

## ARTICLE

## Ecology of Critical Zones

# Dynamic disequilibrium: Recent widespread increases in vegetation cover on subarctic floodplains of Interior Alaska

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**Handling Editor:** Steven J. Hall**Abstract**

Boreal forest and tundra ecosystems are undergoing rapid climatic and environmental changes with consequences for ecosystem structure, function, and services. Although riparian zones occupy a small footprint within subarctic landscapes, they have disproportionately high value as foci of hydrological processes, biogeochemical cycling, ecological disturbance, biodiversity, and wildlife activity. Recent observations of increased winter discharge, reduced peak flows, and increased connectivity between catchments, streams, and groundwater in subarctic riparian zones have prompted predictions of altered riverine disturbance regimes, increased channelization, and a decline in the extent of active floodplains. However, few observational data exist concerning the spatiotemporal dynamics of subarctic floodplain vegetation, which can serve as a bioindicator to corroborate such predictions. We analyzed the distribution and extent of riparian ecotypes across a network of streams in 12 Interior Alaska watersheds using high-resolution image pairs from circa 1981–2010. All stream reaches encompassed pronounced elevational gradients and included elevational forest–tundra ecotones. We classified riparian ecotypes using an image-based point-intercept sampling approach, calculated the probability of ecotype transitions, and evaluated relationships between ecotype transitions and environmental covariates. Our results reveal widespread increases in the stature, density, and extent of riparian vegetation spanning gradients of elevation, floodplain morphology, and climate. Ecotype transitions occurred at >20% of sample points, and there was a strong imbalance toward forward successional transitions (16.5%) versus backward transitions (4.0%). That is, we observed a strong tendency toward increasing cover, stature, and density of vegetation communities across our extensive sampling domain across our approximately 30-year sample period. This relatively rapid riparian “greening” signal tended to be most pronounced in our glaciated watersheds. Although the streams we studied displayed high local variability in ecotype transitions, our results support hypotheses of increasing channelization and

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reduced extent of unvegetated surfaces on subarctic floodplains. They also likely reflect a trend toward more rapid and extensive plant recruitment and growth due to processes associated with conspicuous warming in northern ecosystems, consistent with greening documented in other subarctic landscape segments along gradients of elevation and latitude.

#### KEYWORDS

Alaska, boreal forest, climate change, disturbance, floodplain, riparian zone, subarctic, succession

## INTRODUCTION

Subarctic ecosystems have become a focal point of global change research due to their high sensitivity to climate change. Boreal forest and tundra environments have experienced rapid warming in recent decades with a cascade of changes to vegetation, soil hydrology, permafrost, and disturbance processes (Beck, Goetz, et al., 2011; Heijmans et al., 2022; Rogers et al., 2015; Veraverbeke et al., 2017) that feed back to the global climate system (Bonan et al., 1992; Chapin et al., 2005; Walker et al., 2019). In northwestern North America, there has been particular interest in detecting changes to tree and tall shrub extent near forest–tundra boundaries along gradients of climate, latitude, and elevation (Brodie et al., 2019; Danby & Hik, 2007; Dial et al., 2007; Roland et al., 2016; Terskaia et al., 2020). Boreal forest wildfire and successional processes have also been the subject of numerous investigations in the subarctic (Baltzer et al., 2021; Kasischke et al., 2010; Mack et al., 2021; Walker et al., 2021). However, comparatively little is known about vegetation dynamics in subarctic riparian zones, despite their disproportionately high importance as “hotspots” of hydrological processes (Ploum et al., 2021), biogeochemical cycling (Blackburn et al., 2017), species diversity (Andersson et al., 2000; Johansson et al., 1996; Johnson & Almlöf, 2016; Nilsson & Svedmark, 2002), wildlife habitat use (Cooke & Tauzer, 2020), and ecological disturbance (Scrimgeour et al., 1994).

Northern rivers have received considerable attention from hydrologists due to observed changes in seasonal flow regimes (Holmes et al., 2012, 2021; McClelland et al., 2006; Peterson, 2002; Rawlins et al., 2010; Shiklomanov et al., 2021), river ice breakup (Prowse et al., 2006; Prowse & Beltaos, 2002), groundwater relations (Okkonen et al., 2010; Smith et al., 2007), catchment-scale permafrost extent (Dankers & Middelkoop, 2008; Jones & Rinehart, 2010; Quinton et al., 2011; Rouse et al., 1997; St. Jacques & Sauchyn, 2009), and river icings (Pavelsky & Zarnetske, 2017). The combined effects of these processes are thought to promote increased channelization, reduced peak flows

and associated disturbance severity, and contraction of the areal extent of active floodplains (Jansson et al., 2019; Nilsson et al., 2013; Ström et al., 2011, 2012; Thorne, 2011). Less well known are changes in the structure and composition of vegetation on subarctic floodplains, as studies of vegetation have generally emphasized upland and lowland forest ecosystems that dominate boreal forest landscapes on an area basis. In Interior Alaska, retrospective field studies have documented long-term increases in the cover and stature of riparian vegetation at scattered locations (e.g., Brodie et al., 2019; Terskaia et al., 2020), as well as increases on sparsely vegetated surfaces in other landscape positions (e.g., uplands and terraces) (Roland et al., 2016). Similar observations have been made elsewhere in forest–tundra ecotones and Low Arctic tundra (Frost & Epstein, 2014; Lantz et al., 2012; Ropars & Boudreau, 2012), suggesting that changing environmental conditions are most likely to become manifest in open, early successional environments where there is little established vegetation and reduced levels of competition that can otherwise impede the development of new plant communities.

Riparian vegetation mosaics are inherently dynamic because of the continuous interplay between the establishment of vegetation on newly deposited alluvium, and the destruction of riparian vegetation by channel migration, flooding, and sedimentation (Wiens, 2002). This is particularly true on floodplains in glaciated watersheds, which are extensive in northwestern North America. The extent of riverine barrens and early seres at a given time reflects both the contemporary and historical timing and extent of flooding, erosion/deposition events, and the rate and pattern of vegetation colonization (Helm & Collins, 1997; Van Cleve et al., 1996; Viereck et al., 1993; Walker & Chapin, 1986). Given the role of climate and extreme events on biological and physical processes on floodplains, it logically follows that both sides of this dynamic equation may be influenced by recent climatic warming in Interior Alaska, with consequences for the distribution and function of riparian vegetation. For example, the rate of vegetation establishment and development may increase with ameliorating climatic

conditions due to longer and more productive growing seasons, particularly in forest–tundra ecotones (Beck, Juday, et al., 2011; Kharuk et al., 2006; Wilmking & Juday, 2005), whereas changes in hydrological regimes may alter the severity and frequency of riverine disturbance events. Understanding the interplay of these two processes is important for assessing the long-term impacts of continued warming on subarctic floodplains.

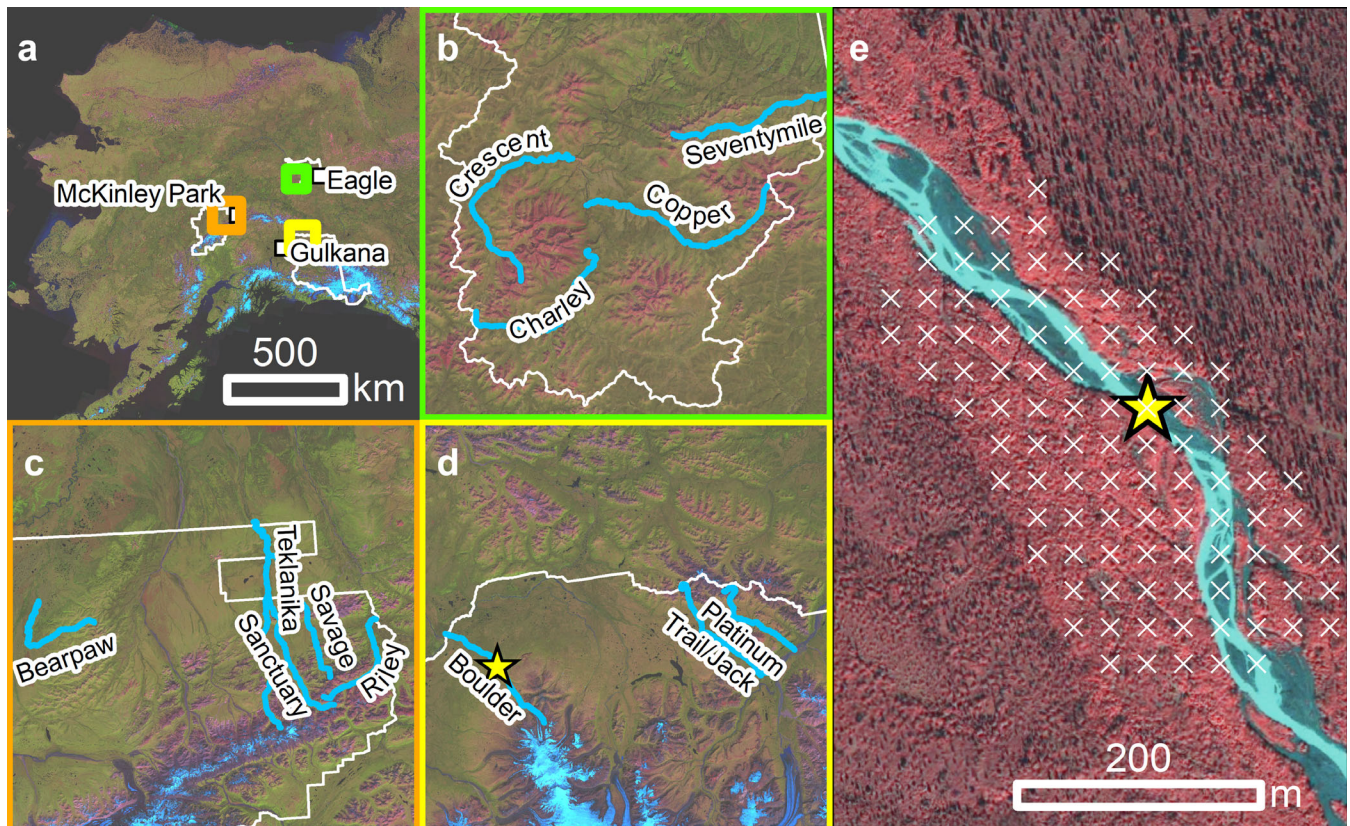
We investigated the trajectory of change in subarctic riparian zones by interpreting high-resolution image pairs spanning circa 1981–2010 and classifying riparian ecotypes and floodplain characteristics for 12 streams in three national park units in Interior Alaska, USA. We used these data to quantify vegetation change over time and identify potential drivers. We focused on vegetation changes in riparian zones for two primary reasons: (1) the high importance of these areas for ecosystem services and wildlife (Mizel & Swanson, 2022; Tape et al., 2015, 2016); and (2) the likelihood that warming-induced changes to subarctic vegetation may become manifest more quickly in early successional settings that lack established, long-lived perennial vegetation that can impede or mask directional changes in ecosystem

conditions (Brodie et al., 2019; Roland et al., 2016). We addressed the following questions:

1. Has there been a geographically widespread trend of increasing vegetation cover on Interior Alaska floodplains in recent decades?
2. What were the most common transitions among riparian ecotypes during this period?
3. What geographic and environmental covariates were associated with the different ecotype transitions, and what do they tell us about the likely drivers of detected changes on Interior Alaska floodplains?

