Running head: variation in leaf isotopes

Disentangling the role of shared ancestry and the environment on leaf stable isotopes

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Abstract

Stable carbon (C) and nitrogen (N) isotopes in plants are important indicators of plant water use efficiency and N acquisition strategies. While often regarded as being under environmental control, there is growing evidence that evolutionary history may also shape variation in stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) among plant species. Here we examined patterns of foliar $\delta^{13}C$ and $\delta^{15}N$ in alpine tundra for 59 species in 20 plant families. To assess the importance of environmental controls and evolutionary history, we examined if average $\delta^{13}C$ and $\delta^{15}N$ predictably differed among habitat types, if individual species exhibited intraspecific trait variation (ITV) in $\delta^{13}C$ and $\delta^{15}N$, and if there were a significant phylogenetic signal in $\delta^{13}C$ and $\delta^{15}N$. We found that variation among habitat types in both $\delta^{13}C$ and $\delta^{15}N$ mirrored well-known patterns of water and nitrogen limitation. Conversely, we also found that 40% of species exhibited no ITV in $\delta^{13}C$ and 35% of species exhibited no ITV in $\delta^{15}N$, suggesting that some species are under stronger evolutionary control. However, we only found a modest signal of phylogenetic conservatism in $\delta^{13}C$ and no phylogenetic signal in $\delta^{15}N$ suggesting that shared ancestry is a weaker driver of tundra wide variation in stable isotopes. Together, our results suggest that both evolutionary history and local environmental conditions play a role in determining variation in $\delta^{13}C$ and $\delta^{15}N$ and that considering both factors can help with interpreting isotope patterns in nature and with predicting which species may be able to respond to rapidly changing environmental conditions.

Keywords: Alpine, $\delta^{13}C$, $\delta^{15}N$, Intraspecific trait variation, Phylogenetic signal

Introduction

Understanding the relative importance of evolutionary history and the environment on physiological and morphological traits is a long-standing question at the intersection of evolutionary biology and ecology (Felsenstein 1985; Lauder 1981; Losos 1990). With the greater availability of functional trait data, trait based approaches in community ecology are becoming more prevalent (e.g., Adler et al. 2013; Carmona et al. 2016; Hulshof and Swenson 2010; Kraft et al. 2008) and there has been an increased interest in linking functional trait data with phylogenetic patterns (Cavender-Bares et al. 2009; Swenson 2011; Webb 2000). As a result of these advances in functional and phylogenetic ecology, it is increasing evident that some plant functional traits are labile and respond rapidly to changes in the environment (i.e., Bloor and Grubb 2004; Gratani 2014), while other plant functional traits are phylogenetically conserved and have maintained functional trait similarity through evolutionary time (i.e., Cavender-Bares et al. 2006; Swenson and Enquist 2007) without a clear indication of when shared ancestry or environmental control are more important (Bhaskar et al. 2016; Flores et al. 2014; Forrestel et al. 2015; Yang et al. 2014). One approach for resolving this issue is to focus on “hard” plant functional traits that correlate strongly with physiological processes (i.e., stable isotope ratios) as opposed to “soft” traits that are influenced by multiple processes simultaneously (i.e., specific leaf area, tissue N; Goud and Sparks 2018). Distinguishing between the contributions of environment and evolutionary history in shaping hard traits will help clarify patterns of functional diversity along environmental gradients, improving our predictions of species responses to global change.

Two key isotopes that are linked to physiological processes are ^{13}C and ^{15}N. Foliar carbon isotope ($\delta^{13}C$) values in a plants are related to the balance of photosynthesis and stomatal conductance and their coupled response to variation in the environment (Cernusak et al. 2013;

Farquhar et al. 1989; Farquhar et al. 1982). Specifically, $\delta^{13}C$ is controlled by the ratio of intercellular (c_i) to ambient (c_a) CO_2 concentrations where plants become enriched in $\delta^{13}C$ by any process that increases the difference between c_i and c_a (Farquhar et al. 1982). Importantly, there is a significant relationship between c_i/c_a and plant water use efficiency (WUE) where $\delta^{13}C$ provides an estimate of the long-term WUE of a plant (Ehleringer 1989; Farquhar et al. 1989). Due to this relationship plants adapted to more xeric environments often have lower $\delta^{13}C$ (and WUE) when grown in more mesic environments, or vice-versa (Anderson et al. 1996; Korner et al. 1991; Yang et al. 2015), suggesting strong evolutionary control on $\delta^{13}C$. However, in other cases individual plants respond to decreased water availability by increasing their WUE and thus $\delta^{13}C$, suggesting stronger environmental control (Corcuera et al. 2010; Farquhar et al. 1989; Ramírez-Valiente et al. 2010).

Foliar nitrogen isotope ($\delta^{15}N$) values in plants can shed light on short-term dynamics of the N cycle (Craine et al. 2015), though variation in $\delta^{15}N$ is much more difficult to explain than variation in $\delta^{13}C$. Variation in observed foliar $\delta^{15}N$ within and among species is dependent on a combination of available nitrogen from atmospheric deposition, soils, or bedrock (Kolb and Evans 2002) and symbioses (e.g. mycorrhizal fungi and N-fixing rhizobia; Hobbie et al. 2000; Hobbie and Hobbie 2006). As seen with $\delta^{13}C$, foliar $\delta^{15}N$ may be under stronger evolutionary control where species maintain $\delta^{15}N$ values across habitat types (Miller and Bowman 2003; Yang et al. 2015), or alternatively $\delta^{15}N$ may vary greatly between conspecific individuals in response to differences in soil N availability (Bustamante et al. 2004).

To date there have been relatively few tests of a phylogenetic signal in plant foliar stable isotopes with most studies assuming strong environmental control. In one of the few studies to examine the relative roles of environment control and phylogenetic signal in $\delta^{13}C$ and $\delta^{15}N$ for plants, Goud and Sparks (2018) found that both δ^{13}C and δ^{15}N exhibited significant trait conservatism (closely related species were more similar than expected by chance) for a group of 57 plant species in the Ericaceae. Moreover, by sampling over broad environmental gradient including swamps and riparian zones in the south-eastern United States, California chaparral, and arctic tundra in northern Canada, they found that evolutionary history played a stronger role in influencing isotope values than the environment, except in some specialized environments (Goud and Sparks 2018). While this work by Goud and Sparks (2018) provides an excellent broad scale assessment, they used very broad scale environmental gradients (vapor pressure deficit from nearby weather stations) and we lack a clear picture of if these patterns are consistent across a broader phylogeny (multiple families) or if the relative importance of phylogenetic signal and the environment differs at smaller spatial scales.

