Plant Successional Patterns at Sperry Glacier Foreland, Glacier National Park, MT, USA

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ABSTRACT

Regional and local changes in the climate have been driving rapid glacial retreat in many glaciers since the Little Ice Age. This retreat provides a unique opportunity to study succession across the chronosequences of glacier forelands. Patterns of plant colonization and succession on terrain exposed by retreating glaciers give insight into factors influencing alpine ecosystem change and recovery. Understanding these patterns and processes is important for conserving alpine landscapes and flora as glaciers disappear. This study sought to investigate how various biotic and abiotic factors influence plant successional patterns in the dynamic alpine environment of Sperry Glacier, a Little Ice Age, mid-latitude cirque glacier in Glacier National Park, Montana. Through field data collection, additional Geographic Information System (GIS) derived variables, and subsequent geostatistical analysis, I specifically assessed: (1.) vegetative trends (percent cover, species richness, Shannon's diversity, species evenness, composition, and species turnover) over a 170-year chronosequence, and (2.) vegetative trends over field and GIS-derived site conditions (e.g., surface fragmentation, concavity, flow accumulation, and solar irradiance). Sixty-one plots (each 8 square meters) were placed throughout the glacier foreland using a random sample stratified by terrain date. Percent cover, species richness, Shannon's diversity, and species evenness were calculated for each plot. All sampled vegetation was identified with taxonomic resolution down to species whenever possible. I assessed vegetative trends across terrain age ranges using Kruskal-Wallis and Dunn's tests. I used two models, generalized linear models (GLMs) and Classification and Regression Trees (CARTs), to assess field and GIS-derived biophysical correlates (e.g., surface fragmentation, concavity, terrain variables, and solar irradiance with vegetative trends), followed by Kruskal-Wallis tests, Dunn's tests, and scatterplots. Species richness and vegetation cover were greater on older terrain. Plant composition changed over terrain age, with *Penstemon ellipticus* favoring older terrain and *Boechera lemmonii* favoring moderately aged terrain. Moderate drainage and concave plots, which were important in the GLMs, explained increased species richness and Shannon's diversity across different site conditions. The CARTs were able to predict species richness, vegetation cover, Shannon's diversity, and species evenness with surface fragment sized from gravel to cobble, topographic position index, and flow accumulation. These findings show that both temporal and biophysical site conditions influence successional trends across the foreland, though different vegetation measures are most influenced differently.

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GENERAL AUDIENCE ABSTRACT

Regional and local changes in the climate have been driving rapid glacial retreat in many glaciers since the Little Ice Age. This retreat provides a unique opportunity to study succession across glacier foreland terrain that has been uncovered for different lengths of time. Patterns of plant colonization and succession on terrain exposed by retreating glaciers give insight into factors influencing alpine ecosystem change and recovery. Understanding these patterns and processes is important for conserving alpine landscapes and flora as glaciers disappear. This study sought to investigate how various biotic and abiotic factors influence plant successional patterns in the dynamic alpine environment of Sperry Glacier, a Little Ice Age, mid-latitude glacier in Glacier National Park, Montana. Through field data collection, additional Geographic Information System (GIS) derived variables, and subsequent geostatistical analysis, I specifically assessed: (1.) vegetative trends (percent cover, species richness, Shannon's diversity, species evenness, composition, and species turnover) over terrain uncovered between zero and 170-year, and (2.) vegetative trends over field and GIS-derived site conditions (e.g., surface fragmentation, concavity, flow accumulation, and solar irradiance). Sixty-one plots (each 8 square meters) were randomly placed within each terrain age range throughout the glacier foreland. Percent cover, species richness, Shannon's diversity, and species evenness were calculated for each plot. Shannon's diversity is a measurement of a community's diversity and uses both species richness and evenness to calculate diversity. All sampled vegetation was identified with taxonomic resolution down to species whenever possible. I assessed vegetative trends across terrain age using several statistical comparison tests. I used two types of statistical models to assess field and GIS-derived biophysical correlates (e.g., surface fragmentation, concavity, terrain variables, and solar irradiance with vegetative trends), followed by comparison tests and scatterplots. Species richness and vegetation cover were greater on older terrain. Plant composition changed over terrain age, with the species *Penstemon ellipticus* (rocky ledge penstemon) favoring older terrain and *Boechera lemmonii* (Lemmon's rockcress) favoring moderately aged terrain. Moderate drainage and concave plots explained increased species richness and Shannon's diversity across different site conditions. Species richness, vegetation cover, Shannon's diversity, and species evenness could be predicted with surface fragments sized from gravel to cobble, topographic position index, and flow accumulation. These findings show that both temporal and biophysical site conditions influence successional trends across the foreland, though different vegetation measures are most influenced differently.

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Chapter 1 – Introduction

Succession refers to the processes associated with plant colonization and the development of an ecosystem over time (Clements, 1916; Walker & Del Moral, 2003). Primary succession, the transition from barren land to a more developed ecosystem, occurs after a disturbance, such as a volcano eruption or glacier activity, and removes all or most organic matter from an area (Clements, 1916; Walker & del Moral, 2009). Understanding primary succession, including the role environmental and topographical factors play in this process, provides fundamental information about how ecosystems develop and adjust as conditions change. Successional studies are especially relevant for preserving and rehabilitating ecosystems (Matthews, 1992; Walker & Del Moral, 2003), developing farmland on barren lands (Walker & Del Moral, 2003), and giving insight into anthropogenic and climatic effects on ecosystems. At locations where anthropogenic disturbance is minimal, successional studies can provide baseline trajectories of ecosystems under a changing climate and environmental disturbances (Matthews, 1992). These trajectories can be compared to locations with human disturbance to better understand how anthropogenic disturbances alter these ecosystems (e.g., Schumann et al., 2016; Young, 2014). Therefore, successional studies are especially needed to understand the trajectory of relatively untouched and anthropogenically altered landscapes.

Glacier forelands, the areas of land exposed after glacial retreat and confined between the glacier tongue and the lateral and terminal moraines, provide a unique opportunity for studying succession. Instead of the entire landscape developing simultaneously, such as after a forest fire or similar disturbance, the terrain closer to the glacier has a progressively greater delay to successional development due to the gradual retreat of the glacier. Once the terrain is uncovered, successional processes begin to change the landscape. Therefore, the entire foreland does not start successional processes simultaneously, rather there is a gradient of terrain ages, depending on when the landscape became exposed from under the glacier. This gradient of terrain age since exposure enables a ‘space for time’ substitution (Stevens & Walker, 1970; Walker & Del Moral, 2003; Walker et al., 2010). This space-for-time substitution is possible using a chronosequence, which allows succession patterns to be studied by sampling terrain representing different successional time periods. Sampling across terrain rather than over time allows researchers to observe the effect of time at a coarse temporal scale, including any time scale between decades to centuries (Stevens & Walker, 1970; Walker & Del Moral, 2003; Walker et al., 2010). Therefore, these studies observe succession at a much greater scale than can otherwise be achieved in a single study.

The main criticism of using a space-for-time substitution is that it assumes similar histories across the entire landscape (Pickett, 1989; Walker et al., 2010) and assumes younger sites represent the older sites’ past condition (Walker et al., 2010). Since glacier forelands don’t always meet these assumptions, the successional patterns found in chronosequence studies will not give a complete picture of the land’s successional history. The suggested alternative to using a chronosequence is permanent plot studies (Erschbamer et al., 2008; Johnson & Miyanishi, 2008; Pickett, 1989; Walker & Del Moral, 2003). Although permanent plot studies directly observe temporal patterns of succession (Pickett, 1989), they are limited to the timescale of a single study. Permanent plots cannot efficiently be maintained long enough to study coarse temporal scales and are unable to study temporal patterns before the start of the study. Chronosequences are only limited to the age range of the exposed landscape. Permanent plots may be more precise, but chronosequences currently are the best tool we have for studying long-term successional patterns on glacier forelands. However, it is important to know the history of the landscape before using a time-for-space substitution (Walker et al., 2010).

Some glacier forefields and alpine systems have had a long anthropogenic land use history. For example, in the European Alps (Schumann et al., 2016) and areas of the Tropical Andes (Young et al., 2018) land use for millennia has included grazing, and hunting (Matthews, 1992; Walker & Del Moral, 2003; Winkler, 2020). However, the relative remoteness of some glaciers allows for natural processes to be studied apart from direct human influence, contributing to their usefulness in the study of successional processes. Many glaciers and alpine environments have remained largely unaffected by direct human activity due to their remote locations (Matthews, 1992).

Finally, the study of glacier forefields can provide an abundance of information on successional processes and their influencing factors as influenced by changing geomorphic and climate conditions. The vegetation dynamics are influenced by many biotic and abiotic processes operating at various temporal and spatial scales, allowing the full complexity of succession to be assessed (Matthews, 1992; Wojcik et al., 2021). Various factors influence succession and distribution on a landscape or site-specific level (e.g., Glausen & Tanner, 2019).

Landscape-level factors of specific interest at glacier forelands include the age of the terrain (time) and climate. Overall, vegetation presence and growth tend to increase with time under favorable conditions. Time is required for seeds to disperse to an area and for vegetation to establish and grow. Climate influences the range and composition of plant communities (Bueno de Mesquita et al., 2018; Young, 2014), including the ability of invasive species to encroach on alpine environments (McDougall et al., 2005). Alpine communities are especially affected by changes in the climate (Cannone et al., 2008; Haeberli et al., 2007; Johnson, 1980; Jumpponen et al., 1999), partially due to the limited upward ability of plant range, sometimes leading to “mountain-top extinction” (Dullinger et al., 2012; Zimmer et al., 2018). This sensitivity to the climate makes glacier forefields appropriate for observing early signs of the climate’s impact on alpine ecosystems (Matthews, 1992; Young, 2014).

Factors influencing primary succession on a site-specific level include biotic and abiotic site-specific characteristics that vary across the landscape. Biotic factors include plant composition, fungi and bacteria, and biofeedback effects between vegetation and the environment. Abiotic factors include microtopography, resource availability, and the presence of safe sites. These factors influence vegetation dispersal and establishment, determining plant communities' spatial distribution and successional patterns. These abiotic factors are important initially for seed capture and sheltering seedlings and saplings (Jumpponen et al., 1999; Perez, 2009). Once plants establish, the vegetation can start shaping the local environment through biofeedback, such as stabilizing slopes or trapping resources (Klaar et al., 2015; Perez, 2009) and act as safe sites for arriving individuals, protecting them from harsh wind and solar conditions (Erschbamer et al., 2008; Haussmann et al., 2010; Schlag & Erschbamer, 2000). These site-specific conditions are key to successional trends (L. Walker & Del Moral, 2003).

Knowledge of successional processes and their driving factors is still limited at both a site-specific and landscape-level scale. One gap includes the discovery of factors that cause ecosystems on the same foreland and exposed by the same deglaciation process to develop differently. Various local terrain features and geomorphic processes may be responsible for these different developmental trajectories (e.g., Bayle, 2020; Glausen & Tanner, 2019). However, the roles specific terrain features play in these various trajectories are not fully understood. Some aspects of this question have been addressed. For example, one study observed different vegetative growth rates and communities on different slopes (Glausen & Tanner, 2019). In another study, fluvial processes influenced the frequency of disturbances along the glacier foreland, which, in turn, influenced vegetation growth (Bayle, 2020). However, this question of why ecosystem recovery varies over a landscape is understudied since most successional studies either focus on the main vegetative trends across the chronosequence (e.g., Cutler, 2010; Fischer et al., 2019; Jones & Henry, 2003) or on differences between different glacial landscapes (e.g., Andreis et al., 2001; Fickert, 2020; Schumann et al., 2016). Understanding what drives these variations in ecosystem changes would allow scientists to better understand succession and predict or direct ecosystem recovery.

Another gap is understanding how different landscape conditions affect succession. A deep understanding of how different factors influence succession requires conducting a multitude of studies in many locations and conditions (Carrara & McGimsey, 1981; Fickert, 2020). Many locations and conditions are needed because researchers best understand how landscape-scale factors affect the rate of change and trajectory of ecosystem recovery by comparing the factors and ecosystem changes between glacier forelands around the world. A location that has had very little research on plant succession is the mid-latitude cirque glaciers of Glacier National Park (GNP). The patterns of glacial retreat have been well studied in this area (Goff & Butler, 2016; Key et al., 2002), but little has been done to investigate successional trends along the forelands of these same glaciers.

Additionally, some of the glaciers in GNP have rocky terrain with little to no soil (Soil Survey Staff et al., n.d.), making them different from many previously studied glaciers. Glaciers with rocky terrain have been under studied compared to soil-covered forelands (e.g., Franzetti et al., 2020; Klaar et al., 2015; Knelman, 2012). The consequences of this relatively soil-free terrain on plant succession rates and the future of the plant community are unknown. This lack of soil may affect the availability of nutrients to the colonizing vegetation, especially since many alpine ecosystems tend to already be nitrogen limited (e.g., Dawes et al., 2013; Körner, 2003; Soudzilovskaia et al., 2005). The nitrogen pool tends to increase toward older soil, mainly due to the nitrogen-fixing bacteria living in the soil (Nemergut et al., 2007). However, nitrogen may also come from the meltwater supply, resulting in less of a nitrogen limitation near the snowfields (Björk & Molau, 2007; Bowman, 1992). Overall, the effect of this lack of soil on plant successional trends has not previously been explored. Therefore, studying glacier forelands and the ecosystem change in this area would contribute to previous studies and help researchers understand how ecosystems develop under different landscape conditions, including across a landscape with little to no soil.

This study worked to fill the gaps relating to both the landscape and site-specific spatial scales by studying plant distribution and successional trends at Sperry Glacier, a mid-latitude, Little Ice Age cirque glacier in Glacier National Park, Montana, USA. I focused on what biophysical site conditions influence variation in plant growth and on the overall vegetation trends across the soil-limited foreland. Through a mixed-method approach involving field-derived information and geospatially-derived terrain variables, the specific objectives of our study were to:

1) Characterize plant successional patterns, specifically vegetation cover (VC), species richness (SR), species evenness (SE), Shannon's diversity (SD), and composition along a chronosequence extending from the 1850 Little Ice Age (LIA) moraine to the glacier terminus.

2) Determine biophysical terrain correlates/predictors of VC, SR, SE, and SD trends, using Classification and Regression Trees (CARTs) and Generalized Linear Models (GLMs), using a suite of field and Geographic Information System (GIS)-derived biophysical variables.

This study provides one of the first case studies to examine how both temporal and biophysical site conditions direct plant succession at a North American, mid-latitude location. Specifically, it is the first study to examine plant successional patterns at Sperry Glacier's foreland. New case studies on vegetation change in recently deglaciated regions, such as the one conducted here, deepen our knowledge about how geomorphological processes operating in different topographic and geographic settings influence vegetation shifts and ultimately landscape change. This improved understanding of succession trends allows for a better understanding of how to manipulate conditions to preserve natural ecosystems, direct rehabilitation of damaged land, and shape environments for greater fertility, diversity, or productivity (L. Walker & Del Moral, 2003).

Chapter 2- Literature Review

2.1. Subdisciplines

This research lies at the intersection of fields including botany, ecology, and phytogeography. The focus on plant communities falls within the field of botany, the study of plants. Ecology, the study of interactions, is involved through investigations of the interaction among physical environmental features and plant composition. The examination of these botanical and ecological patterns across a glacier forefield, which represents processes and patterns that occur and have occurred over different spatial and temporal scales, is provisioned via a geographic lens. Specifically, this work is framed under the approach of phytogeography, which emphasizes the spatial and temporal distribution of plants (Thomas & Goudie, 2009).

Phytogeography-centered studies have a research scope that includes topics such as climate and anthropogenically-induced plant range shifts (Young, 2014), the distribution of seed arrival (Erschbamer et al., 2008), and microbial-plant composition (Franzetti et al., 2020; Knelman, 2012). Phytogeomorphology-focused research applies to physical properties of the environment and plant systematics, such as plant growth, boulders, and slope stability interactions (Perez, 2009) and the role of disturbance in the primary succession of plants (Schumann et al., 2016; L. Walker & Del Moral, 2003; Wojcik et al., 2021). Phytogeography and phytogeomorphology often overlap. The geomorphic processes studied in phytogeomorphology are often a major component in plant species distribution, studied in phytogeography. Likewise, the distribution of a plant community can influence what geomorphic processes it is exposed to. Therefore, these subdisciplines are often intertwined with each other and are both important when researching plant succession.

2.2. Site-Specific Terrain Factors

Fine-scale terrain factors, such as the local topography, topographic differences within a landscape, and rock fragments, influence resource availability and thus ecological patterns and processes, such as plant succession. The first step of plant succession is recruitment via seed arrival and establishment. Recruitment is influenced by factors such as microtopography, substrate, solar exposure, and moisture availability. A site's suitability for seed arrival and establishment is vital to succession and overall spatial aspects of community assembly (Erschbamer et al., 2008). An increased number of seeds increases the rate of succession (Erschbamer et al., 2008), however, Matthews & Vater (2015) found that seeds begin to arrive at deglaciated sites almost immediately and concluded that seeds have few limitations hindering their ability to reach sites. Therefore, seed arrival has less to do with the ability for seeds to travel to a location and more to do with the suitability of a site to trap and support seeds, though the composition of plants arriving at these sites may depend on the plant's dispersal mechanism and seed morphology.

The ability of seeds to immediately reach newly exposed terrain may be due to most seeds on glacier forelands being wind dispersed, allowing the seeds to travel further than other dispersal mechanisms in the foreland (Fischer et al., 2019; Jumpponen et al., 1999). Many plants across glacial forelands have seeds with winged fruit or pappi to help catch the wind and stabilize the descent toward the ground (Gan et al., 2022; Grohmann et al., 2019). Wind dispersal allows seeds with such structures to disperse long distances and potentially travel to higher elevations (Tackenberg et al., 2003). Other dispersal mechanisms are more limited. Animal dispersal is limited to areas the animals frequently travel through. Gravity and water only disperse seeds downhill, away from the newly exposed terrain. Therefore, wind dispersal is the most effective method for transporting seeds across the glacial foreland to colonize terrain of all ages. The factors influencing the site's suitability include slope, orientation, elevation, and degree of soil development because they determine moisture availability, solar radiation, and shelter for seedlings of colonizing species in alpine environments (Corenblit et al., 2011; Eichel et al., 2013; Jumpponen et al., 1999). Further, characteristics of surficial geology, including rock type and degree of consolidation, influence chemical and mechanical weathering rates and the potential for plant colonization (e.g., Dixon & Thorn, 2005).

Wind, which governs most seed dispersal at glacial forefields (Fischer et al., 2019; Jumpponen et al., 1999), is influenced by topography. For example, flat and barren land has no topographic features to alter airflow, whereas locations with fine-scale topographic variation cause friction that deflects wind current, creating areas sheltered from the wind (Kondo et al., 2002; Resler, 2006). When seeds are deposited in areas with limited wind current, they are less likely to be blown from that location. Therefore, features that shelter seeds from the wind in alpine areas such as concavity (Jumpponen et al., 1999), boulders (Jumpponen et al., 1999; Perez, 2009), and stone gaps (Perez, 2009), tend to have greater seed arrival and increased vegetation. Areas with less shelter, such as bare-ground sites, have very little plant recruitment (Carrara & McGimsey, 1981). A lack of seeds is one of the main reasons a site is not colonized (Chapin et al., 1994). Therefore, a site must be able to shelter and collect seeds for colonization to begin. However, even the artificial addition of seeds to bare ground does not have much of an effect on the succession rate (Erschbamer et al., 2008). Bare ground's ability to eliminate the effect of increased seed presence shows that site suitability involves more than just facilitating seed arrival.

A site must also promote seed establishment to have vegetation growth. At wind-swept treeline study areas in Glacier National Park, relict solifluction risers were shown to protect seed arrival and initial tree colonization but failed to provide sufficient protection for vegetative growth, resulting in high plant mortality after seed establishment (Resler et al., 2005). Seed arrival may be vital to initiate colonization, but a site must be able to support vegetation for succession to proceed. This support may be through safe sites or resource availability. Concave surfaces provide low spots that accumulate resources such as water and soil (Jumpponen et al., 1999). Rocks and crevices likewise can collect seeds and create a gradient of moisture and nutrients to support vegetation establishment and growth (Mori et al., 2013). Boulders provide shade, protect seedlings from frost and debris movement disturbances, lengthen the growing season by melting snow earlier in the season (due to the boulders warming in the sun, causing the nearby snow to melt), collect fine material, and provide moisture in the form of dew and the preservation of soil moisture (Jumpponen et al., 1999; Perez, 2009). Pebbles and gravel likewise protect from frost and collect dew (Perez, 2009). These benefits are likely why vegetation tends to be found on concave surfaces (Jumpponen et al., 1999) and around boulders (Jumpponen et al., 1999; Perez, 2009). Species number also tends to increase with coarse material, and species number and vegetation change are negatively associated with the presence of bedrock (Lambert et al., 2020; Schumann et al., 2016). However, the relative importance of each factor's influence on a system's successional trajectory is still unknown. The benefits of rocks may have less of an impact on plant recruitment when other factors are present (Jumpponen et al., 1999), and even in the absence of other factors, the color and size of stones and boulders will change their characteristics and recruitment ability (Perez, 2009).