## STUDY AREA

Our study area included 12 unregulated streams in three US national parklands in Interior Alaska: Denali National Park and Preserve (DNPP;  $n = 5$ ), Wrangell–St. Elias National Park and Preserve (WSNP;  $n = 3$ ), and Yukon-Charley Rivers National Preserve (YCNP;  $n = 4$ ) (Figure 1, Appendix S1). All but one of the streams in



**FIGURE 1** (a) Overview of the three Interior Alaska park units and locations of nearby meteorological stations; (b) four stream reaches in Yukon-Charley Rivers National Preserve; (c) five stream reaches in Denali National Park and Preserve; (d) three stream reaches in Wrangell–St. Elias National Park and Preserve (WSNP); and (e) example station and late period imagery on Boulder Creek in WSNP with 100 sample points in active and inactive floodplain environments.



DNPP are located on the north side of the Alaska Range in the northeastern quarter of the park. Two of these streams (Sanctuary and Teklanika rivers) are headed by alpine valley glaciers, while the other two are unglaciated except for small alpine cirque glaciers (Riley Creek and Savage River). The fifth DNPP stream, Bearpaw River, is in the unglaciated Kantishna Hills in the northwestern quarter of the park. In WSNP, Platinum Creek and Trail/Jack Creek are located on the south side of the Alaska Range and lack extensive glaciation, while Boulder Creek drains the northernmost portion of the Wrangell Mountains and is headed by a large valley glacier. In YCNP, all four study streams are located in the unglaciated Yukon–Tanana Uplands. Although permafrost is generally absent from active floodplains, permafrost occurs in all of the studied watersheds, with the majority of areas corresponding to zones of continuous (>90% of landscape) or discontinuous (50%–90%) permafrost (Jorgenson, Yoshikawa, et al., 2008). The active channels of the study streams mainly exhibit meandering morphology and floodplains are typically >50 m wide, although portions of the three extensively glaciated streams have much wider floodplains with braided channels. For analysis, we focused on active and inactive floodplain environments that are typically flooded at annual or decadal timescales.

All study streams experience a continental climate characterized by long, cold winters and short, warm summers. Eleven streams are in the southeast Interior Alaska climate division, and the twelfth (Bearpaw River) lies on the eastern edge of the Central Interior climate division (Bieniek et al., 2012). We summarize the climate attributes for the base period 1981–2010 for three long-term stations near the study streams: McKinley Park, about 20 km east of most DNPP streams; Gulkana, about 70 km southwest of the WSNP streams; and Eagle, about 100 km east of the YCNP streams (Table 1).

## METHODS

### High-resolution imagery collection

We visually interpreted riparian ecotypes and floodplain characteristics using high-resolution imagery from circa 1981 (1979–1984; hereafter, early period) and circa 2010 (2004–2010; late period) (Appendix S2). All early period imagery came from the airborne Alaska High Altitude Photography (AHAP) program and was downloaded from the US Geological Survey Earth Explorer website (<http://earthexplorer.usgs.gov/>); AHAP imagery has three spectral bands (red, green, and near-infrared) with variable spatial resolution ranging 0.9–1.5 m. For DNPP and WSNP, most late period imagery came in the form of park-wide orthorectified mosaics constructed from IKONOS commercial satellite images acquired by the US National Park Service from DigitalGlobe, Inc.; these data are subject to use restrictions, but the source imagery can be browsed at <https://discover.digitalglobe.com/>. The IKONOS imagery possesses four spectral bands (red, green, blue, and near-infrared) that were pansharpened to a spatial resolution of 1 m. For YCNP, late period imagery came from orthorectified mosaics of aerial photography with spectral and spatial resolutions comparable to IKONOS. Some sample stations lacked cloud-free, midsummer imagery in the park-wide orthomosaics, so we supplemented the imagery collection with more recent commercial imagery where available. Nearly all imagery was acquired during the months of July and August, when vegetation productivity is at peak and seasonal ice and snow are absent except at isolated river icings (aufeis).

We co-registered early period AHAP images to late period imagery by inserting ground control points at stable, readily identified landscape features (e.g., mature spruce trees, boulders) that overlapped the sampling stations. We then applied a spline (i.e., rubber sheet) transformation that maximized the local co-registration

**TABLE 1** Summary of temperature and precipitation climatologies for stations located near the study streams; base period is 1981–2010 (NCDC, 2022).

Station	Mean temperature (°C)			Mean precipitation (mm)		
	Annual	January	July	Annual	Snow season <sup>a</sup>	Warm season <sup>b</sup>
McKinley Park (DNPP)	−2.3	−16.1	13.1	383	112	271
Gulkana AP (WSNP)	−2.1	−19.4	14.2	286	102	184
Eagle AP (YCNP)	−3.5	−23.1	15.8	315	104	206

Abbreviations: DNPP, Denali National Park and Preserve; WSNP, Wrangell–St. Elias National Park and Preserve; YCNP, Yukon–Charley Rivers National Preserve.

<sup>a</sup>Predominantly October–April.

<sup>b</sup>Predominantly May–September.

accuracy near control points and better facilitated point-based change detection compared with systematic transformations. This task was completed in ArcGIS software and was aided considerably by the use of existing park-wide orthomosaics constructed for the parks; although some of this commercial imagery is somewhat dated (2004–2010), for many stations they represent the most current, cloud-free imagery available with appropriate seasonal timing. This approach also maintained a similar period of record for all streams in the retrospective analysis.

## Sampling design and imagery interpretation

We selected a set of 12 streams of roughly comparable size in terms of size, discharge, length, and extent for our study (excluding from consideration both major rivers such as the Yukon River and small-order streams). This allowed us to use similar spacing among our sampling stations and standardize the number of points sampled at each station and still assemble similar samples across our sampled streams. To be included, a stream was required to encompass the transition from an alpine landscape in its headwaters to boreal (forested) lowland ecosystems in its lower reaches. We then developed a hierarchical, spatially balanced sampling design for each stream whereby we selected a series of sampling stations, and then assessed vegetation at 100 sample points at each station. To begin, we established a systematic network of “seed” points representing candidate sampling stations at 500-m intervals along each stream using the stream flowlines from the National Hydrography Dataset (NHD), excluding headwater areas and sections outside of park boundaries. Next, we stratified the candidate stations for each stream by elevation quartiles using a statewide digital elevation map derived from interferometric synthetic aperture radar (hereafter, IFSAR DEM) (USGS, 2020) to ensure consistent sampling intensity across elevation gradients. We then ranked the candidate stations within each elevation quartile using Generalized Random Tessellation Stratified sampling (GRTS), implemented with R statistical software (R Core Team, 2022). The GRTS approach provided a practical means of selecting a spatially balanced sample while also allowing design-based inference. During sampling, we worked sequentially through the GRTS rankings, except when stations occurred on very narrow or incised floodplains, or lacked suitable imagery; in these cases, we skipped to the next ranked station. We began sampling in DNPP and sampled streams roughly in proportion to their length, resulting in an unequal number of stations

(14–32 stations per stream). For WSNP and YCNP, we sampled 10 stations per stream.

At each selected station, we established a systematic grid of potential sampling points at 30-m spacing with points set in the center of Landsat grid cells projected in the Alaska Albers coordinate system, and then identified the 100 grid points nearest to each station that overlapped active and inactive floodplains. We interpreted floodplain environments by referring to the imagery collection, elevation breaks evident in the IFSAR DEM, and available mapping of riverine physiography (Christopherson et al., 2021; Jorgenson, Roth, et al., 2008). Therefore, the spatial configuration and effective length of each sampled stream reach varied; stations on very wide floodplains consisted of 100 points arranged in a disc, while stations on narrower floodplains were more linear in shape. We rejected stations that could not accommodate a minimum of three sample points from one edge of the floodplain to the other.

To classify riparian ecotypes at each sample point, we first referred to existing ecotype classifications for the parks (Christopherson et al., 2021; Jorgenson, Roth, et al., 2008) and developed a simplified classification that was detailed enough to distinguish key differences in riparian vegetation cover, structure, and successional stage, but general enough to be distinguished consistently in images of varying sources (Table 2). Most of the vegetated classes were related to one another along a predictable successional sequence beginning with seral meadow and ending with Spruce. We excluded dwarf shrub, wet meadow, and marsh due to rarity and aggregated the uncommon balsam poplar class with tall shrub. Using our general knowledge of vegetation and ground conditions in each park, we assigned a categorical confidence assessment of high, medium, or low for our interpretation at each sample point for each time period. Classification for this study was performed by two interpreters, who worked together initially to standardize their interpretations of imagery. Once completed, the full set of classifications was then reviewed by the first author to ensure consistency and repeatability of the entire classification dataset.

## Environmental covariates and data analysis

To evaluate spatial patterns of riparian vegetation change and relationships with environmental covariates, we digitized the centerline of all active channels within each sampling station for each time period and calculated the minimum distance from each sample point to a channel centerline. We also measured the maximum active

**TABLE 2** Descriptions of the riparian ecotypes interpreted in high-resolution imagery, listed according to their typical successional sequence.

Ecotype	Description
Water/barren	Perennially flooded river channels, oxbow lakes, and beaver ponds, and barren areas that are typically flooded during high-water events including point bars, lateral bars, and mid-channel bars (islands). We interpreted these ecotypes separately but combined them for data analysis.
Seral meadow	Discontinuous cover of pioneer vegetation dominated by grasses, forbs, and willows ( <i>Salix</i> ).
Low shrub	Shrub patches dominated by willows ( <i>Salix</i> ) <1.5 m height, not casting distinct shadows in imagery. Typically occurs at higher elevations and/or in very early succession.
Tall shrub	Shrub patches dominated by willows ( <i>Salix</i> ) and alder ( <i>Alnus</i> ) >1.5 m height, casting distinct shadows in imagery. Feltleaf willow ( <i>Salix alaxensis</i> ) is typically the dominant shrub. This ecotype includes balsam poplar ( <i>Populus balsamifera</i> ) trees, which occurred infrequently on several streams.
Spruce	White spruce ( <i>Picea glauca</i> ) trees.

