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ORIGINAL ARTICLE

A diverse alpine species pool drives a 'reversed' plant species richness–elevation relationship in interior Alaska

Carl A. Roland[1,2*] and Joshua H. Schmidt[2]

[1]Denali National Park and Preserve, Denali Park, AK 99775, USA, [2]Central Alaska Network, National Park Service, Fairbanks, AK 99709, USA

ABSTRACT

Aim We evaluate whether vascular plant species richness in interior Alaska is highest in the alpine zone. We test the proposition that historical dynamics have influenced the sizes of species pools inhabiting different segments of the landscape by quantifying the contrasting responses of five phytogeographical elements within the flora to changes in elevation and topography.

Location Denali National Park and Preserve, Alaska, USA.

Methods We developed Bayesian hierarchical models for total plant species richness and the richness of five phytogeographical elements with data from a systematic-grid sample containing 1022 plots. We also used rarefaction and extrapolation techniques on these data to estimate species richness for more extensive landscape segments, including across seven elevation bands in the study area.

Results Plot-level species richness had a unimodal response to elevation, reaching its peak in the alpine zone. Overall plant species richness across more extensive areas was also higher in the alpine zone, even though this zone occupies less area overall in interior Alaska. Species richness of Alaska endemic and amphi-Beringian phytogeographical elements showed particularly strong positive responses to elevation, whereas that of the North American and incompletely circumpolar elements declined with elevation.

Main conclusions Our results document a unique pattern in the study of variation in species-pool sizes with elevation, revealing that sparsely vegetated alpine areas contained a larger species pool than adjacent extensive lowlands. This pattern was driven by pronounced increases in phytogeographical elements whose distribution patterns suggest that they evolved or persisted in the region during full-glacial intervals. The persistence of tundra and/or similar open, treeless vegetation in interior Alaska contrasts with the simultaneous periodical elimination of boreal lowland ecosystems in the region. We posit that this has resulted in a regional species pool relatively enriched in alpine species and impoverished in boreal lowland taxa, causing a 'reversed' relationship between species richness and elevation. Increased habitat heterogeneity in high-relief areas of the mountainous landscape are also likely to have contributed to the reported patterns.

Keywords

Alaska, Beringia, Denali National Park, diversity patterns, elevation gradient, phytogeography, species pools, vascular plants.

*Correspondence: Carl A. Roland, National Park Service, 4175 Geist Road, Fairbanks, AK 99709, USA.
E-mail: carl_roland@nps.gov

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INTRODUCTION

Dramatic variation in species richness along elevation gradients has intrigued biogeographers and ecologists for decades (MacArthur, 1972; Rahbek, 1995; Körner, 2000; Whittaker *et al.*, 2001; Mori *et al.*, 2013). Early studies suggested that decreases in species richness with increasing elevation were the rule, a pattern initially considered analogous to decreasing species richness with latitude (see MacArthur, 1972; Stevens, 1992). More recently, field studies have revealed that the relationship between species richness and elevation is variable and is both taxon-specific and scale-specific. Moreover, a unimodal 'humped' response of species richness to elevation is more common than a steady decrease with elevation (Rahbek, 1995). One pattern not reported is the existence of larger species pools in sparsely vegetated alpine landscapes than in adjacent lowland forested landscapes over an extensive area.

Researchers – including the eminent botanist A. E. Porsild, who remarked that '. . .in the unglaciated mountains in Yukon and Alaska, the richest and most varied floras are found above timberline . . . rather than in valleys now occupied by coniferous forest' (quoted in Drury, 1969) – have long noted the high diversity of vascular plants in unglaciated alpine terrain. Recent comprehensive plant inventories in interior Alaska, have suggested that peak plant species richness may indeed occur in the alpine zone in this region (Roland, 2004). Furthermore, the ecological history of eastern Beringia suggests that variation in the relative sizes of the regional species pools may have contributed to this atypical pattern. Specifically, the species-pool hypothesis predicts that, all other things being equal, older and historically larger habitats will contain larger numbers of species than younger and historically smaller habitats (Taylor *et al.*, 1990).

The history of Beringia is characterized by the repeated diminution or elimination of dominant boreal species during glacial maxima, when an open, low-statured vegetation mosaic replaced the large-statured boreal vegetation typical of interglacial periods (Cwynar & Ritchie, 1980; Edwards *et al.*, 2000). Studies of pollen spectra (Edwards *et al.*, 2000), plant macrofossils (Zazula *et al.*, 2006; Reyes *et al.*, 2010) and material from rodent middens (Zazula *et al.*, 2011) dating to the last full-glacial period reveal that currently-forested areas of this landscape were either treeless or mostly so, and were occupied by tundra, steppe-tundra or steppe. Indeed, according to Yurtsev (2001) the vegetation of full-glacial Beringia contained a high diversity of herbaceous plant taxa (grasses, sedges and forbs) occurring within an open landscape mosaic he called steppe-tundra. New evidence supporting the prevalence of diverse, forb-rich tundra in full-glacial Beringia was recently reported by Willerslev *et al.* (2014).