Here, we examined patterns of foliar δ^{13}C and δ^{15}N for 59 species across 20 plant families in alpine tundra. Due to the redistribution of snow by wind in the alpine tundra, strong gradients of productivity, soil moisture, nutrient availability, and physical stress results in a mosaic of habitat types across alpine tundra landscapes (Bowman et al. 2003; Bowman and Fisk 2001; Litaor et al. 2008; Seastedt et al. 2004; Walker et al. 2001). These habitat types include: fellfield, dominated by cushion plants and lichens; dry meadow dominated by xeric sedges and forbs, moist meadow, co-dominated by grasses and forbs; wet meadow, dominated by sedges and mesic forbs; late melting snow banks, dominated by forbs and sedges (May and Webber 1982; Walker et al. 1993; Walker et al. 2001). We sampled across these habitats and asked: 1) are foliar δ^{13}C and δ^{15}N values in alpine tundra plant species phylogenetically conserved traits or are they environmentally driven responses; and 2) is phylogenetic conservatism of these isotopic values tundra wide or restricted to specific habitat types?

Methods

Study location. This study was conducted in alpine tundra at the Niwot Ridge Long Term Ecological Research site (40º03'N, 105º35'W). Located in the Front Range of the Colorado Rocky Mountains. Niwot Ridge has a short growing season (approximately 2–3 months) with a mean annual temperature of -2.3C (6.5 C in the growing season) and an average annual precipitation of 884mm, with the majority of the precipitation (94%) falling as snow (Litaor et al. 2008). Annual daily wind speeds average 8.1 m s-1, with an average annual daily maximum wind speed of 19.8 m s-1 (Losleben and Chowanski unpublished data). Due to these high wind speeds, an important environmental factor in alpine tundra is the redistribution of snow by wind (Bowman and Fisk 2001). Wind keeps Fellfield and Dry Meadow habitats relatively snow-free all winter and these low productivity habitats are characterized by temperature stress, low water availability, and low nitrogen availability (Billings and Mooney 1968; Walker et al. 2001). Blown snow accumulates in Snow Bank habitats which are buffered from wind scour and temperature stresses in the winter and snow melt during the growing season enhances water and nitrogen availability in Moist and Wet Meadow habitats found downhill of Snow Banks habitats which tend to be energy limited due to the large snow accumulation. Soil moisture is significantly correlated with snowfall amounts and terrain factors that affect snow accumulation (Taylor and Seastedt 1994).

Trait collection. We collected leaves from 59 species in 20 plant families and four functional groups (Supplementary Table 1) during the summers of 2017 and 2018. Samples were largely collected next to 88 permanent 1-m^2 plots established in 1989 to track changes in vegetation over time in the different community types found on Niwot Ridge (noted above). Species for collection were chosen haphazardly within each community type and 20 of the 59 species were found in multiple habitat types. For each species in each community type we collected one leaf from 5-20 separate individuals (all individuals were greater than 1m apart to ensure that individuals were not clones connected belowground). Leaves were oven dried at 60°C for 4 days. Approximately 10g of dry material was then shipped to the University of Wyoming Stable Isotope Facility (http://www.uwyo.edu/sif/) where samples were ground with a steel ball mil and analyzed for δ^{13}C and δ^{15}N on a Carlo Erba 1110 Elemental Analyzer coupled to a Thermo Delta V IRMS. Isotope ratios were calculated as

$$\delta[^{13}\mathrm{C}, {}^{15}\mathrm{N}]samples = (\frac{R_{sample}}{R_{standard}} - 1)\ x\ 100$$

Where R_{sample} and R_{standard} are the ^{13}C/^{12}C or ^{15}N/^{14}N molar abundance ratios of samples, with 36-UWSIF-Glutamic 1and 39-UWSIF-Glutamic 2 use as reference samples.

Phylogenetic tree. To evaluate the importance of evolutionary history, we created a phylogenetic tree for all genera in our dataset based on the phylogeny produced by Zanne et al. (2014). Prior to calculations of phylogenetic signal, we resolved polytomies using the multi2di function in the ape package (Paradis et al. 2004). Note that resolving polytomies in this way does not affect branch lengths and consequently maximum likelihood estimates of Pagel's λ do not vary. We then calculated Pagel's λ (Pagel 1999) for both isotopes using the multiPhylosignal function in the PICANTE package in R (Kembel et al. 2010). We used Pagel's λ to quantify phylogenetic signal, because it has been shown to be robust to branch length uncertainty and many of the calibration issues that affect supertrees (Münkemüller et al. 2012). Pagel’s λ is a branch scaling parameter that ranges from 0 to 1 where a λ values of 0 indicate no phylogenetic signal and a λ values of 1 indicates a phylogenetic signal found under a Brownian motion model of trait evolution (Pagel 1999). We then used the contMap function in the phytools package (Revell 2012) to plot isotope values along our trimmed phylogeny. All phylogenetic analyses were conducted in R (R Core Team 2019)

Statistical Analysis. To test for differences in species mean isotopic values among habitat types we used a one-way ANOVA and Tukey post-hoc comparisons to compare each habitat type in To compare intraspecific variation in isotope values among habitats for the 20 species found in multiple habitats we use used a one-way ANOVA and Tukey post-hoc comparisons to compare values among each habitat type. Both analyses were conducted in JMP version 13 (SAS Institute Inc., Cary, N.C.).

To assess the degree to which closely related species were more similar to each other in isotope values than expected by chance, we tested whether Pagel's λ was > 0 by comparing the log-likelihood of the fitted λ with that of λ = 0 using a log-likelihood ratio test using the 'phylosig' function in the phytools R package (Revell 2012). Variables with a λ greater 0.5 (at P = 0.05) have phylogenetic signal (i.e., closely related species are more similar to each other than expected by random chance) (Münkemüller et al. 2012).

Results

Habitat variation. We found that species mean isotope signatures varied among habitats for both $\delta^{13}C$ and $\delta^{15}N$ ($F_{4,81}$=3.29, P=0.01 and $F_{4,81}$=3.31, P=0.01 respectively; Fig. 1) with the least negative $\delta^{13}C$ in dry meadow and the most negative in wet meadow, and the highest values for $\delta^{15}N$ in wet meadow and the lowest in fellfield. Tukey post-hoc comparisons revealed that only dry meadow and wet meadow significantly differed from each other in δ^{13}C (Fig. 1), and only wet meadow and fellfield differed in δ^{15}N (Fig. 1).