*Note:* Three rare ecotypes (dwarf shrub, wet meadow, and marsh) were excluded from analysis and are not shown.

channel width and the maximum floodplain width for each station and time period and assigned these values to all sample points at each station. We then evaluated a series of variables derived from ancillary datasets for local topography, watershed properties, and climatology. Initial evaluation indicated that certain pairs of these variables were highly intercorrelated, for example, elevation was strongly correlated with July temperature and snowfree date. Therefore, in all cases where the correlation between two covariates was  $R > 0.6$ , we selected one covariate with high explanatory power and dropped any duplicative covariates from the model (Table 3).

We used conditional multinomial logistic regression models to estimate the occurrence probability of the five ecotype classes in relation to the selected environmental covariates. This approach is a simple extension of binomial logistic regression that allows for more than two classes. Given that the conditional approach requires one class to be used as the reference for estimation, we treated water/barrens as the earliest stage of succession against which the four vegetated classes were compared. For each time period, we fit a model containing mean daily maximum

**TABLE 3** Summary of environmental variables selected for sampling network design and analysis of ecotype occurrence probability.

Variable	Description	Reference
Stream flowlines	National Hydrography Dataset; for station setup	USGS (2022)
Elevation (m)	IFSAR digital terrain model	USGS (2020)
Mean daily maximum July temperature (°C)	PRISM reanalysis (1971–2000)	Daly et al. (2008)
Snowfree date (Julian days)	Climatological snowfree date (1999–2015)	Macander et al. (2015)
Maximum floodplain width (m)	Interpreted for each station from late period imagery	This study
Distance to active channel (m)	Calculated from interpreted active channel centerlines	This study
Maximum channel width (m)	Interpreted for each station from late period imagery	This study
Aufeis (presence/absence)	Interpreted for each point	This study

*Note:* Several additional variables were dropped because they were strongly correlated with the selected variables.

Abbreviations: IFSAR, interferometric synthetic aperture radar; PRISM, Parameter-elevation Regressions on Independent Slopes Model.

July temperature, snowfree date, maximum floodplain width, distance to active channel, maximum channel width, and presence of aufeis to explain variation in the occurrence probability for each ecotype. We included quadratic mean daily maximum July temperature and snowfree date effects to allow for nonlinear relationships. We also included unique identifiers for each stream and station as random effects to account for spatial autocorrelation. Finally, we derived class-specific probabilities by back-transforming the resulting parameter estimates, allowing for direct comparisons of occurrence probability among classes and between periods for each class. Note that for any given set of conditions, the probabilities across classes must sum to 1.0. By plotting the predicted occurrence probabilities over the range of observed covariate values, we were able to identify patterns in site conditions that were related to ecotype transitions. Note that for graphical presentation it was necessary to condition the plots on the mean values of the remaining covariates, which may produce unintuitive results in some cases (e.g., few cases of high July temperature at mean snowfree date and mean floodplain width).

To assess broad patterns of change across ecotypes, we also reclassified class-specific transitions between the two time periods to: stasis (same ecotype in both years), forward transition (change to a later successional ecotype, e.g., seral meadow to tall shrub), or backward transition (change to an earlier successional ecotype, e.g., spruce to water/barren). We then simply fit the identical model structure described above (both covariates and analysis) to the resulting reclassified dataset; this allowed us to compare overall successional patterns independent of the individual ecotypes. For both sets of analyses, we used the “mclogit” package in R statistical software (Elff, 2020; R Core Team, 2022). In each case, we developed two full models, one that excluded low-confidence sample points, and one that included all points regardless of confidence. The results of both models were very similar; therefore, we present results from the full dataset.

## RESULTS

### Descriptive summary

Our sampling network consisted of 179 stations on 12 Interior Alaska streams, with a total of 17,900 sample points. We excluded 319 points from analysis because they were occupied by rare ecotypes or were affected by excessive shadow, cloud contamination, or human disturbance, resulting in a total of 17,581 sampled points. The three most common riparian ecotypes in the early period were water/barren, low shrub, and tall shrub (Table 4). By the late period, the extent of water/barren decreased by 22.0%, while the extent of tall shrub, low shrub, and seral meadow all increased (Appendix S3).

**TABLE 4** Transition matrix showing the number of points in each of our primary ecotypes in our two sample iterations.

Early period ecotype	Barren/ water	Seral meadow	Low shrub	Tall shrub	Spruce
Barren/ water	4209	<b>1008</b>	<b>433</b>	<b>461</b>	<b>4</b>
Seral	<i>173</i>	518	<b>437</b>	<b>218</b>	<b>2</b>
Low shrub	<i>171</i>	44	3320	<b>283</b>	<b>25</b>
Tall shrub	<i>185</i>	20	38	3402	<b>33</b>
Spruce	<i>31</i>	<i>1</i>	7	35	2523

Note: The rows represent our classifications from the early period and the columns represent classifications from the late period. Numbers in boldface represent “forward” transitions, numbers in italics represent “backward” transitions, and regular font numbers (on the diagonal) represent “stasis” when points were classified the same in both periods.

In contrast, the extent of the late successional Spruce ecotype remained nearly identical. Across the sampling network, we recorded ecotype transitions at 20.5% of all sampling points. Forward transitions occurred at 16.5% of all sampled points and exceeded backward transitions (4.0%) by more than fourfold (Table 5). Forward transitions were far more common than backward transitions at all three parks and for 11 of 12 rivers (Figure 2).

Across all streams except Riley Creek, most forward transitions occurred on surfaces that were unvegetated in the early period, rather than transitions from one vegetated ecotype to another. This pattern was particularly striking on the three glaciated streams, where 38% of points that were unvegetated in the early period showed a forward transition, compared with 24% of initially unvegetated points on nonglacial streams. Four forward ecotype transitions accounted for >60% of all transitions recorded throughout the network: barren/water to seral meadow, barren/water to tall shrub, seral meadow to low shrub, and water/barren to low shrub (Table 6). Collectively, these four transitions accounted for 13.3% of all points sampled across the network.

The most common backward transitions were tall shrub to barren/water, seral meadow to barren/water, and low shrub to barren/water. Although the most common transitions varied from stream to stream, most involved closely related, early successional ecotypes. However, the frequency of specific ecotype transitions varied with elevation (Table 6). For example, the most frequently observed transition—barren/water to seral meadow—was most common in the two highest elevation quartiles. In contrast, forward successional transitions to tall shrub were generally more common in lower quartiles.

### Occurrence probability by ecotype

Our models explained a large proportion of the variation in the data for both study periods, with proportional reductions in deviance values of 0.63 and 0.64 for the early and late periods, respectively. The proportional reduction in deviance for our transition model was 0.53. For both study periods, distance from channel, floodplain width, channel width, snowfree date, July maximum temperature, and presence of aufeis were important predictors of occurrence probability across ecotypes. Several of these covariates represent spatial proxies of vulnerability to riverine disturbance. For example, sample points that were near stream channels, on wide floodplains, or near wide channels were much more likely to be classified as barren/water, while the late successional spruce

**TABLE 5** Summary of prevalent successional trajectories detected for stations and sample points on Interior Alaska streams.

Stream	Total stations	Forward		Backward	
		Percentage of stations	Percentage of points	Percentage of stations	Percentage of points
DNPP					
Bearpaw	20	85.0	10.5	5.0	2.5
Riley	14	100.0	21.7	0	1.2
Sanctuary	19	100.0	30.3	0	2.9
Savage	24	91.7	13.9	8.3	3.7
Teklanika	32	93.8	28.4	3.1	5.7
WSNP					
Boulder	10	90.0	16.7	10.0	6.5
Platinum	10	80.0	9.4	10.0	4.9
Trail/Jack	10	40.0	9.7	60.0	8.5
YCNP					
Charley	10	80.0	7.6	10.0	3.6
Copper	10	80.0	8.3	10.0	3.4
Crescent	10	60.0	5.3	30.0	3.9
Seventymile	10	80.0	5.7	10.0	1.5
Total	179	85.4	16.5	10.6	4.0

Note: Shown for each stream are the percentages of stations in which the majority of successional transitions were forward or backward, and the percentages of all sample points that displayed a forward or backward transition.

Abbreviations: DNPP, Denali National Park and Preserve; WSNP, Wrangell–St. Elias National Park and Preserve; YCNP, Yukon–Charley Rivers National Preserve.

