

Variability in the expansion of trees and shrubs in boreal Alaska

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Abstract. The expansion of shrubs and trees across high-latitude ecosystems is one of the most dramatic ecological manifestations of climate change. Most of the work quantifying these changes has been done in small areas and over relatively recent time scales. These land-cover transitions are highly spatially variable, and we have limited understanding of the factors underlying this variation. We use repeat photography to generate a data set of land-cover changes in Denali National Park and Preserve, Alaska, stretching back a century and spanning a range of edaphic, topographic, and climatic conditions. Most land-cover classes were quite stable, with low probabilities of transitioning to other land-cover types. The advance of woody vegetation into low-stature tundra, and the spread of conifer trees into shrub-dominated areas, were both more likely at low elevations and in areas without permafrost. Permafrost also reduced the likelihood of herbaceous vegetation transitioning to woody cover. Exceptions to the general trend of relative stability included nearly all (96%) of the broadleaf forest-dominated areas being invaded by conifers, an expected successional trajectory, and many open gravel river bars (17.8%) transitioning to thick shrubs. These floodplain areas were distinctly not at equilibrium, as only 0.1% of shrub-dominated areas converted to gravel. Warming temperatures in coming decades and concomitant declines in the extent of permafrost are predicted to enhance the spread of woody vegetation in Denali further, but only by ~3%. Land-cover transitions, notably the rapid advance of trees and shrubs observed in other studies, could be less likely and more spatially heterogeneous here than in other high-latitude systems.

Key words: arctic; boreal; climate change; land cover; shrubification; succession; tree line.

INTRODUCTION

The effects of climate change are being felt most strongly at high latitudes (Serreze et al. 2000, Chapin et al. 2005). Temperatures are warming, permafrost and sea ice melting, and UV penetrance increasing (Hansell et al. 1998). In recent decades, Alaska has warmed more than twice as fast as the rest of the United States (Stewart et al. 2013). Indeed, “the arctic may be the ‘canary in the coal mine’ of our global climate system” (Foley 2005:628). Climate change impacts on natural communities manifest most at high latitudes for several reasons. First, abiotic changes are generally of greater magnitude (Serreze et al. 2000, Chapin et al. 2005). Second, many arctic and boreal species may exist close to their physiological limits to survival and reproduction (Roots 1989); arctic and alpine species can show relatively strong responses to experimental climate

manipulations (Arft et al. 1999, Elmendorf et al. 2012). Finally, the relative simplicity of high-latitude food webs implies that community structure may be importantly affected by impacts on only a few component species (Hooper et al. 2005).

Among the most dramatic climate-driven ecological change occurring at high latitudes is the rapid advance of shrubs and trees into low-statured tundra (Myers-Smith et al. 2011, Lin et al. 2012, Pastick et al. 2018), particularly at low elevations (Rinas et al. 2017). Over the latter half of the 20th century, Alaska has experienced a 43% increase in tall shrub cover (Chapin et al. 2005) as well as upward and northward expansions of tree lines (Harsch et al. 2009). These community changes are thought to be largely driven by warming winter temperatures and associated changes in permafrost (Epstein et al. 2004, Harsch et al. 2009, Elmendorf et al. 2012).

These changes are important globally; shrub expansion increases net primary productivity but also increases respiration, elevates heat absorption, and decreases albedo (Euskirchen et al. 2009); thus high-latitude shrub and tree expansion may exacerbate global climate change

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(Chapin et al. 2009). Indeed, the carbon cycle is increasingly susceptible to climate change and human activities (McGuire et al. 2009). By altering precipitation runoff and hydrology over vast spatial scales, the shift from tundra to tall woody vegetation could also affect global climate by affecting freshwater provisioning to the Arctic Ocean (McGuire and Chapin 2006).

To date, there has been a research emphasis on documenting high-latitude land-cover transitions (Klein et al. 2005, Tape et al. 2006, Dial et al. 2007, Post et al. 2009) and assessing transition rates relative to rates of warming (e.g., Dial et al. 2016). Critically, however, we still have a limited understanding of what drives the variability where shrub expansion, tree-line advance, and other land-cover transitions have occurred and are occurring (Danby and Hik 2007, Lin et al. 2012). Changes from tundra to shrubland or forest are very obvious in some areas, but in other areas are slow or not occurring (Tape et al. 2012, Roland et al. 2016). Though some contributing factors have been identified (e.g., Frost et al. 2013, Swanson 2015, Pastick et al. 2018), the variation in shrub and tree expansion is not well understood and is spatially variable, representing a complex interplay between climate and soil conditions (Brenning 2008, Tape et al. 2012, Roland et al. 2013, 2016), topography (Roland et al. 2013), herbivory (Post and Pedersen 2008, Gornall et al. 2009, Olofsson et al. 2009), and disturbances such as fires (Higuera et al. 2009, Roland et al. 2013, 2016).

Here, we combine several data sets to assess the factors driving variability in land-cover transitions in an iconic high-latitude landscape, Denali National Park and Preserve, in interior Alaska, over a uniquely long time frame. We compiled a database of historical photographs and their modern analogues stretching back nearly a century, which provides a detailed picture of land-cover changes over time. As Denali has been studied in more detail than most other boreal and arctic landscapes, we are able to use high-resolution data on the extent of soils, permafrost, and topography to elucidate the environmental factors associated with land-cover changes.

METHODS

Study system

Denali National Park and Preserve, United States, straddles boreal forest, tundra, and montane glaciers along the Alaska Range in central Alaska. Much of the area is dominated by spruce (*Picea* spp.) forest and dwarf birch (*Betula* spp.), with extensive portions of low-statured tundra and herbaceous vegetation (Roland et al. 2013). Several glacial outflow rivers wind through the park in braided gravel drainages.

Mean annual temperatures at the park headquarters (at the eastern edge of our study area) were -3°C from 1971 to 2000, with peaks in July (20°C) and troughs in

January (-22°C ; Shulski and Wendler 2007). Mean annual precipitation at park headquarters was 38 cm, mostly falling between June and August (Sousanes 2008). A primarily gravel road goes ~ 150 km into the park from the east. Otherwise, recent human disturbance in most of the park (except for the headquarters and visitor center areas and the community of Kantishna at the end of the park road) are relatively minimal.

