1 Patterns and Causes of Arctic Plant Community Diversity

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Attempts to explain and quantify community diversity have been a major paradigm in the development of modern ecology (e.g. Pielou 1975; MacArthur 1960; Whittaker 1965). Questions of the functional significance of diversity, and indeed whether species diversity alone has any functional significance, are also abundant (e.g. Hurlbert 1971; May 1973; Schulze and Mooney 1993). The taxonomic and genetic diversity within a community, the diversity among communities, and the diversity of communities on a landscape all contribute to regional diversity and are all aspects of community diversity. Genetic and species diversity are the building blocks of communities, and define the set of potential plant communities for a given region, but the plant communities into which these taxonomic and genetic units are organized are the most direct and easily measurable indication of overall ecosystem diversity, because they represent the integration of species and landscape. Understanding how the diversity of communities may change following a directional change in climate requires an understanding of the processes that control diversity at different levels.

1.1 Background and Definitions

Whittaker (1972) recognized and defined four aspects of community diversity, each of which have an implicit scale associated with them: (1) alpha diversity, the species diversity within a stand or community, (2) beta diversity, the degree of differentiation among communities within a landscape, (3) gamma diversity, the total species diversity within a landscape, and (4) delta diversity, the change in floras from one landscape or area to another.

1.1.1 Alpha Diversity

One of the key ecological debates of the past century has concerned the ecological importance, or lack thereof, of alpha diversity. This debate has centered on whether diversity acts as a stabilizing influence in a community or ecosystem, with more species resulting in a greater degree of ecological redundancy (May 1973). This debate became mired in problems with defining stability and was

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further complicated by the idea that complexity, rather than simple diversity, was necessary for stability. More central to the present discussion is the large body of work on the mechanisms that control alpha diversity, much of which comes from the field of theoretical population biology (e.g. May 1975). Understanding and explaining these mechanisms are critical to predicting changes in alpha diversity with a changing climate, as climate and diversity are not likely to be simply linked.

Alpha diversity has two main subcomponents: richness (the total number of species) and evenness (the uniformity of their distribution). Many different methods of calculating richness and evenness have been published (Magurran 1988). Studies of the species diversity of natural communities have often found that richness alone gives equally useful information as richness and evenness (e.g. Fridriksson 1989).

1.1.2 Beta Diversity

Beta diversity is a measure of community diversity independent of any classification system. There has been relatively little published on the ecological importance of and underlying controls on beta diversity; most of the contributions are from outside the field of plant ecology (e.g. Cody 1970). Beta diversity can be represented as a ratio between alpha and gamma diversity (Whittaker 1972):

$$D_\beta = \frac{D_\gamma}{\overline{D_\alpha} - 1},$$

where D_β is beta diversity, D_γ is gamma diversity, and $\overline{D_\alpha}$ is the average sample alpha diversity. As average sample alpha diversity decreases relative to gamma diversity, beta diversity increases. Another quantitative measure of beta diversity is the length of the first axis of a detrended correspondence analysis ordination, which is in "SD units" (Gauch and Whittaker 1972). One SD unit represents the average width of a species dispersion along the floristic gradient constructed by the ordination, with the underlying assumption that species have a unimodal, Gaussian response to the gradient. For most data sets, one SD unit represents approximately 50% dissimilarity, and four SD units represent approximately 100% dissimilarity. The richness and evenness of community types (associations) can also be considered as a measure of beta diversity, although not strictly within Whittaker's original definition.

1.1.3 Gamma Diversity

Gamma diversity, or total regional diversity, represents the sum of alpha diversities and a fundamental constraint on those alpha diversities. It can also be considered as essentially equivalent to alpha diversity at the next level of organization, and the same theoretical and quantitative considerations apply.

A problem with quantitative data on species richness of large areas is the log-linear relationship between species and area, which makes simple comparisons of

differently sized areas difficult, because small areas will have disproportionately high numbers of species per unit area compared to larger areas (Gleason 1922; Cailleux 1961; Billings 1992). Given that this log-linear relationship has been shown to hold true for most empirical data sets (Preston 1962 a,b), the most useful index of floristic richness should be a logarithm of species number per some set area. For example, Cailleux (1961) demonstrated a linear relationship betwen mean annual temperature and the logarithm of areally adjusted vascular species richness on a global scale.

