

The exclusive license for this PDF is limited to personal website use only. No part of this digital document may be reproduced, stored in a retrieval system or transmitted commercially in any form or by any means. The publisher has taken reasonable care in the preparation of this digital document, but makes no expressed or implied warranty of any kind and assumes no responsibility for any errors or omissions. No liability is assumed for incidental or consequential damages in connection with or arising out of information contained herein. This digital document is sold with the clear understanding that the publisher is not engaged in rendering legal, medical or any other professional services.

Chapter 7

ECOLOGY AND EVOLUTION OF PLANTS IN ARCTIC AND ALPINE ENVIRONMENTS

***Amy L. Breen¹, David F. Murray², Martha K. Raynolds³,
Ina Timling³ and Donald A. Walker³***

¹International Arctic Research Center, University of Alaska, Fairbanks, Alaska USA

²University of Alaska Museum of the North, University of Alaska,
Fairbanks, Alaska USA

³Institute of Arctic Biology and Alaska Geobotany Center,
University of Alaska, Fairbanks, Alaska USA

ABSTRACT

The main structuring element of a terrestrial biome lies in its vegetation. Hierarchical patterns, from the level of the plant community to the global biome, are at their core a reflection of the evolutionary response of plants to their environment. These processes provide the framework for our chapter on ecology and evolution of plants in arctic and alpine environments. Arctic and alpine plants grow above latitudinal and altitudinal treelines around the world. Short-statured shrubs, herbaceous plants, lichens, and mosses comprise the low vegetation of these regions that is collectively referred to as tundra. Arctic and alpine tundras are viewed as growing in uniformly and predictably harsh environments with low temperatures, even during the growing season. The harshness attributed to the tundra, however, vastly oversimplifies the limitations plants face in these environments. The Arctic is not spatially uniform at any scale; neither is the Alpine. The arctic flora in particular, with a history that exceeds two million years, developed through multiple glacial periods. There is ample evidence of major climatic changes over millennia through which tundra vegetation has persisted despite the perceived harshness. Components of the arctic flora may be ancient, but the modern flora is an amalgam of Tertiary, Quaternary, and Holocene contributions. Herein, we focus on recent insights into the ecology and evolution of arctic and alpine plants gained from molecular ecology, modeling, and remote-sensing studies. We review the history and evolution of arctic and alpine floras and discuss the current status of arctic and alpine plant biodiversity. We then

* Corresponding author: albreen@alaska.edu.

discuss the potential for arctic and alpine plants to adapt to a changing climate. We conclude with an overview of plant cross-kingdom interactions, with a focus on the plant-ectomycorrhizal fungi symbiosis in arctic and alpine environments.

INTRODUCTION

Arctic and alpine plants grow above latitudinal and altitudinal treelines around the world (Figure 1). Treeline is the limit of forest; beyond it conditions limit the growth, survival, and reproduction of trees. Short-stemmed shrubs, herbaceous plants, lichens, and mosses comprise the low vegetation of these regions. The vegetation of this treeless landscape is collectively referred to as tundra. Compact life forms are common, such as plants with dense basal rosettes or forming cushions, which protect vulnerable growing tissues from drying winds in summer and from blowing snow in winter.

Arctic and alpine tundras are viewed by some as uniformly and predictably harsh environments. Growth and productivity are constrained by the physical environment: timing of snowmelt, topography, moisture availability, exposure, and aspect. The vegetation is formed by species sufficiently tolerant of cold summer temperatures at any given location to survive freezing temperatures during the growing season, although frost-hardiness and frost-avoidance are not unique to arctic and alpine plants. The harshness attributed to the tundra, however, vastly oversimplifies the limitations plants face in these environments. To characterize tundra as harsh clearly represents our temperate zone bias (Murray, 1987). This bias makes it difficult to not view tundra plants as perilously close to the limits of life—which is simply not so. As Raup (1969) wrote:

“...what we need is a first class Eskimo(sic) botanist—one who thinks of the tundra as a home, and a very good place to live. I think he would see the plants as they are, members of an ancient flora remarkably well adjusted to the habitat.”

The Arctic is not spatially uniform at any scale; neither is the Alpine. Arctic and alpine environments are climatically variable from day to day, month to month, and year to year, yet they are predictable within limits. The Arctic flora in particular, with a history that exceeds two million years, developed through multiple glacial periods with contrasting demands imposed by the changing biological and physical environments over millennia through which tundra vegetation persisted, although the floristic composition of tundra varied over time—despite the perceived harshness.

Physiognomic similarities among the tundra regions can lead us to equate arctic and alpine environments. Dissimilarity among tundra types exists, however, notably in geographic distribution. Arctic tundra is beyond the latitudinal limit of trees in the northern hemisphere and comprises nearly 5% of the terrestrial surface of the Earth, or over 7 million km² (Walker et al., 2005). Approximately 5 million km² of the Arctic is covered by vegetation, and the remainder is covered by ice. In contrast, the Alpine is beyond the altitudinal limit of trees and comprises 3% of the terrestrial surface of the earth (Körner, 2003). Approximately 4 million km² of alpine tundra is scattered globally, with 82% occurring in the northern hemisphere. Plant species that occur in both the Arctic and Alpine, are designated as arctic-alpine taxa.

Our discussion here of alpine tundra is limited to the northern hemisphere as this is where most high altitude tundra occurs and where it is the most similar to the Arctic.

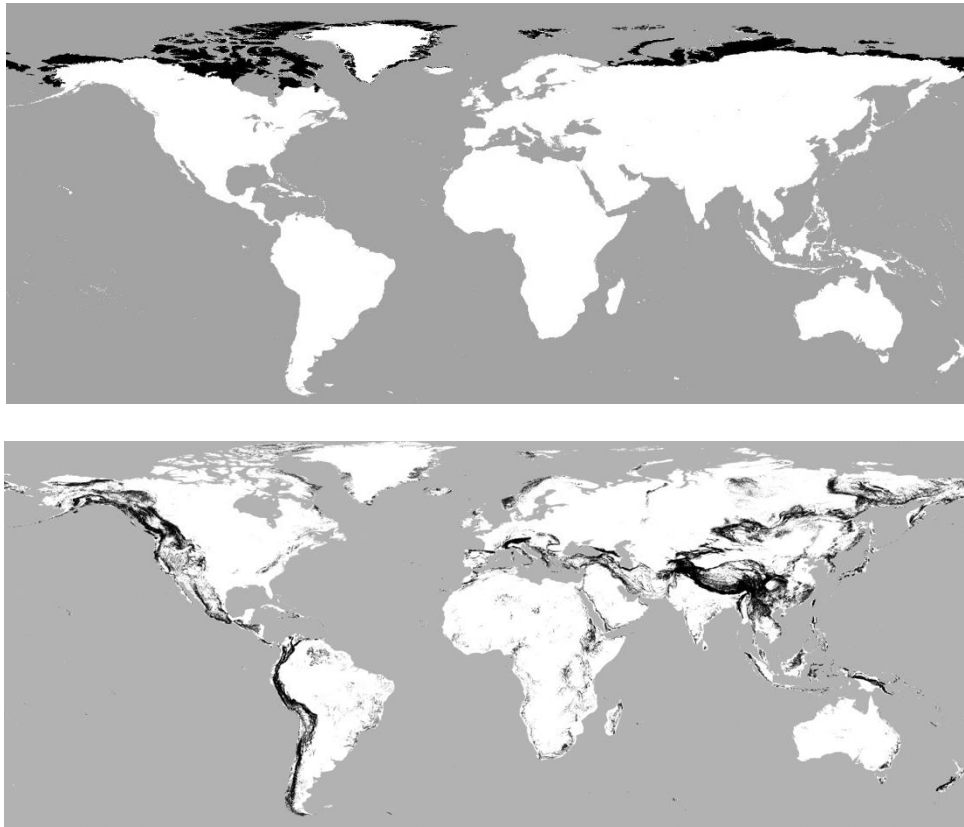


Figure 1. Global geographic distribution of arctic (top) and mountainous (bottom) regions. Alpine regions are fragmented and confined to above-treeline elevations within the mountainous regions, and thus difficult to depict at the global scale. The top panel is adapted from CAVM Team (2003), and the bottom panel is adapted from Körner et al. (2011).

Climate

The critical climatic attribute shared by arctic and alpine environments is low temperatures during the growing season. The arctic photoperiod is continuous during the growing season north of the Arctic Circle (latitude $66^{\circ} 33' 44''$ N). However, during the continuous daylight of an arctic summer, the sun's angle remains low and the solar radiation is less intense than at lower latitudes. Mean July air temperature in the High Arctic is $<6^{\circ}\text{C}$ and can reach $10\text{--}12^{\circ}\text{C}$ at its southern limit in the Low Arctic (Walker et al., 2005). There is a four-fold difference in length of the growing season across this gradient ranging from a few weeks to over three months.

A comparison of mean air temperature of the warmest month across alpine sites in the northern hemisphere shows a range from 5°C in the Austrian Central Alps to 8.5°C in the Rocky Mountains at Niwot Ridge in Colorado (Körner, 2003).

Plant Adaptations

The most profound limitation of the short growing season is its effect on plant reproduction. We discuss plant reproductive adaptations here and then specifically address the process of adaptation through natural selection in the *Adaptation and the Response of Arctic and Alpine Plants to Climate Change* section of this chapter. Plants must progress through anthesis, pollination, and seed set during a relatively short span of summer warmth. It is no surprise, therefore, that annuals are rare; the best example of an arctic annual being the arctic-alpine/bi-polar *Koenigia islandica* (Polygonaceae) (Jónsdóttir, 2011). The primary means to avoid this limitation is through vegetative reproduction; that is, by rhizomes (e.g., graminoids), runners (e.g., *Potentilla anserine* [Rosaceae], *Saxifraga flagellaris*, *Saxifraga platysepalae* [Saxifragaceae]), bulbils (e.g., *Bistorta vivipara* [Polygonaceae], *Saxifraga cernua*, *Saxifraga foliolosa*, viviparous grasses in *Festuca* and *Poa* [Poaceae]), or by producing seeds apomictically (e.g., *Potentilla* spp.).

The majority of arctic and alpine plants can reproduce sexually, despite the prevalence of vegetative reproduction (cf. Murray, 1987), or if apomicts, may nevertheless require pollination. Self-incompatibility is rare and autogamy provides more assured seed set, but this can lead to genetic homogeneity and inbreeding depression. Mixed mating overcomes the many limitations imposed by arctic and alpine environments. Polyploidy buffers plants against the effects of inbreeding and genetic drift (Brochmann et al., 2004). An adaptation that is totally unexpected is heliotropism, the remarkable tracking of the sun by plants such as *Dryas* (Rosaceae) and *Papaver* (Papaveraceae). This occurs in conjunction with parabolic corollas (Kevin, 1972a, 1975; Wada, 1998) such that reflection of solar radiation from the inner surface of the corollas is focused on the reproductive structures thus warming them above ambient temperature and hastening development, as well as providing basking sites for insects (Hocking & Sharplin, 1965).

Advantages accrue to plants capable of producing pre-formed flower buds that overwinter surrounded by scales and leaves. These buds are developmentally advanced, in some cases up to and including meiosis, thus important steps of morphogenesis have already been completed when flowers open the following spring. Sørensen (1941) provided an excellent discussion in which he documented the wintering floral stages with photographs of meticulous dissections and cleared tissue.

Plants that are self-compatible and autogamous are more assured of seed set, although with some genetic cost through reduced recombination that accompanies inbreeding. Most outcrossers are self-compatible and through mixed-mating gain reproductive advantages. The outcrossing species are primarily wind- and insect-pollinated. Some are self-incompatible obligate outcrossers that require the mediation of insects (Kevin, 1972b). These plants offer both attraction and reward to potential pollinators. Attraction lies in flower shape and color, but “colors” not entirely within the spectra visible to humans. Among the white- and yellow-flowered taxa, so numerous in the flora, are ones with spectacular color elaborations in the ultra violet range, invisible to us but sensible to insects (Kevin, 1972c). Floral reward is typically in the form of pollen and nectar.