Another factor that plays an important role in plant succession is substrate. The substrate affects plant establishment and succession on level ground, as well. The composition of the soil dictates what impact the soil has on succession (Andreis et al., 2001). Sand, for example, tends to be negatively correlated with species number, while increased soil moisture is correlated with increased species number (Schumann et al., 2016). Soil pH influences bacterial communities (Franzetti et al., 2020) and correlates with vegetation. Moss cover, herb cover, and the overall species richness were found to decrease as pH increased (Schumann et al., 2016). However, pH is also affected by vegetation, specifically, vegetation tends to decrease pH (Knelman, 2012). Soil properties also change as succession progresses. In a study of four glacier forelands in the Eastern Alps, soil aeration decreased, organic matter increased, nutrient content increased, and pH became more acidic with age (Fickert, 2020). In addition to providing nutrients, soil may also help trap seeds, preventing them from being blown away by the wind. Some seed surfaces contain angled trichomes or spines which create extra resistance for pulling the seeds from the soil without increasing the force required for the seeds to enter the soil, protecting the seeds from being blown away (Grohmann et al., 2019). Overall, as soil forms and becomes more developed, vegetation tends to increase (Andreis et al., 2001).

The substrate can also influence the interaction between other site conditions and plant succession. For example, fine substrates contribute to the instability of slopes (Perez, 2009). Slopes tend to inhibit plant development (Lambert et al., 2020; Perez, 2009) due to their decreased stability and increased risk of disturbances such as debris flows (Perez, 2009). These disturbances can greatly hinder succession by uprooting, burying, and damaging vegetation, which can reset successional progress (Andreis et al., 2001; Matthews, 1992; Perez, 2009; Wojcik et al., 2021). However, all slopes are not the same. Boulders can stabilize slopes, and slopes made of coarser material tend to be more stable than slopes covered with fine material (Perez, 2009). The aspect, or positioning, of a slope can further influence succession because it results in different amounts of solar exposure. For example, while studying at a glacier forefield in southern Iceland, Glausen and Tanner (2019) found that the northeast slope received less sunlight than the southwest slope, which contributed to a greater increase in vegetation cover. While sunlight is required for photosynthesis, exposure to too much solar radiation can cause some plants to overheat, such as cushion plants (Körner, 2003), or dehiscence (Erschbamer & Caccianiga, 2016). Overall, increased solar radiation is associated with increased vegetation cover (Lambert et al., 2020; Schumann et al., 2016), though an intermediate amount of solar radiation exposure may promote the greatest amount of plant diversity (Schumann et al., 2016) due to the need to photosynthesize and risk of dehiscence or overheating (Erschbamer & Caccianiga, 2016; Körner, 2003).

Not only do site characteristics influence the amount and diversity of vegetation growth, but also influence the plant traits found across the forefield. Mesophilic plants survive best in moderate temperatures and with moderate water availability. Xerophilic plants survive well in warm, dry conditions. Distance from the glacier and topography may influence the plant’s traits expressed across the chronosequence. Plants closer to the glacier and snowfields tend to be mesophilic while plants that grow on older terrain tend to be xerophilic due to the decreased reliance on snow melt to provide water (Apple et al., 2022). Mesophilic plants are often found closer to the glacier, which also tends to be at higher elevations, due to the snowfields located at the terminus of the glacier. As meltwater becomes scarcer toward older terrains, plant communities shift from mesophilic to xerophilic. As the snowfields shrink, previous snowfield edge environments become unsuitable for the mesophilic species inhabiting them and these species must migrate to the current snowfield edge to survive (Apple et al., 2022). Steep slopes and windy areas, due to windy areas being drier, also tend to be associated with xerophilic vegetation (Hedding et al., 2020).

These abiotic site conditions, though important to succession, may vary in their influences across different phases or scales of succession. Abiotic site conditions tend to dominate the initial phases of succession due to abiotic factors determining the initial conditions of a site while biotic factors increase in importance as succession progresses (Schumann et al., 2016; Wojcik et al., 2021). In some glacier forelands, abiotic site conditions, such as the microtopography, including factors like aspect, have a greater influence on a smaller scale rather than on a landscape level (Glausen & Tanner, 2019). Topography is the characteristics of a landscape's surface and terrain. Microtopography is the surface and terrain characteristics on a very fine scale, observing the variations within sections of a landscape rather than over the entire landscape. These variations influence the exposure and resources available to vegetation. For example, in Skaftafellsjökull glacier in Southern Iceland, an aspect facing away from the glacial front was more sheltered from glacial winds, providing a more suitable location for plant colonization.

2.3. Biotic Factors

Biotic factors, such as community composition, microbe interactions, and proximity to other species, are also foundational to successional trends. These biotic components also shape abiotic characteristics, often increasing their suitability for colonization. These changes facilitate other species through positive recruitment interaction, especially in harsh environments, through mechanisms such as the nurse-plant effect where one plant shelters the establishment of a neighboring plant (Bertness & Callaway, 1994). Established plants, for example, can provide shelter from wind and terrain stabilization similar to rocks (Perez, 2009). Cushion plants may create better safe sites as well as improve soil nutrients and mycorrhizae (Haussmann et al., 2010). Glausen and Tanner (2019) attribute the increase in species richness and species diversity at a Southern Iceland glacier forefield to facilitation by early colonizers. However, communities are not only influenced by facilitation but also by competition. Facilitation and competition often occur simultaneously in the same area (Bertness & Callaway, 1994; Carrara & McGimsey, 1981). A species that facilitated the establishment of another species may be outcompeted by the species it facilitated. This newly established species may go on to facilitate even newer establishing species (Erschbamer et al., 2008).

Facilitation is not only provided by vegetation. Bacteria help weather rock (Franzetti et al., 2020) and carry out nitrogen fixation (Knelman, 2012), and fungi help develop soil by decomposing organic matter (Franzetti et al., 2020). The presence of vegetation also alters bacterial communities and increases the fungi-to-bacteria ratio (Knelman, 2012). Seed arrival also introduces bacteria to an area, though bacteria also arrive via animals, aerial circulation, or even from the glaciers themselves (Franzetti et al., 2020). Even proximity to treelines contributes to species composition and richness throughout succession (Fickert, 2020; Schumann et al., 2016). This may be partially due to the ability of forests to create updrafts that push wind-dispersed seeds higher in elevation, allowing for longer dispersal distances (Qin et al., 2022). Further, the composition of a community influences successional trends. For example, if a plant community lacks a dominant species, the community tends to have greater species evenness, richness, and diversity (Andreis et al., 2001). Systems with stronger biotic controls by trees tend to have a more convergent successional trajectory, while systems with stronger abiotic control tend to have a more divergent pathway (Matthews, 1992).

Biotic factors are not only important for shaping the physical aspects of an environment but also for shaping the biotic communities themselves throughout the course of succession. However, not all biotic factors are influential to plant succession. Matthews & Vater (2015) found that plants and invertebrates occupying the same areas were both primarily influenced by abiotic features and had little influence on each other, resulting in each developing relatively independently of each other. Raffl et al. (2006) found that the physical differences between two transects, such as the aspect which influenced each transect's solar exposure, resulted in two different successional trends, as opposed to the biotic differences. Biotic and abiotic site conditions have varying impacts on different aspects of succession and different sites. However, site conditions, whether biotic or abiotic, are not the only factors directing succession.

2.4. Landscape Level Factors

Landscape-level factors refer to any factor of the environment or climate that affects the ecosystem on a landscape scale. These landscape-level factors, such as climate, tend to affect the entire landscape rather than vary substantially between specific sites. Climate includes the overall temperature trends of an area. An increase in temperature tends to shift plant ranges higher in elevation (Young, 2014) and expand the range of woody plants while anthropogenic and water influences may shift the range of woody plants to lower elevations (Bueno de Mesquita et al., 2018). Increased precipitation may also expand the range and percent cover of shrubs (Bueno de Mesquita et al., 2018).

The increased deglaciation rate due to rising temperatures can lead to a time lag between ground exposure and colonization, which impacts the composition and interactions of the plant community (Dullinger et al., 2012; Zimmer et al., 2018). Zimmer et al. (2018) found that this lag was especially strong for water and animal-dispersed plants, changing the community composition toward a greater proportion of wind-dispersed species. Wind is less affected by this lag since various weather conditions and forest canopies can create updrafts that lift wind-dispersed seeds allowing them to travel further, including to higher elevations (Qin et al., 2022; Tackenberg et al., 2003). Water-dispersed seeds, however, are always transported downslope, in the direction of flow, and, therefore, will not transport seeds up the foreland. This lag was not only evident in the dispersal of plants, but also in the interactions between plants. The delay in plant establishment decreases the ability of already developed plants to serve as safe sites for seeds and seedlings, due to the decrease in developed plants in these areas (Zimmer et al., 2018). However, in some areas, the rate of colonization and succession appears to be accelerated in alpine communities (Cannone et al., 2008). Cannone et al. (2008) found that in the European Alps, species were still able to colonize on terrain exposed for only a year. In both studies, however, the community composition appears to shift to favor certain strategies, such as wind dispersal (Zimmer et al., 2018) or clonal growth (Cannone et al., 2008), whether plant colonization and establishment are delayed or accelerated.

Lags in plant establishment may be due to the condition of the newly exposed ground. At Twin Glacier in Canada, soil was deposed by the glacier while it melted (Jones & Henry, 2003) while at several forelands in the Italian Alps, soil did not start forming until 70 years of exposure (Andreis et al., 2001). Furthermore, wind, the very thing that allows seeds to reach the area, may also hinder the establishment of these plants by drying them out (Moreau et al., 2005) or blowing away what little soil does develop (Glausen & Tanner, 2019) if sufficient safe sites are not available to collect the soil.

Climate and geography add another layer of complexity to successional differences between glaciers since it does not affect all landscapes equally. In fact, despite glaciers being more sensitive to changes in the climate, small cirque glaciers tend to be more shaded and sheltered than other glaciers, preventing ablation and snowmelt (Kuhn, 1995). As a result, some foreland processes, especially in small cirque glaciers, may be influenced more directly by topography than climate (Kuhn, 1995). Successional processes, community assembly dynamics, and local biodiversity patterns may be constrained or enhanced by these topographic features at multiple spatial scales (Graae et al., 2018), making terrain an important factor on both the site-specific and landscape level.

Terrain age (time since deglaciation) is a main landscape-level factor influencing plant distribution at glacial forefronts (Andreis et al., 2001) and landscape-level changes (Glausen & Tanner, 2019); however, disturbances can greatly disrupt the rate of succession (Matthews, 1992; Wojcik et al., 2021). Time since deglaciation affects both fungal and bacterial communities (Franzetti et al., 2020) and tends to increase floristic dissimilarity (Fickert, 2020). Since succession occurs over time, time is the background over which all other influencing factors are observed. However, time alone cannot be used to predict the trajectory of succession. Along with time, Glausen & Tanner (2019) found that nutrient availability influenced succession on a landscape level.

Knowing landscape-level vegetation trends is vital but does not explain the whole successional process occurring across the foreland. Raffl et al. (2006) demonstrated that transects across the same landscape can show completely different trajectories. Therefore, along with landscape-level analysis, it is important to understand the site-specific factors discussed previously as well. To fully understand succession, both landscape-level and site-specific factors must be studied at various locations.

2.5. Changes Throughout Succession

The relative influence of each factor over succession changes throughout the successional process. One of these changes is a shift from stochastic and allogenic processes dominating the early phases of succession to deterministic and autogenic processes dominating the later phases of succession (Matthews, 1992; Wojcik et al., 2021). Stochastic processes are processes that involve an element of chance, such as where seeds land, while deterministic processes are not random, such as the effect soil has on the seeds once they land. Allogenic processes are processes driven by external factors, such as the abiotic factors in the environment, while autogenic processes are factors driven by the organisms themselves. The influence of allogenic processes, such as disturbances, can initially delay or restart the succession process but has less of an impact as a site becomes well-established. This delay is especially evident on slopes where debris movement is common (Perez, 2009). The shift from allogenic to autogenic processes is mainly attributed to biogeographical feedback (Wojcik et al., 2021). This feedback is evident in the relationship between plants and soil stability on sloped areas. Unstable slopes damage and hinder plant growth, while the plant growth that does occur stabilizes the soil, making debris movement less likely (Perez, 2009). This feedback drives landscapes from being dominated by disturbance events to being influenced by the forming plant community.

This shift from disturbance events to biotic drivers influences successional trends, such as that of species richness, as addressed by the Intermediate Disturbance Hypothesis. The

Intermediate Disturbance Hypothesis is a theory that species richness is greatest with an intermediate amount of disturbance (Moi et al., 2020). If disturbances occur too frequently, the area will be repeatedly cleared of vegetation and a large number of species will not have an opportunity to grow between each disturbance. If an area is rarely disturbed, the vegetation cover will grow, resulting in competition between species. This heavy competition will decrease the number of species in a plot since the dominant species outcompetes the other species (Jones & Henry, 2003). Therefore, species richness is at its greatest when enough disturbances are occurring to prevent a species from dominating a plot without destroying all the vegetation in the plot.

The relative importance of individual factors also appears to shift throughout each of these dominant processes. In a conceptual model based on plant colonization at a glacier foreland in Norway, the relative importance of several abiotic processes changed within the first 35 years of succession. The dominant process during the allogenic-dominated phase is initially water-driven, then shifts to temperature-driven, then to wind-driven (Matthews & Vater, 2015). In the Eastern Central Alps, Fickert (2020) observed a trend of increased preference for temperature and decreased preference for light over time. Schumann et al. (2016) observed greater importance of elevation in mid and late succession than in early succession. The early-stage vegetation composition was relatively consistent at different elevations, while the composition varied with elevation in mid to late succession (Schumann et al., 2016). Schumann et al. (2016) concluded that different elevations were likely similarly harsh at early succession while more factors influenced composition at later successional stages. While it is generally agreed that disturbance is more influential earlier in succession (Perez, 2009; Schumann et al., 2016; Wojcik et al., 2021), there is still some debate about whether safe sites have greater influence over succession during initial successional stages (Schumann et al., 2016) or if they increase in importance later (Wojcik et al., 2021). Safe sites are important for plant recruitment and establishment (Jumpponen et al., 1999; Perez, 2009), but stochastic processes play a large role at the beginning of succession (Wojcik et al., 2021). How protected a site is does not matter if seeds don't land at that location or if slope disturbance destroys the vegetation at the location. Once vegetation is established and the slope is more stable, the protection of safe sites is important for vegetation survival. However, if a seed lands in an unprotected site, the chance arrival is insufficient for vegetation to establish itself. These changes in dominant processes need to be studied to fully understand succession and predict the trajectory of certain landscapes.

Further complicating successional trends, site factors do not influence all plants and landscapes the same. Even landscape-level changes don't affect all species equally. Different conditions are preferred by different species and one factor may impact species in varying ways (Bueno de Mesquita et al., 2018). Woody vegetation, for example, tends to prefer warmer environments with greater solar radiation while herbaceous plants prefer flat and cool terrain (Schumann et al., 2016). These variations in plant preferences and responses further emphasize the need to collect more data on how factors influence succession in different environments, creating knowledge of the general and specific trends of succession.

2.6. Succession and Chronosequences

Initially, succession was thought to have a determined endpoint where an ecosystem reaches an equilibrium or climax stage (Clements, 1916). Currently, succession is thought to not have a predictable endpoint, but rather remain in a state of disequilibrium and fluctuation (Matthews, 1992; L. Walker & Del Moral, 2003). Moreover, succession does not always follow a linear pathway. In one study, succession from a post-glacial water body toward a bog forest even paused and temporarily reversed in some locations, showing the fluctuating nature of succession (Walker, 1970). However, Matthews (1992) believes it's premature to assume this lack of a true endpoint makes studying successional trajectories futile. Rather, studying succession, especially primary succession, is vital to understanding and developing solutions for some of the world's problems, such as habitat loss, species loss, and the presence of disturbed or damaged land that can neither be used for natural habitat nor agriculture.

Ideally, succession is studied using permanent plots so the process can be studied directly rather than assumed or inferred (Erschbamer et al., 2008; Johnson & Miyanishi, 2008; Pickett, 1989; Walker & Del Moral, 2003). Long-term studies in permanent plots also allow for the observation of more detailed succession patterns or changes in trajectories (Pickett, 1989). However, the long timescale of succession makes this method impractical. Scientists often cannot carry out studies long enough to capture succession since succession can often progress longer than a century (e.g., Cutler, 2010; Fickert, 2020; Fischer et al., 2019; Glausen & Tanner, 2019). Though a long-term study would be beneficial, more time-effective alternatives are necessary.

An approach often used to study primary succession is observing plots along a chronosequence. This is the dominant approach used to study glacier foreland succession and was used in this study. However, this method's validity has been previously debated and the findings obtained were questioned. Therefore, before continuing, the limitations of using chronosequences as a space for time substitution must be addressed. To start, a precise definition of chronosequences must be revisited. In ecology, a chronosequence is defined as a sequence of sites with varying times since formation, or deglaciation in the case of glacier forelands, that have similar parent material and environmental conditions (Stevens & Walker, 1970; Walker et al., 2010). These conditions allow researchers to observe phenomena that span decades to centuries, by assuming a space-for-time substitution (Stevens & Walker, 1970; L. Walker & Del Moral, 2003; Walker et al., 2010). This approach relies on a few basic assumptions. One main assumption is that younger sites represent an earlier stage of the older sites, or as Walker (2010) put it, the "present repeats the past." Though this assumption is not always true, chronosequences are still viable if the succession pathway is similar between the different aged sites. The next assumptions are that the sites have similar initial conditions and that they have similar histories (Pickett, 1989; Walker et al., 2010). There will always be slight differences between sites, but chronosequences are still beneficial if the differences aren't great enough to drastically alter the site's successional trajectory.

Chronosequences are best suited for areas with convergence or cyclic successional pathways and areas with a predictable development pattern (Pickett, 1989; Walker et al., 2010). They are less useful in areas with divergent convergence, high disturbance regimes, and slow turnover (Walker et al., 2010). Convergence occurs when the area becomes more alike over time while divergent communities do not converge over time. Cyclic succession is when the species of an area are replaced by a few other species in the absence of disturbance. Walker (2010) also argues that chronosequences should not be used when different soils or topography are involved, however, Raffl et al. (2006) found that chronosequences could be effectively used to compare the effect of different topography by comparing transects that contain different topographic features along a chronosequence. They used this method to assess how different site characteristics impact the overall succession process. Further, Pickett (1989) argues that chronosequences can be used to determine the degree of variability among sites, which would be an unnecessary measure if sites did not vary. Chronosequences should not be used in areas where the history or time since disturbance is unknown (Walker et al., 2010) because differing histories can lead to significantly different successional trajectories. For example, a history of grazing increased the species richness of a site (Schumann et al., 2016) and decreased the resilience of alpine vegetation to drought in Kosciuszko National Park, Australia (Scherrer & Pickering, 2005).

Despite the benefits of chronosequences, they have a few inherent limitations. For example, they have an averaging effect and can miss patterns and variations in dynamics revealed in long-term studies as well as disturbance regimes revealed in reconstruction analysis (Pickett, 1989). Study sites may also have histories that are not on record and are unknown to the researcher, changing the pathway the site follows (Johnson & Miyanishi, 2008). Some argue that these limitations of the chronosequence method invalidate the finding of studies using this method and that chronosequences should no longer be used (Johnson & Miyanishi, 2008).

However, others argue that chronosequences still provide valuable data if used properly (Pickett, 1989; Walker et al., 2010). What chronosequences lack in detailing variations in succession pathways, it makes up for in outlining overall patterns, such as trends used for creating general models and predictions to be studied later in more detail (Pickett, 1989; Walker et al., 2010). They are also the best option for locations where permanent plots cannot be set up or maintained for a long enough period (Walker et al., 2010).

Before conducting a study using chronosequences, it is important to know the benefits and limitations of the method to ensure proper interpretation of the results. Chronosequences are a powerful tool to study trends that cannot be observed otherwise so long as the results are analyzed appropriately and are not used to infer information that is beyond the scope of the method. For the time being, chronosequences should be limited to looking at coarse trends and site variability rather than inferring a detailed history for specific sites. Despite its limitations, chronosequences appear to be a valid research tool, and future research can be built upon the previously mentioned research rather than disregard their findings.

Chapter 3- Study Area

Glacier National Park (GNP), established in 1910 (Carrara & McGimsey, 1981), is in northwestern Montana adjacent to the Canadian border and comprises of the world's first International Peace Park and UNESCO Biosphere Preserve with Waterton Lakes National Park of Alberta, Canada. The glaciers of GNP have retreated rapidly during the past 100 years as the global mean temperature has increased 0.45°C since the late 19th century (Hall & Fagre, 2003), resulting in visible landscape transformations.

According to tree-ring studies, glacial retreat in the area began in 1850 after the Little Ice Age (LIA) (Goff & Butler, 2016; Key et al., 2002), at which time there were 150 glaciers (Carrara & McGimsey, 1981). Less than 20% of those glaciers remain in the park (Carrara & McGimsey, 1981). The Continental Divide runs along the Lewis Range in the park, causing a split in climate. The western side of the divide has a stronger maritime influence while the eastern is described as more continental and extreme (Finklin, 1986), resulting in the park being described as "Continental with Pacific maritime modifications" (Carrara & McGimsey, 1981). An overall increase in both extreme and seasonal mean temperatures (Pederson et al., 2010) is largely responsible for the decrease and disappearance of glaciers (Brown et al., 2010; Carrara & McGimsey, 1981; Goff & Butler, 2016; Johnson, 1980). The mean annual temperature of Glacier National Park has increased by 1.33°C since 1990, which is around 1.8 times the global mean increase (Fagre et al. 2017). However, this temperature increase does not affect all glaciers equally (Brown et al., 2010). Average precipitation varies throughout the park (Lesica, 2002), but typically increases with elevation (e.g., Johnson, 1980). Some cirque glaciers, such as Grinnell Glacier, have increased precipitation due to both easterly and westerly winds pushing moist air to higher elevations (Finklin, 1986). The eastern side of the Continental Divide tends to have less precipitation and more wind (NPS, 2021). However, the difference in precipitation on the east and west sides of the park is very similar when averaged over the area (Finklin, 1986). Glacier National Park is home to several rare arctic-alpine plants, though their populations are on the decline (Lesica & McCune, 2004). The glacier focused on in this study is Sperry Glacier, one of the larger glaciers in the park.

