Latitudinal Dispersal of Southern North American Glacial Refugial Plants within Yukon, Canada

Wayne L Strong[1]

ABSTRACT. This study investigates the distribution of southern North American glacial refugial migrants that have invaded Yukon (Canada) since the Last Glacial Maximum (LGM), which began about 9500 years ago. The analysis was based on indigenous vascular plant occurrences that were stratified according to 0.33° latitudinal bands. Among 90,397 occurrence records, about 37% were postglacial migrants as opposed to former members of the Eastern Beringian flora. Most migrants probably moved northward from LGM refugia in the western U.S. region (Montana-Idaho-Wyoming) and, to a lesser extent, from the midwestern United States, but several were potentially from a Pacific coast refugium in westernmost Washington-Oregon-northern California. Gradients in taxa composition and richness occurred, with Beringian taxa increasing and migrant taxa decreasing at greater latitudes (+3 vs −0.5 taxa per degree, respectively) based on statistically significant regression trends. An interpretation of ordination results based on taxa presence and absence suggests south-to-north migrating plants are strongly influenced by climate. Only half of all Yukon migrant taxa have geographical ranges that extend beyond the latitudinal centre of the territory. Possible constraints on greater dispersal include competition from pre-existing vegetation, colder northward climates, and the presence of the Ogilvie and Wernecke Mountains across the latitudinal centre of the territory. Just over half (24 of 44) of the taxa that occurred in only one latitudinal band were located immediately north of the southern Yukon border, which suggests glacial refugial migrants are still invading Yukon.

Keywords: Beringia; diversity; floristic richness; latitude; migration; species density; vascular plants; Yukon

RÉSUMÉ. La présente étude porte sur la répartition des migrateurs réfugiés glaciaires du sud de l'Amérique du Nord qui ont envahi le Yukon (Canada) depuis le dernier maximum glaciaire, dont le début remonte à il y a environ 9500 ans. L'analyse est fondée sur les occurrences de plantes vasculaires indigènes qui étaient stratifiées dans les zones de latitude de 0,33°. Parmi les 90 397 enregistrements d'occurrences, environ 37 % représentaient des migrateurs postglaciaires par opposition à d'anciens membres de la flore de la Béringie de l'Est. La plupart des migrateurs se sont probablement déplacés vers le nord à partir de refuges du dernier maximum glaciaire situés dans la région de l'Ouest américain (Montana-Idaho-Wyoming) et, dans une moindre mesure, dans la région du Midwest américain, bien que plusieurs provenaient peut-être d'un refuge de la côte du Pacifique, dans la partie la plus à l'ouest de Washington-Oregon-nord de la Californie. Des gradients étaient manifestes sur le plan de la composition et de la richesse des taxons, avec augmentation des taxons de la Béringie et diminution des taxons de migrateurs aux plus grandes latitudes (+3 par opposition à −0,5 taxon par degré, respectivement), d'après les tendances de régression statistiquement significative. L'interprétation des résultats d'ordination en fonction de la présence et de l'absence de taxons suggère que les plantes faisant la migration du sud au nord sont fortement influencées par le climat. Seulement la moitié de tous les taxons migrateurs du Yukon ont des portées géographiques s'étendant au-delà du centre latitudinal du territoire. Parmi les contraintes possibles derrière une plus grande expansion, notons la compétition de la végétation préexistante, les climats plus froids vers le nord et la présence des monts Ogilvie et Wernecke à la hauteur du centre latitudinal du territoire. Un peu plus de la moitié des taxons (24 sur 44) présents dans une seule zone latitudinale se trouvaient immédiatement au nord de la frontière sud du Yukon, ce qui suggère que des migrateurs réfugiés glaciaires envahissent toujours le Yukon.

Mots-clés : Béringie; diversité; richesse floristique; latitude; migration; densité des espèces; plantes vasculaires; Yukon

Traduit pour la revue *Arctic* par Nicole Giguère.

[1] Arctic Institute of North America, University of Calgary, Calgary, Alberta T2N 1N4, Canada; wlstrong@northwestel.net

INTRODUCTION

The floristic composition of a region is the product of its contemporary ecology and climatic and phytogeographical history. The territory of Yukon has a unique phytogeographical history relative to other regions of Canada because ~40% of its area was unglaciated (Eastern Beringia refugium) during the Last Glacial Maximum (LGM, 26,500–16,000 BP; Clark et al., 2009). Most of the unglaciated area occurs west of 135° W longitude and north of 62° N latitude (Fig. 1), but a relatively continuous ice-free zone also extended eastward along the upper elevations of the Ogilvie and Wernecke Mountains to the Mackenzie Mountains (Dyke et al., 2003). As deglaciation progressed, it created new surfaces for colonization by Eastern Beringian plants. Regional deglaciation was essentially complete by 10,000 BP (Jackson et al., 1991). Current evidence suggests that more than half of Yukon's present-day indigenous terrestrial flora occurred in Eastern Beringia (Strong, 2021). The remaining portion consists mostly of postglacial migrants from refugia located south of the Laurentide and Cordilleran glacial fronts in the western and, to a lesser extent, in the midwestern United States during the LGM (Strong, 2023).

Plant migration toward Yukon was initiated ~15,000 BP with the contraction of the Laurentide and Cordilleran glacial fronts along their interface in southern Alberta. However, it was not until ~12,500 BP that a continuous ice-free passageway opened to Yukon (Dyke et al., 2003). Palynological evidence suggests that white spruce (primarily *Picea albertiana* S. Brown emended Strong & Hills) arrived at the southeast and south-central portions of the Yukon border about 9500 BP (Cwynar, 1988; Cwynar and Spear, 1995). In contrast, lodgepole pine (*Pinus contorta* var. *latifolia* Engelmann ex S. Watson) and presumably other ecologically similar plants did not reach these locations until 2500–1500 BP and ~3000 BP years later, respectively (Strong and Hills, 2013). It could be inferred from these examples that members of the same taxon, as well as other taxa, used different migratory routes to reach Yukon. Two possible routes include: (1) migration east of the Rocky Mountains along the ice-free corridor and (2) migration through the Rocky Mountains as deglaciation progressed. Both routes originated in the Montana-Idaho-Wyoming region of the northwestern United States (Strong, 2023). Variation in migration rates could be attributable to different refugial locations and starting times, species-specific biological constraints, and the discontinuity of suitable colonization sites along each route.

There is a fundamental question about the phytogeographical development of Yukon: How far north into Yukon has southern North American refugial migration advanced? A cursory assessment (Strong, 2021) suggested that the higher latitudes of Alaska and the Yukon are dominated by Beringian taxa based on abundance (91% of cover) and floristic richness (83% of taxa). Similar analyses for other portions of Yukon are lacking, and
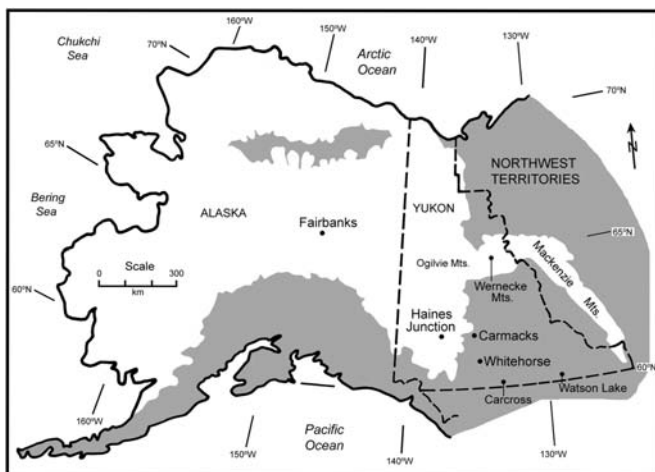

FIG. 1. Location of Yukon in northwestern North America relative to Alaska (U.S.) and the Northwest Territories (Canada). Shaded areas indicate the extent of glaciation during the Last Glacial Maximum (Dyke et al., 2003).

existing taxon distribution maps (e.g., Cody, 2000) are difficult to interpret because of their small size, the small number of reported occurrences per taxon, and the large number of taxa involved.

