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CHECKLIST

Checklist of vascular plants for Wind River Indian Reservation (USA) high-elevation basins: ecological drivers of community assemblages

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Background and aims – Native American reservations in the United States provide biodiversity critical for conservation and ecosystem functions. Unfortunately, botanical inventories are less common for reservations than other land jurisdictions. Such ecological importance and needs are apparent for the Wind River Indian Reservation (WRIR), the 7th largest reservation in the US (>890,000 ha) that is shared by the Eastern Shoshone and Northern Arapaho.
Material and methods – A botanical study for two WRIR high-elevation basins (Saint Lawrence Basin (SLB) and Paradise Basin (PB)) to (1) reconcile a 1960 plant list, and (2) quantify plant communities ecologically was conducted. In 2017, 106 monitoring sites were established to quantify species presence. Across basins, 231 total vascular plant taxa (221 to species and 10 to genus) were identified, or > 3× more plant species than noted in the 1960 list. In SLB, 222 plant taxa (213 to species and 9 to genus) were identified and in PB 98 plant taxa (90 to species and 8 to genus) were identified. In 2018, sites were re-sampled to quantify species abundance, soil pH, organic matter, soil nutrients, CEC, salts, and texture.
Key results – Slope and elevation explained species distributions in the topography ordination and soil organic matter, pH, texture, P, and K explained species distributions in the soil ordination. Eleven exotic species, and one rare endemic species were documented with implications for empowering tribal management. Using a classification approach followed by an indicator species analysis and fidelity (Phi) assessment, we identified 14 unique plant communities and related these to 6 alliances and 7 associations across 6 macrogroups from the US National Vegetation Classification database. These indicator species of communities included sedges (*Carex aquatilus*), grasses (*Pseudoroegneria spicata*, *Elymus elymoides*, *Achnatherum lettermanii*, *Elymus trachycaulus* subsp. *trachycaulus*, *Poa glauca* subsp. *rupicola*), forbs (*Polygonum bistortoides*, *Balsamorhiza incana*, *Castilleja flava*), shrubs (*Artemisia tridentata*, *Betula glandulosa*, *Dasiphora fruticosa* subsp. *floribunda*) and trees (*Pinus contorta*).
Conclusion – The plant taxa, plant communities, and ecological drivers documented in this study will enhance tribal and federal monitoring of these high-elevation WRIR basins.

Keywords – Climate change; indigenous; multivariate analyses; plant communities; plant inventory.

INTRODUCTION

Quantifying botanical diversity patterns is fundamental to conserving global biodiversity, particularly at ecotones and extreme margins within the context of a changing climate (Pauchard et al. 2009; Lesica 2015). Recognizing plant communities as valuable resources, the United States (US) federal government regularly works with researchers to document and study the natural resources in national parks (Carter et al. 2006). Native American Indian reservations also function as pools of biodiversity for a broad spectrum of ecosystems and sizes of conservation units (Luna & Bahls 2017). However, even though the US federal government manages trust land on behalf of tribes, plant inventory projects, or projects quantifying biodiversity of any kind, are less common for reservations than other land jurisdictions such as national parks or forests (Crumpacker et al. 1988; Lesica 1993).

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There are currently 573 federally recognized American Indian and Alaskan Native tribes and villages in the US (Bureau of Indian Affairs 2019). The federal recognition is formalized, particularly in the relationship with the Bureau of Indian Affairs via the following definition: "A federally recognized tribe is an American Indian or Alaska Native tribal entity that is recognized as having a government-to-government relationship with the United States, with the responsibilities, powers, limitations, and obligations attached to that designation, and is eligible for funding and services from the Bureau of Indian Affairs [BIA]" (Bureau of Indian Affairs 2019). In the US there are 326 federal Indian reservations that hold approximately 22.7 million hectares of land in trust by the US federal government (Bureau of Indian Affairs 2019). Trust lands are lands that the federal government holds title on behalf of various tribes, American Indians, and Alaskan Natives (McCarthy 2004; Bureau of Indian Affairs 2019).

These reservations are diverse in terms of size, management, organization, and natural resources. Some tribes have no designated trust land. Many reservations have a complex checker-board arrangement that includes a patchwork of trust, allotted, and fee land (Bureau of Indian Affairs 2019). Trust lands are accessible by tribal members year-round and during the summer months non-tribal members can purchase recreation use permits with varying levels of accessibility across the many tribes and their associated tribal laws. There is a complex history of policy decision-making regarding tribal land involving the US Congress, the Department of the Interior and individual tribes themselves, although tribes currently function with more autonomy regarding natural resource management than in past eras of policy (McCarthy 2004; Wilkins & Stark 2017; Bureau of Indian Affairs 2019). Such autonomy can be reflected in a tribal natural resource, environmental, or wildlife office and current practice demonstrates how tribes have the authority to make decisions regarding the depth and types of land use, which has the potential to reduce or increase human and livestock interactions with ecosystems. It is also common for most tribes to work with BIA staff to further address natural resource issues and such co-management of tribal resources is mandated because the BIA is "charged with carrying out the United States' trust responsibility to American Indian and Alaska Native people, maintaining the federal government-to-government relationship with federally recognized Indian tribes, and promoting and supporting tribal self-determination" (Bureau of Indian Affairs 2019). The federal Indian trust responsibility is a legally enforceable fiduciary obligation by the United States to protect tribal treaty rights, lands, assets, resources and executes the mandates of federal law (McCarthy 2004; Bureau of Indian Affairs 2019).

The BIA Branch of Agriculture and Rangeland Development administers the trust responsibility by improving the management of land and natural resource assets on trust land. BIA staff provide oversight and technical assistance in eight major categories: (1) inventory; (2) farm and range planning; (3) rangeland improvements; (4) rangeland protection; (5) leasing and permitting services; (6) contract monitoring; (7) agriculture extension; and (8) noxious weed eradication (Office of Trust Services 2019). BIA also facilitates cooperative efforts between tribes and other federal agencies for soil survey and rangeland vegetation classification to guide management and rangeland improvement projects (Hodgkinson 1984; Pease et al. 1991; Office of Trust Services 2019). Integrated management and conservation plans have been created for tribes to meet the technical assistance goals expected of the BIA (Fred Phillips Consulting and Bureau of Indian Affairs 2013). While BIA is a federal agency, it is not always the case that national level resource inventories are implemented on trust lands. For example, Ecological Site Descriptions (ESDs) are the world's largest land management framework created by scientists in collaboration with land managers. ESDs can provide detailed information on climate, soil, geomorphology, hydrology and vegetation to assist in land management decisions (USDA 2013; Twidwell et al. 2013), yet on trust lands ESDs either do not exist or often contain gaps of data yet to be determined by ground verification, making these ESDs useless for writing range management plans. Thus, the currently available vegetation inventory data is not always operational.

Such issues of biodiversity, bureaucracy, and opportunities intersect on the Wind River Indian Reservation (WRIR). WRIR is the 7th largest Indian reservation by land area in the US, consisting of more than 890,000 hectares. The WRIR has approximately 26,000 residents (U.S. Census Bureau 2010). The WRIR is located within Fremont and Hot Springs Counties of Wyoming USA and the federally-recognized Eastern Shoshone and Northern Arapaho tribal nations share the reservation (fig. 1). The WRIR is situated in the Wind River Basin and is surrounded by the Wind River, Owl Creek, and Absaroka mountain ranges. The Wind River Mountain Range is the largest mountain range in Wyoming and has the highest peak in the state – Gannett Peak at 4,209 m. The aesthetic and cultural uniqueness of these high-elevation mountains illustrate the societal values that the WRIR and society at large place upon the Wind River Mountain Range. To date, detailed botanical data has primarily been limited to species presence and absence lists with no ecological site information (supplementary file 1).

Due to the expansive rangeland resources of the WRIR and its ecological, agriculture, and cultural importance, a more intricate study of botanical relationships is needed for both conservation and rangeland management. In 2015 a two-year, comprehensive plant inventory study was initiated to (1) reconcile a dated (55-year-old) plant presence/absence study, and then (2) to quantify the plant communities of high-elevation basins with a greater level of ecological detail relative to environment features. Specifically, quantifying plant communities and dominant functional groups in the basins, coupled with topographic, soils and disturbance data is critical to understanding where plant assemblages occur and provides resources to assist in making informed management decisions. The impact of such studies is that more comprehensive data allows tribal land managers to better detect how environmental change such as variation in land use, temperature, precipitation, and snowpack levels impacts sensitive plant communities in these high-elevation basins – information that has been lacking to date.

MATERIAL AND METHODS

Justification

In 1960, Field & Tidd conducted an inventory of the plants in Paradise Basin (or "Paradise Park") and Saint Lawrence Basin in the Wind River Mountain Range with voucher specimens reconciled by C.L. Porter who was the curator of the University of Wyoming's Rocky Mountain Herbarium at that time (see supplementary file 1). A second set of voucher specimens are housed at the Bureau of Indian Affairs (BIA) Wind River Agency in the Range Department Herbarium. This initial inventory, while useful as a basic plant species list, is severely lacking in applicable value for several reasons: (1) it only includes the presence or absence of 74 species with some repeating, (2) makes no estimate of species abundance, (3) makes no differentiation between the two basins relative to the presence of a species, and (4) does not measure any other ecological explanatory information to explain species occurrence. Thus, while this survey has some base-level value, it is not useful in explaining the rangeland plant communities in these high-elevation basins, has no abundance data that would be useful for determining rangeland health and condition, and is unable to develop predictive models for where certain plant species and plant assemblages occur relative to other environmental features. These lacking features of the 1960 inventory preclude the tribal use of the information to understand the current rangeland conditions and development of management plans.

Study area

The study area consists of two adjacent high-elevation basins in the Wind River Mountain Range on the WRIR: (1) Saint Lawrence and (2) Paradise basins (fig. 2). The Saint Lawrence basin is located approximately 26 kilometres northwest of Fort Washakie, Wyoming and has an area of ~94.52 km^2. The Saint Lawrence basin receives, annually, 64.3 cm of precipitation, and temperature ranges from -4 to 8.7°C (1988–2018) with an elevation ranging from 2,560 to 3,352 m a.s.l. (PRISM Climate Group 2019). Dominant land