Sperry Glacier was named after Lyman B. Sperry, who was credited with first observing the glacier in 1897 (Johnson, 1980). Sperry Glacier is a cirque glacier on the west side of the Continental Divide, situated on the northwest slope of Gunsight Mountain at an elevation of around 2450 m. Cirque glaciers tend to be less sensitive to variations in the climate since they are sheltered from solar radiation and ablation by the surrounding mountain range (J. Brown et al., 2010). Sperry Glacier forefront receives a mean annual precipitation of around 218 cm and has an annual temperature of 0.7°C with an extreme high of 30.4°C and an extreme low of -38.8°C according to ClimateNA Map (https://www.climatewna.com/). Sperry Glacier is calculated to have originally been 3.76 km^2 in 1850 (Key et al., 2002). Sperry retreated at a rate of 1 to 5 $m\ a^{-1}$ from 1850 to 1993, 15 to 22 $m\ a^{-1}$ from 1913 to 1945, around 11 $m\ a^{-1}$ from 1945 and 1950, and around 5 $m\ a^{-1}$ from 1950 to 1979 (Key et al., 2002). Though the deglaciation rate has decreased since the mid-1940s, Sperry Glacier has lost much of its area and volume over the years and continues to shrink, especially below the elevation of around 2300 m (Johnson, 1980). By 2002, the glacier had shrunk to about 26% of its previous area. Sperry Glacier went from being one of the largest glaciers in the park to being the 8th largest with an area of around 0.80 km^2 (Fagre et al., 2017; Goff & Butler, 2016). The furthest extent of the glacier in 1850 is marked by a moraine consisting of metasedimentary rock derived till and talus (Soil Survey Staff et al., n.d.). The remainder of the foreland consists mostly of bare rock with a metasedimentary rock parent material and rock fragments derived from this parent material (Soil Survey Staff et al., n.d.). The Sperry Glacier sampling area existed along the foreland within elevations 2200 to 2500 m.

Chapter 4: Methods

4.1. Field Data Collection

4.1.1. Plot Placement

Fieldwork occurred in July-August of 2021 and 2022 to coincide with minimal snow coverage and the fruiting and flowering of many high-elevation plants. The presence of fruit or flowers is often necessary to accurately identify plants to species level and the shrinkage of snowfields allows for closer access to the glacier terminus.

Before entering the field, potential plot locations were determined using a random sampling strategy stratified by terrain age ranges between the LIA glacier moraines and the glacier terminus. I positioned random points a minimum of 50 meters apart and between each terrain margin date line. I limited points to the southern portion of the glacier forefield due to accessibility and safety. Glacier margin date lines based on historic glacier extents were created by the USGS (Fagre et al. 2017) for 1966- 2015 and Key et al. (2002) for 1850 -1966. I generated more plot points than were sampled in the study; all waypoints were uploaded into a Trimble Geo 7X global positioning system (GPS) handheld device with submeter accuracy for field navigation.

4.1.2. Plot Sampling

In the field, I used the GPS for navigating to waypoints. Waypoints selected for field sampling were based on 1) accessibility and safety, and 2) terrain date range to ensure representative cover across all date ranges. Ideally, all generated plot locations would be sampled, but time constraints, mainly due to the tremendous time it took to reach sampling locations (accessibly only via the backcountry), required prioritization.

In total, I sampled 61 plots between the 1850 LIA moraine and the present glacier margin (Figure 1). Each plot was a fixed-area, square sampling plot (8 m^2). Plot size was determined using combined knowledge from species-area curves, landscape layout, and similar studies conducted in mid-latitude locations (e.g., Eichel et al., 2013). Some coordinates positioned in unsafe or inaccessible areas were repositioned by following a random compass heading (within an accessible direction), for a random number of paces between 1 and 25. At that location, a pin was tossed in a random direction and the new plot was centered upon where the pin landed. Plots lying completely in the snow were also repositioned, following the same procedure. The coordinates of each plot centroid were obtained with the GPS to enable resampling. For each coordinate, I used a minimum of 30 waypoints for subsequent differential correction.

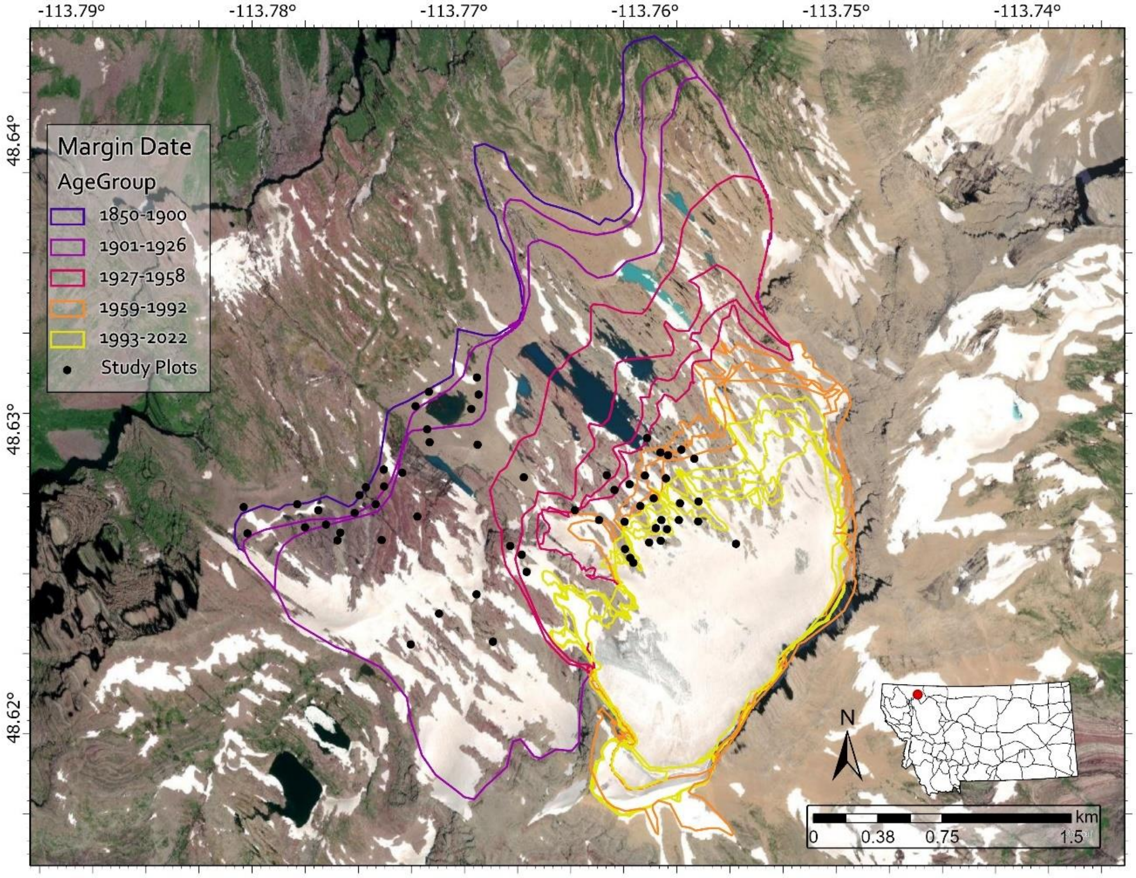

Figure 1: Sperry Glacier and foreland with glacier margin dates and sample plot locations.

I characterized floristics and the local abiotic site conditions within each plot. Floristic data included: species richness (number of different species per plot), percent vegetation cover (including lichen cover, though lichen is not technically vegetation), and composition. Abiotic site conditions included: surface rock fragment cover, observed terrain concavity, drainage, and landform features. I also categorized the dominant geomorphic process domain (Table 1) (e.g., Eichel et al. 2013). Percent vegetation cover was determined through ocular estimation of the proportion of the plot covered by canopy, foliage, and bases of plants. This method enables estimation of the influence a species has on an area and can be applied to any form of vegetative life (Schulz, 2009), and has been shown as an ideal method for capturing rare and infrequent species (Colson & Karl, 2012). The proportion of area covered was based on the outermost outline of the vegetation from a vertical projection and considered overlap. To reduce subjectivity, the percent cover estimates were performed by two field team members simultaneously and averaged. In this study, I estimated all plant cover less than 1% to be 0.5% due to uncertainty.

Table 1: All variables used in the study with their collection method, units, which objective they were used to answer, and why they were chosen for this study.

Dependent Variables	**Source**	**Units**	**Objective**	**Description/Justification**
Species Richness	Field	Count Data	1 & 2	The total number of species.
Vegetation Cover	Field	Percent	1 & 2	The percent cover of vegetation.
Shannon's Diversity	Calculated from Field	n/a	1 & 2	Combines species richness and evenness measures to assess biological variability (Ortiz-Burgos, 2016).
Species Evenness	Calculated from Field	n/a	1 & 2	Measures the relative abundance of each species in a community and how evenly percent cover is distributed among each species (Moore, 2013).
Species Composition	Field	n/a	1	All the identified species that make up the community.

Independent Variables	**Source**	**Units**	**Objective**	**Description/Justification**
Terrain Age Ranges	USGS	Years	1 & 2	Dates of terrain exposure based on glacier margin date lines for analysis of vegetation over time.
Drainage	Field	n/a	2	Drainage was categorized into poor and moderate drainage. Water availability is important for plant germination and survival (Erschbamer & Caccianiga, 2016).
Observed Concavity	Field	n/a	2	Concavity was classified into concave, convex, straight, and undulating. Concavity can create safe sites (Jumpponen et al., 1999).
Landform feature	Field	n/a	2	Landform features were classified into moraines, Roche moutonnée, and others. These features may influence safe site availability.
% Fines-Sand	Field	Percent	2	The percent cover of surface fragments under 2 mm in size. These small surface fragments may contain nutrients and preserve moisture (Perez, 2009).
% Gravel-Cobble	Field	Percent	2	The percent cover of surface fragments from 2 to 256 mm in size. Gravel and cobble provide safe sites (Jumpponen et al., 1999; Perez, 2009).

% Boulder	Field	Percent	2	The percent cover of surface fragments greater than 256 mm in size. Boulders provide shade and wind shelter (Perez, 2009).
Process Domain	Field	n/a	2	The main glacial process that shaped the landscape, classified as depositional or erosional (e.g., Eichel, 2019).
Northness	GIS-Derived	n/a	2	A cosine transformation of aspect, which may influence vegetation cover and composition (Glausen & Tanner, 2019).
Eastness	GIS-Derived	n/a	2	A sine transformation of aspect, which may influence vegetation cover and composition (Glausen & Tanner, 2019).
Slope	GIS-Derived	Degrees	2	A measure of the steepness of the surface. Slopes cause instability and may hinder vegetation development (Lambert et al., 2020; Perez, 2009).
Terrain Roughness Index	GIS-Derived	n/a	2	A measure of average surface roughness or smoothness that influences wind exposure (Lambert et al., 2020; Resler et al., 2005).
Topographic Position Index	GIS-Derived	n/a	2	The relative position/elevation of a location. This position influences erosion and soil development (Román-Sánchez et al., 2018; Temme et al., 2016).
Flow Accumulation	GIS-Derived	n/a	2	The accumulated weight of water flow into each raster cell of a landscape. Flow accumulation influences the water supply in each plot.
Area Solar Radiation	GIS-Derived	WH/m2	2	A measure of insolation, or solar exposure. Solar radiation may increase dehiscence or change plant composition (Erschbamer & Caccianiga, 2016; Schumann et al., 2016).
Profile Curvature	GIS-Derived	1/100 m	2	The curvature parallel to the direction of the maximum slope. Profile curvature influences the acceleration and deceleration of flow (Buckley, 2010).
Tangential Curvature	GIS-Derived	1/100 m	2	The curvature perpendicular to the direction of the maximum slope. Tangential curvature influences the convergence and divergence of flow (Kopp, 2021).

National Parks generally discourage destructive sampling methods or collecting; thus I identified plants in the field to the species level whenever possible using Lesica, (2002) with some assistance from Sullivan (2022). I checked species names against the Integrated Taxonomic Information System (ITIS) to ensure the current taxonomic names were used. Any species that could not be determined in the field were photographed and later identified. Photos obtained to aid identification included images of the overall plant, branching pattern, abaxial and adaxial side of the leaves, detailed images of any fruit, flowers, or sporangium, the receptacle, any pubescence if present, and other distinguishing features. Overall pictures of the plots were also taken in 2022 for later reference, if needed. Online herbarium specimens from databases including Tropicos and SEINet aided identification when necessary. Grasses, sedges, and rushes were identified to family due to the difficulty of accurate identification in the field. Similarly, mosses and lichens were not identified down to family due to 1) efficiency, and 2) an inability to identify them in the field.

Characterizing the abiotic site characteristics of each plot allowed for subsequent analysis of the site conditions underlying ecological processes and the possible effect of local environmental variability on plant succession. For each sampling plot, I estimated the rock fragment surface cover and the observed plot concavity, and characterized drainage class, geomorphic process domain, and landform features (Table 1).

The estimation of the percent rock fragment surface cover was based on the Wentworth scale (Wentworth, 1922). For this study, I considered the surface cover of rock fragments to be representative of the potential suitability of those surfaces for plant colonization. The Wentworth scale divides surface fragments into 6 groups (fines, sand, fine-medium gravel, coarse gravel, cobble, and boulder) depending on the diameter of each fragment. For this study, I simplified the

Wentworth scale into 3 groups (fines-sands, gravel-cobble, and boulders). This simplification groups fines and sands, which are both too small to provide safe sites, but may provide a substrate for vegetation that contains nutrients and preserves moisture (Perez, 2009). Gravels and cobbles were combined because both may provide safe sites for arriving and existing vegetation, capture water and finer material, and protect against needle ice and frost (Jumpponen et al., 1999; Perez, 2009). Similarly, boulders provide safe sites by trapping seeds and resources, shading vegetation, blocking wind, and forming condensation (Perez, 2009).

Observed concavity for each plot was defined as straight, concave, convex, or undulating in the field through visual estimation. Concavity is important for plant recruitment because it can shelter seeds from wind and collect water and sediment (Jumpponen et al., 1999). An undulating plot was a plot that was not clearly straight, concave, or convex. These undulating plots had aspects of the other three categories throughout them. The measure of undulating was included, rather than averaging the shape of the plot, since the concave parts of the plot may provide some shelter while the convex parts may be more exposed, which may influence the plant colonization within these plots. Drainage classes for each plot were poor, moderate, and well-drained. Poor draining plots were those that either pooled water, so that water did not drain, or lacked any surface fragments to become saturated, so that water would either stand on the surface or immediately wash off (Figure 2). Moderate draining plots contained surface fragments and were shaped in such a way that the water could trickle through without pooling or all immediately running off the plot (Figure 2). None of the plots were well-drained in our study area, so that category was omitted. I included drainage since desiccation due to water shortage is one of the main risks to germination found in glacier forelands (Erschbamer & Caccianiga, 2016), while the presence of standing water in poor draining plots may drown vegetation.

Figure 2: A poor drainage, concave plot (left), poor drainage, straight plot (middle), and moderately drained, convex plot (right). Photos: A. Schulte 2022.

I also recorded the dominant geomorphic process domain reflected by that plot (e.g., Eichel, 2019). The two main processes that shaped Sperry Glacier's foreland include depositional and erosional geomorphic process domains. A depositional process domain occurs when glaciers deposit debris during retreat; an erosional process domain occurs when glaciers shape the landscape through erosion by scraping rocks and other debris across the bedrock (Figure 3). These processes influence the history of how the landscape was shaped and formed. Finally, landform features were recorded for each plot. Landform features recorded for this study include moraines and Roche moutonnée (Figure 4). Plots lacking these features were listed as "Other". Moraines are mostly unconsolidated material (till) deposited at the edge of glaciers as they retreat. Since moraines are made of the material pushed and deposited by the glacier, they typically mark the furthest extent of the glacier before retreating. Roche moutonnée landforms are glacially eroded bedrock forming an asymmetrical hill (Benn & Evans, 2010). Roche moutonnée generally consists of more consolidated material compared to moraines. These features shape the topography of the land, which may provide safe sites for vegetation, making this variable important for this study.

Figure 3: Landscape showing evidence of a glacial depositional process through the deposition of till (left) and a glacial erosional process through deep groves and shallow scratches across the bedrock surface (right). Photos: A. Schulte 2021.

Figure 4: Examples of the terminal glacial moraine (left) and Roche moutonnée (right) on the glacier foreland of Sperry Glacier. Photos: A. Schulte 2021.

4.1.3. Additional Variables Derived from Field Data

To fully assess the characteristics of the vegetation in each plot and how these plant communities change across the foreland, I calculated two additional floristics: Shannon's diversity and species evenness for subsequent statistical analysis. I calculated these variables for each plot using species richness and the species percent cover of each species (Shannon, 1948). Shannon's Diversity Index was used to compare the diversity of vegetation among each plot and terrain age range. This diversity index combines species richness and evenness measures to assess the differences in biological variability over space or time (Ortiz-Burgos, 2016). The following equation was used to calculate Shannon's diversity:

$$\mathrm{H} = \sum_{\mathrm{i}=1}^{\mathrm{s}} \mathrm{p_i} \ln \mathrm{p_i}$$

Where H is the diversity, p_i is the proportion of the total vegetation cover by species (i), and s is the number of species. When calculating Shannon's diversity for terrain age, the percent covers of each species were pooled for each range and p_i was the proportion over the range rather than the proportion over the plot.

Species evenness is a measure of the relative abundance of each species in a community or how evenly the percent cover is distributed among each species (Moore, 2013). I measured species richness within each plot and terrain age range. The following equation was used to calculate species evenness:

$$\mathrm{E} = \mathrm{H} \,/\, \ln \mathrm{S}$$

Where E is the evenness, H is Shannon's diversity, and S is the species richness.

Finally, I calculated species turnover and absolute species turnover for each terrain age range, excluding the youngest range since this is the earliest that species start to appear. Species turnover is a measure of the rate species composition changes across a temporal or spatial gradient. Species turnover was important for determining the rate of change in species composition between terrain age ranges and was found by the equation:

$$Turnover = \frac{(\#appearing\ species + \#disappearing\ species)}{(total\ species\ \#)} * 100$$

Absolute species turnover is the numerator portion of the ratio for calculating turnover. Absolute species turnover gives insight into how much the species composition changes between terrain age range by quantifying how many species either appear or disappear. It was determined using the following equation:

$$Absolute\ Turnover = \ \#appearing\ species + \#disappearing\ species$$

4.2. Data derived from GIS

I considered additional abiotic site and landscape variables, related to the shape and orientation of the landscape, that could influence vegetative growth and successional trends (e.g., Glausen & Tanner, 2019; Perez, 2009; Schumann et al., 2016). Many of these variables were GIS-derived, including a Terrain Roughness Index (TRI), a Topographic Position Index (TPI), flow accumulation, solar radiation, aspect, profile and tangential curvature, and slope angle. The derived variables were derived using ArcGIS Pro or SAGA (ESRI Inc., 2020; Conrad et al., 2015) from a USGS 1/3-arc sec DEM (~10 m) DEMs downloaded for the study region from https://apps.nationalmap.gov/downloader/. Data for each variable was extracted by plot centroid using the projected coordinate system NAD_1983_UTM_Zone_12N.

The spatial resolution of the DEM is coarser than plots but provides valuable information for contextualizing the landscape, and the data represented the finest resolution data available at the time of the study for the study area. The spatial resolution of these variables was 1/3-arc sec, which is about an 8.69 m x 8.69 m area at Sperry Glacier (ESRI Inc., 2020). The plots, however, were only 8 m^2, or about 2.83 m x 2.83 m. Each of these derived variables, therefore, measures the respective trait of the 8.69 m x 8.69 m area in which the plot is located, rather than measuring that same characteristic only within the 8 m^2 plot. For example, the overall landscape may have a negative profile curvature, indicating a more convex surface, though the plot itself may be concave. However, knowing the overall characteristics of the landscape around the plot may still give insight into the plot’s conditions. A wide range of spatial resolutions influences the properties of a plot. For example, both landscape-level topography (Bitsuamlak et al., 2007; Ruel et al., 1998) and microtopography (Jumpponen et al., 1999; Perez, 2009) are known to affect wind exposure. Even if the plot itself is relatively smooth, a rough landscape surrounding the plot may still protect it from the wind. Therefore, these variables, despite having a coarser resolution than the plot size, were still important aspects of the area to include and may shape patterns in species richness, cover, diversity, and evenness.

I derived two of these variables, TRI (an indicator of the average roughness or smoothness of an area) and TPI (relative position of an area compared to the surrounding area), using SAGA. TRI and TPI are related measures, however, they were not significantly correlated in this study, so they were both included. Terrain roughness and exposure have been shown to influence plant colonization in alpine environments through the provision of wind-sheltered safe sites that aid plant establishment and growth (Lambert et al., 2020; Resler et al., 2005). More heterogeneous microclimates, found in areas of higher terrain roughness, also encourage greater species richness in alpine ecosystems (Malanson et al., 2023). Alpine microclimatic conditions, including the relative exposure of a site to light and wind (Williamson et al., 2020), may additionally be influenced by elevation. The topographic position may influence erosion and soil development on a fine scale (Román-Sánchez et al., 2018; Temme et al., 2016).