The objective of this study was to determine the latitudinal distribution of postglacial migrant plants in Yukon. An understanding of their contemporary distribution would provide a greater appreciation of how migrants have shaped the floristic composition of Yukon from both a territorial and a regional perspective. Additionally, the results might serve as baseline data for future researchers to determine how ongoing global warming is changing the botanical resources of Yukon.

MATERIALS AND METHODS

Study Area

Yukon has an area of 482,443 km² with rolling to mountainous terrain (Fig. 1). Its regional vegetation includes deciduous, mixedwood, and evergreen upland forests in the south (Mid-Cordilleran ecoclimatic zone; Strong, 2013) and primarily evergreen-dominant forests farther north (Northern Cordilleran ecoclimatic zone). Subalpine and alpine ecosystems occur at mid- and upper elevations throughout the southern quarter of Yukon. These two ecosystems represent one-third of the territory. The elevation boundary between alpine and subalpine ecosystems generally declines at a rate of ~175 m per degree of increased latitude, from 1400–1500 m in southeastern Yukon to <700 m north of 68° N. Subarctic ecosystems dominate the northern half of the territory; they transition to Arctic ecosystems north of 68.33° N. Annual total precipitation (~300 mm) is generally similar throughout the territory, whereas average annual temperatures decline from −1.1°C to −9.9°C from south to north, respectively (Strong, 2013).

Botanical collecting for scientific purposes had begun in the territory by at least 1901, based on specimens collected by J.W. Macoun and J. Maclean (Mid-Atlantic Herbaria Consortium, see Table 1). More intensive collecting occurred during the early to mid-1900s by renowned botanists such as A.E. Porsild (1951; Doubt, 2022) and H.M. Raup (Mid-Atlantic Herbaria Consortium, see Table 1). The lack of ground access was and continues to be a major impediment to the development of a comprehensive botanical survey of the entire territory. This is especially true in its northern half, which is served by a single unpaved road. Most archived Yukon plant specimens reside in herbaria located outside the territory because of inadequate local storage facilities (Table 1). Much of the available information on plant occurrences within Yukon exists as relevé data, which was often compiled for land planning and management purposes rather than scientific analysis.

Data Compilation

Plant occurrence data were compiled from online herbaria databases, privately held and publicly accessible sources, published lists, and vegetation studies (Table 1). It was assumed that individual plant occurrences were accurately located and correctly identified based on the prevailing taxonomic system at the time of collection or reporting. The initial criteria for inclusion of an occurrence record in the analysis were: (1) classification to at least the species level, and (2) an adequately defined location of collection, preferably according to latitude and longitude. Aquatics (e.g., *Potamogeton* spp.), hybrids, and anthropogenic introductions were excluded from consideration. Plant nomenclature was standardized according to the Integrated Taxonomic Information System (ITIS Partners, 2022) or the Canadensys VASCAN database (Brouillet et al., 2022). Before analysis, compiled taxa were classified as either Beringian-related or non-Beringian, depending upon whether they currently exist in easternmost Siberia (Strong, 2021: Supplementary Information, see arctic/alpine and subarctic taxa). Non-Beringian taxa were considered southern North American refugial migrants or endemic taxa, with the latter excluded from consideration (Strong, 2023: Supplementary Information, Table 2). Individual occurrence records were removed from consideration if they were insufficiently differentiated at the intraspecific level of classification. These more detailed levels of taxonomic classification were pertinent when a species had subspecies or varieties that were associated with both Beringian (e.g., grey-leaved willow [*Salix glauca* var. *acutifolia*]) and postglacial migrant floras (e.g., grey-leaved willow [*Salix glauca* var. *villosa*]). The allocation of migrant taxa to a potential glacial refugium was based on Strong (2023: Supplementary Information).

To facilitate comparison of the floristic data on an equitable spatial basis, Yukon was divided into twenty-nine 0.33° latitudinal bands starting at 60° N (the southern border). Each latitudinal band was subdivided into grid cells with widths approximately equal to their latitudinal height (~37 km × 37 km or 1369 km^2). The 141° W meridian (Yukon's western border) was used as the starting point for latitudinal band subdivision. This method resulted in 2–25 grid cells per latitudinal band for a total of 359 cells. The subdivision process resulted in systematically offset grid cell boundaries because the physical distance between longitudinal lines decreases poleward. Grid cells extending outside of Yukon were combined with other partially occupied and adjacent cells, which had similar topography. This procedure was applied primarily along the eastern side of the territory where the boundary is irregular. These mergers usually had little to modest influence on the overall floristic composition of the recipient grid cell due to the lack of comprehensive, if any, floristic data from the added grid cells.

Migration Trends

Plant migration trends relative to latitude were assessed from four perspectives: (1) the total number of reported plant occurrences without regard to biogeographical origin; (2) the number of Beringian and migrant taxa occurrences as separate entities; (3) the average number of Beringian and migrant taxa occurrences according to grid cells; and (4) the percentage of migrant content relative to the total number of taxa occurrences. Most variables were graphed and analyzed according to latitudinal band densities to provide a standardized basis for comparing within and between plant groups. Comparisons of latitudinal bands represented an assessment of gamma diversity based on the definition used by Moreno and Rodríguez (2010).

The northward advance of migrant taxa was assessed based on the following assumptions: (1) all postglacial migrants crossed the southern Yukon boundary (60° N) at sometime after deglaciation; (2) their arrival times were not necessarily simultaneous; and (3) they may or may not currently exist in the area immediately north of the Yukon border nor as a continuum of occurrences from the border to their current northernmost geographical limit in the territory. The northernmost occurrence of individual migrant taxa was identified by the latitudinal band it is currently found in. The number of unique taxa at their northernmost limit by band (d_i) was used to construct a theoretical model of changing migrant taxa numbers at increasing latitudes. The number of migrant taxa that passed through each band (Q_i) was considered equal to $\Sigma d_{i=29 \dots 1}$, with i representing latitudinal bands from north to south, respectively. The results of this procedure are inverse to conventional species accumulation curves.

Taxa that occurred in only one latitudinal band (referred to as single-band occurrences) were identified to assess occurrence patterns and the number of taxa that might represent recent arrivals to the territory. Although these taxa occurred in only one latitudinal band, more than one record was typically available for each taxon.

TABLE 1. Sources of Yukon plant specimen occurrence data.

