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Timberline meadows along a 1000-km transect in NW North America: species diversity and community patterns

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Keywords
Heath; Meadow; OptimClass; Parkland; Subalpine Vegetation; Vegetation Classification

Abbreviations
AIC = Akaike information criterion; FET = Fisher's exact test; NMDS = non-metric multidimensional scaling; UPGMA = unweighted pair group method with arithmetic mean

Nomenclature
Flora of North America Editorial Committee (1993–2007) for vascular plant species except *Pulsatilla*, which is kept separate from *Anemone*; Douglas et al. (1989, 1990, 1991, 1994) for families not covered by the Flora of North America (Apiaceae, Boraginaceae, Campanulaceae, Fabaceae, Hippuridaceae, Parnassiaceae, Poaceae, Onagraceae, Rosaceae, Scrophulariaceae, Valerianaceae and Violaceae). *Polemonium caeruleum* subsp. *amygdalinum* was treated as *P. occidentale*, *Sanguisorba stipulata* is circumscribed to include *S. sitchensis* and *Viola bellidifolia* and *V. adunca* are treated as distinct species.; Esslinger (2010) for lichens; Anderson et al. (1990) for mosses; Anderson (1990) for *Sphagnum*; Stotler & Crandall-Stotler (1977) for liverworts

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Abstract

Question: The mountains of NW North America are home to natural meadows that cover large areas at the timberline. The vegetation of these meadows has been the topic of few local studies, and little is known of species composition turnover across mountain ranges and along the latitudinal gradient. We sampled and analyzed community composition along a 1000-km gradient to answer the following questions: (1) what are the main community types in timberline meadows; (2) what are the most important abiotic gradients underlying their composition; and (3) how is species diversity related to environmental factors and how does it change along the latitudinal gradient?

Location: SE and central British Columbia (Canada), NW Montana (USA).

Methods: We recorded data on cover and presence/absence of vascular plant, bryophyte and lichen species, as well as structure and environmental properties in 4 m × 4 m plots (n = 112). Using the OptimClass approach, we classified plots into distinct community types. We used NMDS and multiple regressions to analyse the relationship between composition, species richness and environmental and geographic gradients.

Results: Despite drawing from a large geographic area, our classification revealed only four meadow communities. Mesic meadows were the most frequent and had a pronounced species turnover along latitude, resulting in two distinct community types. In addition, a three-dimensional ordination showed that vegetation structural properties, macroclimate and geographic predictors were important underlying gradients for species composition. Vascular species richness increased with soil pH, and exhibited a quadratic relationship with litter cover and latitude. Furthermore, in the latter case, it increased towards the southern and northern ends of our gradient.

Conclusions: Detection of only four meadow communities along the 1000-km sampling gradient suggests a relatively recently established flora and a lack of regional differentiation consistent with the low level of endemism in the region. Higher vascular species diversity at the northern and southern edges of our gradient may reflect the geographic proximity to areas unglaciated during the Pleistocene, and suggests that areas farthest from the unglaciated edge may be experiencing colonization debt.

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Introduction

Meadows are a characteristic vegetation type of timberlines in many high-mountain systems of the Northern Hemisphere (Löve 1970; Tuhkanen 1993; Holtmeier 2009). Some timberline meadows were created or expanded by centuries of logging, traditional grazing and mowing, such as in the Alps and the Caucasus (Löve 1970; Tuhkanen 1993; Box et al. 2000). Others appear to be natural, i.e. to have evolved without any human interference, such as in the mountains of Central Asia (Korovin 1962) and western North America (Peet 2000).

The NW North American Cordillera harbours extensive natural timberline meadow vegetation (Franklin & Dyrness 1973, as 'subalpine meadows'; Hämet-Ahti 1978). The meadows are typically dominated by herb-rich communities and are thus distinct from grasslands; in many regions they occur interdigitated with *Cassiope* or *Phyllodoce* heaths. In their composition they further differ from forests in montane zones and alpine tundra communities at higher elevations. Before the arrival of the first European settlers, subalpine habitats in NW North America were used by native people only for hunting and gathering (Burtchard 2003). Unlike meadow and wetland landscapes at lower elevations, haying or cattle grazing have almost never been practised, even after the arrival of European settlers (Shaw 1916; Hämet-Ahti 1978). Although they have never been explicitly mapped, they cover thousands of hectares per mountain range, and range from the southern oceanic regions of Alaska (ca. 61° N) south to around 46–48° N, well into the American Pacific Northwest. Subalpine meadows occur primarily in oceanic to sub-oceanic orographic systems rich in precipitation and with some of the deepest average winter snow covers in the world (Kotlyakov et al. 1997). They tend to form a parkland mosaic, with scattered forest islands of *Abies lasiocarpa*, *Picea engelmannii* and *Tsuga mertensiana*. In the forest classification system of British Columbia, they have been traditionally lumped together with a variety of unrelated plant community types as 'parkland subzones' of major forest biogeoclimatic zones (e.g. Coupé et al. 1991), despite differences in floristic composition.

Timberline meadows are an important habitat for several wildlife species at risk, including as summer range for the endangered mountain caribou (*Rangifer tarandus caribou*; Seip 1990) and as foraging habitat for the Vancouver Island marmot (*Marmota vancouverensis*; Milko 1984; Milko & Bell 1986). Given their colourful plant species composition, they have long been a popular recreational destination and a frequent motif on postcards. However, anthropogenic pressure from off-road vehicle use, snowmobiling and helicopter skiing has grown in recent years, with impacts on vegetation still largely unknown (Price 1985; Rochefort et al. 2006). In addition, empirical observations over the past decades indicate a decline of subalpine meadow habitat to forest and krummholz encroachment, probably due to warming temperatures and lengthening growing seasons (e.g. Landals & Scotter 1974; Rochefort et al. 1994; Klasner & Fagre 2002).

Of the timberline meadows in NW North America, those in the Cascade and Olympic Mountains are among the best studied, having been the subject of several well-known vegetation surveys (Kuramoto & Bliss 1970; Douglas 1972; Henderson 1974). The large, high-elevation meadow formations of the interior mountain ranges, by contrast, have received scant attention, with detailed descriptions provided only in the unpublished work of Landals & Scotter (1974) in Mount Revelstoke National Park, Karen Eady's thesis on alpine and timberline vegetation of Big White Mountain in British Columbia's Okanagan Highland (Eady 1971) and, at the eastern fringe of the formation, Christian Damm's (2001) thesis on high-altitude plant communities of Glacier National Park, Montana. Hämet-Ahti's (1978) work from Wells Gray Provincial Park was the first in-depth study on timberline meadow vegetation in the interior NW North American Cordillera to be published and remains one of the most comprehensive to date. All these studies, however, were focused on local mountain ranges and leave open the question to what extent timberline meadow vegetation varies regionally within NW North America.

