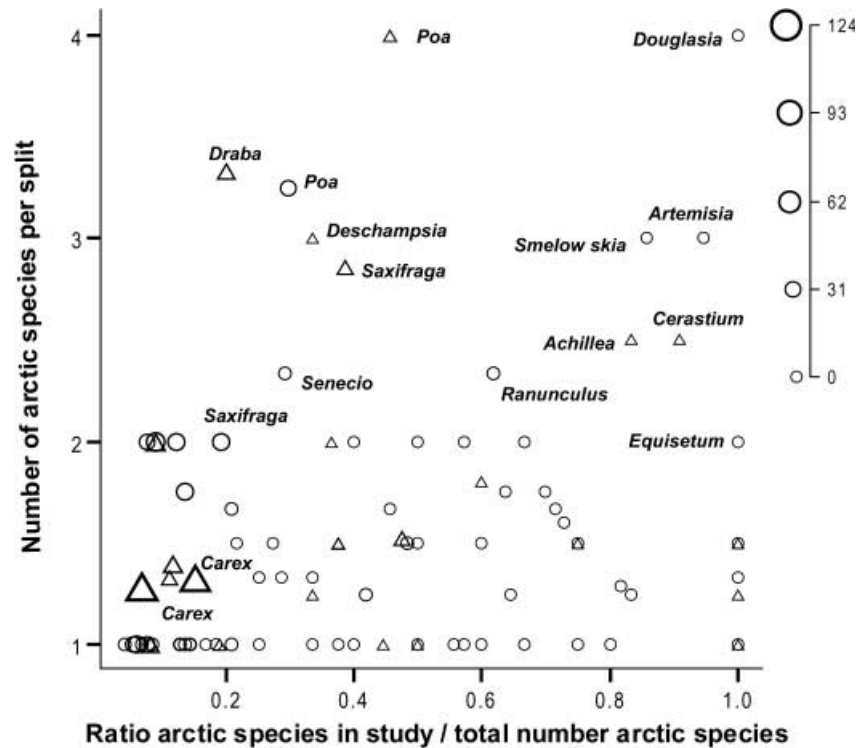
diversification rates (Fig. 4). A linear regression reveals slopes greater than 1 (linear regression coefficient = 1.176, n = 143, P < 0.001 for the highly supported set; linear regression coefficient = 1.399, n = 181, P < 0.001 for the total data set). A regression slope of 1 would indicate that the average number of arctic species per split does not increase with more splits. Slopes greater than 1 indicate that the more splits occur – a feature connected with the sizes of the genera in terms of their species richness – the more arctic species evolve. Large genera thus tend to have, on average, more arctic species per evolutionary split leading to a clade with arctic taxa than smaller genera.

Discussion

The significant positive correlation between the total species number of a genus and the number of its arctic species suggests the overall capability of genera to diversify is an important precondition for the origin of arctic species. The repeated parallel origin of arctic taxa in the phylogeny of many genera indicates that the required changes in physiology or development to adapt to arctic environmental conditions can be accomplished comparatively easily in these genera. Although the number of observed evolutionary splits giving rise to arctic taxa depends in principle on the taxon sampling of the evaluated molecular phylogenetic studies, the absence of major radiations is well supported by the significant correlation between the number of evolutionary splits giving rise to arctic species and the number of arctic species.

The absence of species' radiation in the Arctic is surprising because several prerequisites are seemingly fulfilled: the avail-

ability of new ecological spaces without competitors (Schwarzbach & Kadereit, 1995; Schluter, 2000; Coyne & Orr, 2004) and sufficient time since the emergence of the tundra environments. In most phylogenetic studies of the arctic flora either no molecular clock estimates were available or the clades with arctic taxa were not dated (Table S1). However, for three arctic species of *Androsace* (Primulaceae) Wang *et al.* (2004) obtained very different divergence times when compared with their nonarctic congeners (*A. filiformis, c.* 11 mya; *A. septentrionalis, c.* 5 mya; *A. chamaejasme, c.* 1 mya). By contrast, the small radiation in *Douglasia* (syn. *Androsace* subg. *Douglasia*) appears to be much younger (Schneeweiss *et al.*, 2004). Depending on the method, the split between *Androsace* and *Douglasia* dates between 3.89 and 0.91 mya. The lower limit is close to the estimate for the first appearance of a continuous tundra biome (Matthews, 1979; Matthews & Ovenden, 1990). However, taxa of *Douglasia* present in the Arctic belong to the rather terminal clades in that group and may be much younger. A node within the arctic clade was dated between 1.86 mya and 0.39 mya – clearly younger than the origin of the arctic tundra. Our analysis of divergence times for arctic *Artemisia* also revealed a pattern of a temporal varying evolution of arctic species (Tkach *et al.*, 2008a). One lineage of arctic *Artemisia* species predates the formation of the arctic biome (*c.* 7–17 mya, *A. androsace/ A. senjaviensis/A. glomerata* clade), whereas several other lineages split from their nonarctic congeners after the origin of the tundra (i.e. they are younger than 3 mya). Other time estimates are available for the tree species *Pinus sylvestris* and *Pinus pumila* (Eckert & Hall, 2006) that have wide boreal ranges that extend
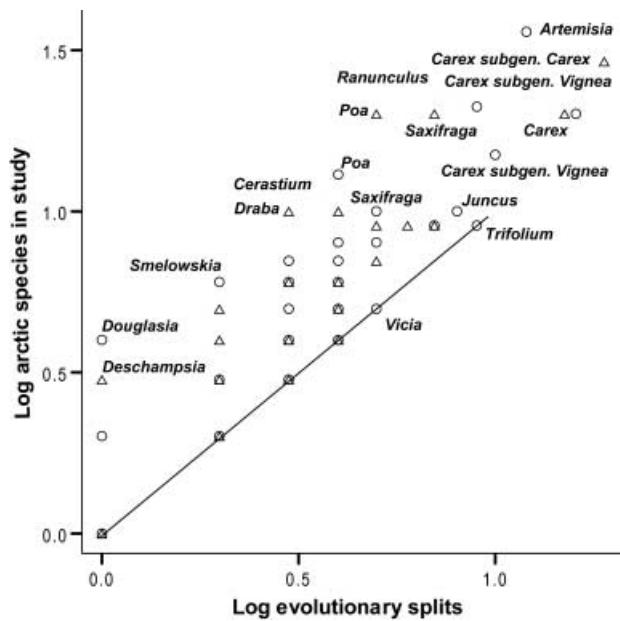
Fig. 4 Number of arctic species and evolutionary splits that gave rise to them. Circles denote splits statistically supported in the original molecular phylogenetic studies, triangles denote unsupported nodes (see the Materials and Methods section). The line is the 1 : 1 diagonal. Several points are shared by different genera (see the Supporting Information, Table S1). The supported data set (circles) has a linear regression coefficient = 1.176, $n = 143$, $P < 0.001$ and the total set a linear regression coefficient = 1.399, $n = 181$, $P < 0.001$.

