

**DISTRIBUTION OF PLANT FUNCTIONAL GROUPS
ACROSS GRASSLAND-FOREST ECOTONES: TESTING THE
ASSUMPTIONS**

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ABSTRACT

Ecotones, transition zones found at abrupt discontinuities in vegetation, are a part of every landscape and have long been considered hotspots for biodiversity and conservation of both plants and animals. However, many assumptions about ecotone characteristics have not been rigorously tested. The most prevalent claim in the literature is that ecotones support higher species richness than adjacent habitats. Patterns of higher species richness in ecotones has been hypothesized to arise from ecological processes ranging from spatial mass effect, increased environmental heterogeneity, seed predation or introduction by animals or insects, to increased dispersal ability by exotic generalists. The purpose of this project is to document patterns of plant functional group richness and abundance across grassland-aspen ecotones in the Lac du Bois grasslands north of Kamloops, British Columbia. Specifically, this research addresses the following questions: 1) Are ecotones more species-rich than surrounding areas in both north- and south-facing aspects? 2) What is the relationship between functional diversity and species richness across the grassland-aspen ecotones? and 3) How does the method of ecotone definition (statistical versus visual) and data analysis (blocking versus gradient approach) impact the results?

Twenty ecotones (10 south-facing and 10 north-facing ecotones) were intensively sampled along 35 m transects for richness and abundance of herbaceous plant species, aspen saplings, soil pH and moisture and tree canopy cover. To compare techniques, the location of each ecotone was defined both statistically using moving window regression analysis and visually using the treeline as an approximate centre. Ecotone locations varied greatly when the statistical method was compared with the visual method. Overall, the results did not support the assumption that ecotones are more species rich than adjacent habitats. However there was variation between richness and abundance of other functional groups (shade tolerance, dispersal method and drought tolerance, for example) in ecotones compared to adjacent habitats. This research also found a strong influence of aspect on the results, especially when grasslands and ecotones were compared.

Keywords: ecotone, grassland, aspen, aspect, functional groups, treeline

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CHAPTER 1 DISTRIBUTION OF HERBACEOUS PLANTS ACROSS GRASSLAND-FOREST ECOTONES: TESTING THE ASSUMPTIONS

ECOTONES: EVOLVING DEFINITIONS

Ecology has long been concerned with both spatial and temporal patterns of species richness (Pausas & Austin 2001; Starzomski et al. 2008), especially with respect to the influence of biotic and abiotic factors (Iverson & Prasad 2001; Midgley et al. 2002). Ecotones were first defined as a “stress line connecting points of accumulated or abrupt change” on a landscape (Livingston 1903). With the rise of conservation and global climate change biology ecotone research has increased significantly in popularity beginning in the 1980s (Kark & Rensburg 2006). Since then, definitions of ecotones and methods used to delineate them have evolved.

At the basic level, ecotones, from the Greek root *oikos* (home) and *tonus* (tension), are the zones of transition where two distinct ecosystems such as forest and grassland meet (Kark & Rensburg 2006). Most researchers follow the definition first outlined by Clements in 1905 in which an ecotone is viewed as an abrupt line between two systems. Curtis and McIntosh (1951) clarified that ecotones are also zones of tension between biogeographic regions. This definition was expanded further to define ecotones as broader landscape elements with more dynamic, somewhat unstable characteristics (Van der Maarel 1990). Odum (1971) added that the ecotone itself may have a large linear extent, but is narrower than the adjacent communities. More specifically, some researchers argue that there should be a distinction in the classification of edge environments as either ecoclines (areas with typically higher species richness) or ecotones (areas with similar or lesser species richness (Van der Maarel 1990)). This idea is based

on a previously held view of edge environments, but recent research seems to be finding support for a return to this concept (Lloyd et al. 2000; Walker et al. 2003; Senft 2009).

ECOTONE CHARACTERISTICS

Recently, ecotones have garnered considerable ecological attention for both conservation and theoretical reasons. The potential of ecotones to contain high species diversity coupled with their role in the flow of energy, nutrients, and genes have led to the argument that ecotones are important landscape elements for conservation of species and habitat (Risser 1995, Fagan et al. 2003, Kark 2013). Like all ecological systems, ecotones can be observed from many spatial scales; from continental i.e., latitudinal vegetation gradients (Gosz 1993), to the local landscape level i.e., riparian zones of small water bodies (Risser 1995). Local scale ecotones can be natural or anthropogenic in origin and range from very young and dynamic to ancient and essentially static. An ecotone's location, extent and sharpness can be influenced by underlying environmental gradients such as soil type, bedrock, site productivity, topography, local hydrology and snow cover (di Castri et al. 1988; Van der Maarel 1990; Bestelmeyer et al. 2006; Gottfried et al. 2011). For example, in reverse treelines, where lower elevations are grassy and trees occur at higher elevations, Coop and Givnish (2007) found that treelines are strongly correlated to shifts in the thermal regime, only weakly associated with soil nutrient and type and not associated with soil moisture.

At the local scale, the study of ecotones has involved two major approaches; the analysis of underlying environmental gradients or the response of populations, species and communities to these gradients (Kark & Rensburg 2006). The plant communities within these ecotonal zones are traditionally thought to be made up of

a blending of the two adjacent systems, with some unique ecotonal species (di Castri et al. 1988). Some studies have found that edge-effects (often equated with ecotones) associated with disturbed or managed forests can extend to fifty metres or more into adjacent ecosystems (Matlack 1994). As a result, an ecotone associated with a treeline, for example, can be very wide, reaching beyond the physical treeline on both sides. Ecotones and plant communities are also strongly influenced by aspect (McLean 1970; Vyse & Clarke 2000; Hylander 2005) since differences in solar exposure, prevailing winds and precipitation patterns impact plant abundance and richness. As a result, it is important to measure plant richness and abundance patterns on both north- and south-facing aspects (Holland & Steyn 1975; Orczewska & Glista 2005).

ECOTONES AND CLIMATE CHANGE

As changing climates impact the location and extent of ecosystems, ecotones will likely migrate or change size (Loehle 2000). This is often noted when treeline ecotones are discussed. Treelines often shift north or upwards in elevation as climate changes locally (Taylor & Taylor 1997; Díaz-varela et al. 2010). Due to this movement and sensitivity to climate, treeline ecotones are often seen as early indicators of future changes and have been identified as potentially useful for evaluating the stability of forest stands under the increasing stresses of climate change (Walker et al. 2003; Senft 2009; Díaz-varela et al. 2010).

The ecological response of ecotone species to disturbances such as climate change may be related, in part, to the distribution of individual species across environmental gradients (Shipley et al. 2011). Ecotones dominated by a large number of species with narrow distributions are likely to experience more compositional shifts than ecotones dominated by species with wide distributions across the ecotone (Hylander 2005). In dynamic ecotones, the age of the ecotone

may also impact patterns of species richness (Halpern et al. 2010).

COMMON ASSUMPTIONS REGARDING ECOTONES

Definitions of ecotones often include several untested assumptions that are important to evaluate empirically. First and foremost, there has been a longstanding assumption that ecotones are areas of high species diversity due to an increased rate of species change across environmental gradients (Camarero et al. 2006). However, several researchers (Lloyd et al. 2000; Walker et al. 2003; Senft 2009) have found evidence that not all ecotones are more species-rich than their surrounding communities. Similarly, a meta-analysis of 21 studies found that riparian ecotones contributed to increased regional species richness through the occurrence of different, rather than more, plant species (Sabo et al. 2005). Other common assumptions regarding ecotone concepts are that ecotones are defined by sharp rather than gradual vegetation transitions, that they encompass changes in physiognomy when compared to adjacent plant communities, that they contain unique ecotonal species (di Castri et al. 1988), or contain more exotic species than in adjacent plant communities (Allen & Knight 1984; Vavra et al. 2007).