We focused our study on the portions of the park north of the Alaska Range, as they constitute a different set of ecoregions from the areas south of the range. Our study area was $3,136\text{ km}^2$ in total, centered at 63.616° N , 150.738° W , with an elevation range of $280\text{--}1,370\text{ m}$ (Fig. 1; Appendix S1: Table S1).

Data collection

We gathered high-resolution scans of historical photographs cataloged in various digital and physical archives. Historical photos of the park and surrounding areas were taken by early scientists, residents, and visitors to the park. For example, ~ 40 images were taken by Joseph Dixon, who conducted some of the first scientific surveys of the area in 1926 and 1932. Dozens of additional photographs in the collection used for analysis were taken aerially as part of a wildlife habitat survey by Fred Dean in 1976. These images are not a random sample or necessarily representative of historical land covers. For our analyses, we chose historical photographs where the location could be identified with certainty through (1) descriptions on the photographs themselves, or (2) land forms visible in the image. We visited sites by vehicle, foot, or aircraft (2005–2016; Appendix S1: Fig. S1; Table S1) and took modern analogues of the photographs, matching angle and field of view as best as possible. All historical photos, matched with their modern analogs, are publicly available at <http://denalirepeat.photos.uaf.edu/> (accessed 15 March 2018).

We used monoplotted (cf. Stockdale et al. 2015) to map the land-cover types visible in the oblique-angle photographs onto three-dimensional landscape maps. To do this, we entered the GPS points where each photograph pair was taken into Google Earth® (Landsat/Copernicus imagery) and rotated the scene vertically and horizontally until the view was the same as in the photographs. We then drew polygons in Google Earth corresponding to the land-cover types in each historical and modern photo (see Appendix S1: Fig. S2 for an example).

Such monoplotted can potentially induce a number of biases, which we sought to minimize. First, in any given photograph pair, the historical photograph had lower resolution, was often gray scale instead of color, and was usually less sharp. Together, this means that it could be much more difficult to ascertain the land-cover types in the historical photograph than in the modern one, which could bias our estimates of land-cover change. To account for this, polygons were only drawn

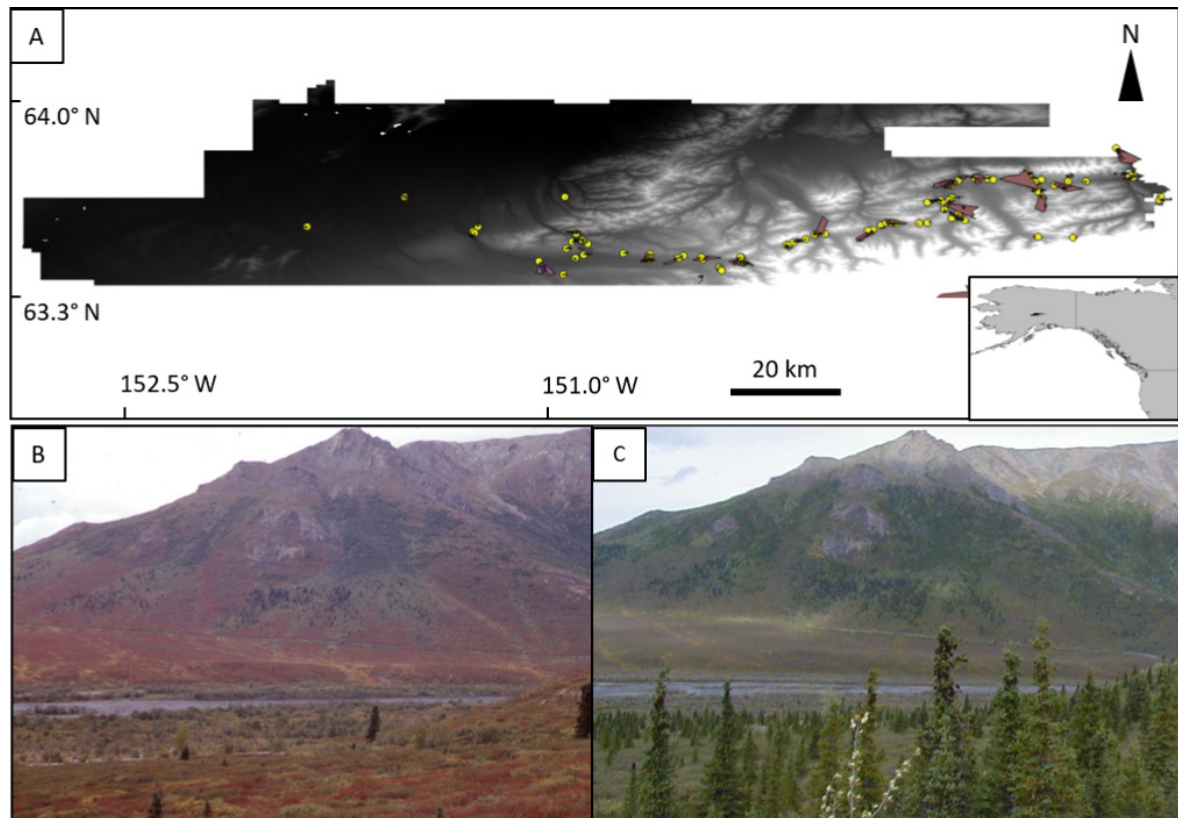


FIG. 1. (A) Elevation map of the study area in Denali National Park & Preserve ranging from 135 m (black) to 2,670 m (white), with repeat-photograph locations (circles) and land-cover polygons. An example photograph pair, the Savage River and Denali park road in (B) 1958 and (C) 2001. Photo credits: L. Viereck.

where land-cover types, and the boundaries between types, were clearly identifiable in both of the photographs. Second, monoplottting is most accurate when mapping oblique photographs onto hillsides or mountain slopes, because the ground surface in those areas is less oblique relative to the observer. The ideal in repeat photography is to have orthophotographs, where the landscape is perpendicular to the observer. Most (68.4%) of the photographs in our data set were taken from ground level, with a mountain or ridge in the midground or background. For these, we drew polygons almost exclusively on the midground of the images, where monoplottting error was lower. This also reduced the influence of any error in relocating the original photograph site, because such errors would result in inaccuracies in the foreground but not areas farther removed from the observer. Therefore, the proportion of each image that was used for our analysis was usually much less than one.