Most data on gamma diversity are not based on equally sized areas but loosely defined regions, referred to as regional or local floras, which are usually some unit representing an area that can be reached conveniently by foot or vehicle from a central location, such as the Toolik Lake region, the Prudhoe Bay region, etc. containing all of the major habitats present in that region. Tolmachev (1931) formalized this concept as a concrete or local flora, which is defined as the flora of the minimal area necessary to include the most characteristic habitats for a given macroclimate. Abundant data on local floras of the Russian Arctic exist, but most have not yet been published or analyzed (V.Yu. Raszhivin and N.V. Matveyeva, pers. comm.). The Russian data represent an untapped source for testing specific theories about controls on arctic species diversity (e.g. Chernov, this Vol.). In practice, the Russian and North American approaches are not that different, as in all cases the investigator is seeking to visit all habitats within an "ecologically homogeneous area", and the species-area curve will tend to flatten in any case unless the size of the study or search increases geometrically.

1.1.4　Delta Diversity

Delta diversity is the functional equivalent of beta diversity at the next level of organization; it is the degree to which local floras are differentiated. Although there are many qualitative comparisons of specific local arctic floras (e.g. Young 1971; Murray 1978), I know of no quantitative analysis of delta diversity in the Arctic, and indeed there are few published analyses of delta diversity of plants for any system (e.g. Kruger and Taylor 1979). Delta diversity is an important component in predicting response to global change, because the degree of differentiation among local floras is one indicator of the potential for invasion of new species.

1.2　Arctic Species Diversity: The First Filter

Community diversity is fundamentally and inextricably linked to species diversity. Körner (this Vol.) explains the causes of diversity of a given site, community, etc. as a function of a series of "filters" with differently sized pores. The first filter is the presence of the species somewhere in the Arctic. Only about 0.4% of the earth's known vascular plant species occur in the Arctic (Billings 1992). The first filter is so fine that relative size differences among additional pores are small, and species that get through the first filter have a high probability of getting through additional ones.

The Arctic is one end of a global gradient of summer temperature, biologically useful heat, and taxonomic diversity. Temperature has strong effects on almost all aspects of arctic ecosystems, including soil stability, moisture, and nutrient availability, and any one or many of these may effectively limit an individual species' presence in the ecosystem. Even habitat diversity, considered an important control on species diversity in all systems, can be strongly related to thermal energy in the Arctic, as periglacial land and surface forms result from the interaction between climate and local geological conditions (Washburn 1973). I refer to the gradient of summer warmth (usually measured in degree-days above 0 °C) and summer temperature (usually measured as mean July temperature) synonymously as a gradient of thermal energy, recognizing that they have different effects and importance. Temperature has direct biological effects that may control species presence and therefore diversity, for example, Q_{10} and key thresholds such as frost resistance (e.g. Körner and Larcher 1988). In other cases, the total seasonal heat energy may be critical, such as for the development of reproductive structures. Callaghan and Jonasson (this Vol.) report an increase in seed set and viability of high arctic populations of *Dryas octopetala* following experimentally increased temperatures. Both temperature and thermal energy are a consequence of latitudinal differences in solar input, and it is their combined influence that ultimately affects species diversity. Biological or physical processes related to either temperature or heat energy may limit individual species at almost any stage in the life cycle and are not expected to be the same among species.

1.3　Biogeographical Patterns Within the Arctic: The Second Set of Filters

Most recent estimates of the size of the arctic flora, which vary depending upon the classification of subspecific taxa and species groups, include about 1500 vascular, 750 bryophyte, and 1200 lichen species (Murray 1992; B. Murray, pers. comm.). Approximately 60% of the vascular flora is in common throughout, increasing to about 90% in common in the most northerly areas (Polunin 1959; Hultén 1962; Young 1971; Yurtsev et al. 1978; Billings 1992). If one begins at some arbitrary point in the southern Arctic, there will be a gradient of decreasing diversity to the north, with species being lost and only a few new truly arctic species being gained (i.e., the rate of loss is much greater than the rate of gain), and a gradient of increasing total diversity to the east or west, with new species coming into the flora and others being lost locally (i.e., the rates of gains and losses are approximately equal).

