CHANGES IN GRASSLAND COMMUNITY COMPOSITION AT HUMAN-INDUCED EDGES IN THE SOUTH OKANAGAN

by

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Abstract

The grasslands of the Okanagan Valley, in southern British Columbia, Canada, are under intense development pressure. Alteration of biotic and abiotic conditions at the edges of remnant habitat patches is one of the key consequences of habitat fragmentation. Such edge effects likely diminish nonlinearly with increased distance from the edge, and significant changes are expected to be greater than the natural spatial variation within the interior of a habitat patch. Furthermore, habitat adjacent to more intensively managed areas, like paved roads and fruit crops, should be more affected at the edge than habitat fragmented by less intensively managed areas, like dirt roads. I used nonlinear canonical analysis of principal coordinates (NCAP), which characterizes nonlinear gradients in species composition, to test if edge effects were present in grassland communities next to roads and cropland. Variation partitioning was also used to determine the relative importance of key environmental factors in predicting compositional change at edges. Nonlinear shifts in community composition were more frequent at the edges of paved roads and fruit crops than at control sites in the interior of grassland patches. On average, 90% of the compositional change occurred within 28 m of the edge. Variation partitioning suggested that nonlinear responses at developed edges were due to true edge effects and not natural gradients, since a significant proportion of the nonlinear change in community composition was related to distance from the edge independently of the soil environmental variables at all types of human-developed edges, but not at the control site. The soil factors that best predicted compositional changes were soil pH and Cu/Mn at paved roads, soil pH and mineralizable N at the edges of fruit crops, and soil resistance at the edges of dirt roads, while soil texture and mobile cations best explained community

variation at one control site with a significant nonlinear gradient. Comparisons between

edge and interior plots revealed decreased cryptogam cover and an increase in the

proportion of exotic species at the edges, but changes were significant only at paved

roads. In sum, biotic and abiotic edge effects were present in the selected grasslands,

particularly at roadsides.

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List of Abbreviations

AICc – Akaike's Information Criterion (corrected)

ANOVA – Analysis of Variance

BEC – Biogeoclimatic Ecosystems Classification

BG – Bunchgrass Zone (BEC)

B.C. – British Columbia

GCC – Grasslands Conservation Council of B.C.

GIS – Geographical Information System

IDF – Interior Douglas-fir Zone (BEC)

MoFR – British Columbia Ministry of Forests and Range

NCAP – Nonlinear Canonical Analysis of Principal Coordinates

NCCorA – Nonlinear Canonical Correlation Analysis

PCO – Principal Coordinate Analysis

PP – Ponderosa Pine Zone (BEC)

REML – Restricted Maximum Likelihood

TRIM – Terrain Resource Information Management

VWC – Volumetric Water Content

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Dedication

To the planet,

my parents,

and me.

Co-authorship Statement

The identification and design of this research program was developed by Tanis Gieselman after discussion with co- advisors Dr. Mark Vellend (UBC-V) and Dr. Karen Hodges (UBC-O), and other UBC faculty members. The field research, data analyses and manuscript preparation was completed by T. Gieselman, with guidance and revision from both Dr. Vellend and Dr. Hodges. Laboratory analyses were conducted by T. Gieselman and hired research assistants, under the advisement of Dr. Les Lavkulich (UBC-V), and the B.C. Ministry of Forest and Range Research Branch soil laboratory.

1 General Introduction

Development and Fragmentation of Natural Landscapes

Human development is increasing at a staggering rate. The human population of the planet is currently about 6.8 billion people, and is expected to reach 9 billion by 2050 (UN Department of Economic and Social Affairs 2009). Humans require a place to live, food, and water like all other living things. However, we have also developed a desire for big houses, shopping malls, golf courses, vineyards, and the roads to connect them, which has resulted in huge areas of land being converted into something that is unsuitable for most other species.

The development of natural landscapes into human-dominated landscapes has a wide range of effects on the remaining natural ecosystems. In addition to the loss of habitat, ecological communities face habitat fragmentation and isolation, invasion by exotic species, chemical alteration of the environment, and increased physical disturbance. The remaining plant and animal communities can be affected on many levels. Development can alter the environment (e.g. chemical pollution, noise pollution, temperature) (Forman and Alexander 1998, Laurance et al. 2002, Gadsdon and Power 2009), the success of a species across a developed landscape (Fischer and Lindenmayer 2007), migration between patches (Soons et al. 2005), colonization and extinction rates within remnant patches (Soons and Heil 2002, Joshi et al. 2006), the number and type of species in a patch (Laurance et al. 2002, Bender et al. 1998), and the distribution of species within a patch (e.g. road avoidance) (Kristan et al. 2003).

The total amount of habitat and the isolation of patches from one another are two main factors affecting the number of species (species richness), the composition of species, and extinction rates in remnant patches (Laurance et al. 2002, Fischer and Lindenmayer 2007, Saunders et al. 1991, Bruun 2000, Krauss et al. 2004, Bisteau and Mahy 2005, Piessens et al. 2005). The effects of patch size and isolation after fragmentation of a landscape differs for different organisms, and depends on the organism's resource requirements and dispersal ability, and the type of land use or cover between the patches (Laurance et al. 2002, Cadenasso et al. 2003, Ries et al. 2004, Ewers and Didham 2006). A meta-analysis of almost 90 studies suggested that the fragmentation effect of patch size and isolation on animal populations are influenced by the type of land use or cover between the patches, with human-developed landscapes having more impact than in patches surrounded by other types of natural cover (Prugh et al. 2008).

Not only are patch size and isolation effects influenced by the type of land use between remnant patches, but edges of habitat patches can also be altered by the type of land use in the surrounding matrix. Physical, chemical, and biological degradation of habitat at developed edges is widespread (Harrison and Bruna 1999, Pickett et al. 2001, Spellerberg 2002, Coffin 2007). Degradation could change the suitability of the edge as habitat, amplifying the effects of size and isolation created by habitat loss. In fact, most recent reviews about the effects of habitat fragmentation recognize edge effects as a primary influence on biodiversity in habitat fragments (Laurance et al. 2002, Fischer and Lindenmayer 2007, Ewers and Didham 2006, Harrison and Bruna 1999, Debinski and Holt 2000, Hobbs and Yates 2003).

The term "edge effect" was first used by Aldo Leopold (1933) to describe patterns of accumulation of game diversity at the boundaries between different habitats. However, this term is now more broadly used to describe patterns of biotic and abiotic change in the transition zone from one habitat type to another (Ries et al. 2004). Studying these edge patterns can help us understand what conditions are needed for certain species to occur, and how they respond to changes in their environment.

Changes in community composition at the edges of a patch can arise through various processes. The first is through the flow of energy, materials or individuals to and from the habitat patch across its edges (Cadenasso et al. 2003, Ries et al. 2004). This process depends on the permeability of the edge of the patch to these flows (Cadenasso and Pickett 2001, Cadenasso et al. 2004). Differences in light, heat, moisture, and wind outside the patch can change the microclimate at the edge, making it intermediate between the conditions on either side of the edge (Laurance et al. 2002, Ries et al. 2004, Harper et al. 2005). The larger the difference between the conditions in the patch and the surrounding matrix, the greater the extent of change is expected to be at the edge of the patch (Harper et al. 2005).

The flow of materials in the form of dust, chemicals, nutrients, as well as plant seeds, pollen, or migrating animals could be increased, decreased, or prevented altogether at an edge (Ries et al. 2004, Bhattacharya et al. 2003, Strayer et al. 2003, Duncan et al. 2008). Changes in the rate of flow of any of these biotic or abiotic factors can alter community composition at habitat edges. Edge effects can be further magnified when plant or animal distributions change to match the changes in climate or distribution of resources such as food, shelter or water (Ries et al. 2004). New species favored by

conditions at the edge could also interact with existing species, assisting or competing with them, and further reinforcing the edge effect (Fagan et al. 1999, Kollmann and Buschor 2003).

Changes to the plant community are particularly important because plants represent the base of the food chain and the primary source of habitat for most other living things. Shifts in plant communities next to human-developed edges have been primarily studied in forests and grasslands along forest clear-cuts and roads. One of the longest running experiments on fragmentation is the Biological Dynamics of Forest Fragments Project in the Amazon Basin (Debinski and Holt 2000). Research conducted over 22 years, before and after fragmentation in the Amazon rainforest, revealed increases in wind disturbance, light infiltration and temperature after fragmentation (Laurance et al. 2002, Kapos 1989, Lewis 1998). This fragmentation resulted in dramatic increases in tree stress, damage and death at the edges of clear-cuts (Laurance et al. 1998). The drier conditions increased leaf litter at the edges, which could suppress the growth of new seedlings, and increase risk of fire (Bruna 1998, Cochrane et al. 1999).

Not all changes at the edge of a patch have negative impacts on all species (Yahner 1988). The fragmentation studies in the Amazon revealed increases in exotic and generalist species adapted to highly disturbed conditions at the edge, while large bodied, rare, and specialist species adapted to the undisturbed interior of large forest patches declined in the fragmented patches (Laurance et al. 2002). The most dramatic changes happened within 100 m of the edges, but shifts in insect community composition were observed up to 400 m from edges. The variety in species' responses to edges, habitat size, and isolation restricts the number of generalizations one can make about

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fragmentation and edge effects (Harrison and Bruna 1999, Debinski and Holt 2000, Hobbs and Yates 2003). However, the creation of edges undoubtedly alters the environment and the composition of communities within remnant patches.

Grasslands and the Okanagan Valley

The grasslands of British Columbia are an endangered ecosystem (Austen et al. 1998, British Columbia Ministry of Environment 2010). They are under intense development pressure because they are easily accessible, and they also have suitable climatic conditions for growing crops. Grasslands are one of the most highly productive ecosystems, with higher rates of primary production than both cultivated and developed areas (Vitousek et al. 1986). In addition to feeding livestock and supporting wild pollinators of food crops, grasslands also support a substantial proportion of regional and global biodiversity. In British Columbia, grasslands cover only 1% of the land area, but they support over 30% of the province's threatened and endangered species (Gayton 2004, Grasslands Conservation Council of British Columbia 2004a). Most of these endangered species are found in the grasslands of the Southern Interior, which is an essential corridor for wildlife from the Great Basin in the south to the boreal forests and grasslands in the north (Austen et al. 1998).

The grasslands of the Southern Interior are found mostly at low to middle elevations in the valley (Figure 1.1), within three Biogeoclimatic Ecosystem Classification (BEC) zones distinguished by characteristics such as vegetation, soil, and climate (Meidinger and Pojar 1991). The Bunchgrass biogeoclimatic zone (BG) is at the lowest elevation. In the Okanagan Valley, the BG zone contains the grasslands from the valley bottom (270 m) up to elevations of ~900 m. These grasslands grade directly into the Ponderosa Pine
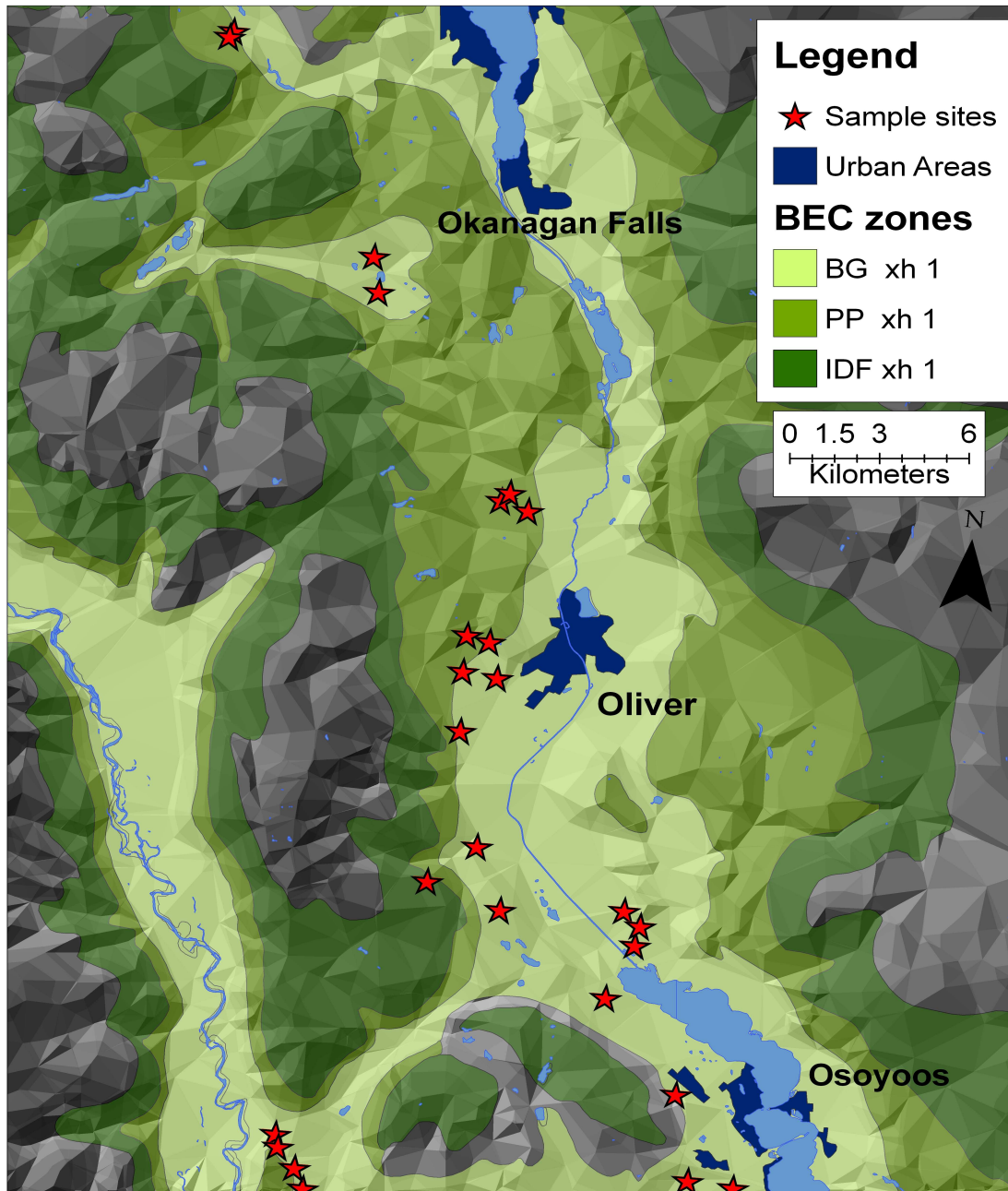
Figure 1.1 The location of grassland study sites within three Biogeoclimatic Ecosystems Classification (BEC) zones in the south Okanagan Valley. The Bunchgrass zone (BG) is represented by the lightest green color, the Ponderosa Pine (PP) zone is intermediate, and the Interior Douglas Fir (IDF) zone is the darkest green color. This map was created with ArcGIS ArcView 9.2 software (ESRI 2007) using digital elevation model data from DMTI Spatial Inc. (2002), BEC zone digital data from the British Columbia Ministry of Forests, Research Branch (2003), waterway data from the Department of Natural Resources Canada CanVec database (2007), and Baseline Thematic Mapping data of land use from the Government of British Columbia Integrated Land Management Bureau (1992).

(*Pinus ponderosa*, PP) and Interior Douglas-fir (*Pseudotsuga menziesii*, IDF) zones at higher elevations, where intermittent fires, along with soil and topographic conditions, maintain large areas of open grassland and parkland among the trees (Meidinger and Pojar 1991). The hot dry grasslands on the bottom of the southern Okanagan Valley are dominated by bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) Á.Löve; formerly *Agropyron spicatum* (Pursh) Scrib. & J.G. Sm.) and big sagebrush (*Artemisia tridentata* Nutt.), while the grasslands at intermediate elevations are dominated by bluebunch wheatgrass and alkali bluegrass (*Poa secunda* J. Presl.), and higher elevation grasslands are dominated by bluebunch wheatgrass and rough fescue (*Festuca campestris* Rydb.*;* formerly *F. scabrella* Torr.) (Meidinger and Pojar 1991, Tisdale 1947).