The relationship between plant and pollinator, attraction and reward, is so well established, co-evolved, that the loss of pollinators can limit the range of plants. Savile (1959) noted that the northern limit of Fabaceae in the islands of the eastern Canadian Arctic correlates well with the disappearance of the bumblebee. To someone accustomed to Low and

Middle Arctic floras (*sensu* Polunin, 1951), when on the ground, the absence of legumes in the High Arctic is noticed.

Vegetation Patterns

The response to summer temperatures is so consistent that the Arctic has been divided into five bioclimate subzones based largely on characteristic vegetation (CAVM Team, 2003). The bioclimate subzones are separated by approximately 2°C in mean July temperature. Similar changes in temperatures occur with elevation in alpine areas in the Arctic, with elevation belts corresponding to the Arctic bioclimate subzones separated by approximately 333-m based on the adiabatic lapse rate of -6° C/1000 m (CAVM Team, 2003), although these subzones have been shown to shift upwards in Greenland due to a more continental climate with earlier snowmelt (Sieg & Daniëls, 2005).

In the Alpine, generally three biogeographical zones or alpine belts are recognized (Wielgolaski, 1997). The lower belt, with no trees and often with tall shrubs, is called the Low Alpine. The next belt, without shrub thickets and with a dominance of graminoids, is the Mid Alpine, although sometimes it is divided into two belts with the upper belt being referred to as Subnival. The belt of limited vegetation beyond the Mid Alpine that occurs on the highest peaks may be called either the High Alpine or Nival Belt. For a comparison of the biogeographical zones and belts of the Arctic and Alpine that pre-dates the Circumpolar Arctic Vegetation Map (CAVM Team, 2003) see Figure 1.1 in Wielgolaski (1997).

Each bioclimate subzone in the Arctic has characteristic plant growth forms. Bioclimate subzone A is the coldest part of the Arctic and includes mountain elevations closest to permanent snow cover. Most of the ground surface is barren, with only sparse vascular plant cover. What little vegetation is present grows mostly in soil cracks related to patterned ground or in sheltered areas provided by topography, where plants are protected from the wind and have a warmer microclimate. Nonvascular plants and biological soil crusts—consisting of a mixture of fungi, algae, and crustose lichens—are dominant, with a few scattered herbs (Vonlanthen et al., 2008). In bioclimate subzone B, there are a few more species of vascular plants and greater plant cover. Bare ground and biological soil crusts are still common, especially on ridges, dry hill slopes, and on the tops of hummocks. In bioclimate subzone C, the vegetation is still patchy, but covers most of the ground in flat, moist areas. Shrubs start to become an important component of the vegetation in sheltered sites. Bioclimate subzone D is mostly vegetated, with a mix of sedges, erect dwarf shrubs, forbs, lichens, and a thick layer of mosses (Kade et al., 2005). Bioclimate subzone E is adjacent to treeline and has the tallest shrubs and the most continuous vegetation cover.

Variation in plant communities at the sub-meter scale also occurs in relationship to patterned ground in most arctic and alpine areas (cf. Murray, 1997). Soil-frost processes create a range of patterned-ground features from 10- to 30-m diameter polygons with centers, rims, and troughs, to 1- to 5-m diameter frost circles and hummocks (Raynolds et al., 2008). Microhabitats associated with small differences in elevation above the water table, or differences in frost activity, are populated by different species. For example, in tussock tundra, shrubs grow on the warmer, well-drained areas, while mosses grow in the cooler, moister depressions.

Winter conditions affect plants mainly through snow and wind. Plants beneath the snow cover are protected from extreme temperatures, desiccation, abrasion, and herbivory, but can experience shorter growing seasons (Walker et al., 2001a). Taller vegetation is sometimes found in areas protected by moderately deep snow cover, but in deeper accumulations, snowbed plant productivity is strongly limited by the short snow-free period. Some evergreen species have developed the ability to photosynthesize beneath thin snow cover, giving them a head start in spring (Starr & Oberbauer, 2003). Plant communities specifically adapted to very short growing seasons are found in these snowbeds (Billings & Mooney, 1968).

Soil pH has a strong effect on arctic and alpine vegetation. Non-acidic areas in Arctic Subzones D and E are characterized by deeper thaw, non-tussock forming sedges and forbs, and frost circles with bare ground in their geomorphically active centers (Walker et al., 1998). In contrast, acidic areas have a deep moss layer, commonly including *Sphagnum* species (Sphagnaceae), which insulates the soil from summer warming. Plants growing in these moist, acidic soils include tussock sedges and ericaceous shrubs. This tussock tundra is found on old soils throughout Beringia, the vast region spanning from northeast Russia east across the Bering Land Bridge to northwest North America, that remained ice-free during Quaternary glaciations (see below). The effects of soil chemistry are especially obvious in areas of thin soil that are common in the Alpine, where plants are growing close to the source bedrock. Limestone bedrock weathers quickly and does not form soil as well as acidic bedrock, resulting in dry, calcium-rich soils, supporting vegetation that is often sparse, but forb-rich (Walker et al., 2001b).

Since the 1960s, many reviews on the topic of the ecology and evolution of plants of arctic and alpine environments have been published. In this chapter we provide a list of recommended readings by topic (Table 1) and summarize the insights gained from molecular ecology, modeling, and remote-sensing studies. We first provide an overview of the history and evolution of arctic and alpine floras and then discuss the biodiversity of arctic and alpine plants and their potential for adaptation to climate change. We conclude with an overview of plant cross-kingdom interactions, with a focus on the plant-ectomycorrhizal fungi symbiosis in arctic and alpine environments.

Table 1. Prominent reviews recommended by the authors on the topic of the ecology and evolution of arctic and alpine plants

Regional focus	Topic focus	Reference
Arctic	Adaptation	Savile (1972)
Arctic	Ecology	Chernov (1985)
Arctic and alpine	Biodiversity	Chapin & Körner (1995)
Arctic	Vegetation ecology	Bliss (2000)
Arctic	Phytogeography	Abbott & Brochmann (2003)
Alpine	Ecology	Körner (2003)
Arctic and alpine	Evolution	Abbott (2008)
Alpine	Vegetation ecology	Ellenberg (2009)
Arctic	Fungal ecology	Timling & Taylor (2012)
Arctic	Ecology & evolution	Brochmann et al. (2013)
Arctic	Biodiversity	Meltofte (2013)

HISTORY OF ARCTIC AND ALPINE FLORAS

There is a distinct arctic flora, one restricted to regions north of the latitudinal treeline, consisting of taxa that do not have ranges south of the Arctic, but including taxa with minor excursions into the northern boreal alpine zone. There are notable disjunctions south from the Arctic, as in North America, into the southern Rocky Mountains, and these comprise the arctic-alpine flora. There is also a distinct alpine flora that does not reach the Arctic, but is restricted to the southern Rocky Mountains and mountain ranges such as the Alps, Carpathians, Altai, and Caucasus.

The classic late 19th century model proposed a once widespread Tertiary arctic flora driven by advancing Pleistocene ice sheets south into high mountains, leaving nothing in their wake, the *tabula rasa* (clean slate) hypothesis (Nathorst, 1892). These southern migrants remained in the mountains and ascended to their summits when the post-glacial climate ameliorated and plants from south of the maximum extent of glaciation could migrate northward to repopulate the Arctic. Thus, the alpine flora was, by this reckoning, a Quaternary derivative of an early Tertiary arctic flora (cf. Darwin, 1859).

Weber (1965, 2003) has sought an explanation for the disjunctions of alpine plants in the Altai of south-central Siberia and in the southern Rocky Mountains of western North America. He presented abundant examples of taxa shared by both mountain systems and absent from the area between. To reconcile the huge geographic separation today, he envisioned (as did Darwin) a once more-or-less continuous blanket of these taxa at some time during late Tertiary and the subsequent destruction of these plants in the intervening area during the Quaternary. His proposal is logical and derives from inferences from long and detailed studies of floras; however, it must be said that this explanation is without empirical evidence.

Tolmachev (1960) proposed that the arctic flora had been derived from the alpine floras from the mountain ranges of Eurasia and North America. Although Hultén (1958) had earlier supposed a circumpolar arctic tundra at the onset of Quaternary glaciations, he accepted Tolmachev's hypothesis and put forward his own argument in favor of this account of history. He was aware of a common floristic core in mountain ranges surrounding the Arctic (W. A. Weber, pers. comm.). Which flora is the antecedent, arctic or alpine, is a question that remains unanswered.

Late Tertiary floras as reconstructed from plant remains at Lava Creek on the Seward Peninsula in Alaska USA (Hopkins et al., 1971) and at Kap København, 82° N latitude in Greenland (Bennike & Bøcher, 1990) do not provide evidence for a continuous late Tertiary arctic tundra. However, from that flora of Tertiary forests and forest-tundra, plants of bogs and similar cold sites, pre-adapted to conditions that would become widespread in the Quaternary, survived the shift from forest to tundra. Plants of pond margins and waterways faced little change in habitat as the cooling progressed. We can presume these plants persisted wherever riparian habitats remained extant (cf. Johnson & Packer, 1965). Macrofossils from the Tertiary Beaufort Formation of arctic Canada (Matthews & Ovenden, 1990) generally support this view. The occurrence of *Saxifraga oppositifolia* and *Dryas integrifolia* (Figure 2) in Canada and Greenland raise an important question: does the presence of quintessential tundra plants in today's world signify tundra in Late Tertiary?

Formation of the circumpolar arctic tundra we see today progressed throughout the nearly 2.5 to 3 million years of the Late Tertiary (Pliocene) and Quaternary. Arctic tundra reached its geographic extent, floristic richness, and current zonation (see Daniëls et al., 2013 for details) in post-glacial time. Those arctic areas wholly covered by ice sheets during the last glacial maximum, of course, were colonized as recently as 6,000 to 10,000 years ago. Components of the arctic flora may be ancient, but the modern flora is an amalgam of Tertiary, Quaternary, and Holocene contributions. As the vast continental ice sheets withdrew and eventually disappeared, plants moved onto the deglaciated terrain, a great many of them from south of the former ice margin, but patterns of plant distribution suggest also other sources, ones from within the area thought to be *tabula rasa*.

Fernald (1925) and Hultén (1937) drew our attention to areas of persistence, where plants adapted to harsh conditions avoided Quaternary glaciations in ice-free periglacial refugia when most of northern Eurasian and North America were otherwise ice covered. This meant *tabula rasa* but with special cases of plant survival. From centers of persistence, plants emerged and became geographically and ecologically sorted according to their dispersing ability and thresholds of tolerance to various abiotic and biotic limiting factors. Some plants moved faster and farther than others and established a circumpolar existence; some developed southern extensions along the Cordillera and formed the arctic-alpine flora. Others have continued to occupy restricted areas despite the millennia since their release from glacial conditions.

Whereas the boundaries of the huge Beringian refugium, as proposed by Hultén (1937), are now well documented by both geological and biological data, the extent and even the existence of smaller arctic and alpine refugia are still debated. Beringia is vast, but nunataks, used here in its broad sense as any non-glaciated area surrounded by glacier ice, are smaller in area, and discrete. Periglacial refugia have been used to explain numerous disjunct distributions, especially in alpine systems. Even so, questions remain: where did nunataks occur, when were they ice-free, when and how did the plants arrive at these locations, how did they survive there, and are they necessary to explain floristic novelties?

With the advent of molecular analysis of the genome in both plants and animals, and the rise of the field of phylogeography (Avice, 1994) there came an additional line of evidence by which to identify refugia, centers of phylogenetic and geographic origin, routes of migration, and instances of long distance dispersal from known sources.