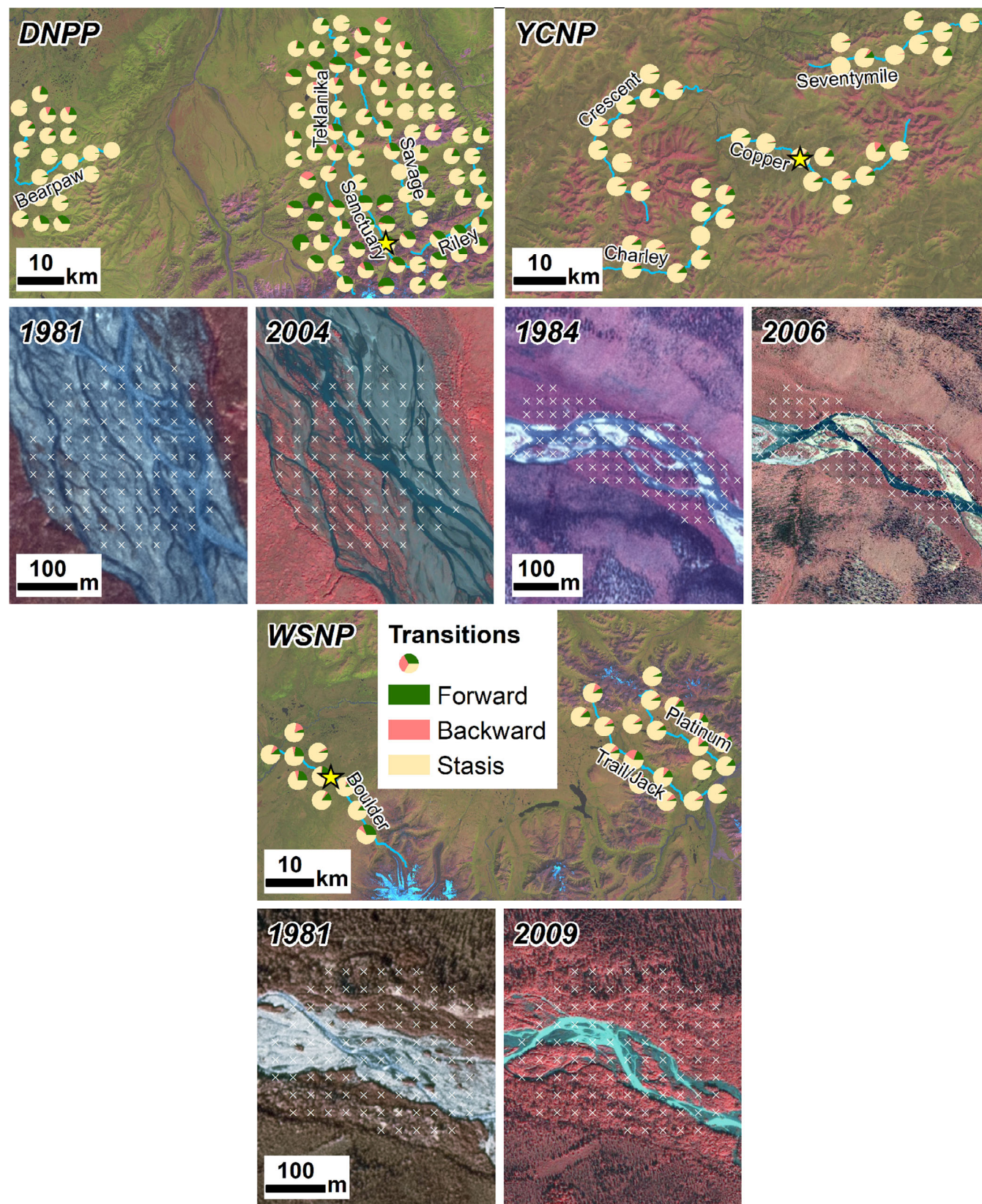
ecotype was most likely to occur far from stream channels, on narrow floodplains, or along narrow streams (Figure 3).

The remaining predictors represented local measures of the length and warmth of the growing season. As expected, the occurrence probability of vegetated ecotypes was generally lower in areas with later snowfree dates, lower July maximum temperatures, and where aufeis was present. Seral meadow was most common in cooler areas with late snowmelt, while Spruce occupied the warmest areas with early snowmelt. Occurrence probabilities of the two shrub ecotypes were relatively invariant across gradients of summer temperature, but were highest at locations with early snowmelt dates.

The occurrence probability of barren/water declined during the study period throughout virtually all environmental gradients, revealing a widespread “greening” trend, particularly on wide (i.e., braided glacial) floodplains and in areas with late-lying snow. Conversely, occurrence probabilities increased for the vegetated ecotypes across a wide range of conditions. Gradients in occurrence probability were similar between the two study periods for most ecotypes; the largest changes were associated with increased tall shrub occurrence on wide floodplains and at sites with late-lying snow.

The spatial and climatic covariates create complex gradients in riparian environments over a range of spatial scales, from microsites (snowfree date), to individual stream reaches (e.g., floodplain width), to the watershed scale (e.g., summer temperature). We find contour plots to be useful in depicting how interactions among spatial and climatic gradients are related to patterns of occurrence and change for each ecotype. Notably, the occurrence probability of barren/water was higher in the early period than the late period throughout multiple spatial and climatic gradients (Figure 4), while the reverse was true for most vegetated ecotypes (Figures 5–8). For vegetated ecotypes, the most striking differences in occurrence probability between periods were evident for seral meadow and tall shrub, which became more frequent on the widest floodplains. These trends also varied predictably along complex gradients of summer warmth and growing season length. For example, increases in seral meadow occurrence were concentrated in the coldest parts of the climate gradient where woody plants are generally less abundant, and Spruce was concentrated in the warmest (low elevation) areas. Increases in tall shrub occurrence were evident across wide climatic gradients but were conspicuously less frequent in spruce-dominated areas.





**FIGURE 2** Regional maps showing the proportion of forward transitions, backward transitions, and stasis observed at riparian stations in the Denali National Park and Preserve (DNPP), Yukon-Charley Rivers National Preserve (YCNP), and Wrangell-St. Elias National Park and Preserve (WSNP) national parklands. Example sampling grids and image pairs are shown below the regional map for each parkland. Stars indicate the locations of the example image pairs. Note that the station locations in the regional maps are approximate.

**TABLE 6** Summary of ecotype transitions (as percentages) observed by elevation quartile.

Transition	Elevation quartile				Percentage of all transitions	Percentage of all points
	1	2	3	4		
<b>Barren/water to seral meadow</b>	11.9	15.0	41.5	31.6	27.9	5.7
<b>Barren/water to tall shrub</b>	28.2	38.4	24.7	8.7	12.8	2.6
<b>Seral meadow to low shrub</b>	19.2	33.4	18.8	28.6	12.1	2.5
<b>Barren/water to low shrub</b>	32.3	21.7	28.6	17.3	12.0	2.5
<b>Low shrub to tall shrub</b>	34.3	23.0	20.8	21.9	7.8	1.6
<b>Seral meadow to tall shrub</b>	20.6	31.7	29.4	18.3	6.0	1.2
Tall shrub to barren/water	40.5	35.7	16.2	7.6	5.1	1.1
Seral meadow to barren/water	8.7	24.9	46.2	20.2	4.8	1.0
Low shrub to barren/water	31.6	17.5	27.5	23.4	4.7	1.0
Low shrub to seral meadow	43.2	18.2	22.7	15.9	1.2	0.3
Tall shrub to low shrub	26.3	34.2	31.6	7.9	1.1	0.2

Note: Forward successional transitions are shown in boldface; only transitions that accounted for >1.0% of all recorded transitions are shown.

Across the network, forward transitions were far more likely to occur than backward transitions throughout multiple spatial and climatic gradients (Figure 9). Forward transitions were most frequent near active channels and were especially frequent on wide floodplains. For example, the occurrence probability of an unvegetated surface on a 500-m-wide floodplain was about 75% during the early period, versus only about 20% during the late period. By contrast, the probability of backward successional transitions was <10% and showed little variation across gradients; however, a modest increase in the probability of backward transitions was evident adjacent to active channels and at stations at the warm end of the summer climate gradient.

## DISCUSSION

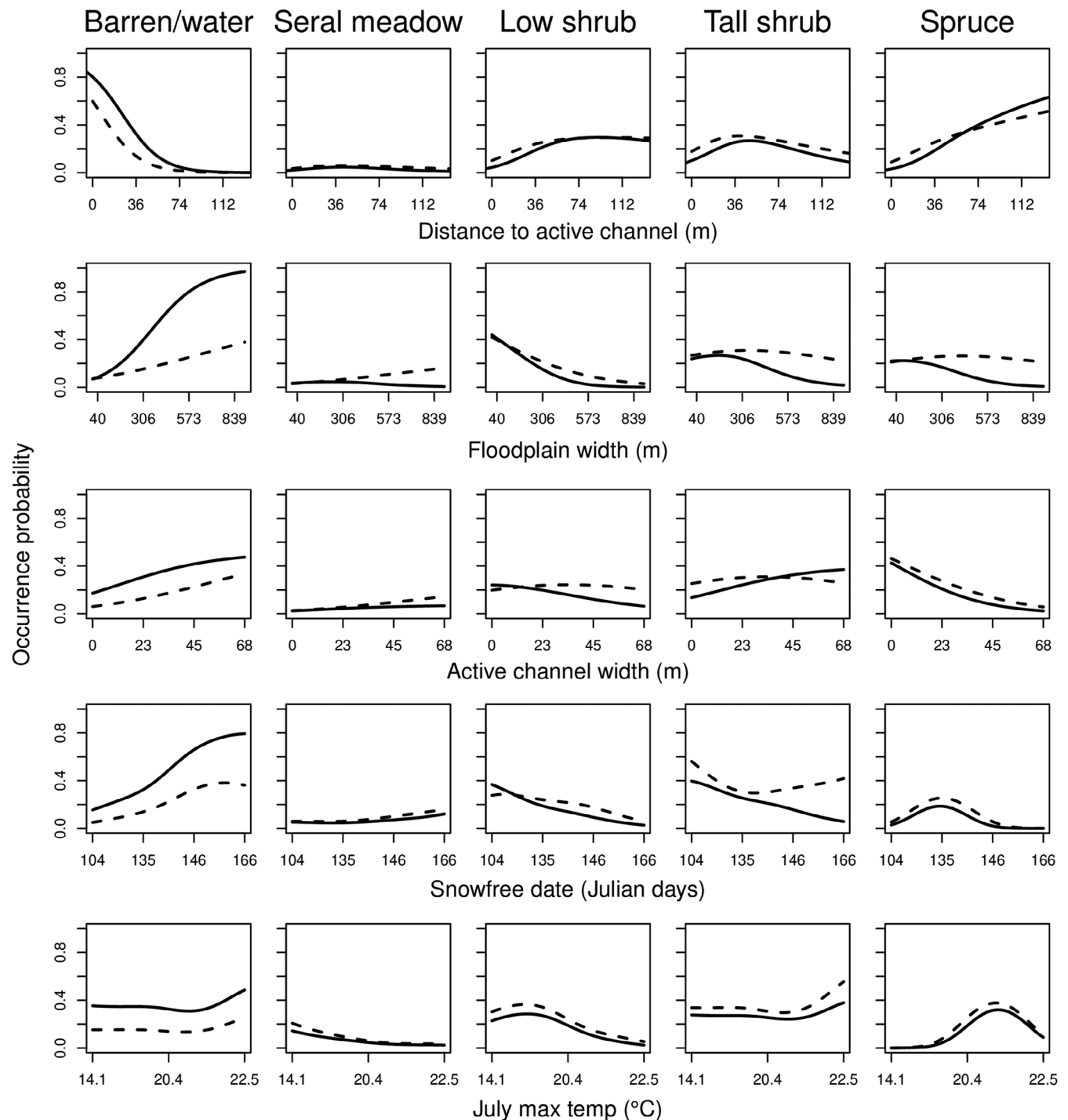
### Vegetation expansion on Interior Alaska floodplains

Our analysis revealed widespread “greening” of riparian corridors over three decades in watersheds spanning a range of subarctic landscape settings across an approximately 85,000-km<sup>2</sup> area of Interior Alaska. Within less than three decades, the extent of unvegetated surfaces decreased markedly throughout gradients of floodplain characteristics, elevation, and climate. Forward successional transitions were far more common than backward transitions at all spatial scales and included both colonization of formerly unvegetated surfaces and successional transitions among vegetated ecotypes. There were, however, substantial regional differences in the extent and

pace of riparian vegetation expansion and ecotype transitions. Floodplain ecosystems were generally more dynamic in the younger, more rugged landscapes of DNPP and WSNP, particularly on wide floodplains in the three glaciated watersheds, and forward successional transitions were more widespread in the wetter DNPP study area than in the other park units.