The soils in the Okanagan grassland regions are mainly Brown to Black Chernozems of glaciofluvial origin, and commonly have a medium to course texture (Kelley and Spilsbury 1949, Wittneben and Columbia 1986). These carbon-rich soils are created by the high productivity of the grasses, and a low rate of organic matter decomposition due to the hot, dry conditions. The climate in the Southern Interior grasslands is semi-arid due to a rainshadow effect from the coastal Cascade Mountains (Williams 1982). Southern Okanagan grasslands receive only about 300 mm of precipitation per year, falling mostly during winter and in June, and temperatures on the valley bottom are on average -2.0^{o}C in January and 22.0^{o}C in July (Williams 1982, Nicholson et al. 1982, Wikeem and Wikeem 2004, Environment Canada 2010). Conditions are cooler and moister at higher elevations and latitudes, resulting in changes in plant composition, increases in plant density and cover of cryptogamic crust (Tisdale 1947, Nicholson et al. 1982). The cryptogamic crust is a very slow growing layer of

mosses, lichen, algae and bacteria that grow on the soil surface between the bunchgrasses, and is important for increasing water infiltration, reducing erosion of the soil, and fixing nitrogen from the air into forms usable by plants (Atwood and Krannitz 1999, Williston 1999).

The grasslands of British Columbia have been influenced by humans for centuries. There is an oral history of First Nations people using prescribed burning to maintain areas of grassland for food production (Blackstock and McAllister 2004). The gold rush of 1858 brought an influx of European and Asian settlers to the Southern Interior, along with cattle to feed them. A "Cattle Ranges Act" was established in 1876, but during the drought of 1930s the grasslands were extremely overgrazed (Fraser et al. 2009). The first orchards and vineyards were also established in the late 1800s (Lea 2009). By the end of the 20th century, the grasslands were recovering under management, but still shrinking due to development and encroachment of the forest after years of fire suppression (Gayton 2009). There is added development pressure in the Okanagan Valley from a thriving tourism industry. Large lakes cradled in rugged terrain make it a spectacular backdrop for outdoor recreation, a large wine industry, golf courses, and suburban sprawl. These qualities can drive the price of the land above what can be supplied by the natural grassland or forage value, making it difficult for ranchers and other private landowners to turn away generous offers for their land (Grasslands Conservation Council of British Columbia 2004b).

The Okanagan Region currently contains 15% (116,600 ha) of the province's grasslands (Grasslands Conservation Council of British Columbia 2004a). By 2004, about 23% of the historic grassland area had been lost to agriculture, and 8.5% to

urbanization (Grasslands Conservation Council of British Columbia 2004a). However, the location of the losses within the three different grassland zones is more significant than the total percentage lost. The tendency for humans is to develop easily accessible, low lying areas, resulting in an uneven spread of development. The steep slopes on the sides of the valley have limited the spread of development into upland grasslands, but agricultural and urban developments have replaced over 60% of low elevation grasslands, and grasslands on gentle slopes (Austen et al. 1998, Lea 2009). Furthermore, it is still unclear how much additional area at the edges of these grasslands is affected by the adjacent agricultural and urban development.

Potential Effects of Agriculture and Roads on the Grassland

Edge effects adjacent to developed areas are caused by a complex combination of interacting processes. In order to determine what effects development has on grassland communities, it is useful to first separate potential causes of grassland community change into an organizational framework, even if some processes can affect more than one category. I have separated the effects of developed edges into physical, chemical, and biological effects.

Physical effects at developed edges

Roads introduce many types of physical disturbance. During construction of paved roads, coarse gravels are deposited for the road footing, and road verges and drainage ditches are excavated, which can alter the soil texture, chemistry and hydrology in a swath on either side of the actual road (Spellerberg 2002, Coffin 2007, Angold 1997). Furthermore, regular maintenance of these roads includes periodic mowing of roadside

vegetation, which can favor growth of fast or low growing ruderal plant species (Frenkel 1977). Other physical effects of roads could range even further than the narrow strip of the road verge. Roads provide access to natural areas, which could increase trampling of vegetation, disturbance to the cryptogamic crust, and compaction of soils by humans, animals and vehicles (Spellerberg 2002, Frenkel 1977, Cole 1990). Any of these types of disturbance could increase the amount of bare ground at the edges, making the edges more vulnerable to soil erosion.

Vehicle traffic and the smooth surface of the road could increase wind speed, which would contribute to soil erosion by facilitating the transport of a larger proportion of fine soil particles from the exposed soil (Spellerberg 1998, Blanco and Lal 2010). The loss of fine soil particles alters the size distribution of soil at the edge, which can change the nutrient and water holding capacity of the soil (Brady and Weil 1999). Road dust could also cover the leaves of adjacent vegetation, clogging leaf pores or reducing photosynthesis, but lichen and moss communities are especially sensitive (Thompson et al. 1984, Farmer 1993). Increased wind along the road corridor could also elevate water evaporation from the soil, intensifying drought stress on the plants (Laurance et al. 2002, Spellerberg 2002). Finally, sound pollution, road-kill and the road structure itself could affect the behavior and distribution of animals within the remnant grassland patches (Forman and Alexander 1998, Kristan et al. 2003, Spellerberg 2002, Coffin 2007, Trombulak and Frissell 2000), which could in turn influence herbivory, seed predation, and seed dispersal.

Agricultural crops like orchards and vineyards are typically fenced, so physical disturbances are not likely to influence the edges of adjacent grasslands much past the

developed area. However, fruit crops often have rough roads surrounding the perimeter. These roads could have many of the same effects as public roads, only to a lesser extent.

Chemical effects at developed edges

In natural ecosystems, nutrient elements used by plants are returned to the soil when the plants shed their leaves, die, or are eaten by something and deposited back into the soil as a digested meal. However, in agricultural systems a large portion of nutrients are exported with the crops, and fertilizers are used to restore nutrients and increase crop productivity. Nitrogen (N), phosphorus (P) and potassium (K) are in highest demand, while other nutrients (Ca, S, Mg, B, Cl, Mn, Fe, Zn, Cu, Mo, Se) are applied as needed (Brady and Weil 1999). Plant tolerance for some of the micronutrients can be very narrow, and if they accumulate in the soil, they can become toxic.

The large scale of commercial agriculture requires that water, pesticides, and fertilizers are often applied by broadcast methods, and can inadvertently spread into adjacent habitat (Duncan et al. 2008). Excessive application of water, pesticides, and fertilizer increases the risk of contaminating surrounding areas. Pesticides and fertilizers can contain heavy metals, which can accumulate within living tissue and have toxic effects on non-target organisms (McEwen et al. 1979, Hopkins and Hüner 1999). Furthermore, over-application of water and fertilizers increases leaching of nutrients, especially N, into surrounding areas (Wilson et al. 1999, Neilsen et al. 2002). Increased availability of water and nutrients could influence plant composition in adjacent areas by facilitating some plants over others (Meidinger and Pojar 1991, Vitousek et al. 1997, Clark and Tilman 2008). However, other outcomes may include increased density of plants, litter cover, or soil N and organic matter (Tisdale 1947, Vitousek et al. 1997,

Pouyat et al. 1997). The application of fertilizers can also increase the acidity of the soil, which can be counteracted with lime application (Goulding et al. 1998). Changes in pH can affect availability of nutrients and metals in the soil (Brady and Weil 1999, Goulding and Blake 1998, Pietri and Brookes 2008), but have also been linked to changes in the composition and cover of the plant and soil microbe communities (Pietri and Brookes 2008, Falkengren-Grerup 1989, Rousk et al. 2010)

Changes in pH, as well as deposition of nitrogen and metals are not only of concern at agricultural edges, but have also been reported to alter the edges of roadsides. Alkaline road dust is associated with increased pH of soil and tree bark at the edges of roads, altering composition, abundance or diversity of plants, cryptogam, and epiphytic lichen (Godefroid and Koedam 2004, Marmor and Randlane 2007, Myers-Smith et al. 2006). Coarse materials deposited during road construction are often from the alkaline sub-soil, which can further alter pH (Spellerberg 2002). Elevated N levels at the edges of roads, from the combustion of fossil fuels, are regularly observed in the air (Gadsdon and Power 2009, Cape et al. 2004, Bignal et al. 2007, Hung-Lung and Yao-Sheng 2009) and in some plant tissues (Bignal et al. 2007, Bernhardt-Romermann et al. 2006). Excess N has been linked to changes in plant composition (Angold 1997, Godefroid and Koedam 2004, Bernhardt-Romermann et al. 2006), decreased species richness (Clark and Tilman 2008), increased insect attack (Bignal et al. 2007), altered phenology and leaf morphology (Honour et al. 2009), and decreased abundance and health of mosses and lichen (Angold 1997). Metals were higher in soils beside urban roads than at non-urban roads in Slovakia (Krcmova et al. 2009), and metal concentration can also increase at roadsides inside leaves (Peachey et al. 2009) and animals (Ash and Lee 1980).

Finally, winter road maintenance often involves using sodium or calcium chloride salts for de-icing. These salts are carried off of the road with meltwater, and can directly damage plant tissues, change species composition, interfere with soil structure, or change the osmotic potential of soil, making it hard for plants to take up water (Spellerberg 1998, Brady and Weil 1999, Trombulak and Frissell 2000, Truscott et al. 2005).

Biological effects at developed edges

When an edge is created, biological transformations can occur in addition to the abiotic effects. Introductions of exotic species are common at developed edges, altering the biological community directly, creating novel species interactions, and often reducing native species diversity (Laurance et al. 2002, Fagan et al. 1999). These foreign species are often transported by human activities, but they can also migrate into newly disturbed areas on their own.

Exotic plant species are introduced by humans through many avenues. Seeds are planted for agricultural forage, for erosion control, and for ornamentals in gardens, but are also inadvertently introduced by vehicles along road corridors (Schmidt 1989, Wilson 1989, Tyser and Worley 1992, Lesica and DeLuca 1996, Dehnen-Schmutz et al. 2007). Some species used in roadside seeding inhibit the germination of native plants (Wilson 1989), and the cover and diversity of native plants and cryptogam is lower in invaded than in un-invaded grasslands (Tyser and Worley 1992). Tyser and Worley (1992) found that the average number of alien species in grasslands declined with distance from paved and unpaved roads, and trail sides in Glacier National Park in Montana, which supports the idea that exotic species spread into adjacent areas from their point of establishment (Williamson 1989).

Many exotic species are adapted to grow in highly disturbed areas, making them especially good at invading new areas. Invasive species often grow fast, have short life spans, and produce numerous long lasting seeds (Smith and Smith 2001). High levels of disturbance along roadsides and amongst cultivated crops favor the establishment of these species over slower growing native species. The disturbed corridors at the edges of roads and crops can act as a constant source of seed for invasion into natural areas. Furthermore, some generalist species can grow in a wide range of conditions, so many rare species can be replaced by a few common ones, causing biotic homogenization in the landscape (Laurance et al. 2002, Harrison and Bruna 1999, McKinney and Lockwood 1999). However, higher native species richness, especially in grasses, can increase resistance to invasion of exotic plant species (Roscher et al. 2009).

Exotic animals can also interact with the native plant community at edges, potentially causing changes in the plant community. For example, corn-rootworm beetles (*Diabrotica barberi*) have been observed to infiltrate remnant tallgrass prairies and feed on native sunflower (*Helianthus* spp.) pollen, reducing seed set (McKone et al. 2001). Natural patterns of herbivory and seed dispersal can be altered by physical disturbances at a developed edge. However, the introduction of exotic species can also alter competition, facilitation, and other types of species interactions (Fagan et al. 1999, Kearns et al. 1998, Tscharntke et al. 2005, Ness and Morin 2008)

Thesis Overview

The effect of developed edges on remnant habitats is complex, with many interrelated processes and outcomes that require a broad but detailed assessment to characterize. The plant community and soil environment are key, and can be studied in

detail to provide insight into the effects of development on the broader ecosystem. The grasslands of the Okanagan Valley represent an important system in which to study physical, chemical, and biological effects of developed edges. The remaining patchwork of grasslands in the Okanagan Valley is conserved within cattle ranches, protected areas, and Crown land. However, a network of orchards, vineyards and roads has fragmented the landscape, and the effects of adjacent agricultural and urban development on the edges of these grasslands have not yet been quantified.

Chapter Two of this thesis describes the results of one study that tests whether edge effects are present in the plant community of the south Okanagan, and whether plant community changes near edges are more extreme than the natural variability within the interior of remnant grasslands. This study also characterizes how edge-related changes manifest in plant community structure, quantifies how far the effects extend from the developed edge, and determines which environmental characteristics are most related to the changes observed at different types of developed edges.

I expect edge effects to be present in grasslands adjacent to roads and fruit crops, with the strength of the effect increasing with intensity of land use in the adjacent developed area. Changes at these developed edges are expected to be greater than observed within the variability of the natural grassland, and could manifest through biotic and abiotic changes at the edge. Such changes include increased proportion of exotic species, more bare ground or leaf litter, increased N, pH, metals or Na, and increased soil compaction, but less total plant and cryptogam cover, and less moisture at the grassland edges.

If the grassland habitat has been degraded along the edges, then the effective area of "quality" grassland that is conserved might be much less than is currently thought. In order to properly manage the sensitive grassland ecosystems of the south Okanagan and the species within it, we need to know how the remaining grassland communities are affected by adjacent human land use. The present study employs a recently developed statistical methodology for characterizing edge responses in community datasets, and the results could elucidate which factors are most implicated in grassland community change, which could be used by stakeholders to mediate further habitat degradation. The information collected herein will be valuable not only for conservation management at edges, but will also catalogue current plant distributions and environmental conditions within grassland patches that can be used as a baseline for tracking future change.

2 Human-induced Edge Effects in the Grasslands of the South Okanagan.

Introduction

Human development has altered vast areas of the earth's surface. The semi-arid shrub-steppe grasslands of the Okanagan Valley, in southern British Columbia, Canada, are no exception. They are under intense development pressure. Much of the lowland area has been developed into a rich wine and fruit growing region, with sprawling suburban areas and the requisite road network. These types of land use are inhospitable for much of the native flora and fauna, resulting in large scale reductions in biodiversity due to the loss of habitat, and the fragmentation and isolation of remaining habitat patches. Recent reviews of habitat fragmentation recognize edge effects as a primary influence on biodiversity in remaining habitat fragments (Laurance et al. 2002, Fischer and Lindenmayer 2007, Ewers and Didham 2006, Harrison and Bruna 1999, Debinski and Holt 2000, Hobbs and Yates 2003).

Edge effects are defined as changes in the environment or the community composition at the edge of a remnant patch of habitat, or at the boundary between two different habitat types. The differences between the two sides of the boundary result in an ecotone, or "zone of transition" (Clements 1907), which is created when environmental conditions or individuals from each side spread across the boundary, influencing many other interacting processes (Ries et al. 2004, Harper et al. 2005). Therefore, the magnitude of an edge effect should be largely dependant on the type and degree of difference between the conditions on either side of the boundary, and the permeability of the edge to individuals and the environment (Cadenasso et al. 2003, Ries

et al. 2004, Cadenasso and Pickett 2001). Since human development contrasts sharply with natural habitat, edge effects along developed edges may be particularly strong.

Edge effects are well studied in forests at clearcuts (Laurance et al. 2002, Harper et al. 2005), and at roadsides (Forman and Alexander 1998, Coffin 2007, Spellerberg 1998), but are not as well characterized in grasslands or at other types of human-induced edges. Changes in the environment and plant composition at forest edges generally extend 50 to 100 m from the edge (Laurance et al. 2002, Ries et al. 2004, Harper et al. 2005), while changes in plant composition at roadsides extend farther (Angold 1997, Bernhardt-Romermann et al. 2006). Effects at roadsides have been attributed to physical disturbances, deposition of dust, nitrogen, heavy metals and other chemical pollutants, altered pH, and invasion of exotic generalist species (Forman and Alexander 1998, Gadsdon and Power 2009, Coffin 2007, Myers-Smith et al. 2006, Tyser and Worley 1992, Santelmann and Gorham 1988).

The effects of pollution, and biological invasion dissipate with increasing distance from the source (Bignal et al. 2007, Williamson 1989). Therefore, changes in community composition due to edge effects are expected to follow a nonlinear saturating distribution, where the rate of change is greatest at the edge, tapering off to an average composition in the interior of the patch (Ries et al. 2004, Ewers and Didham 2006). However, such nonlinear responses have traditionally been difficult to model in multi-species community datasets due to the lack of a suitable statistical technique (Millar et al. 2005).

Typical approaches for studying edge effects have focused on changes in single response variables, such as the abundance of a few key taxa, or broad indices of community structure like species richness (Laurance et al. 2002, Ries et al. 2004,

Marchand and Houle 2006). Nonlinear modeling techniques for analyzing single response variables have been available for some time (Marquardt 1963). However, until recently multivariate models of community structure have been restricted to linear forms. Nonlinear canonical analysis of principal coordinates (NCAP), a new modeling technique proposed by Millar et al. (2005), helps to solve this issue. This method is well suited for characterizing edge effects in community data, as it allows nonlinear models to be fit to multivariate community dissimilarity matrices along an environmental gradient, such as distance from the edge.