More recently, information on plant cover has been gleaned from the bulk DNA extracted from frozen soil cores gathered at several sites in the Arctic: Russia, United States (Alaska), and Canada. Techniques have been developed that provide, for the most part, greater resolving power (*i.e.*, the ability to identify more taxa to species, than could be achieved through palynology alone). Importantly, these cores have been taken from exposures that date back to the last glacial maximum (*cf.* Willerslev et al., 2014).

Prior to molecular genetics, the thinking was that plants isolated for long periods of time in nunatak refugia would exist where, due to isolation, an influx of new genotypes was nil. Random fixation of genes by genetic drift and removal of less fit gene combinations through intense stabilizing selection acting upon these small populations would, theory predicts, result in a gene pool of low diversity but consisting of genotypes admirably adapted to the narrow constraints of a harsh, full glacial nunatak existence. This presumably left the survivors poorly equipped for post-glacial dispersal—except, perhaps, for the polyploid taxa.



A



B

Figure 2. A) *Dryas integrifolia* and B) *Saxifraga oppositifolia* were both a component of the Late Tertiary arctic flora as reconstructed from plant remains at Lava Creek on the Seward Peninsula in Alaska (Hopkins et al., 1971) and at Kap København in Greenland (Bennike & Bøcher, 1990) (photo credits: Martha Reynolds).

A tenet of phylogeography is that plant genomes undergo steady mutation in the neutral, or non-coding, regions of the genome. The longer populations are isolated, the longer the time for the fixation of unique gene combinations and rare alleles; hence, genetic identities form as long as interbreeding with other populations does not occur, as that would swamp any unique haplotypes. In phylogeography, the expectation is for greater genetic diversity as the signal of refugia persistence.

Disjunct occurrences in mountains were taken by some to be *prima facie* refugial survivors; the bicentric distribution pattern in the Scandinavian mountains is an example (Dahl, 1955). Although a thorough reconsideration by Brochmann et al. (2003) concluded that refugia were not necessary to account for both the disjunctions and endemics, a more recent study (Westergaard et al., 2011) has found examples explained by nunatak survival. Thus, these publications are a perfect illustration of the wisdom of Berg (1963):

“...most ... biogeographers explain the arctic-alpine disjunction in terms of glacial survival...It is my opinion that no single explanation can account for all the arctic-alpine disjunctions...a great deal of argumentation has resulted from a futile search for one universal cause.”

The aggregate of disjunct occurrences of Rocky Mountain plants in eastern North America are what first led Fernald to propose his persistence theory (Fernald, 1925). What made some of his examples controversial was the absence of geological evidence for ice-free areas. Ives (1974), in his splendid review of biological refugia and the nunatak hypothesis, chastised those making claims for periglacial refugia without supporting evidence for full glacial, ice-free conditions, even in the face of strong geological evidence against such claims.

A counter-argument to refugial survival was that disjuncts were ecological specialists that arrived at their current position in post-glacial time. Why they remain today as small isolated populations was thought to be the result of drastically reduced ecotypes, the conservative species of Fernald (Fernald, 1925), the rigid species of Hultén (Hultén, 1937), and thus a genetically determined inability to disperse and compete elsewhere. An excellent review of Fernald and Hultén and the debate over refugial existence or post-glacial arrival is provided in Raup (1941, pt. 1).

Long distance dispersal has always been offered as a mechanism to explain disjunct species, but one which we are unlikely to confirm by direct evidence. Savile (1956, 1972), a great field biologist, believed in the efficacy of winter transport by strong winds over a landscape of ice and snow. However, for some geographic problems, greater distances must be traversed. Plant propagules are believed to have been carried across the Atlantic Ocean by migratory waterbirds such as those moving from western Europe to northeastern North America, contributing to the Amphiatlantic flora. The discussion has long gone back and forth, with reasons supporting both why long distance dispersal is probable and why it is not (Dahl, 1963; Löve, 1963).

Abbott & Brochmann (2003) have provided an excellent review of the molecular evidence for transatlantic dispersal. Since then, more examples have appeared: *Carex bigelowii* (Cyperaceae; Schönswetter et al., 2008) and *Saxifraga rivularis* (Westergaard et al., 2010). Moreover, in a remarkable study Alsos et al. (2007) demonstrated how Svalbard could be supplied with plants from elsewhere in post-glacial time, even from distant sources, without involving refugial populations—a suggestion that would have been in conflict with glacial geologists who have said that periglacial refugia did not exist there.

Mountains high enough to support alpine vegetation today were for the most part ice-covered during glacial maxima, certainly during the last glacial maximum, but alpine plants could have persisted in peripheral nunataks at the margins of an ice shield as Schönswetter et al. (2004) postulated for *Ranunculus glacialis* (Ranunculaceae) in the Alps. In the case of *Eritrichium* (Boraginaceae; Stehlik et al., 2002) at high elevations in the Alps, snow and ice would make refugia problematic. Similarly, Marr et al. (2008), having examined the genetics of *Oxyria digyna* (Polygonaceae) over much of the North America Cordillera and elsewhere, reported genetic diversity among disjunct occurrences that they interpreted as the consequence of periglacial refugia, albeit where geological evidence for ice thickness would appear to rule out ice-free areas. The implication is that genetic evidence trumps geological

projections, yet the genetic diversity could be the result of post-glacial secondary contact and the rare alleles, at least in small populations, by fixed random processes.

How did the arctic species disperse southward down the Rocky Mountain chain, getting as far south as Montana, where there are about 100 arctic taxa found in the alpine zone (P. Lesica, pers. comm.)? There are even some arctic-alpine plants on the summits of the San Francisco Peaks of Arizona (Deaver Herbarium; www.nau.edu/deaver). We assume this is due to migrations southward from the Arctic, but it remains unclear when this would have occurred. During the glacial maxima, ice cover was nearly complete and thus, we presume, a barrier to dispersal. Prior to the final glacial advances and/or as glaciers receded in early post-glacial time, there would have been both the arctic environment and open corridors through which plants could have dispersed southward from Beringia (and some southern alpine plants northward). Thus a post-glacial process cannot be ruled out; in fact it seems likely. Despite numerous studies and discussions on the history and evolution of arctic and alpine floras for more than a century, there is still much to be learned.

BIODIVERSITY OF ARCTIC AND ALPINE PLANTS

Species richness of arctic and alpine plants tends to decline with increasing latitude and elevation. Low temperatures and a short growing season are environmental filters that are hypothesized to exclude species from increasingly more severe climates (Chapin & Körner 1995; Walker, 1995). There is no consensus, however, on a single explanation for the decline in biodiversity. Hypotheses fall into two groups, those based on ecological mechanisms of species co-occurrence and those based on evolutionary mechanisms governing rates of diversification and Earth history (Payer et al., 2013). These hypotheses are not necessarily mutually exclusive, as observed patterns may be due to interactions between both abiotic and biotic factors.

On a more regional scale, species richness of arctic and alpine plants is best explained by the ancestral stock of species, long-distance migration following deglaciation, evolution of new taxa, and proximity to a rich species pool as within and near Beringia (Chapin & Körner, 1995; Murray, 1995). Migration is essential for the assemblage of arctic and alpine floras, especially following glacial periods and associated extinctions. In the Arctic, the flora tends to intergrade continuously from a few centers of persistence. In contrast, alpine floras are more discrete due to their restricted habitat and geographic isolation, thereby leading to higher levels of endemism. Thus, mountain ranges in different regions tend to have disparate assemblages of alpine dominants, while the dominant plant species across the Arctic tend to have a circumpolar distribution.

Whereas it is often remarked that the flora of arctic and alpine regions is species-poor, even depauperate, the question arises: species-poor in relation to what? Summer climate is sufficiently cool and winds strong enough to preclude trees and tall shrubs, thus a major component of boreal and temperate vegetation is missing from tundra. But, are there niches unfilled? Are there families, genera, or species missing that we should expect? These questions have not been addressed, but are of interest as we discuss the flora of arctic and alpine regions in this section of the chapter.

Our knowledge of the arctic flora differs for each of the three main taxonomic groups of plants—vascular plants, bryophytes, and algae. Vascular plants are the best-known group. This is due in part to the recent publication of the *Checklist of Panarctic Flora (PAF) Vascular Plants* (Elven, 2011). The Panarctic flora includes 2,218 taxa, 91 families and 430 genera; which is less than 1% of the world flora (Daniëls et al., 2013). There are few gymnosperm taxa: 96% of the flora are angiosperms. Eight species-rich families account for more than 50% of the flora, of which the top three families are Asteraceae (254 taxa), Poaceae (224 taxa), and Cyperaceae (190 taxa). About 5%, or 106 taxa, are endemic. Most endemics are Beringian, occur arctic-wide, and are forbs. There are no endemic woody species.

As a whole, the arctic flora is viewed as taxonomically, ecologically, biologically, and genetically coherent with the many species having a circumpolar distribution. Biodiversity is low in comparison to temperate or tropical ecosystems. Trends in species richness are largely attributed to history, including glaciations, land-bridges, and north-south trending mountain ranges (Yurstev, 1994). Bryophytes are ubiquitous in the Arctic and contribute significantly to species richness, particularly in moist to wet habitats (Daniëls et al., 2013). There are an estimated 900 arctic bryophyte species and approximately 4,000 freshwater and marine algal species. The biodiversity of microalgae is still largely unknown. At present, there are few introduced species (101 taxa; Elven, 2011). The most widespread non-native stabilized introduced species are *Lepidotheca suaveolens* (Asteraceae, pineapple weed), *Plantago major* subsp. *major* (Plantaginaceae, common plantain), and *Trifolium pratense* (Fabaceae, red clover). Most of the introduced species are not invasive and are restricted to disturbed habitats. For example, hay brought in to protect disturbed slopes from erosion where the trans-Alaska oil pipeline passes through the Arctic created an influx of invasive species, but most were gone after the first winter. Although not currently a threat in the Arctic, invasive species are likely to increase due to increasing human activity coupled with climate change. For example, a recent study showed that visitors to Svalbard transport a minimum of four seeds on their shoes. Most of these seeds are from species known to be invasive elsewhere and over a quarter of these seeds were found to be capable of germination under current climatic conditions (Ware et al., 2012).

Plant species diversity of the world-wide alpine flora is much greater than in the Arctic. Körner (2003) estimates 8,000-10,000 vascular plants, comprising 100 families and about 2,000 genera, or nearly 4% of the world flora. The most common families in the Alpine are similar to those also common in the Arctic: Asteraceae, Poaceae, Brassicaceae, Caryophyllaceae, Cyperaceae, Rosaceae, and Ranunculaceae. Regional alpine floras, from the Teton Range in Wyoming to the Hokkaido alpine zone in Japan, typically include 200-280 species, with a mean diversity of 241 species from nine distinct mountain ranges (Körner, 2003). In contrast, in the Arctic, mean species richness of vascular plants from the 21 Panarctic floristic provinces (Elven, 2007) is estimated at 544 species (Daniëls et al., 2013). The most species rich floristic province is Western Alaska (825 species), and the least species rich region is Ellesmere Land-North Greenland (199 species). These data are not directly comparable to estimates of diversity for alpine floras as floristic provinces are not analogous to more regional mountain ranges. Within the alpine zone, total plant species richness within a given region declines by about 40 species of vascular plants per 100 m of elevation (Körner, 2002). Mosses (also see Chapter 12) and lichens (also see Chapter 3) deviate from this pattern as they often increase in abundance with increasing altitude, although their richness

eventually decreases at the highest altitudes. Most alpine species occur at 1,000 m or lower, although a few species have been found as high as 5,900 m in the Tibetan Himalaya (Rongfu & Miede, 1988) or 6,300 m on Mount Everest (Grabherr et al., 1995). Given the geographic isolation of mountains that often are functionally islands, endemism is high with the highest degree of endemism found at moderate, rather than at extreme altitudes.