1.3.1　Climatic Gradients

The south to north gradient of decreasing diversity is essentially a localized version of the equatorial-polar gradient of diversity and productivity, and therefore can be related primarily to changes in thermal energy. The importance

of thermal energy to arctic ecosystems has been a major theme of every comprehensive treatment of these ecosystems (Billings 1974; Ives and Barry 1974; Yurtsev et al. 1978; Aleksandrova 1980, 1988; Chernov 1985; Bliss and Matveyeva 1992). Young (1971) noted that within the Arctic: (1) there is a decrease in overall vascular plant species diversity from south to north, (2) the overall flora is similar throughout relative to other biomes, (3) the vegetation structure is similar throughout, and (4) there are few species endemic to the most northerly regions, although there are some truly arctic species-(see, for example, Beschel 1970; Murray 1992). Young also noted that the northerly floras are primarily depauperate subsets of the southerly floras, indicating that competition is an unlikely factor explaining the lack of species in northerly areas. Young proposed that latitudinally decreasing species diversity could be explained solely by the sum of mean monthly temperatures for all months in which the mean is above 0 °C. This measure is similar to but less precise than thawing-degree days, which represent an annual sum of biologically useful heat (thawing-degree days are the sum of mean daily temperatures for all days when the mean is >0 °C). Mean annual temperature is not as well correlated with species numbers, because low winter temperatures do not necessarily exclude species, and annual means are heavily weighted by winter values.

Young's hypothesis, which was a statement of correlation rather than mechanism or cause, has yet to be refuted, and further studies have supported it. Rannie (1986) made a direct test of Young's supposition that summer temperature is the only variable needed to predict vascular species diversity. Using published floristic data from 38 localities in the Canadian Arctic, she showed a remarkably high correlation between July mean temperature, July degree-days >0 °C, and July degree-days >5 °C, with these various measures explaining 94–95% of the variance in species diversity (Fig. 1.). Temperature had a slightly better correlation with diversity than did degree-days, but the strong correlation between temperature and degree-days makes it impossible to isolate one or the other as a more important casual agent. Although the surveys that went into Rannie's analysis were based on different areas, they were all large enough that the species-area relationship was of minor importance. This is an example of why the
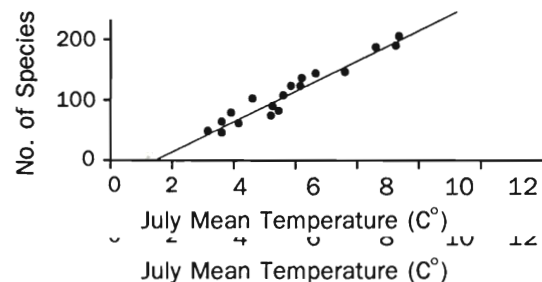
local flora concept may be more useful for comparative purposes than strict equal area comparisons.

At a finer scale, D.A. Walker (1985) divided the Prudhoe Bay region into three zones following a steep coastal-inland temperature gradient of decreasing temperature, and examined the size of the vascular flora and its distribution according to a zonation system developed by Young (1971). Young divided the Arctic into four zones based on northernmost limits of species distribution, so that a species classified as zone 4 (the southernmost of the four zones) has its northern limit somewhere in zone 4. The result of Walker's analysis was an increase in total number of species from 115 in the coastal zone to 188 in the inland zone, a decrease in zone 1 and 2 species from the coast inland, and an increase in zone 3 and 4 species in the same manner (Fig. 2).

The Taymyr Peninsula in Siberia offers almost an ideal gradient of summer temperature from tree line to polar desert, with little change in relief, no difference in winter temperature, and continuous continental landmass (Matveyeva, 1994). The Taymyr is the only place on the globe that offers such a gradient without complications such as islands, complex geology, and strong oceanic climate influences. The diversity of vascular species in local floras of the Taymyr decreases from about 250 in the south to about 50 in the north (Chernov and Matveyeva 1979).

Other climatic gradients also influence diversity. The polar deserts of the Canadian Arctic Archipelago and those of Siberia are both to the north of the 2 °C July isotherm (Aleksandrova 1988). Both areas are mostly barren, with total plant cover of less than 5%. The Canadian communities, on the Queen Elizabeth Islands, are "dominated" by vascular plants, whereas in the Siberian communities,
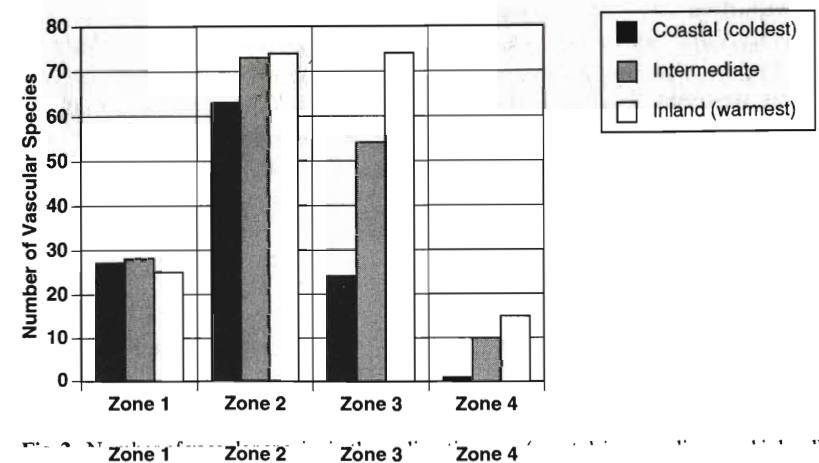