The purpose of the present study was to survey timber line meadow vegetation over multiple inland mountain ranges to assess species composition shifts and the overall diversity of vegetation types over a much larger gradient than has previously been captured in vegetation studies. Specifically, we set out to answer the following questions:

1. What are the main community types in inland timberline meadows?
2. What are the most important abiotic gradients underlying their composition?
3. How is species diversity related to environmental factors and how does it change along the latitudinal gradient?

Methods

Study area

We sampled a total of 112 relevés in timberline meadows from NW Montana (48° N, 114° W; 2060–2220 m a.s.l.) to central British Columbia (54° N, 126° W; 1460–1640 m a.s.l.; Fig. 1), a direct distance of about 1065 km. Southern and central study sites were located in (1) the Whitefish Range (Rocky Mountains, Montana, n = 8 plots), (2) Purcell and Selkirk Mountains (hereafter referred to as the Selkirk complex, n = 57) and (3) Trophy Mountains (all part of the greater Columbia Mountain system, SE and east-central British Columbia, n = 28; Fig. 2). Our north-

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ernmost sampled localities were in (4) the Babine Range (Skeena Mountains, British Columbia, $n = 17$). In each study site we also sampled heath vegetation in order to compare these two common subalpine vegetation types; the only mountain range in which we were unable to sample heaths was the Whitefish Range in Montana, where equivalent communities occurred only in fragmentary microhabitats.

Timberline meadows in inland NW North America are characterized by a cool, sub-oceanic, mountain climate, with some of the largest snow loads of any mountain region in the world. Mean annual temperature is -0.4 ± 0.7 °C SD. Mean annual precipitation varies among study sites, with highest values in the Selkirk Mountains (2180 mm) and lowest in the Babine Range (680 mm; plot-based extrapolated climate data following Wang et al. 2006). Winters are cold and precipitation-rich (mean monthly temperature: −9.9 °C, mean monthly precipitation: 163 mm) whereas summers are cool and dry (9.6 °C, 100 mm). Snowpack usually reaches 2–4 m at the end of winter and snow remains on the ground from late October until June or even the end of July (Evans & Fonda 1990).

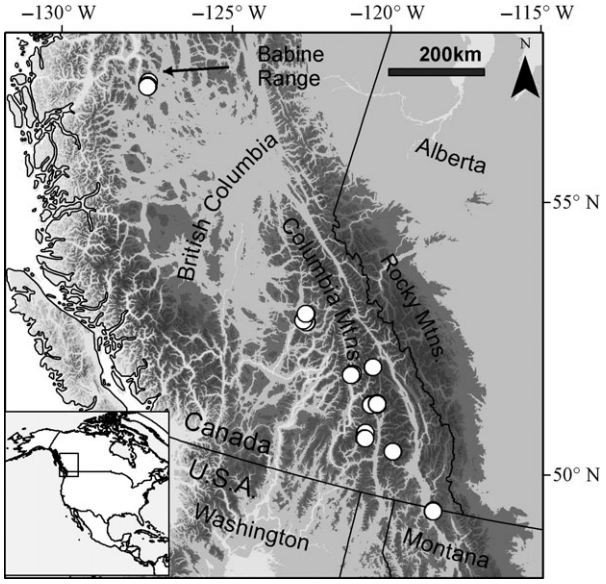

Fig. 1. Map of the study area. White circles indicate study localities ($n = 110$).

The studied vegetation covers gentle plateaus, shoulders and only rarely steep slopes; it is not associated with avalanche tracks. Geological parent material is comprised of various non-calcareous rock types (including metamorphic, sedimentary and igneous rock) and, more rarely, dolomite. These rock types are often overlaid with pockets of glacial till. In the Whitefish Range, the parent material consists of closely interstratified argillites and dolomite, while in the Purcell and Selkirk Mountains granite dominates with a few plots from schistose and quartzitic rock (Cairnes 1932; Holland 1964; Fulton 1983). The Trophy Mountains are overwhelmingly basaltic, while in the Skeena Mountains (Babine Range), bedrock is mostly composed of diorite or volcanic conglomerates (Rice 1948; Holland 1964; Gaba 1992).

During the last glacial maximum (Late Wisconsinian, ca. 17 000 BP), British Columbia and NW Montana were covered by the Cordilleran ice sheet, with the exception of a few nunataks (Clague & Ward 2011). This ice sheet reached SW Yukon and coastal Alaska from the south, while large parts of the Yukon and interior Alaska (Berin-

Fig. 2. Timberline meadow vegetation in British Columbia, Canada. (**a**) 88th Ridge, Trophy Mountains. Photo taken 6 Aug 2006, at ca. 51.76° N, 119.83° W. (**b**) *Erigeron peregrinus* community in the upper Dennis Creek basin, Selkirk Mountains, showing *Lupinus arcticus* subsp. *subalpinus*, *Castilleja miniata*, *Pulsatilla occidentalis*, *Senecio integerrimus* and *Erigeron peregrinus* (bottom right). Photo taken 18 Jul 2006, at ca. 50.08° N, 117.31° W.

gia) remained ice-free (Hultén 1937). In the south, the ice sheet extended to northern Montana, Washington and Idaho. By 10 000 BP, the ice sheet had retreated to approximately its present extent (Fulton et al. 2004). Subalpine soils are therefore relatively young and their development is slowed by a short growing season (Kuramoto & Bliss 1970). In the framework of the Canadian system of soil classification (Agriculture Canada Expert Committee on Soil Survey 1987), subalpine meadows occur on well-drained soils of the sombric brunisol group, in the brunisol order. These soils are characterized by a well developed A horizon (>10 cm), the presence of a B horizon, and soil pH < 5. Heaths tend to occur on soils of the podzol order (Knapik & Coen 1974; Hämet-Ahti 1978; Achuff et al. 1984).