There are several stressors to arctic biodiversity (Meltøfte, 2013). These fall into two categories: anthropogenic and climatic stressors. Anthropogenic stressors include increased development, such as infrastructure associated with oil, gas, and other resource extraction. Further development will be made possible by increased opportunities for transportation including shipping lanes, road building, and regular air service to remote localities. There are also stressors from contaminants, such as persistent organic pollutants, and increased potential for oil spills.

Climatic stressors are the most serious threat to plant biodiversity in the Arctic and equally, or more so, to alpine environments. Climate warming is predicted to lead to migration of plants northward, altering the structure of vegetation through additions or even replacement from the sub-arctic to the low Arctic to the high Arctic. Terrestrial habitats in the Arctic are bounded to the north by a coastline so there is the potential that high arctic ecosystems may only survive in isolated refugia or in mountain habitats. A similar scenario is predicted for the Alpine, with expansion of treeline vegetation to higher elevations. Snowbed specialists, adapted to late snow melt and low soil temperatures are among the most threatened as both conditions are likely to be altered by climate change (Björk & Molau, 2007).

Many studies document changes in arctic and alpine plant distributions consistent with climate warming predictions. Re-sampling studies from over 100 mountains in Scandinavia and Europe, as well as on the arctic islands of Spitsbergen and Greenland, show that species richness on mountain summits has increased (Birks, 2013). This increase is predominantly an altitudinal ascent of grasses, dwarf shrubs, and low shrubs. In central Norway, Klanderud & Birks (2003) showed that changes in species richness from 1930 to 1998 varied by elevation belt. Total plant species richness in the lowest elevation belt (1,600-1,800 m) increased by 8-14 species, while in the mid-elevation belt (1,800-2,000 m) total plant species richness increased by 5-8 species. Above 2,000 m, little or no change in species richness was observed. No high-alpine species had gone extinct, although a few species had decreased in frequency since 1930. In Montana's Glacier National Park, arctic-alpine plant cover declined over two decades of study (1988-2011) with a concurrent increase in mean summer temperature (Lesica, 2014). Plants restricted to high elevations declined more so than those with a broader elevational distribution. In alpine areas of Europe, Gottfried et al. (2012) found increases in warm-adapted species and declines in cold-adapted species over a relatively short time period from 2001-2008. Warming experiments have shown an increase in shrubs in the Low Alpine in Europe (Cannone et al., 2007) and Asia (Klein et al., 2007) and from multiple sites across the Circumpolar Arctic (Elmendorf et al., 2011; Walker et al., 2006). Increases in satellite measures of greenness (related to aboveground plant biomass) have been observed (Epstein et al., 2012), as well as increases in shrub cover based on repeat photography in the warmest parts of the Arctic (*e.g.*, Tape et al., 2006), although grazing by reindeer, lemmings, and voles may limit shrub expansion (Olofsson et al., 2009). Studies in colder subzones of the Arctic have found increased vegetation cover and height, but little change in community

composition (e.g., Hudson & Henry, 2009), except in recently deglaciated areas where succession is occurring.

Equating biodiversity with species richness is one measure, but there is another level to be considered. From molecular studies, we now know that genetic diversity within Linnean, or biological, species can be high. The problem comes in assessing Linnean diversity, for there is often no parallel morphological differentiation to provide visible markers to genotypic boundaries. There is great genetic variation within the species (cf. Brochmann & Brysting, 2008). Reticulate evolution among arctic plants involves multiple genomes, secondary contact, hybridization, and polyploidization, all of which provide raw material for intraspecific variation and differentiation.

Some of the best information on biological species diversity comes from studies of *Draba* (Brassicaceae), initiated by Brochmann and continued by him with students and colleagues in Oslo. Grundt et al. (2006) conducted intraspecific crossing studies of three circumpolar diploid species in *Draba* and found, despite observations of limited morphological and genetic diversity, evidence for cryptic biological species, ones reproductively isolated from one another and thus evolutionarily independent. Hybrids from within populations were mostly fertile (63%), while those from within and among geographic regions (Alaska, Greenland, Svalbard, and Norway) were mostly infertile (8%). These results suggest that intraspecific diversity may be higher in the Arctic than previously realized.

Genetic diversity is essential to long-term persistence of arctic and alpine biodiversity as it provides opportunities for species to respond to changing environmental conditions. As abundance and geographic distributions of species shrink, genetic variability for selection to act upon is also often reduced. For most arctic and alpine plants, we lack information on how genetic variation, and therefore evolutionary potential, is generated and maintained. Species richness is often used as a surrogate for genetic diversity in conservation planning, although we are still learning how these two levels of biodiversity are related. To date, a few studies have addressed whether species and genetic levels of biodiversity co-vary in arctic and alpine plant communities.

Taberlet et al. (2012) showed that for the flora of the Alps and Carpathians, species richness and genetic diversity of high mountain vascular plants are not correlated. Their results showed that genetic diversity is instead associated with glacial history of a species, which in turn was linked with environmental and ecological characteristics of glacial refugia, range shifts, and associated demographic processes. In contrast, Eidesen et al. (2013) showed that patterns of genetic diversity across 17 vascular plant species are analogous to large-scale patterns of species diversity in the Arctic. Diversity was highest in Beringia and decreased gradually into more recently deglaciated regions. It should be noted that both of these studies assessed neutral genetic diversity, which is not under selection.

An aspect of genetic diversity in arctic plants was noted many decades ago as chromosome counts of northern plants were becoming known and diploids and polyploids were identified. It was further noted that there are more polyploids at higher latitudes than at low latitudes (Hagarup, 1928). The relationship between the frequency of polyploids and the northernmost regions became the preoccupation of many, for whom the underlying belief was that polyploidy *per se* gave the plants advantages in cold climates. The advantages of genetic diversity from multiple sets of chromosomes was presumed to endow polyploids with the ability to persist in the rigorous conditions, such as in glacial refugia (see above) and also to have the capacity to spread aggressively during deglaciation (Löve, 1959).

Johnson & Packer (1965, 1967) and Johnson et al. (1965) demonstrated, at Ogotoruk Creek in northwest arctic Alaska, a relationship between the frequency of polyploid taxa along gradients of soil texture, moisture and temperature, depth to permafrost, and degree of geomorphic disturbance. The diploids and low polyploids were found on more stable Tertiary surfaces, and the higher polyploids were found in habitats of the sort that became common and widespread during cold intervals of the Pleistocene, suggesting their more recent divergence.

Brochmann et al. (2004) examined the observations and explanations for polyploidy in arctic plants, particularly what can be concluded from recent molecular studies. Essentially, polyploidy is the means by which reticulate evolution proceeds and by which hybrids can gain fertility, stability, and independence. Research with hybrids showed there is *interspecific* gene flow across ploidy levels (Brochmann et al., 1992a), which demolishes the simplistic but long held belief in strong reproductive barriers between diploids and tetraploids and so-called abrupt speciation. Surprisingly, there can be two or three different parental species, all polyploids sharing parts of their genomes, which form polyphyletic hybrids. These hybrids attain fertility through polyploidization. Hence, taxa of different parental combinations, formed at different times and places, can exist within the same Linnean species (Brochmann et al., 1992b). Recent studies have shown that polyploidy has occurred at different times and places within *Vaccinium uliginosum* (Ericaceae; Eidesen et al., 2007) and that different ploidy levels overlap across the circumpolar distribution of *Saxifraga oppositifolia* (Müller et al., 2012).

Changes in biodiversity, driven by climate and other anthropogenic stressors, will provide new opportunities for recruitment and require adaptation and adjustment of arctic and alpine floras. Crawford (2008) argues that many widespread arctic and alpine plants occupy a range of different habitats, in terms of temperature and soil-moisture content for example, and are ecotypically diverse. If so, this should help buffer these species against extinction with increases in global temperatures. For other plants that are of recent origin or which are narrowly distributed, such ecotypic diversity does not exist. For species that may be outcompeted by more thermophilous species invading from the south, their survival depends on their ability to colonize newly deglaciated land at higher latitude or altitude where temperatures remain low. For alpine species that are already restricted in high altitude mountain ranges, there may be no new suitable habitat to exploit. If so, these species are likely to be among the most endangered in the future (Birks, 2008). In the next section of this chapter, we discuss adaptation and the response of arctic and alpine plants to climate change.

ADAPTATION AND THE RESPONSE OF ARCTIC AND ALPINE PLANTS TO CLIMATE CHANGE

Climate change in recent decades has led to changes in the composition and distribution of vegetation in arctic and alpine environments. These regions are changing, and as a consequence their biodiversity is also changing (Callaghan et al., 2004). Predicted increases in temperatures globally are 0.1°C per decade, which is amplified in the polar region compared to lower latitudes (ACIA, 2005).

In response to temperature increases, shrubs and trees are extending their limits both northwards and upwards. How will arctic and alpine plants be affected by climate change? Birks (2008) stated this question well:

“Will arctic plants be pinched between advancing shrub tundra and forest and the rising sea-level in the low-land Arctic? Will alpine plants be squeezed off the tops of mountains?”

It is likely that some arctic and alpine plants will become extinct, particularly those with small endemic populations at the limit of plant life in the High Arctic or at high altitude. If we look to the past, however, to when the climate warmed in the early Holocene, temperatures were about 2°C warmer in the Arctic. Arctic and alpine plants persisted, and no arctic-alpine species with a fossil record is known to have gone extinct in the Quaternary (Birks, 2008). It therefore is likely that more ecotypically diverse species are resilient to climate change and will survive and adapt as long as some suitable habitat remains.

Ecotypes, variants within species, have long been recognized among temperate plants, where ecotypes show various morphological features adaptive to particular environmental conditions. A selective advantage may also accrue to ecotypes in their native site without a change in morphology as to be recognized as taxonomically distinct. There are many examples of ecotypes along latitudinal and altitudinal gradients, even along local gradients of microtopography where adaptations are less morphological and mainly physiological (Chapin & Chapin 1981; Shaver et al., 1979). Ecological amplitude in geographically wide-ranging species derives from the formation of entities with genetically fixed, adaptive properties. The effectiveness of this process is not fully appreciated. For ecotypes to undergo speciation there would first need to be sufficient genetic variation within them, and second, selection pressure to drive the process of differentiation. Absent one or both, further divergence does not occur; moreover, the infraspecific ecotypes allow for persistence across a range of environmental conditions. Raup (1969) evaluated the breadth of tolerance by species to gradients of soil moisture, plant cover, and geomorphic disturbance and found that some species exhibit great tolerances. This capacity of some tundra plants is a function either of phenotypic plasticity or of genetically fixed ecotypic differentiation, or a bit of both. It is likely that more ecotypically diverse species will have large ecological amplitudes, will be resilient to climate change, and will survive and adapt as long as the thresholds of tolerance to limiting factors are not exceeded.

Temperature, photoperiod, concentration of CO₂, and light intensity all affect photosynthesis and photosynthetic efficiency of plants. Species occurring in both arctic and alpine tundra provide examples of ecotypic differentiation for those environmental parameters. Ecotypes of these species are differentially adapted to the low light intensity and long photoperiod of the Arctic and to the high light intensity and short photoperiod of the Alpine. Even differences in the production of leaves, leaf width and thickness, and concentration of chlorophyll have been identified as part of ecotypic differentiation of physiological traits (cf. Mooney & Billings, 1961; Tieszen & Bonde, 1967).