Fig. 1. Correlation between July mean temperature and number of species for local floras of the Canadian Arctic Archipelago. (Redrawn from Rannie 1986 with permission of the Arctic Institute of North America)

Fig. 2. Number of vascular species in three climatic zones (coastal, intermediate, and inland) at Prudhoe Bay, Alaska, according to Young's (1971) zones of northern limit. Zone 1 species have their northern limit in the polar deserts, and zone 4 species have northern limits in the Low Arctic. Data from D.A. Walker (1985)

on Cape Cheluyskin of the Taymyr Peninsula, lichens and mosses dominate (Matveyeva 1979; Bliss and Svoboda 1984; Aleksandrova 1988; Bliss and Matveyeva 1992). Differences in precipitation and possibly summer fogginess are the most likely causes of these differences; mean annual precipitation is 100–250 mm in the Asian sites versus only 75–150 mm in the North American sites (Bliss and Matveyeva 1992), although a comprehensive comparative treatment of the two systems has not yet been completed.

1.3.2 Gradients of Geological History

Perhaps the most significant historical event in the Arctic has been the series of glaciations that have occurred there over the past million years (Péwé 1975). Although most land areas were covered by large continental glaciers, with only small localized nonglaciated areas, such as nunataks, available as refugia, most of Beringia, covering what is now northern Alaska and the Chukotka Peninsula of eastern Russia, was an extensive, arctic, ice-free area (Hopkins 1967). Lowered sea levels exposed much of the continental shelf between Asia and North America, making a large, contiguous ice-free zone. The modern flora of Beringia is disproportionately high, with a greater number of endemics relative to other arctic areas.

The Beringian species, defined as species that are either endemic to some region of what was the Pleistocene ice-free zone or those that have North American-Asian distributions, and which add to the richness of the Beringian flora, do not dominate the modern communities, but instead are mostly found in specialized habitats with good drainage and often southern exposures (Yurtsev 1982; D.A. Walker 1985; M.D. Walker 1990). M.D. Walker (1990) compared the continental distributions of species that occurred only on pingos[1], a relatively rare habitat which offers good drainage on the otherwise flat wet coastal plain of Alaska, with those species that occurred on pingos but were also found in other more common local habitats. Seventy-one percent of the species that occurred only on pingos had distributions restricted to either Asia and North America, only North America, or only Alaska and the Yukon, with the remaining 29% being circumpolar or nearly so in distribution, whereas the widespread species had 54 and 46% of their species in these respective categories.

Geological history also influences finer scale patterns. When two southern Arctic Foothills, Alaska, landscapes were compared, which differed in their time since release from glaciation but which had the same macroclimate and degree of topographic relief, there was less richness and evenness of vegetation community types on older landscapes (D.A. Walker et al. unpubl. data; Table 1). The causes of the observed differences in diversity are likely related to those observed in other

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[1] Pingos are ice-cored, dome-shaped hills ranging in height to as much as 50m, although normally less than 15 m, and in basal diameter to as much as 1000m, although normally less than 300m. They have constant initial substrate, although zoogenic, pedogenic, and cryogenic processes tend to increase microsite substrate differences over time (D.A. Walker et al. 1985).

Table 1. Richness and evenness of community types on three differently-aged glacial drift surfaces, southern Arctic Foothills, Alaska. The Sagavanirktok drift is broadly mid-Pleistocene (300–500 Ka) in age, the Itkillik I drift is approximately 50 ka, and the Itkillik II drift is approximately 10 ka (Hamilton 1986). Vegetation data are from D. A. Walker et. al (1989 and unpub.)