Data sources		Number of records
Herbarium specimens[1]		
Consortium of Pacific Northwest Herbaria		20,592
http://pnwherbaria.org [2]		
Canadian Museum of National Herbarium (Doubt, 2022)		8294
W.L Strong Yukon Research Herbarium		6421
Smithsonian National Museum of Natural History Herbarium		1737
https://collections.nmnh.si.edu/search/botany/?irn=10334802		
Mid-Atlantic Herbaria Consortium		1556
https://midatlanticherbaria.org/		
University of Alberta, Vascular Plant Herbarium		1150
https://www.ualberta.ca/museums/museum-collections/vascular-plant-herbarium.html)		
SEINet Portal Network		1106
https://swbiodiversity.org/seinet/		
Harvard University, Gray Herbarium		1043
https://huh.harvard.edu/pages/herbaria		
University of Calgary Herbarium		587
https://science.ucalgary.ca/about/faculty-office/collections-room/herbarium.ucalgary.ca/about/faculty-office/collections-room/herbarium		
University of Toronto at Mississauga, Erindale Herbarium and		
https://collections.utm.utoronto.ca/ collections/herbarium		
McGill University and		
https://mcgill.ca/herbarium/		
University of Colorado Museum of Natural History		223
https://botanydb.colorado.edu		
	Subtotal	42,709
Floristic reports		
Yukon Conservation Data Centre, watch and tracking lists		4371
Porsild (1951)		788
Cody (1994)		656
Others:		
(Bennett and Withers, 2010; Bennett et al., 2010; Cody et al., 1998, 2000, 2001, 2002, 2003, 2004, 2005;		
Cwynar, 1983; Harris and Ball, 2004; Nagy et al., 1979; Rosie, 1991; Scotter and Cody, 1979; Wein et al., 1974)		2678
	Subtotal	8493
Vegetation, ecological, and phytogeographical studies		
Yukon Government (2022)		48,388
Others:		
(Access Consulting Group, 2013; Allen et al., 2012; Beatty and Provan, 2010; Birk, 1977, 1980; Chambers, 2010; Darby et al., 2011;		
Davies et al., 1983; Dearborn and Darby, 2017; Doyle et al., 1973; Edwards et al., 2018; Guest and Allen, 2014; Hoefs, 1976a,b;		
Kojima, 1996; Lambert, 1968; Laxton et al., 1996; LGL Limited, 1981; Liposky and McKenna, 2005; Mackenzie and MacHutchon, 1996;		
Marr et al., 2013; McIntire, 1999; Mossop et al., 2002; Ovenden and Brassard, 1989; Parker and Dickinson, 1990; Price, 1970; Ritchie, 1982;		
Smith et al., 1989; Strong, 2009, 2011, 2014, 2015; Thompson and Witton, 2006; Vetter, 2000; Wolters, 2016.		2674
	Subtotal	51,062
Total number of specimen records	Total	102,264
Number of Beringian plant occurrence records		57,259
Number of migrant plant occurrence records		33,138
Deleted records (i.e., introduced taxa and plants with location issues)		11,867
	Total	102,264
Number of Beringian taxa occurrence records among individual grid cells		7889
Number of postglacial migrant taxa occurrence records among individual grid cells		3743
Number of Beringian taxa		610
Number of postglacial migrant taxa		461

[1] Herbaria databases were accessed between May and October 2022.

[2] This database includes specimens from the only formally recognized herbarium in Yukon (BABY).

Data Analysis

Regression by linear or nonlinear procedures and correlation analysis were used to assess latitudinal trends in the floristic data. The midpoint of each latitudinal band was used as the independent variable (x) for correlation. When assessing occurrence data, only latitudinal bands with five or more grid cells were included in the regression analyses to avoid issues associated with the use of very small sample sizes. Detrended correspondence analysis (McCune and Mefford, 1999) was used to ordinate latitudinal bands based on migrant plant presence or absence. A taxon was

included in the ordination dataset if it occurred more than once among all latitudinal bands. Relative Euclidean distance was used to determine the amount of variance (r^2) explained by the ordination.

RESULTS

Reported Occurrence Records

A total of 102,264 terrestrial vascular plant occurrence records were compiled from various sources (Table 1). Of these occurrences, 58% were from vegetation relevés, floristic studies, and literature sources; the remainder were from herbaria databases. Approximately 11.6% of all occurrence records were discarded because the plants were anthropogenic introductions or had location issues; this reduced the size of the dataset to 90,397 records (Table 1). Of these records, the southernmost latitudinal band had the greatest number of reported occurrences ($n = 11,544$; Fig. 2A), but their density was only one-sixth that of the most northerly band (502 versus 3,101 occurrences per grid cell). The number of occurrences by band had a somewhat cyclic latitudinal profile, with a moderately strong trend of decline between 60° N and 69° N (Fig. 2A). As individual entities, Beringian occurrences approximated the latitudinal pattern and correlation ($r = -0.70$, $n = 27$) of Fig. 2A, whereas migrant occurrences (m) decline exponentially from south to north ($m = \exp(20.67 - 0.2482\ Latitude)$, $r = -0.93$, $n = 27$).

The average number of Beringian occurrences per grid cell had no statistically significant latitudinal trend south of 69° N (Fig. 2B). These occurrences averaged 140 (SD 95) taxa per grid cell. North of 69° N, average Beringian occurrence densities were up to 20 times greater (2,857 per grid cell) than those to the south (Fig. 2B).

The average number of migrant occurrences per grid cell decreased from a regression predicted ($ŷ$) 131 to 23 in a south-to-north direction, respectively. This represented a decline rate of 12.7 occurrences per degree of latitude, based on the Fig. 2C regression *beta*-coefficient. The two most northern latitudinal bands had densities of about 265 migrant occurrences per grid cell.

The density of migrants was usually less than the number of Beringian occurrences throughout Yukon (cf. Figs. 2B and 2C *y*-axis scales). The exception was along the southern Yukon border, where similar Beringian (258) and migrant (254) cell densities occurred.

Taxa Occurrences

Approximately 87% of reported Beringian and migrant occurrences represented duplicates at the grid cell level of analysis. Removing them reduced the available dataset to 11,632 unique occurrences. Eastern Beringian taxa represented two-thirds of the reduced total. Beringian and migrant taxa had similar average richness values (19.4 and
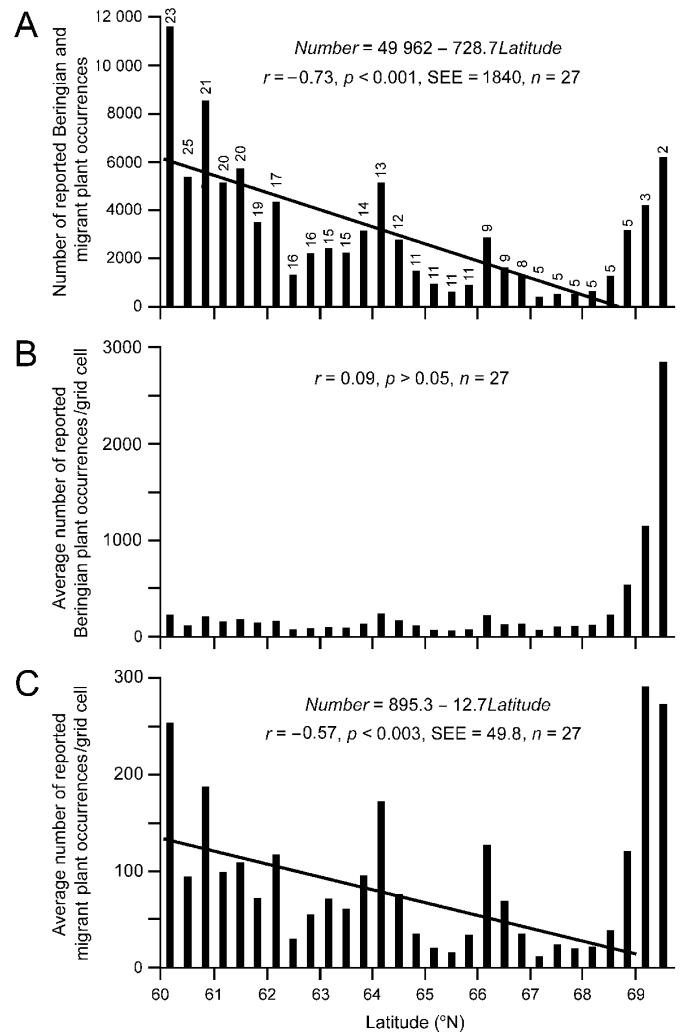

FIG. 2. Total number of compiled Yukon Beringian and postglacial migrant vascular plant occurrences (A), and the number of Beringian (B) and postglacial migrant (C) occurrences as separate entities by latitudinal bands. Regression models developed from latitudinal bands with five or more grid cells. Values included above bars in diagram A indicate the numbers of available grid cells. SEE indicates the standard error of estimate for a regression model.