Floodplains are inherently dynamic environments that experience frequent disturbance arising from channel migration, high-water events, sedimentation, and ice-jam flooding (Scrimgeour et al., 1994). These processes create opportunities for vegetation colonization and then through time to a predictable series of successional changes on floodplain surfaces of varying age, as well as mortality of established vegetation when disturbance recurs. Most of these transitions—particularly in early to mid-succession, and backward transitions arising from disturbance—are readily interpreted in co-registered high-resolution image pairs and conformed to expectations based on general patterns of floodplain succession and disturbance. For example, early and late successional ecotypes were generally found near and far from active channels, respectively. In terms of ecotype transitions, the most obvious spatial relationship we detected was the tendency of seral meadow, low shrub, and tall shrub to develop near channels (Figures 5–7), and a large decrease in the occurrence of unvegetated surfaces at any distance to active channels during the study period (Figure 4). Our results revealed the dynamic side of this process with a clear increase in the probability of forward transitions with decreasing distance to active channels. In contrast, variability in the frequency of backward transitions was much less spatially dependent on



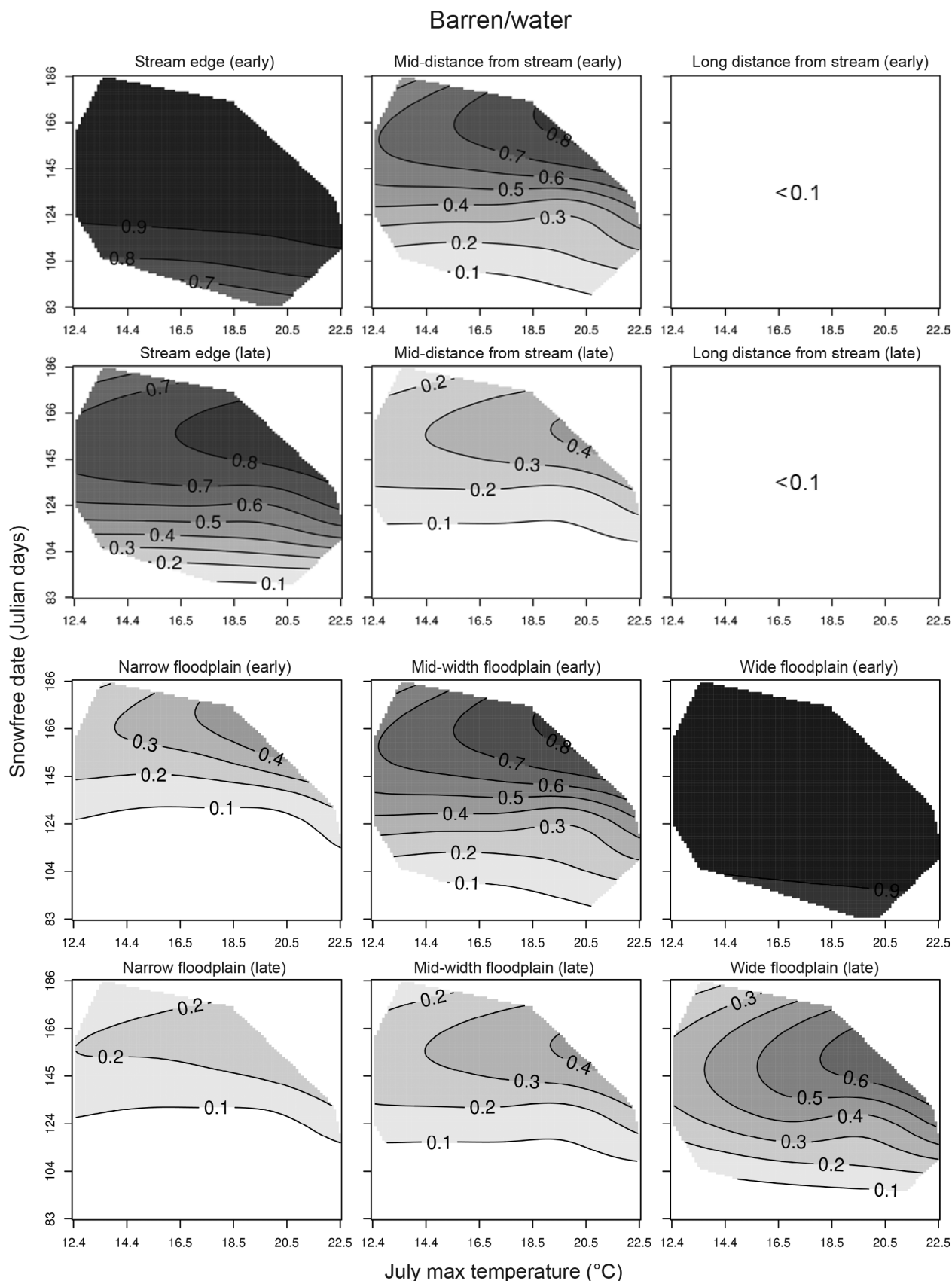


**FIGURE 3** Univariate plots displaying the probability of occurrence for five vegetated riparian ecotypes (columns) along environmental and climatic gradients (rows) in the early (solid lines) and late (dashed lines) study periods on 12 Interior Alaska streams.

channel distance. These patterns indicate that the tempo of plant colonization and succession on one hand, and riverine disturbance and vegetation mortality on the other, were not in equilibrium during the study period, signifying important landscape-level changes in Interior Alaska.

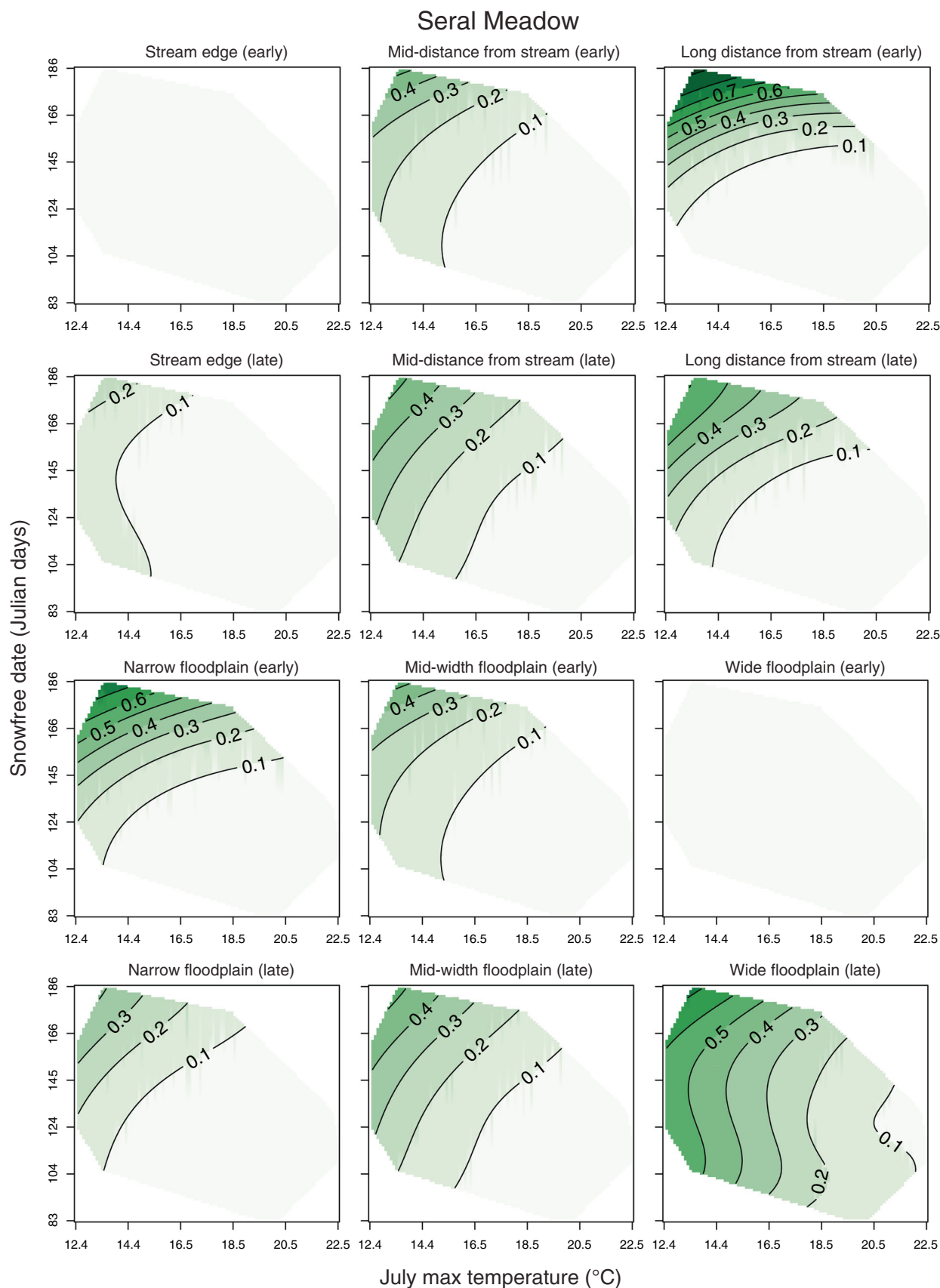
There were many regional- and landscape-scale differences in the most common ecotype transitions. For example, the three glaciated streams supported the highest

frequency of forward transitions observed in our study, and a disproportionately high number of these transitions involved the colonization of previously unvegetated surfaces. All of the most common forward transitions involved closely related early to mid-successional ecotypes, while transitions involving Spruce, the latest successional ecotype, accounted for <3.5% of all observed transitions, and its total extent was nearly identical in the two study periods. Given