Data collection

We collected data from Jul to late Aug 2006 using 4 m × 4 m relevés. Plots in each region were at least 50 m apart, and were chosen based on a combination of targeted habitat sampling and accessibility. All plots were georeferenced using a Garmin Etrex Summit GPS unit, usually to an accuracy of ±10 m. We recorded all vascular plant species and their cover, as well as presence/absence of terricolous bryophyte and lichen species. Cover assignment for bryophytes and lichens was impossible as accurate identification was done after fieldwork was completed, and thus cryptogams were tracked only according to presence/absence. In addition, we assessed structural features (cover of trees, shrubs and herbs, maximum height of herbs, total cover of bryophytes and lichens), as well as environmental properties [folded aspect (linearized to folded aspect = 180°–|aspect°–180°|), slope, cover of rocks, soil and litter, litter depth, soil pH]. Soil was collected and air-dried for later lab analysis. Soil pH was measured in Göttingen in a 1:2 solution of soil: 0.01 M $CaCl_2$ following the methods outlined in Sheldrick (1984). Extrapolated macroclimate data for all relevés were generated using the Worldclim database (2.5′ resolution; Hijmans et al. 2005). Full plot data are archived in the online database GIVD and available for further analysis with permission from the authors.

Species identification followed standard reference literature, except for several critical taxa. For *Castilleja*, hybrid swarms of *C. occidentalis* and *C. miniata* could often not be identified to species and were referred to as *Castilleja* sp. 1. Many bryophytes could not be reliably identified to species level based on sterile material but could usually be placed with confidence in one of a set of operational taxonomic units. Species that could not be consistently named according to present taxonomy, even after checking with bryological experts, were thus numbered, notably in the genera *Bryum*, *Pohlia*, *Lophozia* and *Dicranum*. Distinguishing characteristics of these morphological entities can be obtained from the authors upon request. Most phanerogam and all cryptogam species documented in this study were collected for later identification; voucher specimens including numbered morphotypes are retained in the herbarium UBC with duplicates of some lichens in BG (*Lepraria* spp.) and GZU (*Rinodina* spp.). The lichen species *Micarea subalpina* Coppins & T. Sprib., previously known only from MT, USA (Coppins & Spribille 2004) is reported here for the first time for Canada (representative voucher: British Columbia: Selkirk Mtns., Silvercup Ridge, N 50.59727°/W 117.34953°, plot 160706/2, 16 Jul 2006, V. Wagner L-0136, GZU).

Data analysis

We classified our data based on the combined occurrence of vascular plant, bryophyte and lichen species. Vascular plant abundance was transformed to presence/absence values in concordance with bryophyte and lichen species data. We deleted two outlier plots based on vascular species occurrence, thus retaining data of 110 plots for further analysis.

Several numerical methods are available for vegetation classification. For our data set, we compared the outcome of nine widely used classification methods with the OptimClass approach (Tichý et al. 2010): (1) Flexible beta algorithm ($\beta = -0.25$), (2) Nearest neighbour method, (3) Furthest neighbour method, (4) Median method, (5) Centroid method, (6) modified TWINSPAN algorithm, (7) UPGMA, (8) Ward's method and (9) McQuitty's method. All methods were run for cluster numbers 2–20 and performed using the Sørensen dissimilarity index, except for Ward's method, which was run with Euclidean distance. The OptimClass approach evaluates partitions by inspecting the fidelity of each species to a cluster. As a fidelity measure, OptimClass uses Fisher's exact test (FET; Chytrý et al. 2002). We used mean FET fidelities for each cluster number, calculated as:

$$\text{Mean FET fidelity} = \frac{\sum[-\log_{10}(\text{FET probability})]}{\text{total no. of clusters} * \text{total no. of species}}.$$

The classification method and cluster number that achieved the highest mean FET fidelity was chosen for final analysis of the data set. All analyses were performed in Juice, using PC-ORD (MjM Software Design, Gleneden Beach, OR, US) as external software for hierarchical clustering. Communities were named after one characteristic vascular plant species easily recognizable in the field. Char-

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acteristic species were defined as those with frequency values $\geq 35\%$ per community, whereas diagnostic species were characteristic only in one community.

For further analyses, bryophyte richness, lichen richness, maximum height of herbs and slope were log-transformed; litter depth was $\log_{10}$-transformed; bryophyte cover and lichen cover were logit-transformed. Cover of trees, shrubs, soil and rock had highly zero-inflated distributions and was omitted from the analysis.

To explore how gradients in species composition related to structural and environmental properties, we performed non-metric multidimensional scaling (NMDS; Kruskal 1964a,b; Mather 1976) in the vegan package in R (R Development Core Team 2011, vers. 2.14.0). We chose the Sørensen dissimilarity index, six starting axes and 100 random starting configurations. The correlation between environmental variables and the ordination was tested using a Monte Carlo test with 999 permutations. The final ordination configuration was rotated based on principal components so that the variance of points was maximized in the first dimension.

We analysed how environmental variables (soil pH, litter cover, aspect, slope) and latitude shaped total species richness (sum of vascular plant, bryophyte and lichen species per plot) and vascular plant richness (per plot) using multiple linear regression in R. The final model was chosen based on step-wise backward selection and inspection of the AIC. Both single and second polynomial predictors were included in the initial model to test for linear and quadratic relationships. Altitude, longitude and macroclimatic predictors were dismissed due to multicollinearity. In order to simplify our model, we used only additive effects. The analysis was confined to plots with meadow vegetation (n = 89).

Results

Classification

Our data set comprised 455 species (227 vascular plant, 136 bryophyte and 92 lichen taxa). Nearly all vascular plant species were perennial (97%). Meadows were dominated by herbs, rarely by graminoids. The classification approach with the highest mean FET fidelity was obtained by flexible beta clustering and yielded four meadow communities and one heath community (Fig. 3).

The *Arnica mollis* community was confined to moist soil conditions, as reflected in the presence of hygrophilous diagnostic species (e.g. *Leptarrhena pyrolifolia*, *Juncus mertensianus*, *Trollius laxus*, *Equisetum arvense*; Table 1). The high frequency of *Arnica mollis* and *Agrostis humilis* was characteristic. This community was rich in hygrophilous bryophytes (e.g. *Philonotis fontana*, *Aulacomnium palustre*, *Palustriella commutata*, *Rhytidiadelphus subpinnatus*). This community was found primarily in the mountain ranges, with the best-developed complex meadow mosaics in the Selkirk and Trophy Mountains; it was absent in the Whitefish Range and Babine Range (Table 2).