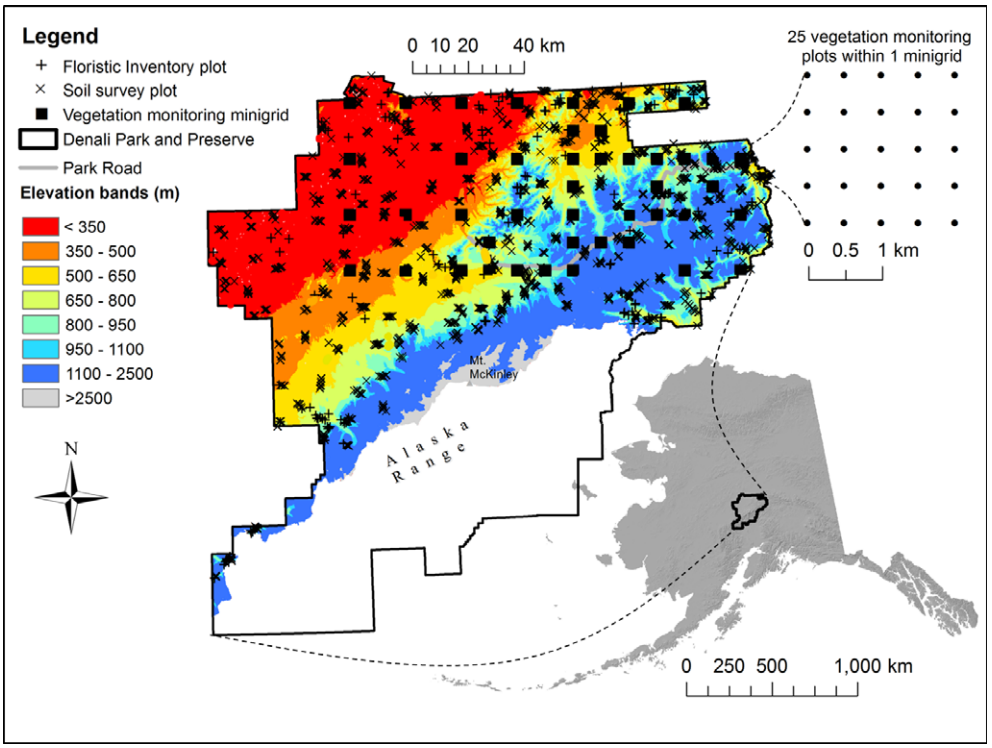


Figure 1 Map of the study area, showing 3023 study plot locations, variation in terrain elevation and the location of Denali National Park and Preserve within Alaska. The area shown in white inside the park boundary is south of the Alaska Range crest and outside the area of inference for this study. The larger black squares are 'minigrids' of 25 vascular plant monitoring plots shown in inset on upper right.

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We address the question of whether the pool of species that occurs in the alpine zone is larger than the species pool at lower elevations, using three datasets from Denali National Park and Preserve (Denali NPP): (1) a grid-based systematic full-coverage survey; (2) a soil survey across the full range of ecotypes; and (3) a targeted plant-inventory survey. Furthermore, we evaluate the hypothesis that strong differences in the responses to elevation of different phytogeographical elements within the flora underlie this pattern. We expected species groups with geographical distributions that reflect residence in full-glacial Beringia (i.e. species endemic to the region and those with amphi-Beringian distributions that were likely to have dispersed across the treeless Bering land bridge) to have higher species richness in the alpine zone. In contrast, we expected that other species groups, which contain larger numbers of species that only migrated to this area after the full-glacial period (i.e. broadly distributed North American species and circumboreal forest and mire plants), would show the more common pattern of decreasing species richness with elevation.

MATERIALS AND METHODS

Study area

The study area encompasses 17,400 km^2 of Denali in south-central interior Alaska (Fig. 1). The area spans 202 km east to west and 190 km north to south with a centre near 63°20.3′ N, 150°49.6′ W. The terrain varies dramatically and includes steep peaks of the Alaska Range more than 4000 m above sea level along its southern boundary. The Alaska Range grades into the surrounding foothill ranges and uplands to the north, and the lowland basins beyond. The study area also contains lower ranges of hills that create additional topographic heterogeneity in the north-central part of the study area, and isolated schist domes that rise from the lowlands along its northern edge.

The mountains are formed of a mix of bedrock types, and Quaternary sediments underlie the adjacent uplands and lowland basins. The Alaska Range portion of the study area is composed mostly of sedimentary or metasedimentary rock, whereas the satellite ranges to the north are formed of metamorphic bedrock (Jones *et al.*, 1983; Csejtey *et al.*, 1992). Pleistocene loess deposits mantle the northern and western areas of Denali NPP (Clark & Duffy, 2006). The basin lowlands are dominated by alluvium, glacial moraines and areas of loess. Permafrost underlies much of the northern lowland terrain, except along river corridors and south-facing hillsides.

The majority of Denali NPP's lowland landscape is forested to some degree, and forest cover declines with elevation, becoming rare above 1100 m elevation (Fig. 2). In contrast, high-elevation areas are occupied by dwarf-scrub tundra or barren screes and fellfields (Fig. 2). The shrub-dominated vegetation peaks in the subalpine zone (*c.* 801–950 m) in Denali NPP (Fig. 2). Similarly, there is considerable variation in soil attributes along the elevation gradient (see Appendix S1 in Supporting Information). Specifically, soil organic mat depth, percentage carbon and percentage moisture generally decrease steeply with increasing elevation, whereas pH generally increases with lower mean pH occurring in the boreal elevation bands, with

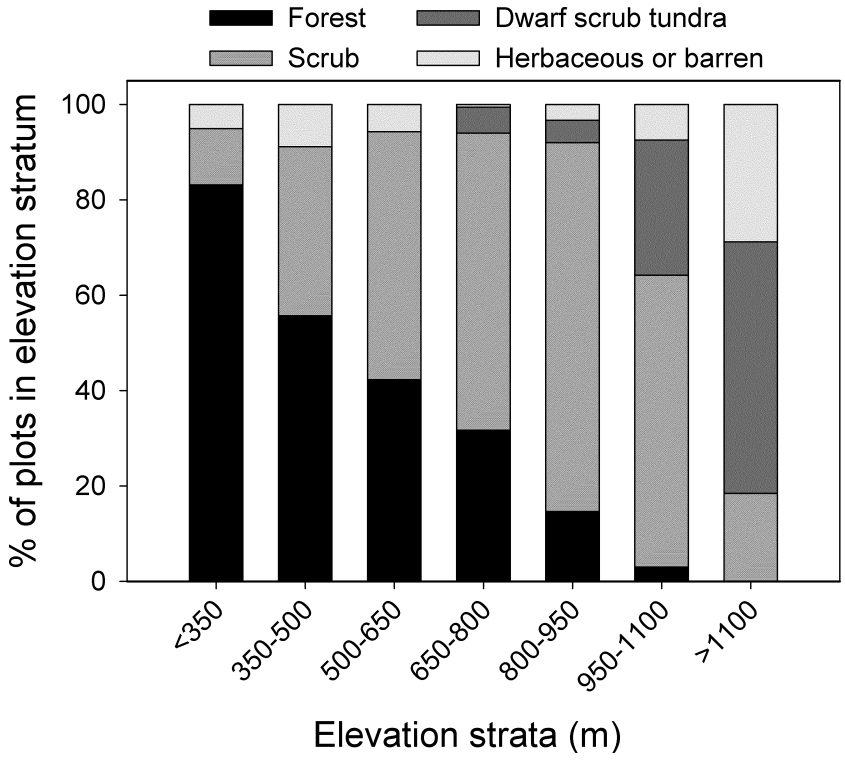


Figure 2 Histogram showing variation in the percentage of vascular plant monitoring plots with different vegetation types across seven elevation bands in Denali National Park and Preserve, Alaska, according to field data recorded on a two-stage systematic grid sample with random start (n = 1022; 200-m^2 plots).