For any given photograph pair, the areas where high-confidence land-cover polygons overlapped in the historical and modern photographs constituted the total area of analysis for that pair. We assessed changes in land cover between the historical and modern photographs only within those areas. In other words, even though a

modern photograph may have had many additional areas where we could reliably determine land-cover type, we did not use those extra areas for analysis.

We assigned polygons to the following land-cover categories: Forest-conifer (white spruce [*P. glauca*], black spruce [*P. mariana*], and larch [*Larix laricina*]), Forest-broadleaf (cottonwood [*Populus balsamifera*], aspen [*P. tremuloides*], and resin birch [*Betula neoalaskana*]), Forest-mixed (conifer and broadleaved species together), Shrub (mostly dwarf birch, willow [*Salix* spp.], and alder [*Alnus* spp.]), Tundra (prostrate shrubs mixed with forbs and graminoids), Graminoid-forb meadow, River bar gravel (in braided glacial outwash floodplains), and Scree (loose gravel on steep slopes). In some cases, it was possible to distinguish subcategories, for example, dwarf birch versus alder shrubs based on their relative height and visual texture, but we considered this to be unreliable in many of the photographs, so we used the more general categories (e.g. “Shrub”).

We overlaid a 100×100 m grid of points across the park; grid points that fell inside land-cover polygons were assigned the historical and modern land-cover values for that polygon. Grid points were then used as the sampling unit in subsequent analyses; in other words, we

assessed land-cover transitions across grid points as a function of the environmental attributes of each point, while accounting for spatial autocorrelation among points (see Data Analysis).

We assessed the accuracy of the monoplotted by validating the predicted land-cover classes against estimated land cover from two other sources. First, we used a park-wide map of land cover based on remote sensing data (Stephens et al. 2001). Second, we used a 1,236-ha land-cover polygon generated from intensive ground-based surveys in the Muldrow Glacier terminus area (Roland et al. 2016). In both cases, we restricted the validation analysis to points within our repeat-photography data set that were obtained within 10 yr of the other data source, to minimize differences attributable to temporal vegetation changes.

Data analysis

We hypothesized that several factors (Appendix S1: Table S2) could affect the probabilities of transition among land-cover types. Warming temperatures have long been suspected of driving land-cover changes at high latitudes (Chapin et al. 2004, Elmendorf et al. 2012, Dial et al. 2016, Rinas et al. 2017), and surface temperatures in this region vary strongly with elevation and other terrain factors (Sadoti et al. 2018). We assessed land-cover transitions as a function of *elevation* in one set of models and as a function of *temperature* in a second set of models (elevation and temperature could not be included together because they are highly correlated: $r = -0.88$). We also included potential *solar radiation* as a predictor variable, which is determined by aspect, slope, and shading from surrounding hills and mountains. Elevation data were extracted from a digital elevation model of the park (see Roland et al. 2013); this same model was used to calculate solar radiation using the RSAGA package (Brenning 2008) in R (R Core Team 2017). Data on current mean temperature were obtained from WorldClim (<http://www.worldclim.org/>; cited 15 April 2018).

Two important dynamics affecting vegetation patterns in Alaska are permafrost (Epstein et al. 2004, Tape et al. 2012) and the disturbance and edaphic conditions influenced by flowing water in floodplain environments (Tape et al. 2012, Roland et al. 2016). We used a binary metric to delineate *permafrost* areas, using the model of Panda et al. (2014). Points were considered to be in floodplain if their underlying lithology was *alluvium*, based on the soil map of Clark and Duffy (2006).

The expansion of forest in Alaska (as elsewhere) depends on the availability of tree seeds (Stueve et al. 2011). Indeed, current forest expansion in interior Alaska and other high-latitude areas could represent ongoing recolonization of areas scoured during the most recent Pleistocene glaciation, potentially sped up by recent anthropogenic climate change (Chapin et al. 2004, Dial et al. 2016). The southern edge of our study area is defined by the Alaska Range massif, which forms

a long barrier to seed dispersal. The core of the study area is separated from boreal lowlands to the north and west by mountainous terrain that impedes dispersal of spruce seeds from boreal regions of interior Alaska, except through river valleys. Thus, large parts of the study area, while they may contain habitat suitable for colonization by spruce, likely experience very limited seed rain. We accounted for this marked variation in spruce seed availability with a binary metric delineating areas subject to *spruce limitation*, determined by expert knowledge by one of us (CR), based on a spatial model predicting *P. glauca* occupancy from a data set containing plant distribution and covariate data for 3,023 sites distributed across the national park (Appendix S1: Figs. S3, S4; also see Roland and Schmidt 2015). Finally, the period of *time* between the historical and modern photographs was included as a predictor variable, as longer periods had more time available for land-cover change to occur. Within the elevation models, correlations among the continuous predictor variables were low (*elevation* and *slope*: $r = 0.39$, *elevation* and *solar radiation*: $r = -0.09$, *slope* and *solar radiation*: $r = 0.03$).

For each land-cover class in the historical photographs we ran a global logistic mixed-effects model, with all of the above factors and a quadratic term for *elevation*, to assess probabilities of binary land-cover transition. As our sampling was spatially clustered (grid points within photograph pairs), we included *photograph* as a random effect. We then used backward-elimination stepwise procedures, sequentially removing nonsignificant variables in order of absolute *z*-score until the final model contained only significant environmental variables. If both elevation and permafrost or alluvium were included in the final model, we added *elevation* $\times$ *permafrost* or *elevation* $\times$ *alluvium* interaction terms and evaluated their significance. We assessed each model's predictive ability using the area under the receiver operating characteristic curve (AUC), including the partial AUC for sensitivity of 80–100%.

Finally, we used the most parsimonious temperature models to predict future land-cover changes across the study area. Of the environmental factors used in our models, temperature and permafrost are predicted to change across the region. We used predicted permafrost distributions from Panda et al. (2014), and predicted mean temperatures from WorldClim to assess how the cover of woody vegetation (shrubs and trees) will change from 2001 (using the estimates of Stephens et al. 2001) to 2050. Specifically, we used an ensemble of three general circulation models used by Panda et al. (2014) that were identified as the best performers for Alaska and that are available in downscaled 30° resolution: GFDL-ESM2G, HadGEM2-AO, and MIROC5 (all based on relative concentration pathway 6.0). To compare the relative effects of warming temperatures and declining permafrost on shrub and tree advance, we predicted woody vegetation cover in 2050 based on changes in each factor alone as well as together.