	Total richness (number of vegetation types)	Areally adjusted richness (number of types per 10 m²)	Shannon-Wiener index[a]	Evenness index[b]	Total area (ha)	Total vegetated area (ha)
Imnavait Creek map area (1:6000 scale)						
Sagavanirktok	29	0.187	0.784	0.536	155 640	154 359
Itkillik I	17	1.81	0.832	0.676	9 405	9 390
Toolik Lake map area (1:5000 scale)						
Itkillik I	20	0.292	0.686	0.527	68 576	67 951
Itkillik II	27	0.373	0.933	0.652	72 288	72 136

[a] $H' = -\sum_{i=1}^{s} p_i \log_{10} P_i$, where H' is the Shannon-Weiner diversity index, s is the number of vegetation types, and p_i is the proportional abundance of the ith vegetation type.

[b] $J = \dfrac{H'}{\log_{10} S}$, where J is the evenness index (Pielou 1969) H' is the Shannon-Weiner diversity index, and s is the number of vegetation types. The denominator is the maximum value for H'; as the maximum approaches the actual value, the types are more evenly distributed.

glacial landscapes over shorter time sequences – that diversity initially increases and then declines as dominance patterns develop (Zollitsch 1969; Reiners et al. 1971; Matthews 1992). *Eriophorum vaginatum* tussock tundra is the dominant community type in these landscapes. Although shifts in species dominance related to moisture and nutrient conditions cause visual variation among tussock tundra stands, its among-sample compositional similarity is consistently high, and its species diversity is low (M.D. Walker et al. 1994). The development of tussock tundra is dependent upon the process of paludification, with development of a *Sphagnum* moss layer resulting in cold soils, decreased depth of thaw, decreased nutrient availability, and increased soil moisture (Jorgenson 1984). A dense canopy of shrubs and tussock grasses forms within this moss layer. The Arctic Foothills pattern is not a simple successional sequence, however, since even the oldest sites would have experienced glacial climates during subsequent advances. The older landscapes were probably sparsely vegetated during the glacial intervals, and the presence of at least some vegetation and soil there, coupled with the existence of an established hydrologic pattern, one of the first geomorphic patterns to appear following deglaciation (Matthews 1992), may have given the older landscapes an "edge" in development.

1.4 Distribution of Species in Communities: The Third Set of Filters

The final set of filters through which a species passes are those within the local landscape. Once a species has found its way into the local flora or landscape, its distribution and abundance there will depend on its internal constraints and their interaction with the environment and its interaction with other species.

1.4.1 Gradients of Biological Interaction

A recurrent theme in the literature of arctic vegetation is an apparent lack of well-structured communities in the most severe arctic environments, which early work explained as reflecting a lack of competition in those environments (Griggs 1934; Savile 1960). These visual impressions were based on visits to high arctic and polar desert areas and were not backed by data or analyses, and the actual role of competition in shaping high arctic communities remains unknown. Even with very few species, competition for safe seedling establishment sites may be intense, and may effectively control what species are present in a region. Rather than invoking competition, or lack thereof, as an important mechanism, it is probably more fruitful to consider the gradient from the southern to northern Arctic as a gradient of potential biological interaction. As both the number of species and the ecosystem productivity decrease, the potential for biotic interaction should also decrease, making physical factors increasingly important. In the north, thermal energy, an important limiting factor not subject to competition, takes on a greater and greater role, until it finally overwhelms all other factors. Although any locality will have some degree of microclimatic variability that will control species distributions, as making physical factors increasingly important. In the north, thermal energy, an important limiting factor not subject to competition, takes on a greater and greater role, until it finally overwhelms all other factors. Although any locality will have some degree of microclimatic variability that will control species distributions, as

temperature becomes increasingly important, the role of secondary environmental gradients in shaping communities should decrease.

Because community diversity is a function of the total number of species available, we expect community diversity at the landscape level to decline as the number of species declines. The number of possible combinations of n species in a single space is $2^n - 1$. Assuming a local flora of only 100 species, there would be 1.27×10^{30} possible combinations of species. In practice, the concrete members of an association have an average similarity of about 50% (Gauch 1982), and the actual number of community types will be far less than this theoretical maximum. Nonetheless, this mathematical relationship indicates that as the total flora decreases, the number of potential community types should also decrease, and the degree of similarity between stands should increase. This effect should occur independently of biological or physical factors that may effect species and community distribution. This also leads to a specific testable hypothesis, i.e., the presence of any other pattern indicates that factors other than simple flora size are influencing community distributions.