Much of what we know about adaptation in arctic and alpine plants is based on common-garden studies as a means of identifying genetically controlled responses among plants grown in different adaptive norms. Work has ranged from the early reciprocal transplant studies of Clausen & Hiesey (1958) with *Potentilla glandulosa* and Clausen et al. (1948) with *Achillea*

lanulosa (Asteraceae) across an elevational gradient in California, to work by Mooney & Billings (1961) with *Oxyria digyna* from a broad latitudinal range of arctic and alpine populations, to work by Tieszen & Bonde (1967) with *Deschampsia caespitosa* (Poaceae) and *Trisetum spicatum* (Poaceae) from arctic and alpine sites. The work of Clausen and colleagues revealed a sequence of climatic races. Mooney & Billings (1961) showed a clear differentiation of physiological traits in *Oxyria digyna* over a latitudinal gradient from northern Alaska south through the Rocky Mountains to Colorado. A more recent study returned to two separate reciprocal transplant experiments in Alaska 30 years later, *Dryas octopetala* subspecies along a snowbank gradient in the Alpine and *Eriophorum vaginatum* (Cyperaceae) along a latitudinal gradient in the Arctic (Bennington et al., 2012; McGraw & Antonovics, 1983; Shaver et al., 1986). For both species, differential survival in the ecotypes' native site provided strong evidence for local adaptation in these long-lived species. These findings show a broad range of ecotypes that would likely respond differently to climate change. Ultimately, the ecotypic differentiation revealed by these and other studies of arctic and alpine plants suggests extinction of wide-ranging species would be unlikely.

Just how the genes underlying genetic variation control ecotypic differentiation in arctic and alpine plants is unknown. Molecular evidence based on non-coding regions of the genome, so usefully applied in phylogeography is, however, neutral to the effects of selection. A focus on adaptive rather than neutral genetic variation will be needed for predicting responses to climate warming (Crawford, 2008). If we assume ecotypic diversity is a surrogate for adaptive genetic variation, it would seem, as discussed above, that species with high ecotypic diversity are likely to survive climate warming. To date, the genetics of adaptation have largely been studied in model organisms with short generation times and not for long-lived arctic and alpine plants.

We must note that an important distinction between arctic and alpine environments is both day length and light intensity. Phenology is often related to day length in plants. For example, arctic and alpine populations of *Oxyria digyna* show ecotypic differences in flower and rhizome production, and in growth responses, to temperature and day length (Mooney & Billings, 1961). Consequently, southern ecotypes cannot simply migrate northward to cooler temperatures in a warming climate, as day length varies from about 15 hours of solar radiation on the summer solstice at Niwot Ridge in Colorado (40° N) to continuous low intensity 24-hour solar radiation north of the Arctic Circle (>66° 33' 44" N). There are clearly limits to arctic and alpine plants escaping climate change by extending their ranges northwards and upwards.

Several recent global modeling studies have shed light on potential future states of vegetation in arctic and alpine environments. Alsos et al. (2012) analyzed range-wide genetic diversity of 27 northern plant species and used species distribution modeling to predict their future distributions and levels of genetic diversity through 2080. Their work predicts range reduction and loss of genetic diversity in nearly all species in their study, according to at least one scenario. Species that were more vulnerable to losses in genetic diversity lacked traits for long distance dispersal and had high levels of genetic differentiation among populations. In another study, Pearson et al. (2013) used ecological niche models, based on statistical associations between vegetation and climate, to predict the future distribution of arctic vegetation. Their study predicts that at least half of vegetated areas will shift to a different vegetation class, for example from graminoid tundra to shrub tundra, by 2050. Moreover, their model predicts woody plant cover, or shrub tundra and forest, will increase by as much

as 52%. In contrast, Breen et al.'s (2014) regional modeling study for Alaska tundra predicts more modest shifts in woody plant cover. Their study used a state and transition model that is driven by both climate and fire dynamics. Treeline advance varies by the climate model used to drive the simulations. With greater tundra fire activity, 12% of tundra transitions to forest, and 11% of graminoid tundra transitions to shrub tundra, by 2100. In contrast, with more modest tundra fire activity, the amount of tundra that transitions to forest nearly doubles to 20%, but there is little change in the relative amounts of graminoid and shrub tundra.

ARCTIC AND ALPINE PLANT INTERACTIONS WITH OTHER ORGANISMS: THE ECTOMYCORRHIZAL SYMBIOSIS

Virtually every plant is full of endophytes (fungi, bacteria, viruses) that occur in all organs of plants. As in other ecosystems, plants in the Arctic and Alpine interact with organisms across kingdoms, including plants, animals (mammals, birds, insects), fungi, bacteria, archaea, and viruses. Many of these complex interactions, both direct and indirect, occur simultaneously. These interactions happen with different degrees of specificity and range from antagonistic to mutually beneficial. The outcome of such interactions depends in large part on the environment (Partida-Martinez & Heil, 2011), which in the Arctic and Alpine are dominated by low temperatures and a short growing season.

The use of molecular methods has not only revealed a great biodiversity of organisms in arctic and alpine environments, but also highlights the complex interactions of plants with other organisms, including fungi (Dahlberg et al., 2013; Gao & Yang, 2010; Timling & Taylor, 2012). Fungi are ubiquitous and benefit plants as mutualistic mycorrhizas (also see Chapters 2, 5) and saprotrophs by providing nutrients and water; they can harm plants as pathogens. We will illustrate how molecular methods have shed light on plant interactions with other organisms through the example of ectomycorrhizal fungi (EMF).

The ectomycorrhizal symbiosis is abundant throughout the Arctic and Alpine, where the fungi associate with shrubs, as well as a few sedges and forbs. Although EMF associate with only about 6% of the vascular plants in the Arctic, these plants are important components of plant communities that cover up to 69% of the ice-free Arctic (Walker et al., 2005). The symbiosis seems especially important in biomes with low nutrient availability, where the fungus provides nutrients and water to the plant and the plant provides carbohydrates to the fungus. In the Arctic, 61-86% of nitrogen in ectomycorrhizal plants is provided by their fungal symbionts while the plant provides 8-17% of photosynthetic carbon to the fungi (Hobbie & Hobbie, 2006).

In contrast to vascular plants in the Arctic, EMF associated with shrubs do not follow the classic pattern of species richness decline with latitude, which suggests that fungal species richness is not governed by temperature (Bjorbaekmo et al., 2010; Timling et al., 2012). The species-rich EMF communities that have been observed on host plants in the Arctic and Alpine are dominated by a few families that are especially species-rich (Thelephoraceae, Cortinariaceae, Inocybaceae) (Blaalid et al., 2014; Gao & Yang, 2010). Similarly, many plant communities are dominated by a few species-rich families (Asteraceae, Brassicaceae, Caryophyllaceae, Cyperaceae, Fabaceae, Poaceae, Ranunculaceae, and Rosaceae; Daniëls et

al., 2013). This suggests that some plant and fungal families are especially adapted to arctic and alpine environments.

Furthermore, EMF communities in the Arctic appear to be dominated by generalist fungi with wide ecological amplitudes and which are excellent dispersers (Geml et al., 2012; Timling et al., 2012). In contrast to boreal (Taylor et al., 2010) and temperate forests (Ishida et al., 2007) and Mediterranean woodlands (Morris et al., 2008), the ectomycorrhizal symbiosis seems to have lower specificity in the Arctic and Alpine (Botnen et al., 2014; Gao & Yang 2010; Timling et al., 2012). While EMF communities in boreal, temperate and tropical climates show distinctive phylogeographic distribution patterns, with restrictions to continents and sub-continental regions (Geml et al., 2008; Talbot et al., 2014), the majority (73%) of EMF species observed in studies from Svalbard and across the entire bioclimatic gradient of North American Arctic have occurred also in other regions within and beyond the Arctic (Geml et al., 2012; Timling et al., 2012). Such wide distributions within the Arctic have been also observed for lichens (Geml et al., 2010) and vascular plants (Alsos et al., 2007). The wide distribution of fungi and lichens might be aided by the smaller size of their propagules. Finally the wide distribution suggests that terrestrial and trans-ocean long distance dispersal must be a common phenomenon in the wide open landscapes of the Arctic, aided by wind, snow, driftwood, sea ice, birds, and mammals (reviewed in Alsos et al., 2007).

Nevertheless, within the Arctic and Alpine, EMF communities show distribution patterns at the regional and local scale that often parallel those of plant communities found there. Ectomycorrhizal fungal communities associated with *Dryas integrifolia* and *Salix arctica* (Salicaceae) change gradually across the five bioclimatic subzones of the North American Arctic, corresponding with climate, plant productivity, glaciation history, geology, and soil factors (Timling et al., 2012). At a local scale, EMF communities often correlate with habitat, successional stage, plant community, and bedrock and edaphic factors such as pH, carbon, and nitrogen (Blaalid et al., 2014; Fujimura & Egger, 2012; Yao et al., 2013; Zinger et al., 2011).

Climatic changes in the Arctic have led to pan-arctic shrub expansion (Tape et al., 2006) and increases in plant productivity (Bhatt et al., 2010) and nutrient cycling (Rustad et al., 2001). Long-term warming experiments show not only changes in plant communities (Walker et al., 2006) but also changes in EMF community structure associated with *Betula nana* (Betulaceae), one of the shrubs most responsive to climate warming (Deslippe et al., 2011). The mutualistic nature of the ectomycorrhizal symbiosis, the low host specificity and the wide distribution support the idea that EMF may play critical roles in the expansion of shrubs in the tundra. Evidence from past climate changes comes from paleobotanical studies which show that plant and fungal communities changed with past glacial and interglacial cycles, with an increase in shrubs and trees and their ectomycorrhizal symbionts since the last glaciation (de Vernal & Hillaire-Marcel 2008; Lydolph et al., 2005). Soil analyses along a bioclimatic gradient in the North American Arctic show that subzone A, which is devoid of woody species, harbors EMF species, probably as spores, and that soil fungal communities in subzone E greatly overlap (74%) with communities of the boreal forests (Timling et al., 2014). Furthermore, a bioassay with soils from above treeline showed that these soils provide sufficient inoculum for a significant growth of conifers (Reithmeier & Kernaghan, 2013). The authors concluded that spores in the soils and shrubs above treeline could facilitate treeline expansion. With a warming climate one might expect changes of EMF community composition with a northward shift of some EMF taxa. Finally EMF may be critical in

facilitating an establishment of woody species in subzone A and a treeline expansion into subzone E.

CONCLUSION

Despite considerable progress made in recent years, there remains much to learn about the ecology and evolution plants in arctic and alpine environments. Molecular ecology, modeling, and remote sensing studies, along with future fossil discoveries, will continue to build upon our knowledge of these biomes and improve our understanding of their potential response to future climate change. Brochmann et al. (2013) write that the species-poor arctic flora is likely to be adapted to environmental change, through selection for high mobility and buffering against inbreeding- and bottleneck-induced gene loss via polyploidy. However, today's flora of arctic and alpine environments will be challenged by a climate warmer than the Holocene and over a shorter period. There is a need to begin focusing on adaptive, rather than neutral genetic variation, to predict how arctic and alpine plants will respond to climate warming over the next century.

There is also a need to intensify biodiversity research on arctic and alpine floras, with an emphasis on vegetation classification, monitoring, and modeling (Daniëls et al., 2013). Efforts such as the Arctic Vegetation Archive (Walker et al., 2013) are underway to improve coordination and cooperation among arctic nations and to produce a pan-arctic vegetation classification. Furthermore, the archive will provide vegetation data from across the Circumpolar Arctic for use in biodiversity and ecosystem models. Jónsdóttir (2013) is also leading an initiative to develop a research framework on biodiversity-shaping forces that considers different spatial and temporal scales and identifies commonalities across biological hierarchies and organisms. This framework will provide for testing hypotheses about biodiversity trends in the face of climate change in the Arctic and Alpine.

ACKNOWLEDGMENTS

We thank Inger Alsos, Teresa Hollingsworth, and two anonymous reviewers for their comments on an earlier version of the chapter that greatly improved its content. We also thank Christian Körner for fruitful discussions about the global distribution of arctic and alpine tundra and for sharing his map of mountainous regions of the world for adaptation and inclusion in the chapter.