If edge effects are present in the grasslands of the Okanagan Valley, and these effects degrade the quality of the edge as habitat for native species, then the effective area of grassland influenced by fragmentation could be much larger than the developed area alone. The Okanagan Valley is ecologically important because it is part of a major North American wildlife corridor (Austen et al. 1998). The shrub-steppe grasslands within the valley are listed as endangered ecosystems in Canada, and are home to many threatened and endangered species (Austen et al. 1998, British Columbia Ministry of Environment 2010). Remnant grasslands in the Okanagan also support the economic stability of the region by providing feed for range cattle and habitat for wild pollinators of the many fruit crops (Grasslands Conservation Council of British Columbia 2004a, Steffan-Dewenter and Tscharntke 1999, Morandin and Winston 2006). In order to manage these ecologically sensitive and economically important grasslands effectively, we need to determine how human development affects grassland community composition, how far the changes extend, and what factors are driving the changes.

Grassland communities may be altered at developed edges through the establishment of exotic plant species, or through physical or chemical changes to the soil environment, which together may influence plant community structure in a variety of ways. Changes in plant community composition are expected to be:

1. stronger and more frequent at developed edges than along natural gradients in the interior of grassland patches; and

2. stronger and more frequent at paved roads than at fruit crops or dirt roads, since paved roads have the most extreme contrast to conditions found within the interior of a grassland patch.

I will use a combination of traditional methods of edge effect analysis, and the recently proposed NCAP method, to characterize and test for edge effects in the plant community, and variation partitioning to determine the relative importance of key factors behind edge-related change in grassland communities.

Methods

Study design and site selection

Vegetation, ground cover, and soil characteristics were surveyed at a total of 26 grassland sites along two 100 m transects per site, set up perpendicularly to the target edge (Figure 2.1). Transects of this length were deemed long enough, based on the literature, to encapsulate most of the edge-related change in community composition, while minimizing the likelihood of encountering confounding effects from changes in topography or habitat type. Eight sites were edged by a paved road, six sites were next to dirt roads, and six sites were adjacent to fruit crops (orchards and vineyards).

Community structure may vary as a function of distance from the edge, but community structure also varies along natural environmental gradients (Gentry 1988). Therefore, six of the grassland sites surveyed were control sites, away from roads and cropland. The control sites were different from edge sites in that they had continuous native grassland vegetation at the both ends of the sampling transect. However, many control sites were set up out of necessity on hillsides, or near forested areas. Therefore, linear and nonlinear gradients in the plant community were expected to be present, but weaker and less frequent at control sites than at human-developed edges. For the purposes of analysis, the end of each control transect that was at the lower end of the slope was designated as the "edge", as most developed edges were also at the bottom of local topographical features.
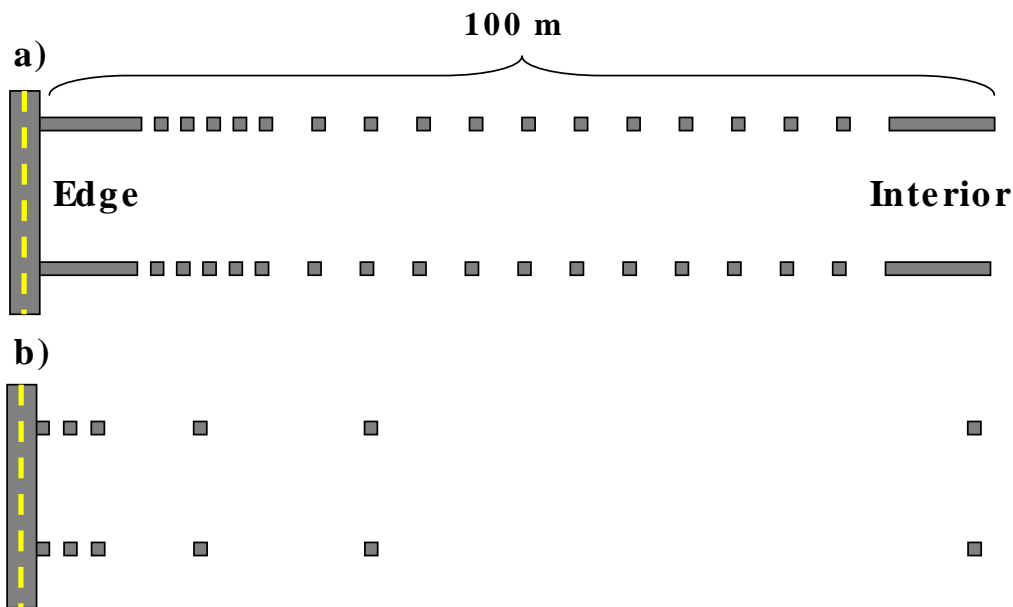
Figure 2.1 Diagrams showing the transect configuration at the edge of each grassland site (e.g. at a paved road), and the sampling locations along each transect for the various analyses. **a)** Species composition and cover was surveyed in 1 m sections along each transect at the locations shown (1-10,12,14,16,18, 20, 25, 30, 35…90-100m). Ground cover was also recorded, and the relative difference in species richness and ground cover between the 10 m sections at the edge and interior of each transect were compared across edge treatments. **b)** Soil samples and environmental data were collected in 1 m sections along the same transects, at the locations shown (1, 3, 5, 15, 30, and 100 m).

The selected paved roads are 50-100 years old and typically carry 100-500 vehicles per day (C. Bianco pers. comm., B. Corbach pers. comm.). These roads are currently maintained with roadside mowing twice per year and application of salts, most commonly sodium and calcium chlorides, in the winter for de-icing (Environment Canada 2001, B. Corbach pers. comm.). Orchards in this region are typically watered, fertilized and sprayed with pesticides using broadcast methods. The types of fertilizer and pesticides that are applied depend on the crop and the quality of the soil. However, nitrogen and phosphorus are likely ubiquitous. The selected dirt roads are used mostly for recreation by hikers and motorized vehicles, and for the passage of cattle.

The study sites were situated within 50 km of each other in the southern Okanagan and Similkameen Valleys of British Columbia, Canada. Sites were located on the east facing side of the valley, or the valley bottom, and ranged in elevation from 280 m to 1000 m (Appendix A). The grasslands in this region are semi-arid bunchgrass, shrub-steppe, and Ponderosa pine savannah. The mean annual precipitation is 280–500 mm, falling mostly during winter and in June (Williams 1982, Environment Canada 2010). The areas of the grassland patches that were sampled ranged from 7 to 100 ha, with slopes from 0 to 30° (Appendix A). Soil substrates in this area formed on glaciofluvial deposits and are medium to coarse textured Brown and Dark Brown Chernozems (Kelley and Spilsbury 1949, Wittneben and Columbia 1986).

Candidate sites were large enough to accommodate sampling up to 100 m from a developed edge, with an additional 100 m buffer to avoid non-target edges. However, site selection was limited due to a high density of dirt roads in remnant grassland patches, and extensive development through most lowland areas, restricting many remnant grasslands to

steep rocky sites where vegetation is inaccessible or discontinuous. I located candidate

sites by combining digital map layers of land use data (from the British Columbia Ministry

of Environment and Ministry of Agriculture and Lands), road information (from Terrain

Resource Information Management (TRIM) and National Road Network datasets), and a

recent map layer of the grasslands of British Columbia created by the Grasslands

Conservation Council (GCC, 2004) into a Geographical Information System (GIS) using

ArcGIS ArcView 9.2 software (ESRI 2007). The GCC layer was created using

government forest cover data, and verified using aerial photos, Landsat imagery, ecosystem

inventories, and regional teams of grassland experts.

Sagebrush (*Artemisia tridentata*, and *A. tripartita*) and antelope brush (*Purshia*

tridentata) generally make up less than 20% of the cover in undisturbed sites (Delesalle et

al. 2009). The dominant native bunchgrasses are *Poa secunda*, *Hesperostipa comata*,

Pseudoroegneria spicata, and *Sporobolus cryptandrus*, while common forbs include *Phlox*

longifolia, *Lomatium* spp., *Achillea millefolium*, *Lupinus sericeus*, *Balsamorhiza sagittata*,

and *Eriogonum* spp. (Meidinger and Pojar 1991, Kelley and Spilsbury 1949). Some

common exotic invasive species in this system are *Bromus tectorum*, *Centauria* spp.,

Tragopogon spp., and *Linaria genistifolia* ssp. *dalmatica*. Native populations of *Poa*

pratensis have been reported, but local populations of this species have been outnumbered

by a more invasive exotic Eurasian variety, and this species is now considered to be

primarily exotic in this area (Tyser and Worley 1992, D. Gayton pers. comm., Cronquist et

al. 1977).

Plant community surveys

The plant community surveys were completed from May to July, 2008. The two line intercept transects at each site were set up at least 10 m apart, along an edge to interior distance gradient as previously described (Figure 2.1). The start of each 100 m transect was placed at the fence-line surrounding fruit crops, and at the vegetation line at the edge of roadsides. Similarly, at control sites, two 100 m transects were set up away from these edge types to assess the variability in the plant community due to natural environmental gradients in the interior of grassland patches. Line intercept transects were used to survey community composition, as they can effectively characterize mixed plant communities containing graminoids, forbs, shrubs and trees (Smith and Smith 2001). Transect locations were pre-selected using the GIS to determine the most topographically uniform areas within each site, along the target edge.

In a subsample of 1 m sections (n = 39) along each transect (Figure 2.1a), I recorded the identity and linear coverage of all vascular plant species and the ground cover to the nearest 0.1 m, while small plants under 0.1 m were designated as 0.05 or 0.01 m. I compared the species richness, and percent cover of cryptogamic soil crust, bare ground, and litter coverage in 10 m sections at the edge and interior (Figure 2.1a). Species were identified using a variety of resources (Hitchcock and Cronquist 1973, Parish et al. 1996, Douglas et al. 1998-2002, Klinkenberg 2009, UBC Herbarium, T. MacIntosh pers. comm.). Nomenclature follows Douglas et al. (2002) and exotic status was determined from E-Flora BC (Klinkenberg 2009). Unique plants that were too immature to identify (31 occurrences) were excluded, and nine taxa were identified only to the genus level, resulting in 126 taxa included in the statistical analyses (Appendix B).

Sampling the soil environment

A random subset of four sites was selected for each edge type in order to evaluate the soil environment along the same transects that plant community data were recorded. Preliminary analysis of the plant community data suggested that the majority of compositional change occurred within 20 – 30 m of the edges. Therefore, the 1 m sections from each transect that were sampled (n = 6) were more frequent within 30 m of the edge, to better characterize any corresponding changes in the plant community (Figure 2.1b). Soil characteristics measured were those that are known to have a strong influence on the growth and success of individual plants in natural settings, such as the level of compaction, water content, soil texture and chemistry (Kelley and Spilsbury 1949, Wittneben and Columbia 1986, Nicholson et al. 1982, Brady and Weil 1999).

Penetration resistance can be used as a proxy for the level of compaction present in the soil (Herrick and Jones 2002). I recorded soil resistance with a dynamic soil impact penetrometer (Synergy Resource Solutions Inc., Herrick and Jones 2002), to a depth of 15 cm. Volumetric water content (VWC) was estimated with a soil moisture probe (HydroSense CS620 by Campbell Scientific, Inc., accuracy: ± 3%) to a depth of 12 cm, and surface air temperature 50 cm above the soil was also recorded. The average of two readings for each sampling meter was recorded for both soil resistance and VWC.

I collected and pooled together three samples of surface soil for each sample meter to analyze physical and chemical properties of the soil. The three samples were taken at the mid-point of each sample meter, and 50 cm to each side of the transect line, to a depth of 15 cm. Six of these pooled samples from each transect were air dried and sieved using a 2 mm sieve.

Particle size distribution (PSD) was determined using a rapid method proposed by Kettler et al. (2001), which uses a combination of sieving and sedimentation to collect the sand and silt fractions, while the clay fraction is calculated by subtraction from the total sample mass. The percent organic matter in the samples was determined through loss on ignition (Kalra and Maynard 1991). Soil pH was measured in both water and 0.01 M calcium chloride (Kalra and Maynard 1991), and the average of the two methods was used for statistical analysis as an index of local soil pH. Exchangeable cation concentrations (Al, B, Ca, Cu, Fe, K, Mg, Mn, Na, P, S, Zn) were extracted with a Mehlich III extractant and quantified using a Teledyne/Leeman "Prodigy" ICP spectrometer (British Columbia Ministry of Forest and Range (MoFR) Research Branch pers. comm.). Mineralizable nitrogen, which is used as an indicator of the long term available N at each sample location, was also measured for cropland and control sites by two-week anaerobic incubation followed by 1N KCl extraction of the ammonium-N, which was measured using an OI-Analytical "Alpkem FSIV" continuous flow analyzer (MoFR pers. comm.).

Data analysis

Overview

First I tested for differences in species richness, proportion of exotic species, and percent ground cover between the edge and the interior of each grassland site. If these aspects of community structure are significantly affected by human-developed edges, then relative differences between the edge and interior for these indices should be greater at edge sites than at control sites between two locations 100 m apart. Next, I determined whether edge effects are present in the grasslands at human-developed edges, by testing for significant linear and nonlinear community responses to distance from the edge. I

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also compared the frequency and strength of significant edge responses at the three types of edges (paved roads, fruit crops, dirt roads), and at control sites in the interior of grassland patches.

To determine the relative importance of the direct edge effects on the plant community, and the indirect edge effects through the soil environment, I partitioned the edge related variation in grassland community composition. A large proportion of community variation related to distance from the edge independent of the soil environment would suggest that direct edge effects, such as invasion of exotic species, are important. However, if the majority of the community variation is explained by both the distance from the edge and the soil environment, changes to the soil environment are likely involved in the edge effects observed in the plant community. Responses of individual species to edges were investigated through correlation of species abundance with the ordination axes, and through the relative bias in frequency of observations of native, exotic, and individual species at the edge relative to the interior. All statistical analyses were completed using the R statistical computing software version 2.9.1 (R Development Core Team 2009).

Does grassland community structure change more at human developed edges than it does within the interior of a grassland patch? What changes occur at edges?

For the species richness, proportion of exotic species present, and ground cover in the first 10 m (edge) and last 10 m (interior) of each transect at all 26 sample sites, I tested whether the relative difference between edge and interior for these indices was

greater at the developed sites than at the control sites. I calculated the relative difference

(d_r) between edge and interior as follows:

$$d_r = \frac{e - i}{\max(e,\ i)}$$

where 'e' is the value at the edge, and 'i' is the value in the interior (Tornqvist et al.

1985). The polarity of the edge to interior difference was preserved by not taking the

absolute value of the numerator. I compared the mean relative differences for the edge

treatments in a one way analysis of variance (ANOVA) using the average of the relative

differences of the two transects for each site. I used Welch Two Sample t-tests to

determine which of the edge treatment means differed significantly from the others, as

this method is insensitive to unequal sample variances (Welch 1947).

Nonlinear changes in community composition

Plant community composition can vary along natural environmental gradients

within a grassland patch, so it is possible to see differences between the edge and interior

of a patch purely due to some natural environmental gradient. However, one can test for

the presence of edge effects by determining if changes in the plant community are related

to the distance from the edge, and whether significant relationships are more frequent or

stronger at an edge than in the natural variation within a grassland patch. If there is no

change in composition with distance from edge, there is no edge effect (Figure 2.2a).