Factors that impact the flow of water and the accumulation of sediment have previously been important for alpine ecosystem processes. GIS-derived surface flow accumulation, slope, and curvature provide estimates of these influences. Flow accumulation represents the accumulated weight of all cells from the DEM flowing into each downslope cell. It was calculated using the deterministic infinity (D-infinity) method which determines the flow direction at any angle toward the steepest slope, rather than sticking to eight discrete directions (ESRI Inc., 2020). I calculated slope (°), which influences stability (Perez, 2009) and runoff, and thus water availability, (Moreau et al., 2005), using ArcGIS Pro.

Whereas surface roughness is a measure of the overall irregularity of the landscape and slope is a measure of the steepness, curvature is the degree of concavity or convexity for an area. For ecosystems, curvature influences the collection and movement of water, wind, and materials (Jumpponen et al., 1999). Here, I calculated two types of curvature in ArcGIS Pro: profile and tangential curvature. Profile curvature is the curvature parallel to the direction of the maximum slope while tangential curvature is the curvature perpendicular to the direction of the maximum slope. Profile curvature influences how flow accelerates or decelerates down the slope (Buckley, 2010) while tangential curvature influences how flow converges or diverges across an area (Kopp, 2021). Plan curvature is sometimes used instead of tangential curvature and similarly measures the flow convergence or divergence (Buckley, 2010). However, plan curvature is calculated using a horizontal cross-section, parallel to Earth's surface, while tangential curvature is calculated using a vertical cross-section, perpendicular to Earth's surface. For this study, I decided to stick with using profile and tangential curvature. These curvatures together influence the overall concavity or convexity of the landscape.

Just as the flow of material over a particular plot is important to the stability and resource availability in that plot, the flow of water across the landscape gives insight into how water is dispersed across the landscape as it flows from higher to lower elevations. Water flow was important to include since water can sustain, drown, transport, or wash away vegetation. Though too much water suffocates vegetation, a lack of water is just as deadly. The potential for desiccation is especially high in glacier forelands with high exposure to solar radiation (e.g., Erschbamer & Caccianiga, 2016) and wind (Moreau et al., 2005), intensified by the exposed bedrock due to limited safe sites. Desiccation from heat is one of the main threats to plant germination on glacier forelands (Erschbamer & Caccianiga, 2016). It is possible that high albedo from snow and ice may intensify desiccation in some species, though the glacial and snowfield melt also provides a water source that protects plants against drying out (Apple et al., 2022). However, the shrinking of permanent snowfields is increasing the bare ground while decreasing meltwater, resulting in a higher risk of desiccation (Apple et al., 2022)

I derived both solar radiation and slope aspect using the Spatial Analyst toolbox in ArcGIS Pro. Area solar radiation (WH/m^2) in ArcGIS Pro calculates the insolation, or exposure to the sun's radiation, across the landscape based on the DEM. ArcGIS Pro uses algorithms to calculate insolation developed by Rich et al. (1994) and Fu and Rich (2000, 2002). In previous alpine studies, high solar radiation not only caused desiccation (Erschbamer & Caccianiga, 2016; Llambí et al., 2021) but also changed the trajectory and rate of succession (e.g., Glausen & Tanner, 2019). The slope aspect also influences solar radiation and affects vegetation cover and composition (Glausen & Tanner, 2019). The circular nature of the slope aspect (measured in degree) necessitated a sine and cosine transformation to create measures of eastness and northness:

$$Eastness = \sin\left(aspect * \frac{\pi}{180}\right)$$

$$Northness = \cos\left(aspect * \frac{\pi}{180}\right)$$

Where the aspect is in degrees.

Finally, to aid statistical analyses, the glacier margins from USGS (Fagre et al. 2017) and Key et al. (2002) were condensed into five age range categories (1850-1901, 1901-1927, 1927-1959, 1959-1993, and 1993-2023) with similar spans of years and a similar number of plots sampled within each (Table 2 and 3). This combined set of ranges ensured the different terrain age ranges were comparable and enabled subsequent statistical analyses. Each range shows the terrain age, or the length of time the terrain has been exposed after deglaciation since the LIA, which determines how long the ground has been exposed for vegetation to start colonizing in the area. I focused on vegetation patterns along terrain age for the first objective, which gave insight into the overall temporal patterns of succession (Walker et al., 2010).

Table 2: Summary of date ranges of glacial margins, and overall statistics for each terrain age range, including time span in years, number of plots, species richness (SR), Shannon's diversity (SD), species evenness (SE), and both species and absolute turnover represented by each range.

Terrain Age Ranges	Years	# Plot	SR	SD	SE	Species Turnover	Absolute Turnover
1850-1901	51	11	49	3.15	0.81	63.75	51
1901-1927	26	18	59	3.17	0.78	69.44	50
1927-1959	32	7	35	2.88	0.81	73.81	31
1959-1993	34	12	18	2.42	0.84	61.54	16
1993-2022	29	13	18	2.50	0.87	n/a	n/a

Table 3: Summary of average plot values per each terrain age range, including species richness (SR), vegetation cover (VC), Shannon's diversity (SD), and species evenness (SE) per plot with standard deviations.

Terrain Age Ranges	Avg SR ± StDev.	Avg VC ± StDev.	Avg SD ± StDev.	Avg SE ± StDev.
1850-1901	9.91 ± 0.32	22.59 ± 1.57	1.74 ± 0.043	0.80 ± 0.015
1901-1927	7.78 ± 0.28	12.89 ± 0.71	1.53 ± 0.031	0.84 ± 0.008
1927-1959	9.14 ± 0.41	17.14 ± 1.60	1.77 ± 0.041	0.83 ± 0.018
1959-1993	3.67 ± 0.21	2.50 ± 0.19	1.06 ± 0.059	0.94 ± 0.011
1993-2022	3.31 ± 0.28	2.85 ± 0.33	0.86 ± 0.069	0.95 ± 0.012

4.3. Variable Summary

Overall, our field and geospatial efforts resulted in a grand total of three field-collected dependent variables (species richness, percent vegetation cover, and species composition) and 17 independent variables for use in subsequent statistical analyses (Table 1). Among the 17 independent variables, seven (drainage, observed concavity, landform feature, percent fines to sand cover, percent gravel to cobble cover, percent boulder cover, and process domain) were estimated in the field during fieldwork. Ten variables were derived from geospatial data sets (terrain age ranges, northness, eastness, slope steepness, TRI, TPI, flow accumulation, area solar radiation, profile curvature, and tangential curvature).

4.4 Analysis

4.4.1 Objective 1: Analysis Over Terrain Age

The first objective investigated was the relationship between vegetation and terrain age using Kruskal-Wallis H tests, Dunn's Kruskal-Wallis multiple comparison tests, and boxplots with an alpha level of 0.05 for significance. The Kruskal-Wallis test is a non-parametric test to determine if the median value differs among more than two categories. Dunn's test is a nonparametric, pairwise test for non-normal data, such as found in this study. It can be used when more than two groups are being compared, and it helps determine if the response variable differs between the compared groups or comes from the same distribution of values. Species richness, vegetation cover, Shannon's diversity, and species evenness were summarized in the bar graphs and each terrain range was compared using the Kruskal-Wallis and Dunn's multiple comparison tests. I also investigated several aspects of plant composition across terrain age. These aspects include plant growth form, trends of frequently encountered vegetation, a calculation of species turnover, and dispersal mechanisms.

Plant growth form was categorized into seven groups: graminoid (which include Poaceae, Juncaceae, and Cyperaceae), bryophytes (only mosses in this study area), pteridophytes, woody (includes trees, shrubs, and subshrubs), semi-woody (vegetation with some woody parts but not considered trees, shrubs, or subshrubs), lichen, and herbaceous (any non-graminoid flowering herbaceous vegetation). The plants were assigned to each group based on their description in Lesica (2002). The proportion of each group was graphed across the terrain ages and the percent cover of each was compared using a Dunn's test.

The most frequently found species, families, and some general categories were also compared using a Dunn’s test across terrain age ranges to determine if the composition changes significantly across terrain age. This comparison occurred with increasing ranking, first at the species level (excluding all cover that could not be identified down to species), followed by family level (excluding bryophytes and lichen which were not identified down to family level), and followed by bryophytes and lichen since they were excluded from the previous comparisons.

Finally, I classified plants according to dispersal mechanisms to determine if the plant composition of any terrain ages was partially determined by the dispersal mechanisms of the plants. Distribution mechanisms play a large part in determining the composition of an ecosystem (e.g., Malanson, 1982; Malanson & Kay, 1980). Different dispersal mechanisms influence a plant's ability to spread its seed greater distances (Nathan & Muller-Landau, 2000). Since younger terrain tends to be further from any potential source of seeds (Johnson & Miyanishi, 2008), plants that can disperse to the older terrain may not be able to reach the younger terrain (McClanahan, 1986). Likewise, since different dispersal methods vary in dispersal distance, some dispersal methods may not be able to reach all areas of the foreland. By looking at dispersal mechanisms, I sought to determine if the plant composition was partially determined by the dispersal mechanism. Dispersal mechanism, a fundamental ecosystem process preceding plant establishment, was determined by examining published research or by observing the fruit and seed structures of the plants. Dispersal mechanisms may influence what species can arrive at a location and are thus of interest here. The four dispersal mechanisms recorded in this study were gravity, water, animals, and wind. I compared the proportion of vegetative cover adapted to engage in each mechanism across terrain ages using a Kruskal-Wallis test, Dunn's test, and bar graph.

4.4.2. Objective 2: Analysis Over Site Conditions

The second objective I investigated was the relationship between vegetation and site conditions. I used two models, General Linear Models (GLMs) and Classification and Regression Trees (CARTs), performed in R Studio version 4.2.1 (R Core Team, 2021) to assess if site conditions influenced patterns in species richness, vegetation cover, Shannon's diversity, or species evenness and which site characteristics were most influential. The site conditions used as predictor variables for these assessments included terrain age ranges, TRI, TPI, flow accumulation, area solar radiation, aspect, profile and tangential curvature, and slope. GLMs are statistical models that create linear models for a response variable with multiple explanatory variables. These explanatory variables can be continuous or categorical and do not need to be normally distributed (Atkinson et al., 1998). However, GLMs assume that the response variable is continuous, all data and errors are independent, the response variable has a linear relationship with the combination of the explanatory variables after they have been transformed, the residuals are normally distributed, and the variance of the residuals is constant. CARTs are machine-learning, statistical algorithms that create decision trees (Loh, 2011). These decision trees split the predictor variables, forming forks that lead to predicted values for the response variables. CARTs are nonparametric and can work with both categorical and continuous variables (Phelps & Merkle, 2008). CARTs can be used even when linear regressions are not appropriate since CART analysis does not assume a specific relationship between the variables. However, CARTs tend to overfit the data, so the number of splits in the tree should be limited to avoid overfitting (Lewis, 2000). The GLMs are useful for identifying which explanatory variables best explain the response variable while CARTs are useful for creating trees that best predict response variable outcomes using the explanatory variables (Resler et al., 2014).

The GLMs were manually selected using backward stepwise selection. Variables were removed one at a time based on their significance in contributing to the model. I generated numerous candidate models and compared several criteria including AIC, BIC, residual deviance, and which model was most parsimonious. The model with the lowest AIC, BIC, and residual deviance was selected as the final model. If two models had similar AIC, BIC, and residual deviance, I selected the model with the fewest variables. If the null model was best, the response variable was determined to not be explained by a GLM in this study. Furthermore, the family used for the GLM depended on the response variable. Species richness used a Poisson family since species richness had a non-parametric distribution. Vegetation cover was transformed into a proportion rather than a percent. This vegetation proportion and species evenness uses a binomial family since their values were between 0 and 1. Shannon's diversity had a relatively normal distribution, so a Gaussian family was used.

Once I selected the best model for each response variable, I ran the Kruskal-Wallis test followed by either a Dunn’s test or Mann-Whitney U test in R Studio to assess any relationships between each explanatory variable and the response variable in the model. A Dunn’s test is a nonparametric pairwise multiple comparison test for explanatory variables with more than two categories, while a Mann-Whitney U test is a nonparametric test for explanatory variables with only two categories (Dinno, 2015; McKnight & Najab, 2010). Both these tests are for continuous response variables and categorical explanatory variables. While the GLM shows which variables best explain the response variable the Dunn’s and Mann-Whitney U tests show the relationships between the explanatory and response variables.

In the CART models, 80% of the points were used to train the data while 20% were used to test the model, resulting in 50 random plots training the data, and the remaining 11 reserved for validation. Since a different tree was formed each time I ran the CART, I bagged the trees using 200 bootstrap replications and a cross-validation method with five folds. This bagging method ranks each explanatory variable in order of importance in the tree models. The importance of variables within one tree is determined by how well the explanatory variable splits the data to improve the prediction of the response variable. The improvement score is calculated by the quality, or accuracy, of a split and by the percentage of data that passes through the split. Therefore, variable splits that have greater accuracy in predicting the response variable and variables listed earlier in the tree are considered more important. The importance value is rescaled to be between 0 and 100, with 100 being the best and 0 being the worst. For the bagged data, the importance of the variables for each of the trees was summarized and rescaled to fit between 0 and 100. This final score is the importance score used in this study.

The relationships between the most important variables for predicting each response variable according to the bagged CART models were investigated by observing multiple possible trees and by scatter plots with regression trend lines. Each time a CART was created in R, a different tree was produced depending on which plots were used as training data and which plots were used as test data. Even though the trees changed, certain patterns could be determined by running multiple trees and observing how the trees divided the variables to predict a higher or lower response variable. I also used scatterplots with regression trend lines run in JMP to observe the overall relationship between each important predictor variable and each response variable.

Chapter 5: Results

Among the 61 total plots, I found 93 species, 62 of which I identified down to species. I also found 25 families and 46 genera, 23 and 40 of which were identified down to family and genera respectively (Table 4). The species that were not identified down to the species level included three grasses, two sedges, one rush, one moss, 10 lichen, and 14 non-graminoid, herbaceous plants. All plant species found at Sperry Glacier's foreland were native to Glacier National Park. Three (*Suksdorfiea violaceae, Phacelia lyallii, and Penstemon ellipticus*) were endemic to the Northern Rocky Mountains. Three species have their status under review (*Silene uralensis, Saxifraga rivularis, and Woodsia oregana*), meaning they may be at risk, but more data is required to make an accurate assessment (Table 5) (https://fieldguide.mt.gov/).

All species with cover < 1% were estimated as 0.5% since a precise percent cover could not be visually estimated under 1%. Since many species' coverages were well under 0.5%, vegetation cover may be slightly overestimated in some plots. I assumed similar-looking unidentified species were the same when calculating the species richness count and assumed the total number of grasses, rushes, and sedges were no greater than the maximum number found in one plot since they were not identified down to species. This method resulted in a more conservative estimation of species richness and, therefore, may slightly have underestimated species richness.

Table 4: List of all species observed, number of associated plots, and average % cover, by species, within each terrain age range.

Taxa	**# Plots**	**Avg Precent Vegetation Cover**					
		1850-1901	1901-1927	1927-1959	1959-1993	1993-2022	Total
Asteraceae:							
Antennaria alpina	1	0	0	0.36	0	0	0.04

Antennaria media	5	0.05	0.11	0.14	0	0	0.06
Antennaria sp.	1	0.05	0	0	0	0	0.01
Arnica cordifolia	7	0.55	0.22	0.07	0	0	0.17
Arnica latifolia	9	0.41	0.58	0.07	0	0	0.25
Arnica mollis	4	0.09	0.06	0	0.04	0	0.04
Arnica sp.	1	0.05	0	0	0	0	0.01
Crepis nana	1	0	0	0	0	0.19	0.04
Erigeron compositus	7	0.18	0.03	0.21	0	0	0.07
Erigeron nivalis	2	0.05	0	0.07	0	0	0.02
Erigeron peregrinus	3	0	0.06	0.07	0	0	0.02
Packera cymbalaria	2	0	0.06	0	0	0	0.02
Packera subnuda	1	0	0.03	0	0	0	0.01
Senecio fremontii	18	0.09	0.25	0.5	0.21	0.15	0.22
Senecio triangularis	1	1.36	0	0	0	0	0.25
Solidago multiradiata	4	0.27	0	0.14	0.04	0	0.07
Taraxacum ceratophorum	1	0.05	0	0	0	0	0.01
Taraxacum sp.	3	0.05	0.03	0.07	0	0	0.02
Unknown Asteraceae sp.	2	0.05	0.03	0	0	0	0.02
Boragenaceae:							
Phacelia hastata	3	0.09	0.06	0	0	0	0.03
Phacelia lyallii	2	0.05	0	0.07	0	0	0.02
Phacelia sericea	1	0.05	0	0	0	0	0.01
Myosotis asiatica	1	0	0.03	0	0	0	0.01
Brassicaceae:							
Arabis nuttallii	1	0	0.03	0	0	0	0.01
Boechera lemmonii	7	0	0.03	0.36	0.04	0.04	0.07
Boechera lyallii	3	0	0.06	0	0.04	0	0.02
Boechera sp.	1	0	0	0	0.04	0	0.01
Draba lonchocarpa	3	0.05	0	0.07	0	0.04	0.02
Draba praealta	1	0.05	0	0	0	0	0.01
Draba sp.	1	0	0.03	0	0	0	0.01
Unknown Brassicaceae sp.	1	0	0.03	0	0	0	0.01
Caryophyllaceae:							
Cerastium beeringianum	5	0	0	0.36	0	0.08	0.06
Sagina saginoides	2	0	0.06	0	0	0	0.02
Silene acaulis	4	0	0.08	0.5	0	0.04	0.09
Silene uralensis	2	0	0	0	0.04	0.04	0.02
Minuartia rubella	3	0	0	0.14	0	0.04	0.02
Crassulaceae:							
Sedum lanceolatum	2	0	0.06	0	0	0	0.02
Cyperaceae:	21	0.41	0.89	1.86	0.17	0.08	0.60
Dryopteridaceae:							
Polystichum lonchitis	3	0.05	0.06	0	0	0	0.02
Ericaceae:							
Phyllodoce empetriformis	1	0	0.17	0	0	0	0.05
Juncaceae:	4	0.64	0.81	0	0	0	0.35

Onagraceae:							
Epilobium anagallidifolium	14	0.05	0.11	0.07	0.17	0.23	0.13
Epilobium clavatum	2	0	0.06	0	0	0	0.02
Ophioglossaceae:							
Botrychium lunaria	1	0	0	0.07	0	0	0.01
Orobanchaceae:							
Castilleja miniata	6	0.27	0.17	0	0	0	0.10
Castilleja occidentalis	1	0	0	0.07	0	0	0.01
Castilleja rhexiifolia	1	0	0.03	0	0	0	0.01
Castelleja sp.	1	0	0.03	0	0	0	0.01
Pinaceae:							
Abies lasiocarpa	4	2.09	0.61	0	0	0	0.56
Picea engelmannii	1	0	0	0.21	0	0	0.02
Plantaginaceae:							
Penstemon davidsonii	1	0.05	0	0	0	0	0.01
Penstemon ellipticus	16	2.14	1.11	0.36	0.04	0	0.76
Veronica wormskjoldii	1	0	0.06	0	0	0	0.02
Poaceae:	39	4.46	2	4.07	0.33	1.23	2.19
Polygonaceae:							
Eriogonum ovalifolium	1	0	0.03	0	0	0	0.01
Oxyria digyna	21	0.32	0.22	0.29	0.17	0.19	0.23
Pteridaceae:							
Cryptogramma acrostichoides	1	0	0.03	0	0	0	0.01
Ranunculaceae:							
Anemone multifida var. tetonensis	2	0	0.03	0.07	0	0	0.02
Anemone sp.	1	0.05	0	0	0	0	0.01
Ranunculus sp.	1	0.05	0	0	0	0	0.01
Rosaceae:							
Dryas drummondii	1	0	0	0.36	0	0	0.04
Dryas octapetala	4	0.46	0.72	2.86	0	0	0.62
Sibbaldia procumbens	1	0	0.11	0	0	0	0.03
Salicaceae:							
Salix arctica	3	0	0.03	0.36	0	0.04	0.06
Salix drummondiana	3	0	0.11	0.21	0.33	0	0.12
Salix nivalis	1	0	0.03	0	0	0	0.01
Salix vestita	1	0	0.17	0	0	0	0.05
Saxifragaceae:							
Micranthes occidentalis	1	0	0	0.07	0	0	0.01
Saxifraga bronchialis	11	1.77	0.14	1.64	0	0.04	0.56
Saxifraga caespitosa	1	0	0	0	0.04	0	0.01
Saxifraga rivularis	6	0.27	0.03	0	0.04	0.08	0.08
Suksdorfia violacea	1	0.05	0	0	0	0	0.01
Valerianaceae:							

Valeriana occidentalis	1	0	0.03	0	0	0	0.01
Woodsiaceae:							
Cystopteris fragilis	3	0.05	0.08	0	0	0	0.03
Woodsia oregana	1	0	0.03	0	0	0	0.01
Other:							
Lichen	17	5.23	1.17	0.07	0	0	1.30
Moss	34	0.64	1.36	1.29	0.71	0.31	0.87
Unknown	6	0.05	0.14	0	0.04	0	0.06
Dead	3	0	0.47	0	0	0.04	0.15

Table 5: Floristic synopsis of the families, genera, and species found in the study, including the number of plots and average vegetation cover (VC) found for the dominant species. The average VC is the actual average cover per plot observed in this study. The standard deviation with the average VC shows the likely range of the vegetation across the entire foreland.