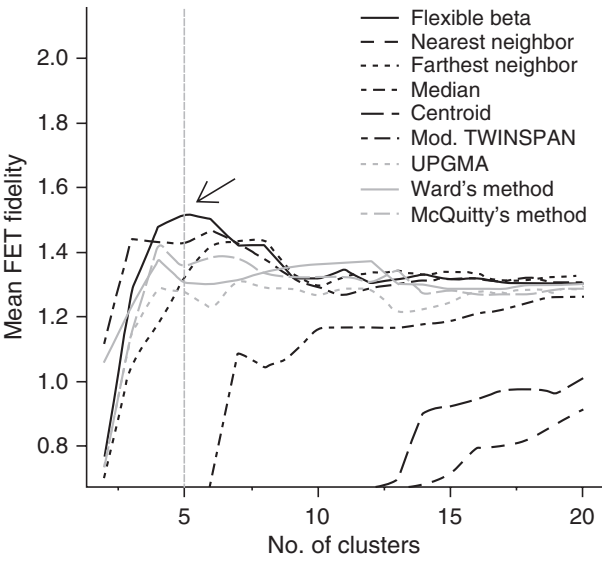

Fig. 3. Comparison of mean FET fidelities across different classification methods. The arrow indicates the highest mean FET value (=1.52).

The *Erigeron peregrinus* community was a widespread mesic meadow community type in SE British Columbia and NW Montana (Table 2, Fig. 2b). Typical species include *Lupinus arcticus* subsp. *subalpinus*, *Erythronium grandiflorum*, *Carex spectabilis*, *Senecio triangularis* and *Valeriana sitchensis*. With the exception of the highly diagnostic *Mitella breweri*, this community is characterized more by the absence than by the presence of a distinguishing suite of species. The name-giving species, *Erigeron peregrinus*, is in fact common across a spectrum of timberline meadow communities but dominates the late-summer physiognomy of this community in particular.

Further north, the latter community was entirely replaced by the species-rich, mesic *Aconitum delphiniifolium* community (Tables 1 and 2). This had a number of diagnostic species that were rare or absent in mesic meadows further south, including the namesake *Aconitum delphiniifolium* as well as *Artemisia norvegica*, *Carex macrochaeta*, *Sanguisorba stipulata* and *Ranunculus occidentalis*. The species turnover associated with the transition northwards to the *Aconitum delphiniifolium* community also extended to the bryophyte composition, with several species (e.g. *Cyrtomnium hymenophylloides*, *Plagiomnium insigne*) found within our data set only in this community.

Species richness was also high in the *Pulsatilla occidentalis* community, which combined heath (*Lepraria caesioalba*, *Cladonia ecmocyna*) and meadow (*Castilleja miniata*, *Valeri-*

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Table 1. Combined synoptic table of average number of species per plot, species frequencies and FET fidelities (superscript above frequency) in classified communities.

Community		1	2	3	4	5
No. of plots		7	15	44	23	21
No. of total species/plot		34.4	46.8	26.7	42.4	29.0
No. of vascular species/plot		21.6	31.2	21.0	25.2	12.9
No. of bryophyte species/plot		11.9	11.7	5.2	10.7	8.9
No. of lichen species/plot		1.0	3.9	0.5	6.5	7.2
		Species frequency and fidelity (superscript) in communities				
Philonotis fontana s.l.	B	**100$^{6.4}$**	13^{-}	11^{-}	9^{-}	0^{-}
Aulacomnium palustre	B	86$^{4.8}$	33$^{1.5}$	0^{-}	13^{-}	5^{-}
Rhytidiadelphus subpinnatus	B	**86$^{6.2}$**	13^{-}	2^{-}	0^{-}	5^{-}
Epilobium anagallidifolium	V	71$^{1.9}$	33	27^{-}	17^{-}	14^{-}
Scapania paludosa	B	71$^{5.0}$	13	2^{-}	0^{-}	0^{-}
Juncus mertensianus	V	71$^{4.1}$	7^{-}	11^{-}	0^{-}	0^{-}
Leptarrhena pyrolifolia	V	71$^{5.5}$	0^{-}	2^{-}	4^{-}	0^{-}
Equisetum arvense	V	57$^{3.2}$	20$^{1.0}$	5^{-}	0^{-}	0^{-}
Trollius laxus	V	57$^{2.0}$	7^{-}	23$^{1.1}$	4^{-}	5^{-}
Viola sp.	V	43$^{1.7}$	13^{-}	9^{-}	9^{-}	0^{-}
Palustriella commutata s.l.	B	43$^{3.2}$	0^{-}	2^{-}	0^{-}	0^{-}
Drepanocladus sendtneri	B	43$^{2.8}$	13^{-}	0^{-}	0^{-}	0^{-}
Castilleja sp.1	V	43$^{1.1}$	0^{-}	18^{-}	22^{-}	5^{-}
Campylium stellatum	B	43$^{2.3}$	20$^{1.3}$	0^{-}	4^{-}	0^{-}
Agrostis humilis	V	100$^{4.8}$	40$^{1.1}$	18^{-}	13^{-}	5^{-}
Caltha leptosepala	V	86$^{4.4}$	53$^{3.7}$	2^{-}	0^{-}	10^{-}
Sanionia uncinata	B	86$^{4.6}$	53$^{3.9}$	5^{-}	0^{-}	0^{-}
Aconitum delphiniifolium	V	0^{-}	**100$^{18.1}$**	0^{-}	0^{-}	0^{-}
Artemisia norvegica	V	0^{-}	**87$^{8.1}$**	11^{-}	17^{-}	10^{-}
Carex macrochaeta	V	0^{-}	**73$^{9.6}$**	0^{-}	0^{-}	10^{-}
Pedicularis bracteosa	V	0^{-}	73$^{3.9}$	27^{-}	35^{-}	0^{-}
Brachythecium oedipodium	B	0^{-}	67$^{3.3}$	32^{-}	13^{-}	10^{-}
Sanguisorba stipulata	V	0^{-}	**60$^{9.0}$**	0^{-}	0^{-}	0^{-}
Ranunculus occidentalis	V	0^{-}	**60$^{9.0}$**	0^{-}	0^{-}	0^{-}
Barbilophozia hatcheri	B	0^{-}	60^{42}	9^{-}	17^{-}	33^{-}
Epilobium lactiflorum	V	0^{-}	53$^{3.7}$	18^{-}	4^{-}	0^{-}
Agoseris aurantiaca	V	29^{-}	47$^{2.5}$	7^{-}	26^{-}	0^{-}
Poa alpina	V	0^{-}	47$^{1.7}$	18^{-}	26^{-}	14^{-}
Rumex acetosa	V	0^{-}	**47$^{6.7}$**	0^{-}	0^{-}	0^{-}
Stellaria calycantha	V	0^{-}	47$^{4.3}$	9^{-}	0^{-}	0^{-}
Cyrtomnium hymenophylloides	B	0^{-}	**47$^{6.7}$**	0^{-}	0^{-}	0^{-}
Luzula piperi	V	0^{-}	40$^{2.6}$	11^{-}	0^{-}	10^{-}
Parnassia fimbriata	V	14	40$^{3.1}$	7^{-}	4^{-}	0^{-}
Gentianella amarella	V	0^{-}	40$^{2.9}$	2^{-}	22$^{1.1}$	0^{-}
Calamagrostis canadensis var. *langsdorfii*	V	14^{-}	40$^{2.6}$	11^{-}	4^{-}	0^{-}
Plagiomnium insigne	B	0^{-}	40$^{4.8}$	2^{-}	0^{-}	0^{-}
Ranunculus eschscholtzii	V	14^{-}	40^{-}	50$^{2.3}$	26^{-}	14^{-}
Lupinus arcticus subsp. *subalpinus*	V	0^{-}	53$^{1.9}$	36$^{1.6}$	17^{-}	0^{-}
Mitella breweri	V	29^{-}	33^{-}	**70$^{7.0}$**	13^{-}	14^{-}
Claytonia lanceolata	V	0^{-}	0^{-}	**84$^{7.0}$**	74$^{1.6}$	24^{-}
Erythronium grandiflorum	V	0^{-}	0^{-}	**80$^{6.1}$**	70$^{1.4}$	24^{-}
Castilleja miniata	V	29^{-}	33^{-}	43^{-}	61$^{2.2}$	0^{-}
Poa cusickii subsp. *epilis*	V	0^{-}	27^{-}	41$^{1.0}$	43^{-}	19^{-}
Sibbaldia procumbens	V	43^{-}	33^{-}	16^{-}	**91$^{9.3}$**	14^{-}
Pseudoleskea radicosa s.l.	B	0^{-}	47^{-}	27^{-}	61$^{2.3}$	29^{-}
Trisetum spicatum	V	0^{-}	67$^{1.9}$	34^{-}	65$^{2.6}$	5^{-}
Brachythecium albicans	B	14^{-}	47$^{1.3}$	16^{-}	57$^{3.5}$	0^{-}
Tortula norvegica	B	0^{-}	20^{-}	30^{-}	**74$^{6.0}$**	0^{-}
Polytrichum piliferum	B	0^{-}	0^{-}	2^{-}	**74$^{8.8}$**	33^{-}