Intraspecific trait variation. We found significant intraspecific trait variation (ITV) in either δ^{13}C or δ^{15}N for 18 out of the 20 species that occurred across multiple habitat types. This ITV varied highly among species and isotopes (Figs. 2 and 3) with 7 species exhibiting ITV in both isotopes, two different sets of 5 species exhibiting ITV in only one isotope, and 3 species exhibiting no ITV in either isotope. Moreover, we found no general patterns in ITV within or among functional groups with some grasses, some forbs, and some N-fixers exhibiting significant ITV and some exhibiting none.

Phylogenetic signal. Tundra wide, we found evidence for a weak phylogenetic signal in δ^{13}C (Pagel's $\lambda = 0.29$, Fig. 3, Table 1) where phylogenetic signal was significantly greater than 0 ($P=0.004$), but not greater than 0.5 which would indicate closely related species are more similar to each other than expected by random chance. For δ^{15}N we found no evidence of a phylogenetic signal (Pagel's $\lambda < 0.01$, Fig. 3, Table 1) and it did not significantly differ from 0 ($P=1$). Within habitats we found evidence for strong trait conservatism in δ^{13}C only in moist meadow and wet meadow (Table 1) and no significant phylogenetic signal in δ^{15}N in any habitat type (Table 1).

Discussion

While many studies have generally assumed strong environmental control on plant foliar stable isotopes (but see Goud and Sparks 2018), we find a much more complex picture where tundra-wide patterns largely mirror the patterns expected under strong environmental control, but individual species and habitat specific phylogenetic patterns suggest evolutionary history also plays an important role in influencing stable isotopes. Together, these results suggest that while species-sorting is occurring generally at the habitat scale (i.e., more water-use-efficient species are generally in more water limited habitats) individual species may have evolved a variety of strategies for coping with the strong environmental gradients in alpine tundra. Importantly, these species specific patterns may be indicative of a species' potential to cope with changing environmental conditions (i.e., Botero et al. 2015) where some species are able to plastically respond to changing environmental conditions and some species are not (Lauteri et al. 2004; Nicotra et al. 2010).

Habitat variation.

We found that when integrating across all species, isotope values generally varied among habitats in a manner mirroring well-established differences among habitats in water and nitrogen availability (e.g., Bowman et al. 2003; Bowman and Fisk 2001; Litaor et al. 2008; Seastedt et al. 2004; Walker et al. 2001). We found the highest average δ^{13}C in dry meadow and the lowest in δ^{13}C wet meadows, which as their names indicate, differ significantly in soil moisture. Although we lack on the ground measurements of soil moisture, we can see predictable changes in δ^{13}C in the tundra, with the driest habitats (dry meadow and fellfield) having the species with the highest WUE, moist meadow having species with intermediate WUE, and the wettest habitats (wet meadow and snowbank) have the species with the lowest WUE. Similarly, we found the highest average δ^{15}N in wet meadow and the lowest average δ^{15}N in the fellfield. Patterns of nitrogen limitation in the alpine largely mirror pattern of water limitation with the lower nitrogen availability in dry meadow and fellfield, and higher nitrogen availability in moist meadow, wet meadow and snowbank habitats (Bowman et al. 2003). Similarly, Yang et al. (2015) found variation in both $\delta^{13}C$ and $\delta^{15}N$ along an elevation gradient in the Swiss Alpine suggesting a key role for environmental control of foliar isotopes in alpine plant species.

Intraspecific trait variation.

In addition to predictable variation among habitats, we found significant intraspecific trait variation (ITV) in either $\delta^{13}C$ or $\delta^{15}N$ for most (18 out of 20) of the species that occurred across multiple habitat types. Twelve of the 20 species exhibited ITV in $\delta^{13}C$ (Fig. 2), suggesting that some species are able to modify their WUE to cope with variation in water availability either through phenotypic plasticity or local adaptation (Albert et al. 2011; Botero et al. 2015; Cleland et al. 2007). Interestingly, 8 species did not respond to the habitat scale gradient in water availability, suggesting that these species may be under stronger evolutionary control (Albert et al. 2011) and may have a bet-hedging strategy for coping with different environmental conditions (Botero et al. 2015). Similarly, 12 of 20 species exhibited ITV in $\delta^{15}N$ (Fig. 3; though not the same 12 species), again suggesting that some species are able modify their phenotype to cope with variation in nitrogen availability and others are not. In total, 7 species exhibited significant ITV in both $\delta^{13}C$ and $\delta^{15}N$ among habitat types. Overall, these results suggest that some alpine plant species are highly variable and are able to adjust their phenotype to a wide range of variability in both water and nitrogen. These species are likely the least threatened by changing environmental conditions in the alpine (Diaz et al. 2003) and likely have the greatest capacity to adapt to changing environments (Botero et al. 2015) if this variation is associated with phenotypic plasticity. Of the 7 species we found to have ITV in both isotopes, 4 out of 7 (*Artemisia scopulorum, Caltha leptosepala, Lloydia serotine, Luzula spicata*) were found to be increasing in abundance over a 21 year period in long term monitoring plots (Spasojevic et al. 2013) while 2 species remained stable (*Bistorta bistortoides*, *Ranunculus adoneus*) and only 1 was declining in abundance (*Geum rossii*).

On the other hand, several of our species are able to adjust their phenotype to a wide range of conditions for one resource (i.e., nitrogen) but are under stronger evolutionary control for another (i.e., water), suggesting their ability to track changing environmental condition will depend on which resource is changing the most rapidly. At our study site, atmospheric nitrogen deposition has reached critical levels (Bowman et al. 2006) and is resulting in changes in some alpine plant communities (Bowman et al. 2018; Simkin et al. 2016). At the same time, Niwot Ridge is experiencing extended summers (prolonged midsummer drought; unpublished data Niwot Ridge LTER) which is reducing soil moisture during the growing season. Interestingly, we find that 4 of the 5 species that exhibit ITV in only $\delta^{13}C$ are increasing in abundance over time in our long-term plots (Spasojevic et al. 2013), while only 2 of 5 species that exhibit ITV in only $\delta^{15}N$ are increasing over time in those same plots. These patterns suggest that species that exhibit ITV in WUE may be less at risk to environmental change than species that exhibit ITV in their nitrogen acquisition strategy. Importantly, these two global changes drivers interact (water availability influences nitrogen availability; Bowman et al. 2003; Bowman et al. 1993) making predictions of species changes much more complex.