RESULTS

Of the approximately 300 photograph pairs in the database, we used 94 for analysis where we were able to identify and classify confidently for each year at least one pair of overlapping land-cover polygons. Dates of the historical photographs ranged from 1906 to 1990 (median = 1956; Appendix S1: Fig. S1). The average length of time between historical and modern photographs within a given pair was 58.6 yr (SD = 26.7; range = 19–106). On average, historical and modern photographs contained 2.3 (0.9; range = 1–4) and 2.3 (1.1; range = 1–5) different land-cover types, respectively. A total of 19,220 grid points fell within the cumulative area of the photographs with identifiable land cover, with an average of 222.1 (355.7; range = 1–2,198) points per photograph pair. Photograph points were concentrated along the park road corridor (Fig. 1).

Validation of the monoplotting suggests that for the transitions from nonwoody to woody vegetation classes (or woody shrub to tree) assessed here, monoplotting generated land-cover estimates that were consistent with estimates from other sources. Differences in shrub classification (i.e., proportions of points that were classified as shrubs in the modern photographs but that were classified differently by other sources) were 0.093, 0.007, 0.063, and 0.005 for conifer forest, gravel, tundra, and graminoid, respectively, using the Stephens et al. (2001) land-cover map, and 0, 0, 0.046, and 0, respectively, using the Muldrow Terminus polygon (there was no conifer forest or graminoid meadow in this polygon). Differences in conifer forest classification were 0.167, 0.003, 0.003, and 0.008 for shrubs, gravel, tundra, and graminoid, respectively, using the land-cover map. (Differences in shrub classification between the Muldrow polygon and the land-cover map at the photograph grid points were 0, 0.003, 0.390, and 0 for conifer forest, gravel, tundra, and graminoid, respectively.)

In the historical photographs, 61.1% of points were Shrub, 26.7% were Forest-conifer, and 5.9% were River

bar gravel (Table 1). In the modern photographs, 60.1% of points were Shrub, 29.2% were Forest-conifer, and 4.5% were River bar gravel (Table 1). Overall, 6.5% of points changed from one land-cover type to another between the historical and modern photographs (Table 1).

Points that were Forest-conifer, Forest-broadleaf, Forest-mixed, and Scree in the historical photographs had too little variation in the dependent variable for models to converge or to provide reliable coefficient estimates; either extremely few or almost all the points transitioned (Table 1). For these land-cover classes, we measured average land-cover transition probabilities (i.e., as presented in Table 1), but could not determine whether those rates varied as functions of environmental variables (i.e., as presented in Table 2).

For points that started as Shrub, 95.6% stayed Shrub (Table 1). Transitions from Shrub to conifer forest (Forest-conifer + Forest-mixed) were more likely at low elevations and in sites without permafrost, that were not subject to spruce seed limitation, and that were outside of alluvial floodplains (Table 2; Fig. 2). Points starting as Graminoid-forb tended to stay Graminoid (81.4%), with some transition to Shrub (18.6%; Table 1). Transition of Graminoid-forb land cover to woody vegetation (Shrub + Forest-conifer) was most likely in areas without permafrost (Table 2; Fig. 3). Points starting as Tundra tended to stay Tundra (76.3%; Table 1). Transitions from Tundra to woody vegetation (Forest + Shrub) were more likely in areas without permafrost (Table 2; Fig. 3). Points starting as River bar gravel either stayed in this class (74.9%) or transitioned to Shrub (25.1%). For this analysis, we did not include *alluvium* in the global model because this land-cover class is, by definition, in floodplain areas. Transitions of gravel to Shrub were not significantly affected by any environmental covariates that we tested (Table 2).

Based on the land-cover map of Stephens et al. (2001), shrubs and trees covered 76.0% of the study area in 2001 (Appendix S1: Fig. S5A). Using our land-cover transition models, we estimated that, in 2050, woody

TABLE 1. Percentage of grid points in each land-cover class in the historical photographs (rows) that transitioned to each land-cover class in the modern photographs (columns). Each row sums to 100% ($\pm$ rounding error). The total number of grid points (sampling units) in each land-cover class in the historical and modern photographs are shown in the last column and row, respectively.

	Forest-conifer	Forest-mixed	Forest-broadleaf	Shrub	Graminoid-forb	Tundra	River bar gravel	Scree	Total number of points
Forest-conifer	99.6	0	0	0.4	0	0	0	0	5,127
Forest-mixed	1.8	98.2	0	0	0	0	0	0	111
Forest-broadleaf	1.1	96.0	2.9	0	0	0	0	0	276
Shrub	4.2	0.1	0	95.6	0	0	0.1	0	11,746
Graminoid-forb	0	0	0	18.6	81.4	0	0	0	102
Tundra	2.9	4.7	0.5	15.6	0	76.3	0	0	596
River bar gravel	0	0	0	25.1	0	0	74.9	0	1,133
Scree	1.6	0	0	0.8	0	0	0	97.7	129
Total number of points	5,620	411	14	11,648	83	455	863	126	19,220

TABLE 2. Final land-use transition models, following stepwise removal of nonsignificant environmental predictor variables from logistic mixed-effects regression models; elevation (E) and temperature (T) were included in separate models because of high correlation. Model predictive accuracy is indicated by the full and partial (80–100% range) area under the receiver operating characteristic curve (AUC and pAUC).

Historical land cover	Transition to	Cases: controls	Model	Estimated model coefficients (SE)		
				E	T	Slope
Shrub	Forest (mixed + conifer)	499: 11233	E	−1.84 (0.27)	–	–
			T	–	0.96 (0.2)	–
Graminoid – forb	Shrub	19: 83	E	–	–	–
			T	–	–	–
Tundra	Shrub or Forest	141: 455	E	–	–	–
			T	–	3.46 (0.68)	1.35 (0.45)
River bar gravel	Shrub	248: 849	E	–	–	–
			T	–	–	–

vegetation would cover 77.5% of the study area because of declines in the extent of permafrost alone, 78.9% because of warming temperatures alone, or 79.2% because of changes in both permafrost and temperature (Appendix S1: Fig. S5B).