By definition, edge effects are most intense at the edge, so they are expected to

dissipate with distance from the edge to some interior average state, following a nonlinear

saturating distribution (Figure 2.2c). The extent of influence of the edge would be the
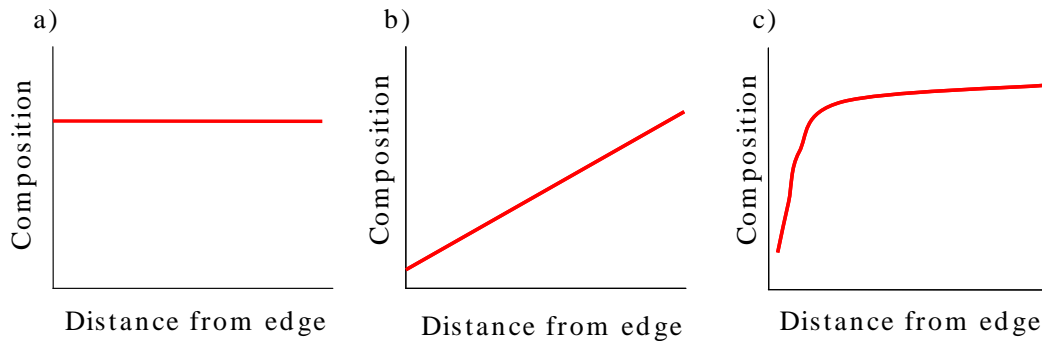
Figure 2.2 Possible relationships between species composition and distance from the edge. **a)** Community composition is the same, regardless of distance from the edge, indicating that there is no edge effect. **b)** Community change is related linearly to distance from edge, which suggests that the transects were too short to encompass the entire nonlinear edge effect, or a linear natural environmental gradient unrelated to the edge is present along the transect. **c)** Community change with distance from edge is a nonlinear rise to an asymptote, as is expected if edge effects are present. However, nonlinear natural gradients may also be present.

distance at which the rate of change in community composition levels off to an average interior composition. Linear relationships between community change and distance from edge may also be observed (Figure 2.2b), and could indicate that the survey transects were not long enough to capture the entire extent of the edge effect. However, natural nonlinear and linear environmental gradients may also be present in the community, so other analyses, such as variation partitioning, may be useful in distinguishing edge effects from natural gradients. The present study focuses on nonlinear edge responses, assuming that they are more likely to represent edge effects than are linear responses.

Nonlinear canonical analysis of principal coordinates (NCAP, Millar et al. 2005) uses a combination of direct and indirect gradient analysis to test for nonlinear community change along an environmental gradient, such as distance from an edge. First, an indirect analysis is employed to organize the multi-species community dataset according to the compositional dissimilarity between pairs of sample plots, and summarize the variation into a manageable number of axes. This step is done with principal coordinate analysis (PCO, Torgerson 1958, Gower 1966), which allows the use

of any dissimilarity metric of choice. Next, nonlinear canonical correlation analysis

(NCCorA) is used to find the best direct correlation between the community axes from

the PCO analysis, and the predictor variables, in this case distance from edge, along an

expected nonlinear link function (Millar et al. 2005). The combination of these

approaches provides a way to test how well nonlinear gradients of change in community

composition can be predicted by distance from edge.

NCAP analyses were completed using modified code from the supplemental

material of Millar et al. (2005). A fourth root transformation was applied to the species

cover data from each site to increase normality in the distribution of the community data,

and square root Bray–Curtis dissimilarity was used as the index of pairwise dissimilarity

between sample plots, to correct for negative eigenvalues (Hawkins and Wixley 1986,

Legendre and Legendre 1998). The first five axes from the PCO analysis, which

generally accounted for over 70% of the variation in the plant community, were selected

for use in the NCCorA portion of the analysis.

The NCCorA step of NCAP tests if the grassland community composition changed

in the expected nonlinear way with distance from the developed edge at each site. This

analysis estimates the proportion of variation in community composition that can be

predicted by distance from the edge along the nonlinear gradient, and tests if the

nonlinear pattern is significantly different from a linear edge response, or a flat (intercept-

only) response (Figure 2.2). Significance was determined with permutation tests (9999

iterations) as described in Millar et al. (2005). If an edge effect is present, the community

response along the distance from edge gradient is expected to change nonlinearly to an

asymptote. This relationship can be modeled using the Von Bertalanffy gradient (1938):

$$\mathbf{Y} = 1 - e^{-b\mathbf{X}}$$

where **Y** is the reduced community matrix from the PCO analysis, **X** is distance from the edge, and *b* is the vector of estimated regression coefficients for this equation that maximize the canonical correlation between the community change and distance from the edge.

To test if nonlinear responses observed at edges were greater than natural variation in the interior of a grassland patch I compared the frequency, extent, and strength of significant nonlinear responses at edge sites to those from control sites. Frequency of significant edge responses between edge treatments was compared with exact binomial tests of homogeneity due to the small number of significant responses at dirt and control sites (Milton 1999, Whitlock and Schluter 2009). The extent of edge influence was calculated as the distance from the edge within which 90% of the change in community occurred. This cut-off value was arbitrary, but has been used in other edge effect studies (Brand and George 2001, Hylander 2005). The canonical correlation from NCAP was used as an indication of the strength of the edge responses. I used Welch Two Sample t-tests with a Bonferroni corrected alpha value ($\alpha = 0.05/3$) to determine if the three edge treatment means differed significantly from the control group for both the extent and strength (Welch 1947, Milton 1999).

Reducing the set of environmental variables

Factor analysis was used to reduce the set of 23 soil environmental variables into 10 key soil factors. Mineralizable nitrogen (hereafter, N) was kept out of the factor analysis as a separate variable as it was not measured for all of the edge treatments, and because N

was highly correlated to organic matter ($r = 0.91$). Percent sand and clay content were included, but silt content was removed to avoid redundancy in the data matrix, since silt content was highly correlated to sand content ($r = -0.99$). Soil resistance and sodium (Na) were also kept as separate variables due to high uniqueness values, meaning that their variance was not well explained by the soil factors ($R^2_{unique} > 0.65$). In the preliminary ordination of the factor analysis, seven soil factors were selected to summarize the dataset using the Kaiser-Guttman Criterion and broken-stick plots (Jackson 1993). Factor analysis was done using the factanal function in R with a varimax rotation. The soil characteristics most related to each of the factors are shown in Table 2.1. Factor scores for these seven soil factors, and the original values for N, Na, and soil resistance, were used in subsequent analyses.

Table 2.1 A list of the factors, and their associated characteristics, that resulted from factor analysis of the soil variables. Soil characteristics with a loading of 0.5 or more on each factor are listed, and negative relationships between factors and soil variables are indicated by (-). Factors with asterisks were not included in the factor analysis because they were deemed to be individually important (see text). Therefore, raw values for these factors were used in variation partitioning.

Factor	Related soil characteristics
1	% Sand (-), % clay, Al, K, Mg, B
2	P, Fe, % organic matter
3	Cu, Mn
4	Ca, S
5	Average VWC (-), air temperature
6	pH
7	Coarse content (-)
8*	Na
9*	Soil resistance
10*	N

Testing effects of environmental variables and distance from edge on community

composition

I used multiple regression and variation partitioning to determine the relative

importance of the direct influence of distance from edge on the community composition,

and the indirect influence through changes in the soil environment. First, multiple

regression models including the edge-distance and best soil variables were fit to the

NCAP scores. I used the original NCAP composition scores from the previous

ordinations, grouped them by edge treatment, and modeled the response at each edge type

with distance from edge, soil environment, and with distance and environment together.

Only sites that showed a significant nonlinear response in NCAP were included. These

models were used for variation partitioning instead of repeating NCCorA ordination with

residualized matrices (as per Borcard et al. 1992), because these ordinations became

unstable with too few data points in the soil subset and too many explanatory variables.

Goodness of fit of the respective models was used to determine how much of the

community variation could be explained by distance and environment together or

individually (Legendre 2007).

For each edge treatment I first fit a global model using all 10 soil variables to

predict the NCAP scores without accounting for edge distance, and then applied all

subsets regression to determine which soil variables best explained the variation in

community composition. All subsets regression was carried out in R using the leaps

package with a function that calculates corrected Akaike's information criterion values

(AICc) from leaps (Schluter 2010), and the best fitting model was selected for each edge

treatment using both Mallows Cp and AICc. Since other models had similar support as

each of the best models, the selected models were likely not comprehensive, including all important environmental variables, but rather indicate the importance of a few key environmental variables in explaining the edge effects present.

Generalized least squares and linear mixed effects models (using the restricted maximum likelihood (REML) method were fit to the NCAP scores using the reduced set of soil variables, with and without accounting for distance (as log meters from edge). Distance was also fit to the NCAP scores without accounting for the soil variables. Attempts to improve model fit were made by including site as a random block, and the best and most parsimonious model structure for each edge treatment was selected using AIC. The variation in the community composition explained by each model was calculated with the adjusted coefficient of determination:

$$R^2_{adj} = 1\text{-residual MS/ total MS}$$

By subtracting the R^2_{adj} values for each model from the total variation in community composition, the variation was partitioned into that which can be explained by distance from the edge, that which is related to the soil environment, and that which can be attributed to both (Legendre 2007).

Which species drive changes in community composition at developed edges?

In order to determine if any individual species were consistently linked to edge-related composition changes at a particular edge type, I calculated the Pearson correlation (*r*) between the NCAP scores and individual species abundance along the transects at each site. Species that were positively correlated with NCAP scores would be those that have a high abundance in the interior and a negative response to the edge. Species with a

strong negative correlation with the NCAP scores would have highest abundances at the edge, which then decrease with distance from edge. Species with abundances that are not highly correlated to the NCAP scores did not respond to the edge.

In addition to the examination of responses of individual species to the edge, I was also interested in determining if native or exotic species showed disproportionately high or low abundance at edges. A species would be edge-biased if it was observed more often near edges than would be predicted if occurrences were located randomly with respect to distance from edge. To calculate the edge bias for each species, I determined the total number of plots each species was observed in, and what percentage of these plots were within 25 m of the edge. This distance roughly corresponds to the average extent of edge influence for all edges. Control sites were withheld from this analysis. Since 40% of the sample plots were within 25 m of the edge, species with >40% of their occurrences in edge plots would be edge-biased, while species with <40% of occurrences avoid the edge. The difference between 40%, and the percentage of total observations within 25 m of the edge, was used to indicate the magnitude of the bias. Species that were rarely observed are more likely to show a strong edge bias by chance, so species observed in fewer than 50 sample plots were analyzed separately from the more common species. One sample t-tests were used to test if the mean biases of native and exotic species were different from zero.

Results

Does the grassland community structure change more at human developed edges than within the interior of a grassland patch? What changes occur at edge sites?

Most of the broad measures of community structure did not change from edge to interior any more at the edge sites than was observed between plots at opposite ends of control transects. The mean relative difference in species richness ($F(3,22) = 0.9934$), percent bare ground ($F(3,22) = 1.5774$), and percent litter cover ($F(3,22) = 0.6274$) were not significantly different between edge sites and control sites ($P > 0.05$). However, the cover of bare ground was greater at the edges of all paved roads than in the interior of the same site (H_o: $\mu = 0$, $t(7) = -3.7103$, $P = 0.0076$), and all but one of the dirt roads ($t(5) = -1.5276$, $P = 0.1871$; data not shown).

The cover of cryptogamic crust was significantly lower (Figure 2.3a, $F(3,22) = 3.0592$, P = 0.0495) at the edges of paved roads (mean = -0.7656, $SD = 0.2422$) than at control sites (mean = -0.0738, $SD = 0.5268$, $t(6.592) = -2.9891$, $P = 0.0217$). Cryptogam cover at the edges of fruit crops (mean = -0.4462, $SD = 0.3506$) and dirt roads (mean = -0.3406, $SD = 0.5815$) appeared to be lower, but was not significantly different than seen in the natural variation at control sites (fruit crops: $t(8.704) = -1.4415$, $P = 0.1844$; dirt roads: $t(9.904) = -0.833$, $P = 0.4245$). However, cryptogam cover at the edges of fruit crops was consistently less than found in the interior of the same site (H_o: $\mu = 0$, $t(5) = -3.117$, $P = 0.0263$).

The relative difference in proportion of exotic species present was not more different between the edge and interior for any of the developed sites than was observed between plots at control sites (Figure 2.3b). The ANOVA indicated that not all mean relative differences were equal for all edge treatments ($F(3,22) = 3.6232$, $P = 0.0290$), but t-tests revealed that none of the edge types were significantly different from the control sites (P > 0.05). However, the exotic cover at paved edges was always greater than the

interior of the same site (mean = 0.6135, SD = 0.3336, H$_o$: μ = 0, $t(7)$ = 5.2016, P = 0.0013).
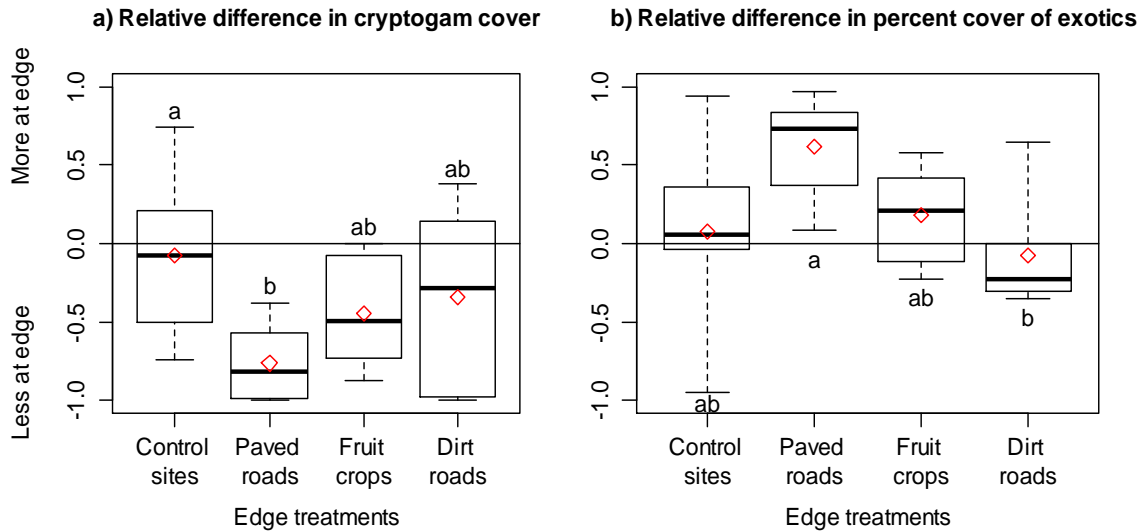
Figure 2.3 Relative differences between the edge and interior of each site within edge treatments for **a)** cryptogam cover and **b)** percent exotic cover. The y-axis is the magnitude of the relative difference, with positive numbers indicating that cryptogam cover at the edge was greater than the interior, and negative numbers indicating cryptogam cover at the edge was less. A relative difference of ±1.0 indicates that either the edge or the interior had no cover for that variable. Boxplots show the median, quantiles and maxima/minima of the data for each edge treatment. Red diamonds indicate the mean relative difference for each edge treatment. Letters indicate significant differences in the mean (α = 0.05).

Are edge effects present? Do edge responses vary among edge types?