Lastly, a few species are under strong evolutionary control for multiple isotopes (2 out of 20 species in our dataset). Similarly, Yang et al. (2015) found that isotope values for several congeners of our study species were insensitive to obvious environmental control and largely under evolutionary control in the Swiss Alps. These species likely have the least ability to cope with rapid environmental change (Botero et al. 2015). Taken together our results suggest a broad range of mechanisms for coping with dynamic environments. It is important to note that while previous studies have noted that phenotypic plasticity occurs in several congeners of our study species, we lack any data on population genetic structure of these species to know if local adaptation or phenotypic plasticity is the mechanism underlying ITV in δ^{13}C or δ^{15}N.

Phylogenetic signal.

Unlike Goud and Sparks (2018) who found a strong phylogenetic signal in δ^{13}C and δ^{15}N, we found a relatively modest (though significant) phylogenetic signal tundra wide and only found a strong signal when we focused in on particular habitat types for δ^{13}C. This difference between our results and the results of Goud and Sparks (2018), may be related to the focus of our studies; Goud and Sparks (2018) focused on a single plant family (the Ericaceae), while we examined 59 species across 20 families including both monocots and dicots. While we lack the resolution do examine phylogenetic signal within families due to using a super tree and having only a few species within a given family, we do see that generally both the Salicaceae (Willows) and Cyperaceae (Sedges) all have species with similar values of δ^{13}C. Interestingly, the Cyperaceae shows the opposite trend with δ^{15}N where we see both the highest and lowest values of δ^{15}N among the species in this family. Nitrogen is a limiting resource in the tundra and evidence suggests that some species coexist by partitioning different forms of nitrogen (Ashton et al. 2008; Miller and Bowman 2003; Miller et al. 2007). While this has not been explored experimentally within the genus Carex for these species, this pattern suggests that these sedges are using potentially using different sources of nitrogen. While some sedge species are spatially segregated (i.e. *Carex rupestris* and *Carex scopulorum* are largely found in different habitats), in our dataset we found 6 species of sedge in dry meadow, and 5 species of sedge in moist meadow, suggesting that nitrogen partitioning may be a way that these closely related species coexist (Silvertown 2004).

While we only found a modest signal of phylogenetic conservatism in δ13C tundra wide we did find a significant phylogenetic signal in δ^{13}C within moist and wet meadow tundra habitats, suggesting that δ13C values were significantly more similar among closely related species than expected by chance. We found no significant signal for the other habitat types. This pattern suggests that plant species in these wetter habitats are converging on similar functional strategies within a given family and that different strategies may have evolved among different families. Lastly, a key source of variation between our results and those of Goud and Sparks (2018) is that they used a more finely resolved phylogeny while we used a super-tree with polytomies at the genus level. Despite the long history of stable isotope studies, few studies have examined phylogenetic signal and our results coupled with the results of Goud and Sparks (2018) suggest that more studies are needed across a greater portion of the plant phylogeny to truly understand the degree of phylogenetic conservatism in plant stable isotopes.

Conclusions.

Our results suggest that isotopes are under both evolutionary and environmental control and that both factors need to be considered when interpreting foliar isotope data in plants. We found significant variation among habitats mirroring predicted resource limitation, but these patterns did not hold for all species and some species did not vary among habitat types. These patterns coupled with some evidence for phylogenetic conservatism in δ^{13}C suggest that some species may have the capacity to adapt to environmental change, while other may not.

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Tables

Table 1. Tundra wide and habitat specific values for Pagel's λ. Bold values indicate that Pagel's λ was significantly greater than 0. Values great than 0.5 indicate closely related species are more similar to each other than expected by random chance.

	Pagel's λ	
Habitat type	$\delta^{13}C$	$\delta^{15}N$
Tundra wide	**0.29**	<0.01
Fellfield	0.43	0.75
Dry Meadow	0.09	<0.01
Moist Meadow	**0.86**	<0.01
Wet Meadow	**1.00**	0.75
Snow Bank	<0.01	0.14

Figure Legends

Figure 1. Variation in A) $\delta^{13}C$ and B) $\delta^{15}N$ among habitat types in alpine tundra. Each data point represents a species level mean. The longer horizontal line represents the mean value for each habitat type and shorter horizontal lines represent the standard error of the mean. Letters represent significant differences among habitat types based on Tukey post-hoc comparisons.

Figure 2. Intraspecific variation in $\delta^{13}C$ among species sampled in multiple habitat types in alpine tundra. Habitats with no data points indicate that species was not present in that habitat type. The longer horizontal line represents the mean value for each habitat type and shorter horizontal lines represent one standard deviation. Letters represent significant differences among habitat types based on Tukey post-hoc comparisons. A) *Artemisia scopulorum* (Artsco, $F_{4,47}=5.26$, $P<0.01$); B) *Bistorta bistortoides* (Bisbis, $F_{3,41}=5.29$, $P<0.01$); C) *Caltha leptosepala* (Callep, $F_{2,27}=10.13$, $P<0.01$); D) *Carex rupestris* (Carrup, $F_{2,26}=2.57$, $P=0.09$); E) Carex scopulorum (Carsco, $F_{2,32}=7.10$, $P<0.01$); F) *Deschampsia caespitosa* (Desces, $F_{3,43}=2.37$, $P=0.08$); G) *Erigeron simplex* (Erisim, $F_{2,23}=0.75$, $P=0.48$); H) *Festuca brachyphylla* (Fesbra, $F_{1,26}=14.71$, $P<0.01$); I) Geum rossii (Geuros, $F_{4,49}=6.39$, $P<0.01$); J) *Kobresia myosuroides* (Kobmyo, $F_{1,13}=3.66$, $P=0.07$); K) *Lloydia serotina* (Lloser, $F_{2,22}=10.75$, $P<0.01$); L) *Luzula spicata* (Luzspi, $F_{1,10}=5.38$, $P=0.04$); M) *Mertensia lanceolate* (Merlan, $F_{2,23}=1.94$, $P=0.17$); N) *Minuartia obtusiloba* (Minobt, $F_{3,36}=10.19$, $P<0.01$); O) *Oreoxis alpina* (Orealp, $F_{1,18}=1.35$, $P=0.26$); P) *Ranunculus adoneus* (Ranado, $F_{1,18}=7.76$, $P=0.01$); Q) *Silene acaulis* (Silaca, $F_{1,18}=12.39$, $P<0.01$); R) *Tetraneuris acaulis* (Tetaca, $F_{1,18}=0.26$, $P=0.63$); S) *Trifolium dasyphyllum* (Tridas, $F_{1,17}=5.72$, $P=0.03$); U) *Trifolium parryi* (Tripar, $F_{2,29}=1.14$, $P=0.33$).