Senft (2009) reviewed hypotheses presented to explain the potential richness of ecotones. In general, Senft found that increased ecotonal richness was predicted to result from: 1) increased environmental heterogeneity allowing increased species packing (Auerbach & Shmida 1987) and a higher species richness overall; 2) an increase in animal-dispersed seeds into ecotones (Russo et al. 2006; Vazquez et al. 2009) or animal grazing (Willson & Traveset 2000); 3) an increase of propagules from adjacent areas (spatial mass effect (Shmida & Wilson 1985)); or 4) an increase in exotic species found in the ecotone.

FUNCTIONAL GROUP APPROACH

Plant richness and abundance within ecotones have traditionally been examined using only taxonomic-based, rather than a functional trait-based, response variables (see Bossuyt et al. 1999; Mast et al. 1997; Kark and Rensburg 2006; Sabo et al. 2005). However, the ecological processes believed to account for the high species richness expected in ecotones would likely influence functional groups of species differently (Kyle & Leishman 2009).

Functional group analyses allow researchers to draw general conclusions on a broader scale (Herault & Honnay 2007), and may help to distinguish between competing hypotheses for an observed pattern (Roscher et al. 2012). As the use of functional traits and groups became more popular in research, there has been an increase in confusion of definitions of the terms (Shipley et al. 2016), much like the disagreement over ecotone definition. In an attempt to clarify the issue, functional traits have been defined as “any trait which impacts fitness indirectly via its effects on growth, reproduction and survival” (Violle et al. 2007). Functional groups, discussed in this study, are collections of plants based on these traits and morphological, behavioural or environmental responses (Steffen 1996). Using functional groups can help to delineate the underlying mechanisms driving an ecosystem and allow predictions in different systems (Sandel et al. 2010). These influences can be made visible through functional traits expressed by the overlying plant community (Kyle & Leishman 2009; Schellberg & Pontes 2012).

The functional group approach is useful for large scale studies where it is important to group species based on their response to environmental variables (Lavorel et al. 2007). This approach could be helpful for meta-analysis, allowing for comparisons across studies regardless of ecosystem or scale (Violle et al. 2007). Additionally, a functional group approach may allow for the comparison of ecotone

effects on both flora and fauna, and help to observe underlying interactions between them (Kark & Rensburg 2006).

IDENTIFICATION OF ECOTONES: BY STRUCTURE OR RATE OF COMMUNITY CHANGE

Conflicting results regarding ecotones and their characteristics may have arisen due to differences in the way ecotones are defined by researchers. Defining the location of an ecotone can be problematic and factors such as temporal dynamics, size, shape and sharpness need to be considered (Kark & Rensburg 2006). In the field, ecotones are often identified by the structural edge created by an obvious shift in vegetation physiognomy i.e., the boles of mature trees (Murcia 1995). However, this approach focuses on a subjective, visually obvious aspect of the plant community rather than a definition based on changes in the community as a whole. In order to objectively define the boundaries of the ecotones, ecotones have been defined as areas with the highest rate of change in species richness or composition (Cornelius & Reynolds 1991; Fortin et al. 2000). Species composition is then plotted graphically through an ordination technique. Delcourt and Delcourt (1992) suggest using moving window analysis to statistically identify the area with the greatest rate of change in species composition which defines the boundaries of ecotones. This analysis helps to define the ecotone and then allow for objective comparison between the ecotone and the surrounding communities. Additionally, richness and/or composition can be compared between objectively identified ecotonal habitats, of any type, found around the globe.

ANALYSIS OF GRASSLAND-ASPEN ECOTONES

In the upper grasslands of Lac du Bois Provincial Park and nearby properties, trembling aspen (*Populus tremuloides* (Michx.)) occur as isolated stands

within a larger matrix of grassland and Douglas-fir (*Pseudotsuga menziesii* (Mirb.)) forest. Aspen stands are important sites of native plant and animal diversity and are sometimes considered “keystone ecosystems” (Stohlgren et al. 1997). Aspen stands provide important habitats for vascular plants, insects, birds, and mammals (Campbell & Bartos 2001; Stohlgren et al. 1997). Vyse & Clarke (2000) found that aspen edges are important winter habitat for sharp-tailed grouse in this area. As a broadleaf, deciduous tree, aspen represent a unique canopy type within the study region which is dominated by grassland and large Douglas-fir stands. In the dry grasslands of Lac du Bois, aspen tend to be associated with depressions or gullies where moisture is likely to accumulate (Giesbrecht 2011).

Aspen forest patches most often expand through clonal reproduction, using lateral shoots that emerge from the soil as suckers. An entire patch can be composed of one organism, known as a clone, connected through the root system (Swanson et al. 2010). Within arid grassland-conifer dominated landscapes such as the interior British Columbia, aspen patches are important for small mammal diversity, ungulate browsing and vascular plant species richness (Oaten & Larsen 2008; Jules et al. 2010; Kuhn et al. 2011). Much of the recent attention devoted to aspen has arisen due to the concern that many aspen populations are in decline around North America (Wooley et al. 2008; Michaelian et al. 2010; Worrall et al. 2010). However, air photo analysis indicates that the aspen patches in the Lac du Bois area have apparently expanded over the last thirty years (Alan Vyse, personal correspondence 2013).

While aspen habitats have elicited much consideration over the last fifteen years (Kuhn et al. 2011), little attention has been paid to diversity patterns found within the ecotones between aspen patches and the surrounding habitat. Relatively few studies have documented patterns of herbaceous species

distribution across low-elevation ecotones, such as the aspen treeline ecotones in Lac du Bois. Hylander (2005) suggests that anthropogenic forest edges, sometimes compared with naturally occurring ecotones, may be optimum habitats for some organisms when there is a trade-off between moisture and sunlight, for example, due to intermediate conditions offered by the edge environment. The ecotones between the aspen patches and the grassland may offer a similar intermediate habitat.

In forest edges, the herbaceous community often represents the largest component of plant diversity (Matlack 1994; Bossuyt et al. 1999). The spread of herbaceous plants across forest ecotone boundaries is influenced by individual species' ecological tolerances (specifically soil pH, moisture, and canopy closure conditions), competitive hierarchies, storage within seed banks, dispersal method (Foster & Tilman 2003) and local climatic variations (i.e., snow cover and wind patterns (Camarero et al. 2006)).

Within the interior of British Columbia, aspect has a strong influence and is visually obvious on a broader scale where vegetation cover differs greatly between northern and southern exposures. Here north-facing slopes are generally heavily forested, whereas south-facing slopes are often open grasslands with only sparse trees.

STUDY OBJECTIVES

The potential for ecotones to maintain high species diversity, their role in energy, gene and nutrient flows across a landscape, and their potential early sensitivity to climate change impacts increase their importance for the conservation of both plants and animals. The presence of an aspen-grassland mosaic within the upper reaches of Lac du Bois Grasslands Protected Area provides an opportunity to not only document species richness patterns across a

little examined ecotone (i.e., aspen-grassland), but also provides a natural laboratory in which to critically examine the effects of ecotone definition (statistical versus subjective), and experimental design approach (block versus gradient) on observed species richness patterns. Finally, the presence of aspen-grassland ecotones on both north- and south-facing slopes provides a unique opportunity to examine the universality of observed species richness patterns on ecotones differing in aspect within one system. This study will add to our understanding of ecotones in general and will specifically evaluate the following questions:

- 1) *Are ecotones more species-rich than surrounding areas in both north-and south-facing aspects?*
- 2) *What is the relationship between functional diversity and species richness across the grassland-aspen ecotones?*

This thesis is divided into four chapters, the introduction, two data chapters and one conclusion chapter. Chapter Two evaluates the evidence for the four competing hypotheses that could lead to increased species richness in ecotones with a functional plant approach. This chapter also defines ecotone centre location, boundaries and width using a statistical analysis based on the evaluation rate of change of species composition. Once the ecotones were identified, plant functional group richness and abundance were compared across grassland, ecotonal and forested habitats, separated by aspect.