16, respectively) in the 60° N to 60.33° N latitude band (Fig. 3). From this starting location, Beringian taxa densities increased (Fig. 3A). Migrant taxa decreased with greater latitude (Fig. 3B). The rate of density change was much greater for Beringian than migrant taxa based on regression *beta*-coefficients (+3 vs −0.54, respectively). Regardless of the pattern of change, both sets of taxa were reported far more frequently in the two most northern latitudinal bands (Fig. 3). Almost two-thirds of migrant taxa (54 of 87) were reported five or fewer times in the two northernmost bands, which had a combined area of about 6160 km^2 compared to the largest band (60.33° N to 60.67° N, with an area of 33,574 km^2). In comparison, only one-third of Beringian taxa (123 of 362) were reported five or fewer times.

Migrant taxa composed 51% of the indigenous taxa occurrences reported immediately north of the southern Yukon border. The percentage of migrant taxa declined,
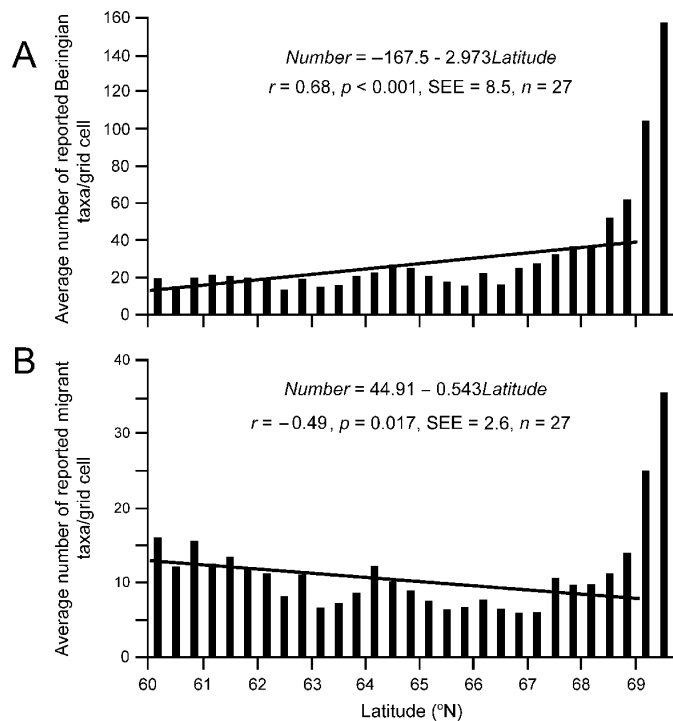
FIG. 3. Average Beringian (A) and migrant (B) taxa densities per grid cell. Regression models developed from latitudinal bands with five or more grid cells. SEE indicates the standard error of estimate for a regression model.

FIG. 4. Percent Yukon Beringian taxa occurrences by latitudinal band.

and Beringian taxa correspondingly increased with greater latitude (Fig. 4), with the rate of change increasing northward. Migrants comprised only 8% of the terrestrial flora in the most northerly latitudinal band (Fig. 4), despite an atypically large sample size (Fig. 2C). Migrant taxa occurrences by latitudinal band are provided in Supplementary Table 1, which includes the full scientific names of taxa.

Of the 610 Beringian taxa, seven (<1.2%) were reported in all latitudinal bands: alpine sweetgrass (*Anthoxanthum monticola*), Aleutian mugwort (*Artemisia tilesii*), black crowberry (*Empetrum nigrum*), one-sided wintergreen (*Orthilia secunda*), northern Labrador tea, (*Rhododendron tomentosum*), Rocky Mountain goldenrod (*Solidago multiradiata*), and long-stalked starwort (*Stellaria longipes* ssp. *longipes*). An additional 12 taxa occurred in 28 of 29 bands. Western white spruce (*Picea albertiana* ssp. *albertiana* [inclusive of *P. glauca*]) and dwarf birch (*Betula glandulosa*) were the only migrants reported in all latitudinal bands; red bearberry (*Arctous rubra*) and Canadian buffaloberry (*Shepherdia canadensis*) were found in 28 bands. In contrast to these cold-hardy plants, the flora of the southernmost latitudinal band included tall deciduous shrubs (devil's club [*Oplopanax horridus*] and Sitka mountain-ash [*Sorbus sitchensis*]) and cold-adverse herbs (such as leafy aster [*Symphyotrichum foliaceum*] and Canada violet [*Viola canadensis* var. *rugulosa*]).

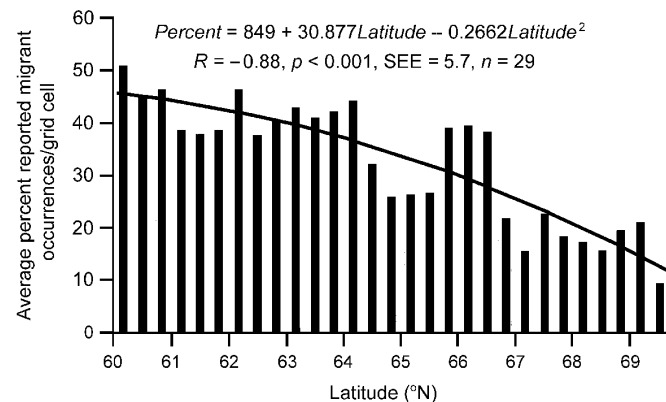Most Yukon migrant plants were probably derived from LGM refugia located primarily in the western and, secondarily, in the midwestern United States. However, several migrants were potentially from a Pacific coast refugium in the westernmost portions of Washington, Oregon, and northern California (including coast mountain draba [*Draba ruaxes*], variegated scouring-rush [*Equisetum variegatum* ssp. *alaskanum*], Arctic lupine [*Lupinus arcticus*], seaside plantain [*Plantago maritima*], slender cinquefoil [*Potentilla gracilis* var. *gracilis*], Nootka alkaligrass [*Puccinellia nutkaensis*], American glasswort [*Salicornia depressa*], McCalla's willow [*Salix maccalliana*], and Sitka mountain-ash [*Sorbus sitchensis*]). Only *Lupinus arcticus* was reported north of 62.33° N in Yukon.

Northernmost Migration Limits

Figure 5 identifies the number of migrant taxa that have theoretically reached each latitudinal band in Yukon (Q_i). Taxa richness was inversely, linearly, and very strongly correlated with latitude (explained variance 98%). The most southern and northern values ranged from 461 to 68 taxa, respectively (Fig. 5). Regionally, migrant numbers declined moving northward at a rate of about 40 taxa per degree of latitude. The northward advance of half of the migrant taxa did not extend beyond 65° N (Fig. 1). Regression residuals were small, although a continuous series of overestimated values occurred between 64° N and 66° N (Fig. 5).