Figure 3. Intraspecific variation in δ^{15}N among species sampled in multiple habitat types in alpine tundra. Habitats with no data points indicate that species was not present in that habitat type. The longer horizontal line represents the mean value for each habitat type and shorter horizontal lines represent one standard deviation. Letters represent significant differences among habitat types based on Tukey post-hoc comparisons. A) *Artemisia scopulorum* (Artsco, $F_{4,47}$=4.19, P<0.01); B) *Bistorta bistortoides* (Bisbis, $F_{3,41}$=4.01, P=0.01); C) *Caltha leptosepala* (Callep, $F_{2,27}$=1.86, P<0.01); D) *Carex rupestris* (Carrup, $F_{2,26}$=1.48, P=0.25); E) *Carex scopulorum* (Carsco, $F_{2,32}$=1.09, P=0.35); F) *Deschampsia caespitosa* (Desces, $F_{3,43}$=4.78, P<0.01); G) *Erigeron simplex* (Erisim, $F_{2,23}$=7.19, P<0.01); H) *Festuca brachyphylla* (Fesbra, $F_{1,26}$=1.34, P=0.26); I) *Geum rossii* (Geuros, $F_{4,49}$=7.59, P<0.01); J) *Kobresia myosuroides* (Kobmyo, $F_{1,13}$=16.18, P<0.01); K) *Lloydia serotina* (Lloser, $F_{2,22}$=10.28, P<0.01); L) *Luzula spicata* (Luzspi, $F_{1,10}$=14.15, P<0.01); M) *Mertensia lanceolate* (Merlan, $F_{2,23}$=15.44, P<0.01); N) *Minuartia obtusiloba* (Minobt, $F_{3,36}$=1.09, P=0.36); O) *Oreoxis alpina* (Orealp, $F_{1,18}$=1.00, P=0.33); P) *Ranunculus adoneus* (Ranado, $F_{1,18}$=28.88, P<0.01); Q) *Silene acaulis* (Silaca, $F_{1,18}$=0.00, P=0.97); R) *Tetraneuris acaulis* (Tetaca, $F_{1,18}$=13.92, P<0.01); S) *Trifolium dasyphyllum* (Tridas, $F_{1,17}$=1.42, P=0.25); U) *Trifolium parryi* (Tripar, $F_{2,29}$=0.08, P=0.92).

Figure 4. Tundra wide variation in A) δ^{13}C and B) δ^{15}N among plant species in alpine tundra. We found a weak phylogenetic signal in δ^{13}C (Pagel's $\lambda = 0.29$) where phylogenetic signal was significantly greater than 0 (P=0.004), but not greater than 0.5 which indicates closely related species are more similar to each other than expected by random chance.

Figures

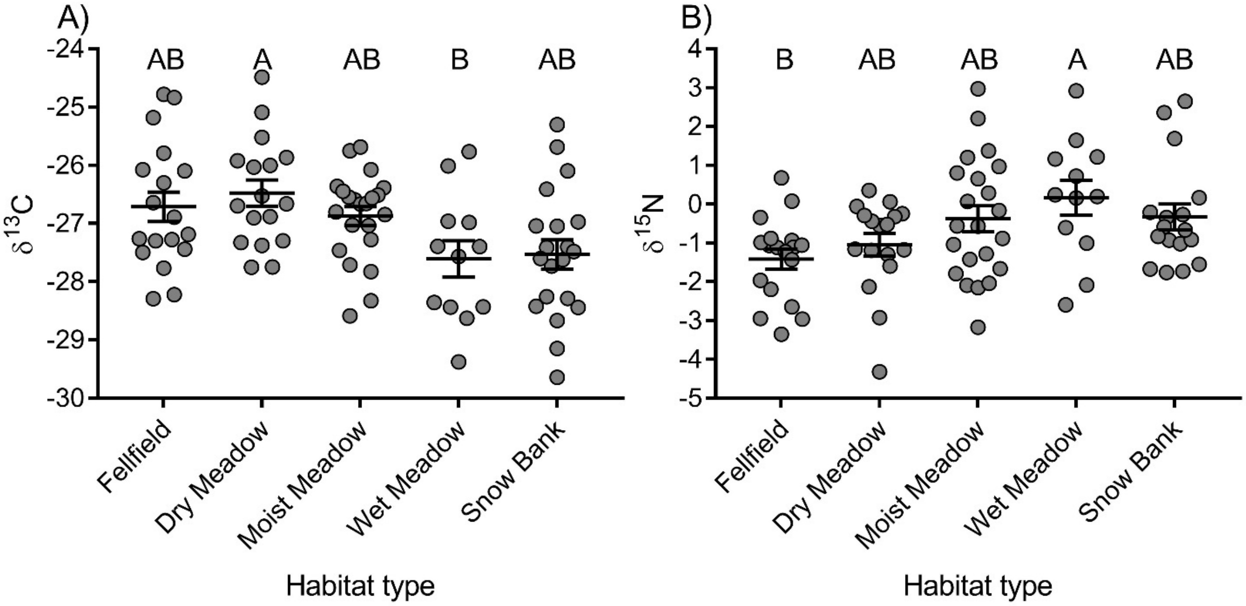

Figure 1.