The importance of competition versus individual species' response to gradients in shaping communities is difficult to quantify, and there has been little experimental work on this question for the Arctic. I used north- and south-facing slopes of pingos in the Prudhoe Bay and surrounding regions as microcosms of larger climatic gradients (M.D. Walker 1990). Temperature differences on these opposing surfaces are equivalent at least to a gradient from Low to High Arctic. From a sample of 41 pingos, overall (gamma) vascular species diversity was lower on north-facing slopes (92 total species on north-facing slopes versus 140 species on south-facing slopes), as was average alpha diversity (mean of 14 versus 18 species) and beta diversity (sum of SD units for four DCA ordination axes 9.0 versus 14.3). Ordinations of north-facing slopes also had lower eigenvalues, indicating noisier patterns in the floristic gradients, and there were fewer and weaker relationships between environmental variables and ordination axes. The first axis of the north-facing slope ordination was significantly rank correlated with five environmental variables, with a mean rank correlation coefficient of 0.378; the south-facing slope axis was correlated with six environmental variables, with a mean rank correlation coefficient of 0.443. Although it is clear from the ordinations that factors other than temperature are affecting community composition on both north- and south-facing slopes, it is also clear that there is an apparent increase in "randomness" to the distribution of species on north-facing slopes, which might be explained by a decrease in the importance of competition on these slopes.

1.4.2 Habitat Diversity

The mosaic of habitats present on a landscape at a point in time are a result of disturbances at all spatial and temporal scales, including those of geological proportion (Table 2). Although disturbance is a primary factor in shaping any landscape and therefore the diversity of that landscape (During et al. 1988), the Arctic differs from other biomes in having a great diversity of mesoscale patterns disturbances at all spatial and temporal scales, including those of geological proportion (Table 2). Although disturbance is a primary factor in shaping any landscape and therefore the diversity of that landscape (During et al. 1988), the Arctic differs from other biomes in having a great diversity of mesoscale patterns

Table 2. Hierarchy of natural disturbances, northern Alaska. (Walker and Walker 1991)

Hierarchical domain (Delcourt and Delcourt 1988)	Disturbance	Geomorphic effect	Vegetation effect	Spatial scale (m²)	Event frequency (years)
Megascale (continental to global)	Continental drift and uplift of Brooks Range	Formation of physiographic provinces and bedrock types, establishment of regional drainage patterns	Evolution of arctic Flora	$>10^{12}$	$>10^6$
Macroscale (regional)	Climate fluctuations associated with ice ages	Formation of glacial surfaces, marine terraces, sand sea, loess deposits, alluvial deposits, regional paludification, sediment deposition, development of second-order and higher drainages	Speciation and extinction; development, movement, and displacement of plant communities	10^4–10^{10}	10^4–10^6
Mesoscale (regional)	Climatic fluctuations during the Holocene	Development and alteration of permafrost, colluviation of steep slopes, development and alteration of many periglacial features (e.g. icewedges, pingos), thaw-lake cycle, development of water tracks and first-order drainages, soil formation	Species migration, ecotene displacement, changes in landscape mosaic, movement of tree line	10^2–10^{10}	10^3–10^5
Microscale (site) Macrosite	Loess deposition	Alkaline silty soils, dilution of organic matter	Addition of nutrients, calciphilous flora	10^6–10^{10}	10^1–10^2
	Tundra fires	Local fluvial and thermal erosion	Burning, recycling and loss of nutrients, opening of canopy	10^4–10^8	10^3–10^4
Mesosite	Growth and erosion of ice wedges	Formation of ice-wedge-polygon microtopography, thermokarst pits	Changes in vegetation mosaic by alteration of microenvironment	10^0–10^3	10^0–10^4

Table 2. (contd.)

Hierarchical domain (Delcourt and Delcourt 1988)	Disturbance	Geomorphic effect	Vegetation effect	Spatial scale (m²)	Event frequency (years)
Mesosite	Major storms and storm surges	Debris flows, large rock falls, floodplain alteration, coastal erosion, rill formation	Burial and removal of vegetation, salt kill in coastal areas	10^{-1}–10^6	10^0–10^2
	Annual snow and runoff cycle:	Springs, icings, solifluction features	Summer-long water source, alteration of soil temperature and growing season length	10^4–10^6	10^0
	Groundwater discharge, melting of active layer Snowback formation and melting	Annual erosion and sedimentation, formation of nivation hollows[a]	Unstable substrate, short growing season, summer-long water source, winter protection	10^2–10^5	10^0
	Spring flood	Fluvial erosion and sedimentation	Addition of nutrients, burial, removal of plants		
Microsite	Oil seeps	Deposition of hydrocarbons	Killing of vegetation	10^2–10^4	10^{-2}–10^1
	Animal disturbances	Caribou trails, animal dens, craters, local erosion, krotovinas	Removal of plants, addition and recycling of nutrients	10^{-2}–10^2	10^{-1}–10^2
	Daily and annual freeze-thaw cycle	Needle ice formation, frost scars	Physical disturbance of plant roots and seedings	10^{-4}–10^4	10^{-2}–10^0