Significant nonlinear relationships ($P < 0.05$ using 9999 randomizations) were observed between community composition and distance from the edge at 75% of paved road sites, 83% of sites adjacent to fruit crops, 33% of dirt road sites, and 33% of control sites (Figure 2.4). Paved road and fruit crop sites that did not have significant nonlinear responses to the edge had linear responses ($P < 0.05$ using 9999 randomizations), while the remaining dirt road and control sites had either linear responses, or no relationship with distance from edge. Binomial exact tests of homogeneity indicated that nonlinear edge responses at paved roads and fruit crops were significantly more frequent than
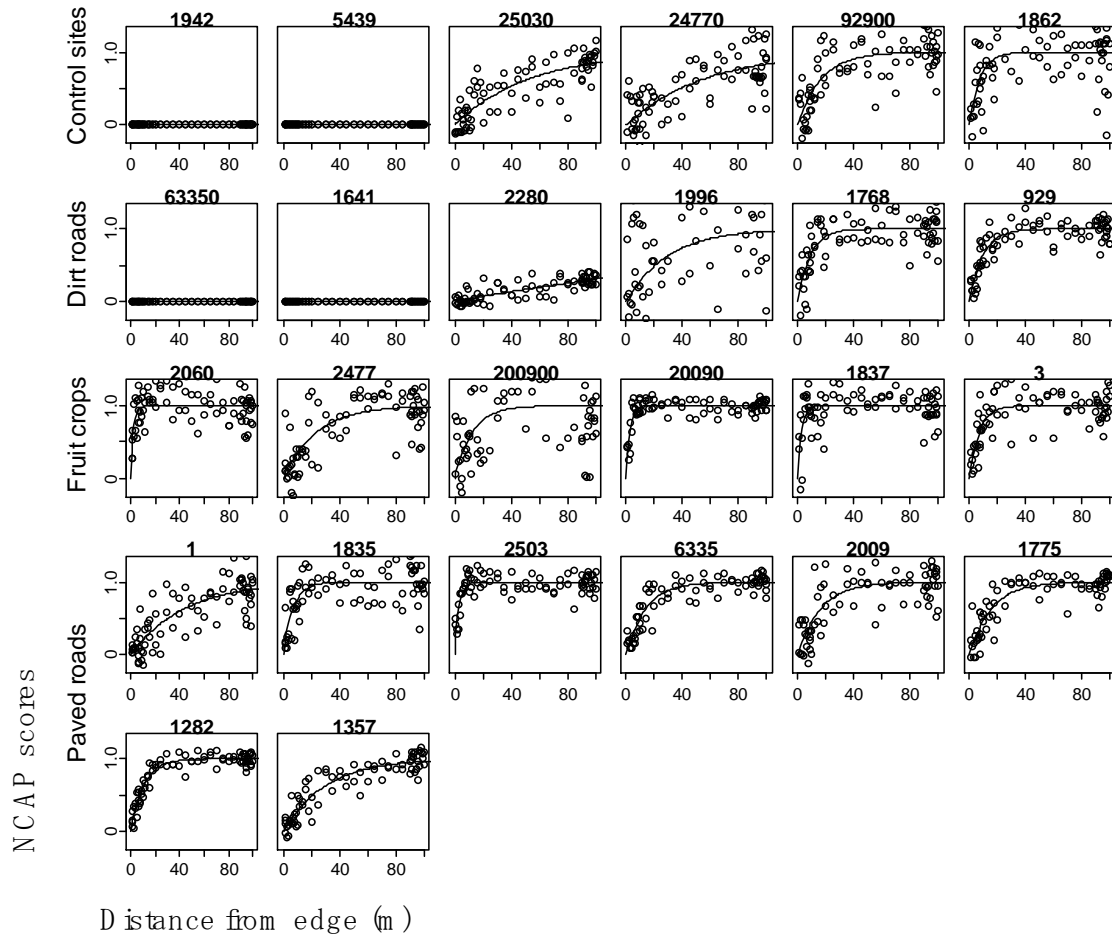
Figure 2.4 NCAP model fits for each sample site, within each of the four types of edge treatment. The site ID numbers are shown above each plot (see Appendix A). The x-axes are the distance from the edge in meters, with the edge located at zero. The y-axes are the NCAP gradient, representing the primary axis of variation in community composition that varies as a nonlinear function of distance-to-edge. Models are constrained between zero and one, with the asymptote approaching an average interior community composition at a value of 1.0; therefore, some data points fall outside of the standardized graphical plotting area. Sites with plots showing average composition at zero had no relationship with distance from edge, so the ordination failed.

nonlinear gradients observed within control sites (paved: $B(8, 2/6)$, $P = 0.019$; fruit: $B(6, 2/6)$, $P = 0.017$). Edge responses at dirt roads were observed with the same frequency as natural nonlinear gradients.

At sites with significant nonlinear composition-distance relationships, the depth and strength of edge effects, as represented by the mean extent of edge influence and mean

canonical correlation values, were not significantly different between any of the edge types and the natural gradients at control sites ($P > 0.0167$ (after Bonferroni correction), Figure 2.5). However, due to the small number of significant nonlinear responses at dirt road and control sites, comparisons between edge treatments required the use of conservative tests. The extent of influence extended on average 34 m from the edge at paved roads, 22 m at fruit crops, and 21 m at dirt roads (average extent for all edges was 28 m), while nonlinear gradients at control sites extended 27 m. Average canonical correlation of NCAP models was 0.68 for paved road sites, 0.51 for fruit crop sites, and 0.59 for dirt road sites, while control sites had average correlation values of 0.46.
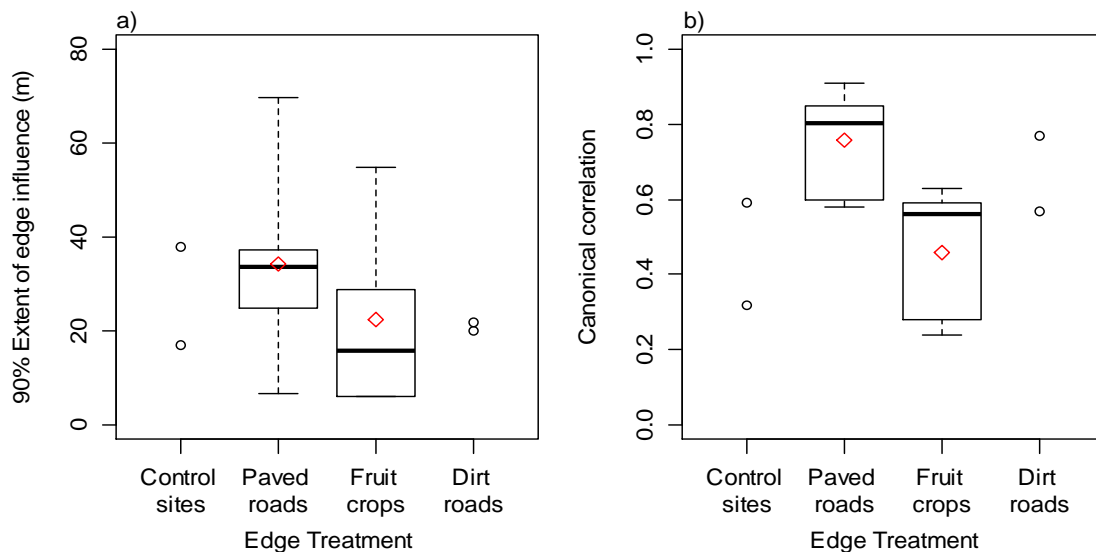
Figure 2.5 Extent and strength of nonlinear composition-distance relationships. The boxplots show the ranges of **a)** Extent of edge influence and **b)** canonical correlation (strength) for the NCAP relationships for each site within the different edge treatments. Boxplots indicate the median, quantiles and maxima/minima of the data for each edge treatment. Red diamonds indicate the mean for each edge treatment with more than two data points. None of the edge treatment means were significantly different from the control mean, and these results were no different when sites with linear relationships were included (data not shown).

Indirect or direct edge effects?

Three of the four paved road sites, four out of four fruit crop sites and two of the four dirt road sites where the soil environment was sampled showed significant nonlinear relationships between community composition and distance from edge in the NCAP. One of the four control sites where the soil environment was sampled also had a significant nonlinear composition-distance relationship. For these sites, all-subsets regression suggested that the soil factors that best explained the variation in plant community composition were soil pH and a Cu/Mn factor at paved roads, soil pH and mineralizable nitrogen at agricultural sites, and soil resistance (compaction) at dirt roads, while the natural nonlinear response seen at the control site was most related to changes in soil texture and some mobile cations (Table 2.2, Appendix C). All factors related to compositional change were increased at edges, except Cu and Mn, which showed variable responses to edge, and were seen at much higher levels at one control site (data

Table 2.2 Soil factors that best predict community change with distance from edge, and other factors in the models with equal support. Only factors in the best model were used for variation partitioning, except for the control group where the best model included all 10 factors. In that case the second best model was used, which included only one soil factor related to soil texture and some mobile cations. Factors with negative relationship to NCAP score indicated by (-), but note that individual variables within each factor may have the opposing relationships.

Edge Treatment	Soil factors in the best model predicting community change	Soil factors in the models with equal support as the best model
Paved road	Soil pH, Cu/Mn	VWC/air temperature(-), Na and soil texture/Al/K/Mg/B(-)
Fruit crop	Soil pH, N	coarse content, soil texture/Al/Mg/B, Cu/Mn, Ca/S(-)
Dirt road	Soil resistance	VWC/air temperature(-), Cu/Mn(-), P/Fe/% organic matter(-), coarse content(-)
Control site	All 10 soil factors	Soil texture/Al/K/Mg/B(-)*, Na(-)*

*these factors did not have equal support as the best model, but were included in the next best models.

not shown). Other models that had equal support (ΔAICc < 2) included combinations of these best factors, and those shown in Table 2.2.

Variation partitioning revealed that, for the developed edges, a small but significant proportion of the edge-related change in community composition was related to distance from edge independently of the best fitting soil factors (Table 2.3). Conversely, community change at the control site was not directly related to distance independently of the soil environment. The shared variation (Table 2.3) indicates how much of the change in grassland composition is related to both the distance from edge and the soil environment. A small proportion of community variation was also related to the soil environmental factors independently of distance from edge, except at the dirt road sites. For these sites, the community variation explained by the best soil factor, soil resistance, was completely related to distance from the edge (Table 2.3). However, only 42% of the total variation in plant community composition at dirt roads was explained by this factor and distance from edge together.

Table 2.3 The results of variation partitioning for sites where soil was sampled and where significant nonlinear community shifts with distance from edge were found in NCAP. Soil environmental factors used in variation partitioning were those selected from all subsets regression (see Table 2.2).

Edge Treatment	# of sites (/4) with significant nonlinear edge responses	Variance explained by distance alone (%)	Variance shared by distance and environment (%)	Variance explained by soil environment alone (%)	Total variance explained by distance and environment (%)
Paved road	3	11	70	5	86
Fruit crop	4	11	24	15	50
Dirt road	2	20	22	0	42
Control site	1	0	47	16	63

Which species drive changes in community composition at developed edges?

One or a few individual species were not responsible for all of the changes in community composition seen at edges. Instead, each site had different combinations of species that changed in abundance with distance from the edge (Appendix D). *Poa bulbosa* and *Sisymbrium altissimum* were the exotic species most frequently associated with community change alongside paved roads (50% and 37.5% of sites, respectively). *Poa secunda* and *Hesperostipa comata* were the most edge-affected native species at paved roads (50% and 37.5% of sites, respectively), and *P. secunda* was also frequently associated with compositional change next to fruit crops (50% of sites).
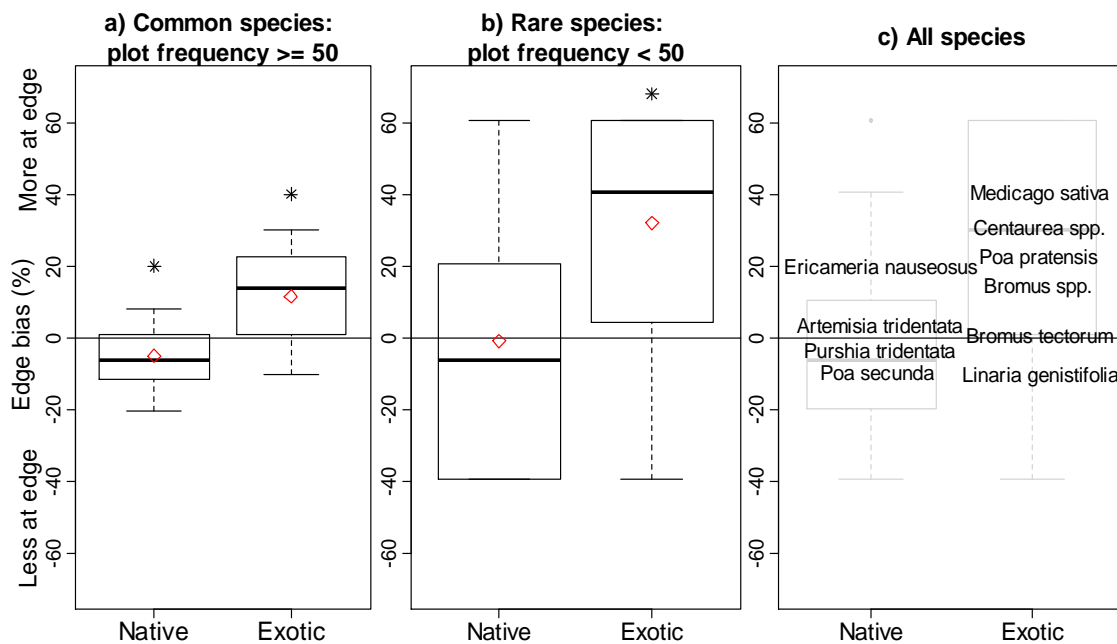
Figure 2.6 The edge bias of plot presence for native and exotic species. Plots show a) common species b) rare species, and c) all species, with the names of select species of interest overlayed. Edge bias indicates how much more often than random each species was located within 25 m of the edge. If species were randomly distributed within a grassland patch, then there would be an equal chance of a species being found in any plot along the transect, and the species would all be clustered evenly around zero. Boxplots indicate the median, quantiles and maxima/minima of the data for each edge treatment. Red diamonds indicate the mean bias for each group. Asterisks indicate means that are significantly different than zero.

The analysis of the edge bias of each species (Figure 2.6a) revealed that, on average, common native grassland species avoid the edge, while exotic species were significantly edge-biased. Mean bias values were significantly different from zero for both native (mean = -5.08, 95% CI [-8.48, -1.68], P = 0.0051) and exotic species (mean = 11.59, 95% CI [0.30, 22.89], P = 0.0454). Rare exotic species were also significantly edge-biased (mean = 31.94, 95% CI [17.87, 46.01], P < 0.0001). However, rare native species were more evenly distributed (Figure 2.6b). The edge biases of some common native and exotic species are shown in Figure 2.6c (see also Appendix B).

Discussion

Shifts in grassland community structure were detected at developed edges, and the frequency of the edge effects increased as intensity of land use in the developed area increased. In particular, evidence of edge effects at paved roads was found throughout this study, while evidence for edge effects at fruit crops and dirt roads was more limited. The magnitude of the edge effects at fruit crops and dirt roads were difficult to distinguish from the natural variability along environmental gradients in the interior of remnant grasslands.

Significant shifts in community structure at paved roads were observed in the reduced abundance of cryptogam cover (Figure 2.3a), increased proportion of exotic plant species (Figure 2.3b), and the increased frequency of nonlinear edge responses in plant composition (Figure 2.4). The nonlinear edge relationships also appeared to be strongest at paved roads (Figure 2.5b). However, on average, the extent of influence of the paved roads was not greater than the ranges of natural nonlinear gradients present at control sites (Figure 2.5a). Therefore, the extent of the nonlinear responses was not

useful for distinguishing whether shifts in composition were edge effects or natural gradients.

The high frequency of nonlinear shifts in composition at paved road and fruit crop sites, as well as changes in cryptogam and exotic cover, indicated that significant changes were present at many of the developed edges. Furthermore, variation partitioning revealed that some of the community change near edges was related to the distance from edge, independent of the soil environment at edge sites, while none of the change at the control site could be attributed to distance alone (Table 2.3). The lack of direct influence of distance at control sites suggests that the nonlinear responses at developed edges were in fact due to some influence from the edge, while nonlinear responses at control sites were due to natural gradients.

In addition to providing evidence for the presence of edge effects at edge sites, the direct distance effects (Table 2.3) indicated that some of the effects from the edge on the plant community could be the result of one or more factors unrelated to the soil environment. Edge-related alterations in the interactions between species, such as the behavior of pollinators or seed dispersers (Bhattacharya et al. 2003, Fagan et al. 1999, Kollmann and Buschor 2003, Kearns et al. 1998, Ness and Morin 2008), could alter plant composition at the edge independent of the soil environment, and contribute to the direct distance effect observed. However, quantifying such species interactions was outside of the scope of this study. It is also possible that the direct effect of distance could be explained by unmeasured soil variables. However, the wide range of soil variables measured makes this explanation doubtful. Given the increased exotic cover (Figure 2.3b) and frequency (Figure 2.6) observed at developed edges, it is likely that the

introduction of exotic plant species from road corridors and agricultural areas (Schmidt 1989, Lonsdale and Lane 1994, Gelbard and Belnap 2003, Benvenuti 2007) has altered the plant composition at developed edges, resulting in a direct edge effect.

The proportion of exotic cover at paved roads (Figure 2.3b) was always higher at the edge than the interior of the same grassland site. However, the differences between edges and interiors were not significantly greater than observed between plots at control sites, which suggests that the interior of grasslands can have equally large spatial variation in the proportion of exotics present. Previous studies have found similar patterns, with increased exotic cover in grasslands at the edges of roads, and some interior invasion (Tyser and Worley 1992, Cilliers et al. 2008).

In addition to the effects of distance-from-edge *per se*, there was also evidence that the nonlinear changes in community composition at edges were related indirectly to the edge, through the soil environment. The shared variation (Table 2.3) indicates how much variation was explained by both the distance from edge and the soil environment. However, it was not possible to determine how much of this shared variation in community composition was due to an indirect edge effect, and how much might be due to natural gradients along the transects. Over half of the total variation explained by distance and environment at the control site was shared variation, which indicates that the soil environment is both spatially structured and strongly related to grassland composition, even without the influence of an edge. At the paved roads an even greater proportion of the total variation in community composition (70%) was shared variation, and spatially structured shifts in community composition were much more frequent than observed at control sites. Furthermore, all of the variation related to the soil environment

at dirt roads was also explained by distance from edge (Table 2.3). Together these results suggest that although natural environmental gradients can result in nonlinear shifts in community composition, indirect edge effects via the soil environment likely play some role in the edge-related community changes observed.