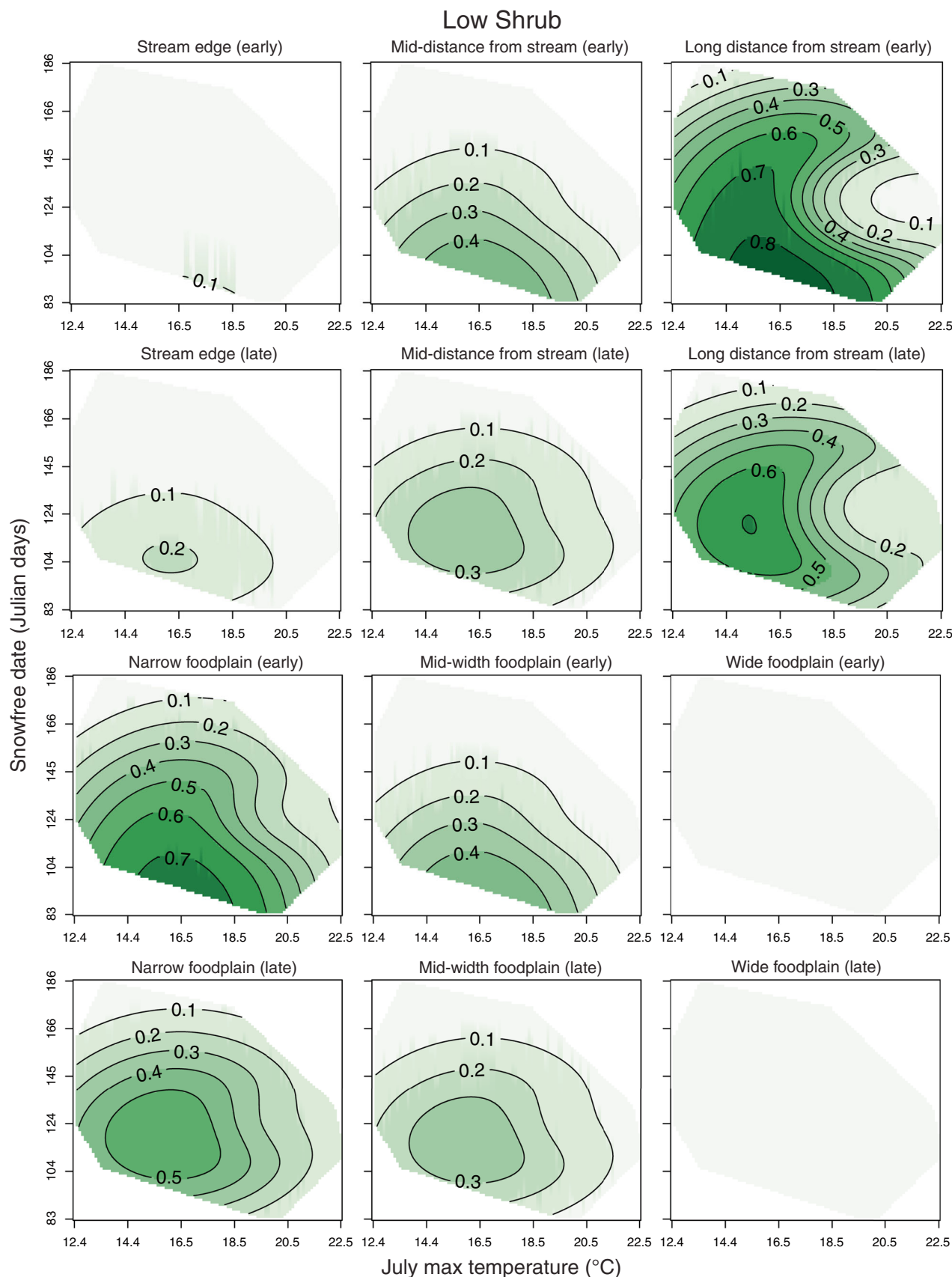


**FIGURE 4** Contour plots showing occurrence probabilities for barrens/water in the early and late periods based on joint variation in maximum July temperature and snowfree date at (top) different distances from an active channel and (bottom) at different floodplain widths. Contours are truncated to the range of observed values for each covariate.

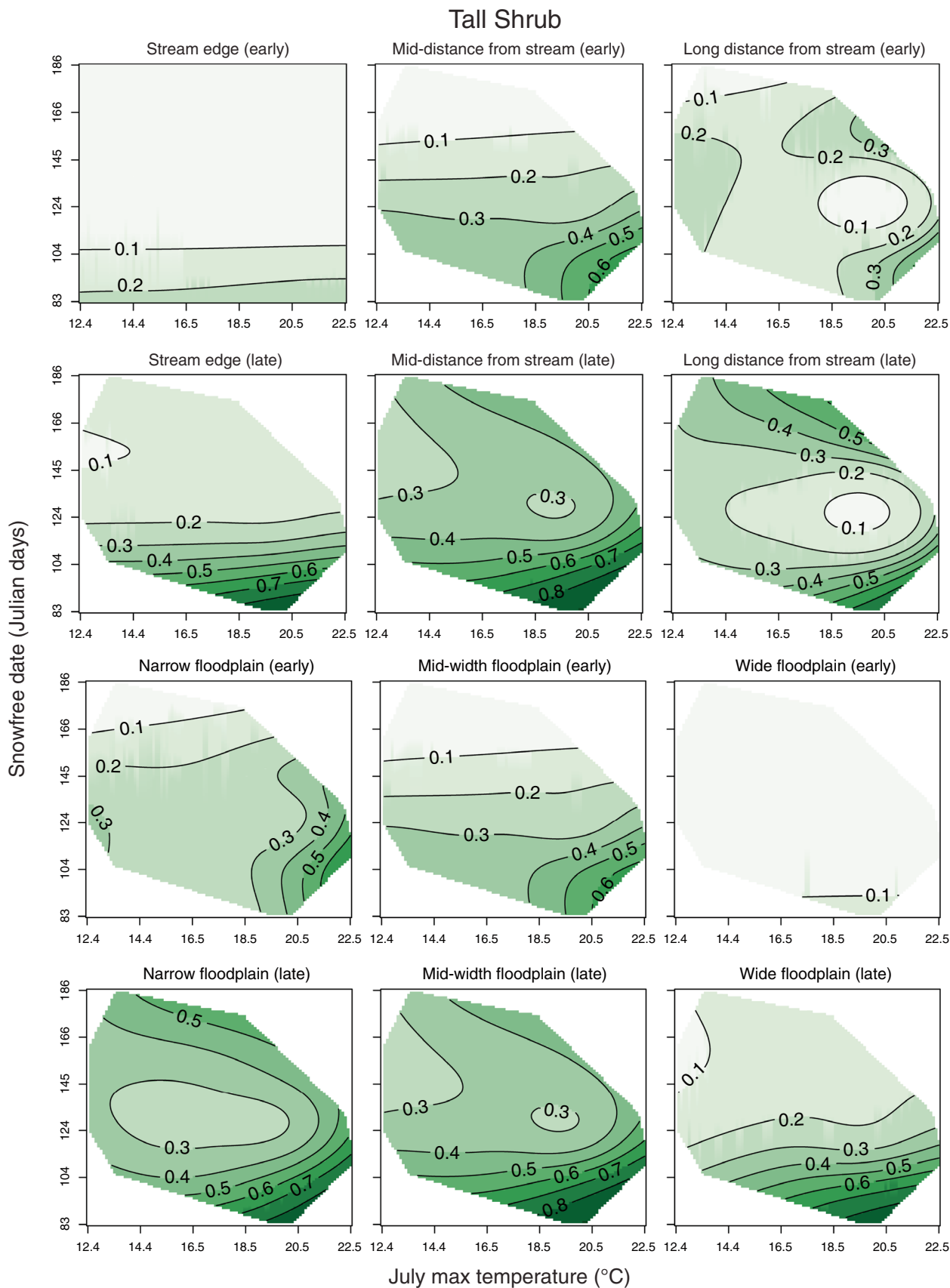




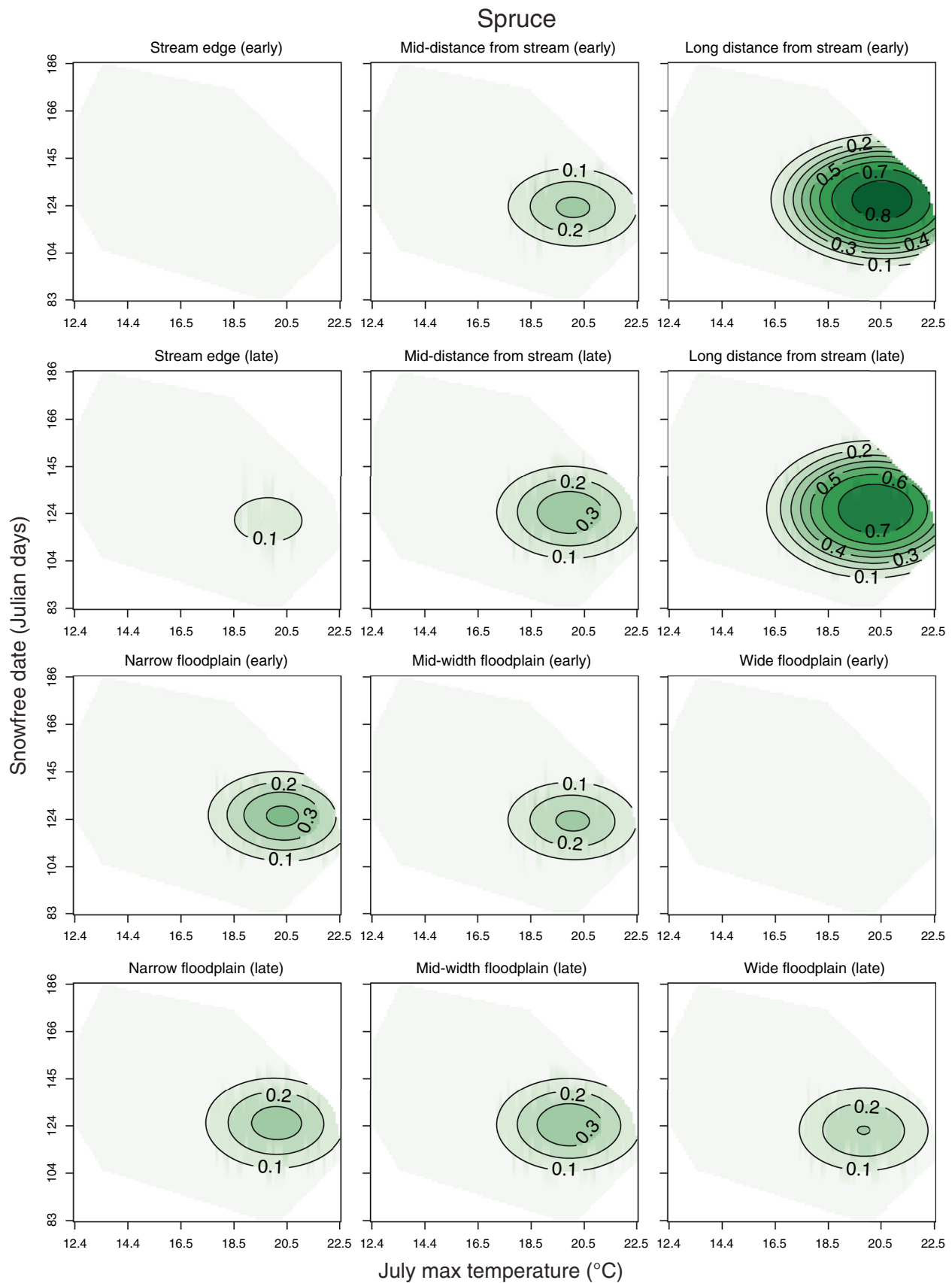
**FIGURE 5** Contour plots showing occurrence probabilities for seral meadow in the early and late periods based on joint variation in maximum July temperature and snowfree date at (top) different distances from an active channel and (bottom) at different floodplain widths. Contours are truncated to the range of observed values for each covariate.