REFERENCES

- Abbott, R. J. (Ed.). (2008) Special issue: History, evolution and future of arctic and alpine flora. *Plant Ecology & Diversity* 1, 129-349.
- Abbott, R. J. & Brochmann, C. (2003) History and evolution of the arctic flora: In the footsteps of Eric Hultén. *Molecular Ecology* 12, 299-313.
- ACIA (2005) *Arctic climate impact assessment*. Cambridge: Cambridge University Press.

- Alsos, I. G., Eidesen, P. B., Ehrich D., Skrede, I., Westergaard, K., Jacobsen, G. H., Landvik, J. Y., Taberlet, P. & Brochmann, C. (2007) Frequent long-distance plant colonization in the changing Arctic. *Science* 316, 1606-1609.
- Alsos, I. G., Ehrich, D., Thuiller, W., Eidesen, P. B., Tribsch, A., Schönswetter, P., Lagaye, C., Taberlet, P. & Brochmann, C. (2012) Genetic consequences of climate change for northern plants. *Proceedings of the Royal Society Series B*, DOI: 10.1098/rspb.2011.2363.
- Avise, J. C. (1994) *Molecular markers, natural history and evolution*. New York, NY: Chapman & Hall.
- Bennike, O. & Bøcher, J. (1990) Forest-tundra neighbouring the North Pole: Plant and insect remains from the Plio-Pleistocene Kap København Formation, North Greenland. *Arctic* 43, 332-338.
- Bennington, C. C., Fetcher, N., Vavrek, M. C., Shaver, G. R., Cummings, K. J. & McGraw, J. B. (2012) Home site advantage in two long-lived arctic plant species: Results from two 30-yr reciprocal transplant studies. *Journal of Ecology* 100, 841-845.
- Berg, R. (1963) Disjunctions in the Norwegian alpine flora and theories proposed for their explanation. *Blyttia* 212, 133-177, in Norwegian with an English summary (cited in Brochmann et al., 1996).
- Bhatt, U. S., Walker, D. A., Raynolds, M. K., Comiso, J. C., Epstein, H. E., Jia, G., Gens, R., Pinzon, J. E., Tucker, C. J., Tweedie, C. E. & Webber, P. J. (2010) Circumpolar arctic tundra vegetation change is linked to sea ice decline. *Earth Interactions* 14, 1-20.
- Billings, W. D. & Mooney, H. A. (1968) The ecology of arctic and alpine plants. *Biological Review* 43, 481-529.
- Birks, H. H. (2008) The Late-Quaternary history of arctic and alpine plants. *Plant Ecology & Diversity* 1, 135-146.
- Birks, H. J. B. (2013) Alpine plants and recent climate change. *Climatica*. Online: <http://climatica.org.uk/alpine-plants-and-recent-climate-change>. Accessed July 1, 2014.
- Bjorbaekmo, M. F. M., Carlsen, T., Bryisting, A., Vralstad, T., Hoiland, K., Ugland, K. I. & Geml, J., Schmacher, T. & Kauserud, H. (2010) High diversity of root associated fungi in both alpine and arctic *Dryas octopetala*. *BMC Plant Biology* 10, DOI:10.1186/1471-2229-10-244.
- Björk, R. G. & Molau, U. (2007) Ecology of alpine snowbeds and the impact of global change. *Arctic, Antarctic and Alpine Research* 39, 34-43.
- Blaalid, R., Davey, M. L., Kauserud, H., Carlsen, T., Halvorsen, R., Hoiland, K. & Eidesen, P. B. (2014) Arctic root-associated fungal community composition reflects environmental filtering. *Molecular Ecology* 23, 649-659.
- Bliss, L. C. (2000) Arctic tundra and the polar desert biome. In: M. G. Barbour & W. D. Billings (Eds.) *North American terrestrial vegetation*. Second edition (pp. 1-40). Cambridge, UK: Cambridge University Press.
- Botnen, S., Vik, U., Carlsen, T., Eidesen, P. B., Davey, M. L. & Kauserud, H. (2014) Low host specificity of root-associated fungi at an Arctic site. *Molecular Ecology* 23, 975-985.
- Breen, A. L., Bennett, A., Hewitt, R. E., Hollingsworth, T. N., Genet, H., Euskirchen, E. S., McGuire, A. D. & Rupp, T. S. (2014) Tundra fire and vegetation dynamics: Simulating the effect of climate change on fire regimes in Arctic ecosystems. In prep to submit to *Ecology Letters*.

- Brochmann, C. & Brysting, A. K. (2008) The Arctic—An evolutionary freezer? *Plant Ecology & Diversity* 1, 181-195.
- Brochmann, C., Stedje, B. & Borgen, L. (1992a) Gene flow across ploidal levels in *Draba* (Brassicaceae). *Evolutionary Trends in Plants* 6, 125–134.
- Brochmann, C., Soltis, P. S. & Soltis, D. E. (1992b) Recurrent formation and polyphyly of Nordic polyploids in *Draba* (Brassicaceae). *American Journal of Botany* 79, 673-688.
- Brochmann, C., Gabrielsen, T. M., Nordal, I., Landvik, J. Y. & Elven, R. (2003) Glacial survival or *tabula rasa*? The history of North Atlantic biota revisited. *Taxon* 52, 417-450.
- Brochmann, C., Brysting, A. K., Alsos, I. G., Borgen, L., Grundt, H. H., Scheen A. C. & Elven, R. (2004) Polyploidy in arctic plants. *Biological Journal of the Linnean Society* 82, 521-536.
- Brochmann, C., Edwards, M. & Alsos, I. G. (2013) The dynamic past and future of arctic vascular plants: Climate change, spatial variation and genetic diversity. In: K. Rhode (Ed.). *The balance of nature and human impact* (pp. 133-152). Cambridge, UK: Cambridge University Press.
- CAVM Team (2003) *Circumpolar Arctic vegetation map, scale 1:7 500 000*. Conservation of Arctic Flora and Fauna (CAFF) map no. 1. Anchorage, AK: U.S. Fish and Wildlife Service.
- Callaghan, T. V., Bjorn, L. O., Chernov, Y., Chapin, F. S., Christensen, T. R., Huntley, B., Ims, R. A., Johansson, M., Jolly, D., Jonasson, S., Matveyeva, N., Panikov, N., Oechel, W., Shaver, W., Elster, J., Henttonen, H., Laine, K., Taulavuori, K., Taulavuori, E. & Zockler, C. (2004) Biodiversity, distributions and adaptations of arctic species in the context of environmental change. *AMBIO* 33, 404-417.
- Cannone, N., Sgorbayi, S. & Guglielmin, M. (2007) Unexpected impacts of climate change on alpine vegetation. *Frontiers in Ecology and Environment* 5, 360–364.
- Chapin, F. S. III & Chapin, M. C. (1981) Ecotypic differentiation of growth processes in *Carex aquatilis* along latitudinal and local gradients. *Ecology* 62, 1000-1009.
- Chapin, F. S. III & Körner, C. (Eds.) (1995) *Arctic and alpine biodiversity: Patterns, causes and ecosystem consequences*. Berlin: Springer-Verlag.
- Chernov, Yu. I. (1985) *The living tundra*. Studies in Polar Research. Cambridge: Cambridge University Press.
- Clausen, J. & Hiesey, W.M. (1958) *Experimental studies on the nature of species. IV. Genetic structure of ecological races*. Publication 615. Washington, DC: Carnegie Institution of Washington.
- Clausen, J., Keck, D. D. & Hiesey, W. M. (1948) *Experimental studies on the nature of species. III: Environmental responses of climatic races of Achillea*. Publication 581. Washington, DC: Carnegie Institution of Washington.
- Crawford, R. M. M. (2008) Cold climate plants in a warmer world. *Plant Ecology & Diversity* 1, 197-208.
- Dahl, E. (1955) Biogeographic and geological indications of unglaciated areas in Scandinavia during the glacial ages. *Geological Society of America Bulletin* 66, 499-519.
- Dahl, E. (1963) Plant migrations across the North Atlantic Ocean and their importance for the paleogeography of the region. In: A. Löve & D. Löve (Eds.). *North Atlantic biota and their history* (pp. 173-188). London: Pergamon Press.
- Dahlberg, A., Bültmann, H., Cripps, C. L., Eyjólfsson, G. G., Gulden, G., Kristinsson, H. & Zhurbenko, M. (2013) Fungi. In: H. Meltøfte (Ed.). *Arctic biodiversity assessment: Status*

- and trends in Arctic biodiversity* (pp. 354-371). Akureyri: Conservation of Arctic Flora and Fauna (CAFF).
- Daniëls, F. A., Gillespie, L. J. & Poulin, M. (2013) Plants. In: H. Meltofte (Ed.). *Arctic biodiversity assessment: Status and trends in Arctic biodiversity* (pp. 310-353). Akureyri: Conservation of Arctic Flora and Fauna (CAFF).
- Darwin, C. (1859) *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. London: John Murray.
- de Vernal, A. & Hillaire-Marcel, C. (2008) Natural variability of Greenland climate, vegetation, and ice volume during the past million years. *Science* 320, 1622-1625.
- Deslippe, J. R., Hartmann, M., Mohn, W. W. & Simard, S. W. (2011) Long-term experimental manipulation of climate alters the ectomycorrhizal community of *Betula nana* in Arctic tundra. *Global Change Biology* 17, 1625-1636.
- Eidesen, P. B., Alsos, I. G., Popp, M., Stensrud, Ø., Suda, J. & Brochmann, C. (2007) Nuclear vs. plastid data: Complex Pleistocene history of a circumpolar key species. *Molecular Ecology* 16, 3902-3925.
- Eidesen, P. B., Ehrich, D., Bakkestuen, V., Alsos, I. G., Gilg, O., Taberlet, P. & Brochmann, C. (2013) Genetic roadmap of the Arctic: Plant dispersal highways, traffic barriers and capitals of diversity. *New Phytologist* 200, 898-910.
- Ellenberg, H. H. (2009) The vegetation above the alpine treeline. In: H. H. Ellenberg. *Vegetation ecology of Central Europe*. Fourth edition (pp. 388-454). Cambridge: Cambridge University Press.
- Elmendorf, S.C., Henry, G.H. R., Hollister, R. D., Björk, R. G., Boulanger-Lapointe, N., Cooper, E. J., Cornelissen, J.H. C., & Day, T. A., et al. (2012) Plot-scale evidence of tundra vegetation change and links to recent summer warming. *Nature Climate Change* 2, 453-457.
- Elven, R. (2007) *Checklist of the panarctic flora (PAF): Vascular plants*. Oslo: University of Oslo, National Centre of Biosystematics, Natural History Museum.
- Elven, R. (2011) *Annotated checklist of the panarctic flora (PAF): Vascular plants*. Oslo: University of Oslo, National Centre of Biosystematics, Natural History Museum.
- Epstein, H. E., Raynolds, M. K., Walker, D. A., Bhatt, U. S., Tucker, C. J. & Pinzon, J. E. (2012) Dynamics of aboveground phytomass of the circumpolar arctic tundra over the past three decades. *Environmental Research Letters* 7, 015506. DOI:10.1088/1748-9326/7/1/015506.
- Fernald, M. L. (1925) Persistence of plants in unglaciated areas of boreal America. *Memoirs of the American Academy of Arts and Sciences* 15, 237-342.
- Fujimura, K. E. & Egger, K. N. (2012) Host plant and environment influence community assembly of High Arctic root-associated fungal communities. *Fungal Ecology* 5, 409-418.
- Gao, Q. & Yang, Z. L. (2010) Ectomycorrhizal fungi associated with two species of *Kobresia* in an alpine meadow in the eastern Himalaya. *Mycorrhiza* 20, 281-287.
- Geml, J., Laursen, G. A. & Taylor, D. L. (2008) Molecular diversity assessment of arctic and boreal *Agaricus* taxa. *Mycologia* 100, 577-589.
- Geml, J., Kauff, F., Brochmann, C. & Taylor, D. L. (2010) Surviving climate changes: High genetic diversity and transoceanic gene flow in two arctic-alpine lichens, *Flavocetraria cucullata* and *Flavocetraria nivalis* (Parmeliaceae, Ascomycota). *Journal of Biogeography* 37, 1529-1542.