Chapter Three compares how two methods used in ecotone research impact the results. In this chapter, ecotones and their attributes (plant functional group richness and abundance) that were defined using the statistical method used in Chapter Two were compared to ecotones defined by a structural, subjective approach. This subjective approach involves using a visually-defined

location (the treeline created by the boles of mature aspen) to identify the ecotone centres. This chapter also compares a blocked data treatment (used in Chapter Two) to a gradient treatment. Chapter Four discusses conclusions, future research suggestions and management implications related to ecotones.

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CHAPTER 2 TESTING THE ASSUMPTIONS: PLANT FUNCTIONAL GROUP RICHNESS AND ABUNDANCE ACROSS GRASSLAND-ASPEN ECOTONES IN LAC DU BOIS

INTRODUCTION

Within ecology, evolving definitions are not uncommon. Ecotones were first defined by Livingston (1903) as a “stress line connecting points of accumulated or abrupt change.” However, at the turn of the 21st century variable and non-exclusive use of the term “ecotone” led to a call for a consensus on ecotone definition in order to facilitate interpretation and comparison of different studies (Hufkens et al. 2009). Part of the ambiguity surrounding the use of the term ecotone undoubtedly arises from the multiple causes and origins of these ecological boundaries; ecotones can arise from either anthropogenic or non-anthropogenic causes, occur in diverse landscapes and can be found at widely varying spatial and temporal scales (Risser 1995). Ecotone characteristics such as width and species richness can also vary in response to aspect, solar radiation, wind patterns, precipitation and grazing (Harper & MacDonald 2001; Harper et al. 2005; Hylander 2005; Orczewska & Glista 2005).

Variably referred to as edges, borders, or interfaces (Danz et al. 2012), ecotones have been delineated using a variety of approaches (Lloyd et al. 2000; Harper & MacDonald 2001; Walker et al. 2003; Hufkens et al. 2009; Senft 2009), yet characterization of ecotones remains contentious. Attempts to characterize ecotones have included both boundary delineation as well as ecotonal community descriptions. As ecotones can rarely be delineated by a fine line, identifying the boundary of ecotones is complex (Fortin et al. 2000; Erdős et al. 2011; Kark 2013). While numerous ecotone studies have used subjective or poorly documented

means to identify boundaries, such as changes in vegetation height, there has been an increasing reliance on the use of statistical methods to objectively identify the ecotonal community boundaries (Chen et al. 1996; Fortin et al. 2000; Walker et al. 2003; Hennenberg et al. 2005). Of the multiple methods used (see Hufkens et al. 2008 for a review), one objective approach uses the moving window regression (Cornelius & Reynolds 1991; Fortin et al. 2000; Walker et al. 2003; Hennenberg et al. 2005; Kent et al. 2006).

Moving window regression allows for the objective identification of ecotone centres and boundaries from which analysis of species and functional group richness can be completed (Walker et al. 2003). This analysis identifies the midpoint of an ecotone by regressing the ordination scores of species composition measured along transects. The peak in the first axis ordination scores identifies the midpoint of the ecotone and the inflection points along the second ordination scores delineate the boundaries of the ecotone. In this way ecotones are defined based on a statistical change in species composition rather than being defined by a visual change such as a treeline. Proponents of this statistical approach argue that this helps to standardize ecotone research and allow for comparisons between very different systems in an effort to articulate general ecotone characteristics (Fortin et al. 2000; Walker et al. 2003). The moving window approach allows for repeatable and comparable ecotone definition, but requires intensive sampling methods. As a result, ecotone studies using this approach are often based on relatively small sample sizes which could lead to potentially misleading results and conclusions about the general characteristics of ecotones (Luczaj & Sadowska 1997; Lloyd et al. 2000; Walker et al. 2003; Orczewska & Glista 2005).

Although there is little consensus regarding which specific method is best to define, delineate or characterize ecotones, few doubt the importance of

ecotones as landscape elements (Murcia 1995; Kark 2013). The potential of ecotones to contain high species diversity coupled with their role in the flow of energy, nutrients, and genes have led to the argument that ecotones are important for conservation of species and habitat (Risser 1995; Erdős et al. 2011). For instance, Hylander (2005) suggests that even anthropogenic ecotones – such as agricultural edges – are optimal habitat for species with a preference for intermediate conditions. Although ecotones have garnered considerable attention for both conservation and theoretical reasons, there has been little research completed to address assumptions about specific characteristics such as richness, diversity or uniqueness (di Castri et al. 1988; Walker et al. 2003; Kark & Rensburg 2006).

In one of the few studies to explicitly evaluate the high species richness of ecotones, Senft (2009) identified four separate hypotheses that had been proposed to explain increased species richness in ecotones:

- I. Increased environmental heterogeneity leading to increased species packing
- II. Spatial mass effect leading to increased richness/diversity within ecotones
- III. Animal seed predation and dispersal impacts plant richness
- IV. Easily dispersed generalists and exotics lead to increased richness

Although Senft (2009) found little evidence for increased richness in anthropogenic ecotones between deciduous forest and a mowed meadow, she analyzed only composite community-level response variables such as species richness and diversity. When patterns in ecotone species richness are examined using only taxonomic-based response variables (Mast et al. 1997; Bossuyt et al. 1999; Sabo et al. 2005; Kark & Rensburg 2006), the differential response of different plant functional groups may be swamped by opposing

responses of species within the same taxonomic group. Certainly, as a community-level response variable, species richness will provide little information about what ecological factors could be driving shifts (or lack thereof) in species richness across ecotones.

However, a plant functional group approach that allows for the examination of a large number of organisms and their interaction with environment factors (Garnier & Navas 2012) could help to distinguish between the competing hypotheses identified by Senft (2009), as potential drivers of species richness within ecotones (Table 2.1). For instance, spatial mass effect is defined as the addition of propagules from adjacent systems into an area where the adult plants generally do not survive to reproduce (Shmida & Wilson 1985). The influence of spatial mass effect on patterns within the ecotone could be evaluated using *a priori* defined functional groups composed of indicator species from adjacent habitats. The impact of animal seed predation and/or dispersal can be measured by the analysis of the richness of seed type functional groups across an ecotone. Likewise, comparing the number of exotic versus native functional groups in ecotones and adjacent habitats would provide evidence for the importance of easily-dispersed species in ecotone communities. The final ecological process hypothesized to lead to higher richness in ecotones is increased environmental heterogeneity. Evidence for this process could be detected by examining species or functional group turnover within the ecotone boundary. In addition, evidence for this hypothesis could be collected if high rates of species composition change are used as a proxy for increased species packing. Then high species richness would be predicted to occur in the same locations where high species composition change occurred. In general, functional group analyses may allow generalization of observed findings rising above the taxonomic specifics of a

single locality (Herault & Honnay 2007).

Although many studies have investigated conifer or riparian ecotones (Maher et al. 2005; Mason et al. 2005; Sabo et al. 2005; Danby & Hik 2007; Bai et al. 2011; Griesbauer et al. 2011), few studies have examined species richness over aspen-grassland ecotones. The importance of grassland and aspen patches as separate reservoirs of diversity and critical habitat is well recognized for both plants and animals (Oaten & Larsen 2008; Kuhn et al. 2011). In British Columbia (BC), grasslands form a unique and important habitat for many species and are home to 42% of the province's 2854 vascular plants species including many red and blue listed species, even though they only cover about 1% of the province (Wikeem & Wikeem 2004; Lee 2011). Likewise, aspen stands in western North America have been described as "keystone ecosystems" for native plant and animal diversity (Stohlgren et al. 1997; Campbell & Bartos 2001; Swanson et al. 2010; Kuhn et al. 2011).

Aspen-grassland mosaics in the southern interior of BC provide an opportunity to document species richness patterns across a little examined ecotone. Furthermore, the presence of north- and south-facing aspen-grassland ecotones allow for the evaluation of the universality of the observed results across ecotones differing in a fundamental characteristic within one system. Using the moving-window regression approach to statistically identify ecotones, this chapter evaluates the following questions: 1) *How does species richness and abundance of functional groups (taxonomic, shade tolerance, growth form, dispersal method, status, drought tolerance and habitat indicator species) vary over grassland-aspen ecotones?* 2) *How do the observed patterns vary across north- and south-facing ecotones in the same system?*

Table 2.1 Processes (after Senft 2009), predictions and potential evidence that could be used to test individual predictions correlating with potential species and functional group richness patterns across the ecotones. Evidence gathered in this study is bolded.