**FIGURE 6** Contour plots showing occurrence probabilities for low shrub in the early and late periods based on joint variation in maximum July temperature and snowfree date at (top) different distances from an active channel and (bottom) at different floodplain widths. Contours are truncated to the range of observed values for each covariate.

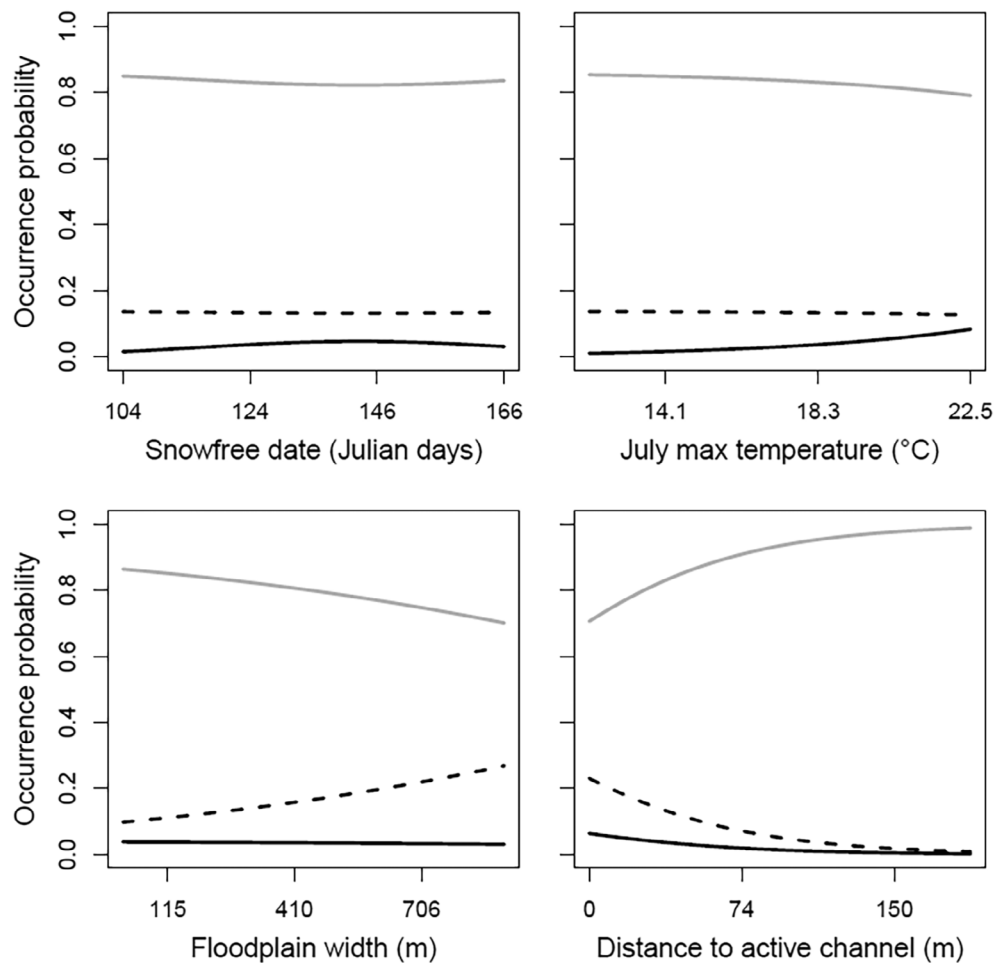


**FIGURE 7** Contour plots showing occurrence probabilities for tall shrub in the early and late periods based on joint variation in maximum July temperature and snowfree date at (top) different distances from an active channel and (bottom) at different floodplain widths. Contours are truncated to the range of observed values for each covariate.



**FIGURE 8** Contour plots showing occurrence probabilities for spruce in the early and late periods based on joint variation in maximum July temperature and snowfree date at (top) different distances from an active channel and (bottom) at different floodplain widths. Contours are truncated to the range of observed values for each covariate.





**FIGURE 9** Univariate plots displaying the probability of occurrence of forward successional transitions (dashed lines), backward successional transitions (solid black lines), and stasis (solid gray lines) along spatial and climatic gradients on 12 Interior Alaska streams.

our relatively short sample interval, this is not surprising because the development of the spruce ecotype requires many decades, and this ecotype can persist for long periods of time in the absence of disturbance. However, should vegetation continue to expand on Interior Alaska floodplains, we would expect a progressive increase in spruce extent to occur over time as recently established vegetation patches are colonized by spruce during succession, especially in those areas with abundant nearby seed sources.

Our results revealed that the frequency of some transitions varied according to gradients of elevation and summer temperatures. For example, the most commonly observed transition—barren/water to seral meadow—was concentrated in the two highest elevation quartiles, and the overall cover of seral meadow actually decreased over the study period in the lower quartiles as woody ecotypes expanded there. Although transitions to tall shrub were much less extensive in the highest elevation quartile in our network compared with lower zones, the relative increase in tall shrub at high elevations (27.6%) was the

highest observed in any quartile. These patterns are consistent with known limitations on tall shrub growth (Swanson, 2015), and observations of increasing tall shrub abundance in forest–tundra ecotones along gradients of elevation and latitude at widely distributed sites in Alaska and elsewhere in the pan-Arctic (Lantz et al., 2012; Myers-Smith et al., 2011).

Although observational studies of riparian vegetation dynamics are limited in Alaska and across the circumboreal region in general, local increases in riparian vegetation have been documented using repeat ground photography in northern Lake Clark National Park and Preserve, about 450 km southwest of DNPP (Jorgenson et al., 2007). Similarly, our findings of riparian vegetation expansion in DNPP are corroborated by analyses of repeated historical photographs dating to the early 20th century (Brodie et al., 2019). In addition, quantitative sampling of vegetation at long-term plots in DNPP has demonstrated striking increases in vegetation cover on abandoned riverine terraces near the McKinley River

since 1958 (Roland et al., 2016). These terraces no longer undergo extensive riverine disturbance, but surficial materials are the same as those of modern floodplains, vegetation was historically discontinuous, and the composition of the recently established vegetation resembles that found on floodplains. On western Alaska's Yukon River Delta, dramatic increases in tall willow and alder abundance since the mid-20th century have been widely reported by regional elders (Fienup-Riordan et al., 2021; Rearden & Fienup-Riordan, 2014) and are corroborated by long-term increases in the normalized difference vegetation index (NDVI), a spectral proxy of vegetation biomass (Frost et al., 2021). Riparian zones have also been highlighted as hotspots of positive NDVI trend in regional-scale time-series analysis in northern Quebec (McManus et al., 2012), and riparian zones have been well documented as foci of tall shrub expansion in Low Arctic environments of Alaska's North Slope (Naito & Cairns, 2015; Tape et al., 2011). Information from unregulated Eurasian floodplains is quite limited in the English language literature; existing studies have shown increases in the cover of trees and tall shrubs (albeit with high local variability) on several widely separated, but relatively short floodplain sections in Siberian forest-tundra ecotones (Frost & Epstein, 2014). Taken together, retrospective studies suggest that subarctic riparian zones have undergone persistent increases in vegetation cover since at least the mid- to late 20th century across wide spatial scales and environmental gradients. Should changes at the rate and scale we have detected continue, it would likely portend profound consequences for a range of physical and biological processes in subarctic riparian zones.

## Sources of uncertainty

Our retrospective analysis focused on state-level changes in vegetation in dynamic floodplain environments, where disturbance processes and succession produce conspicuous changes in vegetation cover and structure over decadal timescales. Nonetheless, several sources of uncertainty need to be considered. The spatial resolution of the early period AHAP imagery was lower compared with the late period imagery, and the color saturation of AHAP color-infrared images was somewhat variable from frame to frame, potentially impacting our interpretation of ecotype at sample points. In practice, we had high confidence in interpreting barrens and water regardless of imagery source or time period. Some vegetated ecotypes were more difficult to distinguish, particularly in AHAP imagery for the early period. We mitigated the potential for classification errors by being conservative in recording ecotype transitions in cases where the visible

signature of ecotypes at a point was indistinct and we had low confidence in the interpretation. In total, we identified only 319 sample points as having low interpretation confidence (1.8% of all points) and found that the results were relatively insensitive to classification errors, particularly in the direction of overstating forward successional transitions. Therefore, we are confident that differences among image sources had negligible impact on our conclusions, and may actually have made measures of riparian "greening" somewhat conservative, since the impacts of disturbance on vegetation were much more likely to be visible in the imagery collection than incremental increases in live cover within vegetated ecotypes.

Other potential confounding factors for retrospective imagery analysis include interannual variability in vegetation phenology and water levels, as well as registration errors affecting the alignment of early and late period imagery. We mitigated phenology differences by restricting our analysis to imagery from the months of July and August to the greatest extent possible, when vegetation productivity is at peak and seasonal snow cover is absent; when necessary, we supplemented the late period imagery collection with additional scenes in cases where the park-wide orthomosaics included images with suboptimal (September) timing. We also avoided the use of imagery from early summer, when water levels could be influenced by seasonal snowmelt; although differences in water level likely affected the relative proportion of barrens and water between periods at some stations, we combined these ecotypes as a single unvegetated class for analysis, and visual interpretation of imagery indicated no surface water in vegetated areas except in rare cases (e.g., beaver ponds). For imagery co-registration, we applied spline transformations that maximized the local registration accuracy at control points. Although we cannot determine systematic registration errors arising from these transformations, we were able to visually review the registrations by considering numerous stable landscape features (usually long-lived trees) simultaneously and inserting additional control points as needed.

