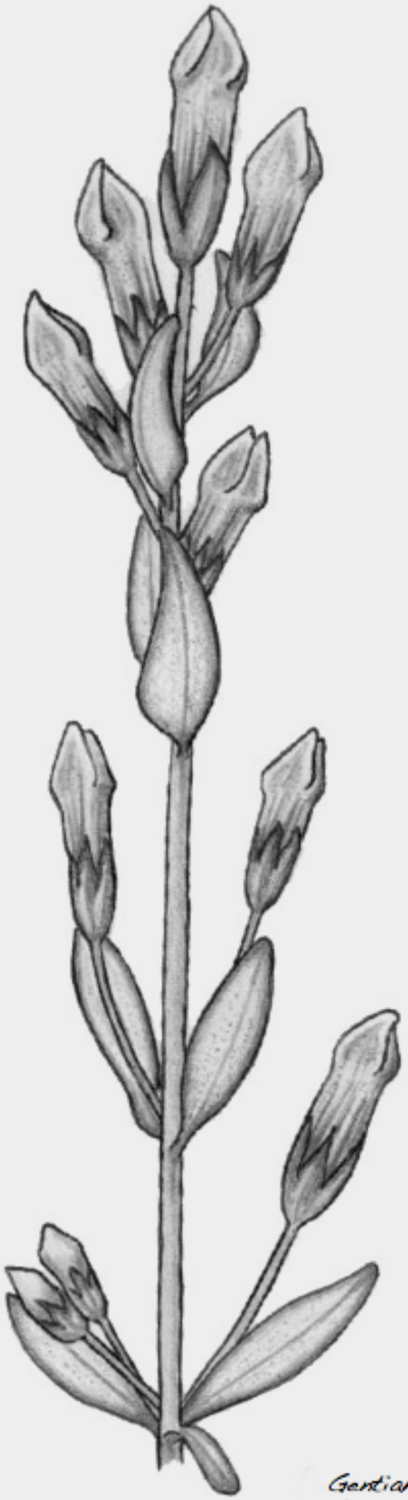

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The Impact of Recreational Activities on an Alpine Vascular Plant Community in the Canadian Rockies

by

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Abstract

Alpine tundra is notorious for its fragility and slow recovery following disturbance. Tourism is increasing in alpine areas, creating the need to improve our understanding of the impacts of recreation in these ecosystems. This study examined the impacts of hiking and off-highway vehicle use on the vascular flora of dry alpine meadows in the Canadian Rockies by comparing community data, including rare plant distributions, on recreational trails, on intact tundra meadows, and on sparsely vegetated gravel steps formed by frost disturbance. The trails were found to be different from both undisturbed and naturally disturbed tundra in terms of vascular plant cover, diversity, species composition and soil compaction. Rare plants do not seem to be adversely affected by recreational activities. Trampling leads to environmental conditions that will likely make regeneration of abandoned trails an extremely slow process; and it is advisable to limit the extent of trail networks in alpine areas.

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Figure & Tables

Figures

Tables

1. Introduction

The tundra, Earth's coldest biome, can be defined as the treeless regions that lie above altitudinal (alpine) and latitudinal (arctic) treelines. Life in the tundra is shaped by the extreme climatic conditions found in these regions. Outside of the tropics (which even at the highest altitudes have very different environmental conditions than most tundra regions), alpine and arctic plant communities experience cold temperatures, high winds (particularly in alpine areas), and short growing seasons. Tundra soils are often nutrient-poor (Bowman et al. 1993; Bliss 1962b), and are sometimes waterlogged in areas underlain by permafrost (Munroe & Bockheim 2001).

Plant life in the tundra is characterised primarily by species of short stature as well as an ability to grow and reproduce in cold climatic conditions (Billing & Mooney 1968). Beyond this there is a great deal of diversity in tundra plant communities; different areas are characterised by different "types" of tundra. These differences appear to be driven by moisture, which is partly a function of local topography (Billings & Mooney 1968). For example, the low-lying region around Barrow, Alaska, has saturated soils and supports communities dominated by cottongrasses (*Eriophorum* spp.), while in drier areas, such as polar deserts in the high arctic, plant communities often consist of scattered cushion plants. Other regions support tundra communities that are dominated by shrubs (often *Betula* and *Salix* spp.), by dwarf shrubs, by graminoids, by forbs or by lichens. Some tundra communities are densely vegetated, while in others vegetation is sparse and scattered.

Topography is particularly important in shaping alpine communities. High winds in the alpine create variations in moisture among different microhabitats (e.g., ridgetop, slope, gully) due to their effect on snow distribution (Körner 2003; Billings 1974). Snow is a major source of moisture in many alpine communities (Billings & Mooney 1968); strong winds redistribute snow from higher, more exposed locations to lower or more sheltered areas (Isard 1986). As a result of this, ridgetops and mountaintops tend to be quite dry and have little snow cover to shelter plants from harsh winter temperatures and winds (Billings & Mooney 1968). At the other end of the spectrum, snow accumulates in depressions resulting in later spring snowmelt. As a result, the growing season for plants in these "late snowbeds" is very limited, and snowbed plants must be able to grow, flower and set seed within a very short period of time (Isard 1986). Aspect, as it relates to wind and sun exposure, also has an important influence on the environmental conditions that plants experience in the alpine (Billings & Mooney 1968; Körner 2003; Isard 1986). South-facing slopes are warmer than north-facing slopes in the northern hemisphere (the opposite is true south of the equator), while slopes with windward aspects have less snow than leeward slopes (Billings 1974).

Disturbance in tundra ecosystems

Like all natural communities, tundra ecosystems experience a variety of natural disturbances including fire, landslides, solifluction, cryoturbation, and trampling and digging by wildlife. Cryoturbation, or frost disturbance, is a type of disturbance that is created by freeze-thaw cycles. Repeated freezing and thawing causes the movement of soil and the sorting of stones and rocks, and can result in considerable instability in affected soils (Bliss 1962b). Frost disturbance is common in high alpine regions, and can lead to root damage and breakage in tundra plants (Benninghoff 1952).

Disturbances such as these were once thought to be a rare force that disrupted the equilibrium of otherwise stable ecosystems (Sousa 1984). In recent decades, however, they have become understood as important environmental factors that shape ecological communities in many ways. Human activities such as logging, mining, and road building constitute a form of disturbance that is increasingly modifying natural ecosystems. While human disturbance sometimes approximates the effects of natural disturbance, in many cases the impacts of the two are obviously quite different. Given the scale of current human involvement in, and alteration of, the natural environment, it is necessary for us to understand the effects of disturbance on ecological communities in order to predict, manage, and remediate the impacts of human activities.

Arctic and alpine regions in North America have only recently begun to experience substantial human disturbance, and the response of tundra communities to disturbance is still not well understood. Human disturbance in the arctic has mainly been the result of large-scale industrial developments that have been initiated in the last 50 years: the North Slope oilfields, seismic exploration in the Mackenzie Delta, and diamond mining in the Northwest Territories are all examples. In mountainous areas, recreational activities such as hiking and downhill skiing have been increasing since the post-war period (Billings 1973; Dearden & Sewell 1985), and are likely the dominant sources of human disturbance in the alpine. Arctic areas have also seen an increase in tourism and recreation in recent years (Forbes et al. 2004).

Low productivity communities such as the tundra are believed to be easily disturbed and slow to recover (Liddle 1975). The precise timeframe for recovery from disturbance in tundra communities is not known and is likely a function of disturbance type, timing and severity. For example, studies from the Colorado Rockies suggest that recovery of trampled tundra might take several centuries (Willard et al. 2007; Willard & Marr 1971), while Racine et al. (1987) found that burned tussock tundra communities returned to pre-disturbance cover values within 6-10 years after fire. Tundra plants grow slowly (Atkin et al. 1996), and recovery might be further delayed by side effects of recreational activities such as soil compaction and erosion. The natural beauty and ecological uniqueness of both arctic and alpine ecosystems are attracting increasing numbers of recreational visitors (Parsons 2002; Forbes et al. 2004), and although many alpine areas in particular are found in protected areas, this designation seems to make these places even more appealing to visitors (Parsons 2002), leaving managers struggling to maintain a balance between recreation and conservation. The intrinsic fragility of tundra ecosystems, along with the increased human presence in these areas and the predicted stresses of climate change, create a growing need to increase our understanding of how human activity impacts these communities and how these impacts can best be managed.

Despite this need, the response of tundra communities to human disturbance has not been as extensively studied as that of other biomes, such as boreal or temperate forests, and most of the work that has been done has focused on the arctic, leaving alpine communities severely under-represented in the literature. The majority of the arctic disturbance literature examines the impacts of large-scale industrial disturbances, but there is little work on the impacts of recreational activities. In contrast, though the literature on human disturbance in alpine ecosystems is sparse, it is generally more focused on recreational impacts.

Studies of the impacts of recreation in tundra communities cover a variety of activities; the most commonly addressed are skiing, hiking and camping, and, to a lesser degree, horse riding. They also focus on different elements of the affected system: plant community studies alone have looked at changes in vegetation cover, composition, biomass and structure. The geographic scope of these studies includes mountain ranges on every continent, all of which experience different environmental conditions and support a wide variety of plant communities. Tropical alpine ecosystems, for example, are very different from alpine communities in temperate regions in terms of temperature cycles (Billings & Mooney 1968), snow cover (Billings 1974) and the strength of insolation (Billings

1974). Communities in the midlatitudes can also be very different from one another: for example, the Australian alpine environment is milder and wetter than that in Colorado (Growcock 2005), though both occur at latitudes of roughly 40 degrees. As a result, the tundra communities found in these two regions are very different. Even within a local area, tundra can include a wide range of community types, largely due to differences in topography and soil moisture. Unlike other biomes, the tundra is not characterised by a dominant life form (such as grasses or trees in prairies and forests, respectively: Bliss et al. 1973). There are many different types of tundra (shrub tundra, sedge tundra, fellfields, etc.) within a single region and this presents a challenge when it comes to identifying processes and patterns that are common to the biome as a whole.

Given the variation in tundra communities, as well as the geographical reach of the studies of recreational impacts on tundra, it is not surprising that the findings of tundra disturbance studies vary widely. The distribution of tundra spans the globe, from the tropics to the poles, and the plant communities found in different locales can differ dramatically as a result of differences in environmental conditions such as insolation, growing season length and daily maximum temperature. For this reason it is difficult to extrapolate the results from one study to another region or community type. A better understanding of the effects of disturbance in tundra communities as a whole might require studies to be undertaken in different community types and in different geographical areas.

The goal of this project was to examine how recreational activities impact an alpine tundra community in the front ranges of the Canadian Rocky Mountains. I examined the vegetation on, near and away from trails, as well as abiotic changes such as soil compaction. This project is primarily being done to obtain information that will be useful for the management of the study area, but it will also make an important contribution to the body of knowledge in the field, as it has a couple of attributes that make it unique. First, this study was conducted in the Canadian Rockies, which are under-represented in the alpine disturbance literature, and second, it looked at the impacts of human activity both on established trails and on the trailside environment, whereas most similar studies only look at trail conditions. In addition, I compared the effects of natural and human disturbance within a single alpine community, to gain insight into how their effects differ.

The importance of alpine conservation

The conservation value of the tundra is not always as clear as that of other biomes. Tropical forests, for example, are known for their high levels of biodiversity (Olsen & Dinerstein 2002), while the economic importance of the boreal and temperate forests of North America creates an impetus for the proper management of these ecosystems. Alpine tundra has little in the way of large-scale extractable resources, and tundra communities are often species-poor compared to communities in more temperate climates. However, there are several reasons why alpine tundra should be a conservation priority in Alberta.

First, the alpine tundra sub-region in Alberta is not very extensive, covering only 2.3% of the province's land base (Alberta Conservation Information Management System [ACIMS] 2006). ACIMS describes this sub-region as being "largely unvegetated", which indicates that the amount of land that supports tundra plant communities is likely much less than 2.3%. Despite its limited extent, however, and despite the fact that alpine areas are typically not hotspots of biodiversity, mountain regions often *are* hotspots for rare and endemic species (Gould 2007), and this holds true for Alberta's alpine sub-region, which contains 15% of the province's tracked plant species (species which are provincially rare and/or threatened; Kemper 2009).

Another reason why it is important to conserve the alpine tundra in Alberta is that it is primarily located in protected areas. Between Jasper, Waterton and Banff National Parks, Willmore Wilderness Park, and a number of smaller provincial parks in the Rockies, the majority of the alpine sub-region in Alberta falls into either federal or provincial protected areas. These protected areas share broadly similar mandates: they aim to conserve ecological integrity while providing opportunities for recreational activities (Government of Canada 2000; Government of Alberta 2009), and it is important that the latter part of this mandate does not interfere with the former. In addition, alpine areas are recognised for their outstanding aesthetic value, and because perceived impact affects visitor experience (Leung & Marion 2000), degradation of these areas could hinder their recreational value as well as their ecological integrity.

The remainder of this introduction will focus on reviewing the literature about disturbance in tundra communities, with an emphasis on the impacts of recreational activities on plants and soils at the individual, community, and ecosystem level. I will also discuss factors that influence communities' susceptibility to damage by disturbance, as well as observed and projected recovery times for disturbed tundra.

The impacts of recreational activities on alpine and arctic tundra

As mentioned above, the literature in this field is diverse: it includes studies from several continents and covers a wide range of topics. In order to organise the findings of these studies, I will discuss different types of recreational impact studies, and then go on to discuss their findings. The focus of my thesis is human impacts on alpine tundra in temperate regions, thus studies from tropical alpine areas will not be reviewed because of the many environmental and ecological differences between the two. Arctic tundra, however, is similar to North American alpine tundra in many ways, including many of the plants and plant communities that each supports (Billings 1974). Because of this, I have chosen to review studies from the arctic along with studies from mid-latitude alpine regions. Before continuing it is important to make one clarification of the terminology that will be used in this thesis. The vast majority of studies examining the impacts of recreational activities on plant communities have only looked into the impacts of foot traffic. The impacts of vehicle traffic on plants has not received nearly as much attention. For this reason the term “trampling” is often used when discussing recreational impacts on vegetation. Although the word trampling connotes foot traffic, I will use the term to refer to both foot and vehicle use on plant communities.

Experimental vs. descriptive studies

Studies of the impacts of recreational activities on tundra communities have been either descriptive or experimental in nature. Descriptive studies look at an ecosystem once it has been disturbed and note how trampled areas differ from undisturbed areas, while experimental studies involve first disturbing an intact system and then noting how it subsequently changes. The experimental studies have the advantage of being able to control variables such as the intensity and the type of disturbance (e.g.: hiking, horse riding, etc.). Their weakness is that they usually provide a very short-term and spatially-limited look at the system in question: many of these studies look at the effects of trampling over a single season (Cole 1995a, 1995b; Monz 2002; Whinam & Chilcott 1999; Whinam et al. 1994), though some studies have applied experimental trampling over a longer time frame, typically three or four years (Cole & Monz 2002; Whinam & Chilcott 2003). Descriptive studies have the advantage of analysing the state of an ecosystem after a longer history of chronic stress, and as a result they might be more representative of actual long-term community responses. The biggest disadvantage of this type of study is the lack of controls: the intensity of use and the types of activities that occur on the study site are not controlled and in some cases might be unknown.

Previous research has focused on a number of different response variables. The most commonly studied responses are changes in vegetation structure, including changes in plant cover (Monz 2002; Cole 1995a, 1995b; Whinam & Chilcott 1999, 2003; Cole & Monz 2002; Bell & Bliss 1973; McDougall & Wright 2004), vegetation height (Cole & Monz 2002; Monz 2002; Gremmen, et.al. 2003) and biomass (Whinam & Chilcott 1999, 2003). Changes in species composition (Cole & Monz 2002), richness (Gremmen, et al 2003; Monz 2002) and diversity have received much less attention than structural changes. There are a number of studies that look at the attributes of trampling-tolerant plants versus those of more sensitive plants (e.g.: Cole 1995b). Abiotic changes, such as surface profile change (Whinam & Chilcott 1999, 2003), percent bare ground (Monz 2002) and soil compaction (Monz 2002; Grabherr 1982) have also been studied.

Individual Plant Responses

Recreational activities lead to the trampling of plants, which can result in the breakage of leaves and stems, causing the plant to become weakened, and sometimes leading to plant death. Damage to and loss of leaves compels the plant to spend more energy growing new leaves, and, as a consequence, the development of the root system suffers, potentially leading to a further weakening of the plant (Liddle 1997). Trampled plants are often smaller in size and have reduced reproductive capacity compared to undamaged plants (Hartley 1979).

Not all plant species are equally sensitive to trampling, and there are a number of studies devoted to examining the characteristics that make some plants more sensitive to trampling damage than others. One of the most important characteristics in determining a plant's ability to withstand trampling is its morphology (Cole 1995b). Morphology can describe many aspects of a plant's structure, such as leaf-stem architecture (also called growth form), structural group (herb, shrub, graminoid), woodiness, stature, and leaf shape and size. Christen Raunkiaer's life form classification system (Raunkiaer 1934) classifies plants according to where on the plant the perennating bud is located; this system has also been used as a basis for comparing trampling tolerance.

Some studies separate species' ability to withstand trampling into three distinct categories. The first of these is resistance, which is the ability to withstand trampling without breakage or other changes to the plant. The second is resilience, which is the ability to recover following a period of trampling, and the third is tolerance, which is the ability to withstand repeated cycles of trampling and recovery (Cole 1995b). While some authors distinguish clearly between these three terms, others appear to use them in a generic fashion, or use the term "durability" to discuss species' ability to withstand trampling without defining precisely what this term means (e.g., Gremmen et al. 2003; Willard & Marr 1970; Whinam & Chilcott 2003; Pounder 1985). Because this thesis is not solely concerned with the relationship between morphology and the ability to withstand trampling, and because I want to keep this overview brief, I will not distinguish between these three characteristics in the following summary. Throughout the rest of this thesis I will use the term “tolerance” to discuss the ability of plants to withstand (i.e., survive in the face of) trampling, as the definition of tolerance given above focuses on species’ ability to survive repeated trampling, which is what plants growing on recreational trails experience.

Morphological characteristics that are commonly associated with greater ability to withstand trampling include: caespitose (tufted), rosette or matted growth forms (Cole 1995b; Cole & Monz 2002; Kuss 1986), short stature (Price 1985), cryptophytic or hemi-cryptophytic life form (Cole 1995b), strong, flexible leaves and flexible stems (for woody species) (Cole 1995b; Cole & Monz 2002; Monz 2002;). Grabherr (1982) found that trampling-tolerant species in the Austrian Alps tended to have narrow leaves and relatively large rhizomes, and graminoids in general tended to fare well (Pounder 1985; Cole 1995b; Bates 1935; Price 1985; Whinam & Chilcott 2003; Gremmen et al. 2003). Plants that have one or more of these characteristics might even increase in abundance in high-traffic hiking areas (Price 1985).

Plants that do not tolerate trampling well include brittle woody plants (Price 1985; Cole 1978), tall herbaceous plants (Price 1985; Cole 1995b), upright growth forms (Cole 1995b) and chamaephytes (Cole 1995b; Cole & Monz 2002). Lichens, particularly fruticose species, also appear to be quite sensitive (Liddle 1997; Grabherr 1982; Monz 2002). Cushion plants do not appear to be hardy to trampling (Whinam & Chilcott 2003; Gremmen et al. 2003) although if trampling pressure is low enough, they might be able to persist in trampled areas as they are well-adapted to the harsh environmental conditions that are often found on alpine trails. Their closely packed stems and leaves can moderate the cushion's internal temperature by trapping warm air, and cushions have been found to be able to conserve moisture in the soil beneath them (Körner 2003). In addition, the cushion life form acts as a litter trap, allowing the plant to access extra nutrients in nutrient-poor environments (Körner 2003).

Some morphological groups, including shrubs, have shown mixed responses to trampling (Cole 1995b; Whinam & Chilcott 2003). Monz (2002) found that low levels of trampling had little effect on tundra dominated by prostrate shrubs, while Gremmen et al. (2003) found that shrub cover was lower on trails than in the surrounding tundra. Forbs and bryophytes have also shown mixed responses to trampling (Cole 1995b; Whinam & Chilcott 2003; Gremmen et al. 2003; Grabherr 1982; Cole & Monz 2002).

Community Level Responses

Richness & Diversity

The most obvious change that trampling causes in alpine plant communities is a decrease in plant cover on trafficked areas. Effects on species richness and diversity are less straightforward. Although the Intermediate Disturbance Hypothesis (IDH; Connell 1978) predicts that diversity will peak at moderate levels of disturbance, there is reason to believe that the IDH should not apply in tundra ecosystems. This is because the IDH is based on a trade-off between the ability to colonise and the ability to compete, but competition is not believed to be an important factor in tundra communities (Callaway et al. 2002; Pierce et al. 2007). Actual study results have been mixed, however. Gremmen et al. (2003) noted a decline in richness following trampling, while Growcock (2005) and Monz (2002) found that richness did not decrease significantly after experimental trampling. Richness appears to be the only measure of diversity that has been examined in tundra trampling studies; other common indices such as Shannon's H' have not been used.

Exotics

Introduced exotics are believed to be less of an issue in tundra communities than in more temperate ecosystems, because common ruderal species are usually not well-adapted to the stresses of the tundra environment (Price 1985). There have, however, been some cases of exotic plants invading tundra communities. Some hardy species, such as *Taraxacum officionale* Weber, can survive in disturbed alpine environments where native species are less competitive (Price 1985). In northern Russia there is evidence that exotics have moved into some arctic-alpine communities in the Ural Mountains (Forbes et al. 2004), and exotics were found along trails on subantarctic Marion Island (Gremmen et al. 2003) as well as on alpine trails in Australia (Hill & Pickering 2006) and the western United States (Weaver et al. 2006). Weaver et al. (2006) did note, however, that the abundance of exotics in tundra communities was far lower than it was in lower-altitude communities surveyed. Only a few studies that have looked for invasion by exotic species in disturbed tundra systems have failed to find evidence of its occurrence

(Whinam & Comfort 1996; Grabherr 1982), suggesting that the colonization of tundra by exotic species might be more common than previously thought. However, the paucity of studies that reported an absence of exotics might not be representative of the actual situation: most recreation impact studies do not discuss exotics – possibly because none were encountered at the study site.

In many cases the main vector for the introduction of exotics is horses (Price 1985). In other cases humans introduce these species to the tundra environment for the purpose of revegetation. Hardy (and non-native) grasses are common components of revegetation seed mixtures, which are sometimes used to restore abandoned trails (Scherrer & Pickering 2006). In some cases these introduced grasses can persist, at least in the short- to medium-term (Scherrer & Pickering 2006).

Changes in composition

When an alpine system undergoes chronic, intense trampling, we might expect to see a shift in community composition in favour of plants that are able to withstand the trampling. Graminoids and species with caespitose or rosette growth-forms, for example, might increase at the expense of sensitive plants, such as tall forbs or brittle shrubs. Very few studies of recreational impacts have actually looked at compositional changes, however. Cole & Monz (2002) did examine the effects of trampling on species composition in Wyoming, and found that changes in composition were minor in the alpine communities studied. In a study of experimentally denuded plots in Colorado, Ebersole (2002) found that the composition of the regenerating plots was indistinguishable from undisturbed controls. However, the experimental plots were not trampled, and did not experience the chronic stress and soil compaction that accompanies recreational activities. As a result these plots might not be a very good predictor of the effects of trampling on species composition.

Ecosystem Level Responses

Soil compaction and erosion

Recreational activities are usually channeled along a particular route, which results in trail formation and local soil compaction. Erosion often follows as the vegetation that would normally anchor the soil is lost. The severity of erosion is partly determined by slope angle (Liddle 1997) as well as the geomorphological and climatic characteristics (precipitation & wind) of the trail environment (Summer 1986). Soil compaction can result in reduced permeability to water (Liddle 1997; Pounder 1985), which in turn can put increased stress on the plants living in this soil. Soil compaction can also aggravate erosion by increasing surface runoff (Batey 2009). The loss of soil pores can hinder the establishment of seedlings by making it difficult for them to develop sufficient root biomass (Bassett et al. 2005) and can also impede a mature plant’s ability to expand its root network (Liddle 1997).

Only a couple of studies have specifically addressed the effects of recreational traffic on soil compaction and erosion in tundra ecosystems. Monz (2002) found no appreciable increase in soil compaction following even the highest levels of experimental trampling on dry shrub tundra in Alaska, but he did find that soil compaction increased significantly after trampling in a cottongrass community. Willard & Marr (1970) noted that trampling led to patches of bare ground; in these patches erosion washed away the finer particles, leaving behind a gravelly substrate.

Effects on litter

Trampling can affect plant litter in a variety of ways: by reducing the amount of litter present, by breaking litter up into finer components, or by compacting the litter layer (Liddle 1997). In a forest, trails can have a substantial litter layer because of the leaves that fall from the trees above the trail. In alpine areas, though, all the plants are low-lying and as a result, litter deposition is quite localised. Thus, on alpine trails we would expect to see very little litter, as there is very little plant cover. Litter is an important source of nutrients which can be recycled back into the soil system (Brady & Weil 2000). Thus, a loss of plant litter on trails would likely result in a loss of soil nutrients. The loss of litter can also result in increased runoff and erosion (Frissell 1978) and colder soil temperatures as the insulating effect of the litter is lost (Edwards & Cresser 1992).

Effects on cryptogamic soil crusts

Cryptogamic soil crusts (also known as biological soil crusts, cryptobiotic crusts, or simply soil crusts) are thin crusts made up of mosses, lichens, bacteria, fungi and/or algae that often form on the soil surface in arid regions, particularly in deserts and tundra (Belnap & Gillette 1998). Soil crusts have several important ecological functions. They can moderate soil temperatures – either increasing or decreasing ground surface and soil temperatures, depending on the colour of the crust (Gold 1998). Cryptogamic crusts also fix nitrogen (Belnap & Gillette 1998), which is believed to be a limiting factor in the growth of tundra plants (Bowman et al. 1993), and can increase soil nutrient retention (Belnap 1993). The impacts of trampling on soil crusts in desert environments have been fairly well-examined; these studies have found soil crusts to be sensitive to trampling by humans (Belnap & Gillette 1998). Tundra soil crusts have not investigated to the same degree, but a study of caribou trampling found that low-intensity trampling can benefit soil crust organisms as it creates variations in soil microtopography and microenvironments (Csotonyi & Addicott 2004). However, these microtopographical variations and their benefits to cryptogams are lost when trampling pressure is high.

Soil nutrients

The loss of litter and of nitrogen-fixing plants and cryptogamic crust can lead to changes in the levels of nitrogen and other nutrients on disturbed areas in the tundra. There is some disagreement as to the importance of nutrients in alpine systems: some say that because alpine plants are adapted to low nutrient levels and use available nutrients very efficiently, soil nutrient losses are not terribly problematic for these plants (Körner 1989). On the other hand, Theodose & Bowman (1997) found that fertilization of dry alpine tundra with nitrogen and phosphorus led to an increase in plant species diversity, indicating that tundra plants do respond to changes in soil nutrient levels. As explained above, soil compaction can cause changes in nutrient status of the soil as well as the ability of plants to uptake these nutrients (Batey 2009).

Factors that influence the degree of damage

Not all recreational activities produce the same degree of impact, and different types of tundra communities have different levels of susceptibility to human disturbance. While the impacts of different activities have not been compared in tundra communities, Weaver & Dale (1978) found that in forests and grasslands, horses had the highest impact in terms of vegetation compaction, loss of vegetation cover, soil compaction and trail incision. Weaver & Dale found that hiking had the lowest impact on the community, while the effects of motorcycles were intermediate. Kay (1981) found that off-highway vehicle (OHV) use resulted in more erosion and a greater loss of species richness compared to hiking in montane and subalpine environments in Utah.

Vegetation type also influences how well a community can tolerate recreational traffic. As mentioned above, morphology is one of the strongest predictors of a plant's ability to withstand trampling pressure. All other factors being equal, a community that is dominated by a highly tolerant morphotype, such as grasses or sedges, would likely be able to tolerate trampling better than one dominated by more fragile vegetation types, such as lichens or tall forbs. Indeed, Cole & Monz (2002) found that graminoid-dominated alpine communities were highly resistant to trampling damage, while Cole (1995b) found that heath communities dominated by *Phyllodoce empetriformis* (Smith) D. Don were only moderately tolerant of trampling.