Processes	Testable predictions	Evidence gathered
1. Increased environmental heterogeneity leads to increased species packing (Auerbach & Shmida 1987)	<p>1a. Ecotonal area will have increased species turnover compared to adjacent habitats</p> <p>1b. Competitive effects will be reduced under ecotonal conditions compared to adjacent habitats</p> <p>1c. Germination rates will be higher under ecotonal conditions</p>	<p>1a. Use rates of high species composition change as a proxy for species packing. Analyze if species richness highest in these areas of high species turnover.</p> <p>1b. Analyze how dominance varies between belt types</p> <p>1c. Compare soil seed banks in ecotones and adjacent habitats.</p>
2. Spatial mass effect: the addition of propagules from adjacent systems into an area where the adult plants generally do not survive to reproduce (Shmida & Wilson 1985)	<p>2a. Ecotone habitat will have increased richness and/or abundance of grassland-associated species than forest habitats, and increased abundance of forest-associated species than adjacent grassland areas.</p> <p>2b. Ecotonal areas will have higher richness of forest seeds than grasslands; and higher richness of grassland seeds than forested areas.</p>	<p>2a. Richness and abundance of grassland or aspen indicator species compared across ecotones and adjacent habitats.</p> <p>2b. Seed bank study across ecotones.</p>
3. Animal seed distribution/predation will impact species richness in ecotones. (Willson & Traveset 2000; Russo et al. 2006; Vazquez et al. 2009)	<p>3a. Ecotonal areas will have a greater richness and/or abundance of animal-dispersed species than adjacent habitats.</p> <p>3b. Ecotonal areas will have higher richness and/or abundance of animals and invertebrates than adjacent areas.</p>	<p>3a. Richness and abundance of seed dispersal functional groups compared across ecotones and adjacent habitats.</p> <p>3b. Animal sign/trapping across ecotones and adjacent habitats</p>
4. Generalist and exotics which are easily dispersed lead to increased richness (Vavra et al. 2007)	4a. Ecotones contain a greater richness and/or abundance of exotics and generalists than adjacent areas.	4a. Richness and abundance of exotic and functional group generalist species compared over ecotones and adjacent habitat types.

METHODS

STUDY AREA

The study area is located on the traditional territory of the Tk'emlúps te Secwépemc in the BC Southern Interior Plateau, near the city of Kamloops. This plateau is in the rain shadow of the coast mountains and experiences hot, dry summers with an average annual temperature of 6.4°C (Vyse & Clarke 2000; Wikeem & Wikeem 2004). The southern interior of BC is characterized by rolling grasslands dotted with sagebrush (*Artemisia tridentata* (Nutt.)) and ponderosa pine (*Pinus ponderosa* (C. Lawson)) at lower elevations, and Douglas-fir (*Pseudotsuga menziesii* (Mirb.)) and lodgepole pine (*Pinus contorta* (Douglas ex Louden)) forests at higher elevations. Topography has a strong influence within this region. Moisture increases with elevation creating distinct vegetation bands and lower treelines. Aspect also influences the elevation of treelines where trees grow at lower elevations on northern slopes than on southern slopes. Within the interior plateau, grasslands are divided into three elevational bands where the upper grassland (850-975 m) is the wettest and coolest (Tisdale 1947; Wikeem & Wikeem 2004).

The study site is located in the Lac du Bois Grasslands Protected Area and adjacent Nature Conservancy of Canada property about 30 km north of Kamloops, BC. This upper grassland matrix receives approximately 190 mm rainfall during the growing season, and the average temperature during this period is 11.5°C (Vyse & Clarke 2000). This grassland matrix is bordered at the upper edge by the Douglas-fir treeline. The study site includes the lower edge of the IDFxh2 and the top edge of the BGxw1 biogeoclimatic zones (Vyse & Clarke 2000) and the soils in this zone are classified as sandy loam to loamy sand (Lee

2011).

Aspen patches within Lac du Bois Grasslands Protected Area are primarily found in the upper grasslands matrix where they tend to be associated with moist depressions or gullies, and north facing slopes (Ryswyk et al. 1966; Vyse & Clarke 2000; Giesbrecht 2011). Small aspen patches, ranging from approximately 2500 m² to 38000 m², are found throughout this upper grassland, creating ecotones where these two systems meet. These aspen stands range in age from approximately 24 to 148 years old (Jones et al. 2015). Common species within the aspen stands include common snowberry (*Symphoricarpos albus* (L.)), prickly rose (*Rosa acicularis* (Lindl.)), saskatoon (*Amelanchier alnifolia* (Nutt.)), wild strawberry (*Fragaria virginiana* (Duchesne)) and common harebell (*Campanula rotundifolia* (L.)). The upper grassland matrix in this area is characterized by Kentucky bluegrass (*Poa pratensis* (L.)), bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh)), rough fescue (*Festuca campestris* (Rydb.)), yellow salsify (*Tragopogon dubius* (Scop.)), timber milk vetch (*Vicia americana* (Muhl. ex Willd.)) and arrowleaf balsamroot (*Balsamorhiza sagittata* (Pursh)) (Vyse & Clarke 2000; Jones et al. 2015).

Historically, this area was intensively grazed by sheep and cattle, and was home to approximately 200 people in the early 1900s, but it is now parkland with no human inhabitants, limited human use and minimal cattle grazing (Vyse & Clarke 2000; Lee 2011). Air photo analysis indicates that the aspen patches in the Lac du Bois area have expanded over the last thirty years, likely as a result of decreased human use (Alan Vyse, personal communication 2013).

Site Selection

Satellite imagery was used to identify aspen stands within the Lac du Bois grasslands (Google Earth, 2012). Aspen stands were chosen randomly and visited to assess suitability; rejection criteria included stand size and proximity to roads

and fences. Only those forest patches that were large enough to accommodate 30 meter transects placed perpendicular to the edge were included in the study; none of the transects crossed the patch centres at suitable sites. The length of the transect was chosen based on previous studies and constrained by the average aspen stand size available (Kunin 1998; Walker et al. 2003; Orczewska & Glista 2005; Senft 2009). Each transect extended 15 m into the grassland and in order to ensure that transects were longer than the average tree height (16m), each transect extended 20 m into the forest. Pure aspen stands were selected to minimize the impact that other tree species might have on the understory, although the presence of some non-target species seedlings was unavoidable. Forest patches which were smaller than 0.25 ha were rejected, to minimize the influence of nearby edges. Sample site locations and characteristics are summarized in Table 2.2.

STUDY DESIGN

Vegetation Sampling

Within each study site 10x35 m sampling grids were established perpendicular to the structural edge of the forest, between June and September 2012. Each transect extended 20 m into the aspen patch and 15 m into the grassland (Figure 2.1). In order to record the pattern of understory vascular plant species occurrence across each ecotone, species presence and abundance was measured in three 1x1 m plots within each 1x10 m belt transects, located at the centre and at each edge. Abundance was measured using percent cover within the plots. Mean values for all data collected in each 1x10 m belt was used in the analysis. Each plot was examined for percent cover of non-vascular plants; however these were not identified to species but were recorded as a group. Tree seedlings and saplings were recorded within the plots and along each belt, and tree canopy in each belt was recorded. Plant identification was confirmed using

the Illustrated Flora of British Columbia (Douglas et al. 1998-2000). See Table 2.3 for terminology used in this study.