DISCUSSION

The advance of tall shrubs and trees into tundra is one of the most striking ecological changes of arctic and

montane tundra ecosystems, but drivers of the variation in these transitions have been poorly understood. Our study provides an assessment of land-cover transitions in the vegetation mosaic of a high-latitude ecosystem spanning a century of change. Perhaps surprisingly, we found that most of the land-cover types in the portions of the landscape covered by our photograph pairs were quite stable over this interval. Forest encroachment of shrubs and shrub encroachment of tundra were relatively low. The rapid advance of arctic and boreal woody

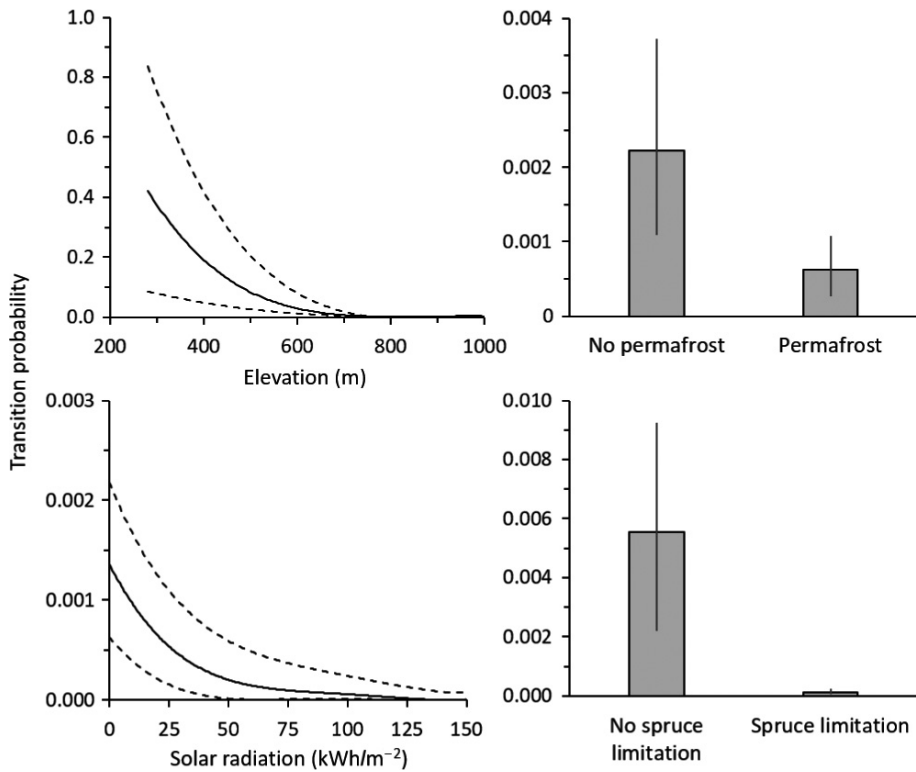


FIG. 2. Environmental factors significantly related to the probability of shrub transitioning to forest. Dashed lines and error bars show 95% bootstrap confidence limits.

Solar radiation	Permafrost	Alluvium	Spruce limitation	Elevation: permafrost	AUC	pAUC
−0.7 (0.3)	−1.22 (0.22)	—	−3.56 (1.24)	−0.55 (0.24)	0.96	0.93
−0.84 (0.29)	−1.03 (0.2)	−1.03 (0.53)	−4.79 (1.18)	—	0.96	0.93
—	−2.35 (1.15)	—	—	—	0.97	0.94
—	−2.35 (1.15)	—	—	—	0.97	0.94
—	−2.23 (0.48)	—	—	—	0.99	0.98
—	−3.2 (0.88)	−4.93 (1.32)	—	—	0.99	0.99
—	—	—	—	—	0.84	0.78
—	—	—	—	—	0.84	0.78

vegetation reported in other studies (e.g., Tape et al. 2006, Harsch et al. 2009, Dial et al. 2016) could be more spatially sporadic than has been generally appreciated (Tape et al. 2012, Myers-Smith and Hik 2018). Factors causing spatial variability may relate to interactions among factors such as variation in landscape age (deglaciation) and associated soil development and dispersal dynamics of different elements of the biota, among other factors.

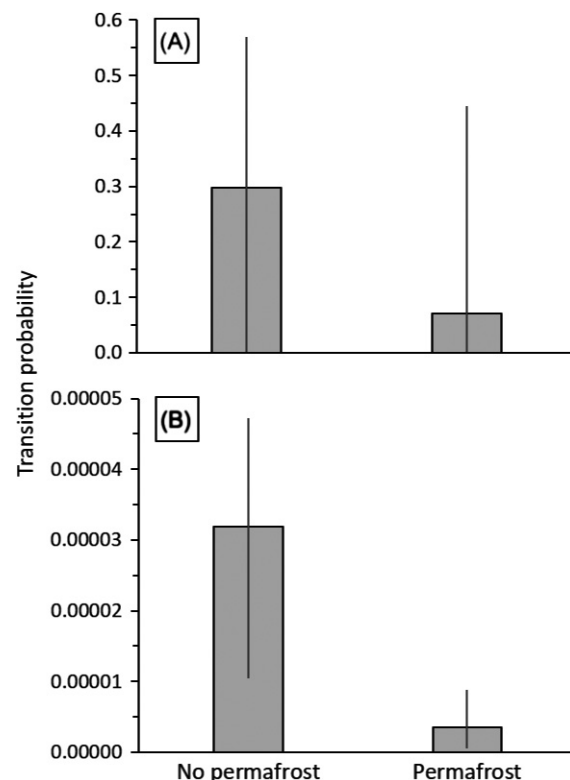


FIG. 3. Effects of permafrost on the probability of (A) graminoid-forb meadow and (B) tundra transitioning to woody vegetation (shrub or forest). Error bars show 95% bootstrap confidence intervals.