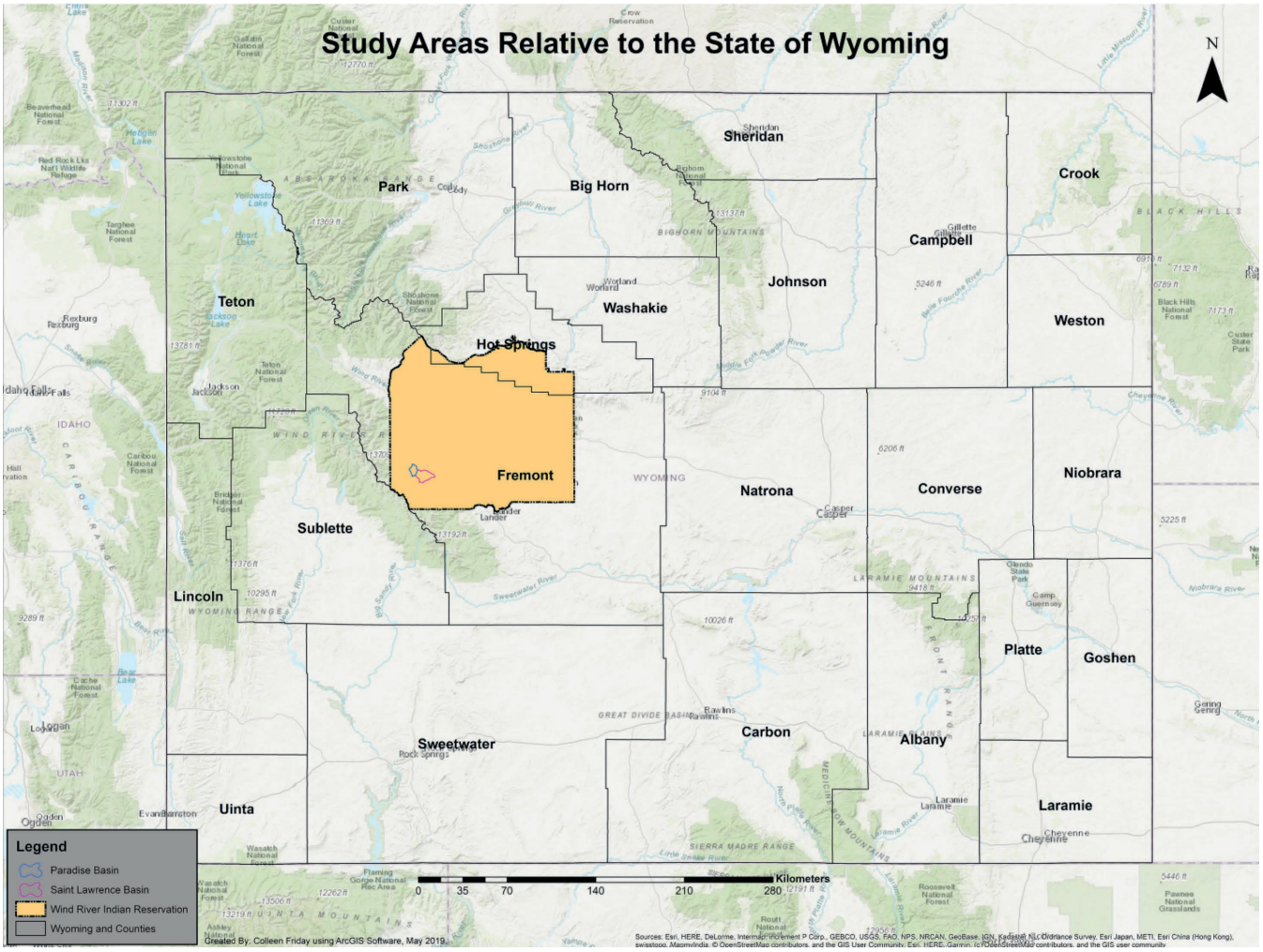

Figure 1 – Map indicating the location of the study areas located in the Wind River Range on the Wind River Indian Reservation in Fremont and Hot Springs Counties, Wyoming, USA. Map created by C. Friday using ArcGIS version 10.7 (Esri 2019). © OpenStreetMap contributors and the GIS User Community, Esri, HERE, Garmin; all rights reserved. This image is not distributed under the terms of the Creative Commons licence of this publication. For permission to reuse, please contact the rights holder.

uses in Saint Lawrence basin are livestock grazing, firewood harvesting, outfitter operations (June–September annually) and outdoor recreation. Paradise basin is located approximately 35 kilometres northwest of Fort Washakie, Wyoming and encompassing an area approximately 41.73 km^2 (fig. 2). Paradise basin receives, annually, 78.8 cm of precipitation and temperature ranges from -4.7 to 6.7°C (1988–2018) with an elevation ranging from 2926–3429 m asl (PRISM Climate Group 2019). Within Paradise basin, outdoor recreation and outfitter client services are the dominant uses.

The geology of the Wind River mountains is very complex as it spans a long time period dating back over 3 billion years with multiple episodes of major developments particularly sea inundations, intense magmatism and tectonic plate activity, and ultimately dramatic uplift and thrusting of Paleozoic and Mesozoic sediments (Wells et al. 2015). For the specific basins in this study, the parent material is primarily Precambrian rocks consisting of mostly granites and gneisses of sedimentary origin (Donohue & Essene 2005). The older strata near the mountains rise to elevations almost as tall as the main peaks themselves. The combination of geologic parent material, alpine glaciation, and geologic forces have formed high-elevation basins as these foothills transition to high peaks and they are dominated by herbaceous vegetation important for livestock and wildlife. For both basins, forested areas are dominated by Lakehelen–Hazton complex soils and steeper slopes and ridges are dominated by Alpine Ridges Rubbleland–Tundra complex soils. For Paradise Basin, sedge-rush areas are dominated by Venapass–Silas loam soils and graminoid-shrub dominated areas are dominated by Nathale–Pishkun–Rock outcrop complex soils. For Saint Lawrence Basin graminoid-shrub dominated areas are dominated by Barbarela–Hapjack–Sawcreek complex soils and sedge-rush areas are dominated by Vensora clay loam soils (USDA NCRS 2020).

Most of the study area is designated as a roadless area and named the Wind River Reserve (Cornell Law School 2019). The roadless area was created in response to the WRIR tribal councils' concerns about the future construction of mountain passes for highways for tourists travelling to

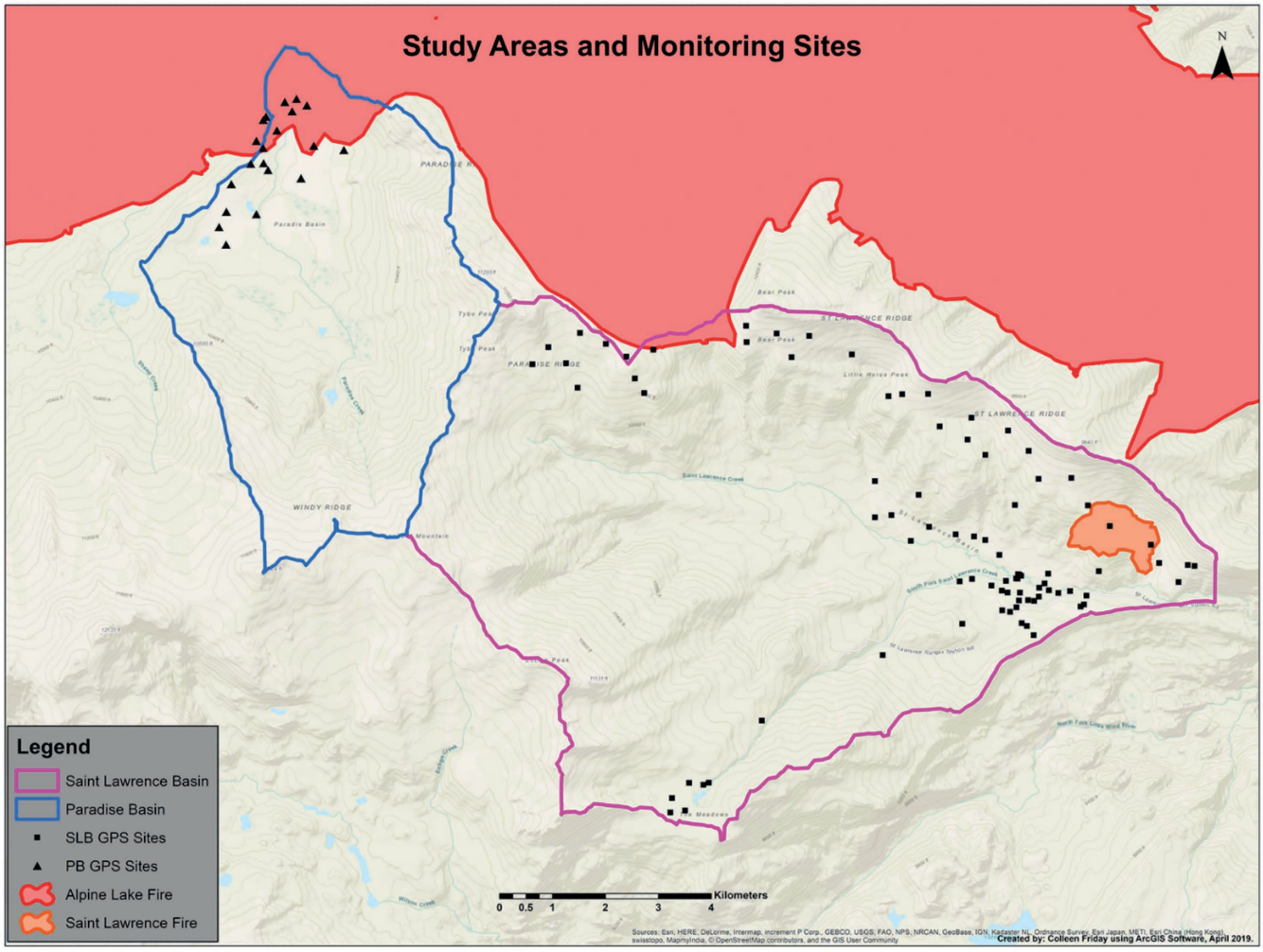

Figure 2 – Map indicating the study area boundaries of Saint Lawrence and Paradise basins with the 106 monitoring sites. The basins are in the Wind River Range on the Wind River Indian Reservation in Fremont County, Wyoming, USA. Map created by C. Friday using ArcGIS version 10.7 (Esri 2019). © OpenStreetMap contributors and the GIS User Community; all rights reserved. This image is not distributed under the terms of the Creative Commons licence of this publication. For permission to reuse, please contact the rights holder.

visit Yellowstone or the Grand Teton National Parks (Aragon 2007). The Wind River Reserve sets aside ~73,000 hectares of land as roadless area and restricts the construction or establishment of roads, highways, truck trails, work roads, and all other types of motor transportation passage ways (Aragon 2007; Cornell Law School 2019). More than half of Saint Lawrence basin is designated roadless area. Paradise basin is designated entirely as roadless area with no livestock grazing permitted and the use of motorized vehicles and tools is restricted unless approved by the BIA Wind River Agency Superintendent (Cornell Law School 2019).

Study design

The BIA Wind River Agency Range Program's assessment and monitoring protocol (originally adapted from Wyoming Range Service Team 2008) was used as the foundation for data collection. The protocol consists of a 30.5 m transect that is established in a north to south direction, photos are taken in four cardinal directions at the north end, line point intercept data is recorded every 0.3 m (i.e., a foot), and quadrats for cover data are placed every 7.62 m starting from zero (Wyoming Range Service Team 2008). The protocol is used for long-term vegetation monitoring by range staff and interested livestock producers are trained with the protocol throughout the WRIR. Prior to conducting this study, the Field & Tidd plant list from 1960 (see supplementary file 1) was reconciled and updated with current taxonomic designations and a determination of plant species status (native/exotic, conservation status, rare/endangered, toxic/poisonous, etc.). Random points were generated from Geographic Information System (GIS) analysis of digitized soil maps (Soil Survey Staff 2019) and study area maps using ArcGIS Software (Esri 2019). One hundred and six (106) total monitoring sites for sampling were selected from the random points maps to establish data collection sites during the study and for long-term monitoring by the BIA Wind River Agency Range staff. Transects were randomly established in both basins across habitat types (riparian, meadow, upland, or forested). For each transect, we noted aspect, slope, and elevation. Additionally, in Saint Lawrence basin we established 4 transects inside and outside of a pre-existing BIA exclosure. In 2012 a wildfire named the Alpine Lake fire burned ~16,732 hectares and in September 2017 another wildfire burned 66 hectares in Saint Lawrence basin. We thus also established transects within each burn area.