Soil moisture and pH

To relate understory species occurrence across ecotones to environmental attributes, moisture and pH data were measured within each plot. Soil moisture along each transect (measured using a 12 cm probe, Field Scout TDR 300 Soil Moisture Meter, Spectrum Technologies, Illinois) was evaluated as each transect was surveyed. This data was collected within a half hour period to minimize temporal variations in evaporation or drainage. As biotic processes and forest canopy can alter soil chemistry (Finzi et al. 1998), the pH of mineral soil exposed in each 1x1 m plot was determined using a Hellige-Truog Soil pH Test Kit. Soil samples were collected in the same 1x1 m plots in which the herbaceous species data was gathered.

Functional groupings

Vascular plant species were categorized into functional groupings based on shade tolerance, growth form, dispersal mode, origin status, drought tolerance and indicator status (Table 2.4). Functional group information for each plant species was gathered from USDA Plants, E-Flora BC and Kew Gardens (Klinkenberg 2013; Royal Botanic Gardens Kew 2015; USDA, NRCS 2015). Abundance data for plant functional groups was calculated by summing the percent cover (rounded to 1%) of all species within each functional group, sampled in the 1x1 m quadrat (Krebs 1999).

Table 2.2 Transect locations and characteristics of measured transects. Azimuths were measured from forest to grassland.

Aspect	Transect	Azimuth	Coordinates (UTM) 10U	Elevation (m)	Aspen stand dimensions (m)	
					Maximum Length	Maximum width
North	2	335	10U 680059E 5629572N	912	102	51
	4	18	10U 679694E 5631522N	915	123	62
	6	24	10U 680538E 5630655N	946	328	54
	8	36	10U 680470E 5632016N	964	184	55
	9	46	10U 680312E 5631975N	954	205	83
	11	20	10U 680259E 5632202N	964	299	92
	12	27	10U 680343E 5632290N	975	299	92
	17	20	10U 680750E 5631993N	1000	259	160
	18	10	10U 680637E 5631962N	981	259	160
	19	44	10U 680678E 5632210N	993	202	74
<i>Mean±SD</i>				960.4±29.7	226±76.0	88.3±40.7
South	1	172	10U 680077E 5629491N	909	102	51
	3	217	10U 680089E 5630246N	927	138	53
	5	230	10U 680641E 5630579N	958	328	54
	7	226	10U 680405E 5631835N	948	196	71
	10	220	10U 680249E 5632239N	965	299	92
	13	256	10U 680588E 5632094N	980	192	65
	14	220	10U 680554E 5631860N	969	276	244
	15	198	10U 680603E 5631778N	972	276	244
	16	222	10U 680633E 5631743N	974	276	244
	20	218	10U 680223E 5631923N	947	205	83
<i>Mean±SD</i>				954.9±22.6	228.8±73.6	120.1±86.5

Table 2.3 Sampling terminology used in this study.

Term	Description
Transect	Sampling zone laid out perpendicular to aspen treeline. Each transect is 10x35 m and is made up of 35 1x10 m belts. 20 transects were sampled.
Belt	Contiguous 1x10 m sections of the transects, each running parallel to the treeline.
Plot	1x1 m plot were located systematically at 1, 4.5 and 9 m across each belt. 2100 plots were sampled.

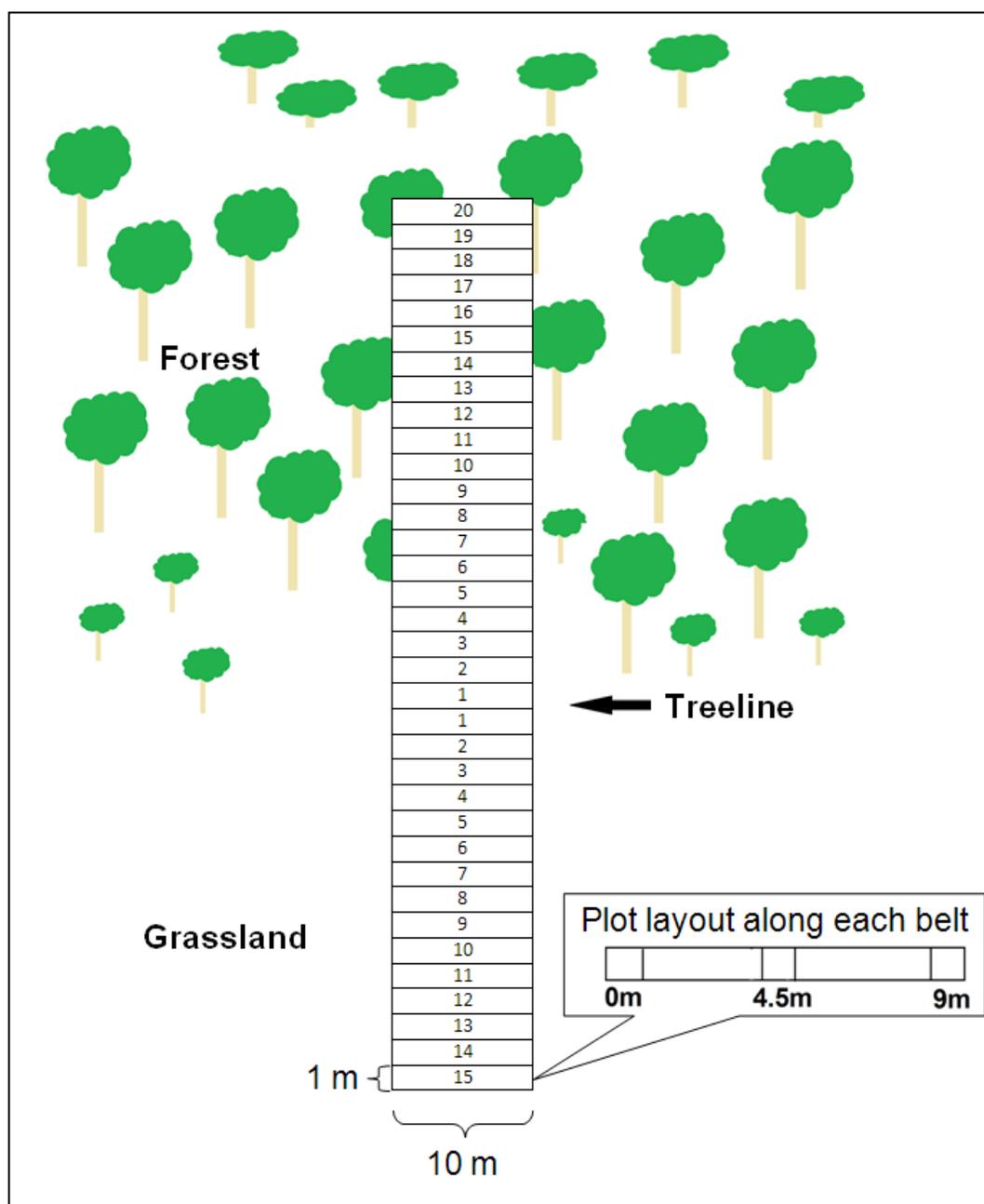


Figure 2.1 Transects were composed of 35 contiguous 1x10 m belt transects, oriented perpendicularly to the treeline. Within each 1x10 m belt transect, the abundance of herbaceous species, soil pH and moisture was recorded in three 1x1 m plots systematically located at 0, 4.5 and 9 m from the transect edge.

Table 2.4 Functional groups and specific categories used in this study, and related *a priori* hypotheses that may explain results.

Functional group	Categories	Related <i>a priori</i> hypothesis
Shade Tolerant Groups	Tolerant/Intermediate/ Intolerant	Increased species packing
Growth Form Groups	Forb/Graminoid/Shrub/Tree sapling	Increased species packing
Drought Tolerant Groups	Tolerant/Intermediate/ Intolerant	Increased species packing
Indicator Species Groups	Aspen stand/Grassland	Spatial mass effect
Dispersal Method Groups	None/Wind/Animal/Generalist	Animal dispersal impact richness
Status Groups	Native/Exotic	More exotics lead to increased richness

DATA ANALYSIS

Ecotones were defined statistically using the moving window regression method to identify areas of rapid change in species composition as measured by mean abundance in 1x1 m plots sampled within each belt (Walker et al. 2003). Ecotone boundaries were defined using the first and second derivatives of ordination scores (first axis) based on species abundance data (Kark & Rensburg 2006). Non-metric multidimensional scaling (NMDS) was used to characterize variation in species composition along each transect with the Bray-Curtis dissimilarity. Species that occurred less than twice along each transect in question were omitted from this analysis to reduce the impact of rare species on the ordination and to improve interpretability of ordination results. All data were checked for homogeneity of variance and normality, and transformed as needed for analysis. To evaluate the relationship between belt type and functional group richness and abundance, normal linear regression was used with functional group richness and abundance logarithmically transformed (where necessary) and belt

type (grassland, ecotone, forest) entered as a categorical variable in the model.