Moisture level appears to be one of the strongest predictors of how easily tundra communities are disturbed. By and large, studies of trampling as well as other human and natural disturbance types have found that wet communities are more easily disturbed than dry communities (Ebersole 2002; Forbes et al. 2001; Gremmen et. al 2003; Monz 2002; Willard & Marr 1970). It is not clear why this is the case, though Gremmen et al. (2003) hypothesised that this is because footsteps in wet environments tend to sink into the substrate, causing soil compression and damage to underground organs.

Slope is another factor that affects an ecosystem's susceptibility to damage from recreational acitivities, partly because there is more erosion on slopes than on flat ground (Leung & Marion 2000). Weaver & Dale (1978) and Kay (1981) found that erosion on slopes was much higher than on flat ground on both OHV and hiking trails. On the other hand, trails on slopes are often narrower (Price 1985; Gremmen et al. 2003); it appears that hikers are more likely to fan out and walk abreast in flatter areas, but tend to remain single file on slopes. So while the rate of erosion might be greater on slopes than on flat land, the affected area is smaller. Gremmen et al. (2003) also noted that while there was more bare ground (less plant cover) on trails on slopes than on paths in flat terrain, species richness was greater on these trails.

Regeneration of disturbed tundra communities

Natural (unassisted) revegetation in tundra communities is reputed to be extremely slow, but in reality, time frames for recovery are largely unknown. Willard et al. (2007) estimated that it would take over 100 years for a disturbed alpine community in Colorado to fully recover from trampling. Interestingly, they found that total plant cover increased and then sharply declined over a 42-year recovery period during which sample plots were protected from trampling. This indicates that recovery might not be a linear process. Willard & Marr (1971) found that alpine tundra in Colorado that had only experienced trampling over one season recovered completely within a year, while areas that had been trampled for nearly 40 successive seasons did not show any signs of recovery after four years of protection from trampling.

A number of factors contribute to this slow recovery rate. First, seedling establishment can be difficult in alpine environments due to needle ice (which uproots the seedling) (Körner 2003). Bare, compacted soil and the absence of associated vegetation cover to offer shelter from the wind and cold result in a less than ideal seedbed. Ebersole (2002) hypothesized that low soil nitrogen can also slow the establishment and growth of seedlings. Finally, tundra plants in general tend to be slow-growing and long-lived by nature (Willard et al. 2007).

Soil moisture seems to be the biggest driver of recovery times in tundra communities. Generally, wet communities recover faster than mesic communities, which in turn recover faster than dry communities (Forbes et al. 2001). This pattern has been found in both the arctic (Forbes et al. 2001) and in the alpine (Ebersole 2002). The reasons why soil moisture is so important are unclear. One possibility is that wetter substrates remove the danger of desiccation for young seedlings, allowing for higher survivorship and a faster return to pre-disturbance cover values (Ebersole 1987). Differences in recovery times could also be due to the growth forms of dominant species in wet communities – most wet communities that have been studied have been sedge meadows, and the quick recovery times might be a function of the rhizomatous nature of these species (Khitun 1997).

As seen in the above review, much has been learned over the past few decades about the impacts of recreational activities on tundra plant communities. However, there remain many unanswered questions. This project aims to add to the knowledge base already established, as well as to answer some questions that have been neglected thus far in the literature.

Objectives

The goal of this project was to assess the impact of recreational activities on the alpine plant communities at a site in the Front Ranges of the Canadian Rockies. I approached this goal by addressing the following three objectives:

Objective 1: Examining trail conditions

This objective was broken down into three smaller questions:

Question i: how does the vascular plant community on an alpine trail differ from the adjacent tundra? There is no way of quantifying exactly how recreation has changed conditions on the trail, as there are no pre-disturbance data for the area.

However, the area where the trail is now located was presumably similar to the adjacent tundra meadows prior to disturbance, so comparing the trail to nearby tundra allowed me to get a sense of what changes trampling has caused.

Question ii: How does the plant community on the trail compare to that in a naturally sparsely-vegetated alpine area? Naturally barren environments, such as scree slopes and fellfields, are superficially similar to trails (i.e.: rocky, exposed and sparsely vegetated). However, the two have never been compared to see how ecologically similar they are. In this section I will address the question about whether the trail environment is unique compared to the surrounding alpine ecosystem, or whether trampling simply causes a shift from one naturally occurring community type to another.

Question iii: How do conditions on a multi-use trail compare to conditions on an OHV trail? Although Cardinal Divide has been used by OHV users in the past (and low-levels of this use continue to this day), the Cardinal River Headwaters trail likely experiences heavier usage than the Divide ever did, with up to 700 passes/month during the summer (Alberta Sustainable Resource Development, unpublished data). OHVs are much heavier than the average hiker, and this difference in weight could result in different degrees of disturbance to plants and soils on the trail. OHV wheels also churn up soil and tear vegetation.

Objective 2: Examining trailside conditions

For this objective I addressed the question of whether the impacts of recreational activities are limited to the trail, or whether there is evidence of off-trail effects in terms of soil and plant community conditions. While previous studies have examined on-trail conditions, the issue of possible edge effects associated with trails has been poorly addressed in the literature. The tundra adjacent to established trails might show signs of impact due to low-intensity trampling caused by trail users wandering off the trail to take photos, examine plants or rocks, or to avoid degraded areas on the trail. For this reason I decided to look into changes in the vascular plant community along the gradient from the trail edge to 50 m away.

Objective 3: Examining the impacts of recreation on rare species

Finally, I wanted to examine the response of rare vascular plants to recreational activities. Because the study area contains a large number of rare plant species, and because of the land's protected status, it is important to know whether human activities are impacting these populations. I approached this by analysing the location of rare plants in relation to the trail, to see if proximity to the trail is associated with lower abundances of rare plants.

2. Methods

Study Site

Most of the fieldwork for this project was carried out in Whitehorse Wildland Provincial Park, which is located in the Nikanassin Range of the Canadian Rockies, near Cadomin, in Alberta, Canada (Figure 2.1). Alberta has seven different types of provincially protected areas which span a continuum: those at one end of the continuum are focused primarily on recreation, while those at the other end are focused on ecological conservation. Wildland Provincial Parks lie roughly in the middle of this continuum: their purpose is to protect natural ecosystems while also providing opportunities for backcountry recreation, including limited use of motorised vehicles in some areas (Government of Alberta, no date). Whitehorse Park can be sub-divided into two areas: 1) Cardinal Divide and the Tripoli-Prospect ridge, both of which are predominantly alpine, and 2) the Whitehorse Creek basin, which lies mostly below treeline. The majority of the data for this project were collected on Cardinal Divide.

Cardinal Divide (Figure 2.2) is a road-accessible alpine ridge located in the southern portion of the Park (52˚53'N, 117˚15'W). The area is believed by some to be a glacial refugium (Packer & Vitt 1974, but see Strong 1999) and is a hotspot for rare and disjunct species (Achuff 1984). At approximately 2000m a.s.l., it is a dry, exposed ridge underlain by calcareous substrate. The bedrock geology of the area is dominated by limestones, sandstones, shales and dolomites

(Achuff 1984). Despite its relatively low altitude, the Divide is primarily an alpine environment. The most common plant community is dry tundra meadows dominated by *Dryas integrifolia* M. Vahl. *Carex rupestris* All., *Hedysarum alpinum* L. ssp. *americanum* (Michx.) and *Hedysarum boreale* Nutt. are also abundant in this community type. Depressions and gullies support snowbed communities that differ in composition from the surrounding tundra. Krummholz patches, made up of *Picea engelmanii* Parry *ex* Engelm. and *Abies lasiocarpa* (Hook.) Nutt., and surrounded by heath communities dominated by *Phyllodoce* spp. and *Cassiope tetrgona* (Bong.) D. Don are common on the Divide. The south-facing slope of the Divide is treed, while the north face for the most part is not.

In terms of climate the Divide is located at the interface of two Köppen climate categories: Dfc (cold, wet forest) and ET (tundra) (Achuff 1984). Specific climate information is not available for the Divide, but some data have been collected at two nearby locations: Grave Flats lookout (2075m) and Mountain Park (1780m), located 25km southeast and 4km northeast of the Divide, respectively. These records show that the mean warmest month (July) temperature in the area is about 10°C while the mean coldest month (January) temperature is around -17°C. Mean annual precipitation is approximately 700mm, the majority of which falls outside of the summer months (June – August) (Achuff 1984).

From the 1970's to the late 1990's the Divide was open to off-highway vehicle

(OHV) users, horseback riders, mountain bikers and hikers (Joyce Gould, personal communcation). These activities led to extensive damage to the alpine vegetation, including the formation of multiple, parallel trails, the creation of ruts and tire tracks, denudation of previously vegetated areas and soil compaction. In the late 1990's the Alberta Native Plant Council began restoration work on the Divide, which involved delineating a single "main" trail with rocks in an effort to channel traffic onto that trail while allowing secondary paths to revegetate. These efforts were mainly focused along the first few hundred metres of the trail on either side of the access road. In addition they planted locally-sourced native species in denuded areas and built water bars in an attempt to control erosion on slopes by diverting water away from the path. Since the incorporation of Whitehorse Wildland Park in 1998, recreational activity on the Divide has been limited to foot traffic; however, there remain some OHV users who ignore the new restrictions (V. Crisfield, unpublished data). Currently two main trails remain on the Divide, one on each side of the access road. Both trails are about 2km long, and both have varying degrees of braiding. Secondary trails (which are more vegetated than the main trail) are still present in many places. While the trail on the west side of the road follows a fairly flat ridgetop, the trail on the east side of the road ascends a steep thrust fault. Erosion channels are prominent on the steeper portion of the east trail. All of the fieldwork on the Divide was done west of the access road.

We also surveyed a second alpine site, which was located in the Cardinal River

Headwaters (Figure 2.3). The Cardinal Headwaters valley is located on the southwest side of the Tripoli-Prospect ridge (Cardinal Divide is located on the northeast side of the same ridge). This valley is located outside of Whitehorse Wildland Park, with the upper valley – generally the area above treeline – falling into the Coal Branch Forest Land Use Zone (FLUZ). The Headwaters valley contains a 15km long trail that has been used by OHVs for approximately 15 years, though it existed as a horse trail before that. It is uncertain exactly how long the trail has been there, though it is no older than 30 years (J. Gould, personal observation). The area is ecologically similar to the Divide except that it is a valley rather than a ridge, and is therefore wetter, as evidenced by the abundance of willow communities in the area. However, the uppermost part of the valley supports *Dryas*-dominated tundra communities very similar to those on the Divide; confining sampling to this area allowed for comparison of the effects of OHVs to those of hikers.

Sampling Design

Field work for this project was done during the summers of 2008 and 2009. In order to answer the questions laid out in my objectives, I needed to collect data on established trails, on intact tundra, and on naturally rocky areas. Data regarding conditions on trails and on the adjacent tundra were collected in a series of transects that covered both the main trail and the surrounding tundra on Cardinal Divide and in the Cardinal River Headwaters. Data about conditions on naturally barren alpine environments were collected on a series of naturally-formed gravel steps located approximately 2km away from the main trail site on Cardinal

Divide. A rare plant survey was also done on the Divide.

Conditions on and adjacent to trails on Cardinal Divide and in the Cardinal River Headwaters

In order to address the questions laid out in Objectives 1 and 2, we set up 42 transects in *Dryas*-dominated tundra perpendicular to the trail on the Divide in a study area beginning at the trailhead and extending 1.5km along the trail on the west side of the access road. To avoid having the transects clumped within a certain section of trail, we first separated the working distance into five 300m sections. An equal number of transects were then placed at random locations within each of these sections. If the tundra off either side of the trail was equally appropriate for sampling (i.e.: the trailside community was *Dryas*-dominated tundra on both sides) we flipped a coin to determine off which side of the trail the transect would extend.

Each transect started on one side of the trail, crossed it, and then extended 50m away from the trail edge into the surrounding tundra. We placed six 0.5 m x 1 m survey plots at the following distances along each transect: one on the centre of the trail, one on the edge of the trail, and one each at 2 m, 5 m, 10 m, 15 m and 50 m from the trail edge (Figure 2.4). The edge to 15 m section of the transects were considered to be useful for assessing changes in conditions near the trail, where there is likely some low-intensity trampling occurring. The 50 m plots were considered as the reference, the assumption being that at this distance the tundra was most likely experiencing little to no human trampling. In some cases plots fell on areas that showed clear signs of human impact, such as secondary trails or tire tracks. These plots were removed from the dataset.

Unfortunately, because of the ridgetop location of the trail, the effects of slope and topography might be confounded with the effects of human trampling. Many, though not all, of the 50 m plots were located in areas with greater slope than was found in the areas nearer to the trail. In addition, because areas further downslope are less exposed to wind than the ridgetop, they are likely covered by a thicker snowpack in the winter, which can result in differing light and temperature conditions on the ridgetop versus lower slopes. However, this was unavoidable, and was accounted for when considering the implications of the results.

In order to compare impacts found on a multi-use trail to those found on an OHV trail (Objective 1-iii), we laid out 20 vegetation transects along a 1.5km section of the trail in the Cardinal River Headwaters, using the same methods as for the Divide transects. Due to time constraints we did not do 50 m plots in the Headwaters.

Comparison of the trail to natural gravel steps

The movement and sorting of soil sediments by frost disturbance can also lead to the formation of certain groundcover patterns, including sorted rings and nets, steps and stripes. Steps are common on moderate to steep slopes (Nicholson 1976), and are composed of strips of fully vegetated tundra alternating with more sparsely-vegetated gravel patches. These gravel steps bear some superficial resemblance to conditions on the trail: the environment is open, exposed and gravelly and supports only a sparse plant community. By comparing the trail to these naturally disturbed areas, I addressed the question of whether plant communities on the trail are similar to those found on other sparsely-vegetated, rocky alpine environments, or whether they are different due to the presence of human traffic on the trail (Objective 1-ii). An additional dimension of this particular project is that it compared two types of disturbance – one human and one natural.

We carried out this survey on a knoll at the base of Tripoli Mountain, where the vegetation was similar to that on the Divide. Frost disturbance has resulted in stone sorting on this knoll, forming a series of terraced gravel patches that run parallel to the slope contours of the rise (Figure 2.5). To select the locations for our plots, we laid out a series of parallel transects, 5 m apart, placed perpendicular to the gravel steps (Figure 2.6). We walked along each transect until we found a gravel patch that was large enough to accommodate the 1 m x 0.5 m survey plot. We repeated this process until we were able to complete 20 survey plots. Finally, in order to ensure that differences found between these plots and those on the trail were not reflective of overall site differences between the knoll and the Divide, we collected data in five reference plots located on the fully vegetated tundra adjacent to the steps.

Rare plant survey

To address Objective 3 we surveyed for six rare plants on and near the trail on

Cardinal Divide: *Antennaria monocephala* DC., *Braya purpurescens* (R.Br.) Bunge*,* *Campanula uniflora* L., *Carex misandra* R.Br., *Pedicularis flammea* L. and *Saxifraga nivalis* L. *Antennaria monocephala* has been removed from the provincial tracking list since the survey was carried out (Kemper 2009). Rarity was determined by provincial S-ranks, which are an index of how rare and/or threatened species are within sub-national jurisdictions (e.g.: provinces; Kemper 2009). S1- and S2-ranked species were considered 'rare' for the purposes of this project. Species were selected for inclusion in this survey on the basis of S-ranks as well as their likelihood of occurring in the area, based on habitat and previously assembled species lists for the area (primarily Achuff 1984). Ease of identification in the field was also considered when selecting species. In order to maximise our coverage of the ridge, we conducted a number of linear surveys extending perpendicular to the trail down to treeline on both sides of the trail. These surveys were done at every 50 m between the trailhead and 1500 m mark, and at every 100 m from 1500 m to 1800 m along the trail. In a few cases the treeline was only about 50 m from the trail, so some of the surveys were very short. The majority of time though, the surveys extended at least 100 m from the trail, and in a few cases they were well over 200 m long.

Data collection

Vegetation data

Vegetation plots

Data for the vegetation transects at both sites (Divide and Headwaters), as well as for the gravel steps, were collected in 1 m x 0.5 m plots. In each plot, we listed the vascular species present and visually estimated the percent cover of each. I aimed for accuracy levels of 0.1% for cover values between 1-2%, 0.5% for cover values of 2-5%, 1% for cover values between 5-25%, 5% for cover values between 25-50%, and 10% for cover values over 50%. Cover values of less than 1% were simply recorded as <1%; these were then transformed into a value of 0.25% for the purposes of the analyses.

Rare plant survey

Each time we encountered a rare plant we recorded the species, the number of individuals present, the distance from the trail, the distance from the road, slope (if greater than 5°), aspect, moisture level (dry, mesic or wet, based on visual assessment), growth stage (vegetative, in bud, flowering, in seed), and the dominant species in the rare plant's immediate surroundings.

Taxonomy

Species identification was done in the field where possible. A sample of each vascular species encountered was collected and pressed, unless the species was believed to be rare, in which case photographs were taken. Species that could not be identified in the field were keyed out in the lab. All identified species were then compared to herbarium specimens to confirm identification. A few samples were sent out to be identified by a more experienced botanist. Two taxa, *Antennaria* and *Draba*, were only identifiable to the genus level in some plots because they were not in flower and are very difficult to identify with confidence from the leaves alone. To ensure that these taxa were not double counted in richness calculations, I made sure that the plant in question was present as identified either at the species level or at the genus level, but not both, within a single plot.

There were a number of samples that I was unable to identify due either to their extremely small size or to lack of development (e.g.: lack of seedheads on graminoids, etc.). As long as I felt confident that these samples were not members of any of the species we encountered in our surveys, I included them in analyses as taxa at the genus level or as unknown “species”.

Nomenclature follows Moss (1983).

Abiotic and non-vascular data collection

Abiotic and non-vascular substrates

Along with the vascular plant survey that was carried out in the 1 m x 0.5 m vegetation plots, we also recorded percent cover values for rock, soil, lichens, bryophytes, and the exposed cryptogamic soil crust. Lichen and bryophyte species were not individually identified.

Soil compaction

We measured soil penetration resistance (“soil compaction”) in each 0.5 x 1m plot using a Humboldt H-4200 pocket soil penetrometer. This instrument had a scale of 0-4.5kg/cm^2, divided into 0.25kg/cm^2 increments. Compaction measurements were taken on mineral soil as close to plot centre as possible, but in many cases this was not ideal (i.e.: plot centre was covered by a rock or a mat of intact vegetation). In these cases we took the measurement where it would cause a minimum amount of disturbance to the vegetation community. In some cases we had to use a trowel to dig under the vegetation mat in order to expose soil to take measurements on. When doing this we kept the trowel at a low angle relative to the ground in order to not compress the underlying soil while digging. The overlying vegetation mat was pulled back (but not ripped out) in order to expose the mineral soil, on which the measurement was taken. Afterwards we replaced the vegetation mat.

We took additional measures of soil compaction on the trail at the first 20 transect locations on the Divide and at all the transect locations in the Headwaters. At each location we took five penetrometer readings to get a profile of soil compaction across the trail. These were taken at the following positions: one measurement at the trail centre, two at quarterpoints located halfway between the centre and the trail edge (one on either side of the centre), and two 10 cm away from the trail edge (again on both sides of the trail). We also recorded trail width at these locations.

Trail profiles

We measured the depth of incision on the trail by documenting the cross-sectional trail profile. This was done by stretching a measuring tape taut across the trail, 20 cm above ground at the edge on either side of the trail. Every 20 cm along the tape we measured the distance between the measuring tape and the ground surface in order to create a profile of local relief on the trail in relation to the surrounding terrain.

Slope and aspect

Slope and aspect were generally measured at the transect level, using a compass and a clinometer. The exception to this is the 50 m plots: because they were located so far away from our other plots, we measured their slope and aspect separately. In the case of the rare plant survey, slope and aspect measurements were taken for each occurrence of rare plants, except where slope was less than 5°.

Data Analysis

Overview

Analyses consisted of comparing different plot locations (trail, tundra, gravel steps) in terms of several response variables, including total vascular plant cover, vascular species diversity, vascular species composition (cover by species), morphological composition (cover by growth form, Raunkiaer life form or structural group), abiotic and non-vascular cover and soil compaction. Below is a brief explanation of each of these variables and a rationale for including them in my analyses. Analysis of the rare plant data involved examining spatial relationships between the trail and rare plant occurrences.

Vascular plant cover

Vascular cover is an important variable in studies of recreational impacts because one of the most obvious and well-studied effects of trampling is change in vegetation cover. While the trail will obviously have less vascular plant cover than the surrounding tundra, differences in vascular plant cover between plots close to the trail and those further away could be an indication that these communities are being affected by trampling, albeit at lower levels than found on the trail.

Species diversity

Species diversity was quantified using four different indices: species richness (S), two diversity indices (H', D) and evenness (E). Species richness is the number of species found in a plot. Shannon's H' is a very commonly-used index that incorporates both richness and evenness (Magurran 2004). Simpson's D is a robust statistic, which, when presented in its reciprocal form (1-D), forms a diversity index that is easy to understand intuitively, as larger values are indicative of greater diversity (Magurran 2004). It also places less emphasis on rare species than does Shannon's H' (Magurran 2004). Both measures are commonly used in community ecology and allow for comparisons of community conditions under different environmental circumstances. Shannon-Weiner evenness ($E=H'/\ln[S]$) is a measure of how evenly distributed species are within a sample plot: a plot where a number of species occupy roughly the same proportion of the plot will have high evenness, whereas a plot where one species is heavily dominant will have low evenness (Magurran 2004).

Species composition

Because species differ in their ability to tolerate trampling by hikers or vehicles, recreational activities could cause changes in species composition in areas that experience heavy use. Species composition has also been scarcely addressed in studies of recreational impact on tundra communities; more data regarding this dimension of community structure will be useful in the field.

Morphological composition

Because previous research has shown that plant morphological characteristics can affect a species' ability to withstand trampling, I separated my species data into morphological groups and analysed cover according to these groups to see which ones are more common on the trail versus the adjacent meadows and the natural gravel patches. Based on previous literature I decided to categorise species in three different ways: by growth form, by Raunkiaer lifeform, and by structural group.

I used five growth form categories: caespitose, rosette, matted, upright and cushion (Figure 2.7). Four Raunkiaer life forms were present in my study plots: chamaephytes, hemi-cryptophytes, cryptophytes and therophytes (Figure 2.8). In cases where it wasn't obvious which category a species belonged in, I referred to one of a number of publications or websites to find out (Talbot et al. 2006; Bruun et al. 2008; Wang 2004; Crane 1991; Fryer 2008; Gucker 2007; Howard 1996; Williams 1999a, 1999b; Fitter and Peat 1994; Aiken et al. 1999; Martin 1999). Finally, species were divided into structural groups (forb, shrub or graminoid).

Once each species was allocated into one of these groups, I calculated the total cover that was comprised by each group in each plot (e.g.: I summed the cover of all caespitose plants for each plot, all rosette plants for each plot, etc.). I then transformed these values into relative cover values for each morphological group – that is, the percent of the total vascular cover that each group comprised in each plot. This was done by dividing the total cover for each group by the total vascular cover for the plot. Cover was relativised in order to prevent differences in total vascular plant cover between the trail and the off-trail plots from obscuring differences in the proportional representation of the various life forms in the community.

Abiotic and non-vascular cover

Although this study was mainly focused on vascular plant cover and composition, the cover of abiotic substrates (rock & soil) and non-vascular plants and lichens might also tell part of the story. For example, lichens, particularly the fruticose forms, have been found to be very sensitive to trampling (Grabherr 1982). A decline in lichen cover could be an indication that an area has been negatively affected by trampling, even if there are no obvious signs of human impact, such as a decline in total vascular plant cover.

Soil compaction

Trampling can result in an increase in soil compaction. Soil compaction is important in a study like this one because previous studies have found that there is a close relationship between trampling pressure and soil compaction (Cole 1987), and that compaction can be used as a proxy for trampling (Tejedo et al. 2009). At a study site such as this one, where human use has been variable and largely unmanaged, this is particularly useful to get a sense of how trampling pressure varies at different distances from the trail, and between different types of trails (OHV versus multi-use).

Statistical Analyses

For all analyses except for the rare plant survey, location (distance from trail, or trail versus gravel steps) was the predictor variable; ‘transect’, which accounted for the spatial blocking of plots, was a random variable (where applicable); and the various plant and abiotic parameters (cover, richness, etc.) were the response variables. For the rare plant survey, distance from trail and distance from the trailhead were predictor variables, while the presence or absence of rare plants was the response variable.

ANOVA

Depending on the question being addressed and the dataset being used, I used either one-way analysis of variance to test for the effects of location (as explained above), or two-way analysis to test for the effects of site (e.g., Cardinal Divide versus the Headwaters), location (e.g., trail versus off-trail) and interactions between the two. Data were tested for normality and homoscedasticity before proceeding with ANOVA tests. In the case of data that were non-normal or heteroscedastic I used test the Mann-Whitney test for unpaired two sample comparisons, Wilcoxon’s test for paired two sample comparisons, Kruskal-Wallis for multi-sample comparisons, or Friedman’s test, which is a multi-sample non-parametric test for randomised complete block designs (Friedman 1937). The

Shapiro-Wilk test was used to test for normality, while Levene’s test was used to assess variance. Analyses were done using SAS 9.2, PC-ord 4, and R.

For two-way analyses on non-normal or heteroscedastic data I used the Scheirer-Ray-Hare extension of the Kruskal-Wallis test, which is a non-parametric equivalent of the two-way ANOVA. This test involves ranking the original data and running a two-way ANOVA on the ranks. The resulting sums of squares and degrees of freedom are then used to calculate a chi-square statistic, which gives a measure of significance for each variable tested (Scheirer et al. 1976). I chose not to use this test in cases where the data were heavily tied, as it is not designed to deal with tied data. In such instances I used the Kruskal-Wallis test: this test is also not designed for tied data, but SAS provides an option (EXACT) in the NPAR1WAY procedure that is recommended for datasets that contain a high number of ties, and adjusts the p-value accordingly (SAS Institute 2004).

Pair-wise follow-up tests for significant one-way and two-way tests were done using planned comparisons (in the case of normal data) or the Mann-Whitney test (in the case of non-normal data).

Regression & Correlation

Univariate linear regressions were used to assess the significance of patterns of change with increasing distance from the trail; Spearman-rank correlation was used in cases where data could not be normalised. Logistic regression was used to model the presence/absence data collected in the rare plant survey as a function of distance from the trail and from the trailhead, as well as the interaction between the two.

Multivariate analyses

Non-metric multidimensional scaling (NMDS, McCune & Grace 2002) was used to visualise patterns in species composition in relation to plot locations, and distance-based redundancy analysis (db-RDA, Legendre & Anderson 1999) was used to assess the relationship between community composition and the environmental variables measured. Both of these methods allow the user to choose which measure of community similarity to use. In both cases I used the Sørenson (Bray-Curtis) distance measure, because of its suitability for ecological data.

Permutational MANOVA (perMANOVA) is a non-parametric analogue of the MANOVA test (Anderson 2001). It is also a distance-based technique which allows the user to compare the similarity of pre-defined groups using a distance measure of their choice. This method compares within-group distances to between-group distances to come up with a measure of the significance of the differences between groups. PerMANOVA requires balanced data.

Multi-response permutation procedure, or MRPP, is another distance-based technique that works along the same lines as perMANOVA (McCune & Grace 2002). However, MRPP tends to be overly generous in finding significant differences, making it a generally poorer choice for multivariate analysis than perMANOVA. However, this method does not require balanced data, which was an issue with one of the datasets used in this project. In addition, it provides test statistics besides the usual p-value that can also be used to assess the results. These include the test statistic, or T-value (McCune & Grace 2002): a larger negative T is indicative of greater differentiation between groups. For these analyses I once again chose to use the Sørenson distance measure.

Indicator species analysis (Dufrêne & Legendre 1997) detects species whose abundance and frequency are strongly correlated with a certain pre-identified group. An indicator value (IV) is assigned to a species based on its level of fidelity and exclusivity to a single group. There is no hard and fast system for determining which species are important indicators and which are not; however, a p-value of <0.05 and/or an IV of 20 are often used at cut-off points for significance (McCune & Grace 2002).

Objective 1: comparing the trail to the surrounding environment

1-i: Comparisons of the trail to the adjacent tundra

I compared trail plots to edge plots and to the 15 m plots in terms of total vascular plant cover, evenness and diversity, vascular species composition, morphological composition (growth form, Raunkiaer life form, structural group), abiotic and non-vascular cover and soil compaction. I chose to compare the trail to the edge plots because the edge plots are spatially closest to the trail, and for this reason they might be the best estimate of what ridgetop conditions would look like in the absence of human use. However, the trail edge is also likely to be moderately impacted by trampling if hikers and OHV users do not confine themselves strictly to the trail. For this reason I decided to compare the trail to the presumably less-impacted 15 m plots as well (the 50m plots might have been a better representative of undisturbed tundra, but the Cardinal River Headwaters survey did not include plots at this location).