Field methods and data

In 2017, plant species presence/absence inventory was recorded by identifying plant species present within a 180 m^2 plot centred on a 30.5 m transect. Of the 106 monitoring sites, 86 sites are located in Saint Lawrence basin and 20 sites are located in Paradise basin (fig. 2). We then compiled a species list for both basins from the presence inventory (supplementary file 2) and taxonomical nomenclature follows USDA NRCS (2019). In some instances, a specimen could only be identified at the genus level, including for *Arnica*, *Artemisia*, *Astragalus*, *Carex*, *Cirsium*, *Erigeron*, *Eriogonum*, *Lupinus*, *Potentilla*, and *Salix*. These 10 genera were included in all analyses with the exception of functional group summaries. Plant voucher specimens were prepared for storage at the BIA Wind River herbarium for a majority of the plant species that were identified. Each specimen included at a minimum the following information: (1) collection number; (2) date collected; (3) identification of the plant; (4) location, including township, range, section, county, elevation and vegetation type; (5) environmental aspects, including aspect, slope and elevation; (6) notes on flower colour, plant size, variability; and (7) collector name (Elzinga et al. 1998; Martin 2010).

Soil samples were taken at every 3 m along a 30.5 m transect line for a total of 10 samples per transect. Soil samples of 10 cm in depth were extracted using a standard cylindrical soil core sampler with a 2.54 cm diameter. The soil samples were air dried on paper bags in full sunlight and stored in 1-quart plastic bags. At the end of the field season the soil samples were shipped to Ward Laboratories, Inc. in Kearney, Nebraska, USA for chemical and texture analysis. In addition, soil compaction data was recorded in the field using a pocket soil penetrometer at 0 m, 8 m, 15 m, 23 m, and 30 m along a 30.5 metre transect line. The measurements were then averaged and recorded in kg/cm^2. Soil characteristics included in analyses included soil pH, organic matter (OM), total nitrogen (N), total phosphorus (P), potassium (K), cation exchange capacity (CEC), soluble salts, and soil texture percentages (clay, sand, and silt).

Statistical analysis

We first calculated the number of species by functional group (forb, grass, sedge/rush, shrub, tree) and origin (native or exotic) for each basin. Varieties and subspecies were included as distinct taxa in all analyses. Then to understand ecological relationships and plant species distributions relative to topographic and soil features within the two high-elevation basins (combined for all subsequent analyses), we first used multivariate statistical techniques and CANOCO version 5 statistical software to perform analyses (Šmilauer & Lepš 2014). This approach allows for the assessment of complex community data relative to variation and similarity and the identification of primary drivers in multi-dimensional space (Frye 2009). We performed a Detrended Correspondence Analysis (DCA), an unconstrained ordination technique, to quantify plant species in multidimensional space data. DCA has been widely used in ecology because of its non-linear model, its ability to address arch effects of correspondence analysis, and its application for predicting vegetation patterns (Zhang et al. 2008; Shetie et al. 2017). We then performed two Canonical Correspondence Analyses (CCA) to quantify plant species distributions relative to topographic features and soil data. In the topographic CCA, we used the topographic features of percentage slope, aspect northness, aspect eastness, and elevation as explanatory variables. In the soil CCA, we used soil pH, CEC, OM, soluble salts, N, K, P, texture percentages (silt, clay, and sand), and SC as explanatory variables (Dingaan et al. 2017). The species response data was binary (i.e., presence/absence or 1/0), data were not transformed, there was no downweighting of rare species, sample diversity was expressed as number of species, and all the first axis and then all constrained axes com-

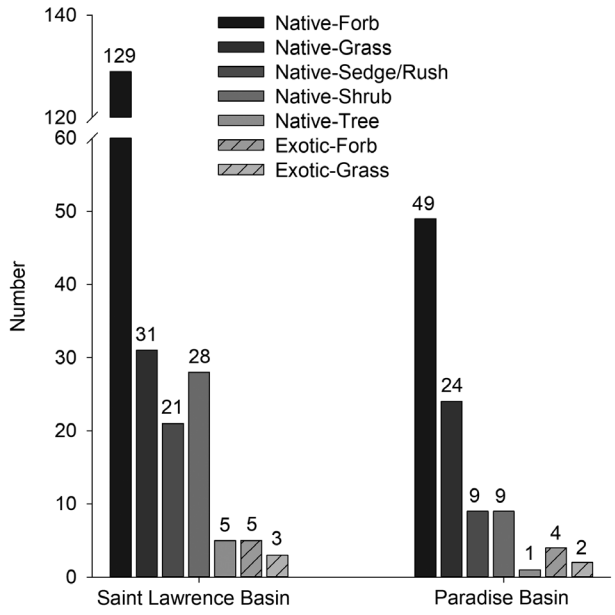

Figure 3 – Total number of plant taxa per functional group (forb, grass, sedge/rush, shrub, tree) relative to plant origin (native or exotic) and comparison between the Saint Lawrence and Paradise Basins in the Wind River Indian Reservation in Fremont County, Wyoming, USA.

bined were tested with a permutation test (1,000 iterations) for significance in each of the CCAs.

In order to move towards identifying plant communities and classification, we then applied a hierarchical clustering approach to initially identify groups of sites using a classical Ward's method algorithm (PAST version 3.0; Hammer et al. 2001). In this step we used a distance cut-off criterium of 12.5 to identify fourteen groups (number of plots within groups ranged from 3 to 14). We then conducted an indicator species analysis using the "indicspecies" package in R (De Cáceres 2020). We then calculated adjusted phi (φ) coefficients (adjusted for some groups having more sites than others; Tichý & Chytrý 2006) as indicators of fidelity to each group and an indication of a positive or negative preference of a species for a group (Chytrý et al. 2002) using CANOCO version 5 (Šmilauer & Lepš 2014). Finally, we evaluated the presence, significance, and fidelity of species within groups and compared to classifications in the United States National Vegetation Classification (USNVC), relative to indicator species and invasive species, to identify similar USNVC alliances (A) or associations (CEGL) and macrogroups when possible (USNVC 2020).

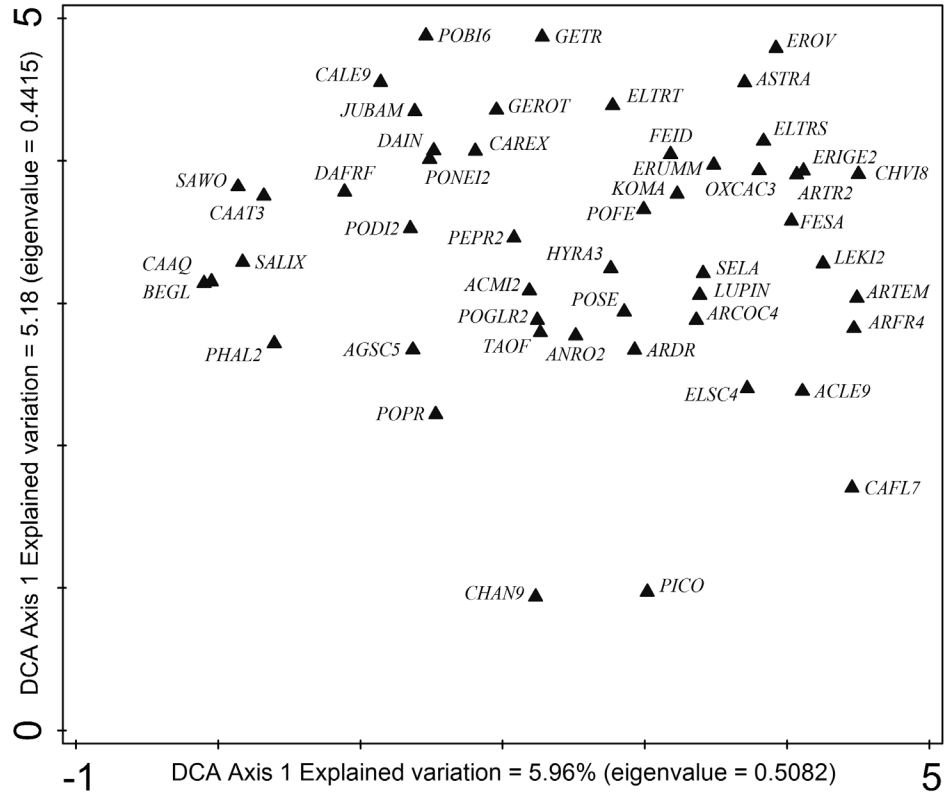

Figure 4 – Detrended Correspondence Analysis (DCA) of species presence/absence data. DCA explained 5.96% of the variation for axis 1 (eigenvalue 0.5082) and 5.18% of the variation for axis 2 (both axes cumulative explained 11.14% of the variation). Plant taxa are represented by a four to five letter code assigned by the USDA Plants database. Other letter codes are associated with Daubenmire cover classes (Daubenmire 1959).

RESULTS

Plant species distributions – unconstrained ordinations

In Saint Lawrence Basin (SLB) 222 plant taxa were identified (213 to species and 9 to genus), with 96% native, and the dominant functional group was forbs followed by native grasses (fig. 3). In Paradise Basin (PB) 98 plant taxa were identified (90 to species and 8 to genus), with 94% native, and similarly forbs are the dominant functional group followed by native grasses. 89 of the plant taxa occurred in both basins, so there were 9 unique species to PB. The total number of exotic taxa was less in PB than in SLB (6 and 8 respectively) (fig. 3).

The DCA explained 5.96% of the variation for axis 1 (eigenvalue 0.5082) and 5.18% of the variation for axis 2 (both axes cumulative explained 11.14% of the variation) (fig. 4). As expected, some species were closer in multi-dimensional space. For example, species associated with wet meadows, ponds, or stream banks such as willows (*Salix* species; SALIX), resin bog birch (*Betula glandulosa*; BEGL), Wolf's willow (*Salix wolfii*; SAWO), shrubby cinquefoil (*Dasiphora fruticosa* subsp. *floribunda*; DAFRF), Baltic rush (*Juncus balticus* var. *montanus*; JUBAM), and water sedge (*Carex aquatilis*; CAAQ) are in close proximity (fig. 4). Species associated with upland rangeland environments such as *Lupinus* species (LUPIN), buckwheat species (*Eriogonum ovalifolium*; EROV, and *Eriogonum umbellatum* var. *majus*; ERUMM), and cool-season C3 grasses (*Elymus trachycaulus* subsp. *trachycaulus*; ELTRS, *Festuca idahoensis;* FEID, and *Festuca saximontana*; FESA) are grouped closer together in multidimensional space (fig. 4).