In order to statistically define the center of each ecotone, ordination scores of each belt were regressed against the distance along the transect. Ecotone centers were identified as the location of maximum rate of change in species composition which can be observed as “peaks” in the regression slopes. To determine the width of each ecotone, a second moving window regression was performed on the rates of change (slopes) of the first regression analysis. In this second analysis, the inflection points of the second regression identifies the boundaries of the ecotone within each transect (Figure 2.2, Walker et al. 2003). As window widths used in the analysis can influence the outcomes, regressions with window widths ranging from five to eight belts wide were used to find the clearest peaks and valleys in the regressions, before adopting a standard moving window size of 5 m. The moving window analysis is represented graphically in Figure 2.3.

Associations of environmental and plant functional group variables with ecotone and adjacent habitats were evaluated using generalized linear models. Models incorporated transect as a blocking variable and belt type (grassland, ecotonal, forested) as a categorical variable, using specific planned comparisons (ecotone: grassland and ecotone: forest) rather than all pairwise comparisons. In order to simplify interpretation, analyses were completed separately for all north- and south-facing transects, regardless of ecotone definition. When completing the moving window analyses five of the transects did not have a single clearly defined ecotone, as a result all analyses were completed using the data from all twenty transects (all transects) and then again using only the fifteen with clearly defined ecotone centres (acceptable transects).

Two different measures of alpha diversity are reported: 1) mean plot richness averaged from all plots within a belt and 2) total species richness derived

from plots and visual surveys of belts. Comparison of species richness and abundance among belt types were made using the functional groupings. Linear models compared abundance and richness of functional groups in statistically defined ecotone belts versus forested and grassland belts, with transect as a blocking variable and belt type as a categorical variable in each model with north and south aspects analyzed separately.

RESULTS

ECOTONE DEFINITION

A standard moving window size (5 m) was used throughout the study to ensure comparisons were equal. Although most transects showed a secondary peak in the first ordination plot, the majority of those were minor and were not considered separate ecotones. Table 2.5 outlines the results of the moving window analysis used to define ecotone centres and boundaries. Ecotone widths ranged from 5 to 10 m; where the mean width at north-facing aspects was 6.1 m and 6.6 m at south-facing aspects. Eleven of the twenty ecotone centres sampled were located in the grassland; eight were located inside the aspen canopy and only one ecotone directly straddled the structural treeline (Table 2.5). The majority of ecotone centres were not equidistant from ecotone boundaries; often the centres were skewed towards one boundary or the other.

Transects marked with asterisks (numbered 2,3,7,8 and 11) did not display a single clear peak using the moving window analysis (Table 2.5). As the results did not differ substantially between the full data set and the “acceptable” transects, I discuss only the results from ecotones with clearly identifiable centres and boundaries. However, results from the analysis of all sampled transects can be found in Appendix A (Tables A.1, A.2 and A.3).

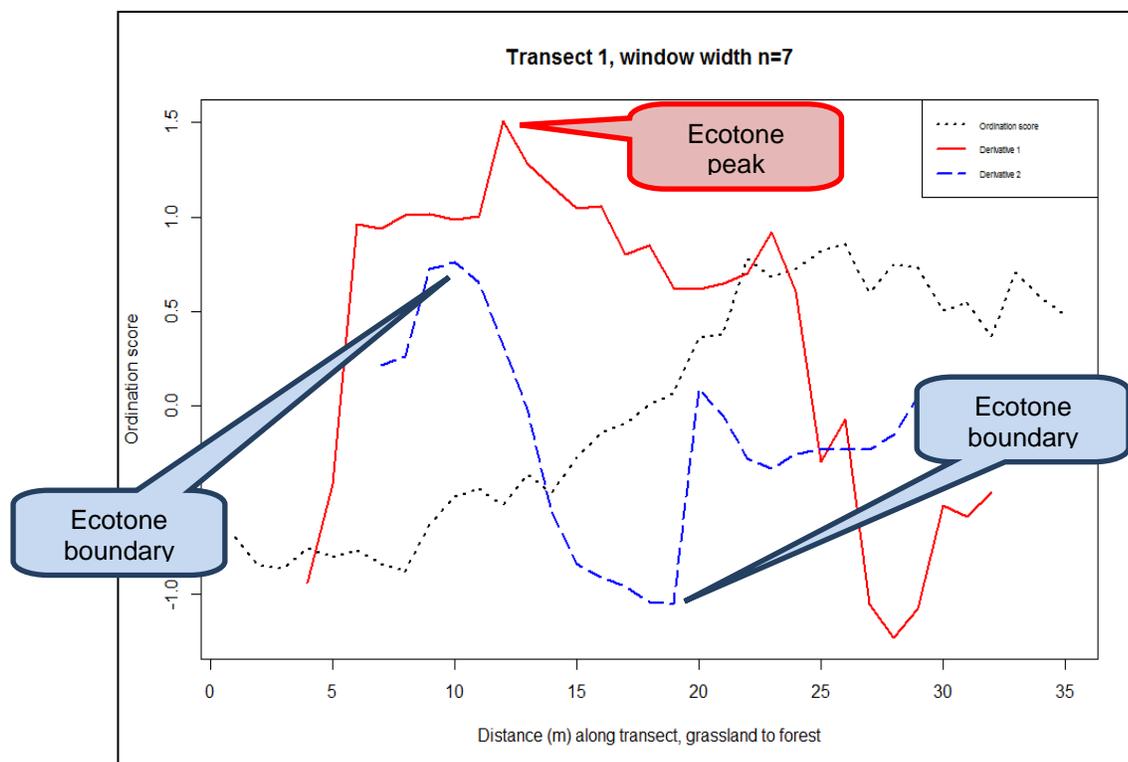


Figure 2.3 Illustration of ecotone boundaries as identified by the moving window analysis. The dotted line shows the ordination score of the change in species composition over the transect. The ecotone peak, or centre, is defined by the first derivative of the ordination (Bray-Curtis dissimilarity) score measuring species turnover along each transect. The boundaries are defined by the second derivative of the ordination score.

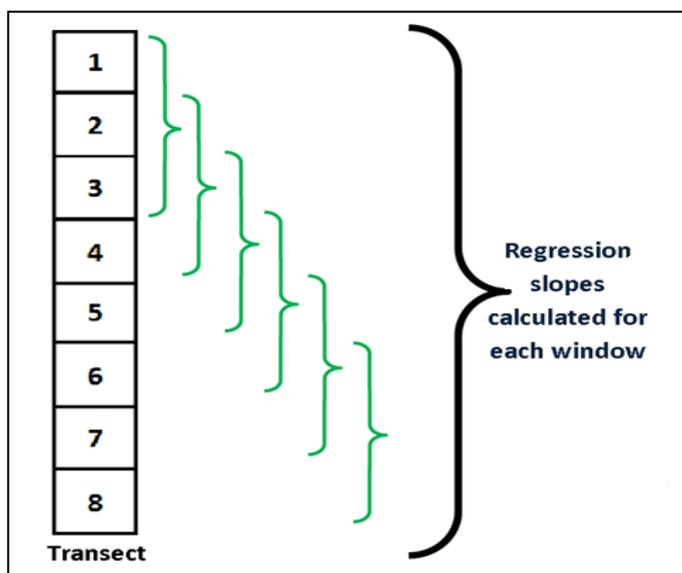


Figure 2.2 Graphical representation of the moving window analysis.