Because trail use and conditions differ between the Divide and the Headwaters, these analyses were done for both sites. However, the Headwaters trail had very little vegetation cover, so analysis for this site was limited to comparisons of non-vascular substrates and soil compaction. All the univariate analyses in this section were done using paired tests (trail versus edge and trail versus 15 m): t-tests for normally-distributed data and Wilcoxon's for non-normal data. Species composition was analysed using perMANOVA and an indicator species analysis.

1-ii Comparisons of the trail to an area of natural disturbance

I compared the trail to frost disturbance formed gravel steps in terms of vascular plant cover, richness, diversity and vascular species composition, morphological composition, and non-vascular and abiotic cover. The locations that were compared in this analysis were the trail plots, the 50 m plots ("trail reference"), the gravel steps, and the plots surveyed on the tundra adjacent to the gravel steps ("gravel step reference"). Two-way ANOVAs were used when possible to compare site (Divide vs. gravel step site) and condition (disturbed vs. undisturbed) as well as the interaction between the two. The disturbed locations included the trail and the gravel steps, while the trail reference and gravel reference plots were considered to be undisturbed. If the data were not amenable to two-way ANOVA or the Sheirer-Ray-Hare extension of Kruskal-Wallis (e.g.: if the data were non-normal and heavily tied), I used one way ANOVAs or Kruskal-Wallis to compare the four locations. If significant differences were found between locations, post-hoc planned comparisons were used to compare the trail to the gravel steps and the trail reference and gravel step reference plots. The rationale behind comparing the two sets of reference plots was to compare the two sites in their undisturbed condition to make sure that the vegetation communities they support were similar. Bonferroni adjustments of the alpha were applied to post-hoc comparisons in order to control Type I error: two post-hoc comparisons were made, so the alpha was adjusted to 0.025 (0.05/2).

NMDS, MRPP and an indicator species analysis were used to look for compositional differences among the four locations. Two pair-wise MRPPs were done for post-hoc comparisons: the trail was compared to the gravel steps, and the trail reference and gravel reference plots were compared. A Bonferroni-adjusted alpha of 0.025 was used.

1-iii Comparisons of an OHV trail to a multi-use trail

Data analysis for this section consisted of comparisons of trail conditions between the Headwaters trail and the Divide trail. I compared soil compaction at the various positions across the trail (edge, centre, and quarter-points), to look for differences in compaction levels at each position on the two trails. To ensure that differences in soil compaction on the trail were not confounded by site differences in soil characteristics, I also ran the same analysis using relativised soil compaction values (i.e.: a ratio of trail:15 m compaction measures), using paired values from within the same transect to calculate each ratio. Both of these analyses were done using the Mann-Whitney test. I also compared trail incision using all the profile measurements from the two sites. This was done using a mixed model ANOVA with transect (nested in site) as a random factor. Finally, I compared the width of the trails between the two sites, again using the Mann-Whitney test.

Because the Headwaters trail had almost no plant cover (only one plot had vegetation growing in it, and it comprised less than 1% of the plot area) I did not make comparisons of vascular cover, richness or diversity between the trails at the two sites.

Objective 2: Trailside effects

Because the objective of this analysis was to look at changes over the distance gradient from the trail edge to 50 m away, I chose regression as the primary method for analysis in this section. Univariate regressions as well as two-sample analysis of variance tests were used to look for changes in morphological composition, non-vascular cover types, soil compaction, richness, evenness and diversity. Because of the absence of data between 15 m and 50 m, a regression of the entire distance gradient would be of questionable validity. Regressions were therefore used to assess changes from the edge to the 15 m plots, while further changes between the 15 m and 50 m plots were analysed using paired t-tests or Wilcoxon's test. Plots from within the same transect were paired for these tests. Blocks (transects) were included in the regressions as a random variable. In addition, I graphed within-transect trends for each of the variables tested in order to visualise the effects of the blocks. Exploratory graphs were used to visualise patterns in the data before regressions were done. Some variables, including total vascular cover, the cover of mosses and soil crust, and the majority of the morphological groups, did not show any distinct pattern with increasing distance. These were not analysed further, but box plots showing the trends for these variables are presented in Appendix 1.

NMDS was used to visualise differences in composition between plots at different distances from the trail, and dbRDA was used to assess how distance, soil compaction and aspect affect species composition. Although slope and aspect were both measured at the transect level, slope was excluded from this analysis because it varied too much within transects to accurately reflect any effects that slope might have on composition. Aspect, on the other hand, was generally consistent within transects. Models using all possible combinations of these variables were run and AIC values were used to select the best model. An indicator species analysis was also run on the off-trail plots.

Objective 3: The impacts of recreation on rare plants

Data regarding the distribution of rare species in relation to the trail were analysed using logistic regression. I separated the transects along which we surveyed for rares into 10 m segments: segments from 0 m to 100 m from the trail were included in the regression. Any rare plants found further than 100 m away from the trail were excluded. This is because our surveys stopped at treeline, and as a result of this they differed greatly in length. Low densities of rare species very far from the trail might indicate that few of our surveys extended to that distance, rather than reflecting a true decrease in the occurrence of rare plants. Most of our surveys did extend at least 100 m, though, making this a safe cut-off point. A total of 96 rare plants were recorded in this survey; 25 of these were excluded from analysis because they were found more than 100 m from the trail.

For each transect, if one or more rare plants were found in a particular segment, I would assign that segment a "yes." If no rare plants were found in that segment, I would assign it a "no." Results from all segments from 0-100 m, from all surveys (50 m -1800 m from the trailhead) were pooled into a single table for analysis. Distance from the trail and from the trailhead were both used as predictor variables, and were considered to be continuous.

Of the four species of rare plants we encountered in our surveys, one species (*Pedicularis flammea*) accounted for the vast majority of occurrences recorded. To find out if these species show individual responses that differ from the overall response as tested above, I analysed the patterns of this species by itself.

Figures

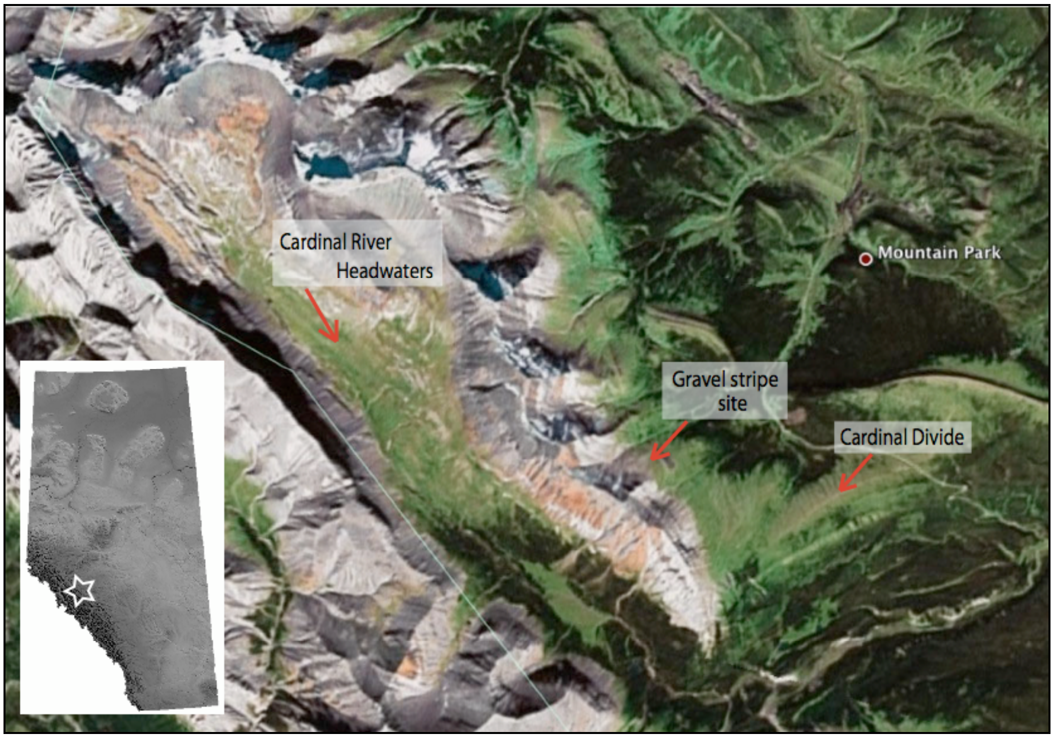

Figure 2.1: Map of Cardinal Divide and the Cardinal River Headwaters. (Image: Google Earth)

Figure 2.2: Looking southwest onto Cardinal Divide. The trail (study site) is visible along the ridgetop. The road intersecting the trail is the access road.

Figure 2.3: The Cardinal River Headwaters trail.

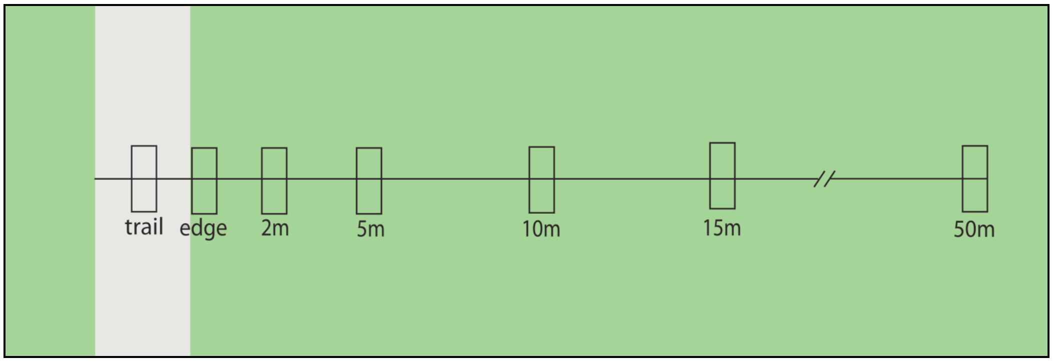

Figure 2.4: The sampling design for the vegetation transects, showing placement of the plots along the transect. The lighter stripe on the left side of the diagram represents the trail and the line represents the transect.

Figure 2.5: Gravel step site. Stone steps are visible in the foreground, running parallel to the slope contours.

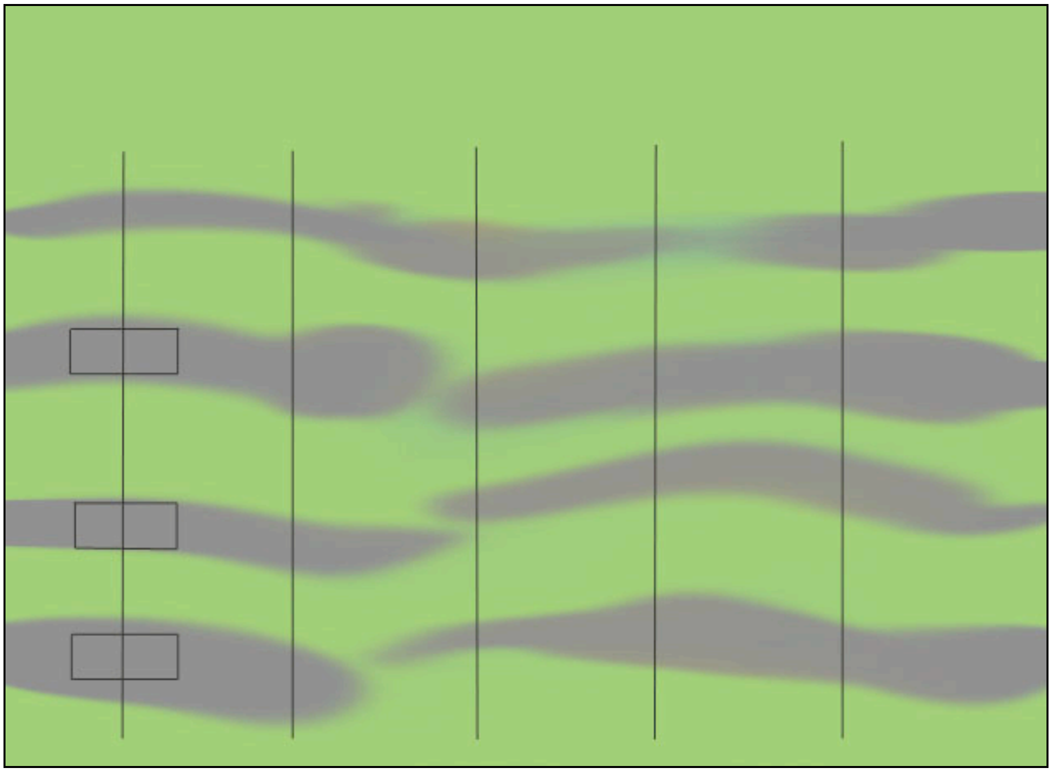

Figure 2.6: The sampling design for the gravel step data collection. Wavy stripes represent the gravel steps, while the background colour represents fully-vegetated tundra. The vertical lines represent the transects we laid out. When the transect intersected with a patch of gravel large enough to accommodate the 0.5mx1m sample plot, we collected data.

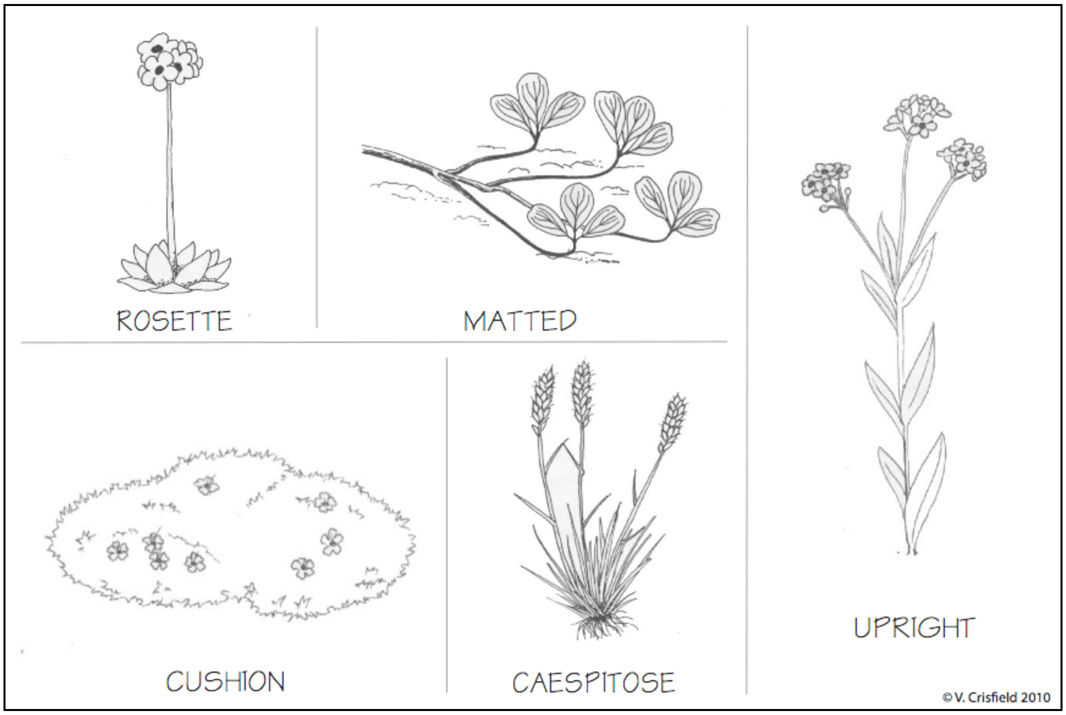

Figure 2.7: Growth forms.

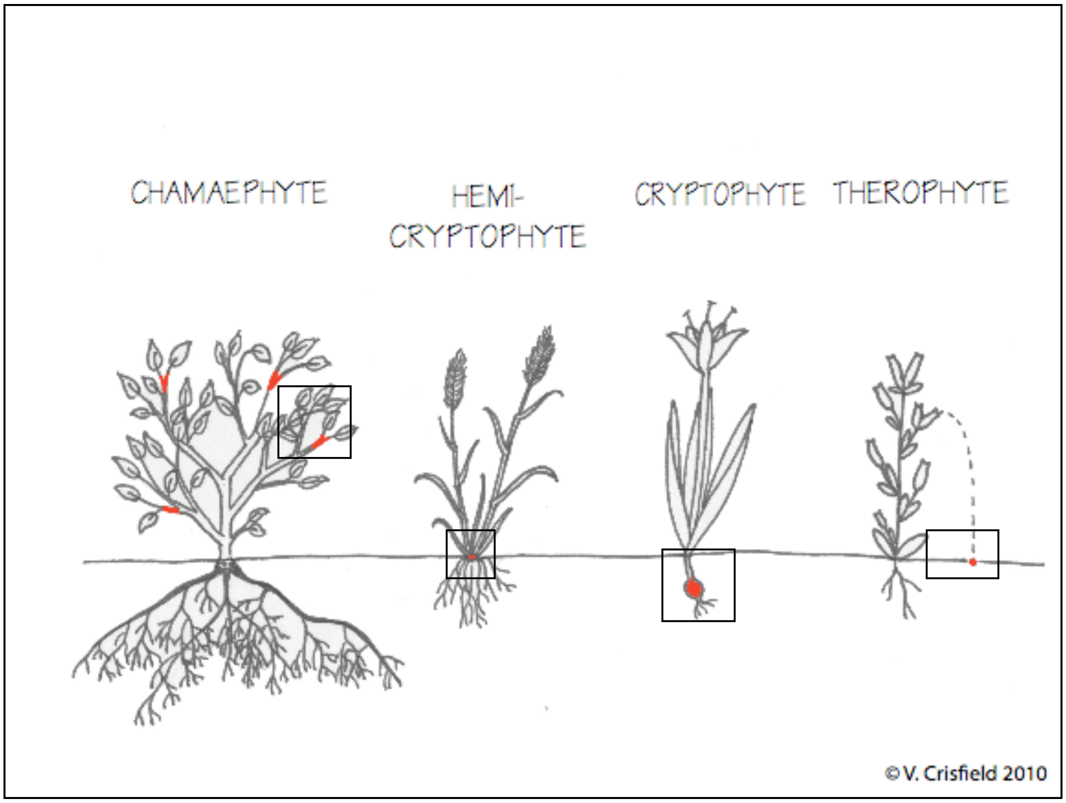

Figure 2.8: Raunkiaer life forms. Perennating buds are outlined.

3. Results

Results will be presented following the same organisational structure that was used to present the objectives; each of the three sections of results will address the questions presented in one of the objectives. First I will present the results of the analysis that examined trail conditions and compared them to the surrounding environment, which addressed questions about how the trail differs from the adjacent environment, including naturally barren areas, as well as the differences in impacts on a multi-use versus an OHV trail. The second main section looked at changes in the community with increasing distance from the trail, to see if there was evidence of impact on the near-trail environment. Finally, the rare plant analysis allowed me to interpret spatial relationships between the trail and the occurrence of rare plants.

We found a total of 73 vascular species on Cardinal Divide, including the gravel step site, 67 of which were identified to the species level (Table 3.1). One taxon, *Minuartia*, was only identified to the genus level due to difficulties with correct identification in the field. Germinants of *Picea engelmanii* and *Abies lasiocarpa* were present, but because of the difficulty of distinguishing between the two species at this stage of development they were lumped together under the heading of “conifer germinant”. Seven species remain unidentified, but as I am confident that all seven were individual species, and do not belong to other species identified at the study site, they were included in the analyses. At the Headwaters site 71 species were found. Five of these remain unidentified and were treated the same as the unidentified species on Cardinal Divide, while another 11 were only identified to the genus level (Table 3.2).

The majority of the data used in these analyses were non-normal; for this reason I will present the median rather than the mean as a measure of central tendency in most cases.

Section 1: Conditions on the trail, and comparisons with the surrounding environment

Differences between the trail and the surrounding environment

The multi-use trail on Cardinal Divide was found to be drastically different from the surrounding community in terms of vascular plant cover, diversity, species composition and morphological composition. Because the OHV trail in the Headwaters was almost completely devoid of plants (only one of 20 plots had any vegetation, and even that comprised <1% of the plot), the only variables that were analysed for that site are the non-vascular and abiotic cover types and soil compaction. Both trails were radically different from the adjacent meadows in terms of these variables.

Vascular plant cover and diversity

Vascular plant cover on the Cardinal Divide trail was significantly lower than on the non-trail plots (both the edge and 15 m plots): mean cover values on trail plots were about 4%, as compared to ~33% for both the edge and 15 m plots (Table

3.3). The trail also had lower richness than did the adjacent tundra; the median number of species on the trail plots was seven, versus nine in the edge plots and 11 in the 15 m plots. In contrast, diversity (both Shannon's and Simpson's indices) and evenness were higher on the trail.

Species composition

Four species were found to be significant indicators for the trail: *Poa alpina* L., *Trisetum spicatum* (L.) Richt. ssp. *molle* (Michx.) Hult., *Deschampsia cespitosa* (L.) Beauv, ssp. *cespitosa*, *Gentiana prostrata* Haenke, *Festuca braychyphylla* Schultes and *Minuartia* spp. (Table 3.4). Several significant indicators were found for each the other two locations, of which four species – *Betula glandulosa* Michx., *Carex rupestris*, *Dryas integrifolia*, *Hedysarum boreale, Kobresia myosuroides* (Vill.) Fiori & Paol. and *Polygonum viviparum* L. – came out as significant for both the edge and 15 m plots. Aside from these four species there were a number of other indicators found for one of the two locations; these are listed in Table 3.4. Two perMANOVA tests comparing the trail to the edge and to the 15 m plots found significant differences ($p<0.001$ in both cases); transects were included as a blocking (random) factor in this test, but were not found to be significant ($p=0.1$ and $p=0.19$ respectively).

Abiotic and non-vascular cover

The trail plots on Cardinal Divide differed significantly from the edge and 15 m plots in terms of all six categories of non-vascular and abiotic cover estimated (Figure 3.1). Rock was by far the dominant cover type on the trail, comprising a median of 71% cover per plot (Appendix 3), versus <20% on off-trail plots. There was also substantially more exposed soil on the trail than on the edge plots and 15 m plots. The other four cover types were more abundant off the trail: lichens, mosses and cryptogamic crust all had fairly low cover values off the trail, but were present only in minute traces on the trail. Litter was the most abundant cover type on off-trail plots, with median cover values of 30-50%, but was only present in small amounts on the trail, with a median cover of 2.5%.

The Cardinal River Headwaters trail was made up almost entirely of rock and soil; other cover types were present only in very small proportions on a few plots (Figure 3.2, Appendix 3). The trail had significantly more soil than the edge plots, but the cover of rock did not differ significantly. The 15 m plots had significantly lower levels of both of these cover types when compared to the trail. Lichen and litter were only present in trace amounts on a few trail plots, while moss and soil crust were completely absent from the trail; unsurprisingly, the differences between the trail and the edge and 15 m plots were highly significant for all of these variables.

Morphological composition

i. Growth forms

The trail on Cardinal Divide had very different morphological composition than the adjacent tundra (Figure 3.3). Caespitose, rosette, cushion and upright growth forms were significantly more abundant on the trail, while matted plants were more abundant in the off-trail plots (Appendix 3). The upright form was the dominant growth form on the trail, comprising nearly half of the trail vegetation.

Caespitose plants were also much more abundant on the trail than off, with a median cover of 12% versus <1% for both the edge and 15 m plots. Cushions were not very abundant on the trail, accounting for only 2% of trail vegetation, but were nearly absent from off-trail plots. Rosettes were more abundant on the trail than off, accounting for 8% of trail vegetation, but only 1-2% on the edge and 15 m plots. Matted plants were the dominant growth form on the off-trail plots, where they made up about 65% of off-trail vegetation. By contrast, they only accounted for 6% of the plant cover on the trail.

ii. Raunkiaer life forms

Three of four Raunkiaer life forms had different proportional abundances on the trail as compared to the off-trail plots on Cardinal Divide (Appendix 3). Hemicryptophytes, mainly graminoids, were the dominant life form on the trail, where they accounted for nearly 75% of the vegetation, versus less than 25% on the edge and 15m plots (Figure 3.4). Conversely, chamaephytes, mainly dwarf shrubs, made up approximately 70% of the cover on the off-trail plots, compared to only 13% on the trail. Therophytes were a minor component of the community overall, but were significantly more abundant on the trail, with 4% cover on the trail versus 1% on the edge and 15 m plots. Cryptophytes were the only group that did not show a clear pattern.

iii. Structural groups

The trail on Cardinal Divide differed from the surrounding tundra in terms of the proportional cover of all three structural groups (Figure 3.5). Graminoid cover was higher on the trail (median cover 55%), compared to the adjacent tundra, where graminoids only made up 5-10% of cover (Appendix 3). Forbs were also more abundant on the trail. Shrubs were much more abundant off the trail, with median covers of approximately 70% on both the edge and 15 m plots, versus only about 6% on the trail.

Soil compaction

Soil on the trail plots was significantly more compacted than on the surrounding tundra at both sites. The median compaction level on the Cardinal Divide trail plots was 2.75kg/cm^2, while the medians for the edge and 15m plots were 1.875kg/cm^2 and 1.5kg/cm^2, respectively (Figure 3.6). The Headwaters trail also had significantly higher compaction levels than both the edge and 15m plots (Figure 3.7). Median compaction on this trail was 4.5kg/cm^2, as compared to 2kg/cm^2 for the edge and 1kg/cm^2 for the 15m plots.

Differences between the trail and natural rocky environments

This analysis was focused on examining differences between the trail and naturally occurring barren environments in the Cardinal Divide area. Four plot locations were used in these analyses: trail, gravel steps, trail reference and gravel step reference. Several differences were found between the trail and the gravel steps, while the two sets of reference plots were, by and large, found to be similar.

Richness and diversity

Vascular plant cover was higher on the gravel steps than on the trail, with a median of 4% on the trail versus 8% on the gravel steps (Table 3.5), while the two sets of reference plots did not differ. Richness was higher overall on the gravel step site than on the Divide, however, follow-up contrasts showed that while the difference between the trail and the gravel steps was significant, the difference between the trail reference and gravel step reference plots was not. The trail had a mean of eight species per plot, while the gravel steps had 11 species per plot. The interaction between site and condition was significant for evenness, and a comparison of LSmeans showed that evenness was higher on the trail than on the gravel steps, while the reference plots did not differ. The only significant difference in Shannon's H was between the trail reference and gravel step reference plots, and there were no significant differences between locations for Simpson's D.

Species composition

The NMDS (Figure 3.8) showed a clear separation of the trail and gravel step plots from the two sets of reference plots. The gravel step plots were clustered closer to the reference plots, while the trail plots were more variable and were generally more different from the two reference locations. Meanwhile, the two sets of reference plots were not distinct in terms of composition. The MRPP showed that the four locations were significantly different overall. Follow-up tests (pairwise MRPPs) found significant differences between the trail and the gravel steps as well as between the trail reference and gravel step reference plots ($p<0.0001$). However, T-values, which are a measure of effect size, were variable: for the comparison of the trail to the gravel steps T was -22.86, and for the trail reference versus gravel step reference it was -8.99 (Table 3.6). These results suggest the trail is more compositionally dissimilar from the gravel steps than the two sets of reference plots are from each other.

Four species were found to be indicators of the trail in this analysis: *Trisetum spicatum*, *Poa alpina*, *Deschampsia cespitosa* and *Minuartia* spp. (Table 3.7)). Significant indicators for the gravel step plots were *Antennaria* spp., *Arnica angustifolia* M. Vahl, *Festuca brachyphylla*, *Oxytropis podocarpa* A. Gray, *Salix reticulata* L. ssp. *nivalis* Löve, Löve & Kapoor and *Saxifraga oppositifolia* L. The gravel step reference plots also had several significant indicators: *Anemone lithophila* Rydb., *Arnica angustifolia*, *Dryas integrifolia*, *Kobresia myosuroides*, *Oxytropis podocarpa*, *Potentilla nivea* L., *Polygonum viviparum* and *Salix reticulata*. Finally, there were five indicators for the trail reference plots: *Betula glandulosa*, *Dryas integrifolia*, *Hedysarum boreale*, *Pedicularis lanata* Cham. & Schlecht. and *Polygonum viviparum*.

Non-vascular and abiotic cover

Non-vascular and abiotic cover types dominated both the trail and gravel step plots, comprising >90% of total plot cover on average. Rock was the primary component of both, and did not differ significantly between these two locations (Figure 3.9; Appendix 4). There were significant differences between the trail and the gravel steps in terms of the other five cover types. The proportion of exposed soil was higher on the trail, while there was more cover of lichens, mosses, litter and cryptogamic crust on the gravel steps. Lichen cover was generally low at both locations, with a median of 0% on the trail and 0.25% on the gravel steps, but the steps were more variable in terms of lichen cover, with values of up to 5%.