- Geml, J., Timling, I., Robinson, C. H., Lennon, N., Nusbaum, C. H., Brochmann, C., Noorderloos, M. E. & Taylor, D. L. (2012) An arctic community of symbiotic fungi assembled by long-distance dispersers: Phylogenetic diversity of ectomycorrhizal basidiomycetes in Svalbard based on soil and sporocarp DNA. *Journal of Biogeography* 39, 74-88.
- Gottfried, M., Pauli, H., Futschik, A., Akhalkatsi, M., Barančok, P., Benito Alonso, J. L., Coldea, G., Dick, J., Erschbamer, B., Fernández Calzado, M. R., Kazakis, G., Krajči, J., Larsson, P., Mallaun, M., Michelsen, O., Moiseev, D., Moiseev, P., Molau, U., Merzouki, A., Nagy, L., Nakhutsrishvili, G., Pedersen, B., Pelino, G., Puscas, M., Rossi, G., Stanisci, A., Theurillat, J.-P., Tomaselli, M., Villar, L., Vittoz, P., Vogiatzakis, I. & Grabherr, G. (2012) Continent-wide response of mountain vegetation to climate change. *Nature Climate Change* 2, 111-115.
- Grabherr, G., Gottfried, M., Gruber, A. & Pauli, H. (1995) Patterns and current changes in alpine plant diversity. In: F. S. Chapin III & C. Körner (Eds.). *Arctic and alpine biodiversity: Patterns, causes and ecosystem consequences* (pp. 167-181). Berlin: Springer-Verlag.
- Grundt, H. H., Kjølner, S., Borten, L., Rieseberg, L. H. & Brochmann, C. (2006) High biological species diversity in the arctic flora. *Proceedings of the National Academy of Sciences (USA)* 103, 972-975.
- Hagarup, O. (1928) Morphological and cytological studies of *Bicornes*. *Dansk Botanisk Arkiv* 6, 1-27.
- Hobbie, J. E. & Hobbie, E. A. (2006) N-15 in symbiotic fungi and plants estimates nitrogen and carbon flux rates in Arctic tundra. *Ecology* 87, 816-822.
- Hocking, B. & Sharplin, C. D. (1965) Flower basking by arctic insects. *Nature* 206, 215
- Hopkins, D. M., Matthews, J. V. Jr., Wolfe, J. A. & Silberman, M. L. (1971). A Pliocene flora and insect fauna from the Bering Strait region. *Paleogeography, Paleoclimatology & Paleoeecology* 9, 111-231.
- Hudson, J. M. G. & Henry, G. H. R. (2009) Increased plant biomass in a High Arctic heath from 1981–2008. *Ecology* 90, 2657–2663.
- Hultén, E. (1937) *History of the arctic and boreal biota of the Quarternary* [sic] *Period*. Stockholm: Bokförlags Aktiebolaget.
- Hultén, E. (1958) The Amphi-Atlantic Plants and their phytogeographical connections. *Kungliga Svenska Vetenskapsakademiens Handlingar* 7, 1-340.
- Ishida, T. A., Nara, K. & Hogetsu, T. (2007) Host effects on ectomycorrhizal fungal communities: Insight from eight host species in mixed conifer-broadleaf forests. *New Phytologist* 174, 430-440.
- Ives, J. (1974) Biological refugia and the nunatak hypothesis. In: J. Ives & R. Barry (Eds.). *Arctic and alpine environments* (pp. 605-636). London: Methuen.
- Johnson, A. W. & Packer, J. G. (1965) Polyploidy and environment in arctic Alaska. *Science* 148, 237-239.
- Johnson, A. W. & Packer, J. G. (1967) Distribution, ecology, and cytology of the Ogororuk Creek flora and the history of Beringia. In: D. M. Hopkins (Ed.). *The Bering land bridge* (pp. 245-265). Stanford, CA: Stanford University Press.
- Johnson, A. W., Packer, J. G. & Reese, G. (1965) Polyploidy, distribution, and environment. In: H. E. Wright, Jr. & D. G. Frey (Eds.). *The Quaternary of the United States* (pp. 497-507). Princeton, New Jersey: Princeton University Press.

- Jónsdóttir, I. S. (2011) Diversity of plant life histories in the Arctic. *Preslia* 83, 281-300.
- Jónsdóttir, I. S. (2013) Shaping forces of biodiversity in the Arctic – exploring the feasibility of a coherent research framework. *International tundra experiment 2013 meeting abstract*. Online: http://www.wsl.ch/epub/itex/sessions/detail_EN?id=147&session=37. Accessed July 1, 2014.
- Kade, A. N., Walker, D. A. & Raynolds, M. K. (2005) Plant communities and soils in cryoturbated tundra along a climate gradient in the Low Arctic, Alaska. *Phytocoenologia* 35, 761–820.
- Kevin, P. G. (1972a) Heliotropism in some arctic flowers. *Canadian Field Naturalist* 86, 41-44.
- Kevin, P. G. (1972b) Insect pollination of high arctic flowers. *Journal of Ecology* 60, 831-847.
- Kevin, P. G. (1972c) Floral colors in the high arctic with reference to insect-flower relations and pollination. *Canadian Journal of Botany* 50, 2289-2316.
- Kevin, P. G. (1975) Sun-tracking solar furnaces in high arctic flowers: Significance for pollination and insects. *Science* 189, 723-726.
- Klanderud, K. & Birks, H. J .B. (2003) Recent increases in species richness and shifts in altitudinal distributions of Norwegian mountain plants. *The Holocene* 13, 1-6.
- Klein, J. A., Harte, J. & Zhao, X. (2007) Experimental warming, not grazing, decreases rangeland quality on the Tibetan Plateau. *Ecological Applications* 17, 541–557.
- Körner, C. (2002) Mountain biodiversity, its causes and function: An overview. In: C. Körner & E. M. Spehn (Eds.). *Mountain biodiversity: A global assessment* (pp. 3-20). New York, NY: Parthenon.
- Körner, C. (2003) *Alpine plant life: Functional plant ecology of high mountain ecosystems*. Second edition. Berlin: Springer-Verlag.
- Körner C., Paulsen J. & Spehn E. M. (2011) A definition of mountains and their bioclimatic belts for global comparisons of biodiversity data. *Alpine Botany* 121, 73-78.
- Lesica, P. (2014) Arctic-alpine plants decline over two decades in Glacier National Park, Montana, U.S.A. *Arctic, Antarctic and Alpine Research* 46, 327-332.
- Löve, A. (1959) Origin of the arctic flora. Problems of the Pleistocene and Arctic. *Publications of the McGill University Museum* 1, 82-95.
- Löve, D. (1963) Dispersal and survival of plants. In: A. Löve & D. Löve (Eds). *North Atlantic biota and their history* (pp. 189-205). London: Pergamon Press.
- Lydolph, M. C., Jacobsen, J., Arctander, P., Gilbert, M. T., Gilichinsky, D. A., Hansen, A. J., Willerslev, E. & Lange, L. (2005) Beringian paleoecology inferred from permafrost-preserved fungal DNA. *Applied Environmental Microbiology* 71, 1012-1017.
- Marr, K. L., Allen, G. A. & Hebda, R. J. (2008) Refugia in the Cordilleran ice sheet of western North America: Chloroplast DNA diversity in the arctic-alpine plant *Oxyria digyna*. *Journal of Biogeography* 35, 1323-1334.
- Matthews, J. V. Jr. & Ovenden, L. E. (1990) Late Tertiary plant macrofossils from localities in Arctic/Subarctic North America: A review of the data. *Arctic* 43, 364-392.
- McGraw, J. B. & Antonovics, J. (1983) Experimental ecology of *Dryas octopetala* ecotypes. I. Ecotypic differentiation and life cycle stages of selection. *Journal of Ecology* 71, 879–897.
- Meltofte, H. (Ed.) (2013) *Arctic biodiversity assessment: Status and trends in Arctic biodiversity*. Akureyri: Conservation of Arctic Flora and Fauna (CAFF).

- Mooney, H. A. & Billings, W. D. (1961) Comparative physiological ecology of arctic and alpine populations of *Oxyria digyna*. *Ecological Monographs* 31, 1-29.
- Morris, M. H., Smith, M. E., Rizzo, D. M., Rejmánek, M. & Bledsoe, C. S. (2008) Contrasting ectomycorrhizal fungal communities on the roots of co-occurring oaks (*Quercus* spp.) in a California woodland. *New Phytologist* 178, 167-176.
- Müller, E., Eidesen, P. B., Ehrich, D. & Alsos, I. G. (2012) Frequency of local, regional, and long-distance dispersal of diploid and tetraploid *Saxifraga oppositifolia* (Saxifragaceae) to Arctic glacier forelands. *American Journal of Botany* 99, 459-71.
- Murray, D. F. (1987) Breeding systems in the vascular flora of Arctic North America. In: K. M. Urbanska (Ed.). *Differentiation patterns in higher plants* (pp. 239-262). Orlando, FL: Academic Press.
- Murray, D. F. (1995) Causes of arctic plant diversity: origin and evolution. In: F. S. Chapin III & C. Körner (Eds.) *Arctic and alpine biodiversity: Patterns, causes and ecosystem consequences* (pp. 21-32). Berlin: Springer-Verlag.
- Murray, D. F. (1997) Regional and local vascular plant diversity in the Arctic. *Opera Botanica* 132, 9-18.
- Nathorst, A. G. (1892) Über den gegenwärtigen Stand unserer Kenntnis der Verbreitung fossiler Glazialpflanzen: Bihang til Kungliga Svenska Vetenskaps Akademiens. *Handlingar* 17, Afd. III, 5, 1-35.
- Olofsson, J., Oksanen, L., Callaghan, T., Hulme, P. E., Oksanen, T. & Suominen, O. (2009) Herbivores inhibit climate-driven shrub expansion on the tundra. *Global Change Biology* 15, 2681-2693.
- Partida-Martinez, L. P. & Heil, M. (2011) The microbe-free plant: Fact or artifact? *Frontiers in Plant Science* 100, 1-16.
- Payer, D. C., Josefson, A. B. & Fjeldså, J. (2013) Species Diversity in the Arctic. In: H. Meltøfte (Ed.). *Arctic biodiversity assessment: Status and trends in Arctic biodiversity* (pp. 66-77). Akureyri: Conservation of Arctic Flora and Fauna (CAFF).
- Pearson, R. G., Phillips, S. J., Loranty, M. M., Beck, P. S., Damoulas, T., Knight, S. J. & Goetz, S. J. (2013) Shifts in Arctic vegetation and associated feedbacks under climate change. *Nature Climate Change* 3, 673-677.
- Polunin, N. (1951) The real Arctic: Suggestions for its delimitation, subdivision, and characterization. *Journal of Ecology* 39, 308-315.
- Raup, H. M. (1969) Studies of vegetation in northwest Greenland. In: K. N. H. Greenridge (Ed.). *Essays in plant geography and ecology*. Halifax: Nova Scotia Museum.
- Raup, H. M. (1941) Botanical problems in boreal America. *Botanical Review Part 1*, 7, 147-208; *Part 2,7*, 209-248.
- Raynolds, M. K., Walker, D. A., Munger, C. A., Vonlanthen, C. M. & Kade, A. N. (2008) A map analysis of patterned-ground along a North American Arctic transect. *Journal of Geophysical Research* 113, DOI:10.1029/2007JG000512.
- Reithmeier, L. & Kernaghan, G. (2013) Availability of ectomycorrhizal fungi to black spruce above the present treeline in eastern Labrador. *PLoS One* 8, e77527. DOI:10.1371/journal.pone.0077527
- Rongfu, H. & Miehe, G. (1988) An annotated list of plants from Southern Tibet. *Willdenowia* 18, 81-112.
- Rustad, L. E., Campbell, J. L., Marion, G. M., Norby, R. J., Mitchell, M. J., Hartley, A. E., Cornelissen, J. H. C., Gurevitch, J. & CGTE-NEWS (2001) A meta-analysis of the