Topography and soil influences on plant species – constrained ordinations

The topographic CCA explained fitted variation for axis 1 was 38.36% and axis 2 explained fitted variation was 29.38% (fig. 5), a substantial improvement over the explained variation in the DCA alone (fig. 4). The first axis is strongly explained by slope and northness/eastness, the

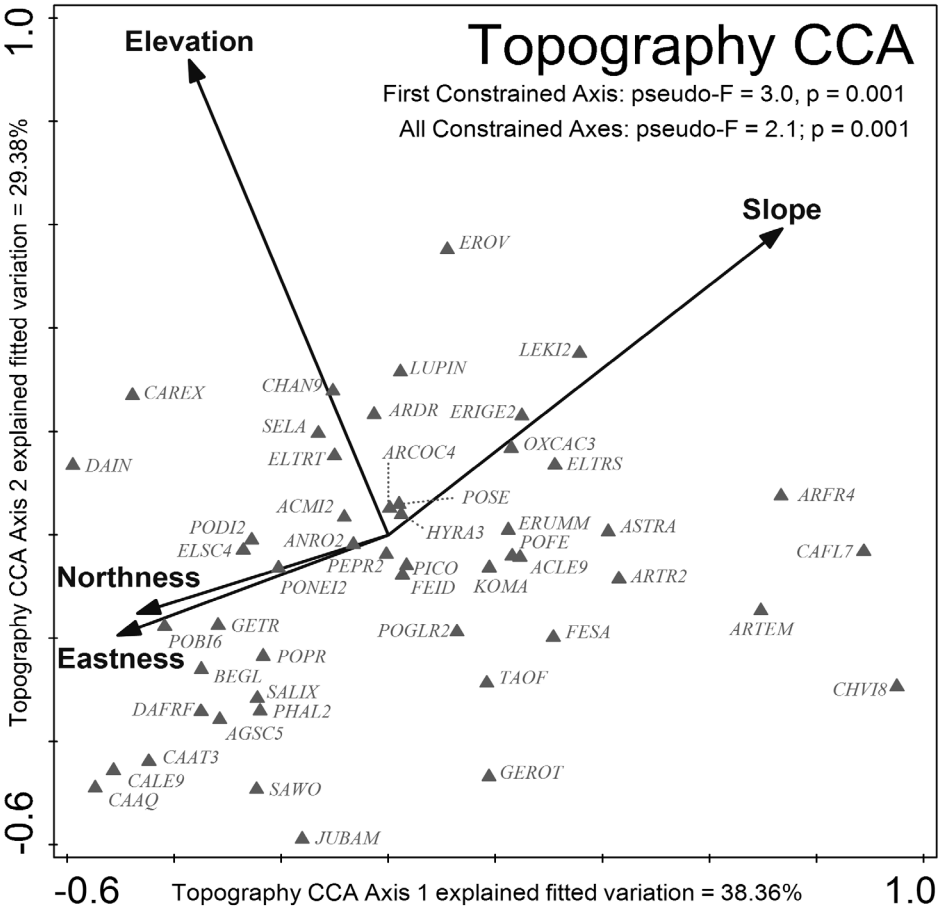

Figure 5 – Topographical Canonical Correspondence Analysis (CCA) of vegetation composition relative to topography features. Explained fitted variation for axis 1 was 38.36% and axis 2 explained fitted variation was 29.38%. The first axis is explained by slope and northness/eastness and the second axis is explained by elevation. The pseudo-F value for the test on the first constrained axis was 3.0 and p = 0.001 and for all four axes was 2.4 and p = 0.001, indicating that the topographic covariates are significant explanatory variables for the plant community data. Plant species are represented by a four to five letter code assigned by the USDA Plants database. Other letter codes are associated with Daubenmire cover classes (Daubenmire 1959).

second axis is strongly explained by elevation. Regarding slope, species such as *Artemisia* (ARTEM), spike fescue grass (*Leucopoa kingie*; LEKI2), prairie sagewort (*Artemisia frigida*; ARFR4), yellow Indian paintbrush (*Castilleja flava*; CAFL7), and slender wheatgrass (*Elymus trachycaulus* subsp. *subsecundus*; ELTRS) seem to be explained by increasing slope, while sedges and rushes such as water sedge (*Carex aquatilis*; CAAQ), Sierra hare sedge (*Carex leporinella*; CALE9), slenderbeak sedge (*Carex athrostachya*; CAATS), Baltic rush (*Juncus balticus* var. *montanus*; JUBAM), and certain shrubs such as willows (*Salix* species; SALIX), resin bog birch resin bog birch (*Betula glandulosa*; BEGL), and shrubby cinquefoil (*Dasiphora fruticosa* subsp. *floribunda*; DAFRF) are associated with gentler slopes and more north and/or east facing aspects. Several species seem to be explained by increasing elevation such as cushion buckwheat (*Eriogonum ovalifolium*; EROV), fireweed (*Chamerion angustifolium*; CHAN9), spearleaf stonecrop (*Sedum lanceolatum*; SELA), Drummond's rockcress (*Arabis drummondii*; ARDR), slender wheatgrass (*Elymus trachycaulus* subsp. *subsecundus*; ELTRS), and lupines (*Lupinus* species; LUPIN). The pseudo-F value for the test on the first constrained axis was 3.0 and p = 0.001 and for all four axes was 2.4 and p = 0.001, indicating that the topographic covariates are significant explanatory variables for the plant community data (fig. 5).

The soil CCA explained fitted variation for axis 1 was 32.72% and axis 2 explained fitted variation was 16.14% (fig. 6), a substantial improvement over the explained variation in the DCA alone (fig. 4). The first axis is strongly explained by organic matter (OM), pH, and potassium (K), while the second axis seems to be strongly explained by phosphorous (P) and salts. A soil texture gradient is also apparent from sand (left) to clay (right). Regarding this first axis, species of willow (*Salix* species; SALIX), shrubby cinquefoil (*Dasiphora fruticosa* subsp. *floribunda*; DAFRF), water sedge (*Carex aquatilis*; CAAQ), and resin bog birch (*Betula glandulosa*; BEGL) are associated with greater OM, greater percentage silt and clay, and lower pH. In contrast, species such as *Artemisia* species generally (ARTEM), big sagebrush (*Artemisia tridentata*; ARTR2), prairie sagewort (*Artemisia frigida*; ARFR4), *Astragalus* species generally (ASTRA),

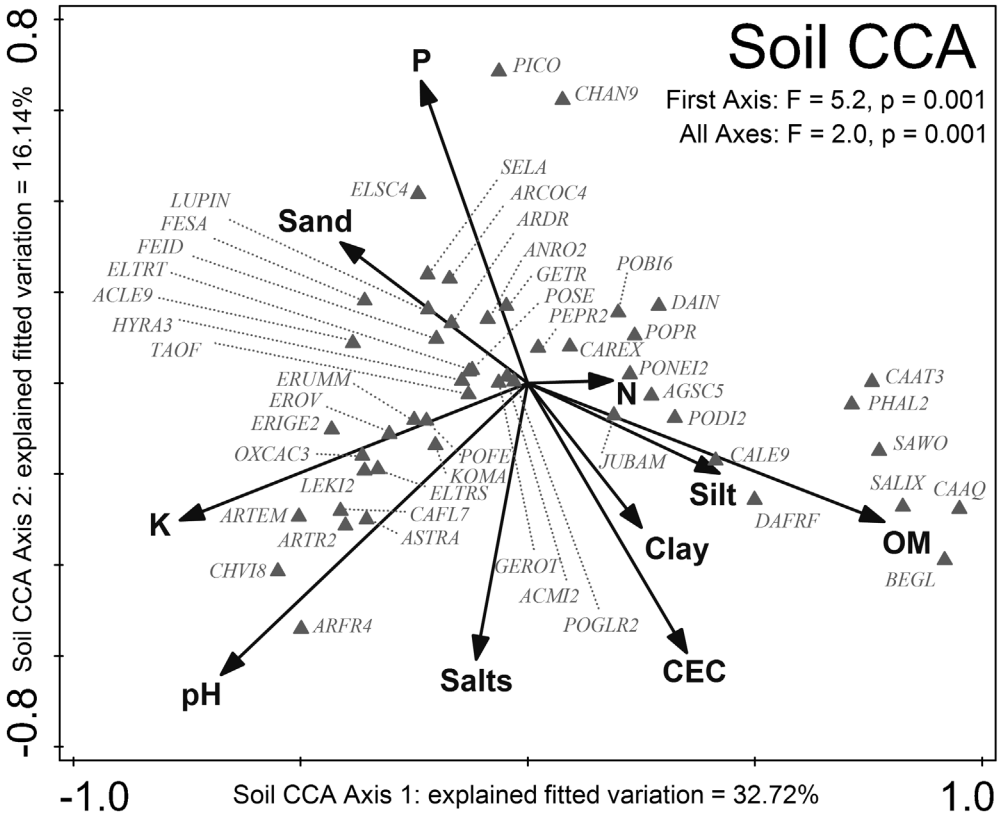

Figure 6 – Soil Canonical Correspondence Analysis (CCA) of vegetation composition relative to soil variables. The soil variables are soil pH (pH), cation exchange capacity (CEC), organic matter (OM), soluble salts (Salts), nitrogen (N), potassium (K), phosphorus (P), and texture percentages (silt, clay, and sand). Explained fitted variation for axis 1 was 32.72% and axis 2 explained fitted variation was 16.14%. The first axis is explained by organic matter (OM), pH, and potassium (K), the second axis seems to be explained by phosphorous (P) and salts, and a soil texture gradient is also apparent from sand (left) to clay (right). The pseudo-F value for the test on the first constrained axis was 5.2 and p = 0.001 and for all four axes was 2.0 and p = 0.001, indicating that the soil covariates are significant explanatory variables for the plant community data. Species are represented by four to a four to five letter code assigned by the USDA Plants database. Other letter codes are associated with Daubenmire cover classes.

Table 1 – **Resin bog birch (*Betula glandulosa*) plant community in the Wind River Indian Reservation in Wyoming, USA.**
[Group 1 plot means (n = 3): Elevation 3,207 m, % Sand-Silt-Clay 58-25-17, Organic Matter 20.7%, pH 5.8]. Phi (φ) is an indicator of fidelity and the asterisk (*) suggests this is the preferred group for this species.

Code	Name	Scientific name	p-value	Phi (φ)
LUPA4	Smallflowered woodrush	*Luzula parviflora*	0.0001	0.9945*
CASC12	Mountain sedge	*Carex scopulorum*	0.0001	0.9699*
BEGL	Resin bog birch	*Betula glandulosa*	0.0001	0.8814*
PHAL2	Alpine timothy	*Phleum alpinum*	0.0001	0.8758*
SAWO	Wolf's willow	*Salix wolfii*	0.0001	0.8748*
POPR	Kentucky bluegrass (**exotic**)	*Poa pratensis*	0.0389	0.8083*
SALIX	Willows (species unknown)	*Salix* sp.	0.0001	0.8012*
DAIN	Timber oatgrass	*Danthonia intermedia*	0.0001	0.7975*
PIEN	Engelmann spruce	*Picea engelmannii*	0.0012	0.7071*
CACA4	Bluejoint	*Calamagrostis canadensis*	0.0002	0.6999*
DAFRF	Shrubby cinquefoil	*Dasiphora fruticosa* subsp. *floribunda*	0.0001	0.6990
CAREX	Sedge (species unknown)	*Carex* sp.	0.0001	0.6926
PHPR3	Timothy (**exotic**)	*Phleum pratense*	0.0008	0.6737*
POAV	Prostrate knotweed (**exotic**)	*Polygonum aviculare*	ns	0.4353*

and spike fescue grass (*Leucopoa kingii*; LEKI2) are associated with decreasing OM, more K, greater percentage sand, and higher pH (fig. 6). Regarding the second axis, lodgepole pine (*Pinus contorta*; PICO), fireweed (*Chamerion angustifolium*; CHAN9), and spreading wheatgrass (*Elymus scribneri*; ELSC4) are associated with more P and sand, and lower salt content and CEC. The pseudo-F value for the test on the first constrained axis was 5.2 and p = 0.001 and for all four axes was 2.0 and p = 0.001, indicating that the soil covariates are significant explanatory variables for the plant community data (fig. 6).