Table 1 Terrain attributes, sample sizes (including area sampled) and mean plot sizes for plots on systematic vegetation monitoring grid (n = 1022) and for the full plot datasets (n = 3023) across seven elevation bands in Denali National Park and Preserve, Alaska.

Elevation bands	Map area (km^2)	Surface area (km^2)	Number of vegetation monitoring plots	Total number of plots	Area sampled (m^2)	Mean plot size [m^2 ($\pm$ SD)]
Plots < 351 m	4714	4720	176	627	176,340	281 ($\pm$ 217)
351–500 m	1724	1739	79	294	61,230	208 ($\pm$ 156)
501–650 m	2002	2026	165	412	75,590	183 ($\pm$ 121)
651–800 m	1726	1763	145	344	66,920	195 ($\pm$ 134)
801–950 m	1629	1678	142	489	85,700	175 ($\pm$ 130)
950–1100 m	1249	1325	129	398	83,370	209 ($\pm$ 194)
Plots > 1101 m	4011	4643	186	459	96,860	211 ($\pm$ 139)

highly organic soils and higher pH occurring in more mineral alpine soil profiles (Appendix S1).

The area has a continental climate characterized by long, cold, dry winters and short, warm summers. The mean annual temperature at the headquarters of Denali National Park (Fig. 1; 63°43′ N, 148°58′ W; 628 m elevation) was −3 °C, with a mean high of 20 °C in July and a mean low of −22 °C in January, and a mean annual precipitation of 381 mm over the period 1971–2000 (Shulski & Wendler, 2007). Most precipitation in Denali NPP falls during the summer (June to August).

Field data

We used plant occurrence data from three landscape-scale field projects completed during 1998–2010, which included all terrestrial habitats and regions in the study area from boreal wetlands to alpine fellfields (Roland, 2004; Roland *et al.*, 2005; Clark & Duffy, 2006). We classified vegetation monitoring plots in the field according to the standard vegetation classification for Alaska (Viereck *et al.*, 1992), and we calculated the percentage of plots in each elevation band based on the following primary vegetation categories: forested, scrub, dwarf-scrub tundra, herbaceous and barren (open water and barren sites). Detailed methods for the surveys used for the current project are described elsewhere (Roland, 2004; Clark & Duffy, 2006; Roland *et al.*, 2013) and summarized below.

The foundational dataset for this study comes from 1022 200-m^2 vegetation monitoring plots surveyed within a two-stage systematic grid in which 44 'minigrids' consisting of 25 plots each (five rows of five plots on a 500-m grid) were arranged on a macrogrid of 10–20-km spacing (Fig. 1). Species composition was recorded in identical circular plots, within which a set of four nested 1–4-m^2 quadrats were placed on bisecting tapes delimiting the plot. Four sequential quarter-plot searches were then performed to arrive at a complete species list for the entire plot. Infrequently, plots were inaccessible (e.g. located on a cliff or in a river), resulting in fewer than 25 sampled plots for some minigrids. Soil conditions were recorded at a set of four points on the plot perimeter. We measured surface horizon depths, and a composite soil sample was extracted to measure pH, texture and soil moisture percentage (see Roland *et al.*, 2013).

The second dataset contained 1805 plots from the Denali NPP soil survey, an ecological site survey using variable-sized plots (depending on site characteristics) centred on a soil pit (Clark & Duffy, 2006). Soil survey plots were arrayed along 631 catena transects (4–8 plots per transect) selected to represent the full spectrum of soils and ecotypes across the study area. A complete species list of vascular plants was recorded during the measurement of these plots. The third dataset contained 170 plots surveyed as part of a floristic inventory project with the objective of completing the vouchered flora for Denali NPP through targeted collecting (Roland, 2004). The inventory employed gap analyses for general site selection and the occurrence of plant species was recorded within variable-sized, non-randomly selected plot areas. Elevation values for plots from each dataset were determined as follows: (1) differentially corrected GPS field data for vegetation monitoring plots; (2) uncorrected field GPS data for the soil survey plots; (3) field altimeter readings for floristic inventory plots.

Geographical information system analyses

We divided the study area into seven elevation bands to examine variation in species pool sizes (Fig. 1, Table 1) and then calculated the area within each of these bands using a satellite-derived bare-earth DEM (DTM; available at http://ifsar.gina.alaska.edu/). Estimates of total annual solar radiation for each plot were made using the Solar Analyst tool (Dubayah & Rich, 1995) in ArcGIS 10.2.

Taxonomy, nomenclature and classification of species

Species determinations were completed by C.A.R., Al Batten, Carolyn Parker and David Murray (University of Alaska, Museum of the North), Don Farrar (Iowa State University; *Botrychium*) and Tony Reznicek (University of Michigan; *Carex*). We used taxonomies in Hultén (1968), Cody (1996) and the *Flora of North America* (Flora of North America Editorial Committee, 1993 onwards) to develop the species lists. The global distribution of each species was evaluated by

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consulting range maps and species descriptions in Hultén (1968), Cody (1996), the *Flora of North America* (Flora of North America Editorial Committee, 1993 onwards) and the USDA Plants database (USDA-NRCS, 2013). We assigned each species to one of five phytogeographical elements based on its global distribution:

1. Circumpolar (CP) – widely distributed species that occur on all circumpolar continents including Greenland.

2. Incompletely circumpolar (INC) – species with similar overall range to the circumpolar group, but with large gaps in their distribution, such as an absence from Greenland.

3. Amphi-Beringian (AB) – species that occur on both sides of the Bering Strait, with range centred on Beringia, including species that radiate far into North America, Asia or both.

4. North American (NAM) – species restricted to North America.

5. Alaska–Yukon endemics (AK) – species whose range is restricted to Alaska, Yukon Territory and adjacent areas.

We included only species-level taxa, except for six species for which two subspecific taxa were reported. We included only terrestrial plant species native to Alaska in our analysis.