Floristic Synopsis		
Families:	25	
Genera:	46	
Species:	93	
Identified to species:	62	
Native:	62	
Status Under Review:	3	
Endemic:	3	
Dominant Families	**# of Plots**	**Avg. VC**
Poaceae:	39	2.19 ± 4.76
Asteraceae:	36	1.34 ± 3.02
Polygonaceae:	22	0.24 ± 0.39
Cyperaceae:	21	0.60 ± 1.58
Plantaginaceae:	18	0.79 ± 2.40
Saxifragaceae:	18	0.66 ± 2.35
Pinaceae:	5	0. 58 ± 2.86
Rosaceae:	4	0.70 ± 3.30
Prevalent Species	**# of Plots**	**Avg. VC**
Oxyria digyna:	21	0.23 ± 0.39
Senecio fremontii:	18	0.22 ± 0.49
Penstemon ellipticus:	16	0.76 ± 2.41
Epilobium anagallidifolium:	14	0.13 ± 0.27
Saxifraga bronchialis:	11	0.56 ± 2.31
Arnica latifolia:	9	0.25 ± 0.82
Dryas octapetala:	4	0.62 ± 3.02
Abies lasiocarpa:	4	0.56 ± 2.86
Other	**# of Plots**	**Avg. VC**
Moss:	34	0.87 ± 1.79

Lichen:	17	1.30 ± 5.03

5.1. Objective 1: Vegetative Trends Across Terrain Age Using Dunn’s Tests and Box Plots

Overall, species richness is greater on older terrain age ranges at the Sperry Glacier foreland (Figure 5). The results of the species richness differed significantly among the terrain age categorical ranges ($H(4) = 22.19$, $p < 0.001$). The Dunn’s multiple comparison test and box plots revealed that species richness in the two most recent date ranges (1959-1993 and 1993-2022) is significantly less than it is within the 1850-1901 ($p = 0.0048$ and 0.0033, respectively) and 1927-1959 date ranges ($p = 0.03$ and 0.026, respectively) (Figure 5). A total of 48 species were observed in the 1850-1901 terrain age range, 59 in 1901-1927, 36 in 1927-1959, 18 in 1959-1993, and 19 in 1993-2022 (Table 2).

The mean percent vegetation per plot was 10.9%. The Kruskal-Wallis test revealed that vegetation cover differed significantly across the terrain age ranges ($H(4) = 24.78$, $p < 0.0001$). Post hoc comparisons revealed vegetation cover in the two most recent age categories (1959-1993 and 1993-2022) to be less than 1850-1901 ($p = 0.0033$ and 0.0013, respectively), 1901-1927 ($p = 0.054$ and 0.027, respectively), and 1927-1959 ($p = 0.030$ and 0.017, respectively) date ranges (Figure 5). According to the Kruskal-Wallis test, both Shannon’s diversity ($H(4) = 11.18$, $p = 0.025$) and species evenness ($H(4) = 20.15$, $p < 0.001$) differed across the terrain age range, yet there were no significant pairwise comparisons. The average Shannon’s diversity per plot was 1.36 ±0.72 SD and the average species evenness per plot was 0.86 ± 0.14 SD (Table 3).

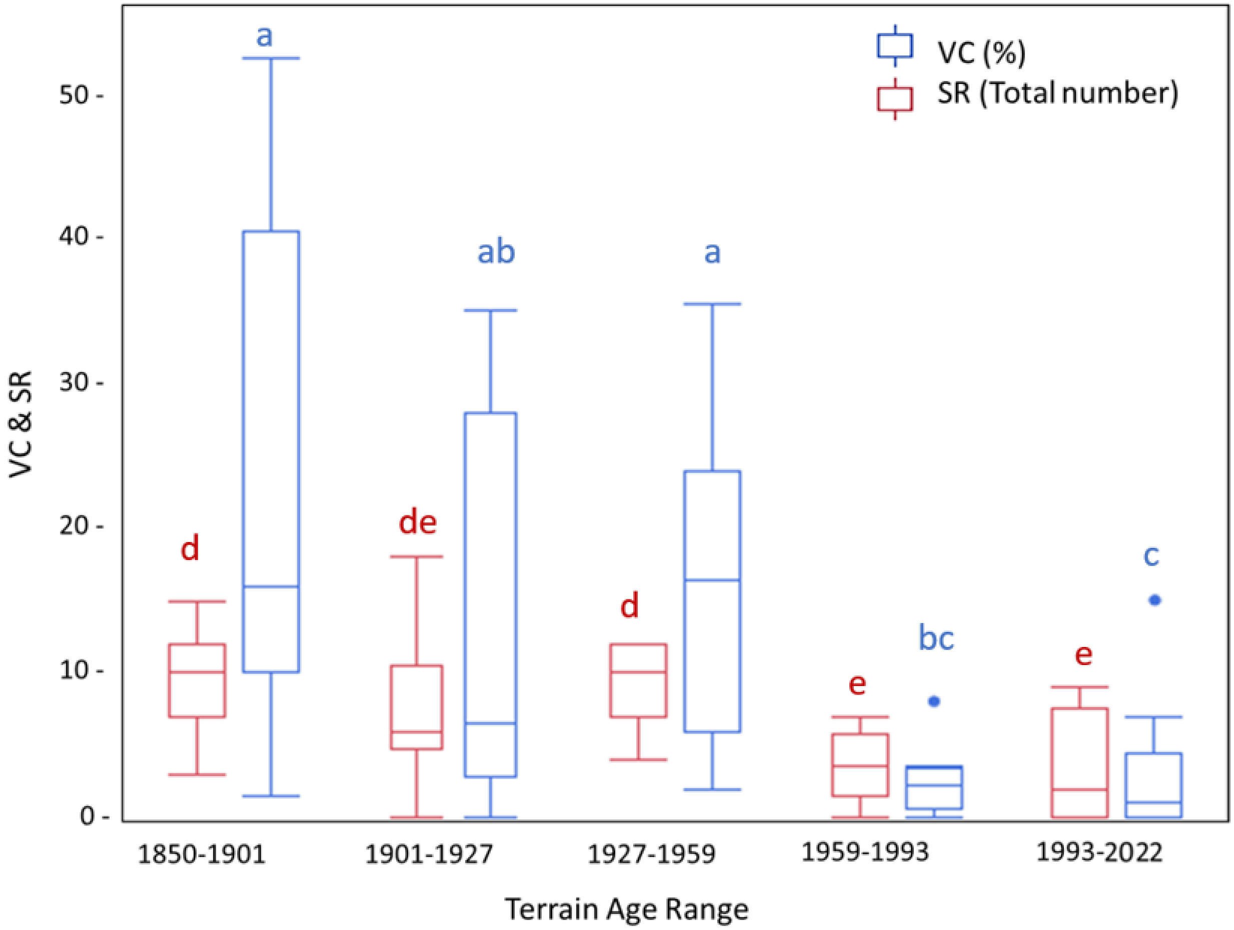

Figure 5: Box plots depicting the distribution of vegetation cover and species richness within terrain age ranges. The letters depict post hoc test groups with ranges sharing a letter if not significantly different.

Kruskal-Wallis tests also revealed significant differences among age range categories in median cover of lichen ($H(4) = 21.17$, $p < 0.001$);, herbaceous ($H(4) = 16.72$, $p = 0.0022$), graminoid ($H(4) = 12.95$, $p = 0.012$), and woody vegetation ($H(4) = 12.10$, $p = 0.017$) changed between different terrain age ranges while bryophytes ($H(4) = 2.49$, $p = 0.65$), pteridophytes ($H(4) = 4.61$, $p = 0.33$), and semi-woody ($H(4) = 7.71$ $p = 0.10$) vegetation did not significantly differ among age range categories. Through Dunn's test post hoc comparisons, I found that lichen and herbaceous cover in the 1850-1901 range was greater than in 1959-1993 ($p = 0.0089$ and 0.020, respectively) and 1993-2022 ($p = 0.0079$ and 0.020, respectively; Figure 6). Lichen cover in 1901-1927 was greater than vegetation cover in 1959-1993 and 1993-2022 (p = 0.020 and 0.018, respectively). Shannon's diversity and species evenness, however, had no significant difference between terrain ages. I found mild support that graminoid and herbaceous cover in 1927-1959 was greater than in the most recent age ranges of 1959-1993 (p = 0.047 and 0.058, respectively) and 1993-2022 (p = 0.079 and 0.063, respectively) with the p-values being significant at a 0.1 alpha level. Woody vegetation cover in the 1850-1901 range was greater than woody vegetation cover from 1993-2022 (p = 0.021). Within the woody vegetation, trees (*Abies lasiocarpa* and *Picea engelmannii*) were found within 5 plots in age ranges between 1850 and 1959, shrubs (*Salix drummondiana* and *Salix vestia*) were found within 3 plots in age ranges between 1901-1993, and subshrubs were found in plots across the entire age range. Lichen and pteridophytes were only found in the three oldest terrain ranges. However, pteridophytes were found in a small enough quantity that their presence in the older terrain rangers was not significantly different from their absence in the younger terrain ranges (Figure 6).

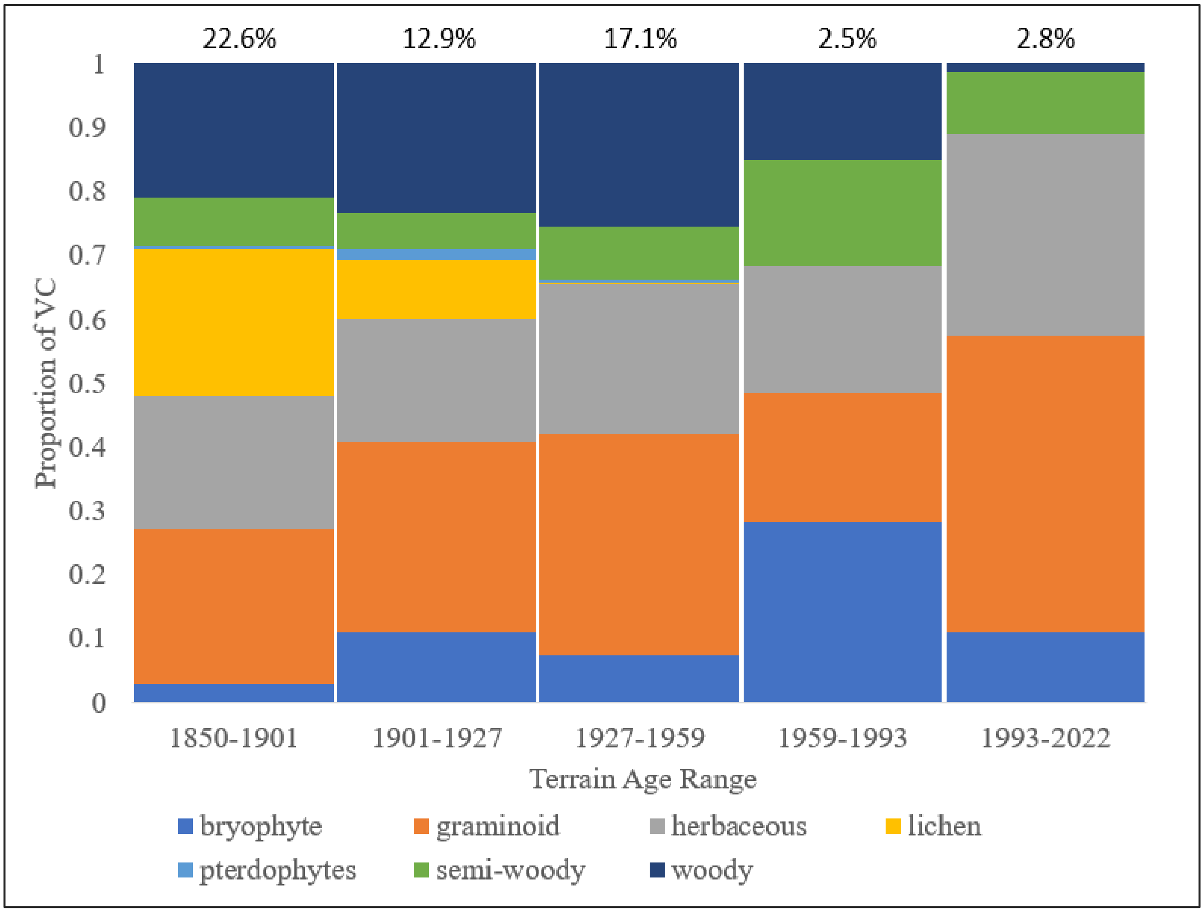

Figure 6: The proportion of cover by each vegetation and lichen group within each terrain age range. The overall % vegetation cover for each age range is listed at the top of each column.

The most frequently encountered plant families (listed from greatest to least) included Poaceae, Asteraceae, Polygonaceae, Cyperaceae, Saxifragaceae, and Plantaginaceae. *Oxyria digyna, Senecio fremontii, Penstemon ellipticus, Epilobium anagallidifolium, Saxifraga bronchialis, and Arnica latifilia* were the most frequently encountered species (listed from greatest to least) on the foreland (Table 5). Similarly, Poaceae, Asteraceae, Plantaginaceae, Rosaceae, Saxifragaceae, Cyperaceae, and Pinaceae were the families that contribute to the most vegetation coverage (listed from the greatest to least percent cover). Two species contributed to the Pinaceae family: *Abies lasiocarpa* and *Picea engelmannii*. *Abies lasiocarpa* was found in four plots, all located within terrain exposed between 1850 and 1927, and *Picea engelmannii* was found in one plot in the terrain age range 1927-1959. These families covered over 0.5% of the entire landscape and contributed to over 5% of the total vegetation cover. *Penstemon ellipticus*, *Dryas octapetala, Saxifraga bronchialis, and Abies lasiocarpa* were the species that contributed most to vegetation coverage (listed from the greatest to least cover) (Table 5). These species also covered over 0.5% of the entire landscape and contributed to over 5% of the total vegetation cover.

Using the Kruskal-Wallis test, our study found that the median cover differed across the landscape in the Poaceae ($H(4) = 9.93$, $p = 0.042$), Cyperaceae ($H(4) = 10.32$, $p = 0.035$), Asteraceae ($H(4) = 13.50$, $p = 0.0091$), and Plantaginaceae ($H(4) = 16.90$, $p = 0.0020$) families. Post-hoc comparisons indicate that Poaceae and Cyperaceae vegetation cover is higher in the 1927-1959 range than in the younger 1959-1993 range ($p = 0.053$ and 0.027, respectively). Asteraceae appeared to primarily grow on the oldest terrain over the youngest terrain ($p = 0.023$) while Plantaginaceae primarily grew on the oldest terrain over the two youngest terrain ranges of 1959-1993 and 1993-2022 ($p = 0.015$ and 0.0038, respectively). Of the dominant species, only the median cover of *Penstemon ellipticus* ($H(4) = 13.72$, $p = 0.0082$) and *Boechera lemmonii* ($H(4) = 16.89$, $p = 0.0020$) differed significantly across the terrain ages. Significantly greater cover of *Penstemon ellipticus* occurred within the 1850-1901 age range compared to the 1959-1993 and 1993-2022 ranges ($p = 0.045$ and 0.012, respectively), and greater cover of *Boechera lemmonii* occurred within the 1927-1959 age range over the younger terrain ranges of 1959-1993 and 1993-2022 ($p = 0.0082$ and 0.0068, respectively; Figure 7).

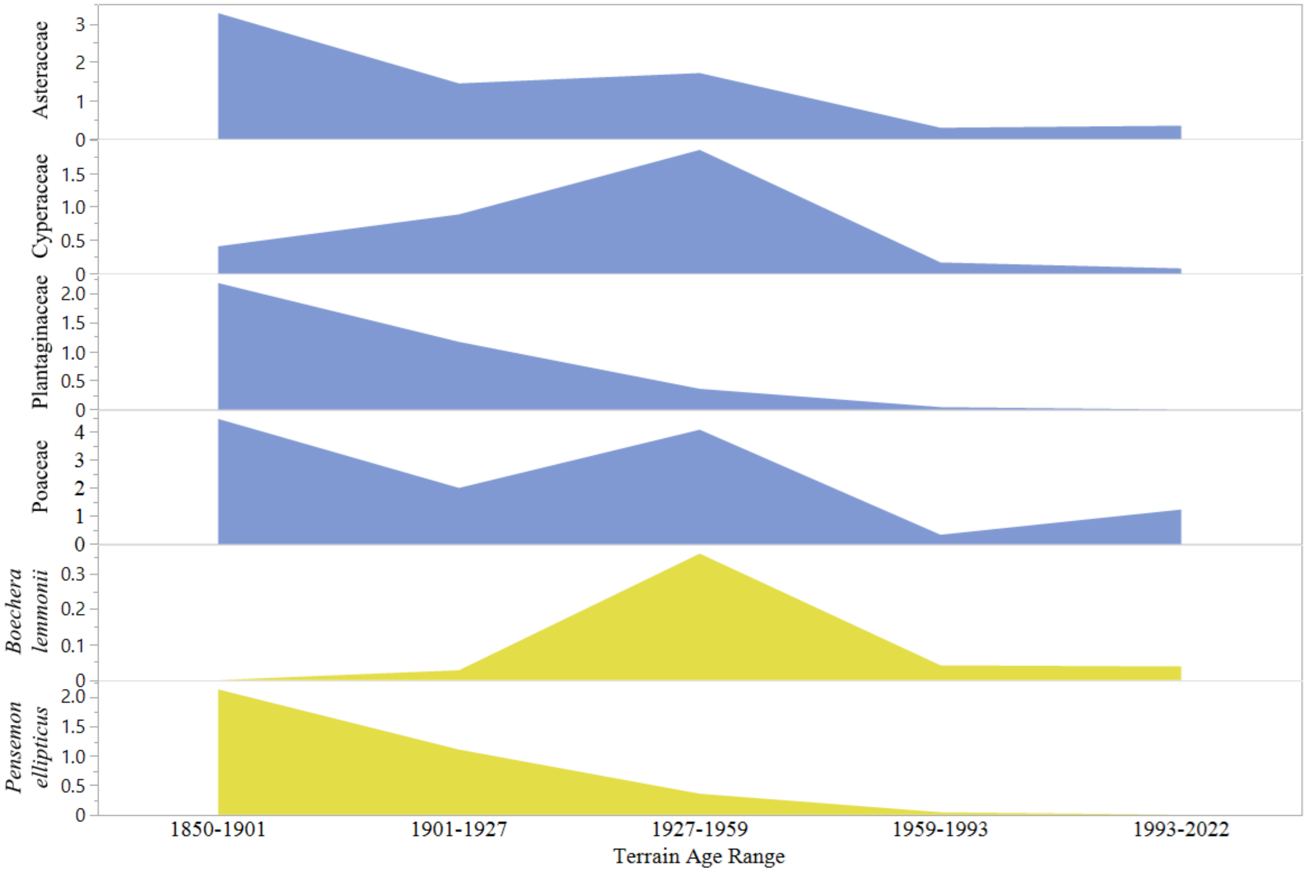

Figure 7: Average percent cover of the families Asteraceae, Cyperaceae, Plantaginaceae, and Poaceae (blue), and of the species *Boechera lemmonii* and *Penstemon ellipticus* (yellow) across the terrain age range. Of the dominant families and species found across the foreland, these four families and two species were the only ones that showed a significant change in vegetation cover between at least two terrain age ranges.

As determined by the percent of the species composition that changed across the different terrain age ranges, species turnover remains relatively consistent between all terrain age ranges. The total species between two age ranges increases as the terrain gets older. Additionally, the number of new species appearing or established species disappearing also increases with terrain age (Table 2). The average species turnover score is 67.14 ± 5.56 SD. However, the absolute species turnover, as determined by the quantity of appearing or disappearing species, increased between each terrain age range from a value of 16 to 51 (Table 2).

Plants found at Sperry Glacier foreland are dispersed by gravity, water, animals, and wind. Each of these mechanisms is represented by plants in age ranges, however, the majority of seeds, specifically 81.5%, were able to be dispersed by wind. The next most common dispersal mechanism was gravity, with 22.2% of plant coverage commonly gravity dispersed. Animal dispersal was less common, with only 9.2% of plant coverage commonly dispersed by animals. Finally, only eight percent of the plant coverage can be dispersed through water. No plants found in the foreland are solely dependent on animals or water. Additionally, the proportion of different dispersal mechanisms remains relatively similar across all terrain ages (Figure 8).

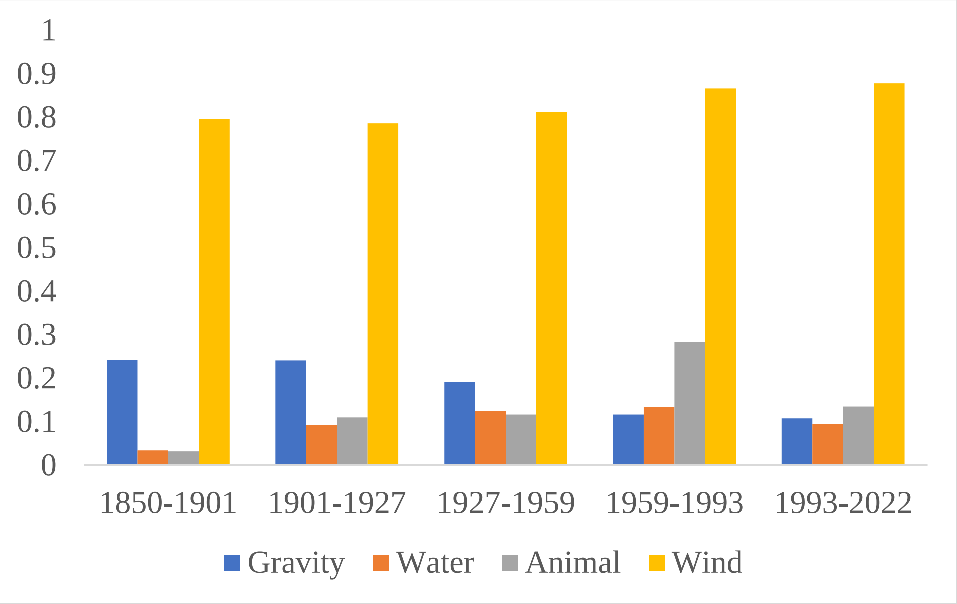

Figure 8: The proportion of vegetation cover with dispersal mechanisms suitable for four different dispersal strategies graphed across terrain age.