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Table 1. *(Continued).*

Community		1	2	3	4	5
Ceratodon purpureus	B	0^{-}	7^{-}	14^{-}	$65^{5.9}$	19^{-}
Desmatodon latifolius	B	0^{-}	0^{-}	25^{-}	$52^{3.8}$	0^{-}
Cladonia sp.	L	0^{-}	13^{-}	23^{-}	$48^{1.8}$	33^{-}
Eremogone capillaris	V	0^{-}	0^{-}	0^{-}	$\mathbf{48^{8.5}}$	0^{-}
Bryum sp. 2	B	0^{-}	0^{-}	14^{-}	$48^{4.7}$	0^{-}
Juncus parryi	V	0^{-}	0^{-}	0^{-}	$\mathbf{43^{6.6}}$	5^{-}
Sedum lanceolatum	V	0^{-}	0^{-}	5^{-}	$39^{5.1}$	0^{-}
Carex phaeocephala	V	14^{-}	7^{-}	23^{-}	$35^{1.6}$	0^{-}
Selaginella scopulorum	V	0^{-}	0^{-}	0^{-}	$35^{4.4}$	10^{-}
Polytrichum lyallii	B	14^{-}	13^{-}	30^{-}	$57^{1.2}$	$71^{2.9}$
Lepraria caesioalba s.l.	L	0^{-}	0^{-}	0^{-}	$43^{2.3}$	$62^{5.4}$
Bryum sp. 4	B	29^{-}	27^{-}	14^{-}	$39^{1.0}$	38^{-}
Cladonia ecmocyna s.l.	L	0^{-}	13^{-}	0^{-}	$35^{1.7}$	$43^{2.7}$
Cassiope mertensiana	V	29^{-}	13^{-}	7^{-}	9^{-}	$\mathbf{90^{11.9}}$
Trapeliopsis granulosa	L	14^{-}	7^{-}	2^{-}	17^{-}	$\mathbf{76^{9.3}}$
Phyllodoce empetriformis	V	14^{-}	13^{-}	2^{-}	17^{-}	$\mathbf{76^{8.9}}$
Dicranum sp. 4	B	29	7^{-}	5^{-}	17^{-}	$\mathbf{76^{8.4}}$
Dicranum scoparium	B	29^{-}	27^{-}	0^{-}	22^{-}	$62^{5.1}$
Luetkea pectinata	V	29^{-}	7^{-}	2^{-}	0^{-}	$\mathbf{62^{7.9}}$
Cladonia carneola	L	14^{-}	0^{-}	0^{-}	4^{-}	$\mathbf{62^{9.2}}$
Barbilophozia floerkei	B	$43^{1.2}$	7^{-}	0^{-}	4^{-}	$52^{5.7}$
Tuckermannopsis subalpina	L	14^{-}	20^{-}	0^{-}	13^{-}	$48^{4.2}$
Lophozia sp. 2	B	29^{-}	7^{-}	0^{-}	4^{-}	$48^{5.3}$
Cladonia pyxidata	L	0^{-}	27^{-}	7^{-}	17^{-}	$48^{3.1}$
Barbilophozia quadriloba	B	29	13^{-}	2^{-}	22^{-}	$43^{2.7}$
Dicranum sp. 1	B	29	20^{-}	2^{-}	9^{-}	$43^{3.2}$
Dicranum pallidisetum	B	0^{-}	0^{-}	0^{-}	9^{-}	$38^{4.8}$
Micarea subalpina	L	0^{-}	0^{-}	0^{-}	4^{-}	$38^{5.4}$
Antennaria lanata	V	57 -	0^{-}	16^{-}	$83^{5.6}$	$62^{1.8}$
Hieracium gracile	V	57 -	33^{-}	18^{-}	$65^{1.4}$	$\mathbf{95^{6.4}}$
Carex nigricans	V	$100^{2.1}$	0^{-}	50^{-}	43^{-}	$86^{3.4}$
Carex spectabilis	V	57^{-}	0^{-}	$89^{3.5}$	70^{-}	$86^{1.2}$
Luzula hitchcockii	V	0^{-}	20^{-}	41^{-}	$57^{1.2}$	48^{-}
Pulsatilla occidentalis	V	14^{-}	0^{-}	45^{-}	$\mathbf{91^{6.4}}$	38^{-}
Arnica latifolia	V	29^{-}	73^{-}	61^{-}	$83^{1.6}$	52^{-}
Phleum alpinum	V	29^{-}	$73^{1.8}$	45^{-}	$65^{1.6}$	5^{-}
Veratrum viride subsp. *eschscholzianum*	V	57 -	$60^{1.5}$	$50^{2.1}$	13^{-}	5^{-}
Arnica mollis	V	$86^{2.8}$	20^{-}	$41^{2.1}$	9^{-}	5^{-}
Juncus drummondii	V	43^{-}	33^{-}	39^{-}	43^{-}	33^{-}
Valeriana sitchensis	V	43^{-}	$93^{1.6}$	$91^{4.3}$	61^{-}	29^{-}
Veronica wormskjoldii	V	57^{-}	$67^{1.0}$	55^{-}	52^{-}	14^{-}
Senecio triangularis	V	$100^{1.5}$	$93^{2.3}$	$84^{4.2}$	39^{-}	5^{-}
Abies lasiocarpa	V	57^{-}	47^{-}	27^{-}	26^{-}	43^{-}
Erigeron peregrinus	V	86^{-}	87^{-}	$93^{2.9}$	74^{-}	43^{-}
Vahlodea atropurpurea	V	86^{-}	60^{-}	73^{-}	48^{-}	81^{-}