The indirect influence of edge on the grassland community through the soil environment appeared to be driven by different factors at the different edge types. Community change at paved roads was related to changes in soil pH and Cu/Mn. Soil pH increased at the edges of paved roads, which follows previous studies (Marmor and Randlane 2007, Myers-Smith et al. 2006), and can result from deposition of road dust, and from coarse alkaline parent materials spread on the soil surface during road construction. Levels of Cu were also expected to be elevated near roads (Coffin 2007, Ash and Lee 1980), while Mn availability was expected to decrease with increased pH (Brady and Weil 1999). However, the responses of Cu and Mn to the edge were variable, and the maximum values at roadsides were much smaller than the values seen within one of the control sites (data not shown). Interestingly, Zn is another heavy metal that has exceeded critical threshold limits at roadsides (Nabulo et al. 2006), but Zn levels were not elevated at the selected roads in the present study.

The cryptogam cover at the edges of paved roads could be lower due to physical disturbance or structural alterations along the road verge. However, lichens are also sensitive to changes in N, pH, and metal deposition near roadsides (Marmor and Randlane 2007, Tuba and Csintalan 1993, Purvis et al. 2003). I found no evidence that N was related to community change at roadsides. Mineralizable N was not measured directly for paved road sites, but N was highly correlated with organic matter, and the

factor most related to organic matter was not included in any of the best fit models explaining community composition. Furthermore, the cover of vegetation and litter were not increased at the edges compared to the interior (data not shown), as would be expected with higher N availability. Since N did not have a strong influence on the plant community, it is also possible that N deposition may not have been enough to influence the lichen community. However, soil pH and Cu were strongly related to community composition and distance from the edges of paved roads, and could be contributing to the reduction of the cryptogamic crust.

Compositional change at the edges of fruit crops was related to soil pH and mineralizable N. The N status at the edges of fruit crops was expected to increase, since intensive cropping requires the addition of fertilizers, which could leach into adjacent areas with excess application. Soil acidity increases with the addition of fertilizers, and requires applications of lime to counteract changes in pH (Goulding et al. 1998, Goulding and Blake 1998, Sverdrup et al. 1995). Increased nitrogen and decreased acidity at the edges of fruit crops in the present study indicate that fertilizer or lime applications may have spread over the edges of the crops into the grassland, and are linked to compositional change in the grassland plant community. Emissions from agricultural machinery could also contribute to the changes in pH and N observed.

At dirt roads with significant nonlinear edge effects, the soil factor that best predicted the variation in plant community composition was related to soil resistance. All of the variation explained by soil resistance was related to distance from the edge (Table 2.3), which suggests that increased accessibility to natural areas by dirt roads can increase compaction of the soil at the edge, and alter plant composition. Further support should be

reflected in a decline in the cover of cryptogamic crust at the edge. Although the difference in cryptogam cover at the edges of dirt roads was not more different than between plots at control sites, the cryptogam cover was reduced at most of the dirt roads compared to the interior of the same site (Fig. 2.3a), and the cover of bare ground was increased.

All of the variation in the plant community explained by distance at the control site could be explained by a single soil factor (Table 2.3), which represented changes in soil texture and some mobile cations. Soil texture can modify plant composition, and nutrient mobility is often a function of soil texture (Brady and Weil 1999), so the factor characteristics are complementary and naturally related to plant composition. Soil texture could vary at edges as a function of bare ground, which makes the soil increasingly susceptible to erosion, or as a function of distance, if soil particles were deposited on the surface progressively more over a distance. However, nonlinear shifts in soil texture large enough to be reflected in changes to the plant composition are more likely the result of deposition patterns in the subsoil rather than changes in the surface texture from erosion and deposition. The different environmental factors important in explaining compositional change at edges and control sites further demonstrates that nonlinear responses at edges are likely the result of edge effects, while responses at the control sites are natural nonlinear gradients.

Conclusion

Edge effects are present in south Okanagan grasslands, especially next to paved roads. Changes in community composition at developed edges are related to establishment of exotic species, changes in the soil environment, and reduction of

cryptogamic crust at the edge. The intensity of land use on the developed side of the edge does seem to determine the frequency with which edge effects are present in the grassland, but not necessarily the extent or the strength of the effect. Paved roads had a strong influence on grassland composition, even with relatively low traffic volume, and fruit crop sites showed more edge effects than were seen at dirt roads.

The majority of change in the grassland plant community occurred on average within 28 m of developed edges. In small patches of remnant grassland 1-3 ha in size, the reduction in effective patch size is substantial: edge effects of this extent would influence the vegetation in half of the area or more, depending on patch shape. While protected areas in the south Okanagan are much larger, mostly 100 ha in size (Wikeem and Wikeem 2004), the area of affected grassland within 28 m of the edges would still equate to at least 10% of the total area.

This study suggests that monitoring changes in cryptogam cover, exotic species establishment, soil pH, metal and N content at the edges of roads and fruit crops would be prudent, and management steps to mediate these types of edge effects would be beneficial to maintaining the ecological integrity of the grasslands in this region. Reducing the extent of soil disturbance and exposed ground during and after road construction will help prevent invasion of exotic species. Planting buffer zones on road verges using native species instead of fast growing, exotic grasses will also help reduce establishment of exotic species within the interior of the grasslands (Tyser and Worley 1992), especially if the buffers are designed to reduce and withstand frequent disturbance, such as mowing. Road verges could also be engineered to provide a structural barrier to help prevent biological, physical and chemical edge effects from penetrating into adjacent grasslands.

This could be achieved by building the road lower than the surrounding landscape,

creating impenetrable rock barriers on either side, or by planting trees and shrubs

alongside the road to decrease edge permeability.

3   General Discussion

Habitat fragmentation can have a wide range of detrimental effects on the remaining natural communities. The research outlined in Chapter 2 confirms that the ecological integrity of the grasslands in the Okanagan Valley, in British Columbia, Canada, have been altered at developed edges, with the frequency of effects increasing with intensity of land use in the adjacent developed area. Nonlinear changes in the plant community were more frequent at the edges of paved roads and fruit crops than at dirt roads, or within the interior of grassland sites. These changes extended on average ~30 m from developed edges. Increased establishment of exotic plant species, and changes to the soil chemistry likely contributed to the nonlinear shifts in community composition. However, the extent and strength of changes near edges were often similar to those of natural gradients (where such gradients were present), and the magnitude of the changes was greater than the natural variability of the grasslands only for the amount of cryptogam cover at paved roads. In this chapter, I will further discuss some of the findings from Chapter 2, linking the results with previous research, and offering suggestions for future research.

General ecological theory, such as the theory of island biogeography (MacArthur and Wilson 1967), can be helpful as a framework for thinking about patterns of species distributions in habitat patches, but cannot predict the responses of all species in an ecosystem. This theory has been useful for predicting the effects of area and isolation on the number of species in a fragmented patch, but it does not predict anything about species composition, and does not account for edge effects or the type of land use in the surrounding matrix (Prugh et al. 2008, Laurance 2008). Edge-effect theory has a basis in

earlier ecological principals, but has its own unique set of hypotheses. Edge effects are caused primarily by ecological flows across the habitat boundary, and are reinforced through species interactions and resource mapping (Ries et al. 2004). The contrast between the two sides of the edge and the permeability of the edge to the ecological flows are considered the major determinants of the magnitude and extent of effects (Cadenasso and Pickett 2001, Harper et al. 2005).

Harper et al. (2005) suggested that including comparisons of observed edge effects with the natural variation in the interior of study communities should be standard in edge effect studies, and that evaluating edges with differing contrast to the plant community would help fill gaps in knowledge about edge effects at developed edges. In the present study, the comparison of community change at edge sites to that at control sites was clearly necessary to avoid making conclusions that exaggerated the severity or importance of the observed edge-related changes. However, this study showed that the significance of some edge effects, such as the invasion of exotic species, may be concealed when interior areas are also influenced by other disturbances, such as cattle grazing (Figure 2.3).

Comparing edge types with various levels of contrast to the natural habitat confirmed that the magnitude and frequency of edge effects increased with greater intensity of land use for some aspects of community structure (e.g. cryptogam cover and exotic invasion, Figure 2.3). However, the extent of edge influence, when present, was not different among edge types, and the edge effects observed had similar extents as natural gradients at control sites (Figure 2.5a). While significant edge effects can be detected only when their magnitude is greater than the natural variability within the

community, it is important to note that significant edge effects can be present even if their extent of edge influence appears similar to the spatial "grain" of natural environmental gradients.

The present research is significant to the study of edge effects in that it demonstrates the use of a new statistical method for characterizing edge effects, namely NCAP, which allows more direct modeling of nonlinear effects in community datasets. It is also one of the first studies to compare the magnitude of edge effects at various edge types to the natural variability in the study area. However, the strength of the research described in Chapter 2 comes not only from the comparisons between different edge types and the natural community variability. Quantifying the relative differences between edge and interior locations within each site before calculating the treatment means or comparing the effects across edge treatments mitigates the problems associated with making comparisons across a diversity of sites with potentially different plant communities. Testing for nonlinear community responses at the edge with the NCAP method was also done at each individual grassland site for this same reason. Furthermore, NCAP and variation partitioning allowed community responses at developed edges to be more explicitly modeled than with basic edge-interior comparisons and traditional linear modeling methods. Variation partitioning also helped edge effects to be distinguished from natural gradients, and the relative importance of environmental characteristics to be determined. The replication of transects within each study site also ensured that changes observed were not the product of selecting an atypical edge location for study, and evaluating community responses at many sites helps this study to be generally applicable to the region.

Even with the large amount of data collected, there were still some analyses which suffered from a relatively small sample size. For example, over 500 soil samples were collected, but the prohibitive cost of some analyses reduced the number of sites, and the number of locations within each site, in which the soil environment could be characterized. Furthermore, the low number of nonlinear responses at dirt road sites and control sites, while expected, made comparisons of strength and extent between the different edge treatments difficult, and further reduced the data available for variation partitioning. Future edge effect studies interested in characterizing the environmental factors related to edge effects should select sites of particular interest for soil characterization, namely those found to exhibit nonlinear responses, rather than randomly selecting sites before community analysis has occurred.

Indications that exotic plant species were involved in the shifts in community composition observed at developed edges came from the comparisons of edge and interior plots, and from the edge bias analysis of individual species. These analyses showed that exotic species were, on average, located more often within 25 m of the edges than would be expected if the exotic species were distributed randomly or uniformly within the remnant grassland patches. Furthermore, the proportion of total vegetation cover that consisted of exotic species was always greater at the edges of paved roads than the interior. These results are similar to those found in previous studies (Gelbard and Belnap 2003, Hansen and Clevenger 2005, Flory and Clay 2006), indicating that edges represent a potentially important target for exotic species management.

Bromus tectorum was one of the earliest exotic species to establish in the Okanagan Valley, and is now the most common invader (Lea 2009, Mack 1981). This species was

the most frequently observed, and had the highest overall cover of any exotic or native

species present in the sample sites (Appendix B). However, *B. tectorum* was not highly

edge-biased, as was expected for exotic species (Figure 2.6c). This species was

moderately correlated with the edge-related change in the plant community at 50% of

fruit crops, and some of the road sites (Appendix D). However, it was positively

correlated with the NCAP scores just as often as it was negatively correlated. The

correlation results indicate that *B. tectorum* can contribute significantly to edge-related

shifts in community composition, but it can be more or less abundant at developed edges.

It is possible that *B. tectorum* does not show an edge-bias because of the considerable

time since introduction, the ability to self perpetuate after establishment by increasing fire

frequency, and the disturbance and seed transport by cattle, all of which help *B. tectorum*

successfully invade the interior of grassland areas (Meidinger and Pojar 1991, Tisdale

1947, Lea 2009, Longland and Bateman 2002)

Other introduced species of *Bromus* (*B. hordeaceous, B. racemosus, B. secalinus,*

B. squarrosus) were also frequent, and were moderately edge-biased (Appendix B). Like

B. tectorum, these other species are all invasive weeds (Klinkenberg 2009), but they have

not had as much time to become established within the interior of the grasslands as *B.*

tectorum, which may explain their biased distribution. These introduced bromes were

significantly correlated to the edge-related community change at 50% of the dirt roads,

but did not seem to have as much of an effect at the edges of paved roads as other exotic

species, such as *Poa bulbosa* or *Sisymbrium altissimum* (Appendix D). However, the

combined abundances of *B. tectorum* and the other introduced bromes together are

considerable at many edge sites. It is possible that these species will continue to move

into the interior of remnant grasslands, and have distributions similar to *B. tectorum* in the future.

The soil variables that best predicted compositional changes at paved roads were soil pH and Cu/Mn. Soil pH, along with mineralizable N, was also related to community composition at the edges of fruit crops, and changes from the edges of dirt roads were best explained by soil resistance. While these factors may not be completely responsible for the edge effects observed in the plant community, it is clear that different environmental variables are involved in edge effects at different sites. Further research is needed to determine the mechanisms underlying how these soil variables interact with the plant community at edges, and what critical levels of pollutants are required before changes occur.

Edge effects on individual plants, animals, and their physical and chemical environment could extend much farther from human developed edges than is observed in plant community composition. The extent of an edge effect can be altered by season, slope, wind direction, aspect and habitat quality (Forman and Alexander 1998, Ries et al. 2004, Bernhardt-Romermann et al. 2006, Gelbard and Belnap 2003, Cadenasso et al. 1997). Some edge effects are also expected to increase over time (Ranney et al. 1981, Gascon et al. 2000, Harper and Macdonald 2002). Permeability of the edge also influences how far edge effects can penetrate into the surrounding areas (Cadenasso and Pickett 2001). Grassland edges are more structurally permeable than forest edges, and so exotic species invasion from roads may be greater in grasslands than in forests (Hansen and Clevenger 2005), and presumably other effects on animals and their physical and chemical environments could also extend farther in grasslands than in forests. However,

contrast between habitat and developed areas is much larger for forests than for grasslands, which is likely why the grassland edge effects observed in the present study did not extend as far as was reported in the forest literature. All of these factors make comparisons between edge effect studies in different ecosystems difficult (Harper et al. 2005), and large scale estimation of affected area complex.

The results of the present thesis can help inform the planning of future development and grassland management. Future researchers could expand on these findings by experimentally testing how the soil factors related to compositional change in the present study can cause shifts in the grassland, and try to determine what threshold levels of these factors are needed to alter plant community structure. Furthermore, determining how edge effects in the grassland community affect other organisms in the food web, or the ecosystem services provided by the grasslands, is essential for quantifying and mitigating effects of edges on this ecosystem. The distributions of weeds, such as the introduced bromes, and their effects on the grassland community structure in conjunction with *B. tectorum*, should also be monitored and controlled. With informed management, the integrity of this important grassland ecosystem can be conserved for the future.

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Appendices

Appendix A Study site attribute data. Site ID's are based on GCC grassland mapping project ID numbers from their GIS layer. Approximate areas were rough calculations using the area calculation tool in ESRI ArcView. Longitude and latitude are displayed in decimal degrees.