Indicator species analysis – plant communities and indicator species

The classification and indicator species analysis revealed 14 unique plant communities. These plant communities generally had similar classifications to the United States National Vegetation Classification (USNVC) with two exceptions. Here, we provide details about each plant community relative to indicator species, invasive species, and USNVC similar Alliances (A) or Associations (CEGL) and/or gaps in the USNVC system relative to our findings. We note that the classifications were derived from six USNVC macrogroups, including: M020 (Rocky Mountain Subalpine-High Montane Forest), M034 (Rocky Mountain-Great Basin Montane Riparian & Swamp Forest), M048 (Central Rocky Mountain Montane-Foothill Grassland & Shrubland), M168 (Rocky Mountain-Vancouverian Subalpine-High Montane Mesic Meadow), M169 (Great Basin-Intermountain Tall Sagebrush Steppe & Shrubland), M893 (Western North American Montane Marsh, Wet Meadow & Shrubland), and have also noted these for each plant community (USNVC 2020).

Resin bog birch (*Betula glandulosa*) plant community (table 1) – This was the preferred group for shrubs and trees that prefer moist environments such as resin bog birch (*Betula glandulosa*), Wolf's willow (*Salix wolfii*), Engelmann spruce (*Picea engelmannii*). Similarly, smallflowered woodrush (*Luzula parviflora*) and alpine timothy (*Phleum alpinum*) preferred this group. All these species had a significant association (p < 0.01) and a high level of fidelity (φ > 0.7) (table 1). This group was also preferred by three exotic species (Kentucky bluegrass (*Poa pratensis*), timothy (*Phleum pratense*), and prostrate knotweed (*Polygonum aviculare*)). This group is similar to USNVC CEGL000357 *Picea engelmannii* / *Caltha leptosepala* Swamp Forest (M034) with additional similarities to A4096 *Dasiphora fruticosa* / *Festuca campestris* - *Festuca idahoensis* Shrub-steppe Alliance because of the invasion by *Phleum pratense* and *Poa pratensis* (M048) and to A3770 *Salix wolfii* - *Salix brachycarpa* - *Betula glandulosa* Wet Shrubland Alliance (M893).

Water sedge (*Carex aquatilus*) - Willow (*Salix* species) plant community (table 2) – This was the preferred group for two sedges including water sedge (*Carex aquatilis*) and Sierra hare sedge (*Carex leporinella*). In addition, this was the preferred group for the forb redpod stonecrop (*Rhodiola rhodantha*). All these species had a significant association (p < 0.02) and a moderate to high level of fidelity (φ = 0.8903, 0.6820, and 0.4171 respectively) (table 2). This group included similar shrubs found in the resin bog birch plant community (resin bog birch (*Betula glandulosa*), willows (*Salix* species), and shrubby cinquefoil (*Dasiphora fruticosa* subsp. *floribunda*), as well as other sedges and rushes. This group is similar to USNVC A3770 *Salix wolfii* - *Salix brachycarpa* - *Betula glandulosa* Wet Shrubland Alliance (M893); *Salix wolfii* was present but non-significant in the data.

Shrubby cinquefoil (*Dasiphora fruticosa* subsp. *floribunda*) - Idaho fescue (*Festuca idahoensis*) plant community (table 3) – This group included shrubby cinquefoil (*Dasiphora fruticosa* subsp. *floribunda*) and Idaho fescue (*Festuca idahoensis*) both of which were significantly associated with the group (p < 0.001) and displayed high fidelity (φ >

Table 2 – **Water sedge (*Carex aquatilis*) - Willow (*Salix* species) plant community in the Wind River Indian Reservation in Wyoming, USA.**
[Group 2 plot means (n = 14): Elevation 2,834 m, % Sand-Silt-Clay 46-30-24, Organic Matter 34.3%, pH 5.5]. Phi (φ) is an indicator of fidelity and the asterisk (*) suggests this is the preferred group for this species.

Code	Name	Scientific name	p-value	Phi (φ)
CAAQ	Water sedge	*Carex aquatilis*	0.0001	0.8903*
SALIX	Willows (species unknown)	*Salix* sp.	0.0001	0.8012
BEGL	Resin bog birch	*Betula glandulosa*	0.0001	0.7206
DAFRF	Shrubby cinquefoil	*Dasiphora fruticosa* subsp. *floribunda*	0.0001	0.6990
RHRH4	Redpod stonecrop	*Rhodiola rhodantha*	0.0001	0.6820*
CAAT3	Slenderbeak sedge	*Carex athrostachya*	0.0001	0.6050
CALE9	Sierra hare sedge	*Carex leporinella*	0.0121	0.4171*
PEGR2	Elephanthead lousewort	*Pedicularis groenlandica*	0.0494	0.3431
JUBAM	Baltic rush	*Juncus balticus* var. *montanus*	0.0001	0.2860
SOMU	Rocky Mountain goldenrod	*Solidago multiradiata*	0.0086	0.2189
DEEL	Slender hairgrass	*Deschampsia elongata*	0.0117	0.1897

Table 3 – **Shrubby cinquefoil (*Dasiphora fruticosa* subsp. *floribunda*) - Idaho fescue (*Festuca idahoensis*) plant community in the Wind River Indian Reservation in Wyoming, USA.**
[Group 3 plot means (n = 7): Elevation 2,608 m, % Sand-Silt-Clay 58-21-21, Organic Matter 5.7%, pH 6.9]. Phi (φ) is an indicator of fidelity and the asterisk (*) suggests this is the preferred group for this species.

Code	Name	Scientific name	p-value	Phi (φ)
CASU12	Sulphur Indian paintbrush	*Castilleja sulphurea*	0.0001	0.9298*
JUBAM	Baltic rush	*Juncus balticus* var. *montanus*	0.0001	0.7702
GEROT	Ross' avens var. turbinatum	*Geum rossii* var. *turbinatum*	0.0007	0.7149*
DAFRF	Shrubby cinquefoil	*Dasiphora fruticosa* subsp. *floribunda*	0.0001	0.6990
FEID	Idaho fescue	*Festuca idahoensis*	0.0001	0.6113
KOMA	Prairie junegrass	*Koeleria macrantha*	0.0001	0.5242
LULE2	Pacific lupine	*Lupinus lepidus*	0.0196	0.5064*
POBI6	American bistort	*Polygonum bistortoides*	0.0001	0.4956
ARTR2	Big sagebrush	*Artemisia tridentata*	0.0001	0.4936
DEEL	Slender hairgrass	*Deschampsia elongata*	0.0117	0.4873*
PEPR2	Littleflower penstemon	*Penstemon procerus*	0.0047	0.4746*
POGLR2	Timberline bluegrass	*Poa glauca* subsp. *rupicola*	0.0004	0.4432

0.6). This was the preferred group for four forbs including sulphur Indian paintbrush (*Castilleja sulphurea*), Ross' avenus (*Geum rossii* var. *turbinatum*), Pacific lupine (*Lupinus lepidus*), littleflower penstemon (*Penstemon procerus*), and one grass (slender hairgrass (*Deschampsia elongata*)) (all p-values < 0.02; all φ > 0.4) (table 3). Big sagebrush (*Artemisia tridentata*) was also present ($p < 0.001$; φ > 0.4). This group is similar to USNVC A4096 *Dasiphora fruticosa* / *Festuca campestris* - *Festuca idahoensis* Shrub-steppe Alliance (M048).

American Bistort (*Polygonum bistortoides*) - wet meadow plant community (table 4) – This was the preferred group for American bistort (*Polygonum bistortoides*) and several sedge/rush species including longstyle rush (*Juncus longistylis*), western singlespike sedge (*Carex scirpoidea* subsp. *pseudoscirpoidea*), and slenderbeak sedge (*Carex athrostachya*); all of which were significantly associated with the group ($p < 0.001$) and displayed high fidelity (φ > 0.6). This was also the preferred group for tufted hairgrass (*Deschampsia cespitosa*) ($p < 0.001$; φ > 0.6) (table 4). Wolf's willow (*Salix wolfii*), shrubby cinquefoil (*Dasiphora fruticosa* subsp. *floribunda*), and other sedges and rushes were significantly associated with the group ($p < 0.001$) and displayed high fidelity (φ > 0.6). In addition, two exotic clover species (white clover (*Trifolium repens*) and red clover (*Trifolium pratense*)) were noted to prefer this group although significance and fidelity levels were low for both ($p > 0.05$; φ < 0.3) (table 4). For this group it was difficult to find a comparable USNVC classification although there are some features in common with A3770 *Salix wolfii* - *Salix brachycarpa* - *Betula glandulosa* Wet Shrubland Alliance (M893).

Table 4 – **American Bistort (*Polygonum bistortoides*) wet meadow plant community in the Wind River Indian Reservation in Wyoming, USA.**
[Group 4 plot means (n = 9): Elevation 2,602 m, % Sand-Silt-Clay 51-25-24, Organic Matter 5.7%, pH 6.9]. Phi (φ) is an indicator of fidelity and the asterisk (*) suggests this is the preferred group for this species.

Code	Name	Scientific name	p-value	Phi (φ)
JULO	Longstyle rush	*Juncus longistylis*	0.0002	0.8333*
JUBAM	Baltic rush	*Juncus balticus* var. *montanus*	0.0001	0.7702
PHAL2	Alpine timothy	*Phleum alpinum*	0.0001	0.7488
SAWO	Wolf's willow	*Salix wolfii*	0.0001	0.7478
CASCP3	Western singlespike sedge	*Carex scirpoidea* subsp. *pseudoscirpoidea*	0.001	0.7152*
DAFRF	Shrubby cinquefoil	*Dasiphora fruticosa* subsp. *floribunda*	0.0001	0.6990
POBI6	American bistort	*Polygonum bistortoides*	0.0001	0.6857*
DECE	Tufted hairgrass	*Deschampsia cespitosa*	0.0006	0.6831*
CAAT3	Slenderbeak sedge	*Carex athrostachya*	0.0001	0.6688*
SALIX	Willows (species unknown)	*Salix* sp.	0.0001	0.6667
CAAQ	Water sedge	*Carex aquatilis*	0.0001	0.6476
CAHEE	Different-nerve sedge	*Carex heteroneura* var. *epapillosa*	0.0019	0.5892
TRRE3	White clover (**exotic**)	*Trifolium repens*	ns	0.2425*
TRPR2	Red clover (**exotic**)	*Trifolium pratense*	ns	0.2425*

Table 5 – **Slender wheatgrass (*Elymus trachycaulus* subsp. *trachycaulus*) forb plant community in the Wind River Indian Reservation in Wyoming, USA.**
[Group 5 plot means (n = 4): Elevation 3,180 m, % Sand-Silt-Clay 57-23-20, Organic Matter 3.9%, pH 7.6]. Phi (φ) is an indicator of fidelity and the asterisk (*) suggests this is the preferred group for this species.