Data analysis

Vegetation monitoring plots from systematic grid

We restricted our quantitative analyses to the systematic-grid dataset, because it has identical plot sizes and a randomized, quantitative sampling design. We used a hierarchical generalized linear mixed modelling approach in a Bayesian framework to help account for the systematic, nested sampling scheme (i.e. plots within minigrids). Our primary objective was to investigate the response of plot species richness to elevation, which integrates multiple microclimatic factors that influence plant distribution. To help control for other major sources of variation that are likely to influence richness, however, we included three additional topographic parameters: slope angle, solar radiation receipt and permafrost class (Roland *et al.*, 2013). In order to control for additional unexplained heterogeneity among plots and possible correlation of plots within minigrids, we included random-effect terms at both the plot and minigrid levels. To improve convergence, continuous covariates were scaled to a mean of 0 and a standard deviation of 1 before analysis, which also allowed direct comparisons of the effect sizes for the resulting parameter estimates. We assumed that the observed species counts were Poisson-distributed, and our hierarchical model can be written as:

$$\log(count_i) = class_i + \beta_1 elevation_i + \beta_2 elevation_i^2 + \beta_3 slope_i + \beta_4 slope_i^2 + \beta_5 solar.rad_i + \beta_6 solar.rad_i^2 + e.grid_j + e.plot_i,$$

where *class* represents the permafrost classification for each *plot, i*, $e.grid_j$ represents the random effect of minigrid, *j*, for each plot and $e.plot_i$ is the random effect for each plot. Permafrost class was modelled as a categorical variable with three levels – continuous, discontinuous and sporadic – resulting in a separate intercept estimate for each of the three categories.

We fitted this model to plot-level species counts for all species, as well as the counts of species from each of the five phytogeographical elements. This approach allowed us to investigate the overall pattern of plot species richness with increasing elevation and compare the patterns among species groups. We were also able to compare parameter estimates for the other covariates in order to identify important predictors of species counts.

We fitted models with WinBUGS 1.4.3 (Lunn *et al.*, 2000) using Markov chain Monte Carlo (MCMC) methods, and used R 2.14.2 (R Core Team, 2012) as an interface. We used diffuse normal priors on parameters with $class_{1:3} \sim N(0,100)$ and $\beta_{(1:6)} \sim N(0,100)$; the prior for the standard deviation for each of the random effects terms was $\sigma \sim U(0,10)$. For each analysis, we ran two MCMC chains for 20,000 iterations, discarding the first 5000 from each as burn-in, and thinning the remainder by half. We used the Gelman–Rubin diagnostic (Brooks & Gelman, 1998) and visual inspection of the chains to ensure that convergence had occurred. In the few cases where one of the random effects did not converge due to sparse data, the model was rerun with only the minigrid-level random term.

To investigate patterns in species richness beyond the plot level, we used a rarefaction approach to estimate total and phytogeographical-element species richness for each of the 44 minigrids, and then for all data (i.e. 1022 systematic grid plots) within seven elevation bands. For the minigrids, we estimated the rate of increase in species richness with increasing sample size and used the rarefaction–extrapolation approach to create the observed accumulation curve across 30 samples (Colwell *et al.*, 2012). Bootstrap methods were used to construct confidence intervals for the species richness of the extrapolated sample (100 bootstrap samples). We employed the iNEXT software incidence data model, which uses the species frequencies from each sample group as input data (Hsieh *et al.*, 2013), to derive estimates of species richness. We used iNEXT to derive estimates of species richness for each of seven elevation bands, by using species frequency data across all of the systematic grid plots in each band and estimating richness across 400 samples for all bands with 100 bootstrap samples.

Dataset summary

In addition to the quantitative analyses, we assembled and summarized a comprehensive plant distribution dataset from 3023 plots across all three field projects, including nearly the entire known flora of the study area. We used MS Access 2010 (Microsoft, Redmond, WA, USA) database software to calculate the total species richness and the number of species in each of the five phytogeographical elements across the seven elevation bands (Table 1). Because site selection was non-random, plot sizes were variable (see Appendix S2) and

sample size differed among bands, we only present general data summaries for the full 3023-plot dataset.

RESULTS

Grid dataset summary

We recorded the distribution of 491 terrestrial vascular plant species across 1022 200–m^2 plots in 44 minigrids sampled in the two-stage systematic grid dataset (Table 2). Plants with a circumpolar distribution (CP) formed the largest phytogeographical element, representing 37% of the flora, followed by the AB, NAM and IN elements, respectively, with AK species representing 6% of the species in the sample. Every phytogeographical element was represented in each of the minigrids, except for AK, which occurred in 75% (33) of the minigrids.

Hierarchical model of plot species richness in systematic grid dataset

A plot of our raw data showed a trend of increasing species richness with elevation, with the most species-rich plots concentrated in the alpine zone, above 1200 m (Fig. 3). Similarly, the strongest positive influence on plot species richness was the linear elevation term (Fig. 4, Appendix S3). The estimates for the random effects suggested that there was generally more heterogeneity at the grid level than the plot level, although the covariates explained much of the variation among plots and grids (Appendix S3). The lowest species richness was estimated to occur at the lowest elevations (14.9 species $plot^{-1}$ at 150 m) with peak estimated species richness of 31.3 species $plot^{-1}$ at 1050 m, more than double the estimated species richness at the lowest-elevation sites. Estimated species richness declined with elevation above 1050 m, although the estimated plot species richness was 17.8 even in the highest elevations sampled (> 1700 m).

Our models exposed marked variation in the responses of the phytogeographical elements to topographic variables (Fig. 4, Appendix S3). Elevation terms had the largest effects in each of the five models for the phytogeographical elements, although the direction and magnitude of the influence of elevation differed sharply, as did the zones of maximum estimated species richness. Plot-level species richness of AB and AK elements showed strong positive responses to

Table 2 Summary of the number of vascular plant species and frequency of occurrence for species in five phytogeographical elements across all of the 200–m^2 vegetation monitoring plots (n = 1022) measured in two-stage systematic grid sample in Denali National Park and Preserve, Alaska.

Phytogeographical element	Number of species (% of total)	Number of plots (frequency)	Number of minigrids (% of total)	Total number of incidences in plots
Circumpolar (CP)	182 (37%)	1019 (99.7%)	44 (100%)	11,867 (44%)
Incompletely circumpolar (IN)	58 (12%)	952 (93.2%)	44 (100%)	3292 (12%)
Amphi-Beringian (AB)	136 (28%)	1015 (99.3%)	44 (100%)	8321 (31%)
North American (NAM)	88 (18%)	877 (85.8%)	44 (100%)	2971 (11%)
Alaska–Yukon endemic (AK)	27 (6%)	324 (31.7%)	33 (75%)	547 (2%)
Total species richness	491	1022 (100%)	44 (100%)	26,998