- response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia* 126, 543-562.
- Savile, D. B. O. (1956) Known dispersal rates and migratory potentials as clues to the origin of the North American biota. *American Midland Naturalist* 56, 434-453.
- Savile, D. B. O. (1959) The botany of Somerset Island, District of Franklin. *Canadian Journal of Botany* 37, 959-1002.
- Savile, D. B. O. (1972) *Arctic adaptations in plants*. Monograph No. 6. Ottawa: Research Branch, Agriculture Canada.
- Schönswetter, P., Tribsch, A., Stehlik, I. & Niklfeld, H. (2004) Glacial history of the high alpine *Ranunculus glacialis* (Ranunculaceae) in the European Alps in a comparative phylogeographical context. *Biological Journal of the Linnean Society* 81, 183-195.
- Schönswetter, P., Elven, R. & Brochmann, C. (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.
- Shaver, G. R., Chapin, F. S., & Billings, W. D. (1979) Ecotypic differentiation in *Carex aquatilis* as related to ice wedge polygonization in the Alaskan coastal tundra. *Journal of Ecology* 67, 1025-1046.
- Shaver, G.R., Fetcher, N. & Chapin, F.S. (1986) Growth and flowering in *Eriophorum vaginatum*: annual and latitudinal variation. *Ecology* 67, 1524-1535.
- Sieg, B. & Daniëls, F. J.A. (2005) Altitudinal zonation of vegetation in continental West Greenland with special reference to snowbeds. *Phytocoenologia* 35, 887-908.
- Sørensen, T. (1941) Temperature relations and phenology of the northwest Greenland flowering plants. *Meddelelser om Grønland* 125, 1-305.
- Starr, G. & Oberbauer, S. F. (2003) Photosynthesis of arctic evergreens under snow: Implications for tundra ecosystem carbon balance. *Ecology* 84, 1415-1420.
- Stehlik, I., Blattner, F. R., Holderegger, R. & Bachmann, K. (2002) Nunatak survival of the high alpine plant *Eritrichium nanum* (L.) Gaudin in the central Alps during the ice ages. *Molecular Ecology* 11, 2027-2036.
- Taberlet, P., Zimmermann, N. E., English, T., Tribsch, A. & Holderegger, R. et al. (2012) Genetic diversity in widespread species is not congruent with species richness in alpine plant communities. *Ecology Letters* 15, 1439-1448.
- Talbot, J. M., Bruns, T. D., Taylor, J. W., Smith, D. P., Branco, S., Glassman, S. I., Erlandson, S., Vilgalsy, R., Liao, H.-L., Smith, M. E. & Peay, K. G. (2014) Endemism and functional convergence across the North American soil mycobiome. *Proceedings of the National Academy of Sciences (USA)*, DOI: 10.1073/pnas.1402584111.
- Tape, K., Sturm, M. & Racine, C. (2006) The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. *Global Change Biology* 12, 686-702.
- Taylor, D. L., Herriott, I. C., Stone, K. E., McFarland, J. W., Booth, M. G. & Leigh, M. B. (2010) Structure and resilience of fungal communities in Alaskan boreal forest soils. *Canadian Journal of Forest Research* 40, 1288-1301.
- Tieszen, L. L. & Bonde, E. K. (1967) The influence of light intensity on growth and chlorophyll in arctic, subarctic and alpine populations of *Deschampsia caespitosa* and *Trisetum spicatum*. *University of Colorado Studies, Series in Biology* 25, 1-21.
- Timling, I. & Taylor, D. L. (2012) Peeking through a frosty window: Molecular insights into the ecology of Arctic soil fungi. *Fungal Ecology* 5, 419-429.

- Timling, I., Dahlberg, A., Walker, D. A., Gardes, M., Charcosset, J. Y., Welker, J. M. & Taylor, D. L. (2012) Distribution and drivers of ectomycorrhizal fungal communities across the North American Arctic. *Ecosphere* 3, DOI: 10.1890/ES12-00217.1.
- Timling, I., Walker, D. A., Nusbaum, C., Lennon, N. J. & Taylor, D. L. (2014) Rich and cold: Diversity, distribution and drivers of fungal communities in patterned-ground ecosystems of the North American Arctic. *Molecular Ecology*, 23, 3258-3272.
- Tolmachev, A. I. (1960) Der autochthone Grundstock der arktischen Flora und ihre Beziehungen zu den Hochgebirgsfloren Nord- und Zentralasiens. *Botanisk Tidsskrift* 55, 269-276.
- Vonlanthen, C. M., Walker, D. A., Raynolds, M. K., Kade, A. N., Kuss, H. P., Daniëls, F. J. A. & Matveyeva, N. V. (2008) Patterned-ground plant communities along a bioclimate gradient in the High Arctic, Canada. *Phytocoenologia* 38, 23-63.
- Wada, N. (1998) Sun-tracking flower movement and seed production of mountain avens, *Dryas octopetala* L. in the High Arctic, Ny Ålesund, Svalbard. *Proceedings of the NIPR Symposium on Polar Biology* 11, 128-136.
- Walker, M. D. (1995) Patterns of arctic plant community diversity. In: Chapin, F. S. III & C. Körner (Eds.). *Arctic and alpine biodiversity: Patterns, causes and ecosystem consequences* (pp. 3-20). Berlin: Springer-Verlag.
- Walker, D. A., Auerbach, N. A., Bockheim, J. G., Chapin, F. S. III, Eugster, W., King, J. Y., McFadden, J. P., Michaelson, G. J., Nelson, F. E., Oechel, W. C., Ping, C. L., Reeburg, W. S., Regli, S., Shiklomanov, N. I. & Vourlitis, G. L. (1998) Energy and trace-gas fluxes across a soil pH boundary in the Arctic. *Nature* 394, 469-472.
- Walker, D. A., Billings, W. D. & De Molenaar, J. G. (2001a) Snow-vegetation interactions in tundra environments. In: H. G. Jones, J. W. Pomeroy, D. A. Walker & R. W. Hoham (Eds). *Snow ecology* (pp. 266-324). New York, NY: Cambridge University Press.
- Walker, D. A., Bockheim J. G., Chapin, F. S. III, Eugster, W., Nelson, F. E. & Ping, C.-L. (2001b) Calcium-rich tundra, wildlife, and the "Mammoth Steppe." *Quaternary Science Reviews* 20, 149-163.
- Walker, D. A., Raynolds, M. K., Daniëls, F. J. A., Einarsson, E. & Evlvebakk A., Gould, W. A., Katenin, A. E., Kholod, S. S., Markon, C. J., Evgeny, S., Moskalenko, N. G., Talbot, S. S., Yurtsev, B. A. & the other members of the CAVM Team. (2005) The circumpolar Arctic vegetation map. *Journal of Vegetation Science* 16, 267-282.
- Walker, M. D., Wahren, C. H., Hollister, R. D., Henry, G. H. R., Ahlquist, L. E., Alatalo, J. M., Bret-Harte, M. S., Calef, M. P., Callaghan, T. V., Carroll, A. B., Epstein, H. E., Jónsdóttir, I. S., Klein, J. A., Magnusson, B., Molau, U., Oberbauer, S. F., Rewa, S. P., Robinson, C. H., Shaver, G. R., Suding, K. N., Thompson, C. C., Tolvanen, A., Totland, Ø., Turner, P. L., Tweedie, C. E., Webber, P. J. & Wookey, P. A. (2006) Plant community responses to experimental warming across the tundra biome. *Proceedings of the National Academy of Sciences (USA)* 103, 1342-1346.
- Walker, D. A., Alsos, I. G., Bay, C., Boulanger-Lapointe, N., Breen, A. L., Bültmann, H., Christiansen, T., Damgaard, C., Daniëls, F. J. A., Hennekens, S., Reynolds, M. K., Le Roux, P. C., Luoto, M., Pellisier, L., Peet, R. K., Schmidt, N.-M., Stewart, L., Virtanen, R., Yoccoz, N. G. & Wisz, M. S. (2013) Rescuing valuable Arctic vegetation data for biodiversity models, ecosystem models and a Panarctic vegetation classification. *Arctic: Info North* 66, 133-137.

- Ware, C., Bergstrom, D. M., Müller, E. & Alsos, I. G. (2012) Humans introduce viable seeds to the Arctic on footwear. *Biological Invasions* 14, 567-577.
- Weber, W. A. (1965) Plant geography in the southern Rocky Mountains. In: H. E. Wright, Jr. & D. G. Frey (Eds.) *The Quaternary of the United States* (pp. 453-468). Princeton, NJ: Princeton University Press.
- Weber, W. A. (2003) The Middle Asian element in the southern Rocky Mountain flora of the western United States: A critical biogeographical review. *Journal of Biogeography* 30, 649-685.
- Westergaard, K. B., Jørgensen, M. H., Gabrielsen, T. M., Alsos, I. G. & Brochmann, C. (2010) The extreme Beringian/Atlantic disjunction in *Saxifraga rivularis* (Saxifragaceae) has formed at least twice. *Journal of Biogeography* 37, 1262-1276.
- Westergaard, K. B., Alsos, I. G., Popp, M., Engelskjøn, T., Flatberg, K. I. & Brochmann, C. (2011) Glacial survival may matter after all: Nunatak signatures in the rare European populations of two west-arctic species. *Molecular Ecology* 20, 376-393.
- Wielgolaski, F. E. (1997). *Polar and alpine tundra*. Ecosystems of the World 3. Amsterdam: Elsevier.
- Willerslev, E., Davison, J., Moora, M., Zobel, M., Coissac, E., Edwards, M. E., Lorenzen, E. D., Vestergård, M., Gussarova, G., Haile, J., Craine, J., Gielly, L., Boessenkool, S., Epp, L. S., Pearman, P. B., Cheddadi, R., Murray, D., Bräthen, K. A., Yoccoz, N., Binney, H., Cruaud, C., Wincker, P., Goslar, T., Alsos, I. G., Bellemain, E., Brysting, A. K., Elven, R., Sønstebo, J. H., Murton, J., Sher, A., Rasmussen, M., Rønn, R., Mourier, T., Cooper, A., Austin, J., Møller, P., Froese, D., Zazula, G., Pompanon, F., Rioux, D., Niderkorn, V., Tikhonov, A., Savvinov, G., Roberts, R. G., MacPhee, R. D., Gilbert, M. T., Kjær, K. H., Orlando, L., Brochmann, C. & Taberlet, P. (2014) Fifty thousand years of Arctic vegetation and megafaunal diet. *Nature* 506, 47-51.
- Yao, F., Vik, U., Brysting, A. K., Carlsen, T., Halvorsen, R. & Kauserud, H. (2013) Substantial compositional turnover of fungal communities in an alpine ridge-to-snowbed gradient. *Molecular Ecology* 19, 5040-5042.
- Yurstev, B. A. (1994) Floristic divisions of the Arctic. *Journal of Vegetation Science* 5, 765-776.
- Zinger, L., Lejon, D. P. H., Baptist, F., Bouasria, A., Aubert, S., Geremia, R. A. & Choler, P. (2011) Contrasting diversity patterns of crenarchaeal, bacterial and fungal soil communities in an alpine landscape. *PLoS One* 6, DOI:10.1371/journal.pone.0019950.