Mosses showed the same pattern – low overall cover, but significantly greater amounts on the gravel steps. The cover of litter and cryptogamic crust was much higher on the gravel steps than on the trail, with medians, respectively, of 8.75% and 2.5% on the gravel steps versus 2.5% and 0% on the trail.

The two sets of reference plots were similar in their cover of lichen, moss, litter and cryptogamic crust. They differed in terms of soil and rock cover, but in both cases the trends were the opposite of what was found on the disturbed plots at each site. While the trail (Divide site) had more rock and soil cover than did the gravel steps, in the case of the undisturbed plots it was the gravel step reference plots that had higher cover of these two substrates.

Morphological composition

i. Growth forms

Four of the five growth forms varied in proportional abundance between the trail and the gravel steps: cushion plants were the only group that did not differ in abundance between locations (Figure 3.10). Follow-up tests found several significant differences between the trail and the gravel steps, as well as a few between the trail reference and the gravel step reference plots (Appendix 4). Caespitose plants were much more abundant on the trail (median=12%) than on the gravel steps (median=2%). Matted plants showed the reverse trend – they were more abundant on the gravel steps, with a median cover of 69%, versus only 6% on the trail. Although rosette plant cover differed between the four locations, neither of the follow-up tests yielded significant results. Upright plants were more abundant on the trail (median=43%) than on the gravel steps (median=16%). The dominance of the upright growth form on the trail is mostly attributable to non-caespitose graminoids; graminoids in general were not a large component of the plant community on the gravel steps.

Only caespitose plants differed in abundance between the trail reference and gravel step reference plots. Cover was low in both cases, but higher on the gravel step reference plots.

ii. Raunkiaer life forms

Chamaephytes, hemi-cryptophytes and therophytes all differed in abundance between the trail and the gravel steps (Figure 3.11), while there were no significant differences between the two reference locations. Chamaephyte cover was much lower on the trail than on the gravel steps, with median covers of 13% and 72%, respectively (Appendix 4). Cryptophytes also came out as being different in a comparison of all four locations, but follow-up tests did not find significant differences between the locations of interest. Hemi-cryptophytes were more abundant on the trail (median=68%) than on the gravel steps (median=20%). Therophytes were a minor component of both the trail and gravel step communities, but significantly more abundant on the trail.

iii. Structural groups

Cover of forbs, graminoids and shrubs differed between locations (Figure 3.12, Appendix 4). Forb cover did not differ between the trail and the gravel steps. Graminoids were much more abundant on the trail, with a median cover of 50%

versus 6% on the gravel steps, while shrubs displayed the opposite pattern, with a median cover of 6% on the trail and 52% on the gravel steps.

The gravel step reference plots had more forb cover and less shrub cover than the trail reference plots; graminoid cover was not significantly different between the reference locations.

Comparisons of an OHV trail to a multi-use trail

Analyses in this section compared the trail on Cardinal Divide to the one in the Cardinal River Headwaters. Due to the lack of replication as well as the historical use of OHVs on the Divide, this is not a perfect comparison of the effects of OHVs versus those of hiking. Based on what previous studies have found (e.g., Weaver & Dale 1978) the Cardinal Divide trail would likely be a less severely-impacted environment if it had been used solely by hikers since its inception. However, comparing the two sites did allow me to get some sense of how the impacts of these two activities differ. ANOVA-type tests were used for all the analyses in this section. Soil compaction and trail width were compared between sites using the Mann-Whitney test, while incision was compared using a mixed model ANOVA in which transect was included as a random factor, nested within site.

Median soil compaction on the Divide trail plots was 2.75kg/cm^2, while on the Headwaters plots it was 4.5kg/cm^2. Soil was significantly more compacted on the Headwaters trail at all five positions across the trail (Figure 3.13). A comparison of relativised compaction measurements, which were a ratio of compaction on the trail plots over compaction on the 15 m plots, also found that the Headwaters trail had significantly greater soil compaction. This indicates that the difference cannot be attributed to natural variation in soils between sites.

Median trail incision was +3cm on the Divide and –6.5cm in the Headwaters. Sample profiles comparing the two sites are presented in Figure 3.14. The Cardinal Divide trail was wider than the Headwaters trail, with a median width of 4.7 m versus 2.7 m.

Section 2: Trailside effects

This section looked at changes in the vegetation community along a gradient from the trail edge to 15 m away using regressions and correlations. Further changes between 15 m and 50 m were analysed separately using paired two sample tests. Overall, community changes along the gradient were minimal, and do not paint a clear picture of decreasing human impact with increasing distance from the trail. Line graphs showing within-transect trends are presented in Appendix 2.

Soil compaction

I will begin this section by discussing trends in soil compaction because, as previously mentioned, there is a close relationship between trampling and soil compaction. A linear regression of compaction against distance from the trail (up to 15 m away) was not significant. However, soil compaction was significantly lower on the 50 m plots than on the 15 m plots (Table 3.8).

Vascular plant cover, richness and diversity

Vascular plant cover was remarkably consistent from the edge to the 50 m plots, ranging between 33-35%, and as a result was not analysed for differences. Richness, evenness and diversity (both Shannon's and Simpson's indices) all increased with distance, and all four trends were found to be significant in linear regressions, but R^2 values were very low (Figure 3.15): 0.06 for richness, 0.03 for evenness, 0.07 for Shannon's H' and 0.08 for Simpson's D. None of these variables differed significantly between 15 m and 50 m (Table 3.8).

Species composition

The NMDS indicates that there is little differentiation in vascular species composition between plots at different distances from the trail. However, the initial ordination appeared to be strongly influenced by seven outlier plots. Further investigation suggested that these plots belonged to different community types (e.g., heather-dominated or snowbed communities). Given that the aim of this project was to focus on *Dryas* meadows, I decided to remove these plots and rerun the ordination in order to see if the outliers were obscuring other patterns in the data. This new plot is presented in Figure 3.16; the original plot is in Appendix 5.

There was very little detectable change in composition along the distance gradient. The NMDS (with outliers removed) shows some separation between plots at different distances, with the edge plots clumped on the left side of the first ordination axis and the 50 m plots more on the right side. However, this might not be reflective of drastic compositional differences between different plot locations. The plots that are clustered in the centre of the graph share very similar species composition, while the plots that are more loosely scattered around this central cluster differ in terms of the cover of one or two species per plot. Given that relatively small variations in the presence of abundance of one or two species per plot accounts for the majority of the spread along both axes in this ordination, it appears that the effect of distance, which accounts for less of the differentiation between plots, is minimal.

Two variables came out as significant in the dbRDA: distance from trail and soil compaction (p=0.005 for both, (Figure 3.17). The ordination that included these two variables had the lowest AIC value of all possible models, and explained 6.5% of the variation in the species dataset. 78% of this was explained in the first two axes. There is some degree of separation between groups (different distances), particularly the 50 m plots. However, the plots of various distances are, for the most part, clumped together and do not form much in the way of distinct patterns.

An indicator species analysis of the edge-50 m plots found three indicators: *Carex petricosa* Dewey was an indicator for the edge plots while *Pedicularis lanata* was an indicator for the 50 m plots. *Carex rupestris* was significant for the 2 m plots (Table 3.9).

Non-vascular and abiotic cover

Cover values for four of the non-vascular and abiotic cover types (rock, soil, lichen and litter) showed patterns of change along the distance gradient, so regressions and correlations were used to assess the strength of these trends. Cover of mosses and cryptogamic crust showed little change and were not analysed further. Soil and lichen were not normally distributed and could not be normalised through transformations; as a result they were analysed using Spearman rank correlations. Rock and soil cover decreased with increasing distance from the trail, while lichen and litter increased (Figure 3.18 & 3.19). R^2 values for rock and litter were low: 0.09 for rock and only 0.05 for litter. These tow cover types did not differ significantly between the 15m and 50m plots (Table 3.8). There was a significant and positive relationship between lichen cover and distance (rho=0.5; $p<0.0001$) while the relationship between soil cover and distance was significant and negative (rho=-0.29; $p<0.0001$). The 15 m and 50 m plots differed in terms of the cover of lichen and soil, with the 50 m plots having more lichen and less exposed soil than the 15 m plots (Table 3.8). This indicates that the trends that were found in the correlations continue beyond 15 m from the trail edge.

Morphological composition

Most of the morphological groups that I analysed in other sections did not vary in abundance with increasing distance from the trail. Graminoids were the only group to show a distinct response to distance from the trail, and declined significantly with increasing distance from the trail. However, the regression was only able to account for 6% of the variation in the dataset (Figure 3.20). There was a further significant decline in graminoid cover between the 15 m and 50 m plots (Table 3.8).

Section 3: The impacts of recreation on rare plants

Rare plant occurrences were converted into presence/absence data for this section, and logistic regression was used to examine the spatial relationship between the trail, the trailhead and the distribution of rare plants. A total of 96 rare plants of four different species (*Antennaria monocephala*, *Braya purpurescens*, *Campanula uniflora* and *Pedicularis flammea*) were found in this survey of Cardinal Divide; 71 of which were analysed. *Campanula uniflora* and *P. flammea* were far more abundant than the other species, accounting for over 90% of occurrences. *Pedicularis flammea* alone accounted for 75% of occurrences.

About 10-30% of the 10 m segments had at least one rare plant occurrence in them. The logistic regression found that distance from the trail, distance from the road and the interaction between the two were all significant (Table 3.10). When *Pedicularis flammea* alone was analysed, both variables alone were significant, but the interaction was not. In general there was a decrease in the occurrence of rare species with increasing distance from both the trail and the road (Figure 3.21).

Tables

Table 3.1: Species list for Cardinal Divide, including morphological categories for each species.

Species	**Life form**	**Growth form**	**Structural group**
Arctostaphylos rubra (Rehder & Wils.) Fern.	chamaephyte	mat	shrub
Arctostaphylos uva-ursi (L.) Spreng.	chamaephyte	mat	shrub
Androsace chamaejasme Host	hemi-cryptophyte	rosette	forb
Anemone lithophila Rydb.	cryptophyte	upright	forb
Anemone parviflora Michx.	cryptophyte	upright	forb
Antennaria alpina (L.) Gaertn.	hemi-cryptophyte	rosette	forb
Antennaria spp.	hemi-cryptophyte	rosette	forb
Antennaria umbrinella Rydb.	hemi-cryptophyte	rosette	forb
Arnica angustifolia M. Vahl	hemi-cryptophyte	rosette	forb
Artemisia norvegica Fries ssp. *saxatilis* (Bess.) H. & C.	hemi-cryptophyte	upright	forb
Aster alpinus L.	hemi-cryptophyte	rosette	forb
Astragalus alpinus L.	hemi-cryptophyte	upright	forb
Betula glandulosa Michx.	chamaephyte	upright	shrub
Braya purpurascens (R.Br.) Bunge	unknown	mat	forb
Bromus inermis Leyss. ssp. *pumpellianus* (Scribn.) Wagnon	hemi-cryptophyte	upright	graminoid
Campanula uniflora L.	cryptophyte	upright	forb
Carex nardina Fries	cryptophyte	caespitose	graminoid
Carex petricosa Dewey	hemi-cryptophyte	upright	graminoid
Carex rupestris All.	hemi-cryptophyte	upright	graminoid
Carex scirpoidea Michx. var. *scirpoidea*	hemi-cryptophyte	upright	graminoid
Cassiope tetragona (L.) D. Don var. *saximontana* (Small) Porsild.	chamaephyte	upright	shrub
Cerastium beeringianum Cham. & Schlecht.	chamaephyte	mat	forb
Deschampsia cespitosa (L.) Beauv. ssp. *cespitosa*	hemi-cryptophyte	caespitose	graminoid
Draba borealis DC.	chamaephyte	rosette	forb
Draba cana Rydb.	chamaephyte	rosette	forb
Draba spp.	chamaephyte	rosette	forb
Dryas integrifolia M. Vahl	chamaephyte	mat	shrub
Dryas octopetala L. ssp. *hookeriana* (Juz.) Hult.	chamaephyte	mat	shrub
Elymus innovatus Beal ssp. *innovatus*	hemi-cryptophyte	upright	graminoid
Equisetum scirpoides Michx.	cryptophyte	upright	forb
Erigeron compositus Pursh	hemi-cryptophyte	upright	forb
Erigeron peregrinus (Pursh) Greene spp. *callianthemus* (Greene) Cronq.	hemi-cryptophyte	upright	forb
Festuca baffinensis Polunin	hemi-cryptophyte	caespitose	graminoid
Festuca brachyphylla Schultes	hemi-cryptophyte	caespitose	graminoid
Gentiana prostrata Haenke	therophyte	upright	forb

Gentianella propinqua (Richards.) J.M. Gillett	therophyte	upright	forb
Habenaria hyperborea (L.) R.Br.	cryptophyte	upright	forb
Habenaria viridis (L.) R.Br. var. *bracteata* (Muhl.) Gray.	cryptophyte	upright	forb
Hedysarum alpinum L. ssp. *americanum* (Michx.) Fedtsch	hemi-cryptophyte	upright	forb
Hedysarum boreale Nutt.	hemi-cryptophyte	upright	forb
Kobresia myosuroides (Vill.) Fiori & Paol.	hemi-cryptophyte	caespitose	graminoid
Luzula spicata (L.) DC.	hemi-cryptophyte	caespitose	graminoid
Minuartia spp.	chamaephyte	cushion	forb
Oxytropis podocarpa A. Gray	hemi-cryptophyte	mat	forb
Oxytropis sericea Nutt. var. *spicata* (Hook.) Barneby	hemi-cryptophyte	upright	forb
Pedicularis capitata Adams	cryptophyte	upright	forb
Pedicularis flammea L.	unknown	rosette	forb
Pedicularis lanata Cham. & Schlecht.	hemi-cryptophyte	rosette	forb
Phyllodoce glanduliflora (Hook.) Coville	chamaephyte	upright	shrub
Picea engelmannii Parry *ex* Engelm.	chamaephyte	upright	n/a
Pinus contorta Loudon ssp. *latifolia* Engelm.	phanerophyte	upright	n/a
Poa alpina L.	hemi-cryptophyte	upright	graminoid
Polygonum viviparum L.	crytophyte	upright	forb
Potentilla diversifolia Lehm.	hemi-cryptophyte	upright	forb
Potentilla fruticosa L.	chamaephyte	upright	shrub
Potentilla nivea L.	hemi-cryptophyte	caespitose	forb
Potentilla ovina Macoun	hemi-cryptophyte	mat	forb
Pyrola grandiflora Radius	hemi-cryptophyte	rosette	forb
Salix arctica Pallas	chamaephyte	mat	shrub
Salix barratiana Hook.	chamaephyte	upright	shrub
Salix reticulata L. ssp. *nivalis* Löve, Löve & Kapoor	chamaephyte	mat	shrub
Salix sp. 1	chamaephyte	upright	shrub
Salix sp. 2	chamaephyte	upright	shrub
Saxifraga oppositifolia L.	chamaephyte	cushion	forb
Senecio lugens Richards.	hemi-cryptophyte	rosette	forb
Silene acaulis L.	chamaephyte	cushion	forb
Smelowskia calycina (Stephan.) C.A. Mey var. *americana* (Rydb.) Drury & Rollins	unknown	upright	forb
Solidago multiradiata Ait.	hemi-cryptophyte	upright	forb
Taraxacum ceratophorum (Ledeb.) DC.	hemi-cryptophyte	rosette	forb
Taraxacum officionale Weber	hemi-cryptophyte	rosette	forb
Trisetum spicatum (L.) Richt. ssp. *molle* (Michx.) Hult.	hemi-cryptophyte	caespitose	graminoid
Unidentified conifer germinant	chamaephyte	upright	n/a
Zigadenus elegans Pursh	cryptophyte	upright	forb

Table 3.2: Cardinal River Headwaters species list

Species list: Cardinal Divide Headwaters
Androsace chamaejasme Host
Anemone lithophila Rydb.
Anemone parviflora Michx.
Antennaria alpina (L.) Gaertn.
Antennaria spp.
Arnica angustifolia M Vahl
Artemisia norvegica Fries ssp. *saxatilis* (Bess.) H. & C.
Aster alpinus L.
Astragalus alpinus L.
Betula glandulosa Michx.
Betula pumila L. var. *glandulifera* Regel
Calamagrostis purpurescens R.Br.
Carex petricosa Dewey
Carex nardina Fries
Campanula uniflora L.
Carex capillaris L. ssp. *capillaris*
Carex rupestris All.
Carex scirpoidea Michx. var. *scirpoidea*
Carex spp. 1
Carex spp. 2
Carex spp. 3
Carex spp. 4
Cassiope tetragona (L.) D. Don var. *saximontana* (Small) Porsild.
Cerastium beeringianum Cham. & Schlecht.
Deschampsia cespitosa (L.) Beauv. ssp. *cespitosa*
Draba spp.
Dryas integrifolia M. Vahl
Dryas octopetala L. ssp. *hookeriana* (Juz.) Hult.
Elymus innovatus Beal ssp. *innovatus*
Equisetum scirpoides Michx.
Festuca baffinensis Polunin
Festuca brachyphylla Schultes
Gentiana prostrata Haenke
Gentianella propinqua (Richards.) J.M. Gillett
Hedysarum alpinum L. ssp. *americanum* (Michx.) Fedtsch
Hedysarum boreale Nutt.
Kobresia myosuroides (Vill.) Fiori & Paol.
Minuartia spp.
Oxytropis jordalii Porsild ssp. *jordalii*
Oxytropis podocarpa A. Gray
Pedicularis capitata Adams
Pedicularis flammea L.
Pedicularis lanata Cham. & Schlecht.
Picea engelmannii Parry *ex* Engelm.
Poa alpina L.

Poa glauca Vahl
Poa sp.
Polygonum viviparum L.
Potentilla diversifolia Lehm.
Potentilla fruticosa L.
Potentilla nivea L.
Potentilla spp.
Salix reticulata L. ssp. *nivalis* Löve, Löve & Kapoor
Saxifraga aizoides L.
Saxifraga oppositifolia L.
Senecio lugens Richards.
Silene acaulis L.
Smelowskia calycina (Stephan.) C.A. Mey var. *americana* (Rydb.) Drury & Rollins
Solidago multiradiata Ait.
Stellaria sp.
Taraxacum ceratophorum (Ledeb.) DC.
Tofieldia glutinosa (Michx.) Pers. var. *glutinosa*
Tofielda pusilla (Michx.) Pers.
Trisetum spicatum (L.) Richt. ssp. *molle* (Michx.) Hult.
Unidentified conifer germinant
Unknown species 1 (forb)
Unknown species 2 (forb)
Unknown species 3 (forb)
Unknown species 4 (forb)
Salix sp. 1
Salix sp. 2

Table 3.3: Percent vascular plant cover, richness, evenness and diversity for the trail, edge and 15m plots, as well as all off-trail plots combined on Cardinal Divide. Asterisks indicate significant differences from the trail (*<0.05, **<0.01, ***<0.001). Means are presented for normally distributed data, while medians are presented for non-normal data. Analyses were done using paired t-tests (for normally-distributed data) and Wilcoxon's test (for non-normal data).

		Trail	**Edge**	**15m**	**Combined**
Cover	Median	4	**32.5*** **	**33.3*** **	34
	5th/95th percentile	1/12	8/62	13/50	13/54
Richness	Median	7	**9*** **	**11*** **	10
	5th/95th percentile	3/12	6/13	15	7/15
Evenness	Median	0.86	**0.57*** **	**0.60*** **	0.60
	5th/95th percentile	0.68/0.91	0.43/0.78	0.50/0.70	0.46/0.76
Shannon	Mean	1.7	**1.34*** **	**1.46*** **	1.44
	Std. dev.	0.35	0.28	0.24	0.24
Simpson	Median	0.78	**0.60*** **	**0.67*** **	0.66
	5th/95th percentile	0.62/0.87	0.42/0.77	0.53/0.76	0.46/0.79

Table 3.4: Significant indicators for the trail, edge and 15m plots on Cardinal Divide. The criteria used for significance are an indicator value of >20 and a p-value of <0.05.

Trail versus edge				**Trail versus 15m**			
Species	**Indicator value (IV)**		***p***	**Species**	**Indicator value (IV)**		***p***
	Trail	Edge			Trail	15m	
Aster alpinus	3	**29**	0.011	*Anemone parviflora*	0	**46**	<0.001
Betula glandulosa	0	**29**	<0.001	*Betula glandulosa*	0	**51**	<0.001
Carex rupestris	6	**81**	<0.001	*Carex rupestris*	6	**80**	<0.001
Deschampsia cespitosa	**23**	0	<0.001	*Deschampsia caespitosa*	**23**	0	0.002
Dryas integrifolia	2	**91**	<0.001	*Dryas integrifolia*	2	**93**	<0.001
Festuca brachyphylla	**18**	0	0.014	*Festuca brachyphylla*	**21**	0	0.005
Gentiana prostrata	**18**	0	0.014	*Gentiana prostrata*	**21**	0	0.05
Hedysarum boreale	0	**84**	<0.001	*Hedysarum alpinum*	0	**40**	<0.001
Kobresia myosuroides	0	**63**	<0.001	*Hedysarum boreale*	0	**76**	<0.001
Minuartia spp.	**43**	1	<0.001	*Kobresia myosuroides*	0	**50**	<0.001
Poa alpina	**77**	0	<0.001	*Minuartia spp.*	**47**	0	<0.001
Polygonum viviparum	8	**86**	<0.001	*Oxytropis podocarpa*	0	**32**	<0.001
Salix nivalis	0	**20**	0.005	*Poa alpina*	**78**	0	<0.001
Trisetum spicatum	**59**	0	<0.001	*Polygonum viviparum*	9	**80**	<0.001
				Salix nivalis	0	**49**	<0.001
				Silene acaulis	0	**27**	0.002
				Trisetum spicatum	**60**	0	<0.001
				Zigadenus elegans	0	**40**	<0.001

Table 3.5: Diversity indices for the trail, gravel steps, trail reference and gravel step reference plots. Asterisks beside gravel step plot values indicate a significant difference from the trail, while asterisks beside the gravel step reference plot values indicate significant differences from the trail reference plots (*<0.05, **<0.01, ***<0.001). Means are presented for normally-distributed data, while medians are presented for data that are non-normal. In the case of normal data, ANOVAs were used for initial comparisons while contrasts were used for post-hoc analyses. The Kruskal-Wallis test was used for non-normal data; follow-up tests were done using Mann-Whitney.

		Trail	**Gravel steps**	**Trail reference**	**Step reference**
Cover	Median	4	**8*****	35	30
	$5^{th}/95^{th}$ percentile	1/12	5/13	20/49	18/36
Richness	Mean	8	**11*****	12	14
	Std. dev.	2.78	1.96	2.68	2.83
Evenness	Mean	0.83	**0.73*****	0.61	0.69
	Std. dev.	0.08	0.07	0.09	0.07
Shannon	Mean	1.71	1.77	1.53	**1.8****
	Std. dev	0.35	0.23	0.27	0.22
Simpson	Median	0.78	0.76	0.66	0.76
	$5^{th}/95^{th}$ percentile	0.62/0.87	0.42/0.82	0.65/0.81	0.73/0.84

Table 3.6: Results of the multi-response permutation procedure (MRPP). T is the test statistic: a larger negative value indicates a larger effect. A is a measure of within-group homogeneity.

Groups compared	**T**	**A**	***p***
All groups	-42.88	0.25	<0.001
Trail vs. gravel steps	-22.86	0.12	<0.001
Trail ref. vs. step ref.	-8.99	0.07	<0.001

Table 3.7: Indicator species for the trail, gravel steps, trail reference and gravel step reference plots. The criteria used for significance are an indicator value of >20 and a p-value of <0.05.

Species	**Indicator value**				***p***
	Trail	**Gravel steps**	**Trail reference**	**Step reference**	
Anemone lithophila	0	2	0	**32**	0.016
Antennaria spp.	1	**35**	2	0	0.007
Arnica angustifolia	1	**25**	1	**33**	0.028
Betula glandulosa	0	0	**59**	0	0.001
Deschampsia caespitosa	**23**	0	0	0	0.027
Dryas integrifolia	1	12	**55**	**31**	0.001
Festuca brachyphylla	7	**26**	0	0	0.022
Hedysarum boreale	0	0	**80**	0	0.001
Kobresia myosuroides	0	0	18	**64**	0.002
Minuartia spp.	**28**	10	0	3	0.031
Oxytropis podocarpa	0	**23**	2	**71**	0.002
Pedicularis lanata	0	0	**41**	0	0.008
Poa alpina	**59**	8	0	2	0.001
Polygonum viviparum	3	8	**27**	**60**	0.001
Potentilla nivea	2	0	2	**47**	0.002
Salix reticulata	0	**21**	10	**41**	0.024
Saxifraga oppositifolia	0	**25**	6	0	0.03
Trisetum spicatum	**49**	1	1	2	0.002

Table 3.8: Mean or median values for different variables measured in the alpine tundra plots 15m and 50m away from the trail on Cardinal Divide. Asterisks beside mean and median values for 50m plots indicate a significant difference from the 15m plots (* $p<0.05$, ** $p<0.01$, ***$p<0.001$). Means are presented for normally distributed data, while medians are presented for non-normal data. Paired tests were used to analyse these data; either paired t-tests (for normally distributed data) or Wilcoxon's test (for non-normal data).

		15m	**50m**
Soil compaction	Median	1.5	**1.25****
	5th/95th percentile	0.5/3.7	0.7/2
Richness	Mean	11	11
	Std. dev.	3	3
Evenness	Mean	0.61	0.61
	Std. dev.	0.08	0.08
Shannon's H'	Mean	1.46	1.5
	Std. dev.	0.2	0.2
Simpson's D	Mean	0.67	0.68
	Std. dev.	0.08	0.08
Graminoid cover	Median	5	**2***
	5th/95th percentile	1/17	1/9
Rock	Median	3	3
	5th/95th percentile	0/49	0/32
Soil	Median	0	**0***
	95th percentile	0/0	0/3
Lichen	Median	5	**10***
	5th/95th percentile	0/25	3/25
Litter	Mean	43	47
	Std. dev.	17	13

Table 3.9: Significant indicators for the off-trail plots on Cardinal Divide. The criteria used for significance are an indicator value of >20 and a p-value of <0.05.

Species	**Indicator value**						***p***
	edge	**2m**	**5m**	**10m**	**15m**	**50m**	
Carex petricosa	**25**	1	1	0	0	0	0.001
Carex rupestris	16	**23**	19	14	15	5	0.031
Pedicularis lanata	0	1	2	2	3	**21**	0.006

Table 3.10: results of the logistic regressions of rare species (combined) and of *Pedicularis flammea* on Cardinal Divide.

		Estimate	***p***
All species	Distance from the trail	-0.0266	0.008
	Distance from the road	-0.00149	0.006
	Interaction	-0.000022	0.039
Pedicularis flammea	Distance from the trail	-0.0235	0.025
	Distance from the road	-0.00132	0.020
	Interaction	0.000017	0.138

Figures

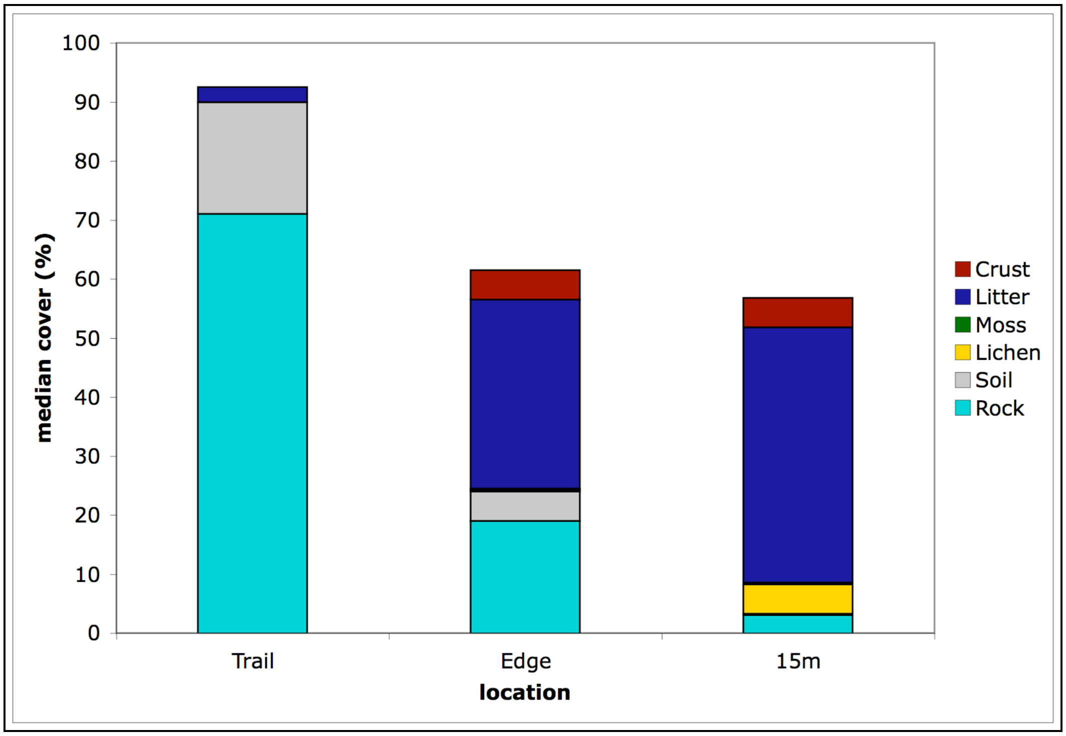

Figure 3.1: Percent cover by non-vascular and abiotic substrates on the trail, edge and 15m plots on Cardinal Divide. Total bar height indicates the median percent of the plots at each location that is made up of non-vascular and abiotic cover.