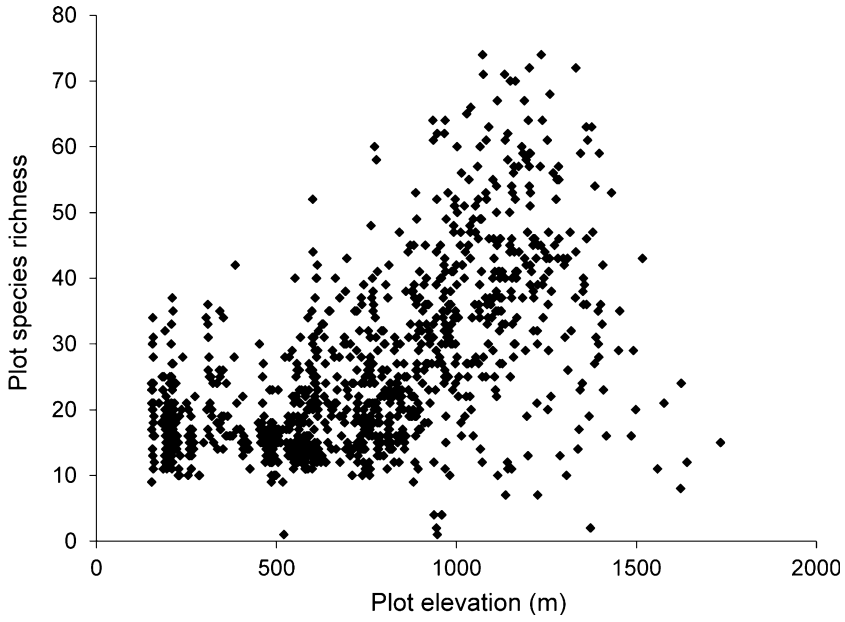


Figure 3 Total number of vascular plant species in each of the 200-m^2 vascular plant monitoring plots (n = 1022) from a two-stage systematic grid sample in relation to plot elevation in Denali National Park and Preserve, Alaska.

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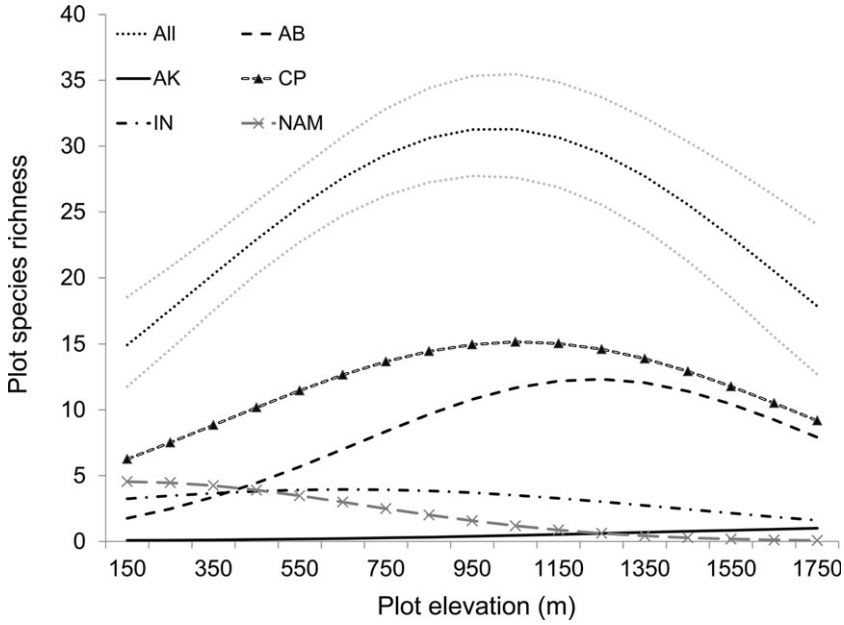


Figure 4 Estimated total vascular plant species richness and estimated species richness of five phytogeographical elements in relation to elevation based on 1022 plot dataset (all plots 200 m^2) from Denali National Park and Preserve, Alaska. Estimates are based on results from the hierarchical model, and all continuous covariates except elevation are set to mean values. The lighter dotted lines bounding the total species richness estimate vector indicate the 95% credible interval. All, total plot species richness; AB, amphi-Beringian species; AK, Alaska–Yukon endemic species; CP, circumpolar species; IN, incompletely circumpolar species; NAM, North American species.

increasing elevation and peaked in high-elevation areas occupied by tundra and fellfields. The influence of elevation on CP species was less strong, but this group also showed a negative quadratic response to elevation, with peak richness occurring at approximately 1100 m. In marked contrast, NAM and IN species richness showed their highest estimated richness at the lowest elevations.

In addition to elevation, other covariates showed significant and contrasting effects on species richness. Each of our models for total and phytogeographical-element richness, except for IN species, identified positive linear responses to slope, and all showed a significant negative response to the quadratic slope term except for NAM species. The NAM element was the only one to show a strong positive response to increasing solar radiation; the remaining elements and total plot species richness were weakly negatively correlated with solar radiation, except for IN species, which showed no significant response (Appendix S3).

In general, plots located in soil polygons classified as continuous permafrost had lower predicted species richness than plots located in discontinuous and sporadic permafrost areas (Appendix S3). The only exception to this was the CP element, which had significantly higher richness in continuous permafrost plots than plots in sporadic permafrost polygons. In contrast, NAM species showed the strongest negative response to increasing prevalence of permafrost.

Variation in estimated species richness among 44 minigrids

The number of species accumulated across 30 plots, estimated by rarefaction-based species accumulation curves for each of 44 sampled minigrids, showed strong differences along the gradient of elevation (Fig. 5). Specifically, the estimates of species richness for the alpine areas were to up to four times greater than those for the low-elevation sampling areas (e.g. nearly 200 species in the high-elevation area versus fewer than 50 at low elevation), and the bootstrapped confidence intervals for high-elevation sample areas do not overlap with those for sampling areas situated in low-elevation regions (< 650 m).

Estimated species richness for the five phytogeographical elements generated by the rarefaction procedure revealed similar general patterns to the results of the plot-level models (Fig 4). For example, the two most pronounced positive responses to increasing elevation were demonstrated by the AB and AK elements with a more than eightfold increase in the estimated total number of species across minigrids observed for both groups. A less pronounced positive response was shown by CP species. At the minigrid level, there was no clear response to elevation by the IN and NAM elements, and confidence intervals overlapped for nearly all sampling areas across the elevation gradient at this spatial scale for these two elements.