A total of 44 migrant taxa occurred only in one latitudinal band (Fig. 5 Inset). More than half (*n* = 24) occurred in the most southerly latitudinal band (Fig. 5 Inset; Supplementary Table 1). In this band, an individual taxon was typically reported fewer than 10 times among the 5850 reported occurrences in ~31,740 km². Northward the frequency of single-band occurrences declined rapidly (Fig. 5 Inset), with only three reported as far north as 65° N (hirsute anemone [*Anemone multifida* var. *Saxicola*], silky phacelia [*Phacelia sericea*], and Arctic buttercup [*Ranunculus gelidus*]).

Ordination of Migrant Taxa

The ordination of latitudinal bands based on the presence and absence of postglacial migrant taxa (*n* = 421
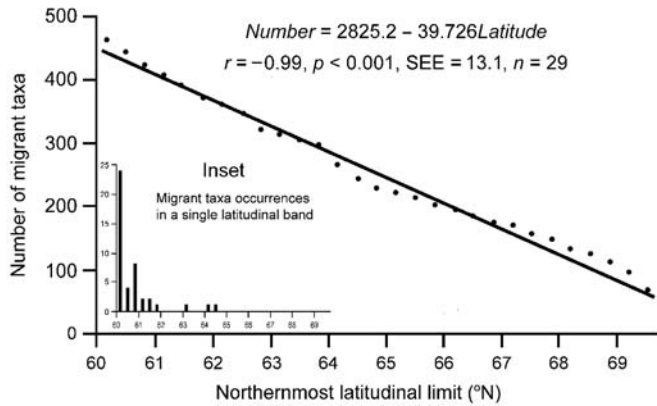
FIG. 5. Theoretical model of migrant plant dispersal based on the most northern occurrence of individual taxa in Yukon. Inset indicates the number of taxa occurring in a single band ($n = 44$ taxa).

taxa) yielded a scatter diagram that was readily partitioned by dominant regional climate zones (Fig. 6). The lowest latitude bands were dominated by a combination of Mid-Cordilleran Boreal and Alpine ecoclimatic zones (A–C) followed by the Northern Cordilleran ecoclimatic zone (Fig. 6). The latter was subdivided according to bands that included (D–I) or lacked (J–N) substantial amounts of the Alpine ecoclimatic zone. Bands A–I had strong within-zone similarity based on their proximity, unlike bands J–N. A trend of increasing northward dissimilarity among bands extended into the Subarctic zone, but not into the Arctic ecoclimatic zone (Fig. 6). The northern portion of the Subarctic zone included bands (V–Z) with a significant amount of Arctic zone areas (Richardson Mountains).

The segments of the ordination approximated the geographical sequence of climate zones as they occur in Yukon. The gradation of latitudinal bands from left to right indicates a progress shift in migrant taxa composition from south to north, with the termini of the sequence having the most dissimilarity. Differences in taxa presence and absence explained 66% ($p < 0.001$) of the variance in the position of latitudinal bands relative to each other, with axis 1 explaining 38%.

DISCUSSION

Data Biases

The difficulties associated with comparing floristic data were recognized more than a century ago and their analysis continues to be controversial (Tjørve et al., 2021). Comparisons are especially problematic when data are derived from unrelated sources and unevenly distributed within large study areas (Turner and Tjørve, 2005). Differences in sample availability were evident in Figs. 2B and 2C, particularly between locations north and south of 69° N. Averaging grid cells reduced the effects of different band sizes but could not eliminate differences in sampling intensity or sample representativeness. Converting migrant
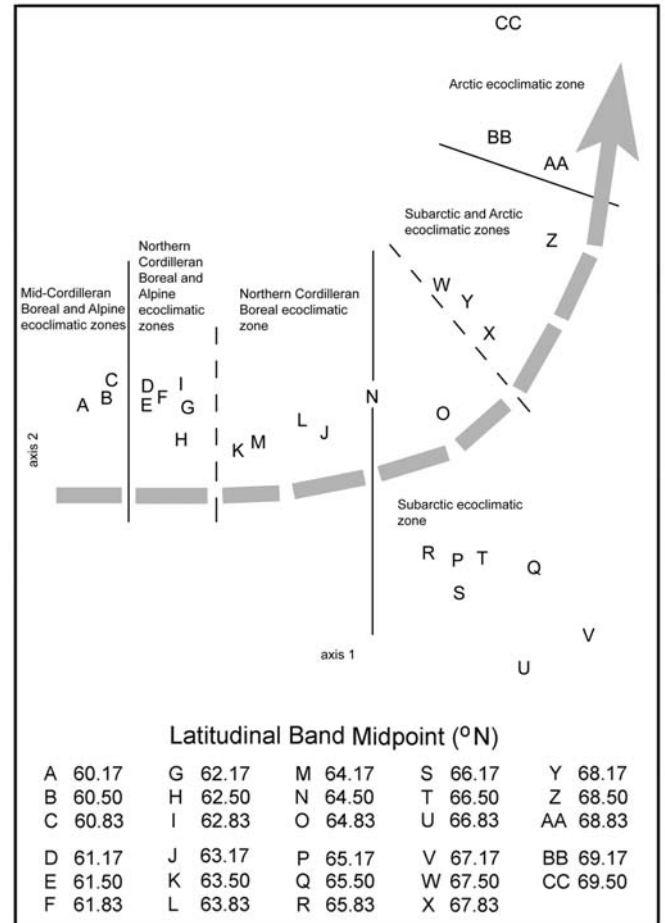

FIG. 6. An ordination of latitudinal bands based on migrant plant presence and absence data. Dominant ecoclimatic zones are assigned to each ordination segment based on Strong (2013). Dashed lines indicated subdivisions within an ecoclimatic zone. The thick shaded line indicates the primary floristic trend in the floristic data.

taxa occurrences to percentages did help to mitigate the importance of differences in sampling intensity among the bands.

The two most northern latitudinal bands were excluded from the occurrence data analyses (Figs. 2 and 3) because of small numbers of cells per band. Their inclusion would have also severely distorted the analysis results, although including them appears to have had little effect when occurrences were reduced to percentages and on presence-absence data. Occurrence data for migrant taxa were more comprehensive in the two northernmost bands than was available for most of the territory. This situation appears to be the result of an exceptionally large amount of sampling within a relatively small area. If this is the case, floristic richness at the southern territory boundary might be 2.5 times greater (40 migrant taxa per cell) than the currently known density based on both regression extrapolation and use of the most northern Arctic richness value in Fig. 3C as a baseline amount. Because band A is very large relative to band CC (31,740 km^2 vs 2358 km^2), it could require 13 times more effort than was employed in band CC to create a density value based on the same intensity of sampling. With

such an effort, the likelihood of finding additional taxa would increase.

Considerably more occurrence records will be needed to reduce data inequities within the territory if more comprehensive migration models are wanted. Sufficient data to resolve this problem is unlikely to be available for decades, if ever, because of the size of Yukon and poor ground access. Regardless of how many botanical records become available, sampling protocols will always be an issue, unless all grid cells are identical in size and sampled at the same intensity with the same degree of thoroughness using identical procedures.