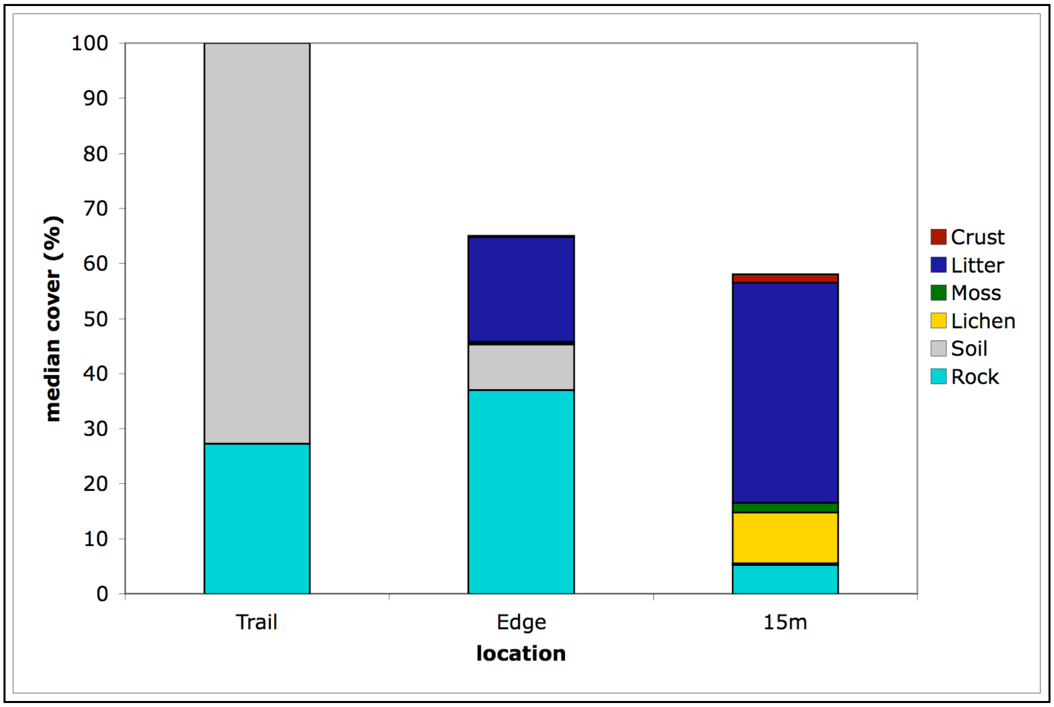

Figure 3.2: Non-vascular and abiotic composition of the trail, edge and 15m plots in the Cardinal River Headwaters. Total bar height indicates the median percent of the plot that is made up of non-vascular and abiotic cover.

Figure 3.3: Growth form composition for the trail, edge and 15m plots on Cardinal Divide.

Figure 3.4: Raunkiaer life form composition for the trail, edge and 15m plots on Cardinal Divide.

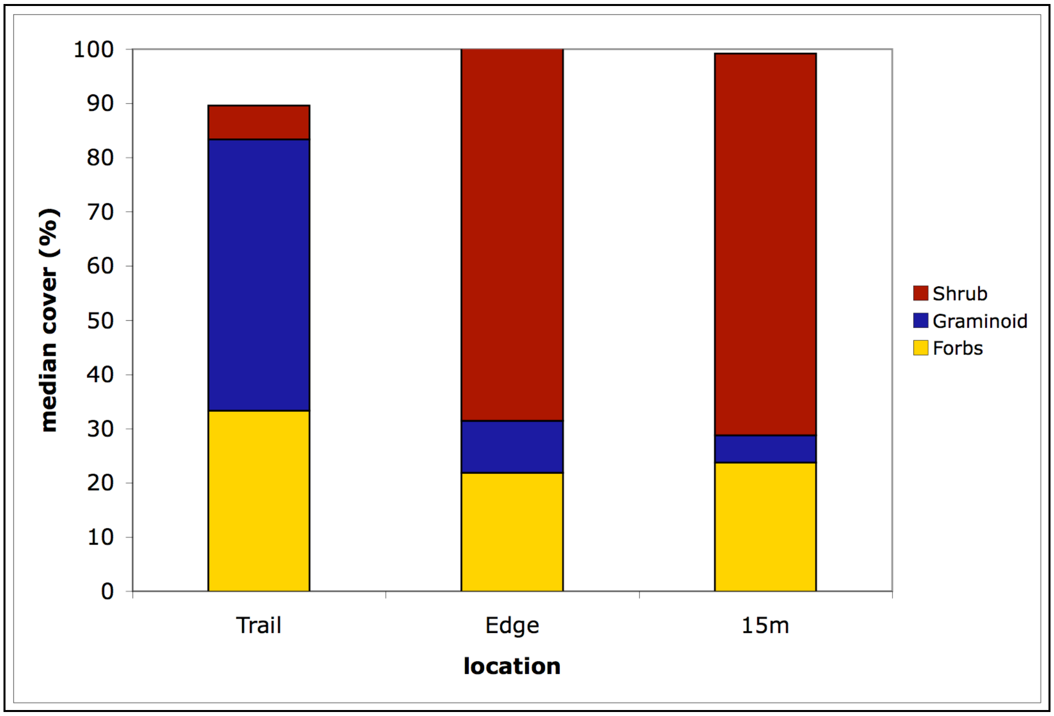

Figure 3.5: Structural group composition for the trail, edge and 15m plots on Cardinal Divide.

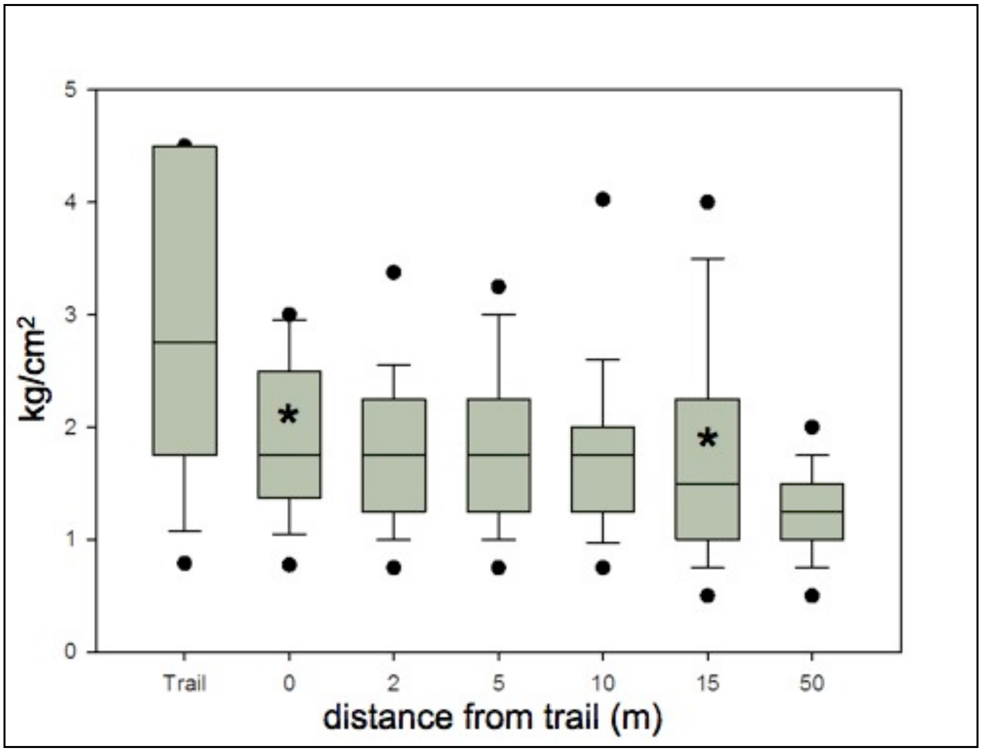

Figure 3.6: Soil compaction versus distance from the trail, Cardinal Divide. Asterisks on the edge (0m) and 15m boxes indicate that these locations were significantly different from the trail. Other locations were not compared with the trail in this analysis. Boxes represent 25th/75th percentiles, whiskers represent 10th/90th percentiles, and points represent 5th/95th percentiles.

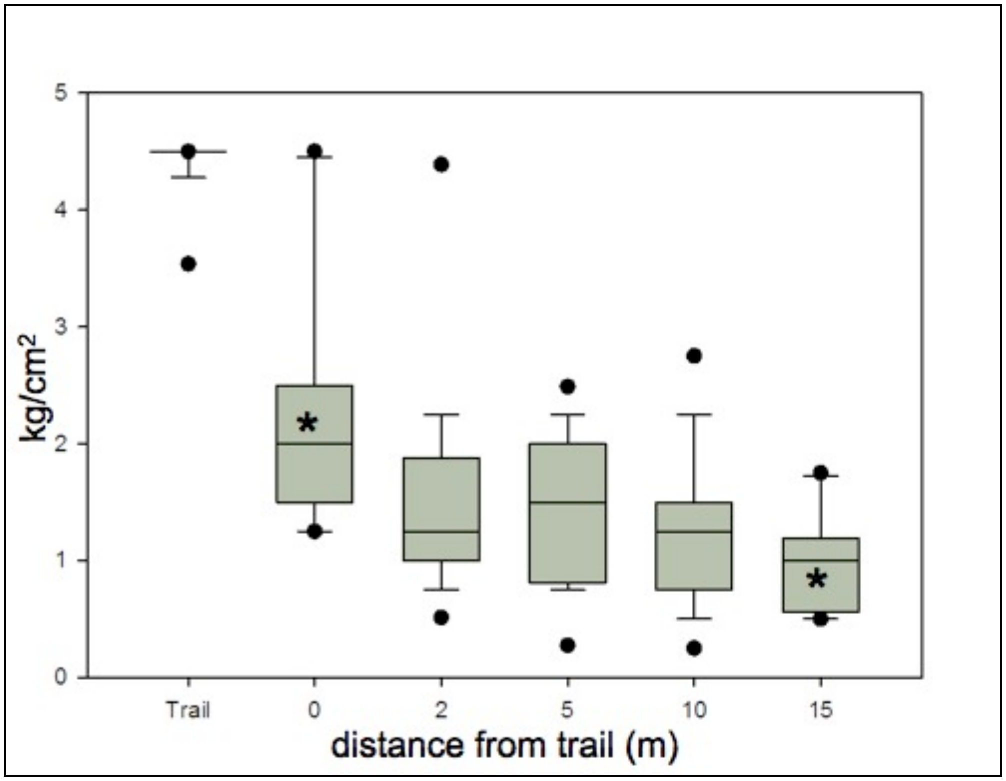

Figure 3.7: Soil compaction versus distance from the trail, Cardinal River Headwaters. Asterisks on the edge (0m) and 15m boxes indicate that these locations were significantly different from the trail. Other locations were not compared with the trail in this analysis. Boxes represent 25th/75th percentiles, whiskers represent 10th/90th percentiles, and points represent 5th/95th percentiles.

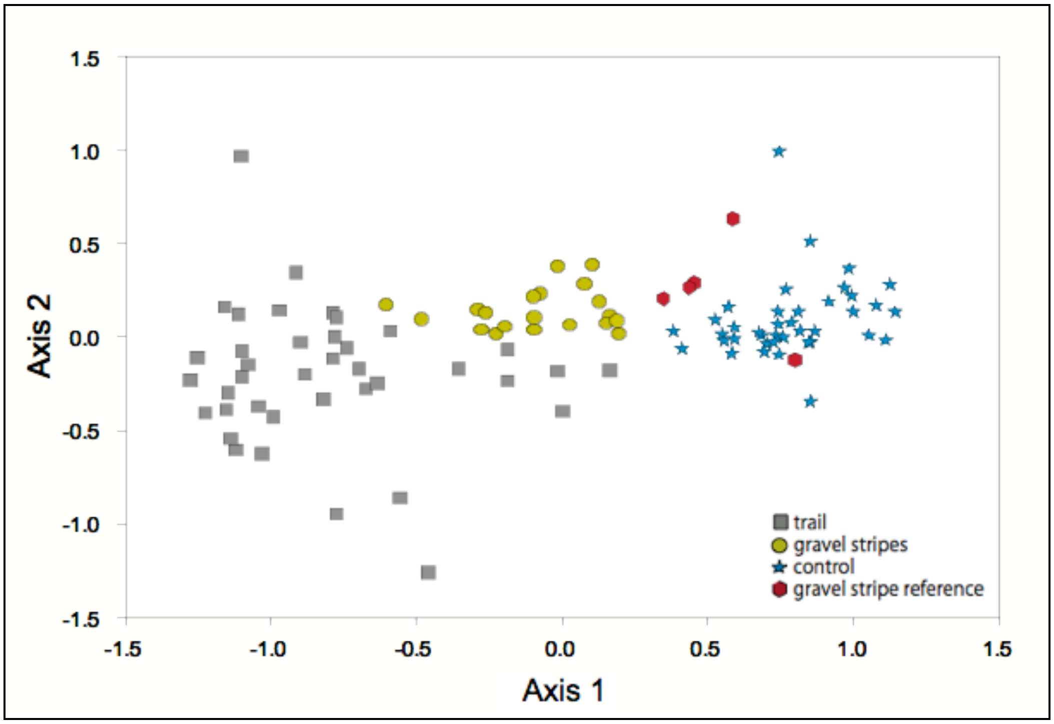

Figure 3.8: Non-metric multidimensional scaling plot of species composition of the trail, gravel step, trail reference and gravel step reference plots. Stress=15.36, variation explained=82.2%.

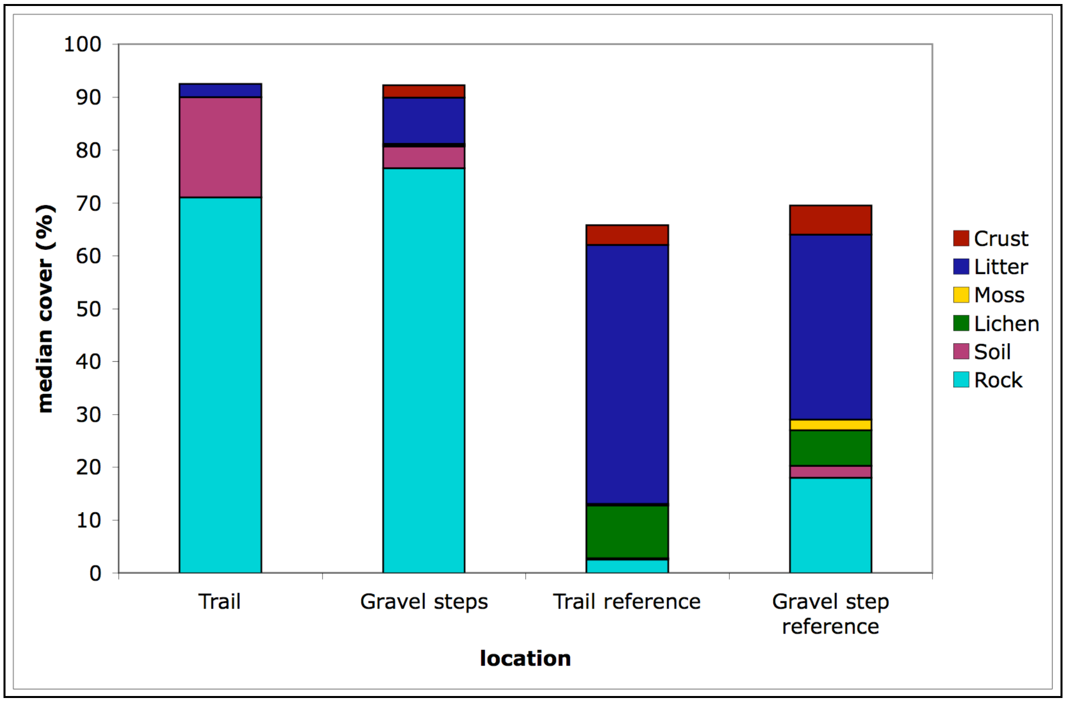

Figure 3.9: Non-vascular and abiotic composition of the trail, gravel step, trail reference and gravel step reference plots. Total bar height indicates the median percentage of the plot that is made up of non-vascular and abiotic cover.

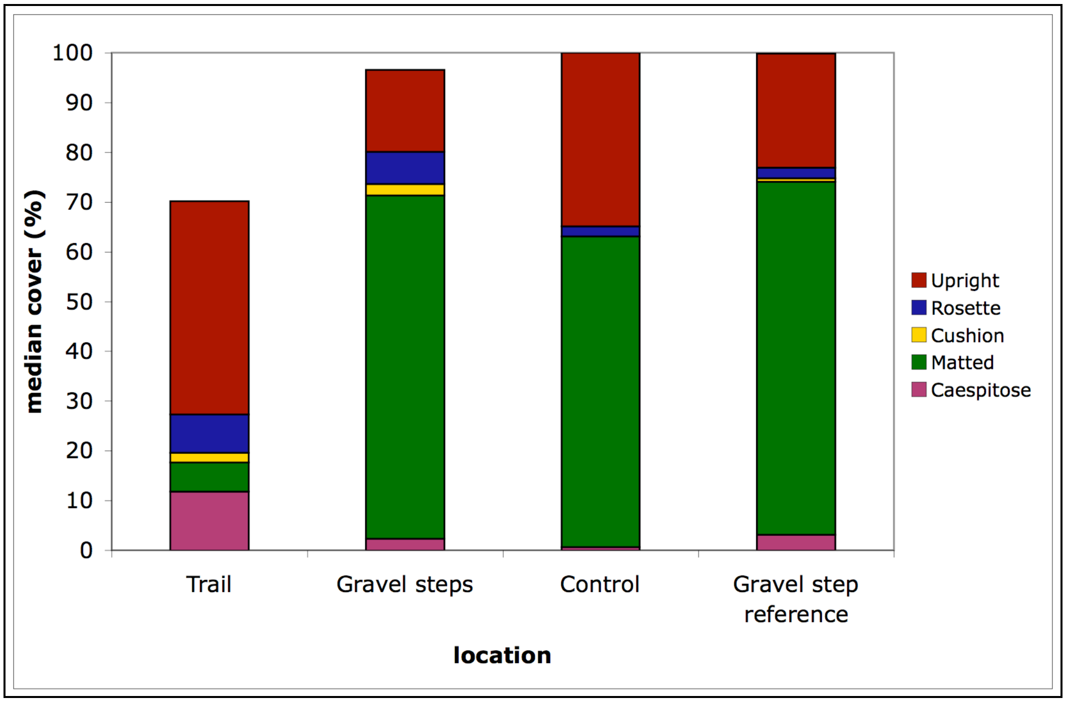

Figure 3.10: Growth form composition for the trail, gravel step, trail reference and gravel step reference plots.

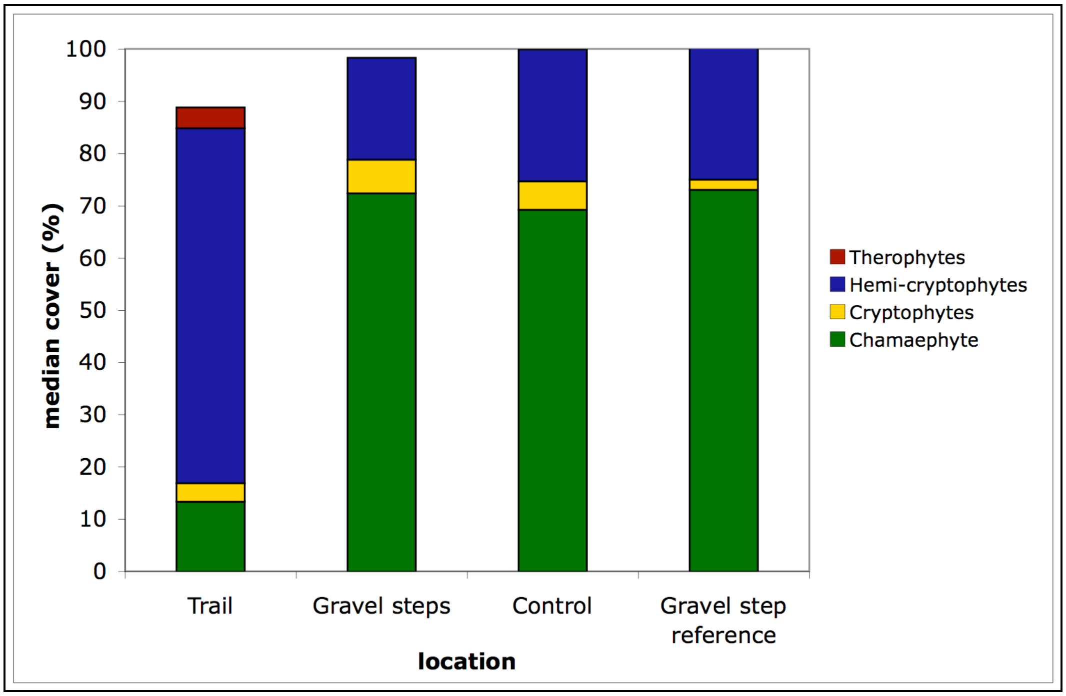

Figure 3.11: Raunkiaer life form composition for the trail, gravel step, trail reference and gravel step reference plots.

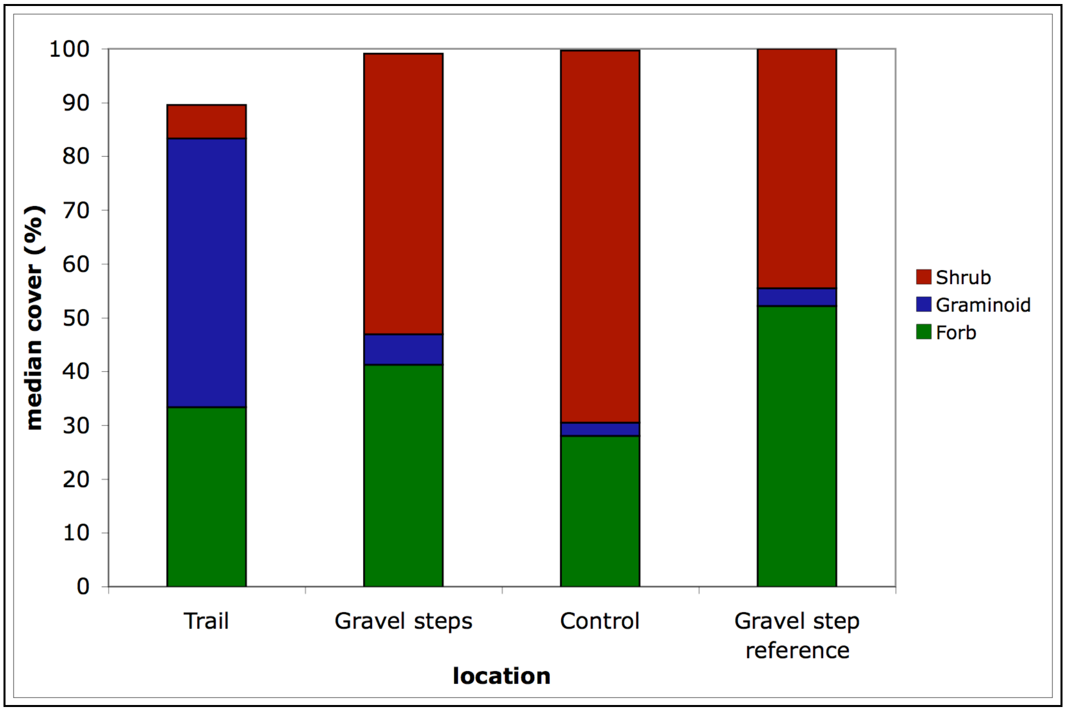

Figure 3.12: Structural group composition for the trail, gravel step, trail reference and gravel step reference plots.

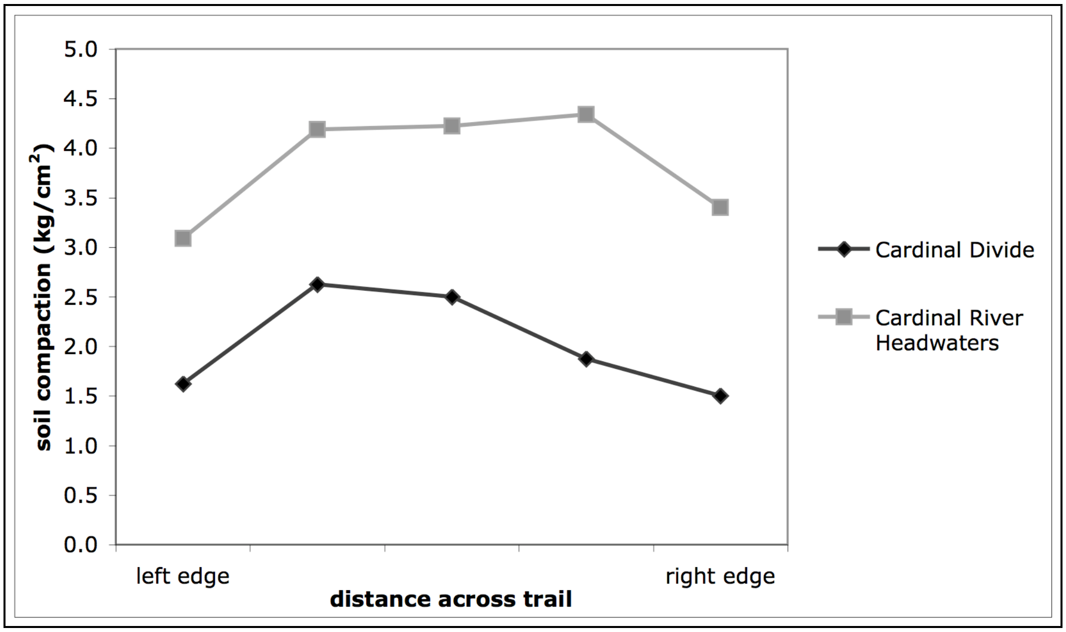

Figure 3.13: Median soil compaction profile of the Cardinal Divide and Cardinal River Headwaters trails.

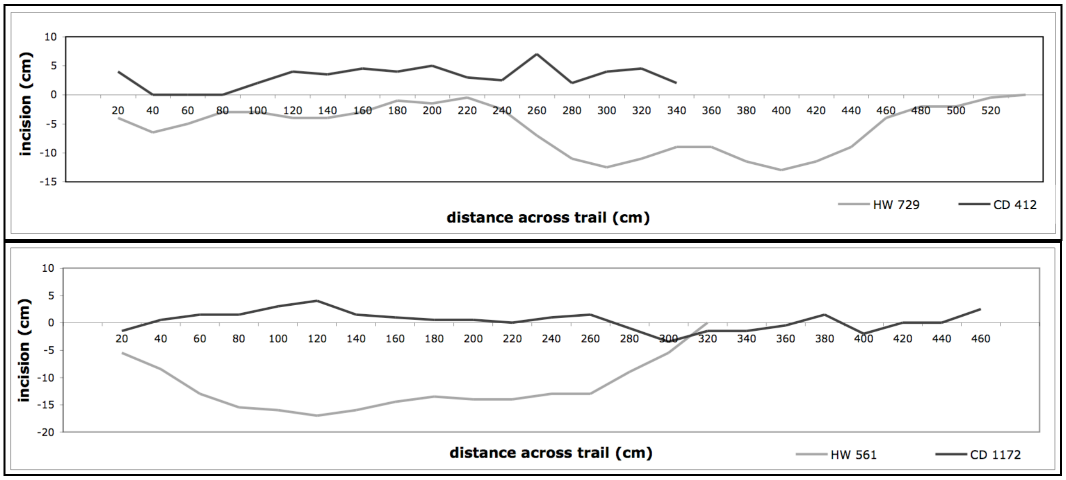

Figure 3.14: Sample surface profiles from the Cardinal Divide (CD) and Cardinal River Headwaters trails (HW). Two profiles from each site were randomly paired together for visual comparison.