[a]Nivation hollows are amphitheatre-like depressions caused by mass wasting and freeze and thaw cycles. They are considered to be the first stage in cirque formation but are not caused by glaciation (Lewis 1939).

related to periglacial activity. Features such as frost boils, high- and low-centered ice wedge polygons, thaw lake basins, and pingos all have major influences on vegetation patterning in arctic landscapes, and many treatments of arctic vegetation have used these landscape features as a primary organizing theme (e.g. D.A. Walker 1985; Matveyeva 1988; D.A. Walker et al. 1989; M.D. Walker et al. 1991).

Changes in substrate or topography at almost any spatial scale will lead to a change in species composition. Matveyeva (1988) considered the vegetation of frost boils (small sorted circles 1–2 m diameter with active frost churning and often mostly bare soil in the center) and the surrounding matrix in upland mesic tundra to be a single plant community, and based on this definition, found alpha diversities as high as 130 to 160 in an area of 100 m², up to 50 species on only 1 m², and up to 25 species on 0.1 m², but only 40, 30, and 20 species, respectively, on similarly sized areas in mires. D.A. Walker (1985), on the other hand, treated the vegetation of different zones (rim, trough, and center) within ice-wedge polygon tundra as a series of separate communities, and he described less diverse communities with almost complete turnover of species with only a few centimeters of change in topographic position.

Frequency and intensity of disturbance also affect diversity. D.A. Walker et al. (1989) compared the community type diversity of five major terrain unit types in a watershed of the southern Arctic Foothills in northern Alaska. They reported the highest diversity on floodplains (Shannon index 0.857), which are frequently disturbed, and the lowest diversity on retransported hillslope deposits (Shannon index 0.471),which are stable sites and the primary areas of tussock tundra development. Bedrock outcrops, glacial till, and basin colluvium had intermediate diversities (Shannon indices 0.624, 0.599, and 0.583, respectively).

1.4.3 Diversity Hot Spots: Focal Points and Oases

Species and community diversity are unevenly distributed in most landscapes, and much of the diversity may be concentrated in relatively small areas. The evenness of community diversity is largely a function of topography, because of its overwhelming importance in controlling the steepness of environmental gradients. In mountainous areas, species turnover is high and relatively continuous. There are many arctic mountain ranges, but the majority of the arctic landscapes consist of gently rolling hills or mostly flat plains. In these less topographically diverse landscapes, turnover tends to be gradual, with community diversity concentrated in areas of unusual resources. These areas of unusual resources represent focal points for the landscape, which I define as an environmental resource patch characterized by high species richness and interaction. An obvious example would be a desert oasis or water hole, where animals interact extensively and plant cover is high.

What determines a focal point depends on what is limiting in a particular landscape. "Oases" have been described from polar deserts, associated with springs or in permanently moist situations below snowbeds (Edlund and Alt

1989; Svoboda and Freedman 1994). These oases have plant cover many orders of magnitude higher than the surrounding barrens, contain most of the local plant species diversity, and may be locally very important to wildlife. Pingos are important focal points in certain arctic regions (D.A. Walker et al. 1985; M.D. Walker et al. 1991; M.D. Walker 1990). On the flat Alaskan coastal plain, topographic relief is in short supply, so the slopes of pingos are rare habitats and landscape focal points. Pingos have very high species diversity in a small area because: (1) their dome shape results in a high degree of habitat diversity in a small area, including north- and south-facing slopes, ablation areas, and snowbeds, (2) their steep slopes discourage peat formation, resulting in warmer soils with higher nutrient availability, (3) their gravel and sand substrates make excellent denning areas for squirrel and fox, creating a moderate level of disturbance and also bringing nutrients into the system. South-facing slopes of pingos are particularly species rich, as the total solar input is much higher on these sites. The "equivalent latitude" of a 15° slope at 70 °N actual latitude is 55° (based on the equation of Lee 1962). Also, pingos may represent relict Beringian habitats which support taxa that were common on the cold, dry Beringian plains during the Pleistocene glaciations and which have now been replaced by mesic taxa following the development of a peat layer at the beginning of the Holocene; the floristic affinities of the pingo species support this concept (Young 1982; M.D. Walker et al. 1991). A few range disjunctions have been described from pingos, mostly lichens to the north of their known ranges, but also some polar desert species that are common to the north but rather rare at that latitude, such as *Draba subcapitata*.