Site ID	Edge Type	Approx. area (ha)	Transect	Transect start point					Transect end point				
				Long.	Lat.	Elevation (m)	Slope (°)	Aspect	Long.	Lat.	Elevation (m)	Slope (°)	Aspect
1	p	45	1	-119.580	49.233	452	10	W	-119.578	49.233	468.55	2	W
			2	-119.580	49.233	454.4	11	NW	-119.578	49.233	471.65	4	W
1282	p	60	1	-119.638	49.315	572.75	1	S	-119.636	49.315	565.85	4	S
			2	-119.638	49.315	571.15	5	SE	-119.637	49.315	559.4	5	S
1357	p	75	1	-119.632	49.302	566.25	10	NE	-119.633	49.301	583	11	NE
			2	-119.628	49.301	567.7	4	NE	-119.629	49.301	565.95	6	NE
1775	p	28	1	-119.596	49.186	492.85	20	E	-119.597	49.186	529.2	24	E
			2	-119.594	49.188	502.45	14	SE	-119.594	49.188	536.65	28	E
1835	p	15	1	-119.597	49.176	469.7	10	SE	-119.596	49.176	455.05	20	S
			2	-119.598	49.176	464.65	10	SE	-119.597	49.175	456.3	11	E
2009	p	90	1	-119.521	49.085	280.25	3	SW	-119.520	49.085	304.1	5	SW
			2	-119.521	49.085	279.75	2	SW	-119.520	49.085	303.35	10	SW
2503	p	>100	1	-119.671	49.004	455.15	5	W	-119.673	49.004	480.75	6	E
			2	-119.671	49.005	455.65	1	W	-119.672	49.005	467.1	8	E
6335	p	>100	1	-119.684	49.021	474.1	8	SW	-119.685	49.021	473.1	1	NE
			2	-119.685	49.022	472	8	SW	-119.686	49.017	471.95	0	NE
3	a	28	1	-119.565	49.230	417.45	1	E	-119.565	49.229	416.9	0	E
			2	-119.567	49.230	424.5	0	NW	-119.567	49.229	422	1	SW
1837	a	21	1	-119.581	49.173	352.5	13	SE	-119.582	49.174	384.9	20	S
			2	-119.581	49.174	354.15	20	SE	-119.582	49.174	390.95	20	SE
2060	a	15	1	-119.532	49.066	390.8	16	NE	-119.534	49.065	422.9	27	NE
			2	-119.533	49.067	392.9	25	NE	-119.534	49.066	436.95	10	N
2477	a	>100	1	-119.474	49.001	318.6	10	SE	-119.476	49.001	344.65	19	SE
			2	-119.474	49.001	316	9	E	-119.475	49.001	337.8	20	NE

Site ID	Edge Type	Approx. area (ha)	Transect	Transect start point					Transect end point				
				Long.	Lat.	Elevation (m)	Slope (^{o})	Aspect	Long.	Lat.	Elevation (m)	Slope (^{o})	Aspect
20090	a	90	1	-119.525	49.096	358.8	1	N	-119.525	49.095	356.6	3	SE
			2	-119.526	49.096	358.1	1	W	-119.526	49.095	357	1	SW
200900	a	90	1	-119.515	49.087	344.75	4	W	-119.517	49.087	338.25	2	SW
			2	-119.516	49.088	347.35	4	W	-119.517	49.088	342.15	0	SE
929	d	48	1	-119.700	49.392	751.45	14	N	-119.684	49.391	767.6	10	NE
			2	-119.700	49.392	751.6	14	N	-119.700	49.391	767.95	10	NE
1641	d	7	1	-119.577	49.236	457.35	6	E	-119.578	49.236	466.25	8	S
			2	-119.578	49.237	462.9	8	SW	-119.578	49.236	470.4	3	W
1768	d	75	1	-119.584	49.185	514.95	9	SW	-119.584	49.186	538.55	28	SW
			2	-119.586	49.186	519.35	8	S	-119.586	49.187	545.85	16	SE
1996	d	>100	1	-119.579	49.094	670.45	4	E	-119.580	49.094	665.95	0	W
			2	-119.579	49.093	661.05	1	S	-119.580	49.093	659.85	4	SW
2280	d	22	1	-119.501	49.033	464.4	14	S	-119.500	49.034	471.9	20	E
			2	-119.501	49.034	469.55	16	S	-119.500	49.034	464.4	14	N
63350	d	>100	1	-119.683	49.016	544.75	5	NE	-119.683	49.017	538.15	13	NE
			2	-119.683	49.016	556.1	2	NE	-119.684	49.017	551.4	23	N
1862	c	35	1	-119.600	49.157	442.65	22	E	-119.601	49.157	477.65	21	E
			2	-119.599	49.155	443.9	7	E	-119.600	49.155	474.25	14	NE
1942	c	>100	1	-119.590	49.115	530.7	23	NE	-119.591	49.114	570.3	10	N
			2	-119.590	49.115	529.65	30	NE	-119.591	49.114	565.65	16	NE
5439	c	12	1	-119.614	49.105	975.75	17	SW	-119.613	49.106	1003	14	S
			2	-119.615	49.105	964.35	10	SW	-119.614	49.105	990	14	SW
24770	c	55	1	-119.498	49.001	544.2	16	E	-119.499	49.001	584.3	27	E
			2	-119.499	49.002	543.65	20	NE	-119.499	49.001	581.9	23	NE
25030	c	>100	1	-119.675	49.009	494.2	23	E	-119.676	49.009	533.4	19	NE
			2	-119.675	49.009	496.25	21	E	-119.676	49.009	530	17	NE
92900	c	48	1	-119.701	49.423	790.8	10	NE	-119.702	49.389	811.9	11	NE
			2	-119.701	49.390	796.25	11	NE	-119.702	49.389	813.15	10	NE

Appendix B Frequency and abundance of taxa included in analysis, and their edge biases. Taxa are ordered by their frequency of plot presence. Control sites were included in frequency calculations but not in edge bias analysis (indicated by*). Consider that rare species have a greater chance of being edge-biased by chance when using edge bias values for species found in only a few plots.

Scientific Name	Common Name	Family	Endemism (native/exotic)	Number of sites present	Frequency of plot presence (/2028)	Total cover by species (m)	% plots present at edge (within 25 m) *	Edge bias (%)*
Bromus tectorum	cheatgrass	Poaceae	e	24	1061	178.01	40.4	1.0
Poa secunda	Sandberg's/Nevada bluegrass	Poaceae	n	24	800	75.3	30.5	-8.9
Hesperostipa comata	needle-and-thread grass	Poaceae	n	23	606	106.79	37.6	-1.8
Pseudoroegneria spicata	bluebunch wheatgrass	Poaceae	n	19	589	139.6	31.2	-8.2
Artemisia tridentata	big sagebrush	Asteraceae	n	15	467	151.83	43.3	3.9
Bromus spp.	introduced bromes	Poaceae	e	18	441	48.4	54	14.6
Stellaria nitens	shining starwort	Caryophyllaceae	n	18	414	26.34	33.4	-6.0
Sporobolus cryptandrus	sand dropseed	Poaceae	n	19	370	51	46.7	7.3
Phlox longifolia	long-leaved phlox	Polemoniaceae	n	19	275	21.26	28	-11.4
Agropyron cristatum	crested wheatgrass	Poaceae	e	10	268	76.86	32.9	-6.5
Artemisia tripartita	threetip sagebrush	Asteraceae	n	19	255	46.09	33.1	-6.3
Poa bulbosa	bulbous bluegrass	Poaceae	e	12	230	45.67	69.6	30.2
Polygonum douglasii	knotweed	Polygonaceae	n	14	226	10.2	27.8	-11.6
Purshia tridentata	antelope-brush	Rosaceae	n	10	181	99.36	36.5	-2.9
Lomatium spp.	desert parsley	Apiaceae	n	20	175	12.22	19.8	-19.6
Balsamorhiza sagittata	arrow-leaved balsamroot	Asteraceae	n	8	173	46.25	35.7	-3.7
Lupinus sericeus	silky lupine	Fabaceae	n	7	171	25.92	34	-5.4
Sisymbrium altissimum	tall tumble-mustard	Brassicaceae	e	17	171	27.5	69.1	29.7
Achillea millefolium	yarrow	Asteraceae	n	19	168	17.44	40.3	0.9
Vulpia spp.	small/six-weeks fescue	Poaceae	n	17	164	8.2	25.8	-13.6
Plantago patagonica	woolly plantain	Plantaginaceae	n	16	158	7.26	38.2	-1.2
Koeleria macrantha	junegrass	Poaceae	n	11	151	15.8	43	3.6
Linaria genistifolia ssp. Dalmatica	Dalmatian toadflax	Scrophulariaceae	e	8	150	16.81	29.3	-10.1
Phacelia linearis	thread-leaved phacelia	Hydrophyllaceae	n	17	115	4.08	30.6	-8.8
Crepis atrabarba	slender hawksbeard	Asteraceae	n	15	114	8.4	25	-14.4
Polemonium micranthum	littlebells polemonium	Polemoniaceae	n	12	102	8.11	47.2	7.8
Tragopogon spp.	salsify	Asteraceae	e	18	94	5.48	48.4	9.0
Astragalus miser	timber milk-vetch	Fabaceae	n	6	86	10.94	26.9	-12.5
Calochortus macrocarpus	sagebrush mariposa lily	Liliaceae	n	20	86	2.32	19.2	-20.2

Scientific Name	Common Name	Family	Endemism (native/exotic)	Number of sites present	Frequency of plot presence	Total cover (m)	% plots present at edge (within 25 m) *	Edge bias (%)*
Festuca idahoensis	Idaho fescue	Poaceae	n	6	86	12.03	36	-3.4
Eriogonum heracleoides	parsnip-flowered buckwheat	Polygonaceae	n	11	85	14.48	8.1	-31.3
Eriogonum niveum	snow buckwheat	Polygonaceae	n	13	84	9.89	43.9	4.5
Opuntia spp.	prickly-pear cactus	Cactaceae	n	12	79	8.32	38.2	-1.2
Phlox gracilis	pink twink	Polemoniaceae	n	11	78	1.88	29	-10.4
Achnatherum nelsonii ssp.dorei	Columbia needlegrass	Poaceae	n	5	69	6.86	47.5	8.1
Arabis holboellii	Holboell's rockcress	Brassicaceae	n	15	65	2.93	25.6	-13.8
Apera interrupta	interrupted apera	Poaceae	e	11	59	3.07	53.4	14.0
Filago arvensis	field filago	Asteraceae	e	5	59	3.11	16.7	-22.7
Comandra umbellata	comandra	Santalaceae	n	13	57	5.69	62.5	23.1
Lactuca serriola	prickly lettuce	Asteraceae	e	13	56	5.39	77.5	38.1
Collinsia parviflora	small-flowered blue-eyed Mary	Scrophulariaceae	n	2	53	2.32	70.8	31.4
Poa pratensis ssp. pratensis	Kentucky bluegrass	Poaceae	e	9	53	6.79	62	22.6
Taraxacum officinale	common dandelion	Asteraceae	e	11	53	3.23	61.5	22.1
Camelina microcarpa	littlepod flax	Brassicaceae	e	8	52	2.16	40	0.6
Erigeron filifolius	thread-leaved fleabane	Asteraceae	n	6	50	3.79	32.1	-7.3
Artemisia frigida	pasture sage/prairie sagewort	Asteraceae	n	7	49	4.54	51.9	12.5
Lithospermum arvense	corn gromwell	Boraginaceae	e	4	40	4.19	25	-14.4
Carex filifolia	thread-leaved sedge	Cyperaceae	n	4	38	8.61	50	10.6
Myosotis stricta	blue forget-me-not	Boraginaceae	e	8	36	3.33	39.4	0.0
Medicago sativa	alfalfa	Fabaceae	e	8	35	9.35	80	40.6
Centaurea spp.	knapweed	Asteraceae	e	14	33	3.79	70	30.6
Aristida purpurea var.longiseta	red three-awn	Poaceae	n	8	32	8.35	36.7	-2.7
Descurainia pinnata	western tansy mustard	Brassicaceae	n	9	31	1.66	31.6	-7.8
Lithospermum ruderale	lemonweed	Boraginaceae	n	9	30	4.25	30	-9.4
Erigeron pumilus	shaggy daisy/fleabane	Asteraceae	n	7	29	1.87	44.8	5.4
Erigeron corymbosis	long-leaved fleabane	Asteraceae	n	7	26	1.73	22.2	-17.2
Saxifraga nidifica	meadow saxifrage	Saxifragaceae	n	5	22	1.31	36.4	-3.0
Antennaria spp.	pussytoes	Asteraceae	n	10	21	1.93	21.1	-18.3
Heterotheca villosa	golden-aster	Asteraceae	n	6	21	2.73	52.4	13.0
Agoseris glauca	short-beaked agoseris	Asteraceae	n	8	20	0.97	50	10.6
Collomia linearis	narrow-leaved collomia	Polemoniaceae	n	7	20	0.78	68.4	29.0

Scientific Name	Common Name	Family	Endemism (native/exotic)	Number of sites present	Frequency of plot presence	Total cover (m)	% plots present at edge (within 25 m) *	Edge bias (%)*
Zigadenus venenosus	meadow death-camas	Liliaceae	n	6	18	0.73	33.3	-6.1
Ericameria nauseosus	common rabbit-brush	Asteraceae	n	8	17	3.66	60	20.6
Pinus ponderosa	ponderosa pine	Pinaceae	n	4	17	13.95	23.5	-15.9
Astragalus collinus	hillside milk-vetch	Fabaceae	n	4	16	1.99	0	-39.4
Bromus inermis	smooth brome	Poaceae	n	3	16	2.9	43.8	4.4
Holosteum umbellatum	umbellate chickweed	Caryophyllaceae	e	4	16	1.33	43.8	4.4
Lappula occidentalis	western stickseed	Boraginaceae	n	3	16	0.32	20	-19.4
Lewisia rediviva	bitterroot	Portulacaceae	n	7	16	0.54	25	-14.4
Medicago lupulina	black medic	Fabaceae	e	5	12	1.53	90	50.6
Lepidium densiflorum	prairie pepper-grass	Brassicaceae	n	6	11	0.23	62.5	23.1
Castilleja spp. (yellow)	paintbrush	Scrophulariaceae	n	7	10	0.58	33.3	-6.1
Erodium cicutarium ssp.cicutarium	common stork's-bill	Geraniaceae	e	4	10	0.77	80	40.6
Rhus glabra	smooth sumac	Anacardiaceae	n	1	10	1.6	30	-9.4
Gaillardia aristata	brown-eyed susan	Asteraceae	n	2	8	0.34	12.5	-26.9
Galium aparine	cleavers	Rubiaceae	n	1	8	0.53	12.5	-26.9
Carex petaseta	broad-wing sedge	Cyperaceae	n	2	7	0.6	28.6	-10.8
Elymus x albicans	Montana wildrye	Poaceae	n	2	7	1.06	100	60.6
Cynoglossum officinale	common hound's-tongue	Boraginaceae	e	3	6	0.9	100	60.6
Delphinium nuttallianum	upland larkspur	Ranunculaceae	n	4	6	0.23	0	-39.4
Equisetum laevigatum	smooth scouring-rush	Equisetaceae	n	1	6	0.61	100	60.6
Toxicodendron rydbergii	poison-ivy	Anacardiaceae	n	1	6	1.05	100	60.6
Dactylis glomerata	orchard grass	Poaceae	e	1	5	1.45	100	60.6
Grindelia squarrosa	curlycup gumweed	Asteraceae	n	3	5	0.81	100	60.6
Heuchera cylindrica	round leaved alumroot	Saxifragaceae	n	2	5	0.55	0	-39.4
Lactuca tatarica	blue lettuce	Asteraceae	n	2	5	0.36	80	40.6
Thinopyrum intermedium	intermediate wheatgrass	Poaceae	e	3	5	0.61	60	20.6
Artemisia dracunculus	tarragon	Asteraceae	n	3	4	0.16	100	60.6
Astragalus purshii	woollypod milk-vetch	Fabaceae	n	3	4	0.22	0	-39.4
Cirsium arvense	Canada thistle	Asteraceae	e	2	4	0.5	100	60.6
Leymus cinereus	giant wildrye	Poaceae	n	3	4	2.2	50	10.6
Lotus denticulatus	meadow birds-foot trefoil	Fabaceae	n	2	4	0.16	50	10.6
Artemisia campestris	northern wormwood	Asteraceae	n	1	3	0.7	33.3	-6.1
Cirsium undulatum	wavy-leaved thistle	Asteraceae	n	1	3	0.25	33.3	-6.1

Scientific Name	Common Name	Family	Endemism (native/exotic)	Number of sites present	Frequency of plot presence	Total cover (m)	% plots present at edge (within 25 m) *	Edge bias (%)*
Gypsophila paniculata	baby's breath	Caryophyllaceae	e	1	3	0.2	100	60.6
Matricaria discoidea	pineapple weed	Asteraceae	e	1	3	0.71	100	60.6
Ribes cereum	squaw currant	Grossulariaceae	n	2	3	2.3	0	-39.4
Verbena bracteata	bracted vervain	Verbenaceae	n	2	3	0.25	100	60.6
Woodsia oregana	western cliff fern	Dryopteridaceae	n	2	3	0.26	0	-39.4
Achnatherum occidentale	stiff needlegrass	Poaceae	n	1	2	0.45	50	10.6
Apocynum androsaemifolium	spreading dogbane	Apocynaceae	n	1	2	0.3	100	60.6
Asparagus officinalis	garden asparagus	Liliaceae	e	1	2	0.2	0	-39.4
Dodecatheon pulchellum	few-flowered/pretty shooting star	Primulaceae	n	1	2	0.15	0	-39.4
Erigeron linearis	linear-leaved daisy	Asteraceae	n	1	2	0.15	0	-39.4
Lolium perenne	perennial ryegrass	Poaceae	e	1	2	0.2	100	60.6
Mertensia longiflora	long-flowered bluebells	Boraginaceae	n	1	2	0.1	0	-39.4
Achnatherum hymenoides	Indian ricegrass	Poaceae	n	1	1	0.4	0	-39.4
Amelanchier alnifolia	saskatoon	Rosaceae	n	1	1	1	0	-39.4
Arnica fulgens	orange arnica	Asteraceae	n	1	1	0.01	100	60.6
Asclepias speciosa	showy milkweed	Asclepiadaceae	n	1	1	0.1	100	60.6
Chenopodium album	lamb's-quarters	Chenopodiaceae	e	1	1	0.05	100	60.6
Claytonia rubra	redstem springbeauty	Portulacaceae	n	1	1	0.05	0	-39.4
Clematis ligusticifolia	white clematis	Ranunculaceae	n	1	1	0.05	100	60.6
Cuscuta spp.	dodder	Cuscutaceae	e	1	1	0.1	0	
Elymus trachycaulus	slender wheatgrass	Poaceae	n	1	1	0.1	100	60.6
Geum triflorum	old man's whiskers	Rosaceae	n	1	1	0.1	0	-39.4
Philadelphus lewisii	mock-orange	Hydrangeaceae	n	1	1	0.7	0	-39.4
Polygonum convolvulus	black bindweed	Polygonaceae	e	1	1	0.1	100	60.6
Potentilla glandulosa	sticky cinquefoil	Rosaceae	n	1	1	0.1	0	-39.4
Potentilla recta	sulphur cinquefoil	Rosaceae	e	1	1	0.1	0	-39.4
Ranunculus glaberrimus	sagebrush buttercup	Ranunculaceae	n	1	1	0.05	0	-39.4
Rosa gymnocarpa	baldhip rose	Rosaceae	n	1	1	0.2	0	-39.4
Salsola kali	Russian thistle	Chenopodiaceae	e	1	1	0.05	100	60.6
Setaria viridis	green bristlegrass	Poaceae	e	1	1	0.01	100	60.6
Symphoricarpos albus	common snowberry	Caprifoliaceae	n	1	1	0.3	0	-39.4
Verbascum thapsus L.	great mullein	Scrophulariaceae	e	1	1	0.1	100	60.6

Appendix C AICc values and supporting statistics for the top 12 models from the all-subsets regression analysis for each edge treatment. Note that for the control sites only the top five models are shown due to the rapid increase in the ΔAICc values. Supporting statitstics were calculated as per Burnham and Andersen (2002).