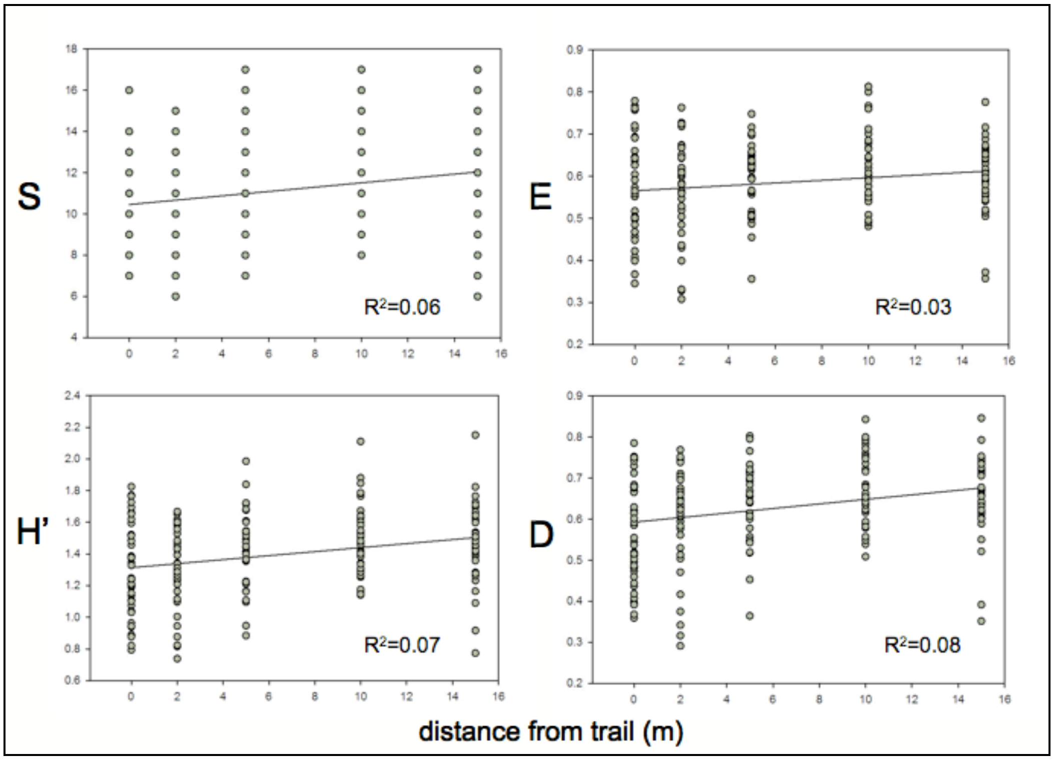

Figure 3.15: Regressions of diversity indices against distance from the trail on Cardinal Divide. S = richness, E = evenness, H = Shannon's Index, and D = Simpson's Index.

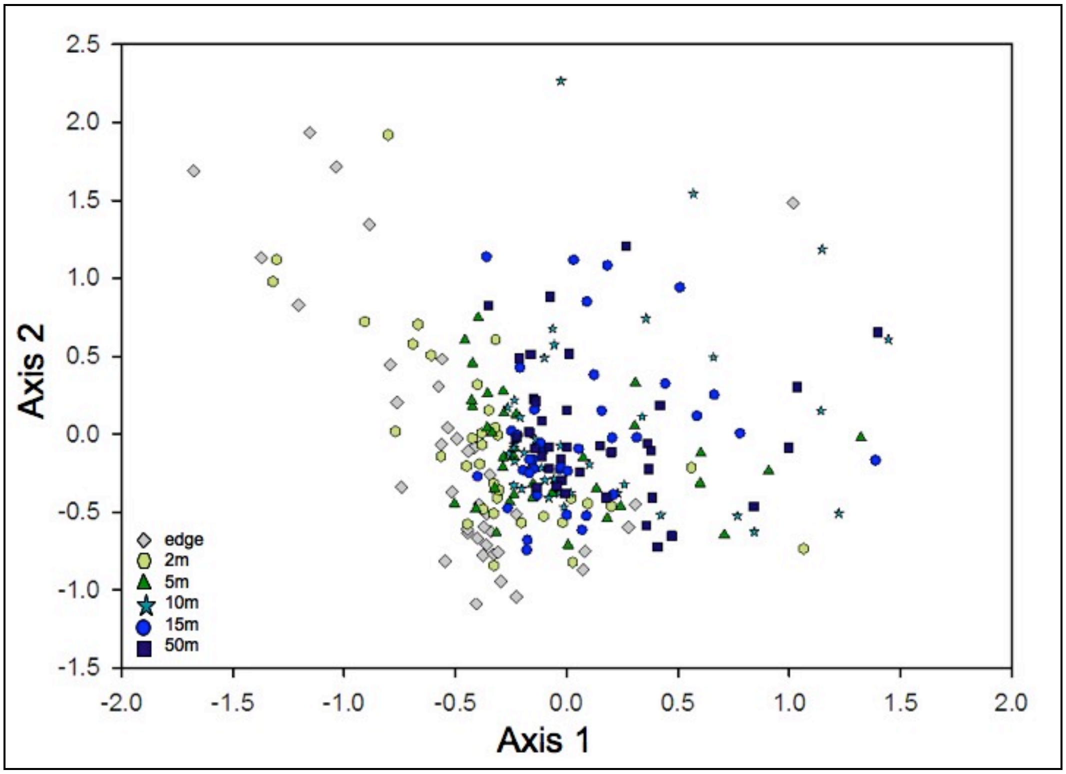

Figure 3.16: Results of the non-metric multidimensional scaling ordination of the off-trail plots on Cardinal Divide. Stress=15.4, variation explained=84.5%.

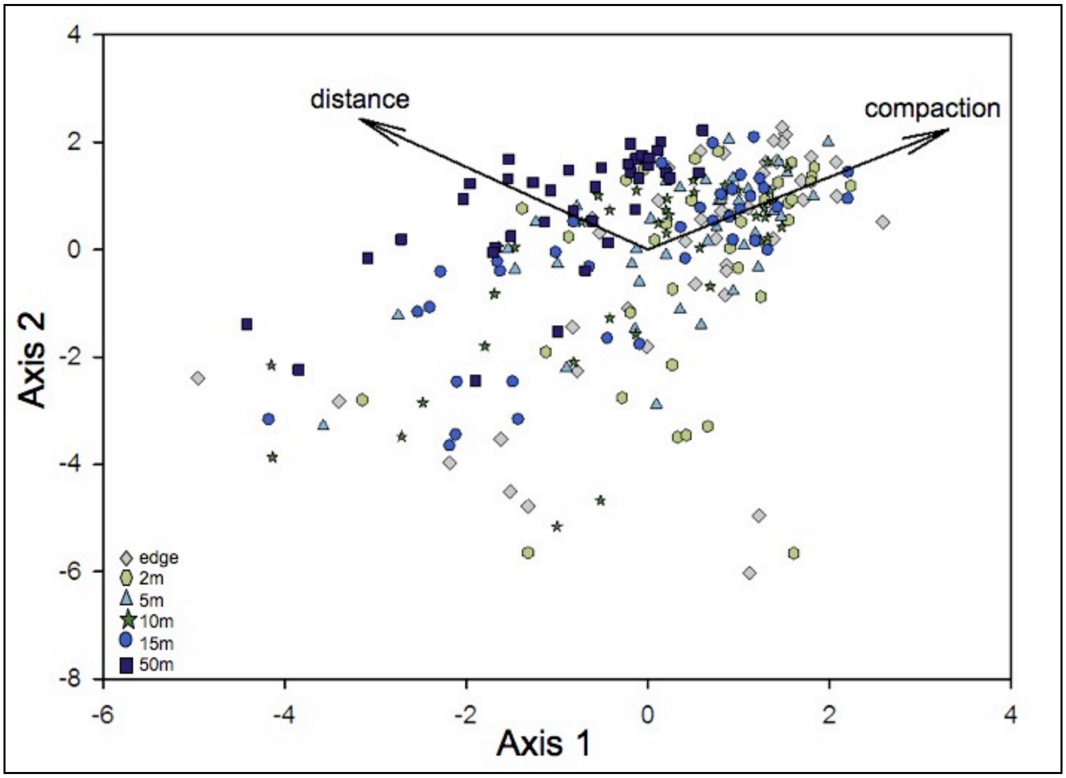

Figure 3.17: Results of the distance-based redundancy analysis plot of the off-trail plots on Cardinal Divide. Variation explained=6.5%.

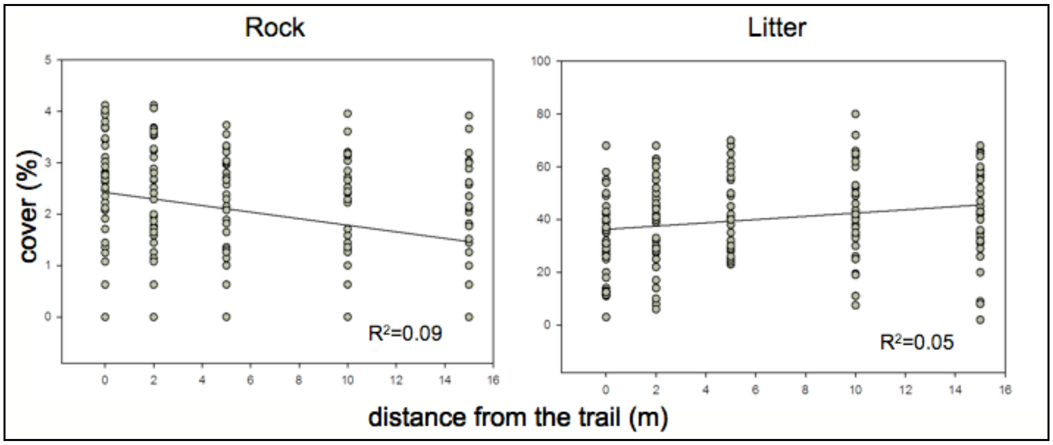

Figure 3.18: Regressions of non-vascular and abiotic cover types against distance from the trail on Cardinal Divide. Cover values are transformed (cubic root) for rock.

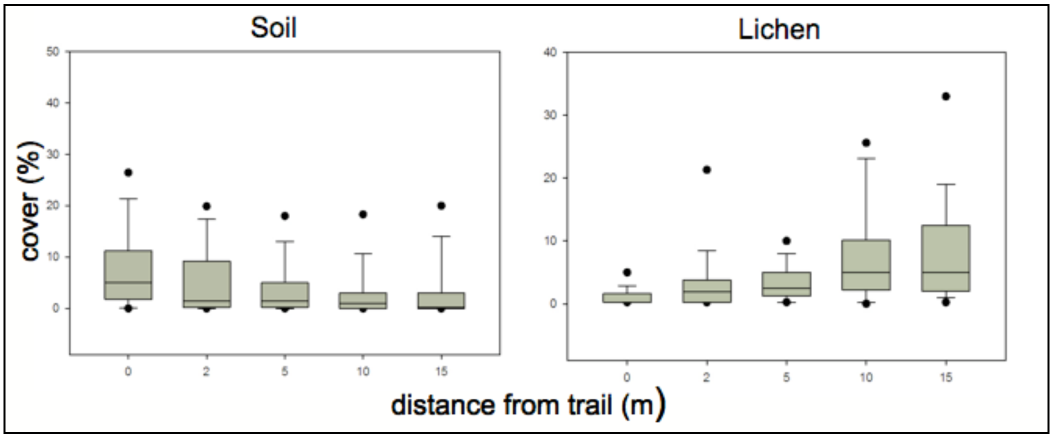

Figure 3.19: Boxplots of lichen and soil cover on off-trail plots on Cardinal Divide. Horizontal bars represent the medians, boxes represent 25th/75th percentiles, whiskers represent 10th/90th percentiles, and points represent 5th/95th percentiles.

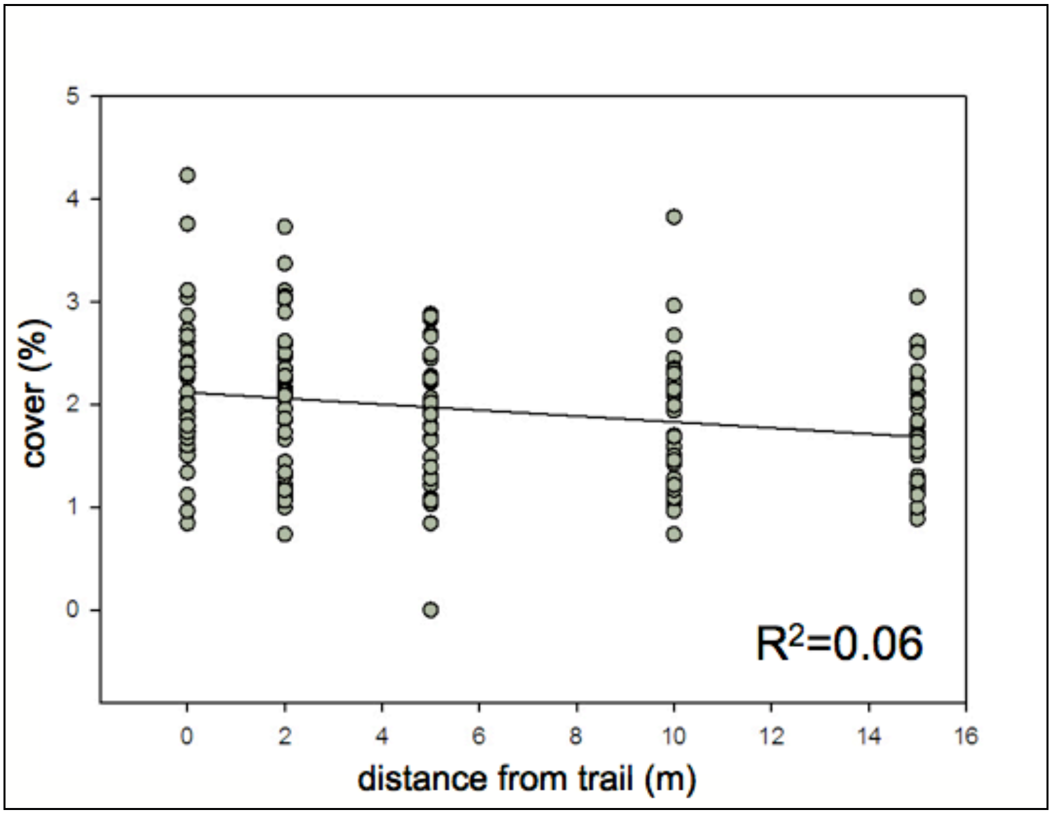

Figure 3.20: Regression of graminoid cover versus distance from the trail on Cardinal Divide. Graminoid cover values are transformed (cubic root).

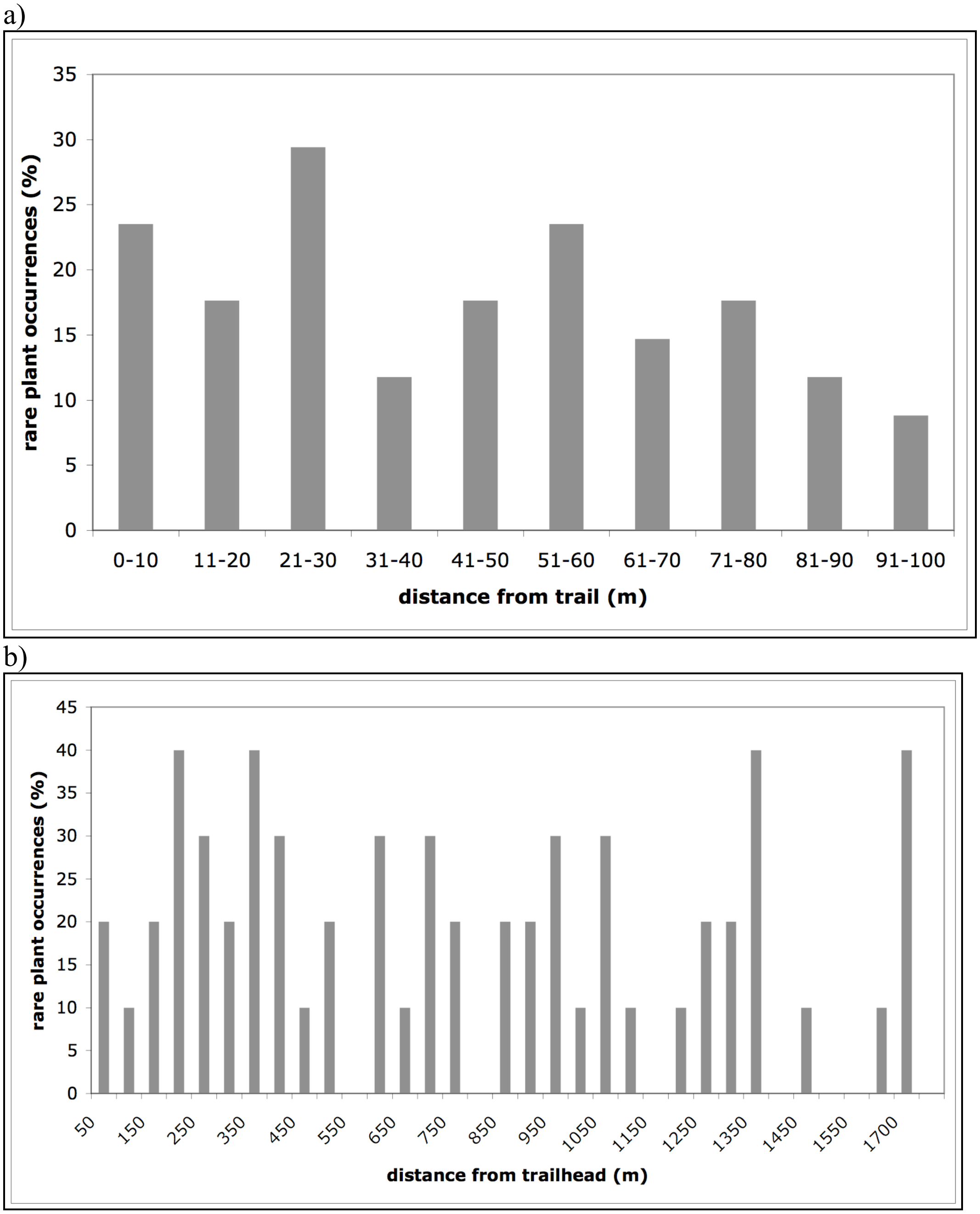

Figure 3.21: Distribution of rare vascular plants in relation to distance from the trail (a) and the trailhead (b) on Cardinal Divide. Rare plant occurrences are expressed as the percentage of 10m segments at a given distance that contained at least one rare plant.

4. Discussion

The trail on Cardinal Divide was dramatically different from the adjacent tundra: it had less biotic cover and more rock and exposed soil than the surrounding meadows, the soil was more compacted, and the vegetation was dominated by species with morphological traits that have been found to be tolerant to trampling. The Cardinal River Headwaters trail was even more radically different from the nearby meadows, and supported almost no plant life. Despite the superficial similarities between the trail and naturally formed steps on Cardinal Divide and the fact that they are both affected by disturbance (trampling on the Divide and frost disturbance on the steps), they supported very different plant communities. Thus, we can conclude that the trail community is unique in the context of the surrounding alpine environment, and the this study shows that the impacts of human disturbance in this ecosystem are both qualitatively and quantitatively different from the effects of natural disturbance. Off-trail impacts appear to be minimal to moderate, as there was very little change in vascular plant cover or composition with increasing distance from the trail. The decrease in lichens and the increase in rock cover, soil compaction and graminoids in near-trail areas indicate that low-level trampling might be having a slight effect, but there are other possible explanations for these changes, such as variations in slope or winter snow cover. Impacts on rare species appear to be equally minor, but because of differences in habitat preference and trampling tolerances, more work is needed in order to ascertain whether this is true for all rare species in the Cardinal Divide area.

Soil compaction

The higher soil compaction on the trail (at both sites) contrasts with what Monz (2002) found in a study of experimental trampling on *Dryas* tundra in Alaska: even after 500 passes, soil in experimentally trampled plots was not significantly more compacted than on control plots. The difference in results could be due to differences in soil type and texture between study sites, but soils were not described in detail in either study (Monz describes the soil at his site as “stony”, but that is also a good description of soils in the two sites surveyed in this study). It seems more likely that the greater soil compaction at my study sites is the result of the cumulative impact of trampling over many seasons on the trails surveyed in this study, as well as the past use of the areas for OHV use and horse riding.

The Headwaters trail, which continues to have active use by off-highway vehicles (OHVs), had more compacted soil than did the one on Cardinal Divide, which has had largely foot traffic for the past decade. This is similar to the findings of Weaver & Dale (1978), who compared the effects of trampling by hikers and by motorcycles in grassland environments, and found that the use of motorcycles caused more soil compaction than did hiking. He did not mention whether these differences were statistically significant, however. It is important to note that 4.5kg/cm^2 is the maximum measurement possible for the penetrometer I used; thus the results presented here are likely an underestimate of soil compaction on the Headwaters trail. In many cases the soil was so compacted that the instrument could not even penetrate the soil surface.

These results (as well as other comparisons of the two trails in this study) cannot be attributed with certainty to the differences between OHVs and hiking. Recall that Cardinal Divide used to be open to OHVs and still sees some such use by those who ignore park regulations. Soil compaction on the Divide is likely influenced by the past use of the area by OHVs; if this trail was exclusively a hiking trail it is likely that the difference between the trails at the two study sites would be even more pronounced.

Trends in soil compaction in off-trail areas are not easily interpreted. If there is more trampling in areas close to the trail as compared to areas further away, previous studies (Cole 1987; Tejedo et al. 2009) suggest that soil compaction should be higher near the trail. There was no significant decrease in soil compaction from the edge of the trail to 15 m away, but soil was significantly less compacted at 50 m from the trail than it was at 15 m. There are a couple possible explanations for these results. One is that areas near the trail, up to at least 15 m away, are experiencing approximately the same level of low-intensity trampling, while areas further away (50 m) are experiencing less human impact. Another possibility is that there is some sort of natural variation in soil between the ridgetop, where the near-trail plots were located, and the environment further downslope, where the 50 m plots were located.

Abiotic and non-vascular cover

Two abiotic (rock and soil) and four biotic (lichens, mosses, litter and soil crust) cover types were surveyed; the trail had higher abiotic cover and lower biotic cover than the surrounding tundra. Lichens and soil crust have been found to be particularly sensitive to trampling (Grabherr 1982; Belnap & Gillette 1998), so it is not surprising that they are almost completely absent on the trail. The near absence of litter on the trail is likely a function of the reduced plant cover. Unlike in a forest, litter does not drop onto an alpine trail from an overhead canopy: rather, litter is deposited in the vicinity of the plants it came from. The low plant cover on the trail means that local litter sources are scarce. Plant litter is an important source of nutrients in alpine tundra (Körner 2003), particularly phosphorus. Litter also functions as a layer of insulation that protects the soil surface from extreme temperatures (Edwards & Cresser 1992). This insulation is not only against cold temperatures: the soil surface in tundra ecosystems can become surprisingly hot on sunny summer days; the resulting high soil surface temperatures can be a significant source of stress for tundra plants (Gold 1998).

The lack of mosses on the trail is more difficult to interpret, as previous studies have shown mixed results: Gremmen et al. (2003) found that pleurocarpous mosses were equally abundant on a trail as they were in adjacent tundra, while Grabherr (1982) found that moss cover was lower in high traffic areas. These results are not very surprising given that mosses are very diverse, and like vascular plants they might show a range of tolerances to trampling. However, it is possible that the trail environment is too dry, and the dessication risk too high, for most species of mosses to thrive on the Cardinal Divide trail. The fact that Gremmen et al. (2003) conducted their study on a humid island, while this study and Grabherr's were carried out on dry ridgetop environments, lends support to this idea.

The gravel steps were intermediate between the trail and the reference tundra in terms of the cover of non-vascular and abiotic substrates. Like the trail, they are dominated by rock, but still have more biotic cover (lichens, mosses, litter and soil crust) than the trail. Frost disturbance on the gravel steps does not appear to have affected the biotic components of the community in the same way, or to the same degree, as human traffic has on the trail.

Lichen and litter cover increased with distance from the trail, while the cover of rock and exposed soil declined. This mirrors the trend in biotic versus abiotic cover that was seen in comparisons of the trail to the adjacent meadow. Though the relationship between litter cover and distance from the trail was statistically significant the regression explained very little of the variation in the data; thus, this might not reflect an ecologically significant trend. The regression for rock cover with distance from the trail also explained little (9%) of the variation, but this might reflect the very high natural variability of rock cover at the study site rather the weakness of the relationship between trampling and rock cover. Naturally occurring gravel patches are common on Cardinal Divide, and plots that fall on these patches would have large amounts of rock regardless of how much trampling they are experiencing. In addition, there are rocks of all sizes scattered across the tundra, which caused large variation in the amount of rock cover from plot to plot. It is possible that trampling does indeed lead to an increase in the cover of rock (by reducing biotic cover), but that the "noise" caused by the scattered rocks and gravel patches obscures this relationship in the regression. There may be some human influence on rock distribution as well: as part of the restoration work in the 1990's, large rocks were placed along the trail edge in the first few hundred metres of the trail in an effort to channel trail users along a single main path. Some of these rocks may have increased the amount of rock present in plots placed at the trail edge. Lichens displayed the strongest response of any of the variables examined in this section; distance explained 50% of the variation in lichen abundance, which is unsurprising in the light of what previous studies have found (Willard & Marr 1970; Grabherr 1982). Grabherr (1982) found that lichens, particularly fruticose species, declined sharply as trampling intensity increased. He noted that moisture conditions strongly affect the ability of these lichens to withstand trampling: when they are wet they are able to tolerate much heavier trampling than when they are dry and brittle. Willard & Marr (1970) found that lichens were absent in areas of concentrated hiking. The high sensitivity of lichens to human traffic might make them good early indicators of human trampling impacts in alpine systems.

Trail width & incision

The greater width of the Divide trail is largely a reflection of the braiding on this trail. Measurements of trail width were taken across all the braids, and included the vegetated strips that separated the narrower trodden sections. It is possible that even without braiding, the Divide trail would still be wider than the Headwaters trail, but not by the same margin. It is not clear why the trail on Cardinal Divide is more braided. The braiding seen could be a remnant of people driving OHVs parallel to one another on the open tundra, but this does not explain why drivers appear to remain single file on the Headwaters trail. There is no reason to believe that OHV use is inherently more likely to form braided trails than hiking; Price (1985) shows evidence of heavy braiding in alpine hiking trails in Banff National Park.

The Headwaters trail was the more deeply incised of the two trails. Weaver & Dale (1978) found the same pattern in grassland and forest trails – hiking trails were less deeply incised than OHV trails – but he did not mention whether the difference was significant. Many of the trail profiles on Cardinal Divide showed that portions of the trail are higher than the surrounding tundra. This might be a result of local topography; given that the trail is on a ridgetop and is generally not deeply incised, it is possible that some points on trail are higher than the trail edges. Large rocks and patches of vegetation on the trail can also account for some of these high points. On the other hand, the apparent lack of incision on the Divide trail might be a result of sampling error. Although we tried to ensure that the measuring tape was stretched taut across the trail, there was often a little bit of a sag in the tape, especially when it was stretched across some of the wider trails on Cardinal Divide. However, based both on our measurements and on visual assessments, I am confidant that if this were corrected, the Headwaters trail would still show greater incision.

Vascular plant cover and diversity

The drastic decline in vascular plant cover on the trail is no surprise, given that the loss of vascular cover is one of the most obvious and well-studied impacts of hiking in tundra ecosystems. Median vascular plant cover on the Cardinal Divide trail was 4%, compared to 33-36% on the off-trail plots. Assuming that the area where the trail is located originally had approximately the same vascular plant cover as the surrounding tundra, this represents a loss of about 88% of the original vegetation cover. This is greater than the losses found in other studies of trampling in tundra communities, which reported declines in vascular cover of 40-80% (Cole 1995a, 1995b; Cole & Monz 2002; Monz 2002; Whinam & Chilcott 1999; 2003; Bell & Bliss 1973; McDougall & Wright 2004). These studies focused on a variety of community types, including forb-dominated, shrub-dominated and graminoid-dominant tundra, so the variation in results might simply be a reflection of differences in trampling tolerance between different types of tundra communities. Monz (2002), who also studied the effects of trampling on *Dryas*-dominated tundra, found that plant cover in this community type declined by 80% after 500 passes. This is just slightly less than the estimated loss on Cardinal Divide from years of human use, including years of use by OHVs.