The relative stability that we observed in most land-cover classes appears to have been particularly high in shallow permafrost and high-elevation areas (Appendix S1: Fig. S6). That permafrost can act to retard the rate of land-cover change has been observed in other studies (e.g., Danby and Hik 2007, Roland et al. 2016). Indeed, cold, poorly drained soils associated with permafrost support slower plant growth for several reasons, including reduced nutrient turnover and availability (Schuur et al. 2007), inhibition of water uptake, and slower root growth (Chapin et al. 1986). But climatic changes over the next few decades are predicted to increase temperatures in interior Alaska, resulting in dramatic melting of permafrost (Panda et al. 2014). Our analysis predicts that changes in temperature alone may increase woody vegetation cover by 2.9% across the study area by 2050, and changes in permafrost alone generate predicted increases of 1.5%. This suggests that the direct effects of warming temperature on plant distributions (which likely integrate both species-specific ecophysiological responses and altered competition dynamics) may be slightly stronger than the indirect effects of temperature via melting permafrost. Nevertheless, even changes in both factors together only lead to a predicted increase in shrub and tree cover of 3.2 percentage points across the study area by 2050, assuming that disturbance dynamics—which are known to have a strong impact on land-cover transitions (Johnstone et al. 2016, Roland et al. 2016)—remain constant.

Several other important site factors that may have impeded the expansion of woody vegetation despite sharply warming temperatures have been identified in arctic Alaska (Swanson 2015). For example, soil limitations restricting tall shrub growth, including poor drainage, shallow rooting depths, and high acidity, can all preclude the formation of closed shrub canopies even if climate warms sufficiently to otherwise allow such expansion in woody plant cover (Swanson 2015). Thus, the interaction of site factors that can impede woody plant expansion and competition within intact late-

successional vegetation have likely acted to reduce the footprint of vegetation transitions on the landscape.

In contrast to our general observations of relative stability, we observed fairly rapid land-cover changes in many of the braided, glacial-outflow river courses. These areas had a high probability (25.1%) of transitioning from bare gravel to thick shrubs. The vegetation dynamics in these areas were not at equilibrium, as evidenced by the very low transition of shrub to gravel (0.1%). There are two likely contributors to this pattern. First, this could reflect the importance of disturbance in catalyzing land-cover change in the context of a warming landscape, wherein newly disturbed areas are much less resistant to change because there is less standing vegetation to compete with arriving propagules (Roland et al. 2016). Newly exposed disturbed areas are thus more likely to support increased recruitment in response to expanded reproductive output of adjacent vegetation. Changes in newly disturbed sites may therefore reflect a release from “resilience debt” (Johnstone et al. 2016), and presage the establishment of a future, and different, trajectory of species composition in the community. Secondly, there was a large flood event that occurred in central Alaska (including Denali) in 1967 (Childers et al. 1972), which likely caused significant scouring and disturbance of many riparian areas within the park. Some of the vegetation expansion observed in our photograph pairs after 1967 may represent recovery and re-establishment of vegetation following this flood event, rather than a directional change.

Indeed, altered disturbance regimes could critically affect many land-cover transitions. Evidence from Denali suggests that flooding events and their geomorphic consequences may be increasing in prevalence (Crossman et al. 2013), and increased disturbance will likely catalyze more rapid vegetation change by removing established plant cover in areas where newly exposed surfaces may follow an altered successional trajectory (Roland et al. 2016). For example, several large landslides have occurred in Denali in recent years. These and other disturbances can dramatically increase the rate of land-cover change by removing the impediment of standing vegetation, allowing recolonization by plant species based on current (rather than historical) climatic preference (Johnstone et al. 2010, Roland et al. 2016).

In more boreal areas of interior Alaska, increasing frequency of fires (Johnstone et al. 2010, Shenoy et al. 2011), and possibly phytophagous insect outbreaks (Volney and Fleming 2000), are posited to drive the replacement of spruce forests with broadleaf forests or grasslands. We found no evidence of this in our cooler, largely montane study area, in that fire and bark beetles have had relatively little impact over the last century in the areas of Denali covered by our photograph pairs. In our study area, the trend in forest composition appears to have been from broadleaf to conifer, an expected successional trajectory (Roland et al. 2013, 2016).

Our analysis focused on transitions among coarse-scale land-cover types. We note that many finer-scale changes in vegetation could have occurred in our study area that we did not detect, as they were not the focus of the study. Altered distributions of individual species have been observed in many systems (e.g., Kelly and Goulden 2008, Rinas et al. 2017) and could very well outpace changes in land-cover type. There may have also been increases in woody plant height (Tape et al. 2012) and cover (Pastick et al. 2018) in areas already classified as Shrub (i.e., that did not undergo a coarse land-cover transition). Indeed, it seems likely that increases in the stature and biomass of existing individuals and clones would be a common initial response to ameliorating conditions in systems such as ours, which are dominated by long-lived perennial species (e.g., Walker et al. 2006).

As with any large-scale mapping of land-cover types, our monoplotting is associated with some amount of error. We validated the land-cover estimates using this method against those from two other methods, and found generally high consistency among them. Land-cover class estimates from the ground-based surveys in the Muldrow Terminus are likely very accurate, but these surveys covered a small area relative to the park as a whole. Importantly, we cannot determine whether the broader-scale Stephens et al. (2001) land-cover map or our monoplotting estimates were closer to the truth, but the fact that all of the estimates were reasonably consistent indicates that the monoplotting methodology used here is reproducible.

Incorporating site-level dynamics that can act to enhance or impede land-cover change is important to avoid bias in large-scale modeling efforts, many of which strictly use climatic factors in predictions of changing distributions of species and functional groups (but see Rinas et al. 2017). Additional research is needed to understand the cumulative impacts of high-latitude land-cover changes on populations and spatial structure of plant (as well as consumer) species in the region, and also to assess overall changes to the distribution of biodiversity across high-latitude systems.

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LITERATURE CITED

- Arft, A. M., et al. 1999. Responses of tundra plants to experimental warming: meta-analysis of the international tundra experiment. *Ecological Monographs* 69:491–511.
- Brenning, A. 2008. Statistical geocomputing combining R and SAGA: The example of landslide susceptibility analysis with generalized additive models. *SAGA—Seconds Out* 19:23–32.