into the low Arctic. *Pinus pumila* diverged *c.* 12 mya and *P. sylvestris c.* 5 mya from their nonarctic congeners. These few data suggest that species of the Arctic may have split at different times from their nonarctic sisters. Perhaps, some species of *Artemisia*, *Androsace* and *Douglasia* may have evolved in arctic ecosystems, whereas the splits in *Pinus* and parts of *Artemisia* and *Androsace* predate the formation of the first patches of arctic tundra *c.* 3.2 mya. Such a temporal varying taxon recruitment has also been reported for other ecosystems (Linder & Hardy, 2004; Barraclough, 2006; Ricklefs *et al.*, 2006). Further examples of ancient and recent speciation in the Arctic, particularly of polyploid origin, were observed in *Saxifraga* and *Draba* (for review see Abbott & Brochmann, 2003). Ongoing diversification of arctic plants may also be inferred from the observation of cryptic species (Brochmann *et al.*, 1993; Grundt *et al.*, 2006) and high levels of genetic diversity among populations of arctic plants (Abbott *et al.*, 2000; Hewitt, 2000). Perhaps, this might indicate a long waiting time to speciation or be a sign of radiation in its infancy.

The relative paucity of species in the Arctic can be attributed to several factors. The short vegetation period in the Arctic seems to act against some life forms. Plants with a rapid generation turnover (i.e. annuals and biennials with a limited life-span between germination, seed production and individual death) are virtually absent from the Arctic. Tree species are only scattered in the southern forest tundra. Most abundant life forms of the

Arctic comprise perennial herbs and low shrubs (species usually having long juvenile periods and a slow generation turnover; Eriksson & Bremer, 1992; Dodd *et al.*, 1999). This life-form may reduce the effective number of generations in many species of the Arctic and thus speciation.

Other potential reasons for the low species number of the Arctic were inferred from global assessments of biodiversity. Current models on worldwide species richness patterns revealed that, in addition to area size and habitat heterogeneity (Ricklefs, 2004; Sarr *et al.*, 2005), relatively few environmental parameters are necessary to explain latitudinal gradients in diversity. Of these, thermal- and water-energy-coupled factors are of great significance (Woodward, 1987; Kreft & Jetz, 2007). Kinetic effects of temperature are discussed for latitudinal clines of speciation and as potential reasons of the paucity of radiations in the North (Allen *et al.*, 2006).

Assuming that earlier glacial–interglacial cycles had detrimental effects on the diversification of the arctic flora at the species level (Hewitt, 2000), the observed pattern of multiple parallel origins of arctic plants could alternatively be explained by the extinction of earlier radiations. If all but one or only a few species from earlier radiations became extinct, particularly if there was insufficient compensation by migration or dispersal, both evolutionary scenarios are hard to distinguish. Some degree of compensation by migration must be expected, since arctic plants show considerable rates of long-distance dispersal (Alsos *et al.*, 2007). The putative extinction may have occurred not only during glacial periods when the arctic areas were largely covered by ice sheets, but also during interglacial periods at times of higher temperatures. During these interglacial periods temperature was sometimes higher than current temperatures (Francis *et al.*, 2006), which certainly affected the space available for the arctic flora. The treeless arctic ecosystem most likely occupied a much smaller area than today.

Questions concerning how and when the arctic flora assembled and how it evolved need to be addressed in the future by in-depth molecular phylogenetic research to complement much better information available from the fields of population genetics and phylogeography (Brochmann *et al.*, 1993; Abbott *et al.*, 2000; Grundt *et al.*, 2006). The first overview on the taxon recruitment of the arctic flora obtained in this study clearly indicates patterns of mostly parallel evolution of arctic taxa from nonarctic lineages, very different ages of their origin, a scarcity of evolutionary radiations and corroborates the rarity of endemics for the arctic flora.

Acknowledgements

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Supporting information

Additional supporting information may be found in the online version of this article.

Fig. S1 Linear regression of the percentages of arctic and nonarctic species treated in the 181 molecular phylogenetic studies evaluated.

Fig. S2 Number of arctic species originated per evolutionary split (maximum number of transitions to arctic species/lineages) in comparison with the taxon sampling density of the molecular phylogenetic studies evaluated.

Table S1 List of molecular phylogenetic studies, from which information on the evolution of the arctic flora were obtained.

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