Rivers, and particularly steep, south-facing river bluffs, may also serve as landscape focal points. The steep slopes of rivers are warm, well-drained habitats, and combined with the possibility for migration along the river corridor are therefore natural concentrations of diversity. Zanokha (1989) has described rare extrazonal communities on steep, south-facing river bluffs of the Rogozinka River on the Taymyr Peninsula. These communities are dominated by boreal taxa in an area that is mostly dominated by *Dryas punctata* mesic tundra. These sites have deep, well-developed soils that rest directly on bedrock. In northern Alaska there are occasional hot springs in the northern foothills of the Brooks Range that support stands of *Populus balsamifera* well to the north of the tree line, which sits on the southern slope of the range, a major topographic barrier (Murray 1980). These are warm-water springs that create localized warm microclimates, and many of these stands support extreme range disjunctions of boreal taxa.

In almost all cases, these hot spots of plant diversity are also locally or regionally important to wildlife. Relative to their spatial extent, the intensity of animal activity on pingos is orders of magnitude higher than in the surrounding landscape. Ground squirrels, arctic fox, various birds of prey, collared lemmings, and grizzly bear are drawn to these points. Rivers are extremely important to wildlife, with steep banks or bluffs offering nesting, denning, and hunting areas, and the floodplains offering forage and cover for many species. Even the small stands of *Populus balsamifera* are locally important to moose. These intense

concentrations of wildlife create disturbances, increase nutrient input, and therefore help perpetuate the high plant species diversity.

1.5 Global Change and Community Dynamics

Existing models of global climate change predict various degrees of temperature shifts in different parts of the Arctic, with increases predicted in some areas and decreases in others (Mitchell et al. 1991). If temperature and thermal energy are indeed the most important ultimate causes of patterns in species diversity, then shifts in temperature should have major consequences for these patterns. It is shifts in summer temperature and degree-days, either positive or negative, that will potentially have the strongest effects on diversity. Changes in mean annual temperature cannot be directly related to diversity, since winter climate will dominate such an average.

Given this overwhelming importance of temperature, and the hypothesized gradient of biological interaction that may exist in the Arctic, a reasonable hypothesis may be that colder areas, which now have fewer species and a stronger direct tie to climate, may be the areas that will experience the most rapid change. Also, the closer summer temperatures are to $0\,^\circ C$, then the more a small change will mean in the total heat energy available throughout the growing season. Alternatively, the lack of carbon and nutrient stores in the soils of these regions could effectively prevent any quick response to a warming. The first species to migrate into the northern areas following a warming should be those which have been lacking due to a threshold response to summer temperature or heat energy but which are able to grow and reproduce under low nutrient conditions. A combination of simulation modeling and field experimentation could be used to test the feasibility of these hypotheses, and long-term monitoring sites should be placed along major gradients of climate.

Focal points may also be critical during a changing climate. In a warming climate, these sites may be important as seed sources. In a cooling climate, these rare areas, which may be of critical importance to certain wildlife species, may lose much of their plant species diversity.

1.6 Conclusions

1. The principles that organize communities do not vary among biomes, but the relative importance of various physical and biological controls may shift substantially, with physical factors being of primary importance in arctic ecosystems.
2. Thermal energy is the main factor correlated with trends in arctic species diversity, both within the Arctic and relative to the rest of the globe.
3. Other major biogeographical gradients within the Arctic include moisture and
2. Thermal energy is the main factor correlated with trends in arctic species diversity, both within the Arctic and relative to the rest of the globe.
3. Other major biogeographical gradients within the Arctic include moisture and geological history.

4. Because thermal energy is not subject to biological competition, the gradient of thermal energy may also represent a gradient of biological interaction, with northernmost communities having the strongest physical controls.
5. Habitat diversity, which is a function of disturbance at all spatial and temporal scales, is the most important factor controlling the distribution of species among communities. Mesoscale periglacial features such as frost boils, ice-wedge polygons, thaw lakes, and pingos are primary controls on the diversity and composition of arctic plant communities.
6. Landscape focal points are uncommon habitats that support high species diversity. Springs, seeps, pingos, and steep river bluffs may all serve this function in certain arctic landscapes.
7. Landscape focal points are usually of great local importance to wildlife.
8. Because of the importance of thermal energy in shaping patterns of arctic community diversity at many scales, either positive or negative shifts in summer temperature should have a dramatic impact on diversity.

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