Grey cells mark frequency values $\geq$35%, bold script marks FET fidelity values >6. Only species with a frequency $\geq$35% are shown (see Appendices S1 and S2 for the entire synoptic table). Community codes: 1 = *Arnica mollis*, 2 = *Aconitum delphiniifolium*, 3 = *Erigeron peregrinus*, 4 = *Pulsatilla occidentalis*, 5 = *Cassiope mertensiana* community. V = vascular plant species, B = bryophyte species, L = lichen species.

ana sitchensis, *Senecio triangularis*) elements. Furthermore, it harboured several snowbed species (e.g. *Eremogone capillaris*, *Juncus parryi*, *Antennaria lanata* and *Sibbaldia procumbens*), which help to distinguish it from the *Erigeron peregrinus* community. Similar to the heath community, it was rich in bryophytes and lichens and lacked the tall, mesophytic *Veratrum viride* subsp. *eschscholzianum*. This community was widespread in the southern study sites but was absent further north, in the Babine Range.

Heaths were frequent in our study sites but species-poor (Table 2), and only one type, the *Cassiope mertensiana* community, was distinguished in our analysis. This was characterized in part by the dominant presence of the mountain heather species *Cassiope mertensiana* and *Phyllodoce empetri-*

Table 2. Frequency of community occurrence (rows) in the studied mountain regions (columns). Values were calculated as the proportion of plots occupied by the community divided by all studied plots in the region.

Community	*N*	Whitefish Range	Selkirk complex	Trophy Mtns.	Babine Range
Arnica mollis comm.	7	0	**0.43**	**0.57**	0
Aconitum delphiniifolium comm.	15	0	0	0	**1.00**
Erigeron peregrinus comm.	44	**0.16**	**0.52**	**0.32**	0
Pulsatilla occidentalis comm.	23	0.04	**0.74**	**0.22**	0
Cassiope mertensiana comm.	21	0	**0.67**	**0.24**	0.10

Numbers in bold mark proportions > 0.1. *N* = Total number of plots for the community.

formis, which contribute extensive litter to a closed, dark, mini-understorey, and lower frequency of major herb species of the meadows (e.g. *Senecio triangularis*, *Veronica wormskjoldii* and *Valeriana sitchensis*). The heaths also harboured a rich cryptogam flora and were unique among the studied communities for their near-continuous mats of hepatics (*Barbilophozia floerkei*, *B. quadriloba*) as well as presence with high frequency of the chionophilous lichen *Cladonia ecmocyna*.

Environmental gradients

The NMDS analysis with three dimensions yielded the lowest stress (14.3) and a convergent solution (Fig. 4). Axis 1 separated heath from meadow vegetation. Meadow plots overlapped with a higher herb cover and taller herb height, whereas heath plots were associated with high shrub cover and increased lichen richness and cover. By contrast, Axis 2 separated plots along altitude and longitude (Fig. 4). The *Aconitum delphiniifolium* community was separated from the remaining communities by its confinement to more western (negative) longitudes and lower altitudes. Axis 3 similarly separated the *Aconitum delphiniifolium* community and some plots of the *Arnica mollis* community from the remaining communities. The former two communities were associated with high vascular plant species richness. The gradient was also related to differences in macroclimatic variables (annual precipitation, precipitation of February, March, April, June and September, minimum temperature of January, precipitation of the driest quarter, precipitation of the driest month and minimum temperature of the coldest month).

Patterns in species richness

Vascular species richness showed a significant relationship with latitude, soil pH and litter cover (Table 3). Specifically, it showed a slight unimodal relationship with litter cover and increased significantly with soil pH (Fig. 5). Notably, species richness increased towards the southern and northern tips of our geographic gradient and dipped in the middle. Overall bryophyte and lichen species richness, by contrast, increased with latitude but decreased with litter cover (Table 3, Fig. 5).