Code	Name	Scientific name	p-value	Phi (φ)
ERBR5	Shortstem buckwheat	*Eriogonum brevicaule*	0.0002	0.7746*
ELTRT	Slender wheatgrass (trachycaulus)	*Elymus trachycaulus* subsp. *trachycaulus*	0.0082	0.7255*
LILE3	Lewis flax	*Linum lewisii*	0.0001	0.6598
ERIGE2	Fleabane	*Erigeron* sp.	0.0026	0.6240*
EROV	Cushion buckwheat	*Eriogonum ovalifolium*	0.0003	0.6236
PHPU5	Cushion phlox	*Phlox pulvinata*	0.0001	0.6035
ASTRA	Astragalus (species unknown)	*Astragalus* sp.	0.0046	0.5797*
CHDO	Douglas' dustymaiden	*Chaenactis douglasii*	0.0052	0.5667*
ERFLF	Alpine golden buckwheat var. flavum	*Eriogonum flavum* var. *flavum*	0.0067	0.5667*
SIAC	Moss campion	*Silene acaulis*	0.0136	0.5515*
ARFR4	Prairie sagewort	*Artemisia frigida*	0.0001	0.5381
KOMA	Prairie junegrass	*Koeleria macrantha*	0.0001	0.5242

Slender wheatgrass (*Elymus trachycaulus* subsp. *trachycaulus*) forb plant community (table 5) – This was the preferred group for slender wheatgrass (*Elymus trachycaulus* subsp. *trachycaulus*) and several forb species including shortstem buckwheat (*Eriogonum brevicaule*), fleabane (*Erigeron* species), *Astragalus* species, Douglas' dustymaiden (*Chaenactis douglasii*), alpine golden buckwheat (*Eriogonum flavum* var. *flavum*), and moss campion (*Silene acaulis*); all of which were significantly associated with the group ($p < 0.02$) and displayed moderate fidelity ($\varphi > 0.5$) (table 5). This group is similar to USNVC CEGL005427 *Elymus trachycaulus* Meadow Association (M168).

Native fescue (*Festuca* species) plant community (table 6) – This was the preferred group for Rocky Mountain fescue (*Festuca saximontana*) and included Idaho fescue (*Festuca idahoensis*) which were significantly associated with the group ($p < 0.02$) and displayed moderate fidelity ($\varphi > 0.4$). Sagebrush (*Artemisia* species) and yellow rabbitbrush (*Chrysothamnus viscidiflorus*) shrubs were also present ($p < 0.001$; $\varphi > 0.5$). This was also the preferred group for Woods' rose (*Rosa woodsii*; $p = 0.0278$; $\varphi > 0.5$) (table 6). For this group it was difficult to find a comparable USNVC classification although there are some features in common with A3986 *Festuca campestris* - *Festuca idahoensis* Mesic Grassland

Table 6 – **Native fescue (*Festuca* species) plant community in the Wind River Indian Reservation in Wyoming, USA.**
[Group 6 plot means (n = 12): Elevation 2,670 m, % Sand-Silt-Clay 66-19-16, Organic Matter 4.9%, pH 6.6]. Phi (φ) is an indicator of fidelity and the asterisk (*) suggests this is the preferred group for this species.

Code	Name	Scientific name	p-value	Phi (φ)
ARTEM	Artemisia (species unknown)	*Artemisia* sp.	0.0001	0.6731
FESA	Rocky Mountain fescue	*Festuca saximontana*	0.0184	0.5692*
CHVI8	Yellow rabbitbrush	*Chrysothamnus viscidiflorus*	0.0001	0.5471
ROWO	Woods' rose	*Rosa woodsii*	0.0278	0.5295*
KOMA	Prairie junegrass	*Koeleria macrantha*	0.0001	0.5242
FEID	Idaho fescue	*Festuca idahoensis*	0.0001	0.4910
ARCOC4	Ballhead sandwort	*Arenaria congesta*	0.0001	0.3262
POGLR2	Timberline bluegrass	*Poa glauca* subsp. *rupicola*	0.0004	0.3049
PEPR2	Littleflower penstemon	*Penstemon procerus*	0.0047	0.2509
ASTRA	Astragalus (species unknown)	*Astragalus* sp.	0.0046	0.2373
ARFR4	Prairie sagewort	*Artemisia frigida*	0.0001	0.1905

Table 7 – **Bluebunch wheatgrass (*Pseudoroegneria spicata*) shrub plant community in the Wind River Indian Reservation in Wyoming, USA.**
[Group 7 plot means (n = 4): Elevation 2,812 m, % Sand-Silt-Clay 61-19-20, Organic Matter 4.8%, pH 7.4]. Phi (φ) is an indicator of fidelity and the asterisk (*) suggests this is the preferred group for this species.

Code	Name	Scientific name	p-value	Phi (φ)
ALCE2	Nodding onion	*Allium cernuum*	0.0001	0.9873
LILE3	Lewis flax	*Linum lewisii*	0.0001	0.9242
CHVI8	Yellow rabbitbrush	*Chrysothamnus viscidiflorus*	0.0001	0.8998
CAFL7	Yellow Indian paintbrush	*Castilleja flava*	0.0001	0.8641
ARFR4	Prairie sagewort	*Artemisia frigida*	0.0001	0.8224
ARTR2	Big sagebrush	*Artemisia tridentata*	0.0001	0.8167
ARTEM	Artemisia (species unknown)	*Artemisia* sp.	0.0001	0.7771
BAIN	Hoary balsamroot	*Balsamorhiza incana*	0.0002	0.6562
CANU3	Sego lily	*Calochortus nuttallii*	0.0030	0.5774
PUTR2	Antelope bitterbrush	*Purshia tridentata*	0.0039	0.5774
PSSP6	Bluebunch wheatgrass	*Pseudoroegneria spicata*	0.0030	0.5774
SYOC	Western snowberry	*Symphoricarpos occidentalis*	0.0075	0.5643
BRTE	Cheatgrass (**exotic**)	*Bromus tectorum*	ns	0.3780*

Alliance (M048), however, *F. campestris* was not present but *F. saximontana* was present.

Bluebunch wheatgrass (*Pseudoroegneria spicata*) shrub plant community (table 7) – Bluebunch wheatgrass (*Pseudoroegneria spicata*) was significantly associated with this group ($p = 0.003$) and displayed moderate fidelity ($\varphi = 0.5774$). In addition, multiple upland shrubs were significantly associated with this group and displayed moderate to high levels of fidelity, including yellow rabbitbrush (*Chrysothamnus viscidiflorus*; $p = 0.0001$; $\varphi = 0.8998$), big sagebrush (*Artemisia tridentata*; $p = 0.0001$; $\varphi = 0.8167$), antelope bitterbrush (*Purshia tridentata*; $p = 0.0039$; $\varphi = 0.5774$), and western snowberry (*Symphoricarpos occidentalis*; $p = 0.0075$; $\varphi = 0.5643$). In addition, the exotic annual grass cheatgrass (*Bromus tectorum*) preferred this group (table 7). This group is similar to USNVC CEGL001032 *Artemisia tridentata* ssp. *vaseyana* - *Purshia tridentata*/*Pseudoroegneria spicata* Shrubland (M169), which also notes the susceptibility to *B. tectorum* invasion.

Sagebrush - Indian paintbrush - Balsamroot (*Artemisia* - *Castilleja* -*Balsamorhiza*) plant community (table 8) – Yellow Indian paintbrush (*Castilleja flava*), hoary balsamroot (*Balsamorhiza incana*), and big sagebrush (*Artemisia tridentata*) were all significantly associated with this group ($p < 0.00$) and displayed moderate fidelity ($\varphi > 0.5$) (table 8). No comparable USNVC classification for this group was found.

Timberline bluegrass (*Poa glauca* subsp. *rupicola*) plant community (table 9) – Timberline bluegrass (*Poa glauca* subsp. *rupicola*) was significantly associated with this group ($p < 0.001$), displayed moderate fidelity ($\varphi = 0.5120$), and

Table 8 – **Sagebrush - Indian paintbrush - Balsamroot (*Artemisia - Castilleja - Balsamorhiza)* plant community in the Wind River Indian Reservation in Wyoming, USA.**
[Group 8 plot means (n = 11): Elevation 2,655 m, % Sand-Silt-Clay 58-21-20, Organic Matter 5.2%, pH 7.4]. Phi (φ) is an indicator of fidelity and the asterisk (*) suggests this is the preferred group for this species.

Code	Name	Scientific name	p-value	Phi (φ)
ARTEM	Artemisia (species unknown)	*Artemisia* sp.	0.0001	0.6640
CAFL7	Yellow Indian paintbrush	*Castilleja flava*	0.0001	0.6593
BAIN	Hoary balsamroot	*Balsamorhiza incana*	0.0002	0.5443
KOMA	Prairie junegrass	*Koeleria macrantha*	0.0001	0.5242
ARTR2	Big sagebrush	*Artemisia tridentata*	0.0001	0.5073
COUM	Bastard toadflax	*Comandra umbellata*	0.0227	0.5021*
ARFR4	Prairie sagewort	*Artemisia frigida*	0.0001	0.4197
ERIGE2	Fleabane (species unknown)	*Erigeron* sp.	0.0026	0.3276

Table 9 – **Timberline bluegrass (*Poa glauca* subsp. *rupicola*) plant community in the Wind River Indian Reservation in Wyoming, USA.**
[Group 9 plot means (n = 9): Elevation 2,812 m, % Sand-Silt-Clay 62-20-18, Organic Matter 3.8%, pH 5.7]. Phi (φ) is an indicator of fidelity and the asterisk (*) suggests this is the preferred group for this species.

Code	Name	Scientific name	p-value	Phi (φ)
POGLR2	Timberline bluegrass	*Poa glauca* subsp. *rupicola*	0.0004	0.5120*
ARCOC4	Ballhead sandwort	*Arenaria congesta*	0.0001	0.4944
ACRCO9	Heartleaf arnica	*Arnica cordifolia*	0.0002	0.4367
PICO	Lodgepole pine	*Pinus contorta*	0.0001	0.3841
CHAN9	Fireweed	*Chamerion angustifolium*	0.0001	0.3195
SHCA	Russet buffaloberry	*Shepherdia canadensis*	0.0249	0.2983
FESA	Rocky Mountain fescue	*Festuca saximontana*	0.0184	0.0985

Table 10 – **Lodgepole pine-limber pine - whortleberry (*Pinus - Vaccinium*) plant community in the Wind River Indian Reservation in Wyoming, USA.**
[Group 10 plot means (n = 6): Elevation 2,832 m, % Sand-Silt-Clay 63-21-17, Organic Matter 6.0%, pH 5.9]. Phi (φ) is an indicator of fidelity and the asterisk (*) suggests this is the preferred group for this species.

Code	Name	Scientific name	p-value	Phi (φ)
PICO	Lodgepole pine	*Pinus contorta*	0.0001	0.8593*
CHAN9	Fireweed	*Chamerion angustifolium*	0.0001	0.8093
ARCO9	Heartleaf arnica	*Arnica cordifolia*	0.0002	0.8063*
ARLA8	Broadleaf arnica	*Arnica latifolia*	0.0031	0.5774*
PIFL2	Limber pine	*Pinus flexilis*	0.0236	0.5388*
FRVI	Virginia strawberry	*Fragaria virginiana*	0.0009	0.4856
ABLA	Subalpine fir	*Abies lasiocarpa*	0.0062	0.4472*
SHCA	Russet buffaloberry	*Shepherdia canadensis*	0.0249	0.4159*
ANUM	Umber pussytoes	*Antennaria umbrinella*	0.0474	0.4062*
PHSE	Silky phacelia	*Phacelia sericea*	0.0109	0.3199
SESP4	Ballhead ragwort	*Senecio sphaerocephalus*	0.0002	0.2856
SOMU	Rocky Mountain goldenrod	*Solidago multiradiata*	0.0086	0.2725
TRDU	Yellow salsify (**exotic**)	*Tragopogon dubius*	ns	0.3015*

Table 11 – **Letterman's needlegrass (*Achnatherum lettermanii*) plant community in the Wind River Indian Reservation in Wyoming, USA.**
[Group 11 plot means (n = 3): Elevation 3,008 m, % Sand-Silt-Clay 53-29-18, Organic Matter 5.0%, pH 6.4]. Phi (φ) is an indicator of fidelity and the asterisk (*) suggests this is the preferred group for this species.