Paved roads

Model	AICc	ΔAICc	Likelihood	Aikaike weights	Evidence Ratio
Factor3 + Factor6	0.0000	0.0000	1.0000	0.1792	1.0000
Factor3 + Factor5 + Factor6	0.5062	0.5062	0.7764	0.1392	1.2880
Factor6 + Na	1.0471	1.0471	0.5924	0.1062	1.6880
Factor1 + Factor6	1.5576	1.5576	0.4590	0.0823	2.1788
Factor5 + Factor6 + Na	1.8758	1.8758	0.3914	0.0702	2.5547
Factor6	1.9053	1.9053	0.3857	0.0691	2.5925
Factor1 + Factor3 + Factor6	2.0494	2.0494	0.3589	0.0643	2.7862
Factor1 + Factor6 + Na	2.0606	2.0606	0.3569	0.0640	2.8018
Factor2 + Factor3 + Factor6	2.1736	2.1736	0.3373	0.0605	2.9648
Factor3 + Factor6 + Na	2.1841	2.1841	0.3355	0.0601	2.9803
Factor2 + Factor6 + Na	2.4385	2.4385	0.2955	0.0530	3.3846
Factor3 + Factor4 + Factor5 + Factor6	2.4719	2.4719	0.2906	0.0521	3.4416

Fruit crops

Model	AICc	ΔAICc	Likelihood	Aikaike weights	Evidence Ratio
Factor6 + Nitrogen	0.0000	0.0000	1.0000	0.1793	1.0000
Factor6 + Factor7 + Nitrogen	1.0434	1.0434	0.5935	0.1064	1.6849
Factor6 + Factor7	1.2479	1.2479	0.5358	0.0961	1.8663
Factor1 + Factor6	1.3836	1.3836	0.5007	0.0898	1.9973
Factor1 + Factor6 + Factor7	1.3852	1.3852	0.5003	0.0897	1.9989
Factor3 + Factor6 + Factor7	1.7985	1.7985	0.4069	0.0730	2.4577
Factor4 + Factor6 + Nitrogen	1.9307	1.9307	0.3809	0.0683	2.6257
Factor6	1.9665	1.9665	0.3741	0.0671	2.6732
Factor6 + Factor7 + Na	2.1458	2.1458	0.3420	0.0613	2.9239
Factor6 + Nitrogen + Soil_Resist	2.3008	2.3008	0.3165	0.0568	3.1595
Factor1 + Factor6 + Nitrogen	2.3115	2.3115	0.3148	0.0565	3.1765
Factor6 + Nitrogen + Na	2.3340	2.3340	0.3113	0.0558	3.2123

Dirt roads

Model	AICc	ΔAICc	Likelihood	Aikaike weights	Evidence Ratio
Soil_Resist	0.0000	0.0000	1.0000	0.2050	1.0000
Factor5 + Soil_Resist	1.4549	1.4549	0.4831	0.0990	2.0698
Factor3 + Soil_Resist	1.5591	1.5591	0.4586	0.0940	2.1805
Factor2 + Soil_Resist	1.7004	1.7004	0.4273	0.0876	2.3401
Factor7 + Soil_Resist	1.7484	1.7484	0.4172	0.0855	2.3969
Factor6 + Soil_Resist	2.1254	2.1254	0.3455	0.0708	2.8942
Factor1 + Soil_Resist	2.2081	2.2081	0.3315	0.0680	3.0163
Factor2 + Factor7 + Soil_Resist	2.3051	2.3051	0.3158	0.0647	3.1662
Factor6	2.4009	2.4009	0.3011	0.0617	3.3216
Factor1 + Factor3 + Soil_Resist	2.4030	2.4030	0.3007	0.0616	3.3252
Factor4 + Soil_Resist	2.6861	2.6861	0.2610	0.0535	3.8307
Soil_Resist + Na	2.8801	2.8801	0.2369	0.0486	4.2209

Control sites

Model	AICc	ΔAICc	Likelihood	Aikaike weights	Evidence Ratio
All 10 Factors*	0.0000				
Factor1	313.7527	0.0000	1.0000	0.4954	1.0000
Factor1 + Na	315.3060	1.5533	0.4599	0.2279	2.1742
Factor1 + Factor3	315.8400	2.0873	0.3522	0.1745	2.8396
Factor2 + Na	316.9091	3.1564	0.2063	0.1022	4.8462

* This model was disregarded because the number of variables in the model was too many for the number of data points available in the dataset.

Appendix D Pearson correlation (*r*) between species abundance and NCAP scores. Positive values indicate species is positively correlated with interior composition and vice versa. Bolded sites had nonlinear relationships, sites with regular script were linear, and grey script is for sites with no significant distance-composition relationship. Species with correlation values ≥ |0.50| are shown, and were highlighted at sites with linear or nonlinear relationships to the edge.

	Paved road sites								Fruit crop sites					
	6335	1282	1357	1775	2009	2503	1	1835	3	1837	200900	2477	20090	2060
Agropyron cristatum	0.00	0.00	-0.42	-0.07	-0.14	0.00	-0.02	0.00	0.00	0.00	0.00	0.29	0.00	0.00
Apera interrupta	-0.22	0.35	-0.12	0.00	0.00	0.00	0.01	0.00	-0.15	0.00	0.00	-0.19	0.00	-0.13
Artemisia tridentata	0.45	0.26	0.24	0.00	0.00	0.09	0.00	0.00	0.00	-0.42	0.00	-0.09	0.00	0.23
Balsamorhiza sagittata	0.00	0.00	0.00	0.41	0.00	0.00	0.00	0.04	-0.54	0.07	0.00	0.00	0.00	0.00
Bromus spp.	0.00	-0.31	-0.60	0.15	-0.22	-0.15	-0.30	0.07	-0.42	0.00	0.00	-0.25	0.00	-0.22
Bromus tectorum	-0.42	0.30	-0.30	0.49	0.57	-0.55	-0.23	0.14	0.27	0.55	-0.14	-0.42	0.50	-0.74
Dactylis glomerata	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-0.57	0.00	0.00	0.00	0.00	0.00
Erigeron pumilus	0.16	0.00	0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-0.08
Eriogonum niveum	0.00	0.00	0.00	0.00	0.01	-0.01	0.00	0.10	0.01	-0.51	-0.37	0.19	0.05	0.14
Filago arvensis	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hesperostipa comata	0.79	0.74	-0.33	-0.14	0.08	0.73	0.36	0.41	0.53	-0.49	0.23	0.11	0.09	0.33
Lactuca serriola	-0.47	-0.18	-0.76	0.03	0.00	0.00	-0.12	0.05	0.00	0.00	0.00	0.00	0.00	0.00
Linaria genistifolia	0.00	-0.17	0.00	0.00	0.61	0.00	0.00	-0.32	0.38	0.39	-0.06	0.00	0.00	-0.06
Lolium perenne	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-0.54	0.00
Lomatium spp.	0.42	0.26	0.12	0.07	0.00	-0.07	0.39	0.23	-0.28	0.00	0.00	0.34	0.00	-0.26
Lupinus sericeus	0.00	0.00	0.53	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.14
Medicago lupulina	-0.22	0.00	0.00	0.00	0.00	0.00	-0.12	0.00	0.00	0.00	0.00	0.00	-0.63	0.00
Medicago sativa	0.00	-0.66	-0.25	-0.13	-0.52	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-0.74	0.00
Phlox longifolia	0.49	0.00	0.00	0.05	0.00	0.30	0.20	0.00	0.20	0.00	0.32	0.02	0.08	0.10
Plantago patagonica	0.29	0.15	-0.04	0.16	0.00	0.18	0.10	-0.17	0.29	0.00	0.00	0.00	0.00	0.05
Poa bulbosa	0.00	-0.57	-0.23	-0.89	0.00	-0.66	-0.75	-0.44	0.00	0.00	0.00	-0.16	0.00	0.00
Poa secunda	0.67	0.62	0.25	0.14	0.00	0.53	0.62	0.37	0.55	0.00	0.78	0.88	0.08	0.28
Polemonium micranthum	0.00	-0.13	0.01	0.00	-0.11	0.00	0.00	0.00	0.00	0.00	-0.54	0.00	0.02	0.00
Polygonum douglasii	0.00	0.51	-0.11	0.07	0.41	0.00	-0.01	0.00	0.39	0.00	0.44	0.00	0.15	0.00
Pseudoroegneria spicata	0.00	0.00	0.66	0.64	0.00	0.01	0.48	0.34	-0.23	0.00	0.00	0.00	0.00	0.08
Sisymbrium altissimum	-0.84	-0.12	-0.79	0.00	-0.44	-0.59	-0.27	-0.02	0.01	0.00	0.04	0.00	0.01	0.00
Sporobolus cryptandrus	-0.24	-0.39	-0.17	-0.65	-0.34	-0.48	-0.05	-0.78	0.44	0.39	0.28	0.16	0.10	0.14
Stellaria nitens	0.00	0.75	0.16	0.20	-0.04	0.00	0.20	0.00	0.46	0.00	0.42	0.00	0.51	-0.03
Taraxacum officinale	-0.04	-0.36	0.07	0.00	0.00	0.00	0.05	0.02	0.00	0.00	0.00	0.00	-0.62	0.00

	Dirt roads						Control sites					
	929	**1768**	2280	1996	1641	63350	**1862**	**92900**	24770	25030	5439	1942
Agropyron cristatum	**0.81**	**0.00**	0.00	0.34	0.78	0.00	**-0.42**	**-0.02**	0.00	0.00	0.00	0.00
Apera interrupta	**-0.53**	**0.00**	0.00	0.03	-0.06	0.00	**0.00**	**0.02**	0.00	0.00	0.00	0.00
Artemisia tridentata	**-0.11**	**0.00**	-0.57	-0.20	0.00	-0.03	**0.00**	**0.30**	-0.66	-0.17	0.00	0.00
Balsamorhiza sagittata	**0.00**	**0.17**	0.00	0.00	-0.07	0.00	**0.00**	**0.00**	-0.15	0.00	-0.10	0.00
Bromus spp.	**-0.63**	**-0.20**	0.00	0.55	-0.67	0.00	**0.24**	**0.00**	-0.72	0.00	0.02	0.80
Bromus tectorum	**-0.60**	**0.60**	-0.45	-0.16	0.07	0.00	**-0.04**	**0.38**	-0.05	0.00	0.07	0.67
Dactylis glomerata	**0.00**	**0.00**	0.00	0.00	0.00	0.00	**0.00**	**0.00**	0.00	0.00	0.00	0.00
Erigeron pumilus	**0.00**	**-0.63**	0.00	0.08	-0.04	-0.04	**0.00**	**0.00**	0.00	0.00	0.00	0.00
Eriogonum niveum	**0.00**	**0.00**	0.09	0.01	0.00	-0.07	**-0.15**	**0.00**	0.00	0.00	0.00	0.00
Filago arvensis	**0.35**	**0.00**	0.00	0.03	0.00	0.00	**0.00**	**-0.78**	0.00	0.00	0.10	0.00
Hesperostipa comata	**-0.24**	**-0.16**	-0.32	-0.56	0.01	0.00	**0.64**	**-0.47**	0.00	-0.78	0.00	-0.12
Lactuca serriola	**0.08**	**-0.03**	0.00	0.20	-0.06	0.00	**-0.08**	**0.00**	-0.17	0.00	0.00	0.51
Linaria genistifolia	**0.00**	**0.07**	0.00	0.00	0.00	0.00	**0.00**	**0.00**	0.00	0.00	0.00	0.00
Lolium perenne	**0.00**	**0.00**	0.00	0.00	0.00	0.00	**0.00**	**0.00**	0.00	0.00	0.00	0.00
Lomatium spp.	**-0.23**	**0.11**	0.22	-0.50	0.00	0.42	**-0.13**	**0.00**	0.04	-0.09	0.57	0.02
Lupinus sericeus	**-0.20**	**0.00**	0.00	0.00	0.00	0.00	**0.00**	**0.19**	0.15	0.00	-0.55	0.33
Medicago lupulina	**-0.36**	**0.00**	0.00	0.00	0.00	0.00	**0.08**	**0.00**	0.00	0.00	0.00	0.00
Medicago sativa	**0.03**	**0.00**	0.00	-0.15	-0.21	0.00	**0.00**	**0.00**	0.00	0.00	0.00	0.00
Phlox longifolia	**0.00**	**-0.34**	0.08	-0.02	-0.01	-0.22	**0.28**	**0.00**	0.16	-0.65	0.00	-0.19
Plantago patagonica	**0.19**	**0.00**	-0.05	-0.51	-0.04	0.00	**0.12**	**-0.63**	0.00	0.00	0.00	0.03
Poa bulbosa	**-0.01**	**-0.59**	0.00	0.00	-0.25	0.00	**0.00**	**0.00**	0.00	0.00	-0.50	0.00
Poa secunda	**-0.23**	**0.15**	0.09	-0.09	-0.32	-0.56	**-0.14**	**0.09**	0.01	-0.22	0.24	-0.10
Polemonium micranthum	**-0.07**	**0.12**	0.00	0.00	-0.08	0.00	**-0.10**	**-0.15**	0.08	0.00	0.00	0.54
Polygonum douglasii	**0.13**	**0.00**	0.00	0.00	-0.21	0.00	**0.10**	**0.09**	0.00	0.00	0.00	0.21
Pseudoroegneria spicata	**-0.24**	**0.44**	0.72	-0.22	-0.17	-0.28	**-0.03**	**0.22**	0.64	0.88	0.35	-0.61
Sisymbrium altissimum	**-0.27**	**0.00**	0.00	0.41	-0.06	0.00	**-0.08**	**-0.47**	0.00	0.00	-0.38	0.71
Sporobolus cryptandrus	**0.00**	**-0.22**	-0.46	0.04	-0.07	0.00	**-0.36**	**0.00**	0.00	0.00	0.00	0.00
Stellaria nitens	**0.00**	**0.00**	0.00	-0.02	-0.03	-0.07	**0.20**	**0.00**	0.41	0.31	-0.02	-0.05
Taraxacum officinale	**-0.05**	**0.00**	0.00	-0.07	0.00	0.00	**0.00**	**0.12**	-0.08	0.00	-0.15	0.00