Some variability in the length of observational periods among stations arose from limitations in imagery available for remote areas of Interior Alaska. Nearly two-thirds of stations had a period of record of 23 or 24 years, but some stations had a period of record of 25–29 years. We mitigated this by calculating ecotype occurrence probabilities categorically and avoided measures of rates of change. Although differences in observational period may have had some influence on the number of ecotype transitions recorded at stations, we maintain that these differences are inconsequential considering the large magnitude of vegetation increase that we observed at all levels of the sample design—parks,

streams, and stations—in less than three decades. In addition, relationships between ecotype occurrence and environmental covariates evident in the contour plots are quite dissimilar for the two study periods, and it is unlikely that broad patterns of change in ecotype occurrence were materially affected by differences in observational period.

## Potential drivers of riparian vegetation change

Our study describes rich spatial patterns of ecotype occurrence and change in riparian corridors of Interior Alaska. Although attributing changes to specific biophysical drivers requires field-based techniques beyond the scope of our study, regional- and landscape-scale variability in the occurrence of ecotypes provide insights into potential mechanisms of riparian vegetation change. We can also place our findings into the context of recent hydrologic changes observed in subarctic rivers, and the predictions they have stimulated concerning the frequency and severity of disturbance in riparian zones.

Several patterns in our dataset suggest direct effects of climate warming as a driver of riparian vegetation expansion, particularly in headwater regions at higher elevations where the distribution of tall shrub and spruce ecotypes is limited to (and in many cases, confined to) riparian zones. While tall shrub extent increased in all elevation quartiles during the study period, the relative increase in tall shrub extent was progressively higher through quartiles of increasing elevation. The dominant canopy-forming species in this ecotype is feltleaf willow (*Salix alaxensis*), which occurs over broad gradients of climate on mineral-dominated, nonacidic, well-drained substrates that lack competing vegetation and organic material (Raiho et al., 2022; Swanson, 2015). The instrumental record indicates that mean June temperatures increased significantly (ordinary least squares regression,  $p < 0.05$ ) during 1975–2010 at the three climate stations near our study streams (i.e., our full study period plus  $\sim 5$  preceding years). No significant changes in summer temperature were evident in July or August during this period; however, other lines of evidence provide clear signals of recent warming in Interior Alaska, such as increases in ground temperatures measured at boreholes since the mid-1980s near DNPP, WSNP, and elsewhere in Interior Alaska (Smith et al., 2021). A large body of dendrochronology and other studies have demonstrated the influence of summer temperatures on tundra shrub growth (Bjorkman et al., 2020; Forbes et al., 2010; Myers-Smith et al., 2015), and the large relative increase in tall shrub occurrence that we observed at high

elevations likely reflects ameliorated growing conditions in recent decades, perhaps dating to the conclusion of the Little Ice Age in the late 19th century. However, we found no evidence of increased spruce development, which may reflect differences in life history and lower potential growth rates, which produce temporal lags that can greatly exceed the relatively short period of our study. Indeed, studies using repeated photo pairs have documented increases in the density and distribution of spruce in DNPP at high elevation (Brodie et al., 2019; Roland & Stehn, 2013).

Additional possible biological drivers of the changes we observed, particularly of vegetation development on barren surfaces, may relate to increases in plant fecundity and seedling recruitment stimulated by ameliorated growing conditions, particularly at higher elevations (Graae et al., 2008; Lantz et al., 2010; Milbau et al., 2009). That is, due to increased plant growth and colonization rates, the temporal lag between deposition of alluvium and development of continuous vegetative cover may be decreasing in our study area over time. Indeed, it has been shown that dispersal limitation can be particularly important early in primary succession (Makoto & Wilson, 2019); we suspect that some fraction of the changes we observed reflect an easing of dispersal limitations imposed by harsher climatic conditions earlier in the 20th century.

We found that vegetation expansion was strongest on wide, braided floodplains with glacial sediment input (Teklanika and Sanctuary rivers in DNPP, and Boulder Creek in WSNP) relative to clearwater streams. While additional work targeting a larger group of glacial streams is necessary to confirm this pattern, one possible explanation for this trend could simply be the greater availability of moist, fine-grained mineral seedbeds on glacial floodplains compared with clearwater streams that lack suspended sediment much of the year. Indeed, in an experimental study of the response of floodplain willow species in Interior Alaska to differing germination substrates, substrate was an important influence on seedling germination rates, which ranged from 0% on dry sandy material to  $>60\%$  on mesic silty substrates (Krasny et al., 1988).

Riparian vegetation expansion could also be attributable to indirect climate impacts on physical processes, including watershed-scale hydrology and permafrost conditions, and their integrative effects on riparian flooding and disturbance regimes. Although none of our study streams are gaged, there have been widespread observations of altered discharge regimes in (usually larger) subarctic river systems (Jansson et al., 2019; Peterson, 2002; Smith et al., 2007), generally leading to reduced peak flows, higher winter base flows, and higher annual

discharge. Reduced peak flows could be expected to reduce the potential for flood-induced vegetation mortality and could account in part for the observed disequilibrium between forward and backward successional transitions. In turn, the colonization and development of vegetation tend to stabilize floodplain deposits and promote increased river channelization (Tape et al., 2011). In addition, thawing and fragmentation of permafrost within catchments and along the margins of floodplains tend to favor increased groundwater input rather than surface discharge and create opportunities for local shifts in vegetation state (Liljedahl et al., 2017, 2020).

An alternative explanation for rapid riparian “greening” is that an extreme event occurred that reduced the cover of vegetation prior to our study period, such that subsequent increases represent ecosystem recovery rather than long-term change. Exceptionally high rainfall occurred in July and August 1967 in the vicinity of Fairbanks and triggered widespread flooding in the Chena River watershed about 150 km northeast of DNPP. Could this or a similar event have affected our study watersheds? The instrumental record from McKinley Park also shows high rainfall in late summer 1967, including a record high for daily total precipitation, suggesting that DNPP watersheds could have experienced severe flooding during the 1967 Fairbanks flood. Indeed, the peak flow measured on the Teklanika River, which was gaged downstream of DNPP from 1964 to 1973, shows a very strong peak flow of nearly 700 m<sup>3</sup>/s in the summer of 1967 coinciding with the flood event in Fairbanks. However, the 1967 flood event is not evident in precipitation records from the vicinity of WSNP and no station data are available for 1967 at Eagle, making it difficult to assess the spatial extent of the event. Overall, the available information indicates that while vegetation on unregulated floodplains is subject to abrupt disturbance resulting from extreme events, the widespread pattern of vegetation expansion that we observed in Interior Alaska parklands cannot be explained by the 1967 flood event—even in DNPP, where repeat photography of the Teklanika River and several other floodplains in our study shows obvious expansion of floodplain vegetation since the early to mid-20th century (Brodie et al., 2019).

## Implications for ecosystem function on subarctic floodplains

The shifts in the cover, structure, and typical stand-age of riparian vegetation that we have documented likely have a web of implications for the properties of riparian habitats for moose, beavers, hares, songbirds, and other

wildlife. In addition, riparian “greening” could impact aquatic biota in clearwater streams, since the addition of coarse woody debris and plant biomass is known to stimulate increases in invertebrate populations, which in turn have cascading aquatic ecosystem effects (Enefalk & Bergman, 2016; Melody & Richardson, 2004). These shifts could also serve as a bioindicator of change to physical processes and disturbance regime on subarctic floodplains. Previous ecohydrological studies of floodplains in northern Europe have given rise to predictions of a narrowing of active floodplain environments due to changes in the seasonal discharge regime of subarctic streams. For example, Nilsson et al. (2013) have predicted a narrowing of most belts of riparian vegetation according to successional stage and elevation relative to active channels, particularly for communities similar to our low shrub, tall shrub, and spruce ecotypes. Overall, our findings of increased vegetation cover on widely separated groups of watersheds in Interior Alaska suggest disequilibrium between riverine disturbance processes and vegetation establishment. We would expect stream channelization to occur, as early successional ecotypes give way to late successional ecotypes, increased vegetation cover and stem density stabilize banks and buffer the severity of flooding, and older floodplain surfaces transition out of the riparian zone as the flood frequency declines.

Although our study encompasses a large portion of Interior Alaska, more work is needed to verify whether riparian vegetation expansion observed in this region is representative of a broader trend across the circumboreal region, and how these trends vary across gradients of stream order, floodplain morphology, and catchment size. In addition, our findings of especially rapid “greening” in glaciated watersheds require further investigation and highlight the need for field-based follow-up work to investigate underlying drivers. However, our findings of recent vegetation expansion on floodplains are, in aggregate, consistent with the expected responses of hydrological, biological, and terrestrial processes to a warming climate at both watershed and local scales. We hope our study motivates further work to corroborate “greening” of subarctic floodplains elsewhere in the circumboreal region and provides a basis for developing and testing hypotheses concerning the response of unregulated subarctic riparian zones to climate change.

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## CONFLICT OF INTEREST

The authors declare no conflict of interest.


## DATA AVAILABILITY STATEMENT

Data supporting the findings of this study are available online at the Integrated Resource Management Applications (IRMA) DataStore hosted by the US National Park Service: <https://irma.nps.gov/DataStore/Reference/Profile/2294338>. Our study made extensive use of historical (circa 1980) and recent (circa 2010) high-resolution imagery to evaluate change in riparian landscapes. All historical aerial photography came from the Alaska High Altitude Photography (AHAP) program and is available to the public at no charge from the US Geological Survey: <https://earthexplorer.usgs.gov/>. Recent high-resolution imagery for Yukon-Charley Rivers National Preserve is available online at the IRMA DataStore: <https://irma.nps.gov/DataStore/Reference/Profile/2293970>. Recent commercial satellite imagery used for the Denali and Wrangell–St. Elias parklands was obtained under license from DigitalGlobe, Inc. This imagery is subject to use restrictions; for more details, please see [High-resolution imagery collection](#). The specific historical and recent images used in our study can be queried using the imagery acquisition dates given for each site in Appendix S2.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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