The second objective focused on vegetation trends (species richness, vegetation cover, Shannon's diversity, and species evenness) across site conditions. However, this next objective is not completely separated from the first objective since some site conditions vary across terrain age. Older terrain, for example, primarily consisted of the terminal moraine, though lateral moraines reached into younger terrain plots. Out of all the plots with a moraine land feature, 83% occurred on terrain age exposed between 1850 and 1927. Eight moraine plots occurred in the 1850-1901 range (73% of all 1850-1901 plots) and 7 moraine plots occurred in the 1901-1927 range (39% of all 1901-1927 plots). All these older moraine plots resulted from a depositional process domain and were moderately drained. Since the majority of the 1850-1901 range consisted of moraine plots, the number of depositional and moderately drained plots was also increased with 82% of the plots formed through a depositional process domain and 82% moderately drained. A Kruskal-Wallis test revealed that flow accumulation also significantly changed across terrain age ($H(4) = 24.48$, $p < 0.0001$) with a greater flow accumulation in the two youngest ranges compared to all other terrain age ranges ($p < 0.05$ for all). Other site conditions, such as observed concavity, surface fragment coverage, TPI, and TRI, did not significantly change across terrain age.

5.2. Objective 2: Vegetative Trends Across Site Conditions Using GLMs and CARTs

Multiple candidate GLMs were run using the species richness, vegetation cover, Shannon’s diversity, and species evenness of each plot as response variables, and a suite of field-collected and GIS-derived site variables as predictors. The final models showed significant site conditions that explained species richness and Shannon’s diversity. However, the null models were best for explaining vegetation cover and species evenness, meaning that none of the site characteristics improved the GLM’s ability to explain the variation in vegetation cover and species evenness.

Species richness was best explained by drainage, terrain age, observed concavity, and process domain. This model has an AIC of 316.49, BIC of 338, and residual deviance of 100.95

compared to the null model's AIC of 429.86, BIC of 432, and residual deviance of 232.32 (Table 6). The Kruskal-Wallis test supports this model's conclusion since species richness differed across the categories within drainage ($H(1) = 22.38$, $p < 0.00001$), terrain age ($H(4) = 22.19$, $p < 0.001$), observed concavity ($H(3) = 8.12$, $p = 0.044$), and process domain ($H(1) = 16.82$, $p < 0.001$). Dunn's test assessed the relationship between observed concavity and species richness, revealing that concave plots had greater species richness than convex plots ($p = 0.026$). Mann Whitney U tests were used to assess the relationships for drainage and process domain categories. Study sites with moderate drainage plots had greater species richness than poor drainage plots ($p < 0.001$). Species richness was greater in depositional plots ($p < 0.001$; Figure 9).

Table 6: The GLM null and best model for species richness including values used to compare the models. The estimate and significance value of each variable was included for the best model.

	Equation	**AIC**	**BIC**	**Degrees of Freedom**	**Res. Dev.**
Best Model:	Formula = SR ~ Drainage + Terrain Age + Observed Concavity + Process Domain	316.49	338	51	100.95
Null Model:	Formula = SR ~ 1	429.86	432	60	232.32

	Intercept	**Erosional**	**Poor Drainage**	**Convex**	**Straight**	**Undulating**	**1850-1901**	**1901-1927**	**1927-1959**	**1959-1993**
Estimate	2.01	-0.47	-0.37	-0.66	-0.32	-0.32	0.71	0.76	0.82	0.22
Std. Error	0.19	0.17	0.16	0.17	0.14	0.14	0.19	0.18	0.20	0.22
Pr(>|z|)	< 2e-16	0.0049	0.022	0.00012	0.026	0.021	0.00025	2.4e-05	5.7e-05	0.32

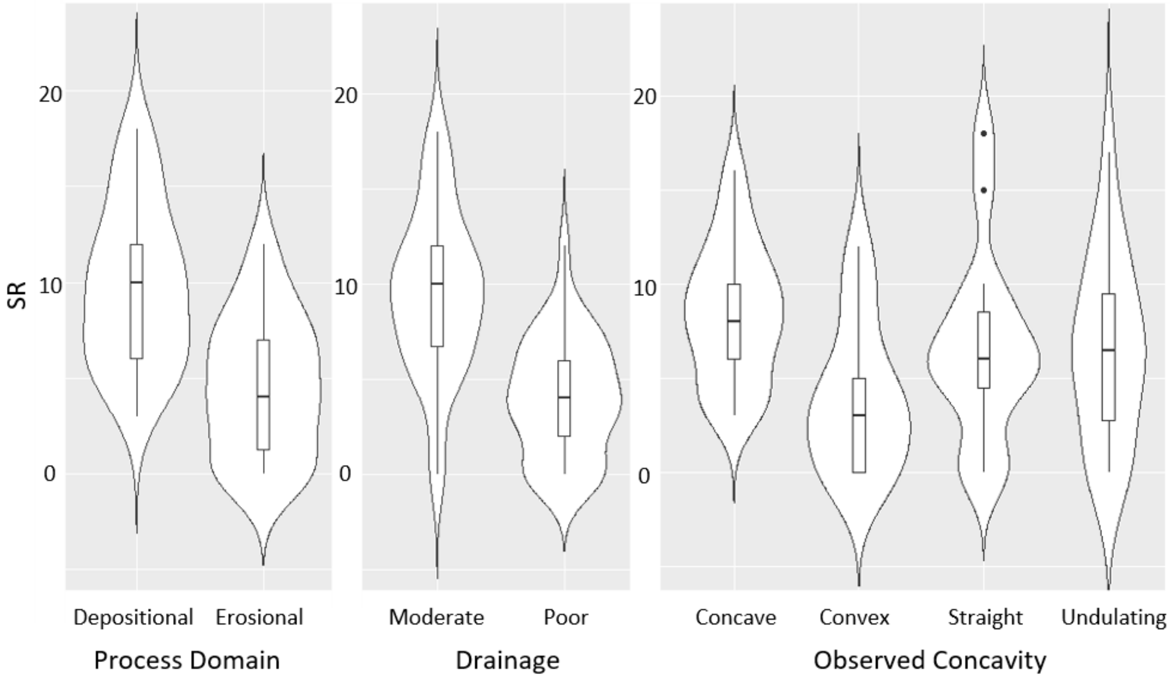

Figure 9: Violin plots showing the differences in species richness (SR) for each variable included in the best GLM model, chosen based on a lower AIC, BIC, and residual deviance.

Shannon's diversity was best explained using drainage and observed concavity. The final GLM had an AIC of 41.103, BIC of 52.7, and residual deviance of 46 compared to the null model's AIC of 58.055, BIC of 61.9, and residual deviance of 50 (Table 7). The Kruskal-Wallis test supports this model's conclusion since Shannon's diversity differed significantly across the categories within drainage ($H(1) = 12.03$, $p < 0.001$) and observed concavity ($H(3) = 14.70$, $p = 0.0021$). Dunn's multiple comparisons test gives strong evidence that concave plots have greater diversity than convex plots ($p < 0.001$) and mild evidence that straight (i.e., no curvature) plots have greater diversity than convex plots ($p = 0.053$). Mann Whitney U tests were used for drainage. Moderate drainage plots had greater diversity than poor drainage plots ($p < 0.001$, Figure 10).

Table 7: GLM null and the best model for Shannon's diversity including values used to compare the models. The estimate and significance value of each variable was included for the best model.

	Equation	**AIC**	**BIC**	**Degrees of Freedom**	**Res. Dev.**
Best Model:	Formula = SD ~ Drainage + Observed Concavity	41.10	52.7	46	5.28
Null Model:	Formula = SD ~ 1	58.06	61.9	50	8.62

	Intercept	**Poor Drainage**	**Convex**	**Straight**	**Undulating**
Estimate	1.92	-0.36	-0.44	0.04	-0.19
Std. Error	0.09	0.10	0.14	0.13	0.12
Pr(>|z|)	< 2e-16	0.00043	0.0028	0.77	0.13

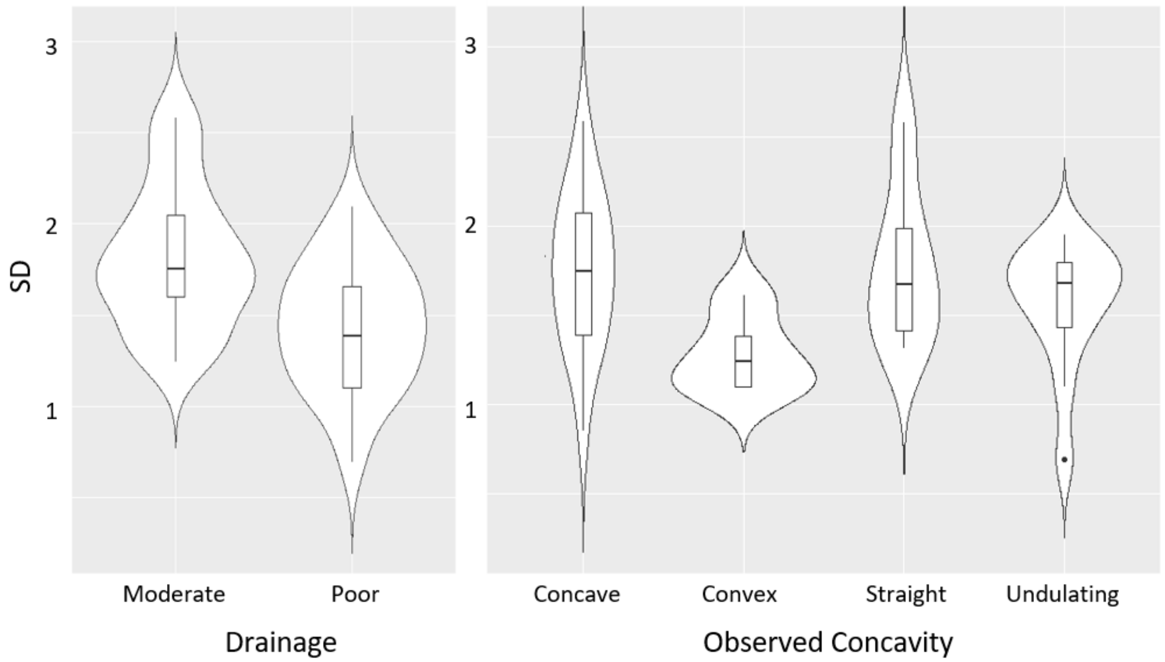

Figure 10: Violin plots showing the differences in Shannon's diversity (SD) for each important variable in the best GLM model.

Bagged CARTs determined which variables are important for predicting species richness, vegetation cover, Shannon's diversity, and species evenness. I used CART models in addition to GLM for their predictive capacities and also for comparative purposes (e.g., Resler et al., 2014).

I thought a comparison would be worthwhile since the CART does not assume any sort of relationship with the variables whereas the GLM assumes that some function of the combined explanatory variables will have a linear relationship with the response variables (Atkinson et al., 1998; Lewis, 2000). Therefore, using CART provides a second way of assessing the data and finding trends.

Results indicated that percent cover of surface fragment size (‘gravel to cobbles’ size category), TPI, and flow accumulation were ranked as the top three important predictors for both species richness and vegetation cover. Variable importance was determined by the calculated influence each variable had on accurately sorting and predicting the species richness and vegetation cover in the bagged CARTs. After these top three ranking variables, the importance of predicting variables for species richness and vegetation cover diverges. For example, the next important factor for predicting vegetation cover is the percent cover of surface fragments sized from fines to sand followed by area solar radiation. For species richness, the next important factor is area solar radiation followed by eastness (Figure 11). Greater gravel to cobble sized surface cover and lower flow accumulation predict a greater species richness and vegetation cover. However, TPI does not show a strong relationship with species richness or vegetation cover. Though when visually observing several trees, lower TPI tends to predict higher vegetation cover and species richness lower in the trees. Similarly, eastness does not appear to relate to species richness in a regression plot, however, greater eastness predicts higher species richness. Area solar radiation does not have a clear relationship with either vegetation trend across the foreland in both the regression plots and the CART models. Different trees showed different relationships between vegetation and solar radiation (Figure 12). The cover of surface fragments sized from fines to sand appeared to predict higher vegetation cover and species richness.

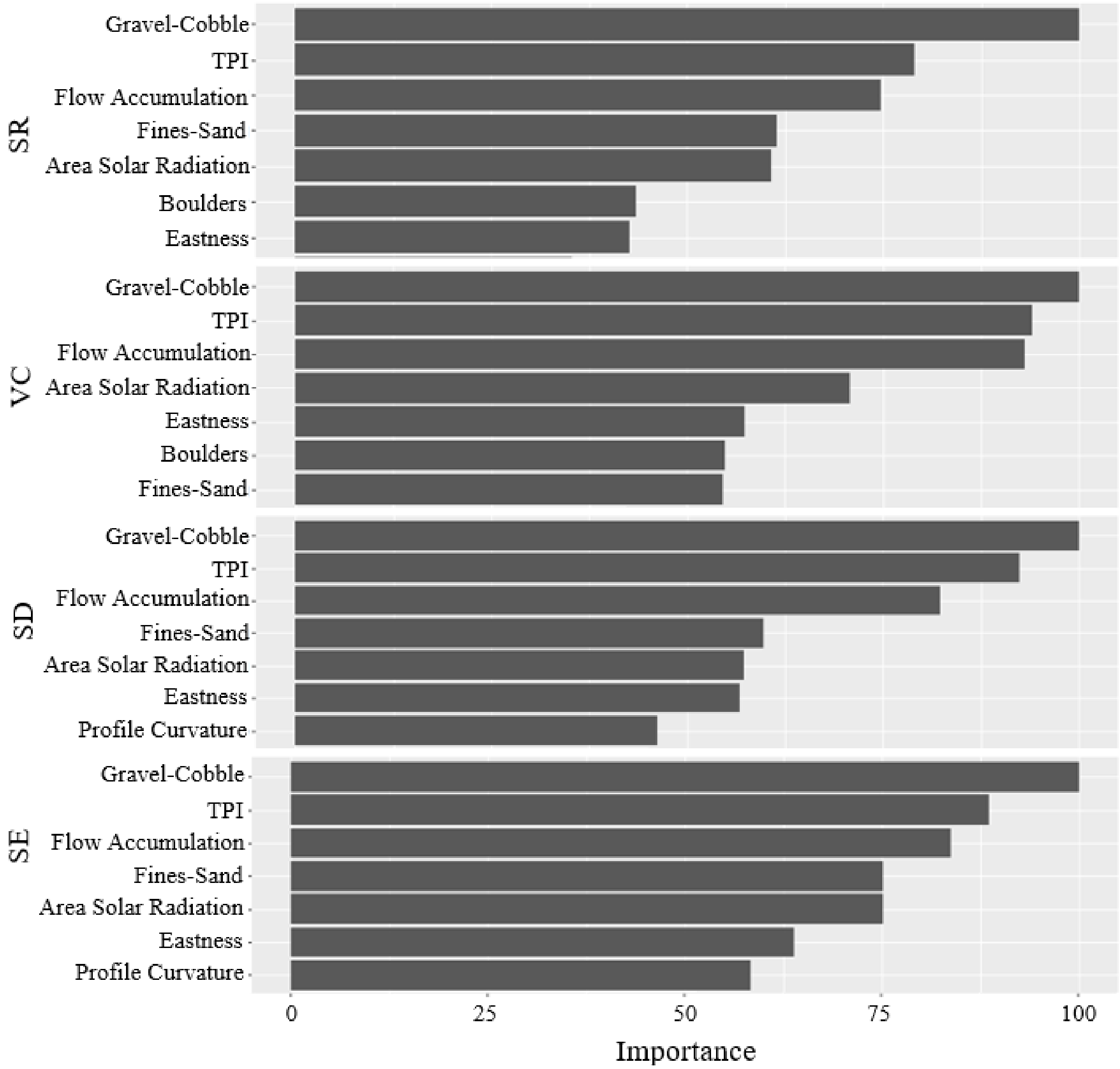

Figure 11: The top seven most important variables for species richness, vegetation cover, Shannon's diversity, and species evenness as determined by the bagged CARTs.

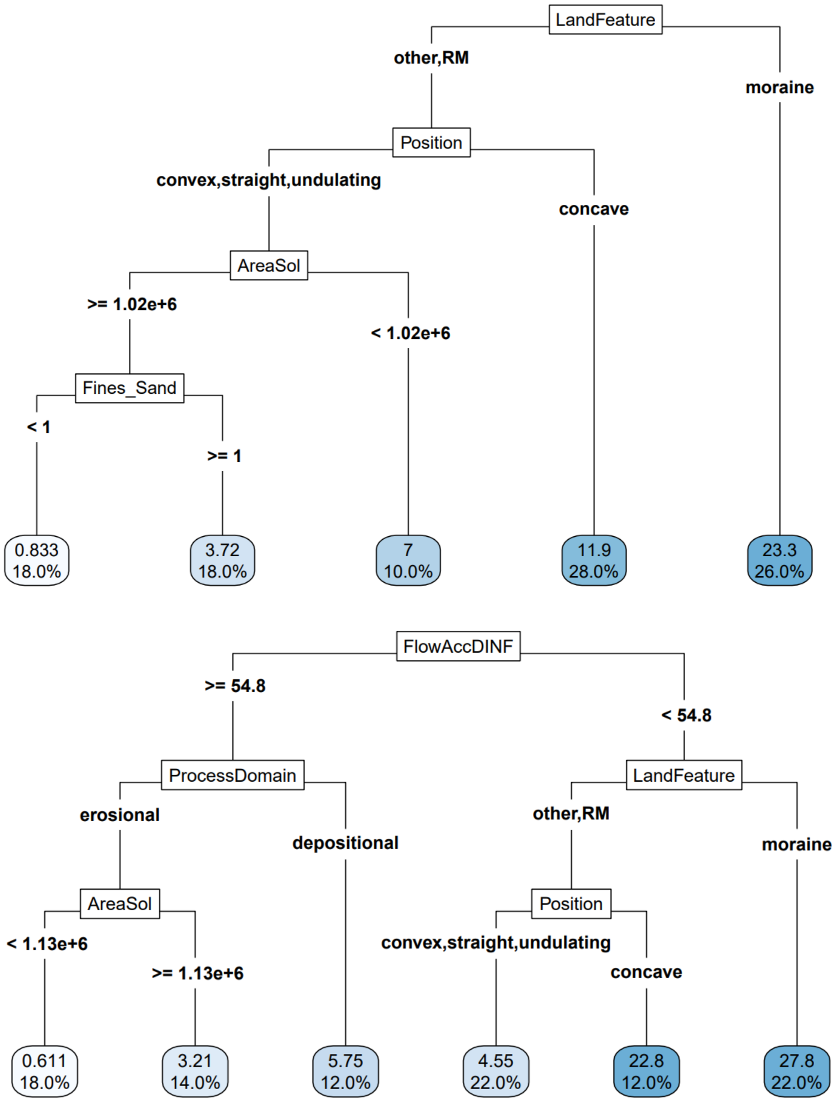

Figure 12: Example trees showing some of the diversity of trees developed using multivariate classification and regression tree (CART) to predict vegetation cover.

The scatter plots with regression trend lines reveal how species richness tends to weakly increase with gravel to cobble-sized surface fragment cover, decreases with flow accumulation, and increases with fines to sand cover (Figure 13). Though none of the vegetation cover regression plots were significant, the overall trend of the plot matched that of species richness and the overall pattern of the trees. Vegetation cover showed a general increase with gravel to cobble surface fragment cover, a decrease with flow accumulation, and an increase with fines to sands.

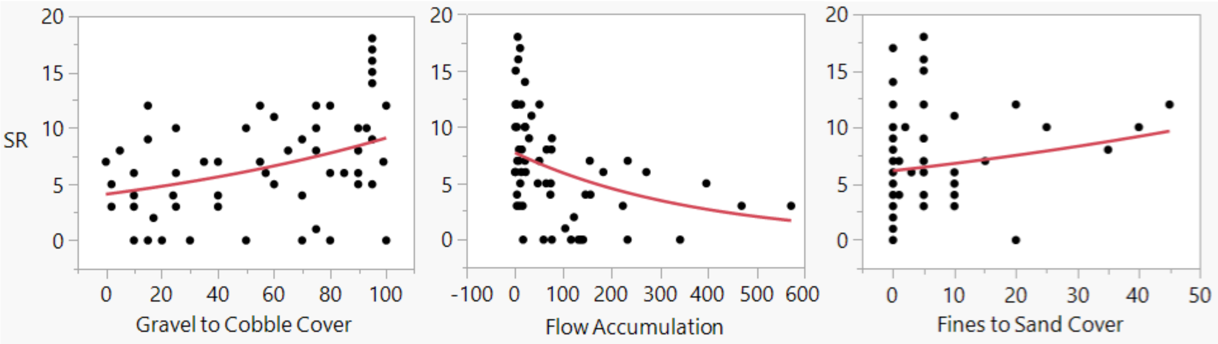

Figure 13: Scatterplots with general regression trend lines showing the relationship between species richness and gravel to cobble cover, flow accumulation, and fines to sand cover.