- Chapin, F. S., T. V. Callaghan, Y. Bergeron, M. Fukuda, J. Johnstone, G. Juday, and S. Zimov. 2004. Global change and the boreal forest: thresholds, shifting states or gradual change? *AMBIO: A Journal of the Human Environment* 33:361–365.
- Chapin, F. S., J. McFarland, A. D. McGuire, E. S. Euskirchen, R. W. Ruess, and K. Kielland. 2009. The changing global carbon cycle: linking plant–soil carbon dynamics to global consequences. *Journal of Ecology* 97:840–850.
- Chapin, F. S., K. Van Cleve, and P. R. Tryon. 1986. Relationship of ion absorption to growth rate in taiga trees. *Oecologia* 69:238–242.
- Chapin, F. S., III et al. 2005. Role of land-surface changes in arctic summer warming. *Science* 310:657–660.
- Childers, J. M., J. P. Meckel, and G. S. Anderson. 1972. Floods of 1967 in east-central Alaska. U.S. Geological Survey, Water Supply Paper Number 1880-A. Government Printing Office, Washington, D.C., USA.
- Clark, M., and M. Duffy. 2006. Soil survey of Denali National Park area, Alaska. National Cooperative Soil Survey. <http://soildatamart.nrcs.usda.gov/Manuscripts/AK651>
- Crossman, J., M. N. Futter, and P. G. Whitehead. 2013. The significance of shifts in precipitation patterns: modelling the impacts of climate change and glacier retreat on extreme flood events in Denali National Park, Alaska. *PLoS ONE* 8: e74054.
- Danby, R. K., and D. S. Hik. 2007. Variability, contingency and rapid change in recent subarctic alpine tree line dynamics. *Journal of Ecology* 95:352–363.
- Dial, R. J., E. E. Berg, K. Timm, A. McMahon, and J. Geck. 2007. Changes in the alpine forest–tundra ecotone commensurate with recent warming in southcentral Alaska: Evidence from orthophotos and field plots. *Journal of Geophysical Research: Biogeosciences*. <http://dx.doi.org/10.1029/2007jg000453>
- Dial, R. J., T. S. Smeltz, P. F. Sullivan, C. L. Rinas, K. Timm, J. E. Geck, S. C. Tobin, T. S. Golden, and E. C. Berg. 2016. Shrubline but not treeline advance matches climate velocity in montane ecosystems of south-central Alaska. *Global Change Biology* 22:1841–1856.
- Elmendorf, S. C., G. H. Henry, R. D. Hollister, R. G. Björk, A. D. Björkman, T. V. Callaghan, L. S. Collier, E. J. Cooper, J. H. Cornelissen, and T. A. Day. 2012. Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time. *Ecology Letters* 15:164–175.
- Epstein, H., J. Beringer, W. Gould, A. Lloyd, C. Thompson, F. S. Chapin, G. Michaelson, C. Ping, T. Rupp, and D. Walker. 2004. The nature of spatial transitions in the Arctic. *Journal of Biogeography* 31:1917–1933.
- Euskirchen, E. S., A. D. McGuire, F. S. Chapin, S. Yi, and C. C. Thompson. 2009. Changes in vegetation in northern Alaska under scenarios of climate change, 2003–2100: implications for climate feedbacks. *Ecological Applications* 19:1022–1043.
- Foley, J. A. 2005. Tipping points in the tundra. *Science* 310:627–628.
- Frost, G. V., H. E. Epstein, D. A. Walker, G. Matyshak, and K. Ermokhina. 2013. Patterned-ground facilitates shrub expansion in Low Arctic tundra. *Environmental Research Letters* 8:015035.
- Gornall, J. L., S. J. Woodin, I. S. Jonsdottir, and R. van der Wal. 2009. Herbivore impacts to the moss layer determine tundra ecosystem responses to grazing and warming. *Oecologia* 161:747–758.
- Hansell, R. I. C., J. R. Malcolm, H. Welch, R. L. Jefferies, and P. A. Scott. 1998. Atmospheric change and biodiversity in the arctic. Kluwer Academic Publishers, Dordrecht, Netherlands.
- Harsch, M. A., P. E. Hulme, M. S. McGlone, and R. P. Duncan. 2009. Are treelines advancing? A global meta-analysis of treeline response to climate warming. *Ecology Letters* 12:1040–1049.
- Higuera, P. E., L. B. Brubaker, P. M. Anderson, F. S. Hu, and T. A. Brown. 2009. Vegetation mediated the impacts of post-glacial climate change on fire regimes in the south-central Brooks Range, Alaska. *Ecological Monographs* 79:201–219.
- Hooper, D. U. et al. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* 75:3–35.
- Johnstone, J. F., C. D. Allen, J. F. Franklin, L. E. Frelich, B. J. Harvey, P. E. Higuera, M. C. Mack, R. K. Meentemeyer, M. R. Metz, and G. L. Perry. 2016. Changing disturbance regimes, ecological memory, and forest resilience. *Frontiers in Ecology and the Environment* 14:369–378.
- Johnstone, J. F., T. N. Hollingsworth, F. S. Chapin, and M. C. Mack. 2010. Changes in fire regime break the legacy lock on successional trajectories in Alaskan boreal forest. *Global Change Biology* 16:1281–1295.
- Kelly, A. E., and M. L. Goulden. 2008. Rapid shifts in plant distribution with recent climate change. *Proceedings of the National Academy of Sciences* 105:11823–11826.
- Klein, E., E. E. Berg, and R. Dial. 2005. Wetland drying and succession across the Kenai Peninsula Lowlands, south-central Alaska. *Canadian Journal of Forest Research* 35:1931–1941.
- Lin, D., D. Johnson, C. Andresen, and C. Tweedie. 2012. High spatial resolution decade–time scale land cover change at multiple locations in the Beringian Arctic (1948–2000s). *Environmental Research Letters* 7:025502.
- McGuire, A. D., and F. S. Chapin. 2006. Climate feedbacks in the Alaskan boreal forest. Pages 309–322 in F. S. Chapin, M. W. Oswood, K. Van Cleve, L. A. Viereck, and D. L. Verbyla, editors. *Alaska's changing boreal forest*. Oxford University Press, Oxford, UK.
- McGuire, A. D., L. G. Anderson, T. R. Christensen, S. Dallimore, L. D. Guo, D. J. Hayes, M. Heimann, T. D. Lorenson, R. W. Macdonald, and N. Roulet. 2009. Sensitivity of the carbon cycle in the Arctic to climate change. *Ecological Monographs* 79:523–555.
- Myers-Smith, I. H., B. C. Forbes, M. Wilmking, M. Hallinger, L. Lantz, D. Blok, K. D. Tape, M. Macias-Fauria, U. Sass-Klaassen, and E. Lévesque. 2011. Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. *Environmental Research Letters* 6:045509.
- Myers-Smith, I. H., and D. S. Hik. 2018. Climate warming as a driver of tundra shrubline advance. *Journal of Ecology* 106:547–560.
- Olofsson, J., L. Oksanen, T. Callaghan, P. E. Hulme, T. Oksanen, and O. Suominen. 2009. Herbivores inhibit climate-driven shrub expansion on the tundra. *Global Change Biology* 15:2681–2693.
- Panda, S. K., S. S. Marchenko, and V. E. Romanovsky. 2014. High-resolution permafrost modeling in Denali National Park and Preserve. Natural Resource Technical Report, Geophysical Institute, University of Alaska, Fairbanks, Alaska, USA.
- Pastick, N., M. T. Jorgenson, S. Goetz, B. Jones, B. Wylie, B. Minsley, H. Genet, H. Knight, D. K. Swanson, and J. Jorgenson. 2018. Spatiotemporal remote sensing of ecosystem change and causation across Alaska. *Global Change Biology* <https://doi.org/10.1111/gcb.14279>
- Post, E., M. C. Forchhammer, M. S. Bret-Harte, T. V. Callaghan, T. R. Christensen, B. Elberling, A. D. Fox, O. Gilg, D. S. Hik, and T. T. Høye. 2009. Ecological dynamics across the Arctic associated with recent climate change. *Science* 325:1355–1358.