Conditions on the OHV trail in the Headwaters were even more extreme than on Cardinal Divide, with almost no plant life on the trail at all. Kay (1981) found similar effects on montane and subalpine trails in the Great Salt Lake region, and estimated that OHV use caused up to five times more devegetation than did hiking. This is likely due to the extra weight of these vehicles as well as the churning motion of their wheels when the rider tries to accelerate quickly.

The lower species richness on the trail (compared to the surrounding community) confirms the findings of Gremmen et al. (2003) in a study of decades-old trails on subantarctic Marion Island. In contrast, Monz (2002) found no significant change in richness in trampled *Dryas* tundra in Alaska, even at the highest level of trampling intensity. However, Monz's study only examined the effects of trampling over a single season. It is possible that richness is impacted differently by long-term, chronic trampling than it is by short-term experimental trampling. Richness was also lower on the trail than on naturally formed gravel steps, while both these locations in turn had lower richness than the reference tundra plots. The trail also showed a greater decline in species-richness compared to the adjacent tundra meadows (trail reference plots) than did the gravel steps compared to the gravel step reference plots. The trail had 33% fewer species than the trail reference plots (the trail had a median of 8 species per plot compared to 12 on the trail reference plots), while the gravel steps had 21% fewer species than the gravel step reference plots (11 species versus 14). This suggests that both trampling and frost disturbance are having the effect of reducing species richness in relation to the surrounding, undisturbed community, but this effect is somewhat more pronounced on the human-disturbed area. Diversity measures included only the vascular plant community; it is possible that there would be greater differences in diversity between disturbed and undisturbed areas if moss and lichen diversity was considered as well.

So far none of the literature in this field has addressed the effects of trampling on diversity; this study provides a basis for comparison for future work. Somewhat surprisingly, species diversity (Shannon's and Simpson's indices) and evenness were higher on the trail than on the adjacent tundra. Further, evenness was higher on the trail than on the gravel steps. One possible explanation for this is that the heavy dominance of the tundra meadows by *Dryas integrifolia* results in low evenness, and by extension, low diversity. In the off-trail plots on Cardinal Divide this species accounted for a median of 60% of the total plant cover while on the trail the median cover of *D. integrifolia* was only 4%. The lower evenness seen in the tundra meadows would result in decreased diversity, as evenness is included in the calculation of both Shannon's and Simpson's indices. Douglas & Ballard (1971) found a similar pattern in burned krummholz/heath communities in the Cascade Mountains: diversity was higher in burned areas 30 years following fire than in it was in unburned sites, and the authors hypothesised that this was driven by the reduced the dominance of *Phyllodoce* spp. The Headwaters trail, on the other hand, had almost no plant life, and by extension, almost no diversity, indicating that trampling does not always lead to increases in diversity and evenness. These results are interesting because they indicate that dominance (and its influence on diversity) might not be solely a function of competitive ability. Competition is believed to be minor in tundra communities (Callaway et al. 2002; Pierce et al. 2007); in stressful environments such as the arctic and high alpine regions, the ability to dominate might be a function of an increased ability to grow or reproduce despite the severity of the environment. It is possible that the intermediate disturbance hypothesis applies to the tundra despite the lack of competition in these communities by reducing the cover of dominant species, which gives the opportunity to other species to invade or expand in the community. However, when disturbance becomes extreme, as on the Headwaters trail, the severity of the environment nullifies this advantage.

The results showing increased diversity and evenness on the trail might also be partially artifacts of the sampling method. As previously mentioned, any species that had a cover value of less than 1% in a plot was given a value 0.25% for analysis. Because most of the plants found on the trail had cover values of <1%, this would give the impression that species found on the trail had very even cover values, despite the fact that some of these plants account for only 0.0001% of cover in a plot, while others account for nearly 1% of the plot.

Although richness, evenness and diversity all increased with increasing distance from trail, changes in these variables between locations were minor: richness ranged between 9-11 species per plot, while evenness ranged from 0.59-0.61 per plot. This indicates that although the regressions were significant, they might not reflect ecologically important trends.

Species and morphological composition: the trail and the adjacent tundra

While the trail community consisted of species that were found in the surrounding tundra, there was a shift in the proportions of different species, and this made the trail community quite different from that of the adjacent meadows. With the exception of *Taraxacum officionale,* all the species that were found on the trail were also found in the adjacent tundra, but in many cases species that were common on the trail, such as *Poa alpina* and *Trisetum spicatum*, were only present in trace amounts in the off-trail community. In a three-year experimental trampling study, Cole & Monz (2002) found that changes in species composition as a result of trampling in dry alpine meadows were minor. In contrast, compositional differences between the trail and the surrounding tundra on Cardinal Divide were substantial. Once again, this might be reflective of differences in community type. The meadows that Cole & Monz studied included forb-dominated and graminoid-dominated communities, whereas the tundra on Cardinal Divide is dominated by dwarf shrubs, which have been found to be intolerant of trampling (Cole 1995b). It is also possible that it takes more than a few seasons of trampling before compositional changes begin to appear. Finally, the past use of the area by motorised vehicles likely contributed substantially to these composition changes.

My results for morphological composition on the trail versus adjacent tundra mostly confirm what other studies have found about the trampling tolerance of different morphological groups. Trail vegetation was dominated by graminoids, hemi-cryptophytes, therophytes and caespitose, rosette and upright growth forms. Three of the four indicator species on the trail were grasses (*Poa alpina*, *Trisetum spicatum* and *Deschampsia cespitosa*), which is in line with previous studies that have found graminoids to be highly tolerant of trampling (Cole 1995b; Grabherr 1982; Gremmen et al. 2003; Cole & Monz 2002). The final trail indicator, *Minuartia* spp., is a genus of cushion plants. The ability of these species to survive on the trail might be indicative of the ability of the cushion growth form to tolerate the dry, cold and windy conditions that are found on the trail.

Although previous studies have found matted plants to tolerate trampling well (Naito 1969; Liddle & Greig-Smith 1975; Rogova 1976; Cole 1987a: cited in Cole 1995b), their cover was relatively low on the Cardinal Divide trail. The most common shrubs on Cardinal Divide – *Dryas integrifolia*, *Salix reticulata* and *Arctostaphylos rubra* (Rehder & Wils.) Fern. – are matted, and as previously mentioned, the matted *shrub* growth form has been found to be quite sensitive to trampling (Cole 1995b). In addition, chamaephytes like *D. integrifolia* have been found to be intolerant of trampling in other studies (Cole & Monz 2002; Cole 1995b). Although Monz (2002) found *Dryas*-dominated tundra communities to be relatively tolerant of moderate levels of trampling, the treatment included only three seasons of trampling. It is likely that chronic trampling over a number of years results in greater and different stresses and leads to different vegetation responses. Indeed, Gremmen et al. (2003) found that shrub cover was reduced on a trail that had experienced many seasons of trampling, and Cole (1995b) found chamaephytes to be intolerant of repeated cycles of trampling and recovery.

The lack of pattern in cover of cryptophytes on and away from the trail was somewhat surprising, given that a previous study (Bates 1935) suggested that cryptophytes are among the most trampling-tolerant life forms. However, this result might not be as contradictory as it appears. Most of the cryptophytes in Bates' study were graminoids, thus Bates' (1935) study might simply be reflecting the high trampling tolerance of graminoids. In contrast, most of the graminoids on Cardinal Divide were hemi-cryptophytes. The cryptophytes on Cardinal Divide were mainly perennial forbs that regenerate via bulbs or root tubers.

Exotics were not common on the trail or in the adjacent tundra community. The only exotic species found in the area was *T. officionale*, and this species showed up in only one of the trail plots, though it was observed several times on the trail. This echoes what Weaver et al. (2001) found in a survey of exotic species in several American ecosystems: *T. officionale* was one of the only exotics to invade alpine communities, and of the three invasive species they found in the alpine, it was by far the most successful.

Species and morphological composition: the trail and the gravel steps

Unlike lower elevation plant communities, associations between alpine plants are believed to be mainly facilitative (Choler et al. 2001; Callaway et al. 2002). At lower elevations where competition is common, increased space between neighbouring plants can be beneficial as it reduces competition between individuals for resources. In contrast, in high alpine communities physical isolation can be a source of stress, as isolated plants are more exposed to the cold, windy conditions of the alpine environment (Choler et al. 2001). Thus, in the alpine, individual plants can benefit from growing in close association with other plants of the same or different species. Plants growing on the trail experience a fairly high degree of physical isolation from their neighbours, and this stress could be selecting for certain species while excluding others from the trail community. Vegetation on the gravel steps is also relatively exposed; if isolation and harsh environmental conditions are shaping the plant communities found on the trail and the gravel steps, we would expect these communities to be fairly similar. However, pronounced compositional differences were found between the two locations. While the plots from both these locations are distinctly different from nearby undisturbed plots (seen in the NMDS) the gravel step community was more similar to the reference tundra than was the composition on the trail. Further evidence of the strong differences between the gravel step and trail communities is the fact that the indicator species for these two locations were completely different. Also, the trail community was dominated by trampling-tolerant species types while the gravel steps were similar to undisturbed tundra in terms of morphological composition. Overall, these results suggest that the trail community is being driven by trampling rather than by the harsh environmental conditions experienced by plants growing in a sparsely vegetated, open location.

The results of the indicator species analysis for the gravel step reference and trail reference plots appear, at first glance, to contradict the results of the NMDS and the MRPP for these two locations. While the latter analyses showed little differentiation between the two sets of reference plots, these locations had two very different suites of indicator species. However, with the exception of *Hedysarum boreale* and *Oxytropis podocarpa,* the indicators for these two locations were very minor components of the community, normally accounting for less than 1% of total cover per plot. This suggests that the differences in indicator species are not indicative of major compositional changes between the two sets of reference plots, and, by extension, that differences between the trail and gravel step plots do not simply reflect differences between the two sites.

Species and morphological composition: off-trail trends

Species and morphological composition did not change radically with increasing distance from the trail (NMDS). However, the dbRDA revealed that compaction does have an effect on species composition – there was a strong separation of plots along the compaction gradient. The relationship between distance and soil compaction was not as straightforward as I had hypothesised: though compaction declined with increasing distance from the trail, the trend was mostly non-significant (only the difference between 15 m and 50 m was significant). This suggests that if there is low-intensity trampling in off-trail areas, it is not necessarily confined to areas near the trail. The fact that soil compaction (presumably driven by human traffic) is having an effect on composition contradicts the findings of Cole & Monz (2002), who found that alpine communities in Wyoming were able to withstand as many as 1000 passes per year with little compositional change. Again, this might reflect the differences in the impacts of experimental trampling versus those of chronic trampling, as well as differences in trampling tolerance among different tundra communities.

The results of the indicator species analysis for different distances from the trail did not provide much insight into any possible gradients in species composition with distance from the trail. They can, however, be explained by the autoecology of the specific indicator species. *Pedicularis lanata*, which was an indicator for the 50 m position, tends to be more abundant in sheltered locations with abundant snow cover (Aiken et al. 1999) This could explain why it was less common on the top of the ridge, where high winds can result in very dry conditions as snow is blown off into more sheltered areas (Billings & Mooney 1968). *Carex rupestris* was found to be a significant indicator of the 2 m plots, but also had relatively high indicator values (though still <20) for all but the 50 m plots, so its occurrence does not seem to be related to trampling. The fact that *Carex petricosa* was an indicator of the edge position might be telling us something about human impacts near the trail. As a graminoid it might be quite tolerant of trampling and might increase in abundance near the trail for that reason; it was also fairly common on the trail. Alternatively, this species is generally found in dry habitats (Moss 1983; Aiken et al. 1999), which is a characteristic of ridgetop environments in the alpine. Thus its association with the trail edge might simply reflect its habitat preference rather than any effect of trampling.

Graminoids were the only morphological group to show a pattern of change in abundance along the distance gradient; they decreased significantly with increasing distance from the trail. This could be explained by their tolerance of trampling and might reflect a decline in trampling pressure at distances further away from the trail. However, the variation explained by the regression was very low (R^2=0.09), making the ecological significance of these results questionable. In addition, this result could be reflective of the habitat preferences of graminoid species that are found on Cardinal Divide. The vast majority of the graminoids in off-trail plots were sedges (*Carex scirpoidea* Michx. var. *scirpoidea*, *Carex nardina* Fries, *Carex rupestris*, *Carex petricosa* and *Kobresia myosuroides*). With the exception of *C. scirpoidea*, all of these species prefer dry environments (Moss 1983; Aiken et al. 1999). Thus the slight decrease in graminoids with distance from the trail could simply be attributable to the change from drier, windier conditions on the ridgetop to moister, more sheltered conditions downslope.

Rare plants

The distribution of rare plants on Cardinal Divide was significantly related to distance from the trail, distance *along* the trail (from the trailhead), and the interaction between the two: rare plants were more abundant near the trail and near the trailhead than they were at greater distances from both. It is difficult to tell whether this reflects an impact of trampling on occurrence of rare species, and it is possible that this really just reflects the influence of natural variation in the ridgetop environment. The area near the road is lower in elevation and has more krummholz patches compared to areas further along the trail, where the tundra is more open and exposed.

Pedicularis flammea was the most commonly found species in the rare plant survey, accounting for 75% of total occurrences. As such, its distribution might have had a disproportionate impact on the results of this analysis. Although there were too few occurrences of the other rare species to analyse them separately, a few trends were noticeable. *Braya purpurescens* was only found areas that have experienced human disturbance. In the rare plant survey it was found twice: once on the trail and once at the edge of the access road, but not in intact tundra meadows. It also appeared a couple of times in the trail plots (from Sections 1 & 2), and there were >50 individual plants growing on the east side of the parking lot at the top of the Divide. Moss (1983) lists alpine screes as *B. purpurescens'* habitat; its ability to survive in this harsh environment might make it better suited than other species to the rocky, exposed conditions found in disturbed areas such as the trail and the access road. *Antennaria monocephala* was most often found in the vicinity of shrubs, particularly willows. This species was not found on the open tundra, and for the most part was only sighted very close to the treeline. Aiken et al. (1999) noted that *A. monocephala* is generally found in mesic and moist areas, so soil moisture might be the driver behind its distribution the Divide. *Campanula uniflora* did not show any distinctive pattern in its distribution.

Synthesis and management implications

The trail and the surrounding environment

One of the questions that I set out to address in this study was whether the impacts of human disturbance in the alpine are similar to the impacts of natural disturbance. The results of this study indicate that the answer to this question is no: trampling and frost disturbance have very different effects on the alpine tundra of Cardinal Divide. While both types of disturbance cause mechanical damage to plants (frost action results in root damage and breakage, and trampling causes the breakage of the above-ground organs), the two disturbed areas support very different community types. This is not entirely surprising, given the different effects that frost disturbance and trampling have on soils; trampling leads to increased soil compaction, while frost heave might loosen soils (Whinam & Chilcott 2003).

It appears that trampling leads to the development of a community type that is unique in the context of the surrounding alpine environment on Cardinal Divide, different from both the tundra meadows and from naturally disturbed, sparsely vegetated gravel steps. Although almost all the species found on the trail are present in the adjacent tundra, the proportions in which these species are found are very different on the trail than off, and while there are similarities between the trail and the gravel steps, by and large the two communities are quite different as well. Unlike the gravel steps, the trail supports a very trampling-tolerant community. These results, along with the lower cover of lichens and soil crust on the trail, suggest that the plant community on the trail is shaped by trampling. Given the radical changes in community composition, along with the increased soil compaction and the increased risk of erosion on the trail, it would be advisable for conservation purposes to limit the extent and number of trails in alpine areas as much as is feasible.

In many cases the impacts of trampling on Cardinal Divide were more severe than the impacts found in the experimental trampling literature: vascular plant cover was lower, soil compaction was greater and species composition on the trail was radically different from that of the surrounding tundra meadows. This is probably partly a function on the intensity of trampling that the Cardinal Divide trail experiences versus that which is applied in experimental trampling studies; most experimental studies use a maximum of 500 passes (although a couple of studies used 800 or 1000 passes as their maximum). In contrast, the Cardinal Divide trail received over 2000 visits (passes) in the summer of 2008 (Alberta Parks, unpublished data). This suggests that experimental trampling studies are underestimating both the intensity of disturbance and the degree of impact that tundra trails experience, and it that it would be advisable to use higher maximum trampling levels in these sorts of studies.

Off-trail impacts

Though the patterns seen along the gradient of increasing distance from the trail were weak, there was some evidence that off-trail areas might be mildly affected by trampling pressure. A decline in lichens and an increase in soil compaction and graminoid abundance nearer to the trail are all consistent with what previous trampling literature has found. However, though the results fit the hypothesis of low-level trampling effects, based on previous literature, I cannot say with certainty that low-intensity trampling is in fact shaping the near-trail community on Cardinal Divide. It is possible to say though, that *if* low-intensity trampling is occurring near the trail (and at least a small amount certainly is, based on observations of visitor behaviour in the field), then the effects of it on this particular system appear to be minor to moderate at this point. Vascular cover and diversity showed very little change with increasing distance from the trail. The loss of lichen and a slight change in species composition associated with soil compaction indicate that continued trampling pressure could eventually have detrimental effects on the system. To this point, however, the ecosystem appears to have been able to sustain low-intensity trampling.

Recreational impacts on rare plants on Cardinal Divide

The findings of the rare plant survey suggest that recreation on Cardinal Divide is not having an adverse effect on rare species in the area; in fact, rare plants became slightly *less* abundant with increasing distance from the trail. However, our survey only included six species, and given that species differ in their habitat preferences as well as their sensitivity to trampling, the results of this survey cannot be extrapolated to all the rare species found on Cardinal Divide. Further surveys of species that are likely to be sensitive to trampling, or that are likely to occur primarily in the ridgetop environment (where the heaviest trampling is), are necessary to ascertain whether recreation on the Divide poses a threat to rare species. The apparent preference of *Pedicularis flammea* for the ridgetop environment underlines the importance of maintaining the current trail on Cardinal Divide: further expansion of the trail network in this area could pose a threat to these species.

The sustainability of recreational activities on Cardinal Divide and in the Cardinal River Headwaters

The trails on Cardinal Divide and in the Cardinal River Headwaters are examples of acute human impact in alpine tundra. In both locations the trail environment and plant community have been severely impacted by human traffic (OHV use and foot traffic) and are radically different from the surrounding tundra. On the other hand, trampling does not appear to have strongly impacted the off-trail communities, and though the damage is severe in areas of high traffic, these high disturbance areas are limited to linear features (the trails) that cover only a small proportion of the alpine environment in the Cardinal Divide area. There are likely other indirect impacts associated with both hiking (e.g., avoidance of the area by animals) and OHVs (e.g., noise and air pollution, deposition of dust on trailside vegetation) but these are beyond the scope of this study.

As long as impacts are contained to the trail and the trail network does not become too extensive, recreational activities should not threaten the ecological integrity of alpine meadows. However, if impacts expand beyond the trail into the surrounding community, or if the trails expand in extent or in number, this could put into question the sustainability of human activity in these ecosystems. Trail expansion (e.g., trail doubling, the abandonment of degraded trails in favour of new ones) could be problematic because regeneration on old trails will likely be a very long-term process, due to the changes in the trail environment associated with trampling. In particular, the small amounts of litter and soil crust that are found on the trail could have implications for the trail community as well as for the revegetation of abandoned trails, as both play roles in nutrient cycling. Litter is an important source of nutrients in alpine communities (Körner 2003), while cryptogamic crust fixes nitrogen, which is believed to be a limiting factor in dry alpine tundra (Bowman et al. 1993). Gold et al. (2001) found that in the absence of cryptogamic crusts, alpine soils had lower levels of both nitrogen and phosphorus. Soil compaction reduces soil porosity and infiltration capacity, and can inhibit root growth (Liddle 1997). Soil temperatures can become more extreme as a result of the loss of the insulating effects of litter and soil crust. Gold (1998) hypothesises that warmer soil temperatures as a result of dark-coloured crusts could increase germination rates in arctic tundra.

Growth rates in alpine plants are slow under natural conditions, but trampling-related changes in the trail environment could further slow down regeneration processes. Trampling results in a situation where many of the natural stresses of the alpine environment are amplified: due to the lack of plant cover the trail is probably colder, windier, and drier than the surrounding tundra and the soil is likely more nutrient-poor as a result of the loss of cryptogamic crust and plant litter. Because of this, trampling could trigger a series of positive feedbacks in tundra systems (Figure 4.1) that inhibit regeneration on disturbed areas and place further stress on plants that have persisted on the trail. These feedbacks could be the mechanism behind the predicted slow recovery rates for tundra communities that have been damaged by recreational activities, and active restoration might be necessary in some cases to reverse this feedback process.

The near complete absence of vegetation and soil crust on the trail is also of concern because the anchoring function that they provide is lost. Erosion is probably a greater concern in the Headwaters, because the trail has more sloped areas and almost no plant cover or cryptogamic crust to anchor the soil. The issue of erosion, trail degradation and trail abandonment, combined with the issues listed above, which could hinder revegetation, could become a serious issue for the management of the Headwaters trail. Combined with increasing levels of trail use in this area (Alberta Sustainable Resource Development, unpublished data), the medium- to long-term sustainability of this trail for OHV use is questionable.

Conclusions

Alpine tundra is widely believed to be a fragile system that lacks ecological resiliency and recovers slowly from disturbance. Despite this, there is a lack of understanding as to how these ecosystems respond to disturbance, even though disturbance in alpine tundra ecosystems has been increasing in recent years, largely due to the increased popularity of these areas for recreation.

While this study has addressed many of the issues regarding the response of alpine tundra to trampling, many questions remain unanswered both in this study and in literature in the field as a whole. The impacts of recreation on soil crusts in tundra ecosystems in particular have received very little attention thus far. Given the fragility and ecological importance of soil crusts, it is important to increase our understanding of how they are affected by recreational activities. More studies looking into the regeneration of soil crusts and possibilities for active restoration would be useful as well. Changes in soil nutrient levels and soil temperatures triggered by the loss of plant litter and soil crust have not been well investigated, even though they could have important ramifications for the revegetation of abandoned trails. More long-term studies looking into the impacts of trampling on alpine tundra, as well as the recovery of tundra communities once trampling pressure is removed, would be helpful to tie together the results of experimental trampling and descriptive studies in the field. In addition, monitoring of recovering areas could provide some insight into predicted recovery times in different types of tundra communities. Finally, it would be useful to directly compare the impacts of different types of recreational activities (hiking, mountain biking, OHV use, horse riding) in the tundra.

Previous literature has for the most part focused on changes in vascular plant cover as well as the characteristics of species that are able to persist in trampled areas, and this study has added to the knowledge base regarding these variables. It has also addressed dimensions of tundra disturbance that have been poorly represented in the literature thus far: there was increased attention paid to species diversity and composition, impacts to the near-trail environment were examined, the distribution of rare species in relation to the trail was analysed, and the effects of human disturbance were compared to those of natural disturbance in a tundra ecosystem. Comparisons of the trail to the surrounding tundra largely confirmed the results of previous studies: the trail had less vascular plant cover than the tundra, and the trail community was dominated by trampling tolerant life forms. There was some evidence that recreation is impacting the tundra close to the trail but the effects, at least on the vascular plant community, appear to be fairly minor at this point. Over time, or if use of the area becomes heavier, off-trail areas might begin to exhibit signs of severe damage from trampling, but at this time there does not appear to be major cause for concern about the ecological integrity of these areas. The trail was found to be very different from naturally formed gravel steps, indicating that the effects of natural disturbance differ from those of human disturbance in tundra communities. Rare plants, at least the species surveyed in this study, do not appear to be adversely affected by trampling in terms of their distribution.

Results of this study suggest the impacts of recreation use are largely confined to the trail, while the surrounding vascular plant communities are little affected. As long as trails and the severe (though localised) impacts associated with them are deemed acceptable by users and managers, recreational activities should not compromise either the ecological integrity or aesthetic quality of alpine areas. However, there is reason to be cautious. Trampling results in an environment that is likely to be extremely hostile for plants, and regeneration on trails will probably be a very slow process. This could become a serious management issue if trails become decreasingly degraded as a result of erosion and are abandoned in favour of newer trails that are easier and more comfortable for users to navigate. Proper maintenance of trails and the prevention of casual expansion (by users) of existing trail networks in necessary in order for recreation to be sustainable in this sort of ecosystem.

Figures

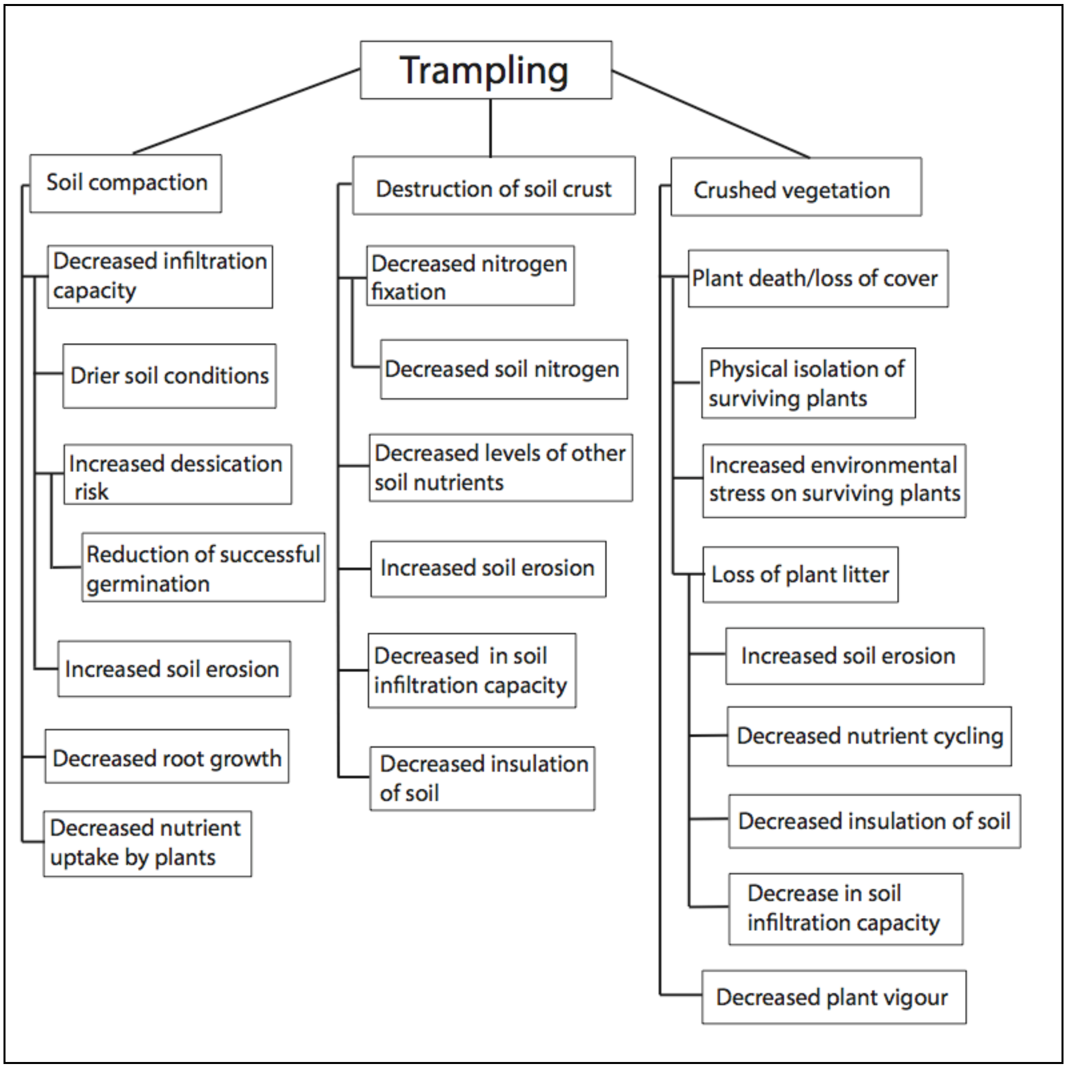

Figure 4.1: Model of predicted positive feedbacks initiated by trampling.