A bagged CART was also used to predict Shannon's diversity and species evenness. The most important variables for predicting both Shannon's diversity and species evenness were the percent cover of gravel to cobble sized surface fragments, TPI, flow accumulation, percent cover of fines to sand sized surface fragments, and area solar radiation (listed in decreasing order of importance) (Figure 11). However, not all these variables appeared to have a consistent trend when running the trees. The general trends observed were that higher gravel to cobble cover and lower flow accumulation predict higher Shannon's diversity, while lower fines to sand cover, greater TPI, and higher flow accumulation predict higher species evenness. Scatterplots of Shannon's diversity support these trends, showing that Shannon's diversity tends to weakly increase with gravel and cobble cover and weakly decrease with higher flow accumulation (Figure 14). The scatterplots of species evenness did not support the trends seen in the trees, revealing no discernable trends between species richness and site characteristics.

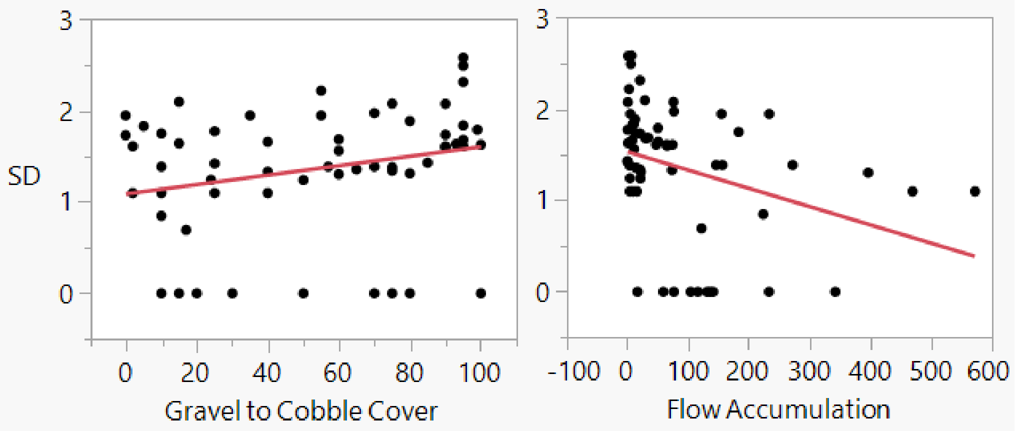

Figure 14: Scatterplots with general regression trend lines showing the relationship of Shannon's diversity with gravel to cobble cover and flow accumulation.

Chapter 6: Discussion

6.1. Vegetation Trend Overview

Species richness, vegetation cover, Shannon's diversity, and species evenness all showed different patterns across terrain age and site conditions. The Kruskal-Wallis test supports an overall increase in species richness and vegetation cover across terrain age (Figure 5), though there appears to be a lag in vegetation colonization and growth compared to other glacier forelands, as described in the literature. The GLMs support the importance of drainage and observed concavity in explaining species richness and Shannon's diversity trends (Tables 6 and 7), as well as the importance of the process domain and terrain age for species richness (Table 6). The CARTs support the importance of gravel to cobble coverage, TPI, and flow accumulation predicting all four vegetation covers (Figure 11).

6.2. Vegetation Patterns Across Terrain Age

At Sperry Glacier's foreland, terrain age is vital for understanding certain vegetative successional trends. As found in other glacier foreland studies, species richness and vegetation cover at Sperry Glacier foreland increased with terrain age. The longer terrain is exposed, the more opportunity there is for species to colonize and establish on the land. However, the establishment and growth of vegetative species and cover are much slower at Sperry than at other glaciers documented in the published literature (e.g., Andreis et al., 2001; Fischer et al., 2019; Glausen & Tanner, 2019; Raffl et al., 2006).

At the Sperry Glacier species richness increased from an average of 18 to 49 species per age range over 170 years (Table 2), with species first starting to appear approximately 8 years after exposure. The initial species to grow in plots exposed for 8 to 15 years (in the 1998-2005 plots) were *Epilobium anagallidifolium*, *Oxyria digyna*, and *Senecio fremontii*, along with some mosses, grasses, and sedges. Of these plants, *Epilobium anagallidifolium*, *Oxyria digyna*, and some species of sedge were previously found to grow near snowfields (Apple et al., 2022). The increase in species richness at Sperry is similar to the species richness found at Jamtalferner Glacier, a temperate valley glacier in the Australian Eastern Alps, with species richness increasing from 13 to 40-50 species over ~ 100 years since deglaciation (Fischer et al., 2019). However, Fischer et al. (2019) measured 13 species within the first 2 years after deglaciation and experienced a doubling of species richness by seven years since deglaciation. By this point in Sperry Glacier's foreland, no vegetation is present. Additionally, the species richness within 15, 25, and 55 years since deglaciation at Jamtalferner Glacier's foreland (with species richness of 20, 20, and 32, respectively) are comparable to 30, 64, and 96 years since deglaciation at Sperry Glacier's foreland (with species richness of 18, 18, and 35, respectively) (Table 2). However, by 122 years since deglaciation, the species richness at Sperry increased to 59, surpassing the recorded species richness at Jamtalferner. Sperry glacier has a similar trend in species richness as that of Jamtalferner, though the increase in species richness is delayed and slower, showing evidence of slower succession at Sperry.

Not only was plant colonization delayed at Sperry, but the vegetation cover remained lower than the corresponding terrain ages at different glaciers. However, the pattern of increasing species richness at Sperry Glacier is comparable to some glacier forelands. This variation in species richness patterns between glacier forelands may be influenced by vegetation cover. Some studies suggest that species richness may decrease later in succession due to competition instigated by high vegetation cover (Glausen & Tanner, 2019; Jones & Henry, 2003). This heavy competition shapes the species richness and composition, demonstrating a shift from allogenic to autogenic factors directing succession, as predicted by Matthews (1992). The highest average percent cover per terrain age category was 22.6% at Sperry, resulting in less competition, and autogenic influences, within the plots. As predicted, the limited vegetation cover at Sperry may explain why the overall trend of species richness keeps increasing, apart from a small decrease at the very end.

This effect of vegetation cover on species richness can especially be seen when Sperry is compared to other glacier forelands. For example, the species richness at Sperry continued to increase past the peak species richness of mid-latitude glacier forelands with high vegetation cover, such as Skaftafellsjökull Glacier in Southern Iceland which had plots with 100% cover as early as 54 years after deglaciation (Glausen & Tanner, 2019). While these glacier forelands with high coverage show a decrease in species richness, Sperry, which has much less vegetation cover, recorded a continued increase in species richness (Figure 15). Species richness at Sperry increased at a similar rate as mid-latitude glacier forelands with a more moderate amount of vegetation cover, such as at Jamtalferner Glacier where vegetation cover did not reach 80% until 100 years after deglaciation (Fischer et al., 2019). However, species richness at Sperry Glacier appears to increase much slower than species richness at tropical glaciers, such as at Humboldt Glacier in Venezuela (Llambí et al., 2021) (Figure 15). The species richness and vegetation cover at this tropical glacier were much higher than that found at Sperry, which could be caused by several factors including temperature vs. tropical differences in productivity, niche relations, spatial relations, and species dynamics (Brown, 2014).

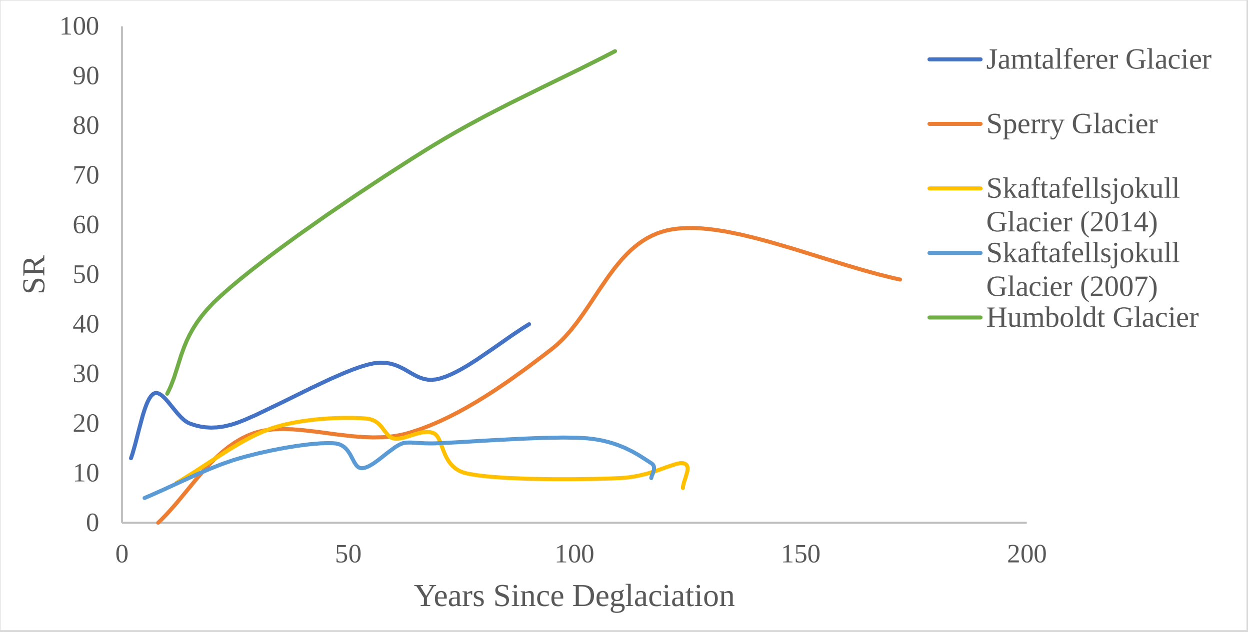

Figure 15: Species richness (SR) over years since deglaciation for Sperry Glacier, Jamtalferer Glacier in the Australian Eastern Alps (Fischer et al., 2019), Skaftafellsjökull Glacier in Southern Iceland sampled in 2007 and 2014 (Glausen & Tanner, 2019), and Humboldt Glacier in Venezuela (Llambí et al., 2021). SR was estimated based on what was reported in each of the published glacial studies.

Overall, the increase of species richness on older terrain at Sperry supports the theory that forelands with lower percent cover can support a greater increase in species richness before species begin competing for space. This high species richness and low percent cover are also supported by the Intermediate Disturbance Hypothesis. The main idea of the Intermediate Disturbance Hypothesis is that a moderate amount of disturbance allows vegetation to grow without allowing any one species to dominate the plot, resulting in high species richness. High disturbance kills vegetation frequently enough to limit species richness and low disturbance allows the competition between species to reduce the species richness (Moi et al., 2020). At Sperry, vegetation cover is low without the vegetation frequently being cleared from the plots. However, instead of a clear disturbance creating these conditions, the low soil cover prevents high vegetation cover without destroying the existing vegetation. Sperry does not have a high vegetation cover, which allows the species richness to continue growing. At the rate of vegetation cover increase at Sperry, many more years may pass before species richness reaches its climax and begins decreasing. Of course, species richness is also limited to the species pool available for colonization into the foreland. Further, this lag results in Sperry Glacier's foreland remaining in the allogenic phase of succession. This delayed shift from allogenic to autogenic controlled succession is also explained by Matthews (1992), who found that severe environments result in autogenic controls primarily controlling succession. The lack of soil at Sperry would make this alpine environment severe compared to other glacier forelands.

A lag in species establishment after terrain is deglaciated is also reflected in vegetation cover trends across the study area. The Sperry Glacier foreland averaged a total species coverage of 10.9% cover across all terrain ages. This cover expanded from zero vegetation cover within 8 years of deglaciation to an average of 2.84% cover within the first 18 years since deglaciation, to an average of 22.59% cover between 120 to 170 years since deglaciation (Table 3). This vegetation cover is much lower than the percent cover found in other glacier foreland studies (Andreis et al., 2001; Fischer et al., 2019; Glausen & Tanner, 2019; Raffl et al., 2006). Further, Sperry's vegetation cover is less than that of the Skaftafellsjokull Glacier due to the glacier foreland containing nutrients from volcanic activity (Glausen & Tanner, 2019). The majority of species found in Sperry's foreland are wind dispersed, as is common for glacier forelands, and wind is prevalent in the area (Figure 16). This availability of wind and wind-dispersed seeds means dispersal distance is likely not a problem at Sperry, as supported by studies that found seeds often aren't limited in their ability to reach newly exposed plots (Matthews & Vater, 2015). Most seed establishment appears to be limited to safe sites such as rocks, boulders, and crevices, which trap and protect seeds (Figure 17). This observation is supported by Erschbamer et al. (2008) who, through natural experiments, found that the manual addition of seeds to bare-ground plots does not affect successional trends. Therefore, unfavorable site conditions, such as bare-ground plots and little to no substrate, are likely the reason for the initial lag in vegetation establishment and may limit vegetation cover on unprotected and early plot locations.

Figure 16: Flagging of a tree showing evidence of strong, directional winds (left) and an example of wind-dispersed seeds found at Sperry (right). Photos: A. Schulte 2022.

Figure 17: Vegetation growing in safe sites created by rocks. Photos: A. Schulte 2022.

The study of soil development has been a key component of glacial foreland successional studies (e.g., Andreis et al., 2001; Franzetti et al., 2020; Jones & Henry, 2003; Klaar et al., 2015; Matthews & Vater, 2015), though it was not explicitly investigated in this study. Soil holds moisture, contains nutrients, and supports microbial and bacterial communities. At some glacier forelands, species richness and diversity are affected by soil type and characteristics along with soil development (Andreis et al., 2001). The lag in succession development may be due to slow soil development in this environment, and a result of exposed, consolidated, metasedimentary bedrock with little to no soil development observed (Figure 18). At Sperry Glacier's foreland, very little soil was observed across all date ranges. What little soil existed was hidden in the cracks of rocks or held among the roots of various vegetation at the moraine. In other studies (e.g., Klaar et al., 2015 for Glacier Bay NP Alaska), reports of soils as deep as 10cm were collected from cores. Conversely, at Sperry Glacier, no plots had deep enough soil for even a shallow soil core to be collected. The dearth of soil at Sperry Glacier foreland very likely results in harsher conditions for germinating and growing vegetation, resulting in a decreased rate of succession compared to other glaciers. Due to this limited soil, microtopography was not only important for capturing seeds but also for capturing the resources necessary for the seeds to germinate. Not only the germination but also the colonization of plants is hindered by the dearth of soil. Some wind-blown seeds have structures that allow them to anchor into the soil. Without soil to anchor into, these seeds are more susceptible to being blown away by the wind, though these anchoring structures may still provide some drag across the bare ground and help the seeds anchor in cracks (Grohmann et al., 2019). This drag also prevents seeds from sliding down a steep slope due to gravity. However, even if a seed manages to attach to the bare ground of a plot, the lack of resources may still prevent germination. Therefore, both plant colonization and germination are limited due to the sparse soil at Sperry. Snowfields may also delay succession since they persist around the glacier late into the growing season (Apple et al., 2022). Though the terrain is no longer covered by the glacier, younger plots may still be blocked from colonizing due to persistent snow fields.

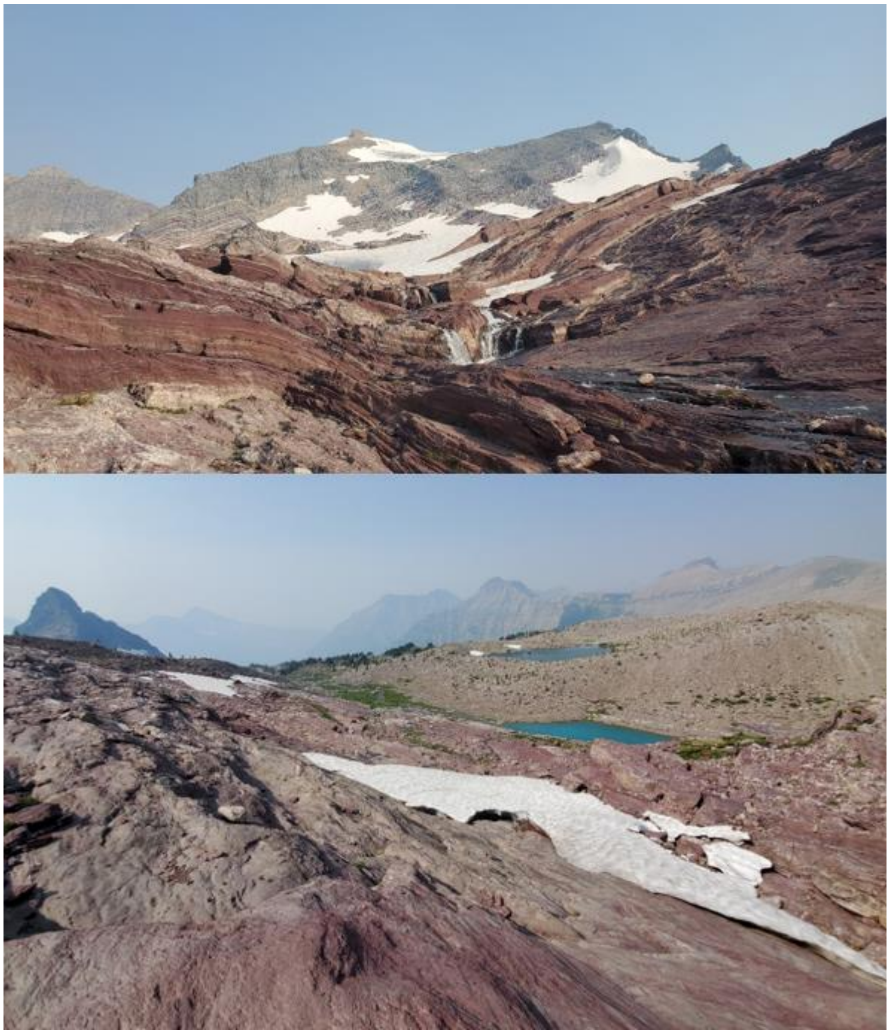

Figure 18: Images of the landscape of Sperry Glacier’s foreland facing southeast, toward Gunsight Mountian (top), and northwest toward the terminal moraines (bottom). Photos: A. Schulte 2021.

Shannon’s diversity, which considers both the number of species in a community and the measure of each species’ percent cover, as well as species evenness did not vary considerably across terrain age, supporting the idea that terrain age is not the main factor affecting diversity or evenness (Table 2). Shannon’s diversity was consistent throughout all the terrain age ranges. Since the youngest terrain age range was 29 years, the diversity at Sperry equalized within 29 years of exposure. Additionally, Shannon’s diversity can be partially explained using site conditions, such as drainage and observed concavity (Table 7; Figure 10), so diversity at Sperry may be dictated more by the landscape characteristics than terrain age, as will be discussed later. Similarly, Sperry's foreland had relatively little change in species evenness across terrain age, averaging a species evenness of 0.86, which is comparable to that reported by Raffl et al. (2006) for Rotmoosferner Glacier and is also comparable to Andreis et al., (2001) for the Italian Alps.

Though Shannon's diversity remained relatively consistent, species composition did vary across the age ranges. Thirty-five of the species observed singularly occurred in one plot (Table 4). This means that, despite diversity being similar across the foreland, the diversity of species is spatially dispersed. Simultaneously, as determined by our sampling, there is low vegetation cover at Sperry Glacier, meaning that each species could be comparatively isolated in the foreland. This isolated spatial pattern may lead to more apomictic reproduction strategies which tend to lower genetic diversity (Jump & Penuelas, 2005) and lead to higher specialization of plants to certain conditions. Furthermore, it may also make adapting to new conditions more difficult, making it harder for plants to adjust to a changing climate (Jump & Penuelas, 2005). However, fragmentation of the population may not limit pollination or gene flow in many alpine species (Frei et al., 2012; Garcia-Fenandez et al., 2012; Pluess & Stöcklin, 2004; Wirth et al., 2010). Therefore, some species may be more strongly affected as the glacier melts and conditions change than other species, depending on continued gene flow from incoming seeds or cross-pollination. Further investigation into the alpine population genetics and pollination mechanisms can help clarify which species are most at risk.

The consistency of species turnover across terrain age shows that the species composition is changing at a relatively constant rate across the terrain age ranges since the number of species appearing or disappearing is proportional to the species richness. In other words, an average of

67.1% of all the species in two consecutive age ranges change between those age ranges. However, since the combined species richness between age ranges keeps increasing, the number of species appearing or disappearing keeps increasing as well, as seen through my results, revealing an increasing absolute species turnover (Table 2). This high disappearance and appearance of species may be due to so many species being found in only one plot. A more intensive survey that collects plant data in more plots may find these species in multiple time ranges, which would decrease the calculated species turnover.