Estimated species richness across seven elevation bands

Species richness estimates for the seven elevation bands indicated clear increases in total AB and AK richness at high elevation over those at low elevation, with no overlap in the confidence intervals at the opposite ends of the elevation gradient (Fig. 6a). The relative magnitudes of the increase in species richness for these groups across the gradient of elevation for the seven bands is quite similar to those estimated in our models for plot-level species richness (but less than those for minigrids). That is, estimated total species richness

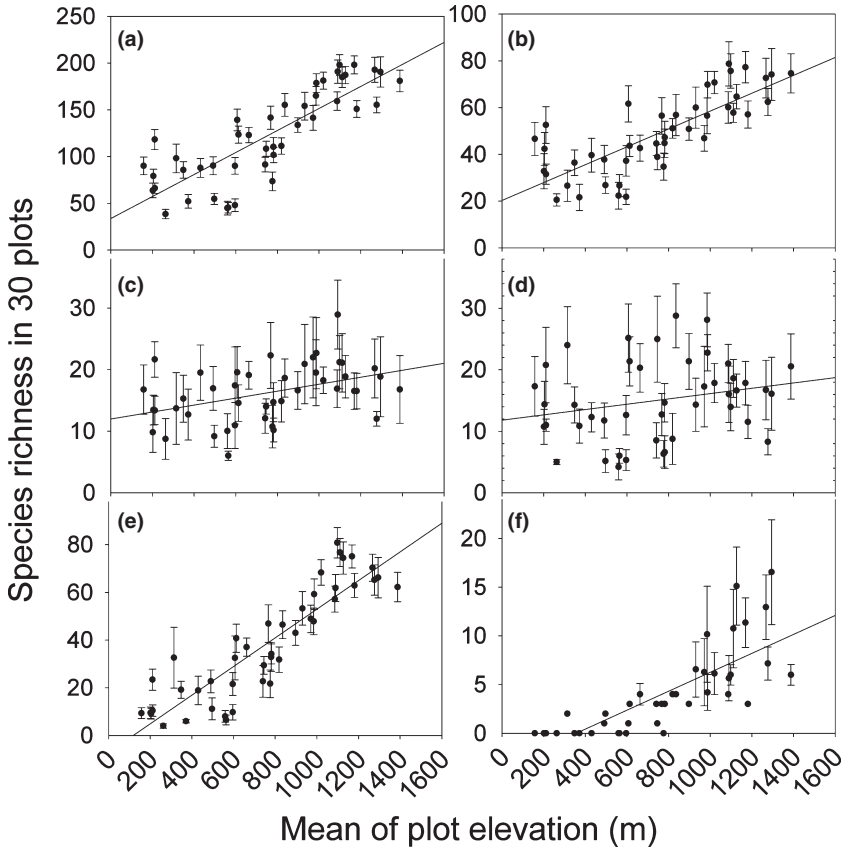


Figure 5 Results of rarefaction and extrapolation analysis across 44 minigrids containing 1022 plots (all plots 200 m^2) in Denali National Park and Preserve, Alaska, estimating (a) the total number of vascular plant species, and the number of species in five phytogeographical elements: (b) circumpolar; (c) incompletely circumpolar; (d) North American; (e) amphi-Beringian; and (f) Alaska–Yukon endemics. Error bars show 95% confidence intervals based on 100 bootstrap samples. Fitted lines are shown for reference purposes only.

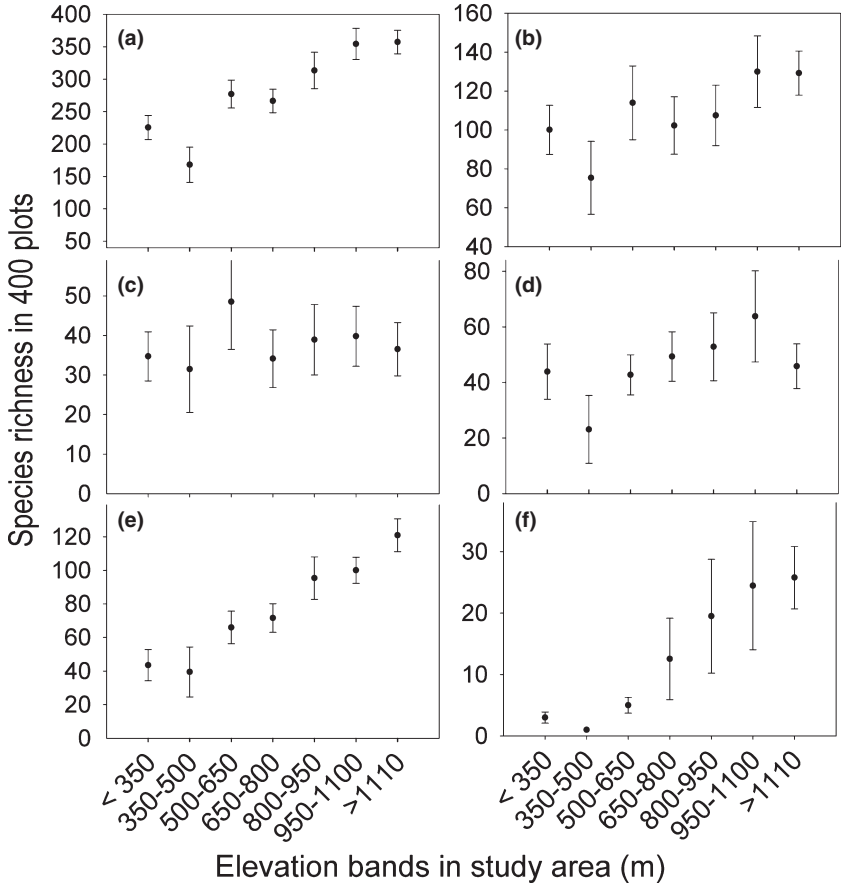


Figure 6 Results of rarefaction and extrapolation analysis across seven elevation bands using the results from 1022 plots (all plots 200 m^2) on a two-stage systematic grid sample in Denali National Park and Preserve Alaska, estimating (a) the total number of species and the number of species in five phytogeographical elements: (b) circumpolar; (c) incompletely circumpolar; (d) North American; (e) amphi-Beringian; and (f) Alaska–Yukon endemics. Error bars show 95% confidence intervals based on 100 bootstrap samples.

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in the > 1100 m band is nearly double that in the lower elevation bands, and AB species richness at high elevation is threefold that estimated for low-elevation bands (Fig. 6b–f). In contrast, the confidence intervals for nearly all of the elevation bands overlap for the IN and NAM phytogeographical elements, with no clear pattern across the elevation gradient.

Summary of the combined dataset

Our full dataset documented the distribution of 641 terrestrial vascular plant taxa across 3023 plots. This represents a nearly complete catalogue of the terrestrial vascular plant flora in the study area. Although Denali NPP has a plant collecting history extending back to the 1920s (Roland, 2004), a comprehensive search of collection records yielded fewer than 10 species that have been collected within the study area but did not occur in at least one of the plots in the full dataset, and each of these 'missing' species was known only from a single locality. The relative contribution of the five phytogeographical elements to the total flora was quite similar for the full and systematic grid datasets (compare Tables 2 and 3).