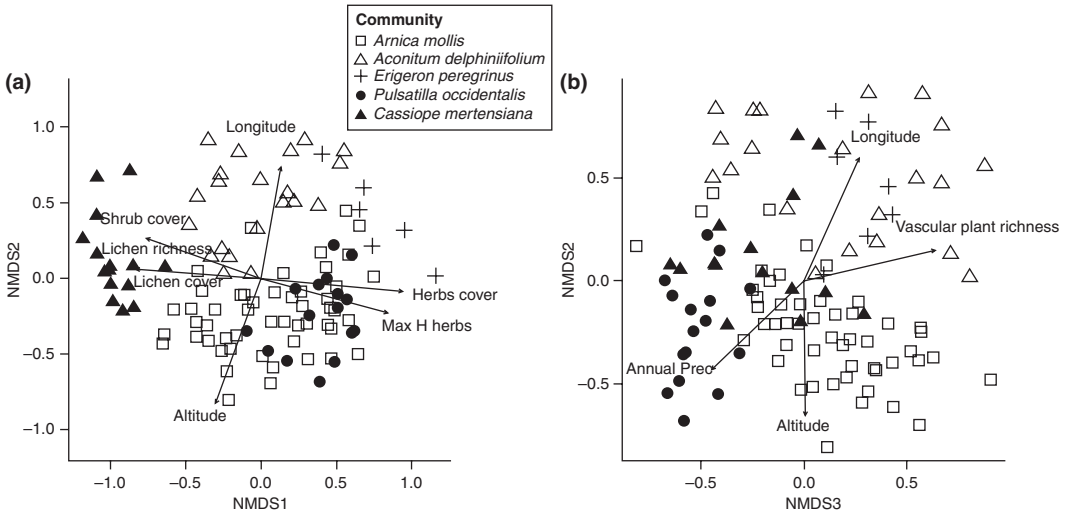

Fig. 4. NMDS ordination for (**a**) Axis 1 vs 2 and (**b**) Axis 2 vs 3. Only those predictors that had $R^2 > 0.4$ ($P < 0.01$) with the main axes are shown as arrows in the joint plot. Not shown as arrows in (**b**) are nine macroclimatic predictors (precipitation in February, March, April, June and September, minimum temperature in January, precipitation of the driest quarter, precipitation of the driest month and minimum temperature of the coldest month), the display of which would clutter the diagram. They were highly correlated with annual precipitation ($R \geq |0.7|$). Prec = precipitation; H = height.

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Table 3. Results of the final multiple linear regression models, inspecting the relationship between environmental and geographic predictors with (A) vascular plant species richness and (B) bryophyte and lichen species richness per plot.

	df	SS	*F*	*P*
A				
Latitude	1	273.7	11.5	0.001
Latitude^2	1	1145.2	48	<0.001
Soil pH	1	788.2	33.1	<0.001
Litter cover	1	241.2	10.1	0.002
Litter cover^2	1	422.1	17.7	<0.001
Residuals	79	1884.3		
B				
Latitude	1	531	12.7	<0.001
Litter cover	1	2202	52.8	<0.001
Residuals	82	3585		

Discussion

Plant communities

Remarkably, despite drawing from a larger number of plots from six mountain ranges, we arrived at nearly the same classification scheme and diagnostic species as Hämet-Ahti (1978) in her study of the Trophy Mountains. Our *Pulsatilla occidentalis* community clearly corresponds to Hämet-Ahti's 'dry meadow' type from the Trophy Mountains. Our *Erigeron peregrinus* community likewise corresponds to her 'mesic meadow' type, while our *Arnica mollis* type corresponds to her 'moist mesotrophic meadows'; the similarity of her 'heath' to our *Cassiope* community is unmistakable. It is thus apparent that the community mosaic originally described from the Trophy Mountains is a recurring suite in climatically similar mountain ranges south all the way to NW Montana, without any significant tandem floristic shifts. Where our classification expands upon Hämet-Ahti's is in recognition of the *Aconitum delphiniifolium* community, which we found only in our northernmost sampling site, in the Babine Range. Here we register a significant shift in the mesic community type towards species of northern coastal subalpine communities, such as the name-giving *Aconitum delphiniifolium*, as well as *Sanguisorba stipulata*, *Ranunculus occidentalis* and *Artemisia norvegica* (compare Sandgren & Noble 1978).

Our analysis of environmental variables confirms Hämet-Ahti's (1978) observation that moisture is one of the main variables determining small-scale timberline meadow community composition. Soil pH, which we had expected to play a greater role over the geographic gradient, was a significant factor only in separating meadow and heath communities. The cause for soil pH differences may, however, not be geological parent material, which typically does not differ between adjacent meadow and heath communities, but may be caused by litter accumulation of the dominant ericaceous shrubs in heaths, lowering pH.

The broader subalpine meadow formation in NW North America appears, based on the available literature, to consist of three main geographic prongs, sharing a set of species that were also frequently observed in our study: *Valeriana sitchensis*, *Erigeron peregrinus*, *Senecio triangularis*, *Lupinus arcticus* subsp. *subalpinus* and *Arnica latifolia*. Recognizing this broader regional pattern, Brett et al. (1998) and later Damm (2001) proposed to unite subalpine meadow communities of NW North America into a phytosociological order, *Valerianetalia sitchensis* Brett et al. *ex* Damm 2001. The first prong, described in this paper, covers the inland mountain ranges from the Columbia Mountains (Landals & Scotter 1974) to northern Idaho and NW Montana (Damm 2001), where vegetation closely related to our *Pulsatilla occidentalis* community is closely linked to open woodland of *Larix lyallii* (Stachurska-Swakoń & Spribille 2002). The second runs along the Coast/Cascade ranges; as Hämet-Ahti has pointed out, many of the main meadow elements appear to be lacking on the rain-ward side of the Coast Ranges as they are here replaced by heath, but rich meadow communities are well known from the Cascades and Olympic Mountains (Brink 1959; Kuramoto & Bliss 1970; Douglas 1972; Franklin & Dyrness 1973; Douglas & Bliss 1977; Crawford et al. 2009) and Vancouver Island (Milko 1984; Milko & Bell 1986). These include an array of species we did not encounter in our study plots, e.g. *Anaphalis margaritacea*, *Bromus sitchensis*, *Eucephalus paucicapitatus*, *Ligusticum grayi* and *Saussurea americana*. The third prong, not previously connected with this formation in the literature, appears to parallel the northern Pacific Coast in SE and south-central Alaska. This northern extension of the subalpine meadow formation appears to involve another tandem shift with the appearance of *Lupinus nootkatensis*, *Sanguisorba stipulata* and *Geranium erianthum*, species reported from oceanic subalpine meadows in Glacier Bay, Alaska (Sandgren & Noble 1978), as well as on the Kenai Peninsula 750 km further northwest (DeVelice et al. 1999). No whole-composition vegetation studies are available from these meadows to our knowledge.

Heath communities, for their part, are species-poor for vascular plants and similar in composition across much of oceanic and sub-oceanic NW North America. Our *Cassiope mertensiana* community is similar in composition to the *Phyllodoco-Cassiopetum mertensianae* described by Brooke et al. (1970) from the southern British Columbia Coast Range, all the way down to details of the bryophyte composition. A detailed overview of the extensive literature on heath communities in NW North America is provided in Damm (2001: 165).