Code	Name	Scientific name	p-value	Phi (φ)
ACLE9	Letterman's needlegrass	*Achnatherum lettermanii*	0.0054	0.8723*
TRSP2	Spiked trisetum	*Trisetum spicatum*	0.0001	0.7460*
SESP4	Ballhead ragwort	*Senecio sphaerocephalus*	0.0002	0.8277*
CHAN9	Fireweed	*Chamerion angustifolium*	0.0001	0.8093
CAREX	Sedge (species unknown)	*Carex* sp.	0.0001	0.6926
PHSE	Silky phacelia	*Phacelia sericea*	0.0109	0.6434*
CAPU	Purple reedgrass	*Calamagrostis purpurascens*	0.0042	0.6414*
CIRSI	Cirsium (species unknown)	*Cirsium* sp.	0.0027	0.6246*
ELEL5	Bottlebrush squirreltail	*Elymus elymoides*	0.0169	0.5469*
PHPU5	Cushion phlox	*Phlox pulvinata*	0.0001	0.5189
PICO	Lodgepole pine	*Pinus contorta*	0.0001	0.4967
ELSC4	Spreading wheatgrass	*Elymus scribneri*	0.0002	0.4785
CIAR4	Canada thistle (**exotic**)	*Cirsium arvense*	ns	0.4314*
CANU4	Nodding plumeless thistle (**exotic**)	*Carduus nutans*	ns	0.4472*

was the only species noted as 'preferred' (table 9). Two forbs, ballhead sandwort (*Arenaria congesta*) and heartleaf arnica (*Arnica cordifolia*), displayed significance ($p < 0.001$) and moderate fidelity ($\varphi > 0.4$) for this group. Lodgepole pine (*Pinus contorta*) and fireweed (*Chamerion angustifolium*) were significantly associated ($p < 0.001$) with this group but displayed low fidelity ($\varphi < 0.39$). No comparable USNVC classification for this group was found.

Lodgepole pine - limber pine - whortleberry (*Pinus - Vaccinium*) plant community (table 10) – Lodgepole pine (*Pinus contorta*), limber pine (*Pinus flexilis*), and subalpine fir (*Abies lasiocarpa*) all preferred this group, were significantly associated with this group ($p < 0.03$), and displayed moderate to high fidelity ($\varphi = 0.8593$, 0.5388, and 0.4472 respectively) (table 10). Additionally, grouse whortleberry (*Vaccinium scoparium*) and common juniper (*Juniperus communis*) were present in this group although they were not noted to be significant and fidelity was low ($\varphi < 0.21$). Two *Arnica* forbs preferred this group (*A. cordifolia* and *A. latifolia*), as did the shrub russet buffaloberry (*Sheperdia canadensis*), all of which were significant ($p < 0.025$) and with moderate fidelity ($\varphi > 0.4$). In addition, the exotic forb yellow salsify (*Tragopogon dubius*) preferred this group (table 10). This group is similar to USNVC CEGL000172 Lodgepole Pine / Grouse Whortleberry Forest Association (M020).

Letterman's needlegrass (*Achnatherum lettermanii*) plant community (table 11) – The grasses Letterman's needlegrass (*Achnatherum lettermanii*) and spiked trisetum (*Trisetum spicatum*) were both significantly associated with this group ($p < 0.01$), displayed high fidelity ($\varphi > 0.7$). Plants in the genera *Cirsium* also preferred this group, including two exotic thistle species (*Cirsium arvense* and *Carduus nutans*). This group only occurred in the Paradise basin. For this group it was difficult to find comparable USNVC classifications although there are some features in common with two groups specifically because of *A. lettermanii*, including CEGL002734 *Achnatherum lettermanii - Oxytropis oreophila* Grassland (however only noted to occur in Nevada) and CEGL001656 *Poa nervosa - Achnatherum lettermanii* Grassland (M168) (however only noted to occur in Colorado and *P. nervosa* did not occur in our plots).

Idaho Fescue - Northern singlespike sedge - Timber oatgrass (*Festuca idahoensis - Carex scirpoidea - Danthonia intermedia*) plant community (table 12) – Timber oatgrass (*Danthonia intermedia*) was the grass with the highest fidelity for this group ($p < 0.001$; $\varphi = 0.5058$) followed by slender hairgrass (*Deschampsia elongata*) ($p < 0.02$; $\varphi > 0.4$). In addition, Idaho Fescue (*Festuca idahoensis*) and Northern singlespike sedge (*Carex scirpoidea*) were both present and significant ($p < 0.02$), although fidelity was low ($\varphi < 0.3$). The exotic species rock dandelion (*Taraxacum laevigatum*) preferred this group (table 12). This group was similar to USNVC A3965 *Festuca idahoensis - Carex scirpoidea - Danthonia intermedia* Central Rocky Mountain Subalpine Dry Grassland Alliance (M048).

Bottlebrush squirreltail (*Elymus elymoides*) mixed shrub - tree plant community (table 13) – This group had seven grass species and one sedge species that were significantly associated with this group ($p < 0.01$) with varying levels of fidelity, including Colorado fescue (*Festuca brachyphylla* subsp. *coloradensis*; $\varphi = 0.7872$), spreading wheatgrass (*Elymus scribneri*; $\varphi = 0.6793$), Idaho fescue (*Festuca idahoensis*; $\varphi = 0.6113$), timber oatgrass (*Danthonia intermedia*; $\varphi = 0.4677$), bottlebrush squirreltail (*Elymus elymoides*; $\varphi = 0.4525$), slender wheatgrass (*Elymus trachycaulus* subsp. *trachycaulus*; $\varphi = 0.3825$), Rocky Mountain fescue (*Festuca saximontana*; $\varphi = 0.3328$), and Sierra hare sedge (*Carex leporinella*; $\varphi = 0.3451$). In addition, big sagebrush (*Artemisia tridentata*) and lodgepole pine (*Pinus contorta*) were significantly associated with this group ($p = 0.0001$ for both

Table 12 – **Idaho fescue - Northern singlespike sedge - Timber oatgrass (*Festuca idahoensis - Carex scirpoidea - Danthonia intermedia*) plant community in the Wind River Indian Reservation in Wyoming, USA.**
[Group 12 plot means (n = 8): Elevation 3,032 m, % Sand-Silt-Clay 59-27-15, Organic Matter 7.7%, pH 5.8]. Phi (φ) is an indicator of fidelity and the asterisk (*) suggests this is the preferred group for this species.

Code	Name	Scientific name	p-value	Phi (φ)
GETR	Prairie smoke	*Geum triflorum*	0.0001	0.7696
CAREX	Sedge (species unknown)	*Carex* sp.	0.0001	0.6926
POBI6	American bistort	*Polygonum bistortoides*	0.0001	0.5333
DAIN	Timber oatgrass	*Danthonia intermedia*	0.0001	0.5058
DEEL	Slender hairgrass	*Deschampsia elongata*	0.0117	0.4171
CAAT3	Slenderbeak sedge	*Carex athrostachya*	0.0001	0.3929
PHPU5	Cushion phlox	*Phlox pulvinata*	0.0001	0.3510
JUBAM	Baltic rush	*Juncus balticus* var. *montanus*	0.0001	0.3423
ARCOC4	Ballhead sandwort	*Arenaria congesta*	0.0001	0.3262
TRSP2	Spiked trisetum	*Trisetum spicatum*	0.0001	0.3097
FEID	Idaho fescue	*Festuca idahoensis*	0.0001	0.2821
CASC10	Northern singlespike sedge	*Carex scirpoidea*	0.0195	0.2628
TALA2	Rock dandelion (**exotic**)	*Taraxacum laevigatum*	ns	0.2582

Table 13 – **Bottlebrush squirreltail (*Elymus elymoides*) mixed shrub - tree plant community in the Wind River Indian Reservation in Wyoming, USA.**
[Group 13 plot means (n = 7): Elevation 2,886 m, % Sand-Silt-Clay 60-23-17, Organic Matter 6.7%, pH 6.1]. Phi (φ) is an indicator of fidelity and the asterisk (*) suggests this is the preferred group for this species.

Code	Name	Scientific name	p-value	Phi (φ)
FEBRC	Colorado fescue	*Festuca brachyphylla* subsp. *coloradensis*	0.0025	0.7872*
GETR	Prairie smoke	*Geum triflorum*	0.0001	0.7696
ELSC4	Spreading wheatgrass	*Elymus scribneri*	0.0002	0.6793*
ARCOC4	Ballhead sandwort	*Arenaria congesta*	0.0001	0.6470
FEID	Idaho fescue	*Festuca idahoensis*	0.0001	0.6113
DAIN	Timber oatgrass	*Danthonia intermedia*	0.0001	0.4677
ELEL5	Bottlebrush squirreltail	*Elymus elymoides*	0.0169	0.4525
ERIGE2	Fleabane	*Erigeron* sp.	0.0026	0.4456
ELTRT	Slender wheatgrass (trachycaulus)	*Elymus trachycaulus* subsp. *trachycaulus*	0.0082	0.3825
ARTR2	Big sagebrush	*Artemisia tridentata*	0.0001	0.3454
CALE9	Sierra hare sedge	*Carex leporinella*	0.0121	0.3451
FESA	Rocky Mountain fescue	*Festuca saximontana*	0.0184	0.3328
PICO	Lodgepole pine	*Pinus contorta*	0.0001	0.2528

respectively), although fidelity was low (φ = 0.3454 and φ = 0.2528 respectively). This group is similar to USNVC CEGL000137 *Pinus contorta* / *Artemisia tridentata* / *Elymus elymoides* Woodland (M020).

Idaho fescue (*Festuca idahoensis*) - forb plant community (table 14) – Four low-growing forb species preferred this group including cushion buckwheat (*Eriogonum ovalifolium*), cushion phlox (*Phlox pulvinata*), alpine clover (*Trifolium dasyphyllum*), and sticky polemonium (*Polemonium viscosum*), and all were significantly associated with the group ($p < 0.05$) with moderate fidelity (φ range = 0.4 to 0.6). Other low growing forbs were also present including ballhead sandwort (*Arenaria congesta*; p = 0.0001; φ = 0.6470) and umber pussytoes (*Antennaria umbrinella*; p = 0.0474; φ = 0.2873). Idaho fescue (*Festuca idahoensis*; p = 0.0001; φ = 0.6113), spreading wheatgrass (*Elymus scribneri*; p = 0.0001; φ = 0.4785), and multiple sedge species were also significant and present. This group is similar to USNVC A3966 *Festuca idahoensis* - *Calamagrostis rubescens* - *Achnatherum nelsonii* Central Rocky Mountain Montane Mesic Grassland Alliance (M048). However, a different *Calamagrostis* species (*C. purpurascens*; p = 0.0042; φ = 0.3917) was present and *Achnatherum nelsonii* was not present.

Table 14 – **Idaho fescue (*Festuca idahoensis*) - forb plant community in the Wind River Indian Reservation in Wyoming, USA.** [Group 14 plot means (n = 9): Elevation 3,089 m, % Sand-Silt-Clay 58-22-20, Organic Matter 6.8%, pH 6.1]. Phi (φ) is an indicator of fidelity and the asterisk (*) suggests this is the preferred group for this species.