Table 2.5 Ecotone identification (centre, width, belt boundaries) based on moving window results. Transects number 2,3,7,8 and 11 (marked with asterisks) did not yield clear results. Belts are numbered from grassland into forest (0 to 35) with the treeline falling between belt number 15 and 16. Lac du Bois Grasslands Protected Area, Kamloops, BC, 2012.

Aspect	Transect ID	Clear primary peak(s) in ordination scores	Ecotone centre location (belt number) ¹⁾	Ecotone centre under forest canopy	Ecotone width (metres) ²⁾	Ecotone belt boundaries (metres)	Belt number of secondary peak(s) (metres)
North	2*	no	19	Yes	7	18-24	many
	4	yes	22	Yes	7	20-26	31
	6	yes	6	No	5	5-9	19
	8*	no	8	No	6	5-10	29
	9	yes	11	No	5	10-14	29
	11*	no	30	Yes	5	25-31	13, 23
	12	yes	17	Yes	9	16-24	8
	17	yes	14	Marginal ³⁾	6	13-18	23
	18	yes	11	No	5	9-13	6
19	yes	8	No	6	6-11	23	
South	1	yes	11	No	6	9-14	24
	3*	no	11	No	10	9-18	30
	5	yes	7	No	10	6-15	20
	7*	no	24	Yes	10	20-29	9, 17
	10	yes	10	No	7	8-14	25
	13	yes	23	Yes	5	21-25	8
	14	yes	28	Yes	7	24-30	7
	15	yes	8	No	5	6-10	29
	16	yes	11	No	5	9-13	27, 30
20	yes	27	Yes	8	23-30	9, 15	

1) As defined by regressing the first ordination scores with distance using the moving window analysis (NMDS)

2) As defined by regressing the second ordination scores with distance using the moving window analysis

3) Ecotone center located at structural edge

SOIL DATA AND NON-VASCULAR PLANT SPECIES

Based on linear models ($lm = \text{soil moisture} \sim \text{belt.type} + \text{transect}$) soil moisture did not vary significantly between ecotones and grasslands, or ecotones and forests for either north or south aspects (Table 2.6). Soil pH generally increased, in all cases, away from the ecotone, however none of these results were significant (Table 2.6). Although there is a general trend of increasing abundance (as measured by percent cover) of non-vascular plants (terrestrial mosses and lichens) in grassland and forest belts as compared to ecotonal belts, none of the results were significant (Table 2.6).

Table 2.6 Results from generalized linear models of acceptable transects comparing canopy cover, soil moisture, soil pH and non-vascular plant species abundance in statistically-defined ecotonal belts versus forested or grassland belts, with transect as a blocking variable and belt type as a categorical variable in each model ($lm = \text{variable} \sim \text{belt.type} + \text{transect}$).¹

Variable	North-Facing Ecotones				South-Facing Ecotones			
	Forest-Ecotone		Grassland-Ecotone		Forest-Ecotone		Grassland-Ecotone	
	Δ in intercept	<i>p</i> value	Δ in intercept	<i>p</i> value	Δ in intercept	<i>p</i> value	Δ in intercept	<i>p</i> value
Canopy cover								
Tree	neg	0.128	pos	0.012	neg	<0.000	pos	0.125
Intermediate	neg	0.406	pos	0.596	neg	0.059	neg	0.757
Shrub	pos	0.517	pos	0.396	neg	0.315	neg	0.587
Soil moisture	pos	0.938	neg	0.107	neg	0.341	pos	0.593
Soil pH	neg	0.113	neg	0.225	neg	0.341	pos	0.593
Non-vascular plants	neg	0.620	neg	0.499	pos	0.207	neg	0.174

¹Change in intercept indicates the direction of change in the variable from ecotonal to adjacent belts (i.e., at north-facing transects there is significant more tree canopy cover in ecotone belts than grassland belts). North and south transects are analyzed separately and *p* values in bold are statistically significant ($p < 0.05$).

FUNCTIONAL GROUP RICHNESS

Overall, the results of the general linear models did not support the assumption that ecotones are more species rich than adjacent habitats (Table 2.7).

However, the richness of individual functional groups did vary significantly when ecotonal belts were compared to adjacent belts. When compared to adjacent forests, south-facing ecotones had greater species richness of those functional groups expected to be associated with grasslands (i.e., shade intolerants, graminoids, wind and generalist dispersers, intermediate drought tolerants and grassland indicators). South-facing ecotones, when compared to adjacent forests, also exhibited a decline in the species richness of forest-associated groups such as shrubs and drought intolerants (Table 2.7). However, when south-facing ecotones were compared to adjacent grasslands, all significant comparisons identified a lower species richness of as rarely occurring species, forbs, and drought intolerants in the ecotone belts.

Within north-facing ecotones, many functional groups expected to be associated with grasslands (i.e., shade intolerants, graminoids, wind dispersed species and drought tolerants) displayed greater richness in ecotonal habitats than in adjacent forested habitats. Also within north-facing ecotones, there was significantly higher species richness of drought intolerants, trees, and generalist dispersers as compared to adjacent forests. When north-facing ecotones were compared to adjacent grasslands, the richness of forbs and shrubs were higher in the ecotone than in the adjacent grassland.

FUNCTIONAL GROUPS ABUNDANCE

Functional group abundance analysis yielded far fewer significant comparisons than the richness analysis (Table 2.8). In contrast to the richness data, the majority of significant comparisons showed decreased abundance within ecotone belts compared to both grassland and forest belts.

Within north-facing ecotones, there was significantly lower abundance of shrubs within ecotone belts as compared to forest belts, but a higher abundance of

drought intolerants. When north-facing ecotones were compared to adjacent grasslands, shade intolerants and generalist dispersers exhibited a lower abundance and intermediate-shade tolerants exhibited a higher abundance.

When south-facing ecotones were compared to adjacent forests, there was lower abundance of aspen-associated groups (shade tolerants, shrubs and aspen indicators) as well as animal dispersers within ecotone belts compared to forest belts. There was a greater abundance of grassland indicators within south-facing ecotone belts as compared to forest belts. When the same south-facing ecotones were compared to adjacent forests, only the abundance of rare species was higher in the ecotone.

Table 2.7 Results from generalized linear models of acceptable transects, comparing richness of functional groups in statistically-defined ecotone belts versus forested and grassland belts, with transect as a blocking variable and belt type as a categorical variable in each model (lm=variable~belt.type+transect).¹

Variable	North-facing Ecotones				South-facing Ecotones			
	Forest-Ecotone		Grassland-Ecotone		Forest-Ecotone		Grassland-Ecotone	
	Δ in intercept	<i>p</i> value						
Mean species richness	neg	0.407	pos	0.373	pos	0.326	pos	0.060
Total species richness	pos	0.826	pos	0.212	pos	0.061	neg	0.958
Rare species	pos	0.387	pos	0.967	pos	0.718	neg	0.026
Shade Tolerant Groups								
Tolerant	pos	0.840	pos	0.635	neg	0.415	neg	0.789
Intermediate	pos	0.671	pos	0.484	neg	0.415	pos	0.687
Intolerant	pos	0.001	neg	0.549	pos	0.001	neg	0.053
Growth Form Groups								
Forb	pos	0.117	pos	0.035	pos	0.142	neg	0.042
Graminoid	pos	0.045	neg	0.708	pos	0.009	neg	0.591
Shrub	neg	0.126	pos	0.050	neg	0.034	pos	0.072
Tree sapling	pos	0.023	pos	0.706	pos	0.065	neg	0.823
Dispersal Method Groups								
None	neg	0.968	pos	0.566	pos	0.332	neg	0.530
Wind	pos	0.020	pos	0.506	pos	0.030	neg	0.111
Animal	pos	0.880	pos	0.336	neg	0.201	neg	0.974
Generalist	pos	0.049	neg	0.249	pos	0.009	neg	0.683
Status Groups								
Native	pos	0.186	pos	0.457	pos	0.050	neg	0.570
Exotic	pos	0.007	pos	0.716	pos	0.448	neg	0.096
Drought Tolerant Groups								
Tolerant	pos	0.013	pos	0.325	neg	0.122	neg	0.220
Intermediate	pos	0.263	neg	0.957	pos	0.032	neg	0.297
Intolerant	pos	0.022	pos	0.992	neg	0.016	neg	0.043
Indicator Species Groups								
Aspen	neg	0.174	pos	0.516	neg	0.004	pos	0.398
Grassland	neg	0.098	neg	0.357	pos	0.002	neg	0.305

¹Change in intercept indicates the direction of change in the variable in ecotonal belts compared to either the forested or grassland belts (i.e., at south-facing aspects, there is significantly lower richness of rare species in ecotone belts than grassland belts). North and south are analyzed separately and *p* values in bold are statistically significant ($p < 0.05$).