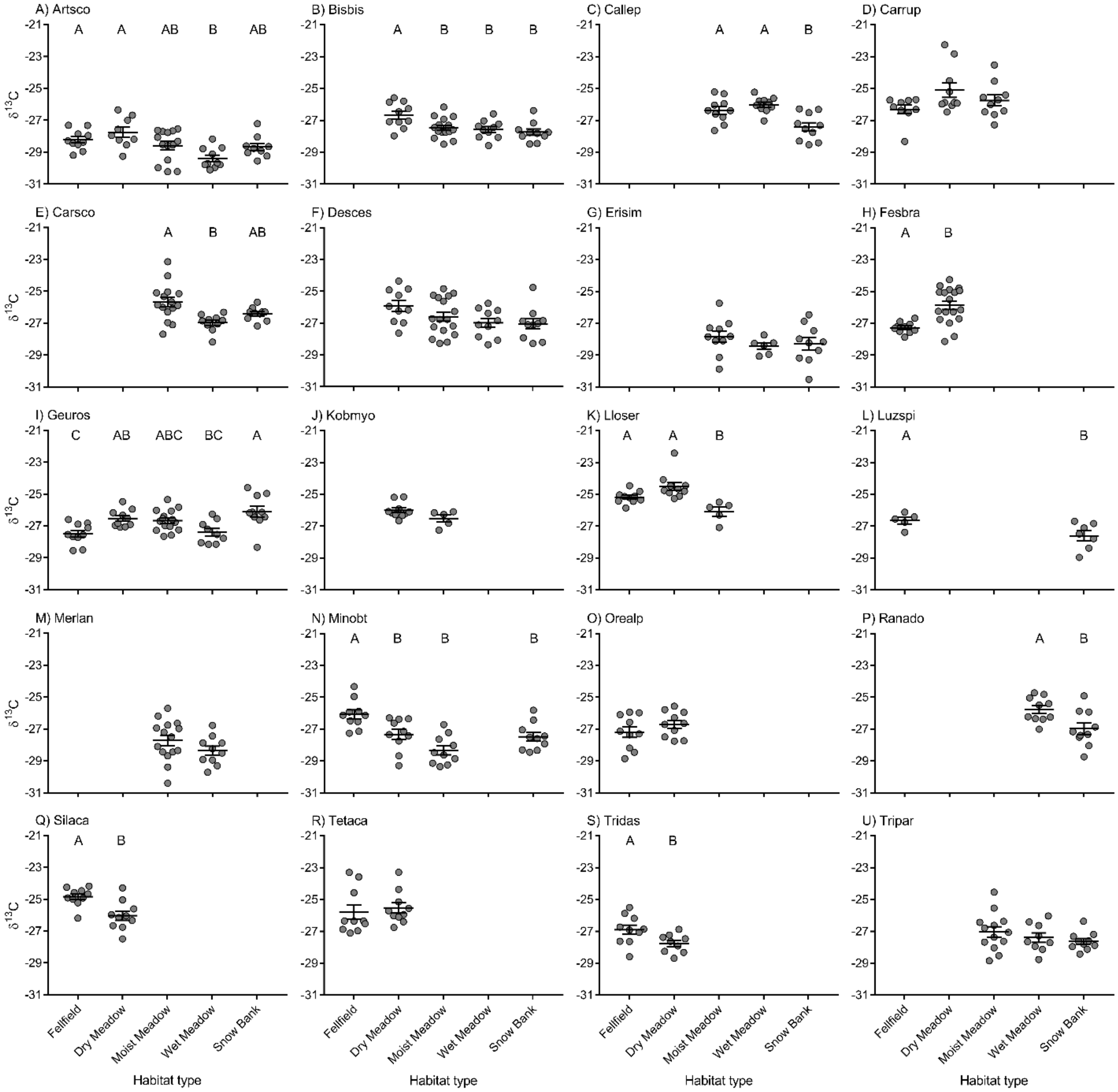
A) Artsco
A A AB B AB
B) Bisbis
A B B B
C) Callep
A A B
D) Carrup
E) Carsco
A B AB
F) Desces
G) Erisim
H) Fesbra
A B
I) Geuros
C AB ABC BC A
J) Kobmyo
K) Lloser
A A B
L) Luzspi
A B
M) Merlan
N) Minobt
A B B B
O) Orealp
P) Ranado
A B
Q) Silaca
A B
R) Tetaca
S) Tridas
A B
U) Tripar
$\delta^{13}C$
-21
-23
-25
-27
-29
-31
Fellfield
Dry Meadow
Moist Meadow
Wet Meadow
Snow Bank
Habitat type

Figure 2.

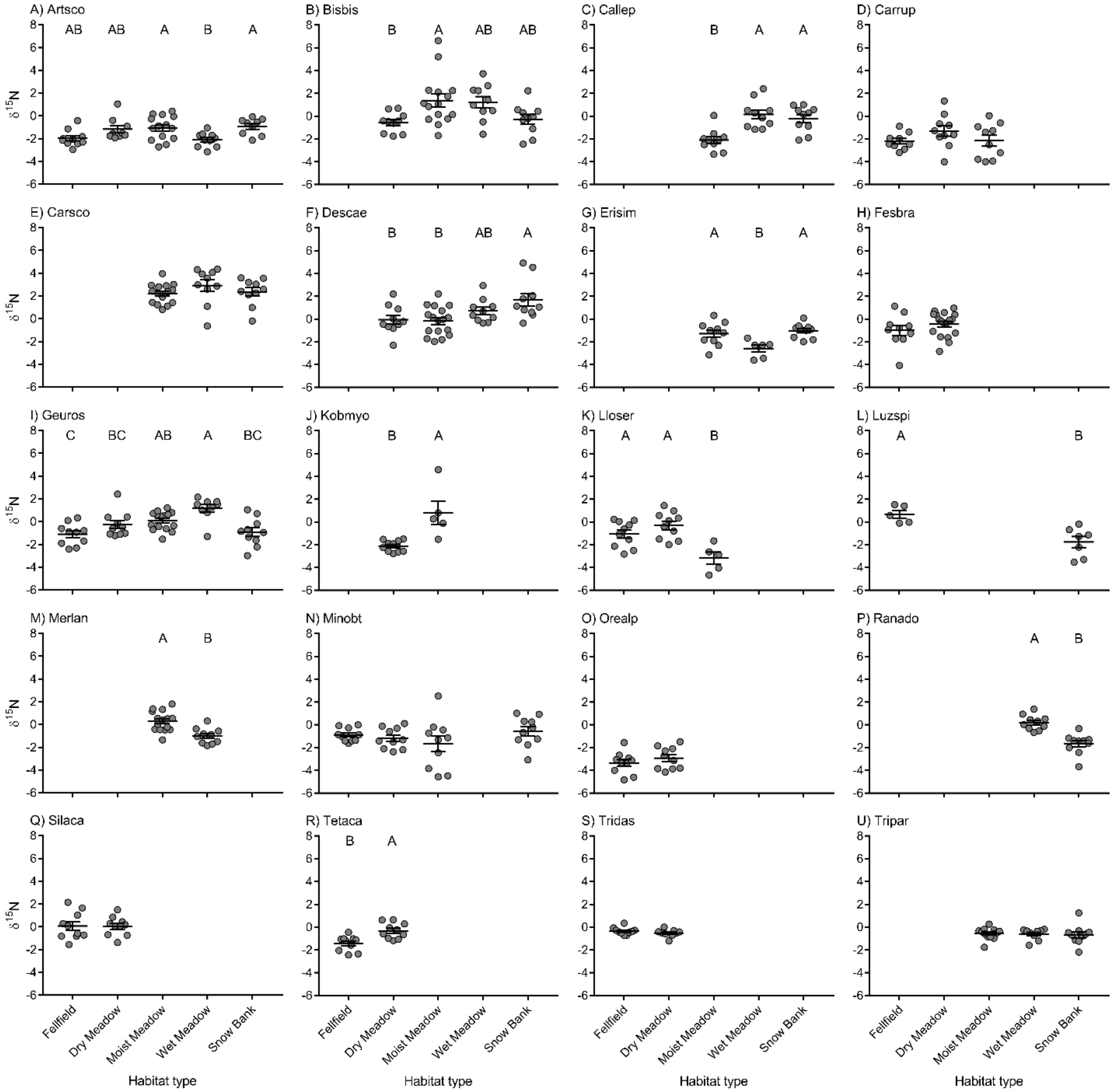
A) Artsco
AB AB A B A
B) Bisbis
B A AB AB
C) Callep
B A A
D) Carrup
E) Carsco
F) Descae
B B AB A
G) Erisim
A B A
H) Fesbra
I) Geuros
C BC AB A BC
J) Kobmyo
B A
K) Lloser
A A B
L) Luzspi
A B
M) Merlan
A B
N) Minobt
O) Orealp
P) Ranado
A B
Q) Silaca
R) Tetaca
B A
S) Tridas
U) Tripar
δ15N
8
6
4
2
0
-2
-4
-6
Fellfield
Dry Meadow
Moist Meadow
Wet Meadow
Snow Bank
Habitat type