Code	Name	Scientific name	p-value	Phi (φ)
EROV	Cushion buckwheat	*Eriogonum ovalifolium*	0.0003	0.6519*
ARCOC4	Ballhead sandwort	*Arenaria congesta*	0.0001	0.6470
PHPU5	Cushion phlox	*Phlox pulvinata*	0.0001	0.6231*
TRDA2	Alpine clover	*Trifolium dasyphyllum*	0.0004	0.6202*
FEID	Idaho fescue	*Festuca idahoensis*	0.0001	0.6113
POVI	Sticky polemonium	*Polemonium viscosum*	0.0304	0.4889*
ELSC4	Spreading wheatgrass	*Elymus scribneri*	0.0002	0.4785
CASC10	Northern singlespike sedge	*Carex scirpoidea*	0.0195	0.4647*
CAREX	Sedge (species unknown)	*Carex* sp.	0.0001	0.4135
CASCP3	Western singlespike sedge	*Carex scirpoidea* subsp. *pseudoscirpoidea*	0.001	0.3917
CAPU	Purple reedgrass	*Calamagrostis purpurascens*	0.0042	0.3917
ANUM	Umber pussytoes	*Antennaria umbrinella*	0.0474	0.2873

Comparison with the 1960 inventory list

Field & Tidd listed 74 plant species on their 1960 collection list from Saint Lawrence basin and Paradise park areas. Through the reconciling process, we eliminated repeat entries and those specimens for which identification was questionable producing a reconciled list of 56 identifiable plant species. Our 2017 plant inventory significantly expanded on the number of plant species in the high-elevation basins to a total of 221 plant taxa and 10 genera for which species identification was not possible (for a total of 231). Of those species, 55 of the 56 (98%) reconciled Field & Tidd plants were confirmed. However, there was one species we did not find on the Field & Tidd list: Northern sweetgrass (*Hierochloe hirta* subsp. *hirta*). In total, 168 additional taxa were identified in Saint Lawrence and Paradise basins in our study. Plant species overlap and occur in both basins, with 222 plant taxa identified in Saint Lawrence basin and 98 plant taxa identified in Paradise basin; and of those 89 were shared between basins.

DISCUSSION

Our study identified 231 plant taxa (221 to species and 10 to genera) across various vegetation communities in the high-elevation Saint Lawrence and Paradise basins of the Wind River Reservation. Previously, for these two basins, Wind River BIA range staff were working with an outdated and insufficient plant list with only 56 reconcilable plants. The plant inventory list and ecological explanatory data collected from our study will serve as comprehensive baseline data for the BIA range staff to effectively monitor plant communities and basin resources in the future. Given Paradise basin's roadless area designation and Saint Lawrence basin's partial roadless designation with limited livestock grazing and logging activities, the data can be used to gauge anthropogenic changes over time which will become increasingly important in these high-elevation basins particularly in the context of climate change forecasts (Gildar et al. 2004). There is also the potential for BIA to consider prescribed burns within the basins in order to reach management objectives by using the baseline data to build GIS-based vegetation mapping and spatial modeling to strategically plan burns (Young et al. 2017).

Topographic, soil, and disturbance data proved to be informative for understanding vegetation in the two high-elevation basins. Slope, aspect, and elevation influence where and how certain plant communities occur. Our vegetation inventory associates topographic data with vegetation data, which we have extrapolated to plant communities. Understanding how plant communities interrelate across varied topography has important management implications (Banta et al. 2005). Soil nutrient content was also an important factor determining where specific plant species grow and their level of abundance (Menzel et al. 2016) and operationalizes soil and vegetation data for BIA range staff. Disturbances identified in the basins were burned areas, livestock grazing, outdoor recreation, two-track roads, and firewood harvesting. In 2012, the Alpine Lake Fire burned a northwest portion of Paradise Basin and in 2017 the Saint Lawrence Fire burned 66 hectares. Establishing long-term transects in burned areas allows land managers to monitor plant species presence and abundance over time (Kost & De Steven 2000) which is important because some plant species are early colonizers of burn areas and monitoring is critical to identify problems or changes.

It is important to thoroughly understand sensitive plant communities that are marginally or extremely distributed to detect changes in plant species abundances caused by environmental changes (Lesica 2015). Kelly & Goulden (2008) found that a dominant plant species identified in 1977 had shifted up ~65 m in elevation in 2007. The researchers attributed the increase in elevation to changes in regional climate that consisted of warming regional temperatures, increasing precipitation variability, and decreased snowpack (Kelly & Goulden 2008). High-elevation environments are also at risk for loss of habitat as plant communities shift higher in eleva-

tion. Species that live and thrive in native plant communities at current elevations can become threatened, endangered, or extinct as dominant plant communities shift upwards in elevation (Dirnböck et al. 2011).

As regional climates warm and native plant species move higher in elevation, habitat loss and inadvertent introductions of invasive plant species to high elevation environments can threaten native plant communities (Pauchard et al. 2009; Expósito et al. 2018). Our study documented eleven introduced species, two of which are designated as noxious weeds by county and state authorities (Wyoming Weed and Pest 2019). Plant species are designated as noxious weeds, a legal designation, when they are harmful to the health and welfare of the environment and/or animals (Wyoming Weed and Pest 2019). We identified Canada thistle (*Cirsium arvense*) in both basins and nodding plumeless thistle or musk thistle (*Carduus nutans*) in Paradise basin – both noxious species in Wyoming. Canada thistle invades plant communities by primarily reproducing by asexual and sexual mechanisms (Wyoming Weed and Pest 2019). Musk thistle generates an excess of 20,000 seeds per plant that are viable in the soil up to 10 years making it difficult to manage the species (Wyoming Weed and Pest 2019). Downy brome (*Bromus tectorum*), more commonly known as cheatgrass, is a declared a noxious weed for Fremont County and it was found in Saint Lawrence basin along a road leading to a popular fishing spot (Wyoming Weed and Pest 2019). Cheatgrass is an introduced winter annual grass that matures earlier than native plant species and has been implicated in dramatic changes in composition and function of western US plant communities (Mealor et al. 2012). The early detection of these noxious species in the high-elevation basins provides the BIA range staff the opportunity to implement management decisions to reduce the abundance and potentially eradicate them from the basins.

From the eleven introduced plant species documented in our study, seven are considered invasive species (Invasive Species Advisory Committee 2006), including: Kentucky bluegrass (*Poa pratensis*), timothy (*Phleum pratense*), prostrate knotweed (*Polygonum aviculare*), white clover (*Trifolium repens*), red clover (*Trifolium pratense*), yellow or western salsify (*Tragopogon dubius*), and rock dandelion (*Taraxacum laevigatum*). An additional five native species are considered invasive: common dandelion (*Taraxacum officinale*), red raspberry (*Rubus idaeus*), thymeleaf speedwell (*Veronica serpyllifolia*), common yarrow (*Achillea millefolium*), and ponderosa pine (*Pinus ponderosa*). Of pressing concern is the warming climate and the possible migrations of exotic species into these high-elevation environments.

Regional climate and environmental changes may stress plant species as ideal growing conditions are altered causing migrations across landscapes or species extirpations (Dirnböck et al. 2011; Thuiller et al. 2005). In Wyoming, there are approximately 485 vascular plant species listed as either 'Species of Concern' or 'Species of Potential Concern' (Heidel 2018) and our study documented two such species. Weber's saw-wort (*Saussurea weberi*) is listed as a 'Species of Concern' and was identified in Saint Lawrence basin. Weber's saw-wort is considered a rare plant species because of its disjunct and infrequent occurrences in alpine habitats. In Wyoming, Weber's saw-wort is considered sensitive and imperilled at the state level and the US Forest Service lists it as sensitive in Region 4 consisting of National Forests in Wyoming: Bridger-Teton, Caribou, Targhee, Wasatch-Cache, and Ashley (including Flaming Gorge National Recreation Area) National Forests (Heidel 2018). At a global level, Weber's saw-wort is considered to be vulnerable and imperilled with a probability of species extinction (Heidel 2018). Limber pine (*Pinus flexilis*) is listed as a 'Species of Potential Concern' and was identified in both Saint Lawrence and Paradise basins. Warmer/drier climate conditions and associated mountain pine beetle (*Dendroctonus ponderosae*) outbreaks are potentially influencing its distribution (Cleaver et al. 2015). In Wyoming, limber pine is considered sensitive and imperiled at the State level but at a global level it is apparently secure (Heidel 2018).

Surprisingly, we did not find Northern sweetgrass (*Hierochloe hirta* subsp. *hirta*; henceforth 'sweetgrass') in either basin. Sweetgrass is commonly used by Indigenous people as a ceremonial smudge or medicine, and as an incense by non-Indigenous people (Cantrell et al. 2016; Shebitz 2005; Shebitz & Kimmerer 2005). The demand for sweetgrass also leads to gathering, braiding, and commercially selling sweetgrass to local businesses or individuals (Dhar et al. 2000; Shebitz 2005). The commercial demand for sweetgrass may have led to overharvesting and its depletion from its natural habitat in at least Saint Lawrence basin (Gaoue & Ticktin 2007; Shebitz 2005; Vihotogbé et al. 2014). Thus, the potential restoration of this culturally important plant species should consider human use, harvesting, economic value, and land use change (Droissart et al. 2019).

CONCLUSIONS

Federally recognized tribes hold roughly 22.7 million hectares (five percent) of trust land designated as Indian reservations in the United States (Bureau of Indian Affairs 2019; Stumpff 2000). The WRIR is an important example as the 7th largest reservation in the US, encompassing more than 890,000 hectares, serving as a pool of biodiversity for conservation with a diversity of ecosystems (Cozzo 2004; Luna & Bahls 2017). This biodiversity is important at a global scale but is also critical at a local scale for local tribal communities. Ultimately, intergenerational transfer and revitalization of Indigenous ethnobotanical knowledge can enhance cultural identity (i.e., people's sense of place) and propel Indigenous perspectives for meaningful management decisions regarding their lands (Serenari et al. 2017).

The WRIR has expansive rangeland resources with ecological, agricultural, and cultural importance that requires understanding of intricate botanical relationships. Our study expanded on outdated plant inventories by identifying an additional 168 vascular plants, collecting data to quantify plant communities, and identifying the dominant functional groups in the Saint Lawrence and Paradise basins. This vegetation data was coupled with topographic, soil, and disturbance data to understand where plant assemblages occur and provides data driven information to guide management decisions of rangelands in the high-elevation basins. This comprehensive study will allow BIA range staff to detect the

occurrence of environmental changes such as variations in land use and regional climate. These changes coupled with disturbances such as outdoor recreation, livestock grazing, and wildfire can introduce non-native species to plant communities. The early detection of noxious weeds and invasive species in the high-elevation basins is critical because they can outcompete native species and this knowledge will empower BIA range staff to act early and make management decisions that will either maintain, reduce, or eradicate these species from the basins. Another consideration associated with regional climate change is the negative stress on plants when ideal growing season shift up in elevations of montane environments. Our study documented two species of concern (Weber's saw-wort (*Saussurea weberi*) and limber pine (*Pinus flexilis*)) enabling BIA range staff to consider these species when developing management plans or making management decisions regarding the basins.

SUPPLEMENTARY FILES

Two supplementary files are associated with this paper:

Supplementary file 1: Identifications of plants from the Saint Lawrence and Paradise basins, Wind River Range, Fremont County, Wyoming, USA, 1960.
https://doi.org/10.5091/plecevo.2020.1682.2177

Supplementary file 2: Identifications of plants from the Saint Lawrence and Paradise basinss, Wind River Range, Fremont County, Wyoming, USA 2017 and 2018.
https://doi.org/10.5091/plecevo.2020.1682.2179

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