It was assumed that the plants included in the dataset were properly identified. To do otherwise would have curtailed the study, because it would be unrealistic to verify the identities of tens of thousands of plants (assuming they were even available for review). If an analysis was limited to herbarium records, which does not guarantee correct plant identifications, the number of available samples might be insufficient to detect regional trends in an area as large as Yukon. Pragmatically, in the absence of a huge volume of high-quality data it is sometimes necessary to make a trade-off between data quality and quantity to facilitate the analysis of large geographical areas. The trends presented in Figs. 4, 5, and 6 appear adequately strong and sufficiently robust to accommodate some taxonomic inadequacies that may have resulted from the classification of a multitude of plants by numerous botanists.

Floristic Trends

A change in postglacial migrant taxa composition and richness with increasing latitude is a trend corroborated by the different approaches used to analyze the occurrence data (Figs. 3 – 6). The migration process has been of sufficient length for 8% of migrants to have reached the northernmost area of Yukon, although a large proportion of the flora consists of miscellaneous occurrences. However, most taxa are concentrated in the southern half of the territory. The occurrence of most single-band taxa in the area immediately north of Yukon's southern border suggests that invasion by postglacial migrants is ongoing. These taxa are often widely distributed in British Columbia and sometimes present at its northern border (Douglas et al., 2002). The pattern of migrant taxa occurrence is probably different from that of the Beringian flora because the latter has existed in the region much longer and has likely reached a quasi-ecological equilibrium with current environmental conditions. Global climatic warming will likely facilitate further northward movement of both the Beringian and migrant plant populations, as well as the invasion of additional migrants. Migrant taxa might also increase in abundance, particular in the southern portion of the territory.

The ordination of migrant taxa based on their presence-absence supports the existence of a south-to-north composition gradient. Being able to partition the ordination

easily into sequential regional biomes highlights the importance of climate in determining how taxa are arrayed latitudinally in Yukon. The degree of (dis)similarity among most latitudinal bands is about what might be expected from this type of analysis, if not better. A strict sequential occurrence of bands (i.e., A → B → ... CC) is unlikely because of mesoscale variation in the types and proportions of terrain and vegetation within individual latitudinal bands.

Migration Constraints

All migrant taxa probably passed through southern Yukon, but only half have extended their range beyond the latitudinal midpoint of the territory. Climate ultimately drives migration, but differences in migration rates and adverse biological (e.g., competition from existing vegetation) and physical conditions can also be hindrances (Normand et al., 2011). The postglacial invasion of Yukon by migrant taxa represents an infiltration of the plants into pre-existing post-Beringian vegetation rather than the colonization of barren deglaciated surfaces—because a vegetation cover existed before the arrival of southern North American migrants (e.g., Ritchie, 1982; Cwynar, 1988). This probably also slowed migration rates. Another important obstacle to plant migration may be the east – west trending Ogilvie and Wernecke Mountains, which extend nearly the entire width of central Yukon. These mountains may obstruct migration because of the occurrence of unfavourable climate conditions at their summits and adverse site conditions, such as extensive areas of exposed bedrock and shallow soils. However, a few low-elevation passes do exist through these mountains, which may perhaps facilitate some south-to-north migration (Strong, 2013). The obvious alternative migration pathway involves skirting the western end of the Ogilvie Mountains (Fig. 1).

The northwest-trending St. Elias Mountains in the southwest and the Selwyn Mountains along the east side of the territory, in conjunction with the Mackenzie Mountains, may have facilitated the latitudinal trends detected in the analysis by funnelling postglacial migrants northward into southern Yukon. These mountains may also act as physical and ecological barriers to both plants from the Pacific coast region and plants moving from east to west at latitudes north of 60° N. In the northern portion of the territory, the north – south trending Richardson Mountains may also act as a barrier to westward migrating plants. As a result, the south-to-north pattern of migration does not appear to have been compromised by substantial plant invasions from other source areas.

CONCLUSIONS

Plant migration is a slow process that is often controlled by climate. Migrant plants from southern North American LGM refugia occur throughout Yukon, but most taxa are

confined to the southern and warmer half of the territory, with the greatest concentration along its southern border. The common presence of single-band occurring taxa immediately north of the border indicates that invasion of Yukon by postglacial migrant plants is an ongoing process. Migrants as a group are currently subdominant to Beringian taxa in the terrestrial indigenous flora of Yukon. Considerably more plant occurrence data are needed to develop a comprehensive understanding of postglacial migrant plant dispersal in Yukon (particularly between 64° N and 69° N latitude) and thus the territory's overall phytogeographical history.

ACKNOWLEDGEMENTS

REFERENCES

Access Consulting Group. 2013. Minto ecosystems and vegetation baseline report, YESAB project proposal Phase V-VI (Appendix S). In: Project proposal: Phase V/IV expansion of mining and milling Minto Mine, Yukon Territory. Vancouver: Minto Explorations Ltd. https://emrlibrary.gov.yk.ca/minerals/MajorMines/minto/phase_V_VI_expansion_proposal/Appendix_S_ecosystems_and_vegetation_baseline.pdf

Allen, G.A., Marr, K.L., McCormick, L.J., and Hebda, R.J. 2012. The impact of Pleistocene climate change on an ancient Arctic-alpine plant: Multiple lineages of disparate history in *Oxyria digyna*. Ecology and Evolution 2(3):649–665. https://onlinelibrary.wiley.com/doi/10.1002/ece3.213

Beatty, G.E., and Provan, J. 2010. Refugial persistence and postglacial recolonization of North America by the cold-tolerant herbaceous plant *Orthilia secunda*. Molecular Ecology 19(22):5009–5021. https://doi.org/10.1111/j.1365-294X.2010.04859.x

Bennett, B.A., and Withers, S. 2010. Spiked saxifrage, *Saxifraga spicata*, rediscovered in Canada after 110 years. Canadian Field-Naturalist 124(1):57–58. https://doi.org/10.22621/cfn.v124i1.1031

Bennett, B.A., Catling, P.M., Cody, W.J., and Argus, G.W. 2010. New records of vascular plants in the Yukon Territory VIII. Canadian Field-Naturalist 124(1):1–27. https://doi.org/10.22621/cfn.v124i1.1025

Birk, H.J.B. 1977. Modern pollen rain and vegetation of the St. Elias Mountains, Yukon Territory. Canadian Journal of Botany 55(18):2367–2382. https://doi.org/10.1139/b77-270

Birk, H.J.B. 1980. The present flora and vegetation of the moraines of the Klutlan Glacier, Yukon Territory, Canada: A study of plant succession. Quaternary Research 14(1):60–86. https://doi.org/10.1016/0033-5894(80)90007-1

Brouillet, L., Coursol, F., Meades, S.J., Favreau, M., Anions, M., Béllisle, P., and Desmet, P. 2022. VASCAN, the database of vascular plants of Canada. https://data.canadensys.net/vascan/

Chambers, J.H.S. 2010. Habitat use and ecologically sustainable carrying capacity for elk (*Cervus elaphus*) in the Takhini Valley, Yukon. MEDes thesis, Department of Environmental Science, University of Calgary, Calgary, Alberta. https://prism.ucalgary.ca/items/bd681286-448f-47b4-9728-b22aed761455/full

Clark, P.U., Dyke, A.S., Shakun, J.D., Carlson, A.E., Clark, J., Wohlfarth, B., Mitrovica, J.X., Hostetler, S.W., and McCabe, A.M. 2009. The last glacial maximum. Science 325(5941):710–714. https://www.science.org/doi/10.1126/science.1172873

Cody, W.J. 1994. The flora of the Yukon Territory: Additions, range extension and comments. Canadian Field-Naturalist 108(4):428–476. https://doi.org/10.5962/p.356832