Figure 3.

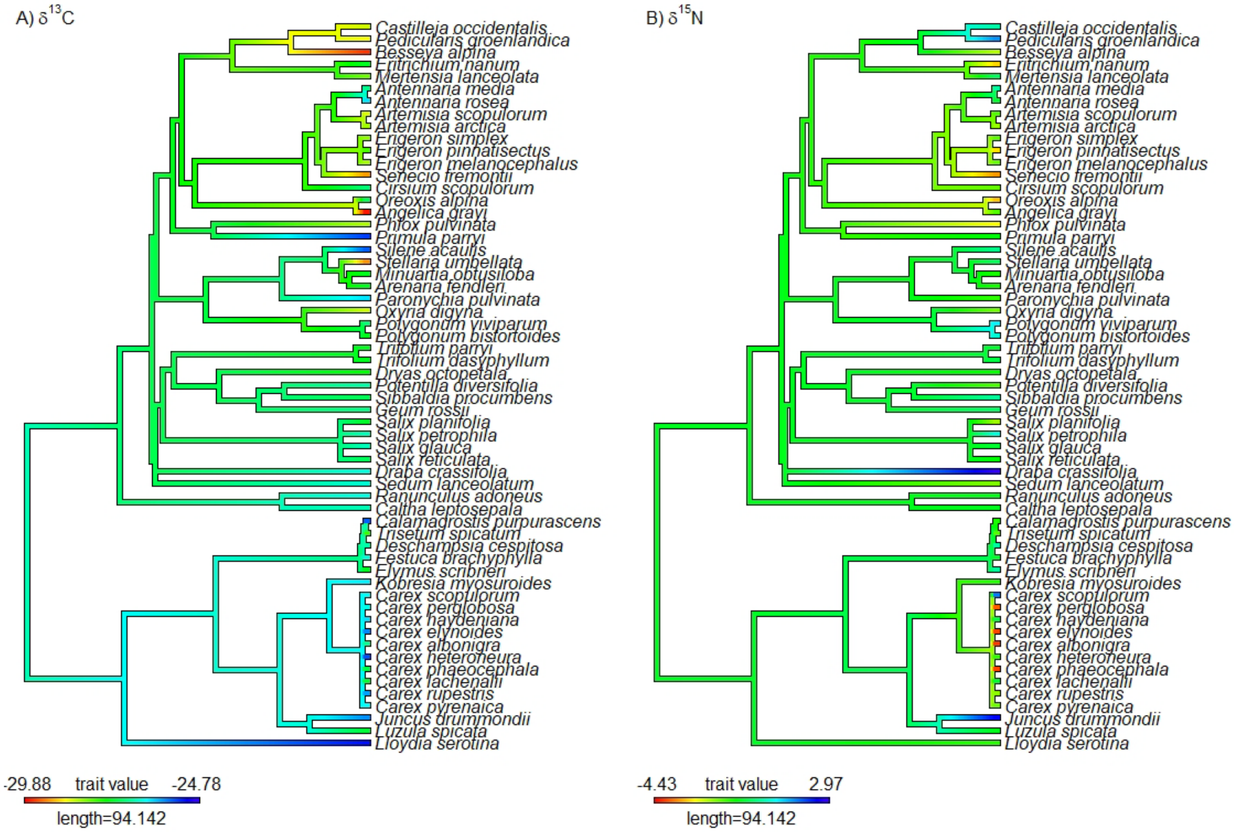
A) $\delta^{13}C$
Castilleja occidentalis
Pedicularis groenlandica
Besseya alpina
Eritrichium nanum
Mertensia lanceolata
Antennaria media
Antennaria rosea
Artemisia scopulorum
Artemisia arctica
Erigeron simplex
Erigeron pinnatisectus
Erigeron melanocephalus
Senecio fremontii
Cirsium scopulorum
Oreoxis alpina
Angelica grayi
Phlox pulvinata
Primula parryi
Silene acaulis
Stellaria umbellata
Minuartia obtusiloba
Arenaria fendleri
Paronychia pulvinata
Oxyria digyna
Polygonum viviparum
Polygonum bistortoides
Trifolium parryi
Trifolium dasyphyllum
Dryas octopetala
Potentilla diversifolia
Sibbaldia procumbens
Geum rossii
Salix planifolia
Salix petrophila
Salix glauca
Salix reticulata
Draba crassifolia
Sedum lanceolatum
Ranunculus adoneus
Caltha leptosepala
Calamagrostis purpurascens
Trisetum spicatum
Deschampsia cespitosa
Festuca brachyphylla
Elymus scribneri
Kobresia myosuroides
Carex scopulorum
Carex perglobosa
Carex haydeniana
Carex elynoides
Carex albonigra
Carex heteroneura
Carex phaeocephala
Carex lachenalii
Carex rupestris
Carex pyrenaica
Juncus drummondii
Luzula spicata
Lloydia serotina
-29.88
trait value
-24.78
length=94.142
B) $\delta^{15}N$
Castilleja occidentalis
Pedicularis groenlandica
Besseya alpina
Eritrichium nanum
Mertensia lanceolata
Antennaria media
Antennaria rosea
Artemisia scopulorum
Artemisia arctica
Erigeron simplex
Erigeron pinnatisectus
Erigeron melanocephalus
Senecio fremontii
Cirsium scopulorum
Oreoxis alpina
Angelica grayi
Phlox pulvinata
Primula parryi
Silene acaulis
Stellaria umbellata
Minuartia obtusiloba
Arenaria fendleri
Paronychia pulvinata
Oxyria digyna
Polygonum viviparum
Polygonum bistortoides
Trifolium parryi
Trifolium dasyphyllum
Dryas octopetala
Potentilla diversifolia
Sibbaldia procumbens
Geum rossii
Salix planifolia
Salix petrophila
Salix glauca
Salix reticulata
Draba crassifolia
Sedum lanceolatum
Ranunculus adoneus
Caltha leptosepala
Calamagrostis purpurascens
Trisetum spicatum
Deschampsia cespitosa
Festuca brachyphylla
Elymus scribneri
Kobresia myosuroides
Carex scopulorum
Carex perglobosa
Carex haydeniana
Carex elynoides
Carex albonigra
Carex heteroneura
Carex phaeocephala
Carex lachenalii
Carex rupestris
Carex pyrenaica
Juncus drummondii
Luzula spicata
Lloydia serotina
-4.43
trait value
2.97
length=94.142