The lowest-elevation band contained by far the largest number of plots and area sampled of any band (Table 1). Nonetheless, each of the elevation bands above 650 m contained more species than the lowest-elevation band (Tables 1 & 4).

There were clear differences in estimated species richness among the five phytogeographical elements in relation to elevation, with the species richness of both AB and AK species groups clearly increasing steadily with elevation. For example, there was, a 4.5-fold increase in AK species richness across this gradient (Table 4) and the highest-elevation band (> 1100 m) contained more than twice as many AB species as the lowest-elevation band (Table 4), even though the sampling effort was far greater at the lowest elevations.

DISCUSSION

Our work revealed that the number of species occurring above 1100 m – a thoroughly alpine fraction of the landscape, which is dominated by open, low and discontinuous vegetation – was significantly larger than the number of species that occurred in adjacent lowlands dominated by boreal forest and wetlands. This essential pattern held true across datasets and spatial scales including the 200-m^2 plot level, the total number of species across minigrids and richness across seven elevation bands. The pattern of higher diversity in the alpine zone was confirmed by quantitative models that controlled for other significant sources of variation in species richness, including slope, solar radiation, permafrost status and correlation among plots and grids. Finally, a qualitative summary of data from 3023 plots that constituted a near-census of the vascular flora occurring in our study area also supported this fundamental pattern. Combined, these findings support our main hypothesis that a 'reversed' relationship between species richness and elevation occurs in Denali NPP.

The diverse alpine flora in Denali NPP was particularly enriched by species from the AK and AB phytogeographical

Table 3 Summary of the number of species and frequency of occurrence for species in five phytogeographical elements across 3023 vegetation plots (full plot dataset) assembled from multiple large field projects in Denali National Park and Preserve, Alaska.

Phytogeographical element	Number of species	Number of plots (frequency)	Total number of incidences across all plots
Circumpolar (CP)	225 (35%)	3004 (99%)	28,648 (42%)
Incompletely circumpolar (IN)	73 (11%)	2750 (91%)	8986 (13%)
Amphi-Beringian (AB)	169 (26%)	2954 (98%)	20,871 (31%)
North American (NAM)	142 (22%)	2483 (82%)	8449 (12%)
Alaska–Yukon endemic (AK)	32 (5%)	764 (25%)	1330 (2%)
Total species richness	641	3023	68,284

Table 4 Total number of species in five phytogeographical elements within each of seven elevation bands recorded in 3023 plots (full plot dataset) in Denali National Park and Preserve, Alaska. CP, circumpolar; INC, incompletely circumpolar; AB, amphi-Beringian; NAM, North American; AK, Alaska–Yukon endemic.

	Elevation bands (m)						
Phytogeographical element	<350	351–500	501–650	651–800	801–950	951–1100	> 1100
CP species richness	141	115	129	153	139	143	141
INC species richness	50	39	46	49	44	45	37
AB species richness	63	66	84	109	132	134	133
NAM species richness	76	60	62	83	73	74	63
AK species richness	6	8	8	11	22	25	27
Total species richness	336	288	329	405	410	421	401

elements and by CP species, which showed a weaker but still positive response to increasing elevation that decreased above 1250 m. Contrastingly, the NAM and IN elements showed the opposite response, matching our initial predictions. These findings support the species-pool hypothesis, which suggests that site-level diversity patterns are causally linked to diversity patterns at regional scales (Zobel, 1997). Indeed, our results suggest that the plot-level species richness reflected the broad-scale variation in species-pool sizes across the elevation gradient. The large species pool (particularly enriched by CP, AK and AB elements) available in the alpine zone allowed higher species richness to occur in alpine plots than in the lowland plots, where the overall number of species available was constrained by a smaller species pool. The consistent responses in species richness of phytogeographical subgroups across the spatial scales (from plot to minigrid to full study area) provided further evidence that plot-level variation reflects the sizes of species pools across the gradient. Whereas ecological processes operating at the plot level, such as competition, disturbance regime and edaphic conditions, also influence the number of species ultimately present in a given plot, the upper limit of species richness is likely to be higher in Denali NPP's alpine zone because of the larger species pool resident there.

Our finding of an alpine species pool that is larger than that of the adjacent lowlands differs dramatically from many previous studies, including those from northern latitudes (e.g. Bruun *et al.*, 2006). If ours is a unique finding, what accounts for the development of this pattern in interior Alaska? We suspect that the prevalence of climate conditions that favoured tundra and related well-drained, open vegetation over the majority of the past 140 kyr (Muhs *et al.*, 2003) applied a strong filter to the vascular flora of Denali NPP, resulting in a regional species pool relatively depauperate in boreal forest and wetland taxa. According to the species-pool hypothesis (Taylor *et al.*, 1990), the 'larger the local and/or global area of a habitat type and the older its geological age, the greater the past opportunity for speciation and hence, the greater the number of available species that are adapted to that particular habitat type'. In the case of Denali NPP, we propose that the larger species pool in the alpine zone may result (at least in part) from two historical influences: (1) the persistence of populations of plant species with affinities for tundra and related facies across glacial and interglacial periods in open, low-statured plant communities confined to mountainous regions; and (2) the diminution or elimination of dominant shade-tolerant and/or thermophilic and mesophytic boreal taxa and ecosystems from the landscape during glacial advances.

We propose that the net result of these influences has been the persistence of a larger and more consistent niche being available over the long term for taxa broadly adapted to well-drained tundra, fellfield and other sparsely vegetated facies in this region, relative to the niche available for taxa adapted to forests and paludified wetlands.

Numerous palaeoecological studies have provided detailed chronologies for the repeated transformations that have characterized the vegetation history of interior Alaska. Denali NPP is situated in the south-eastern part of the former Beringian refugium on the periphery of the Cordilleran ice sheet (Kaufman *et al.*, 2011). The southern region of Denali NPP south of the Alaska Range crest was mostly covered by ice during the Pleistocene glacial advances. Pleistocene sediments in the Denali NPP region indicate that the lowlands and foothills north of the Alaska Range supported graminoid-tundra vegetation during the Last Glacial Maximum (Elias *et al.*, 1996). Holocene sediments show that the (currently forested) northern lowlands of Denali NPP were still dominated by shrub tundra in the early Holocene, and that coniferous forest only became established after 6.5 ka (Elias *et al.*, 1996). The current lowland vegetation mosaic in Denali NPP is thus of recent origin.