———. 2000. Flora of the Yukon Territory. Ottawa, Ontario: NRC Research Press. https://doi.org/10.1139/9780660181103

Cody, W.J., Kennedy, C.E., and Bennett, B. 1998. New records of vascular plants in the Yukon Territory. Canadian Field-Naturalist 112(2):289–328. https://doi.org/10.5962/p.358410

———. 2000. New records of vascular plants in the Yukon Territory II. Canadian Field-Naturalist 114(3):417–443. https://doi.org/10.5962/p.363995

———. 2001. New records of vascular plants in the Yukon Territory III. Canadian Field-Naturalist 115(2):301–322. https://doi.org/10.5962/p.363791

Cody, W.J., Kennedy, C.E., Bennett, B., and Loewen, V. 2002. New records of vascular plants in the Yukon Territory IV. Canadian Field-Naturalist 116(3):446–474.
https://doi.org/10.5962/p.363484

Cody, W.J., Kennedy, C.E., Bennett, B., and Standiforth, J. 2003. New records of vascular plants in the Yukon Territory V. Canadian Field-Naturalist 117(2):278–301.
https://doi.org/10.22621/cfn.v117i2.707

Cody, W.J., Kennedy, C.E., Bennett, B., and Caswell, P. 2004. New records of vascular plants in the Yukon Territory VI. Canadian Field-Naturalist 118(4):558–578.
https://doi.org/10.22621/cfn.v118i4.58

Cody, W.J., Bennett, B.A., and Caswell, P. 2005. New records of vascular plants in the Yukon Territory VII. Canadian Field-Naturalist 119(3):417–436.
https://doi.org/10.22621/cfn.v119i3.154

Cwynar, L.C. 1983. Range extensions of vascular plants from the northern Yukon Territory. Canadian Field-Naturalist 97(2):170–176.
https://doi.org/10.5962/p.354974

———. 1988. Late Quaternary vegetation history of Kettlehole Pond, southwest Yukon. Canadian Journal of Botany 18(10):1270–1279.
https://doi.org/10.1139/x88-196

Cwynar, L.C., and Spear, R.W. 1995. Paleovegetation and palaeoclimatic changes in the Yukon at 6 ka BP. Géographie Physique et Quaternaire 49(1):29–35.
https://doi.org/10.7202/033027ar

Darby, R.K., Koh, S., Hik, D.S., and Price, L.W. 2011. Four decades of plant community change in the alpine tundra of southwest Yukon, Canada. AMBIO 40(6):660–671.
https://doi.org/10.1007/s13280-011-0172-2

Davies, D., Kennedy, C.E., and McKenna, K. 1983. Coal River Springs preliminary biophysical inventory. Whitehorse, Yukon: Yukon Department of Renewable Resources.
https://sis.agr.gc.ca/cansis/publications/surveys/yt/ytcrs/ytcrs_report.pdf

Dearborn, K., and Darby, R.K. 2017. Aspect and slope influence plant community composition more than elevation across forest-tundra ecotones in subarctic Canada. Journal of Vegetation Science 28(3):595–604.
https://doi.org/10.1111/jvs.12521

Doubt, J. 2022. Canadian Museum of Nature Herbarium, dataset/occurrences.

Douglas, G.W., Meidinger, D., and Pojar, J., eds. 2002. Illustrated flora of British Columbia, Vol. 8: General summary, maps and keys. Victoria, British Columbia: British Columbia Ministry of Sustainable Resource Management and Ministry of Forests.
https://www.for.gov.bc.ca/hfd/pubs/docs/mr/mR_illustratedflora.htm

Doyle, P., Fletcher, W.K., and Brink, V.C. 1973. Trace element content of soils and plants from the Selwyn Mountains, Yukon and Northwest Territories. Canadian Journal of Botany 51(2):421–427.
https://doi.org/10.1139/b73-049

Dyke, A.S., Moore, A., and Robertson, L. 2003. Deglaciation of North America. Ottawa, Ontario: Geological Survey of Canada.
https://doi.org/10.4095/214399

Edwards, M.E., Lloyd, A., and Armbruster, W.S. 2018. Assembly of Alaska-Yukon boreal steppe communities: Testing biogeographic hypotheses via modern ecological distributions. Journal of Systematics and Evolution 56(5):466–475.
https://doi.org/10.1111/jse.12307

Guest, H.J., and Allen, G.A. 2014. Geographical origins of North American *Rhodiola* (Crassulaceae) and phylogeography of the western roseroot, *Rhodiola integrifolia*. Journal of Biogeography 14(6):1070–1080.
https://doi.org/10.1111/jbi.12267

Harris, S.A., and Ball, P.W. 2004. New records of Cyperaceae and Juncaceae from the Yukon Territory. Canadian Field-Naturalist 118(2):266–267.
https://doi.org/10.22621/cfn.v118i2.926

Hoefs, M. 1976a. Preliminary biological reconnaissance of the Lower Nisutlin River floodplain. Whitehorse, Yukon: Yukon Game Branch.
https://emrlibrary.gov.yk.ca/environment/preliminary-biological-reconnaissance-of-the-lower-nisutlin-river-floodpain.pdf

Hoefs, M. 1976b. Ecological investigation of dall sheep (*Ovis dalli dalli*, Nelson) and their habitat of Sheep Mountain, Kluane National Park, Yukon Territory, Canada. PhD dissertation, University of British Columbia, Vancouver, British Columbia.
https://open.library.ubc.ca/soa/cIRcle/collections/ubctheses/831/items/1.0093879

ITIS Partners. 2022. Integrated taxonomic information system.
https://www.itis.gov/

Jackson, L.E. Jr., Ward, B., Duk-Rodkin, A., and Hughes, O.L. 1991. The last cordilleran ice sheet in southern Yukon Territory. Géographie Physique et Quaternaire 45(3):341–354.
https://doi.org/10.7202/032880ar

Kojima, S. 1996. Ecosystem types of boreal forest in the North Klondike River valley, Yukon Territory, Canada, and their productivity potentials. Environmental Monitoring and Assessment 39(1–3):265–281.
https://doi.org/10.1007/BF00396149

Lambert, J.D.H. 1968. The ecology and successional trends of tundra plant communities in the low Arctic subalpine zone of the Richardson and British Mountains of the Canadian western Arctic. PhD dissertation, University of British Columbia, Vancouver, British Columbia.
https://doi.org/10.14288/1.0104598

Laxton, N.F., Burn, C.R., and Smith, C.A.S. 1996. Productivity of loessal grasslands in the Kluane Lake Region, Yukon Territory, and the Beringian "production paradox." Arctic 49(2):129–140.
https://doi.org/10.14430/arctic1191

LGL Limited. 1981. An overview study of the vegetation, wildlife and fish resources of the Bonnet Plume Lease, northeastern Yukon Territory. Calgary, Alberta: Pan Ocean Oil Ltd.
https://yma.gov.yk.ca/062150.pdf

Liposky, P.S., and McKenna, K. 2005. Local-scale biophysical mapping for integrated resource management, Watson Lake area (NTS 105A/2), Yukon. Whitehorse, Yukon: Yukon Geological Survey.
https://open.yukon.ca/data/datasets/local-scale-biophysical-mapping-integrated-resource-management-watson-lake-nts-105a2

Mackenzie, W., and MacHutchon, A.G. 1996. Habitat classification for the Firth River valley, Ivvavik National Park, Yukon. Inuvik, Northwest Territories: Parks Canada.