- Post, E., and C. Pedersen. 2008. Opposing plant community responses to warming with and without herbivores. *Proceedings of the National Academy of Sciences* 105:12353–12358.
- R Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.r-project.org/
- Rinas, C. L., R. J. Dial, P. F. Sullivan, T. S. Smeltz, S. C. Tobin, M. Loso, and J. E. Geck. 2017. Thermal segregation drives patterns of alder and willow expansion in a montane ecosystem subject to climate warming. *Journal of Ecology* 105:935–946.
- Roland, C. A., and J. H. Schmidt. 2015. A diverse alpine species pool drives a “reversed” plant species richness–elevation relationship in interior Alaska. *Journal of Biogeography* 42:738–750.
- Roland, C. A., J. H. Schmidt, and E. F. Nicklen. 2013. Landscape-scale patterns in tree occupancy and abundance in subarctic Alaska. *Ecological Monographs* 83:19–48.
- Roland, C. A., S. E. Stehn, J. Schmidt, and B. Houseman. 2016. Proliferating poplars: the leading edge of landscape change in an Alaskan subalpine chronosequence. *Ecosphere* 7:e01398.
- Roots, E. F. 1989. Climate change: high-latitude regions. *Climate Change* 15:223–253.
- Sadoti, G., S. A. McAfee, C. A. Roland, E. Fleur Nicklen, and P. J. Sousanes. 2018. Modelling high-latitude summer temperature patterns using physiographic variables. *International Journal of Climatology* <https://doi.org/10.1002/joc.5538>
- Schuur, E. A., K. G. Crummer, J. G. Vogel, and M. C. Mack. 2007. Plant species composition and productivity following permafrost thaw and thermokarst in Alaskan tundra. *Ecosystems* 10:280–292.
- Serreze, M. C., J. E. Walsh, F. S. I. Chapin, T. Osterkamp, M. Dyurgerov, V. E. Romanovsky, W. Oechel, J. Morison, T. Zhang, and R. G. Barry. 2000. Observational evidence of recent change in the northern high-latitude environment. *Climate Change* 46:159–207.
- Shenoy, A., J. F. Johnstone, E. S. Kasischke, and K. Kielland. 2011. Persistent effects of fire severity on early successional forests in interior Alaska. *Forest Ecology and Management* 261:381–390.
- Shulski, M., and G. Wendler. 2007. *The climate of Alaska*. University of Alaska Press, Fairbanks, Alaska, USA.
- Sousanes, P. 2008. Annual climate summary 2006. Central Alaska Network, Natural Resource Technical Report NPS/CAKN/NRTR-2008/141. National Park Service, Fort Collins, Colorado, USA.
- Stephens, J., K. Boggs, A. Garibaldi, J. Grunblatt, and T. Helt. 2001. Denali National Park and Preserve landcover mapping project volume 1: remote sensing data, procedures and results. National Park Service, Fort Collins, Colorado, USA.
- Stewart, B., K. Kunkel, L. Stevens, L. Sun, and J. Walsh. 2013. Regional climate trends and scenarios for the US national climate assessment: Part 7. Climate of Alaska. NOAA Technical Report NESDIS 142-7. National Oceanic and Atmospheric Association, Silver Spring, Maryland, USA.
- Stockdale, C. A., C. Bozzini, S. E. Macdonald, and E. Higgs. 2015. Extracting ecological information from oblique angle terrestrial landscape photographs: Performance evaluation of the WSL Monoplotting Tool. *Applied Geography* 63:315–325.
- Stueve, K. M., R. E. Isaacs, L. E. Tyrrell, and R. V. Densmore. 2011. Spatial variability of biotic and abiotic tree establishment constraints across a treeline ecotone in the Alaska Range. *Ecology* 92:496–506.
- Swanson, D. K. 2015. Environmental limits of tall shrubs in Alaska's Arctic National Parks. *PLoS ONE*. <https://doi.org/10.1371/journal.pone.0138387>.
- Tape, K., M. Sturm, and C. Racine. 2006. The evidence for shrub expansion in northern Alaska and the Pan-Arctic. *Global Change Biology* 12:686–702.
- Tape, K. D., M. Hallinger, J. M. Welker, and R. W. Ruess. 2012. Landscape heterogeneity of shrub expansion in Arctic Alaska. *Ecosystems* 15:711–724.
- Volney, W. J. A., and R. A. Fleming. 2000. Climate change and impacts of boreal forest insects. *Agriculture, Ecosystems & Environment* 82:283–294.
- Walker, M. D., C. H. Wahren, R. D. Hollister, G. H. Henry, L. E. Ahlquist, J. M. Alatalo, M. S. Bret-Harte, M. P. Calef, T. V. Callaghan, and A. B. Carroll. 2006. Plant community responses to experimental warming across the tundra biome. *Proceedings of the National Academy of Sciences* 103:1342–1346.

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