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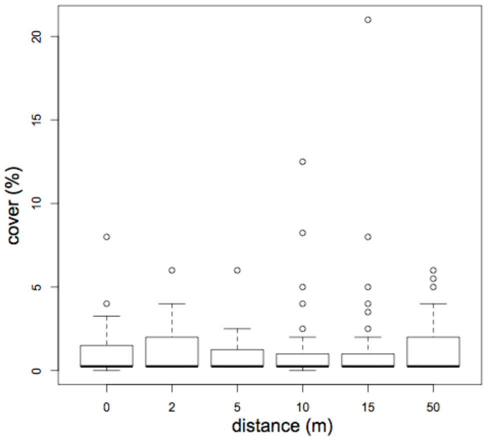
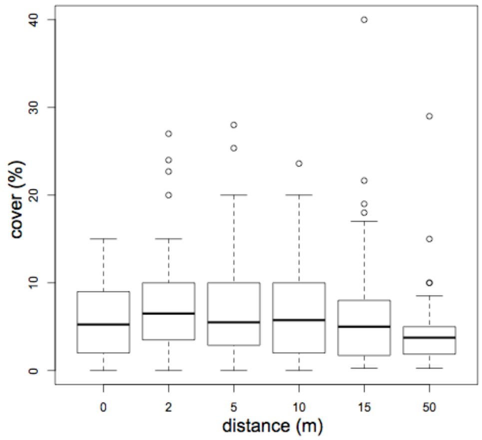
Appendix 1

Box plots of non-analysed variables in Section 2

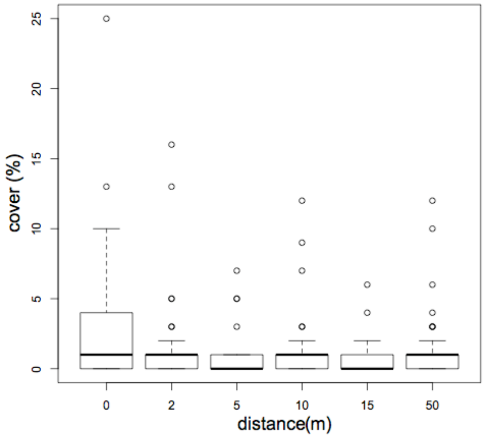
Mosses



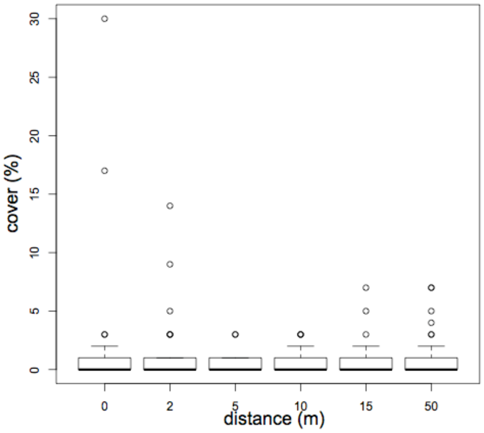
Cryptogamic crust



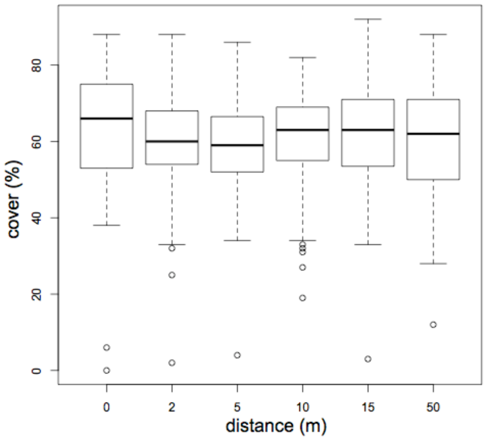
Caespitose growth form



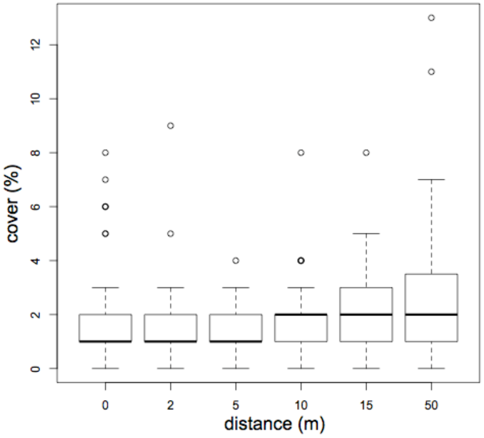
Cushion growth form

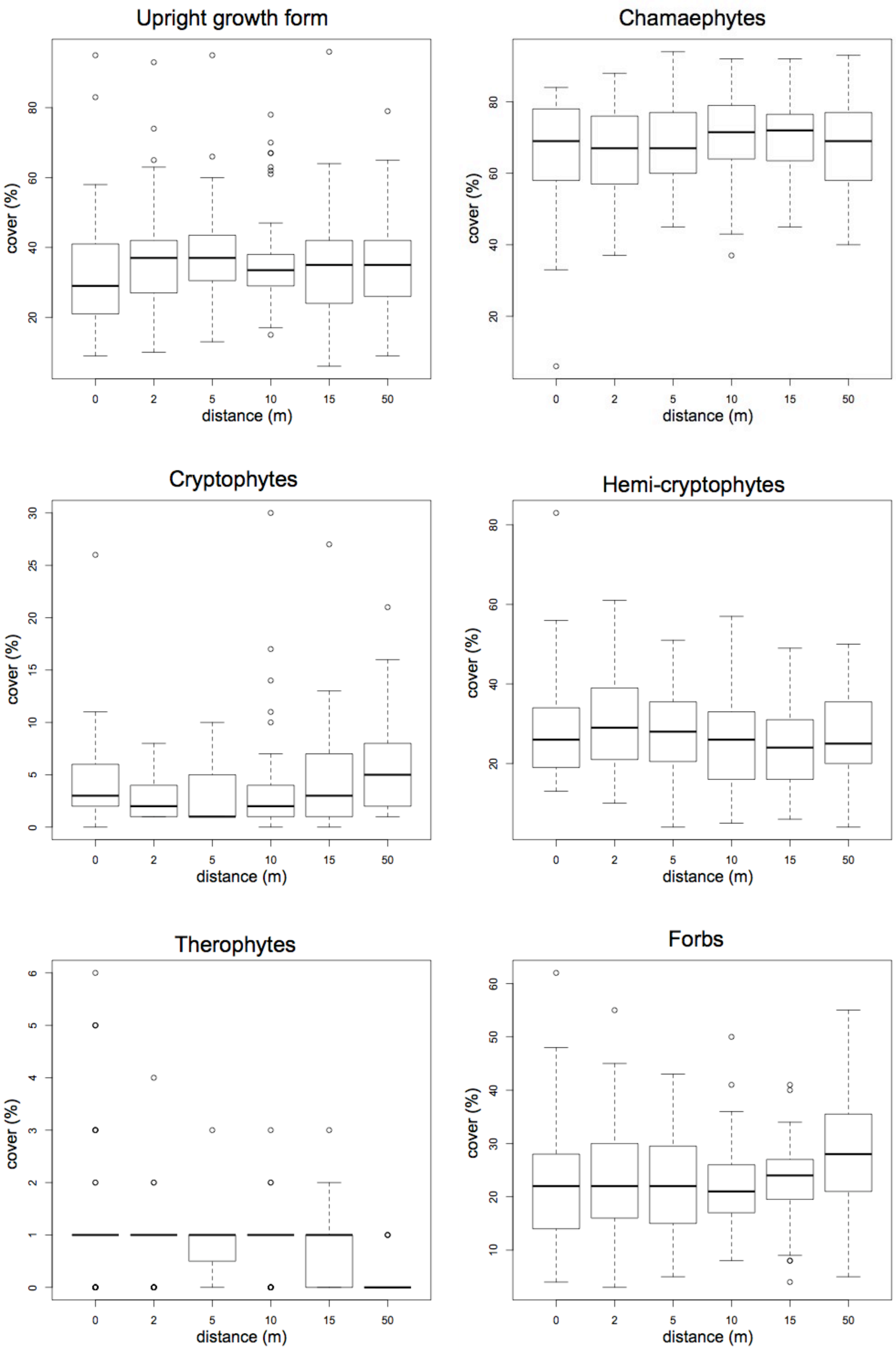


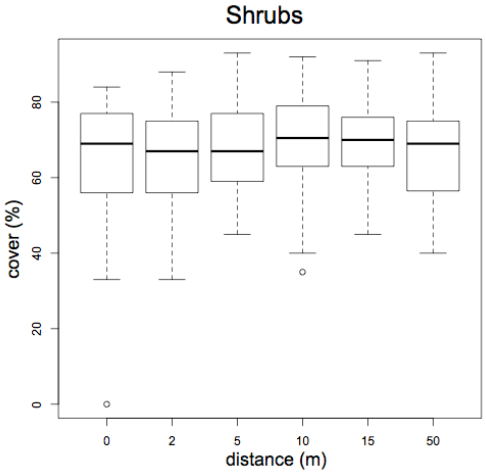
Matted growth form

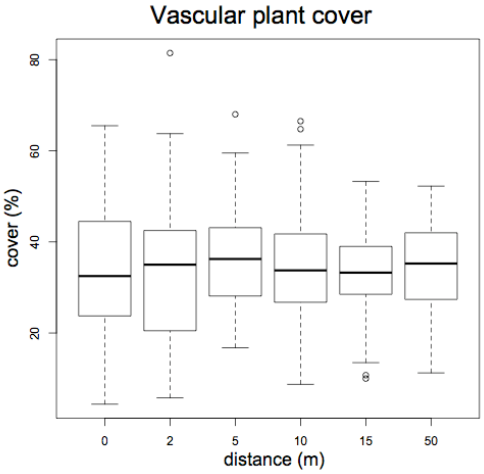


Rosette growth form



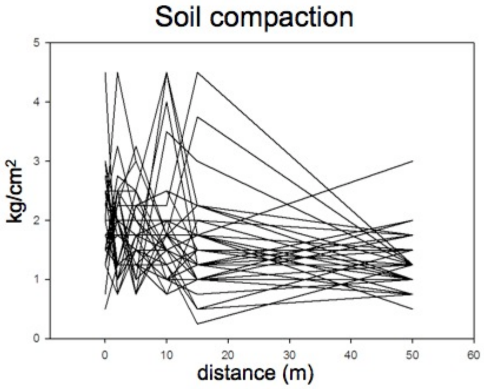

Upright growth form
Chamaephytes
Cryptophytes
Hemi-cryptophytes
Therophytes
Forbs
cover (%)
distance (m)
0
2
5
10
15
50
20
40
60
80
0
5
10
15
20
25
30
0
1
2
3
4
5
6
10
20
30
40
50
60

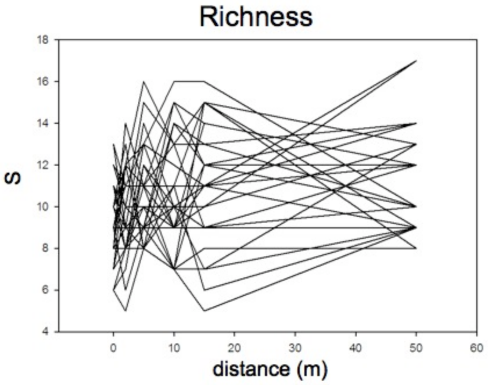

Shrubs
cover (%)
0
20
40
60
80
0
2
5
10
15
50
distance (m)

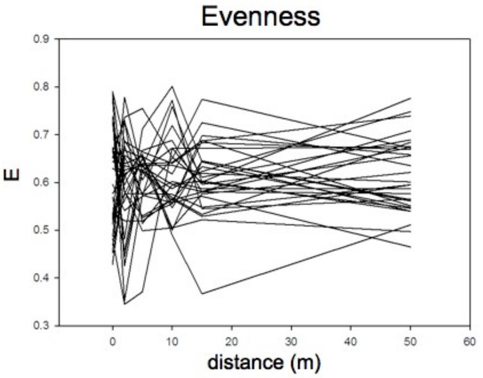

Vascular plant cover
cover (%)
20
40
60
80
0
2
5
10
15
50
distance (m)

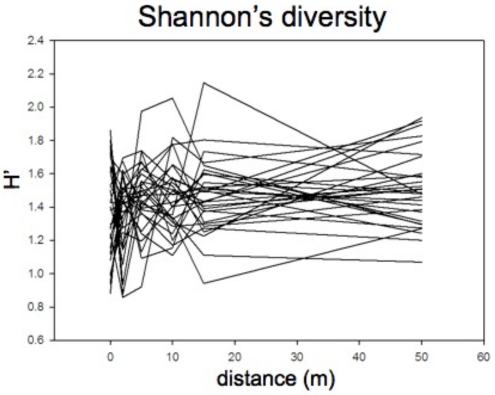
Appendix 2

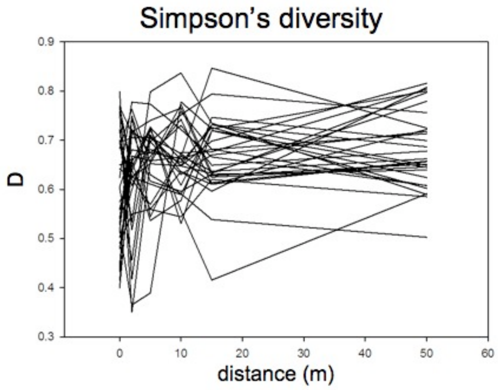
Line graphs of within-transect trends for variables analysed in Section 2

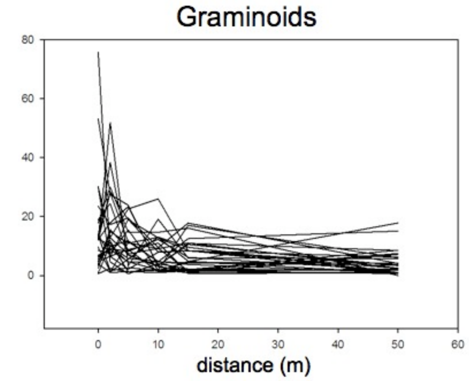


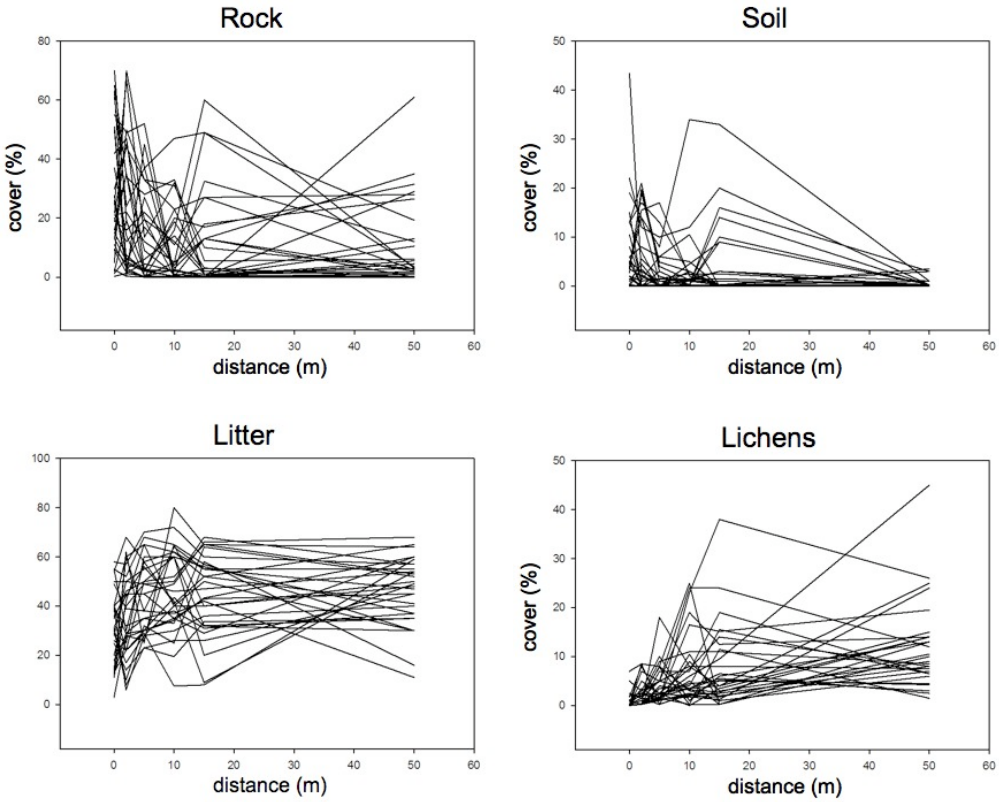











Rock
cover (%)
distance (m)
0
20
40
60
80
0
10
20
30
40
50
60
Soil
cover (%)
distance (m)
0
10
20
30
40
50
Litter
cover (%)
distance (m)
0
20
40
60
80
100
Lichens
cover (%)
distance (m)
0
10
20
30
40
50

Appendix 3

Median non-vascular and morphological covers for the Cardinal Divide and Cardinal River Headwaters trail

Table 1: Median cover of non-vascular and abiotic substrates per plot for the trail, edge, and 15m plots, and for all the off-trail plots combined on Cardinal Divide. The trail plots were compared against the edge and 15m plots separately; asterisks indicate significant differences from the trail (*p<0.05, **p<0.01, ***p<0.001). The combined row refers to all off-trail plots combined, and is presented for reference; these figure were not compared statistically to the trail. Wilcoxon's test was used for this analysis.

		Trail	**Edge**	**15m**	**Combined**
Rock	Median	71	**19*****	**3*****	7
	5th/95th percentile	47/85	0/63	0/49	0/50
Soil	Median	19	**5*****	**0*****	1
	5th/95th percentile	9/85	0/26	0/0	0/18
Lichen	Median	0	**0.25*****	**5*****	3
	5th/95th percentile	0/0	0/5	0/25	0/18
Moss	Median	0	**0.25*****	**0*****	0
	5th/95th percentile	0/0	0/3	0/5	0/4
Litter	Median	3	**32*****	**43*****	41
	5th/95th percentile	0/12	12/55	9/65	12/65
Crust	Median	0	**5*****	**5*****	5
	5th/95th percentile	0/1	0/13	0/19	0/20

Table 2: Median non-vascular cover per plot for the trail, edge and 15m plots, and for all off-trail plots combined in the Cardinal River Headwaters. The trail was compared to the edge and 15m plots separately, asterisks indicate significant differences from the trail (*p<0.05, **p<0.01, ***p<0.001). The combined row refers to all off-trail plots combined, and is presented for reference; these figure were not compared statistically to the trail. Wilcoxon's test was used for this analysis.

		Trail	**Edge**	**15m**	**Combined**
Rock	median	27	37	**5***	17
	5th/95th percentile	6/71	6/85	0/72	0/17
Soil	median	73	**8*****	**0*****	2
	5th/95th percentile	29/94	0/28	0/5	0/17
Lichen	median	0	**0.25*****	**9*****	3
	5th/95th percentile	0/0	0/0	0/24	0/0
Moss	median	0	**0.25*****	**2*****	2
	5th/95th percentile	0/0	0/4	0/11	0/10
Litter	median	0	**19*****	**40*****	33
	5th/95th percentile	0/0	2/39	11/55	6/55
Crust	median	0	**0*****	**2*****	1
	5th/95th percentile	0/0	0/6	0/19	0/17

Table 3: Median cover of different growth form categories by location on Cardinal Divide. Asterisks indicate significant differences from the trail (* p<0.05, ** p<0.01, *** p<0.001). The "combined" column presents values for all the off-trail plot locations combined. These values were not statistically compared to the trail. Wilcoxon's test was used this analysis.

		Trail	**Edge**	**15m**	**Combined**
caespitose	median	12	**0.25*****	**0.5*****	1
	5th/95th percentile	0/59	0/10	0/2	0/7
mat	median	6	**66*****	**63*****	61
	5th/95th percentile	0/55	38/80	36/79	32/81
cushion	median	2	**0****	**0*****	0
	5th/95th percentile	0/30	0/3	0/3	0/3
rosette	median	8	**1*****	**2*****	1
	5th/95th percentile	0/35	0/6	1/4	0/6
upright	median	43	**29****	**35****	35
	5th/95th percentile	11/76	11/58	17/58	14/65

Table 4: Median cover of different life form categories by location on Cardinal Divide. Asterisks indicate significant differences from the trail (* p<0.05, ** p<0.01, *** p<0.001). The "combined" column presents values for all the off-trail plot locations combined. These values were not statistically compared to the trail. Analyses were done using Wilcoxon's test.

		Trail	**Edge**	**15m**	**Combined**
chamaephytes	median	13	**69*****	**72*****	70
	5th/95th percentile	0/64	38/84	57/90	45/88
cryptophytes	median	4	3	3	3
	5th/95th percentile	0/21	1/11	1/12	1/11
hemi-cryptophytes	median	27/73	**26*****	**24*****	26
	5th/95th percentile	92	14/56	8/39	9/49
therophytes	median	4	**1*****	**1*****	1
	5th/95th percentile	0/21	0/5	0/2	0/2

Table 5: Median cover of different structural categories by location on Cardinal Divide. Asterisks indicate significant differences from the trail (* p<0.05, ** p<0.01, *** p<0.001). The "combined" column presents values for all the off-trail plot locations combined. These values were not statistically compared to the trail. Analyses were done using Wilcoxon's test.

		Trail	**Edge**	**15m**	**Combined**
forb	median	33	**22****	**24****	23
	$5^{th}/95^{th}$ percentile	0/64	8/45	8/35	8/43
graminoid	median	50	**10*****	**5*****	6
	$5^{th}/95^{th}$ percentile	7/90	1/30	1/17	1/28
shrub	median	6	**69*****	**70*****	69
	$5^{th}/95^{th}$ percentile	0/56	38/81	55/90	55/88

Appendix 4

Median non-vascular and morphological covers for the trail, gravel steps, trail reference and gravel reference plots

Table 1: Median cover values for non-vascular and abiotic cover types for the trail, gravel step, trail reference and gravel step reference plots. Asterisks beside median values for the gravel steps indicate a significant difference between the trail and the gravel steps; asterisks beside median values for the gravel step reference plots indicate a significant difference between the trail reference and gravel step reference plots (* p<0.05, ** p<0.01, *** p<0.001). Kruskal-Wallis tests were used for the initial analyses, while post-hoc analyses were done using Mann-Whitney.

		Trail	**Gravel steps**	**Trail reference**	**Gravel step reference**
Rock	median	71	77	2.5	**18***
	5th/95th percentile	47/85	63/85	0/32	4/39
Soil	median	19	**4*****	0.25	**2***
	5th/95th percentile	9/46	0/7	0/3	0/3
Lichen	median	0	**0.25*****	10	7
	5th/95th percentile	0/0	0/4	5/25	0/13
Moss	median	0	**0.25*****	0.25	2
	5th/95th percentile	0/0	0/0	0/5	0/4
Litter	median	2.5	**9*****	49	35
	5th/95th percentile	0/12	4/15	29/64	0/51
Crust	median	0	**3*****	4	6
	5th/95th percentile	0/1	0/7	0/11	0/11

Table 2: Median cover of different growth form categories by location. Asterisks beside median

values for the gravel steps indicate a significant difference between the trail and the gravel steps; asterisks beside median values for the gravel step reference plots indicate a significant difference between the trail reference and gravel step reference plots (* p<0.05, ** p<0.01, *** p<0.001). Initial comparisons were done using Kruskal-Wallis; post-hoc analyses used Mann-Whitney.

		Trail	**Gravel steps**	**Trail reference**	**Gravel step reference**
caespitose	median	12	**2*****	1	**3****
	5th/95th percentile	0/59	0/7	0/6	1/12
cushion	median	2	2	0	1
	5th/95th percentile	0/30	0/9	0/6	0/2
matted	median	6	**69*****	62	71
	5th/95th percentile	0/55	45/89	35/76	45/80
rosette	median	8	6	2	2
	5th/95th percentile	0/35	0/15	0/8	0/3
upright	median	43	**16*****	35	23
	5th/95th percentile	0/76	6/38	13/64	6/47

Table 3: Median cover of different life form categories by location. Asterisks beside median values for the gravel steps indicate a significant difference between the trail and the gravel steps; asterisks beside median values for the gravel step reference indicate a significant difference between the trail reference and gravel step reference plots (* p<0.05, ** p<0.01, *** p<0.001). Initial analyses used the Kruskal-Wallis test, while post-hoc comparisons were done using Mann-Whitney.

		Trail	**Gravel steps**	**Trail reference**	**Gravel step reference**
chamaephytes	median	13	**72*****	69	73
	5th/95th percentile	0/64	49/90	43/89	38/76
cryptophytes	median	4	**6***	5	**2***
	5th/95th percentile	0/21	0/15	1/13	0/3
hemi-cryptophytes	median	68	**20*****	25	26
	5th/95th percentile	27/92	7/42	4/43	22/59
therophytes	median	4	**0*****	0	0
	5th/95th percentile	0/21	0/0	0/1	0/0

Table 4: Median cover of different structural categories by location. Asterisks beside median

values for the gravel steps indicate a significant difference between the trail and the gravel steps; asterisks beside median values for the gravel reference plots indicate a significant difference between the trail reference and gravel reference plots (* p<0.05, ** p<0.01, *** p<0.001). Initial comparisons used the Kruskal-Wallis test; post-hoc analyses were done using the Mann-Whitney test.

		Trail	**Gravel steps**	**Trail reference**	**Gravel step reference**
forb	median	33	41	28	**52*****
	5th/95th percentile	0/64	27/62	11/52	44/57
graminoid	median	50	**6*****	2	3
	5th/95th percentile	7/90	2/15	1/9	2/7
shrub	median	6	**52*****	69	**45*****
	5th/95th percentile	0/56	35/68	69/85	38/52

Appendix 5

NMDS ordination of the edge-50m plots with outliers included

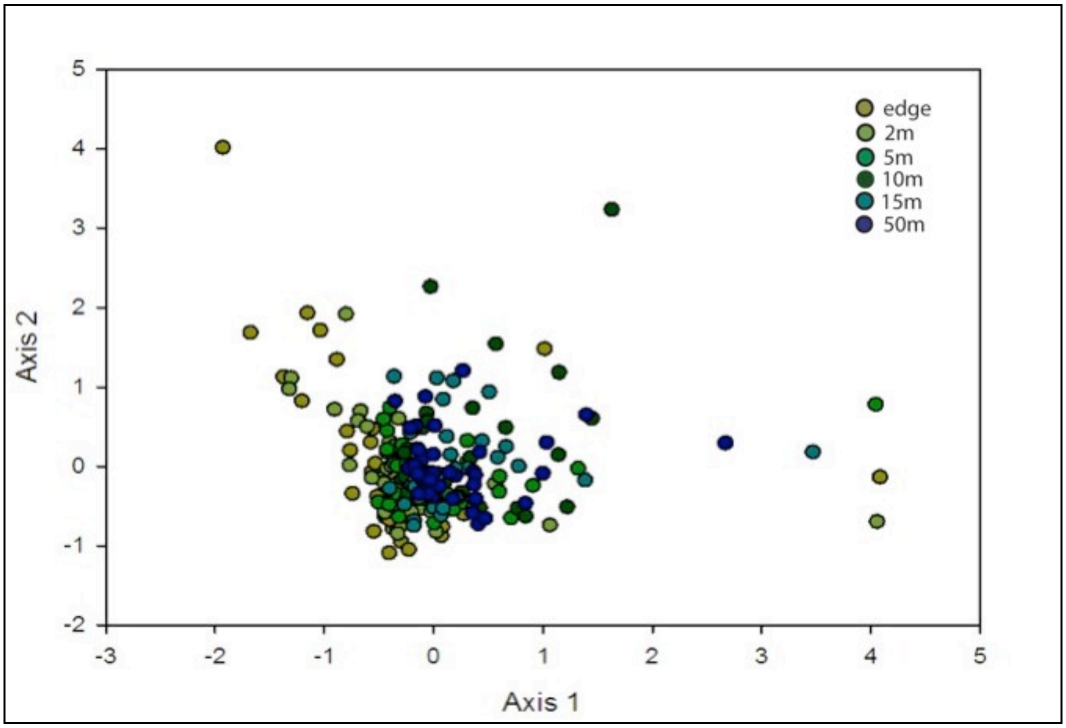


Figure 1: Non-metric multidimensional scaling ordination of off-trail plots on Cardinal Divide, without outlier plots removed. Compare to Figure 3.16. Seven outlier plots (the seven plots that are clearly separated from the main cluster of plots in this figure) were removed as they represent a different community type from the target *Dryas*-dominated community.