Figure 4.

Supplementary Material

Supplementary Table 1. Mean isotope values for each of 62 species

Species	Family	Functional group	Mean ^{15}N	Mean ^{13}C
Angelica grayi	Apiaceae	Forb	-1.42705	-29.8801
Oreoxis alpina	Apiaceae	Forb	-3.13854	-26.9411
Antennaria media	Asteraceae	Forb	0.347703	-26.9023
Antennaria rosea	Asteraceae	Forb	-0.73262	-25.9745
Artemisia arctica	Asteraceae	Forb	-2.03287	-28.1945
Artemisia scopulorum	Asteraceae	Forb	-1.4221	-28.5373
Cirsium scopulorum	Asteraceae	Forb	-1.59712	-26.8806
Erigeron melanocephalus	Asteraceae	Forb	-1.55108	-28.2583
Erigeron pinnatisectus	Asteraceae	Forb	-2.95142	-27.7673
Erigeron simplex	Asteraceae	Forb	-1.48394	-28.1437
Senecio fremontii	Asteraceae	Forb	-3.38198	-29.1469
Tetraneuris acaulis	Asteraceae	Forb	-0.87676	-25.6595
Hymenoxys grandiflora	Asteraceae	Forb	-1.19299	-27.3755
Eritrichium nanum	Boraginaceae	Forb	-2.96747	-27.2604
Mertensia lanceolata	Boraginaceae	Forb	-0.23383	-27.9698
Draba crassifolia	Brassicaceae	Forb	2.965355	-26.3877
Arenaria fendleri	Caryophyllaceae	Forb	-1.06706	-27.2981
Minuartia obtusiloba	Caryophyllaceae	Forb	-1.07875	-27.3032
Silene acaulis	Caryophyllaceae	Forb	0.065092	-25.4342
Stellaria umbellata	Caryophyllaceae	Forb	-0.28723	-29.225
Sedum lanceolatum	Crassulaceae	Forb	-1.79133	-26.4461
Gentiana algida	Gentianaceae	Forb	1.199709	-26.8042
Lloydia serotina	Liliaceae	Forb	-1.17772	-25.0833
Castilleja occidentalis	Orobranchaceae	Forb	0.235086	-28.4376
Pedicularis groenlandica	Orobranchaceae	Forb	1.639541	-28.6262
Phlox pulvinata	Polemoniaceae	Forb	-2.65099	-28.2927
Oxyria digyna	Polygonaceae	Forb	-1.70019	-28.4405
Paronychia pulvinata	Polygonaceae	Forb	-1.22812	-26.0999
Bistorta bistortoides	Polygonaceae	Forb	0.54241	-27.369
Bistorta viviparum	Polygonaceae	Forb	0.966662	-26.8467
Primula parryi	Primulaceae	Forb	-0.83107	-25.3016
Caltha leptosepala	Ranunculaceae	Forb	-0.71647	-26.5955
Ranunculus adoneus	Ranunculaceae	Forb	-0.73883	-26.3695
Dryas octopetala	Rosaceae	Forb	-0.93536	-27.4404
Geum rossii	Rosaceae	Forb	-0.20873	-26.8118
Potentilla diversifolia	Rosaceae	Forb	-1.42432	-26.6574
Sibbaldia procumbens	Rosaceae	Forb	0.165595	-27.0414
Besseya alpina	Scrophulariaceae	Forb	-2.18539	-29.6413
Carex albonigra	Cyperaceae	Graminoid	-4.43429	-26.8349
Carex elynoides	Cyperaceae	Graminoid	-4.30962	-25.5602

Carex haydeniana	Cyperaceae	Graminoid	-0.19473	-26.0505
Carex heteroneura	Cyperaceae	Graminoid	-1.09424	-25.2246
Carex lachenalii	Cyperaceae	Graminoid	-0.34446	-27.4033
Carex perglobosa	Cyperaceae	Graminoid	-4.13385	-26.333
Carex phaeocephala	Cyperaceae	Graminoid	-4.32405	-27.297
Carex pyrenaica	Cyperaceae	Graminoid	-1.59725	-26.2382
Carex rupestris	Cyperaceae	Graminoid	-1.87347	-25.6958
Carex scopulorum	Cyperaceae	Graminoid	2.450562	-26.258
Kobresia myosuroides	Cyperaceae	Graminoid	-1.15172	-26.1738
Juncus drummondii	Juncaceae	Graminoid	2.648734	-25.6878
Luzula spicata	Juncaceae	Graminoid	-0.74869	-27.2016
Calamagrostis purpurascens	Poaceae	Graminoid	-1.11659	-24.7803
Deschampsia cespitosa	Poaceae	Graminoid	0.437937	-26.6307
Elymus scribneri	Poaceae	Graminoid	0.248101	-27.3611
Festuca brachyphylla	Poaceae	Graminoid	-0.6425	-26.3692
Trisetum spicatum	Poaceae	Graminoid	-1.73252	-28.4203
Trifolium dasyphyllum	Fabaceae	N fixing Forb	-0.43103	-27.2997
Trifolium parryi	Fabaceae	N Fixing Forb	-0.61177	-27.3166
Salix glauca	Salicaceae	Shrub	-0.56828	-26.5468
Salix petrophila	Salicaceae	Shrub	0.650729	-26.5646
Salix planifolia	Salicaceae	Shrub	-2.04392	-27.2793
Salix reticulata	Salicaceae	Shrub	-0.88636	-27.0354