The important differences in plant habitat attributes in the Denali NPP lowlands between those extant during glacial periods and the current landscape include the following attributes of the full-glacial landscape that are not seen today:

1. Widespread well-drained soil conditions (Guthrie, 2001; Swanson, 2006; Viau *et al.*, 2008).

2. Predominance of non-acidic, mineral soils (Guthrie, 2001; Swanson, 2006).

3. Increased influence of wind both in the redistribution of winter snowpack and sediments (Muhs *et al.*, 2003).

4. Open vegetation with reduced competition for light (Edwards *et al.*, 2000; Blinnikov *et al.*, 2011).

Conditions in the current alpine zone are thus more similar to these full-glacial lowland habitats than current lowland conditions are. This has resulted in greater continuity for plant populations in alpine areas during a period when dramatic changes have transformed the lowlands from steppe-tundra to coniferous forest and muskeg. This continuity in the alpine zone is likely to have reduced the extirpation of populations of species that inhabited herb-rich steppe-tundra in alpine areas relative to the level of extirpations of the rich full-glacial flora that occurred across the lowlands (and hence the enrichment of AB and AK species currently in alpine areas). Specifically, the increased frequency of geomorphic disturbance on mountain slopes and colder, shorter growing seasons in the alpine zone have reduced the establishment and dominance of large-statured boreal plants that occurred across the lowlands, and also precluded the establishment of the carpet of feather mosses that transforms edaphic conditions in the lowlands.

An exception to the virtual elimination of open, well-drained habitat in interior Alaska's lowlands are the rare open-steppe sites scattered across the boreal zone of eastern interior Alaska, on south-facing bluffs that are too dry for trees. Interestingly, these sites also contain many AB and AK xerophytes that were likely to have been much more widespread on the full-glacial landscape (Murray *et al.*, 1983; Edwards & Armbruster, 1989; Roland, 1996), and many of which now occur in the alpine zone of interior Alaska.

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Another potential contributing factor to the imbalance between lowland and alpine species pools is the repeated (and recent) isolation of eastern Beringia from source populations of the North American boreal flora. Ice-sheets separated Alaska from source populations of southern North American boreal taxa during full-glacial periods, possibly imposing a considerable lag time and/or filter for recolonization.

Variation in species-pool sizes is certainly not the sole factor regulating site-level plant richness. Indeed, our models showed that slope angle, permafrost status and solar radiation all significantly influenced plot-level total and phytogeographical-element species richness. It is likely that other topographic variables influence plot-level species richness to varying degrees, as has been shown elsewhere (Moeslund *et al.*, 2013). One factor that has been suggested to stimulate higher diversity per unit area in mountainous areas, is the increased habitat heterogeneity caused by complex topography and numerous alpine seeps and streams (Grytnes, 2003). Increased heterogeneity in the alpine zone is also caused by frequent small-scale soil disturbances from solifluction and slope processes.

The influence of habitat heterogeneity in our dataset is evident from a comparison of results across spatial scales. Specifically, our estimates of species richness for minigrids across the elevation gradient revealed much more variation in species richness than observed either for the plot-level or for the regional (elevation bands) scales across the same gradient. The exaggeration in the magnitude of species-richness differences among scales was even more pronounced for the AB, AK and CP elements. It stands to reason that the positive influence of environmental heterogeneity on species richness would be most evident at the mesoscale, because a plot contains little heterogeneity due to its small size, and across the very large elevation bands, the large numbers of plots and extensive area sampled ensure that substantial heterogeneity is contained within all of the elevation bands, lessening the differences among bands. At the minigrid level, however, one study area may be relatively homogeneous (such as a gently sloping permafrost plain), or may contain greater topographic relief or other variation.

It is important to note that the total area occupied by boreal ecosystems in the Denali NPP region is far more extensive than the area currently occupied by alpine ecosystems (Clark & Duffy, 2006). Long-established theory suggests that ecosystems occupying a larger area should contain a larger species pool than smaller adjacent ecosystems, all else being equal (e.g. Taylor *et al.*, 1990), but the expected pattern of larger lowland areas containing more species than the smaller islands supporting alpine ecosystems is not the case in Denali NPP. Our interpretation of this unusual pattern is that the influence of the current imbalance in boreal versus alpine habitat area on species diversity is a recent phenomenon that is overshadowed by the historical imbalance in habitat area, in which open and low-statured, treeless vegetation has predominated over long spans of time and thus contributed to the formation of a larger alpine species pool.

We quantified significant topographic influences on species richness across scales in Denali NPP and provided evidence of the positive influence of a diverse alpine species pool on local plot species richness. Our interpretation of the circumstances that produced the larger alpine species pools is predicated on the idea that tundra and related open vegetation types have predominated in this region in the Quaternary period, maintaining a larger fraction of tundra and xerophytic species than forest-adapted and wetland-adapted species in the regional species pool. Although our results cannot demonstrate causation, the best available palaeoecological evidence suggests that the demonstrably species-poor boreal lowlands in our study area are occupied by a forest and wetland mosaic of recent origin (Elias *et al.*, 1996), and that these new communities replaced a pre-existing forb-rich vegetation mosaic that is likely to have supported a flora with considerable affinities to that found today in alpine areas in the region. In addition, these species-poor lowland communities, frequently situated on poorly-drained, paludified soils, are structurally dissimilar to the open, forb-rich vegetation that has occupied interior Alaska's lowland landscapes for long stretches of their recent past (Willerslev *et al.*, 2014). In contrast, adjacent alpine areas of Denali NPP support larger species pools containing a much higher fraction of species with Alaska–Yukon endemic, amphi-Beringian and circumpolar biogeographical affinities. Species with these distribution patterns may have evolved in this region and/or occurred there during full-glacial intervals when the Bering platform was exposed. Taken together, we find this compelling evidence that historical dynamics have played a role in shaping the size and distribution of the vascular-plant species pool resident on the current landscape.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Box-and-whisker plots of soil attributes.

Appendix S2 Frequency distribution of plot sizes by elevation.

Appendix S3 Parameter estimates for Bayesian hierarchical models of vascular plant species richness.

BIOSKETCHES

Carl Roland is the Plant Ecologist for Denali National Park and Preserve. His interests include the phytogeography and botany of Alaska, landscape-level controls on vegetation patterns and processes in the subarctic, as well as the conservation of biological diversity and natural areas.

Joshua Schmidt is the Biometrician for the US National Park Service's Central Alaska Network. His interests include sampling methodology, survey design, population dynamics and the application of hierarchical modelling approaches to complex ecological questions.

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