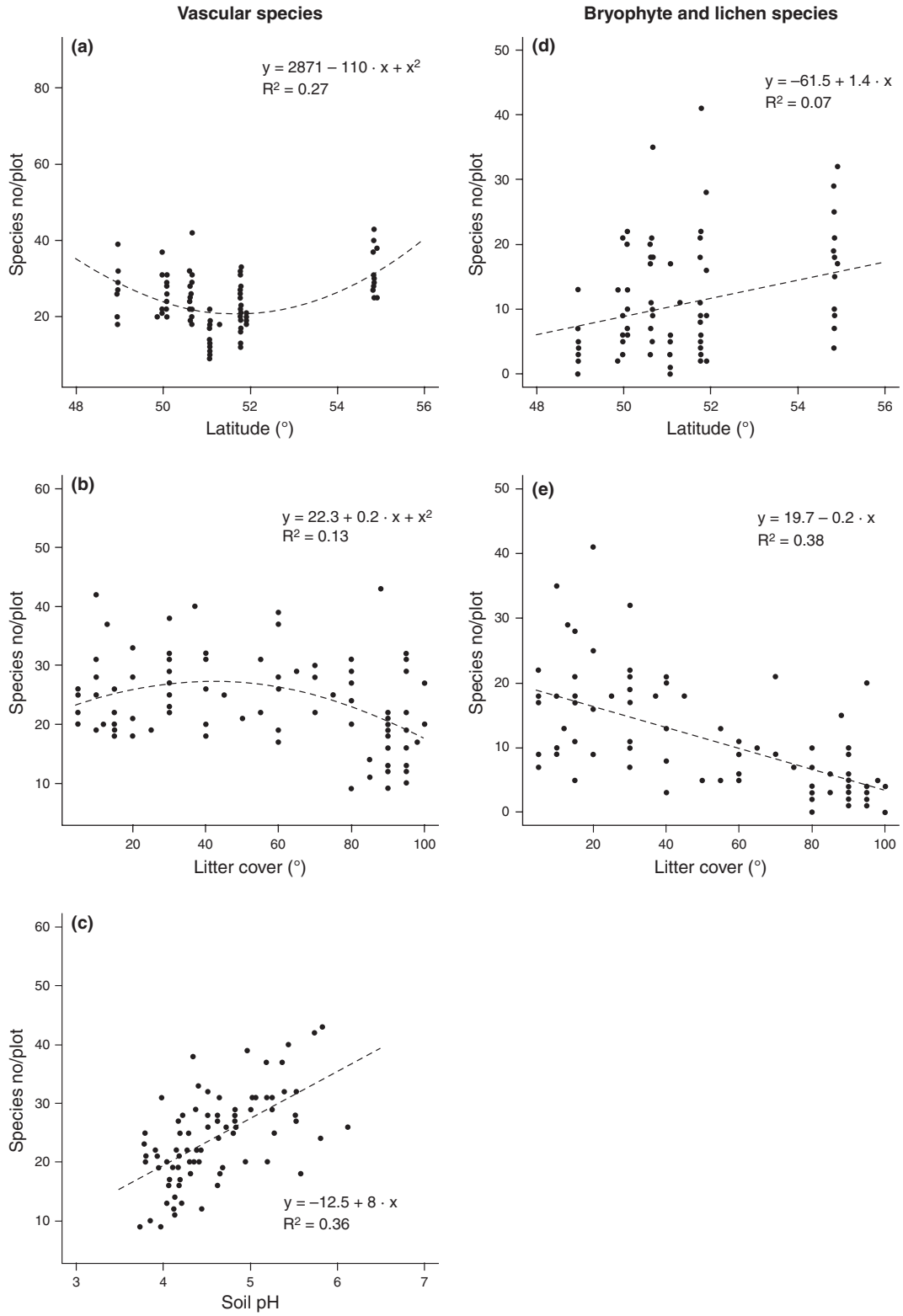

Fig. 5. Change in species richness per plot along (**a**) latitude, (**b**) litter cover and (**c**) soil pH gradients for vascular plants, and (**d**, **e**) for bryophytes and lichens; the relationship of the latter to soil pH was not significant. Formulae refer to single, linear regression models. The coefficient of determination was calculated as an adjusted R^2. The analysis was confined to plots with meadow vegetation; relevés with heath vegetation were excluded.

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Species richness

Our analysis of vascular species richness data from meadows (Fig. 5a) revealed a bimodal relationship with latitude, with highest values at the southern and northern ends of the gradient and a dip in the middle. If this pattern holds true with more intense sampling, it might be explained by historic glaciation and recolonization patterns, similar to that proposed for alpine species in the same region (Harris 2007). Higher species diversity at the northern end of our gradient would be consistent with an influx of colonizers radiating from historically unglaciated areas in Beringia (Hultén 1937), whereas recolonization at the southern tip might have benefited from unglaciated areas in the central Rocky Mountains (Harris 2007) and/or a postulated unglaciated corridor in the Alberta Rocky Mountains (Reeves 1973).

Vascular species richness showed a positive relationship with soil pH. This pattern is a well-known phenomenon in temperate regions and is the subject of a voluminous body of European literature (Pärtel 2002) but has not been described from NW North America. For Europe, this pattern has been explained by the hypothesis of historic bottleneck effects, namely the higher extinction rate of acidophiles compared to calciphiles as a result of a paucity of acidic refugia during the Pleistocene (Ewald 2003). The extent to which the pattern might hold in NW North America would become clear if sampling were conducted on yet higher pH soils, e.g. if our pH gradient were extended over calcareous parent material. Subalpine meadows similar in structure to those sampled here are known to occur e.g. in the limestone areas of British Columbia/Alberta border region of Banff National Park (T. Spribille, pers. obs.), but compatible vegetation data are not available from these communities. However, southern glacial refugia occupy extensive basalt batholiths and other acidic bedrock, and there is no evidence to suggest that Pleistocene glaciation discriminated against acidic refugia, as has been hypothesized for Europe (Ewald 2003).

Conclusion

Vegetation inventory in NW North America has long focused on forest type classification and mapping. However, much of the biodiversity of the Cordilleran landscape is held in yet nameless non-forest plant communities. Describing and mapping the subalpine meadow communities across multiple mountain ranges of this region opens a small window into how biodiversity is arrayed in the landscape, and raises new questions: is the species richness 'dip' a signature of post-glacial colonization patterns from the north and south that may have resulted in a persistent colonization debt in the areas most distant from once-unglaciated regions? Are some species continuing to expand their ranges? Detailed whole-composition studies of high-altitude plant communities in western North America are proving to be invaluable baselines for biomonitoring of climate change (Malanson et al. 2011). Parsing and predicting the effects of climate change in once-glaciated regions will require an accounting for on-going plant migrations and understanding niche shifts across latitudinal and edaphic gradients.

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Supporting Information

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

Appendix S1. Synoptic table of species percentage frequencies in classified communities.

Appendix S2. Synoptic table of species FET fidelities in classified communities.