The results may also indicate that species are specialized to specific terrain age ranges or to different distances from the glacier. This specialization may be due to different resource availability across the foreland. Species growing near snowfields have greater access to water (Apple et al., 2022) and nitrogen (Björk & Molau, 2007) but are more exposed to disturbances (Wojcik et al., 2021) and lack soil. However, vegetation growth on terrain without meltwater may be limited by nitrogen on younger terrain and phosphorous on older terrain (Jiang et al., 2018). This nitrogen limitation may be especially severe at Sperry. Since nitrogen-fixing bacteria often live in association with certain plant species or live free in the soil, a lack of soil may decrease the nitrogen pool by limiting the number of bacteria-fixing nitrogen. Pollution may also change the resource pool by depositing CO_2, nitrogen, and SO_2 may be deposited as fine particles across the environment (Dawes et al., 2013). However, the lack of accumulation of soil particles, especially in younger terrain, may negate this addition. Sperry has a variety of terrain and resources that change across the foreland and throughout the successional process. Leibig's Law of the Minimum states plant growth is limited by the most limited nutrient available. However, different species have different survival strategies and resource needs. Therefore, different species are specialized to survive in specific circumstances. If species are specialized to different terrain ages and distances from the snow fields, the future disappearance of Sperry Glacier may put some of the species at risk since their niche environment will have vanished.

Some frequently occurring plant species, families, and vegetative groups were associated with specific age ranges. According to the results of the Kruskal-Wallis and Dunn's multiple comparison tests, lichens, woody plants, Asteraceae, Plantaginaceae, and *Penstemon ellipticus* appeared to significantly increase in later successional stages while graminoids (including Poaceae and Cyperaceae), herbaceous plants, and *Boechera lemmonii* appeared to increase by mid-successional plots across Sperry's foreland (Figure 7). These results support the idea that different species occur in different stages of succession and are adapted to different conditions associated with each successional stage. The initial conditions that characterize the earliest stages of plant succession are less suitable for some woody, graminoid, and herbaceous vegetation – a pattern also reported in other published research. For example, at Mount Hekla's lava flow in Iceland, which has similar primary succession patterns as glaciers, mosses established a layer to collect wind-blown sediments, providing a substrate for vascular herbaceous plant colonization (Cutler, 2010). Similarly, Sperry's foreland may need time after initial deglaciation for resources to collect and sites to become suitable for further colonization. Some species, such as *Oxyria digyna*, are commonly found on forelands around the world, including in GNP, the Italian Alps, and Austrian Alps (Andreis et al., 2001; Apple et al., 2022; Raffl et al., 2006). In the Italian Alps, *O. digyna* was found consistently across the foreland and was considered an early-stage species (Andreis et al., 2001). *O. digyna* was dispersed across all the terrain ages and was one of the first species to colonize at Sperry. Woody vegetation at other glacier forelands also tends to be a later successional group (Fischer et al., 2019; Glausen & Tanner, 2019) despite having a small presence on young terrain (Glausen & Tanner, 2019). Some of these species play a specific role in the landscape. For example, *Dryas octopetala* does nitrogen fixation (Apple et al., 2022) which may contribute to why *D. octopetala* could grow a large vegetative coverage on the foreland, despite not being frequently encountered in the plots. These changes shape the landscape, facilitating the establishment of other species by providing necessary nutrients, and represent a small shift from allogenic toward autogenic controls directing succession (Matthews, 1992), though allogenic controls still dominate succession across Sperry Glacier's foreland.

This plant-associated nitrogen fixation only occurred on older terrain ages at Sperry. The two species of *Dryas* found at Sperry were only in four plots, all of which were on moraines. Due to this location of nitrogen-fixing plants and the lack of soil for nitrogen-fixing bacteria to inhabit, not much nitrogen is likely to be fixed on younger terrain ages. Therefore, vegetation on these younger terrain ages either have their growth limited by nitrogen availability (Jiang et al., 2018; Soudzilovskaia et al., 2005), or these plants receive nitrogen from meltwater from the snowfields (Björk & Molau, 2007; Bowman, 1992). Unlike plant vegetation, lichen cover decreases with the presence of nitrogen (Soudzilovskaia et al., 2005). The unfavourability of nitrogen-rich plots for lichen coverage may shape the lichen patterns found at Sperry. Lichen was not found in any of the younger terrain ages, exposed between 1959 and 2022. If the meltwater from the snowfields is nitrogen-rich, the plots closer to the snowfields are likely exposed to more meltwater and, therefore, nitrogen (Björk & Molau, 2007). This may make these younger plots unsuitable for lichen growth. Additionally, the till on these younger plots may be unstable (Perez, 2009) or seasonally covered with snow, making them further unfavorable for lichen establishment. Lichen cover was able to continue to increase as terrain age increased since the vegetation growth on the older terrain was not large enough to outcompete or shade the lichen coverage. Additionally, nitrogen did not hinder lichen growth in older terrain age ranges. Any nitrogen fixers or soil was kept separate from the lichen growth due to the variety of microtopography. Most vegetation cover and soil buildup were in cracks or at the bases of rocks. Lichen, however, was often found growing on the top of exposed surface fragments (Figure 2). These locations were unsuitable for vegetation growth and too exposed for soil to collect on them. This would result in lichen growing above the nitrogen available in the plot.

Colonizing plants not only affect the landscape by capturing sediment (Cutler, 2010), changing the soil nutrients (Apple et al., 2022), and facilitating other plants (Erschbamer et al., 2008), but they also provide a food source for animals that may further serve as dispersal agents, which will in turn, contribute to plant establishment (García-Rodríguez et al., 2022; Liu et al., 2023). Throughout the study, I observed *Capra sp.* (goats) traveling through the foreland to graze on some of the vegetation. I also observed *Ursus sp.* (bears), *Lagopus sp*. (ptarmigans), and a variety of insects flying or crawling across the plots, potentially pollinating the flora (Figure 19). Despite the relative isolation of foreland plants, pollination is not limited (Garcia-Fenandez et al., 2012; Pluess & Stöcklin, 2004). Though vegetation at this foreland is sparse compared to other glaciers, this landscape still plays a part in the larger subalpine ecosystem, and the fauna, though not directly studied here, is an active component of this ecosystem that deserves future research attention.

Figure 19: Examples of animal activity on Sperry Glacier’s foreland, including goats (far left), bear footprints in the snowfield (middle left), a mother ptarmigan with a chick (middle right), and an insect (far right). Photos: A. Schulte and L. Resler 2022.

6.3. GLM and CART Supported Vegetation Pattern

Results of the GLM uncovered relationships between associated vegetation patterns and the field- and GIS-derived biophysical variables. However, GLMs were not able to explain the variation in vegetation cover using our selected predictor variables. GLMs revealed that plots characterized by moderate drainage and an overall concave shape were positively associated with species richness (Table 6; Figure 9) and Shannon’s diversity (Table 7; Figure 10). Additionally, the depositional process domain and older terrain ages were positively associated with species richness (Table 6; Figure 9). This finding aligns with those of Matthews & Vater (2015), Jumpponen et al. (1999), and Raffl et al. (2006) who found that water initially dominated the allogenic phase in succession (Matthews & Vater, 2015), and vegetation tends to be found on concave plots due to their ability to provide shelter and accumulate resources (Jumpponen et al., 1999). The p-value for the difference between concave and convex plots, though significant, was not as low as the p-values found for the other variables. This may be due to the variety of conditions within different concave and convex plots. Concave plots tend to be sheltered and convex plots tend to be exposed. However, some of the concave plots may have poor drainage, resulting in water pooling and drowning vegetation, and some of the convex plots may be on the moraines, which contain surface fragments that provide safe sites (Figure 2).

None of the surface fragment size variables were significant in the GLM (Table 6), however, gravel to cobble surface fragment size was important in the CARTs for predicting species richness and Shannon's diversity (Figure 11). The size of the surface rock cover was expected to have a larger impact on species richness due to its ability to provide safe sites and trap seeds (Jumpponen et al., 1999; Perez, 2009). In our study area, however, a large amount of surface fragments was unconsolidated ground till. On sloped areas or areas this ground till may be unstable, and thus non-ideal establishment sites for plants (Perez, 2009). This instability may counter the beneficial effects surface fragment can provide through safe sites, resulting in gravel to cobble coverage not significantly affecting vegetation growth in the GLMs.

Observed concavity, which was positively associated with both species richness and Shannon's diversity, was a plot-level variable measured in the field. This variable performed better in the GLM than other GIS-derived terrain surface measures, including TRI, TPI, and the two measures of curvature. It is possible that this variable performed better at explaining these vegetation patterns at Sperry Glacier due to the resolution captured in the field-derived variable. By visually assessing the concavity of the plot while in the fields, the microtopography of the plot could be assessed, rather than only a measure of the general area around the plot. In fact, most of the variables important in the GLM were field-collected aspects of the microtopography. Concavity was a measure of the plot's surface shape, drainage was a measure of how water would interact with this microtopography, and, though the process domain shapes the overall local topography, the process domain was an assessment of the main force that shaped the plot's microtopography into its current state. Not only do field-derived variables have a greater resolution, but they also more precisely reflect aspects of the plot’s microtopography. These findings demonstrate the continued importance of field data collection and verification along with the need for a higher-resolution DEM at Sperry Glacier for modeling fine-scale vegetation processes.

Based on GLM results, more biophysical variables were statistically important for explaining species richness than Shannon’s diversity, but the pattern of both response variables was effectively explained using GLM (Tables 6 and 7). Shannon’s diversity appears to be driven more by site conditions than terrain age since patterns in diversity arose across these site conditions while diversity remained mostly uniform across terrain age. Species richness varied both across terrain age and across site conditions. The benefits of moderate draining plots and the protection of concave plots may allow more species to thrive in these plots, fostering a higher Shannon’s diversity, while these two variables and depositional process domains may provide more protection for a variety of species to establish in the plots.

I used bagged CART models to rank variable importance for predicting each response variable. These models revealed alignment among the top three most important variables for predicting species richness, vegetation cover, Shannon’s diversity, and species evenness (Figure 11). After the top three predictive variables of 1) surface fragment cover sized from gravel to cobble, 2) TPI, and 3) flow accumulation, the importance rankings of different predictive variables start to diverge between the response variables (Figure 11). Though the top three predictive variables are the same, the response variables are not identical, and will not be influenced identically by all the predictive variables.

The benefit of using CART models is they don’t assume any specific relationship between the predictive and response variables. This makes CART models a good complement to

GLMs, which assume a linear relationship after the predictive variables are transformed. However, since the CART models don’t assume a specific relationship, it is difficult to understand how the important predictive variables relate to the response variables. CARTs are useful for finding variables that are influential in directing succession but have a complicated relationship with vegetation measures. For example, flow accumulation has an overall weak, negative relationship with species richness and Shannon’s diversity. Despite having an overall linear relationship, flow accumulation did not appear as significant in the GLMs. This may be due to the complex relationship flow accumulation may have with vegetation growth. On many plots, large flow accumulation could wash away seeds or drown vegetation. Since water flow transports seeds downhill, water dispersal may decrease the number of plants that colonize the foreland. However, just past the foreland, the glacial streams have lots of vegetation along their edges. Despite heavy flow accumulation, vegetation appeared to be thriving. Therefore, flow accumulation appears to be beneficial to vegetation growth in some circumstances, but not in others. On the foreland, the areas that lacked safe sites to anchor vegetation may have vegetation growth hindered by high flow while downhill locations with more safe sites may be benefited from the input of seeds and the water supply. The CART is a useful tool to know what variables are important to investigate with a focus on how these variables’ effects differ across different conditions. A study with more sample plots would be required to investigate how the impact of these important variables differs across the foreland.

For this study, scatterplots helped show some overall relationships between the important variables and the response variables. Although the CARTs highlighted potentially important site conditions to predict vegetation cover and species evenness, the exact relationships between these variables and these vegetation trends were unable to be explained using a scatterplot with a general regression line, and thus remain uncertain. Therefore, the specific factors directing the variation in vegetation cover and species evenness need additional clarification. Species richness, however, was explained across both terrain age and various site characteristics (Figures 5, 9, and 13). Variation in Shannon's diversity was not explained through terrain age but was able to be explained using site conditions (Figures 10 and 14). Therefore, both terrain age and site conditions are necessary for understanding succession. This conclusion is supported by Raffl et al. (2006) who found two transects on different aspects and slopes created two different successional trajectories and by Walker and Del Moral (2003) who concluded that successional trajectories are sensitive to the local site conditions of the area.

None of the scatterplots showed an association between vegetation cover or species richness and the most important predictive variables, making the patterns of vegetation cover and species evenness hard to identify. Also, like in the GLM, the scatterplots describe more relationships between species richness and the predictive variables than between Shannon's diversity and the predictive variables. However, unlike the GLM, the bagged CART with the scatterplots shows that gravel and cobble surface fragments may be an important source of safe sites as vegetation grows or provide locations for seeds to anchor. The scatterplots revealed both species richness and Shannon's diversity to have a weak positive association with gravel to cobble size clasts and a weak negative association with flow accumulation (Figures 13 and 14). Additionally, species richness appears to have a weak positive relationship with surface fragment sized from fines to sands (Figure 13). This aligns with the GLM findings since the GLM only found models that explained species richness and Shannon's diversity.

At Sperry Glacier's foreland, the suitability of a site to support vegetative growth seems to be more important for creating high-diversity plots (as determined by results of the GLM and

CART for Shannon's Diversity) than the length of time the plot has been exposed for colonization. The importance of site conditions on diversity, as captured specifically by Shannon's diversity index, likely means that a diversity of seeds can reach each plot, and further has sufficient room to grow without outcompeting other species. Thus, site quality seems to be an important factor for diverse plant establishment.

Drainage, observed concavity, and process domain, are variables shown to be most important for explaining the vegetation trends as determined by the CART models (Figure 11). These results likely reflect the capacity of these variables to provide fine scale resources and safe sites, (i.e., the gravel to cobble cover) (Jumpponen et al., 1999; Perez, 2009), or influence water availability (i.e., flow accumulation). These findings align with personal observations made in the field. Most of the plots in which I found running or standing water contained dead, submerged vegetation if vegetation was present (Figure 20).

Percent fines to sand cover surface clast size showed up among the top five important variables for predicting species richness, Shannon's diversity, and species evenness (Figure 11). The importance of higher fines to sand cover as represented in these models may represent the importance of biofeedback. Though microtopographic safe sites, such as rocks and small crevasses, tend to accumulate smaller particles, already-established plants tend to do the same (Cutler, 2010; Perez, 2009). The presence of fines-sands may encourage vegetation colonization, but vegetation also increases the presence of fines-sands. Without vegetation, the fines to sand may be stripped away by the wind, and without the substrate, the presence of plants can be reduced (Glausen & Tanner, 2019).

Figure 20: A 1913-1927 (left) and 1966-1969 (right) plot showing flowing water that either contains dead or no vegetation within the water. Photos: A. Schulte 2022.

Some of the variables listed as important by the CART did not appear to be linearly related to the studied vegetation trends, as seen in scatterplots. This lack of linear relationships may be due to several reasons, including species-specific tolerances to light, moisture, and temperature conditions. In other words, these ‘important’ variables that lack an obvious relationship to the studied vegetation trends may be relevant only under the right conditions. For example, plants in shaded, moist locations may benefit from lots of sunlight, while plants in exposed, dry locations may be burned by sunlight. The CART, therefore, complements the GLM, by showing which variables may be important, though lacking a linear relationship with the vegetation trends. However, discerning these complicated relationships is beyond the scope of this study, but a good topic for future work. The important variables in CART also differed somewhat from the major explanatory variables in the GLMs. However, many of the variable’s relationships seen through the GLM and Dunn’s test could also be seen in the trees. The trees changed each time they were created, due to changes in the test and training data, but variables such as drainage, observed concavity, and process domain, which were emphasized in the

GLMs, appeared to consistently predict greater species richness and Shannon’s diversity in the CART models.

Chapter 7: Conclusion

This study focused on assessing the trends of species richness, vegetation cover, Shannon's diversity, and species evenness across 1) terrain age, with the assistance of Kruskal-Wallis and Dunn's tests, and 2) biophysical site characteristics, with the assistance of GLMs and CARTs. A suite of filed and GIS-derived predictors were used for the site characteristics. Vegetation trends across terrain age were further assessed by comparing species composition, dispersal mechanism, and turnover across terrain age. These two main objectives were used to create baseline measurements of how plant succession changes across different terrain ages and conditions. This baseline can be used to better understand what factors influence succession at Sperry Glacier's forelands and how the alpine ecosystem may change as deglaciation continues. Knowing these trends and changes in the alpine ecosystem could be used to help future conservation and restoration efforts within Glacier National Park.

Overall, a combination of both terrain age and site conditions is important for understanding trends in plant succession at glacier forelands, including Sperry Glacier's foreland. Terrain age explained trends in both vegetation cover and species richness, both of which increase over older terrain. Species composition also varied across terrain age but was not tested across site conditions. Terrain age was important for understanding vegetative successional trends at Sperry Glacier's foreland and across many glacier forelands around the world. However, terrain age is not the only factor directing vegetation distribution and succession. GLMs could explain variations in species richness and Shannon's diversity. Bagged CARTs identified important site conditions that predicted vegetation cover, species richness, Shannon's diversity, and species evenness. However, the relationships between these variables and the corresponding vegetation trends were only clear for species richness and Shannon's diversity. To understand how alpine ecosystems are changing, the entire landscape, along with the chronosequence, must be considered and observed. The unique conditions of Sperry Glacier's foreland, such as the lack of soil and large snow fields, appear to slow the entire successional process compared to succession on other glacier forelands across the world. Finally, the presence of only native species in the study area indicates that this ecosystem is relatively untouched by invasives (Table 5), allowing the study of successional patterns of a native landscape and how native species at Sperry Glacier and similar glaciers respond to deglaciation on a complex landscape. The presence of endemic species and plants which may need conservation emphasizes the need to protect this landscape.

Future research is required to understand just how this slowed-down succession affects the ecosystem's ability to maintain its species composition and diversity. The delay in succession at Sperry could also be further understood by studying the effect different seed mechanisms, which anchor the seed to the ground, have on the ability of species to colonize recently exposed terrain. Future research should also address the risk of invasive species, as dispersed by the growing number of tourists to these remote locations. Due to the uninvaded nature of this landscape and the known presence of invasive species in Glacier National Park, further research should be conducted to test the likelihood of nonnative species invading the glacier foreland by looking at the species composition of neighboring zones and the mobility of the invasive species to spread up in elevation, especially as the planet warms. One last direction for future research is to study the snow fields surrounding the glacier and how they affect the length of the growing season, the species composition, and the plant mortality rate to see if these snowfields contribute to the delayed establishment of vegetation after deglaciation. This research should also address how the availability of resources changes as the snow fields shrink. Since the snow field provides water and nitrogen, the consequence of this shrinking on plants associated with snowfields, such as *Epilobium anagallidifolium* and *Oxyria digyna*. Should be studied.

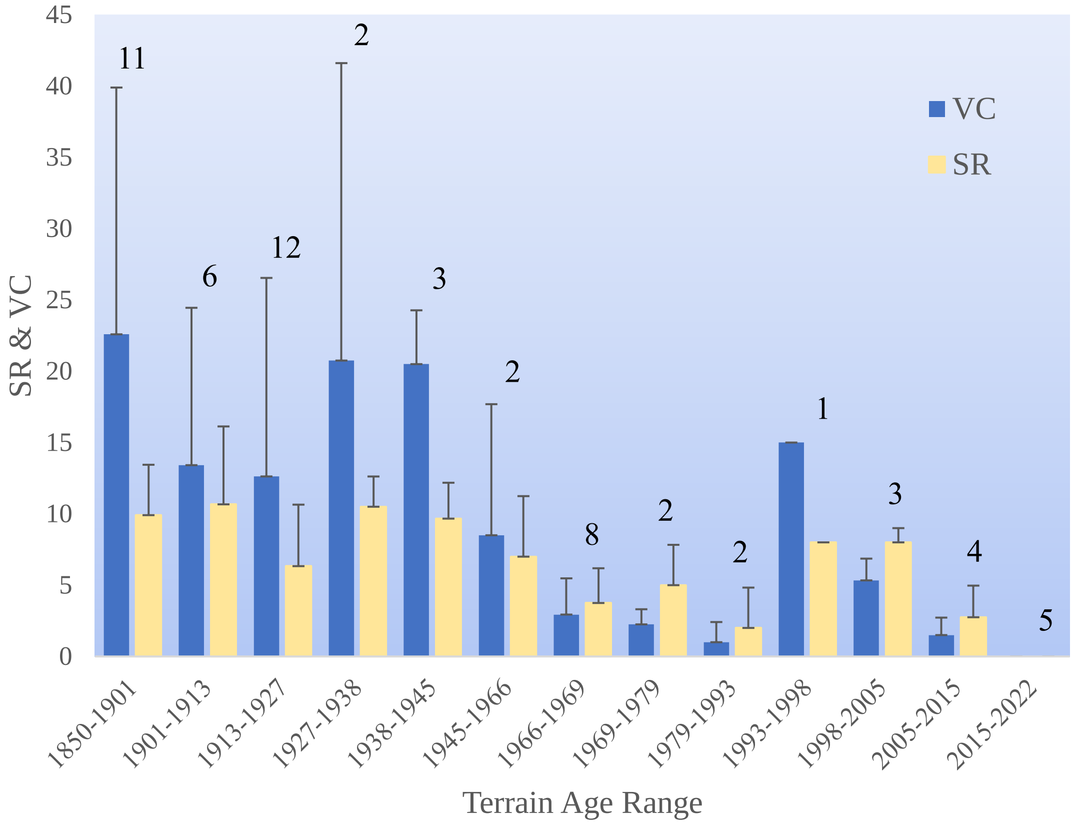

Figure 21: Average species richness (SR) and vegetation cover (VC) per plot for the narrowest terrain age ranges allowed by glacier margin data and standard deviation error bars. The number above the SD error bars indicates the number of plots falling within each date range.

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