Marr, K.L., Allen, G.A., Hebda, R.J., and McCormick, L.J. 2013. Phylogeographical patterns in the widespread Arctic-alpine plant *Bistorta vivipara* (Polygonaceae) with emphasis on western North America. Journal of Biogeography 40(5):847–856.
https://doi.org/10.1111/jbi.12042

McCune, B., and Mefford, M.J. 1999. Multivariate analysis of ecological data, version 4.25. Gleneden Beach, Oregon: MjM Software.

McIntire, E.J.B. 1999. The effect of collared pika grazing on alpine tundra vegetation in southwest Yukon, Canada. MSc thesis, University of Toronto, Toronto, Ontario.
https://www.collectionscanada.ca/obj/s4/f2/dsk2/ftp01/MQ45889.pdf

Moreno, C.E., and Rodríguez, P. 2010. A consistent terminology for quantifying species diversity? Oecologia 163(2):279–282.
https://doi.org/10.1007/s00442-010-1591-7

Mossop, D.H., Rosie, R., O'Donoghue, M., Sinnott, K., and Elias, W. 2002. Ecological reconnaissance of the Chappie Lake wetlands. Whitehorse, Yukon: Yukon Department of Environment, Canadian Parks and Wilderness society, and Yukon College.
https://emrlibrary.gov.yk.ca/ebooks/Northern%20Research%20Institute/ecological-reconnaissance-of-the-chappie-lake-wetlands-2002.pdf

Nagy, J.A., Pearson, A.M., Goski, B.C., and Cody, W.J. 1979. Range extensions of vascular plants in northern Yukon Territory and northwestern District of Mackenzie. Canadian Field-Naturalist 93(3):259–265.
https://doi.org/10.5962/p.346953

Normand, S., Ricklefs, R.E., Skov, F., Bladt, J., Tackenberg, O., and Svenning, J.-C. 2011. Postglacial migration supplements climate in determining plant species ranges in Europe. Proceedings of the Royal Society B 278(1725):3644–3653.
https://doi.org/10.1098/rspb.2010.2769

Ovenden, L., and Brassard, G.R. 1989. Wetland vegetation near Old Crow, northern Yukon. Canadian Journal of Botany 67(4):954–960.
https://doi.org/10.1139/b89-127

Parker, W.H., and Dickinson, T.A. 1990. Range-wide morphological and anatomical variation in *Larix laricina*. Canadian Journal of Botany 68(4):832–840.
https://doi.org/10.1139/b90-110

Porsild, A.E. 1951. Botany of southeastern Yukon adjacent to the Canol Road. National Museum of Canada Bulletin No. 121. Ottawa, Ontario: Canada Department of Resources and Development.
https://doi.org/10.1086/399151

Price, L.W. 1970. Morphology and ecology of solifluction lobe development, Ruby Ridge, Yukon Territory. PhD dissertation, University of Illinois, Urbana, Illinois.

Ritchie, J.C. 1982. The modern and late-Quaternary vegetation of the Doll Creek area, north Yukon, Canada. New Phytologist 90(3):563–603.
https://doi.org/10.1111/j.1469-8137.1982.tb04489.x

Rosie, R. 1991. Range extension and rare vascular plants for southeastern Yukon. Canadian Field-Naturalist 105(3):315–324.
https://doi.org/10.5962/p.358038

Scotter, G.W., and Cody, W.J. 1979. Interesting vascular plants from southeastern Yukon Territory. Canadian Field-Naturalist 93(2):163–170.
https://doi.org/10.5962/p.346910

Smith, C.A.S., Kennedy, C.E., Haragrave, A.E., and McKenna, K.M. 1989. Soil and vegetation of Herschel Island. Yukon Soil Survey Report 1. Whitehorse, Yukon: Agriculture Canada.
http://sis.agr.gc.ca/cansis/publications/surveys/yt/yt15/index.html

Strong, W.L. 2009. *Populus tremuloides* Michx. Postfire stand dynamics in the northern boreal-cordilleran ecoclimatic region of central Yukon Territory, Canada. Forest Ecology and Management 258(7):1110 – 1120.
https://doi.org/10.1016/j.foreco.2009.05.041

———. 2011. Lateral *Picea* shadow effects on *Populus tremuloides* understory vegetation in central Yukon, Canada. Forest Ecology and Management 261(11):1866 – 1875.
https://doi.org/10.1016/j.foreco.2011.02.009

———. 2013. Ecoclimatic zonation of Yukon (Canada) and ecoclinal variation in vegetation. Arctic 66(1):52 – 67.
https://doi.org/10.14430/arctic4266

———. 2014. Northernmost North American *Pinus contorta* var. *latifolia* (lodgepole pine) sociations and vegetation diversity relative to its central range east of the Rocky Mountains. Nordic Journal of Botany 32(2):222 – 232.
https://doi.org/10.1111/j.1756-1051.2013.00126.x

———. 2015. High-latitude Yukon boreal-Cordilleran grassland plant communities. Arctic 68(1):69 – 78.
https://doi.org/10.14430/arctic4453

———. 2021. Potential palaeoflora of Last Glacial Maximum Eastern Beringia, northwest North America. Vegetation History and Archaeobotany 30(5):675 – 684.
https://doi.org/10.1007/s00334-021-00823-4

———. 2023. Potential Late Glacial Maximum refugial areas of Alaska-Yukon postglacial migrant plants. Vegetation History and Archaeobotany 32(1):35 – 48.
https://doi.org/10.1007/s00334-021-00823-4

Strong, W.L, and Hills, L.V. 2013. Holocene migration of lodgepole pine (*Pinus contorta* var. *latifolia*) in southern Yukon, Canada. Holocene 23(9):1340 – 1349.
https://doi.org/10.1177/0959683613484614

Thompson, S.L., and Witton, J. 2006. Patterns of recurrent evolution and geographic parthenogensis within apomictic polyploidy Easter daises (*Townsendia hookeri*). Molecular Ecology 15(11):3389 – 3400.
https://doi.org/10.1111/j.1365-294X.2006.03020.x

Tjørve, E., Matthews, T.J., and Whittaker, R.J. 2021. The history of the species-area relationship. In: Matthews, T.J., Trianthis, K.A., and Whittaker, R.J., eds. The species-area relationship: Theory and application. Cambridge, England: Cambridge University Press. 20 – 48.
https://doi.org/10.1017/9781108569422.005

Turner, W.R., and Tjørve, E. 2005. Scale-dependence in species-area relationships. Ecography 28(6):721 – 730.
https://doi.org/10.1111/j.2005.0906-7590.04273.x

Vetter, M.A. 2000. Grasslands of the Aishihik-Sekulmum Lakes area, Yukon Territory, Canada. Arctic 53(2):165 – 173.
https://doi.org/10.14430/arctic847

Wein, R.W., Hettinger, L.R., Janz, A.J., and Cody, W.J. 1974. Vascular plant range extensions in the northern Yukon Territory and northwestern Mackenzie District, Canada. Canadian Field-Naturalist 88(1):57 – 66.
https://doi.org/10.5962/p.344321

Wolters, J. 2016. Mid- to late Holocene environmental dynamics of the Yukon coastal plain and Herschel Island (Canada): Evidence from polygonal peatlands and lake sediment. PhD dissertation, University of Potsdam, Potsdam, Germany.
https://epic.awi.de/id/eprint/44730/1/Wolter_PhDthesis.pdf

Yukon Government. 2022. Yukon biophysical inventory system – site and vegetation data, Whitehorse, Yukon.