Table 2.8 Results from generalized linear models comparing abundance of functional groups in statistically-defined ecotone belts versus forested and grassland belts, with transect as a blocking variable and belt type as a categorical variable and belt type as a categorical variable in each model (lm=variable~belt.type+transect).¹

Variable	North-facing Ecotones				South-facing Ecotones			
	Forest-Ecotone		Grassland-Ecotone		Forest-Ecotone		Grassland-Ecotone	
	Δ in intercept	<i>p</i> value	Δ in intercept	<i>p</i> value	Δ in intercept	<i>p</i> value	Δ in intercept	<i>p</i> value
Rare species	neg	0.579	pos	0.395	pos	0.062	pos	0.017
Shade Tolerant Groups								
Tolerant	neg	0.482	pos	0.078	neg	0.030	neg	0.529
Intermediate	pos	0.526	pos	0.071	neg	0.350	pos	0.660
Intolerant	neg	0.829	neg	<0.000	neg	0.623	neg	0.487
Growth Form Groups								
Forb	pos	0.180	pos	0.283	pos	0.354	pos	0.427
Graminoid	pos	0.186	neg	0.127	pos	0.090	neg	0.099
Shrub	neg	0.018	pos	0.532	neg	0.010	pos	0.267
Tree sapling	pos	0.152	neg	0.334	pos	0.192	neg	0.179
Dispersal Method Groups								
None	neg	0.193	neg	0.615	neg	0.193	neg	0.615
Wind	pos	0.100	pos	0.130	neg	0.993	neg	0.389
Animal	neg	0.237	pos	0.645	neg	0.006	neg	0.883
Generalist	pos	0.255	neg	0.033	pos	0.100	neg	0.325
Status Groups								
Native	neg	0.363	neg	0.112	neg	0.894	pos	0.702
Exotic	pos	0.217	pos	0.974	neg	0.580	neg	0.680
Drought Tolerant Groups								
Tolerant	neg	0.644	neg	0.079	pos	0.601	pos	0.695
Intermediate	neg	0.468	neg	0.081	pos	0.528	neg	0.074
Intolerant	pos	0.044	pos	0.313	pos	0.316	pos	0.812
Indicator Species Groups								
Aspen	neg	0.174	pos	0.516	neg	0.004	pos	0.398
Grassland	pos	0.098	neg	0.357	pos	0.002	neg	0.305

¹Change in intercept indicates the direction of change in the variable in ecotone belts compared to either the forested or grassland belts (i.e., at south-facing aspects, there is a significantly greater abundance of rare species in ecotone belts compared to grassland belts). North and south are analyzed separately and *p* values in bold are statistically significant (*p*<0.05).

DISCUSSION

ECOTONE ATTRIBUTES

In general, ecotonal attributes were more variable than expected; the width and centre location of the ecotones varied broadly with no obvious pattern. Using the moving window method to identify multiple ecotones along a single long transect covering ground from a mangrove through a woodland to a pasture, Walker et al. (2003) identified two peaks in the rate of change of species composition relatively close to one another within the woodland-marsh interface. They considered these two peaks to signify a single ecotone due to their close proximity. Similarly, during the identification of the ecotones boundaries within this study there was often a second lesser peak in the rate of change of species composition found within the forested portion of the transect. This second peak indicates that there is a second sharp change in species composition that might suggest another ecotone within the forest, in addition to the more significant ones generally found closer to the edge.

Orczewska and Glista (2005), in a comparison of one north- and one south-facing ecotone, found that the south-facing forest ecotone was wider. Although the widest ecotones in this study were in fact south-facing, a *t*-test showed no significant difference in the overall widths between aspects ($p=0.146$). The mean width for south-facing ecotones was 7.3 m and 6.1 m for north-facing ecotones. The aforementioned study only compared two transects one north and one south, so it is hard to draw any strong conclusions. It seems that many ecotone studies involve relatively low sample sizes, likely due to sampling intensity needed to detect patterns (Murcia 1995). In this study the sample size was relatively large and so the results tended to encompass a large range of possible ecotone patterns,

leading to the conclusion that ecotone locations and width patterns are highly variable, and supporting the understanding that ecotones are not discrete lines on the landscape but rather a zone of rapid species turnover.

SOILS AND NON-VASCULAR PLANTS

Based on previous forest soil research (Rhoades 1997; Binkley & Giardina 1998), a difference in pH between forest soils and grassland soils was expected, largely due to influence of leaf litter and rainfall stemflow near tree trunks (Rhoades 1997). Tree species, litterfall quality and rainfall stemflow all influence surface soil pH (Binkley & Giardina 1998, Finzi, Canham & Breemen 1998). Soil pH showed no significant differences between habitat types. It is possible that the pH kit used was not sensitive enough, or that surface soil pH does not vary widely in this region. Surface soil pH might not be a good indicator of deeper soil biotic processes, since this layer of soil is susceptible to desiccation in summer and freezing in winter. Surface soil pH and deeper mineral soil pH may not be strongly correlated (Finzi et al. 1998). It is also possible that the influence of the forest cover on pH may extend much further than expected into the grassland.

FUNCTIONAL GROUP CHARACTERISTICS

The ecotones sampled in this study were not more species rich than the adjacent grasslands and aspen stands, regardless of aspect. These results add support to a growing number of ecotonal studies that question the assumption that all ecotones are species-rich (Van der Maarel 1990; Harper & MacDonald 2001; Walker et al. 2003; Senft 2009). Walker et al. (2003) also found little significant difference in species richness in ecotones and within their study only one of the five identified ecotones displayed greater species richness than the adjacent habitats. They also found this relationship to be scale-dependent; that is,

at a 1 m² scale the results were non-significant but at a 0.5 m² scale they were significant.

Four *a priori* hypotheses were identified to explain expected differences in functional group richness and abundance (Chapter 2, Table 2.1). The first hypothesis proposed that environmental heterogeneity could lead to increased species packing within ecotonal belts. In this study, high rates of species change were used as a proxy for species packing; increased species richness, therefore, was predicted to co-occur with the center of identified ecotones. Overall there was no significant difference in mean or total species richness at the ecotonal belts indicating that the location of the greatest species turnover does not coincide with increased species richness. This means that that even though the ecotone regions are zones of rapid species turnover, they are not necessary zones of increased richness (Table 2.7).

The second *a priori* hypothesis identified by Senft (2009) suggests that spatial mass effects would lead to increased richness. Spatial mass effects results when species dominating one habitat (e.g. aspen indicator species) would have higher richness in ecotones than in the habitat found on the opposite side of the ecotone (e.g., in the grassland). In this study, however, only one of the four relevant comparisons (i.e., grassland indicators compared in south-facing ecotones as compared to forests) showed increased richness and abundance (Table 2.7 and 2.8). This suggests that the influence of spatial mass effect in the ecotones sampled in this study is minimal.

The third *a priori* hypothesis suggests that animal seed dispersal or predation could explain differences in functional group richness and abundance within ecotones. Animal-dispersed seeds differed significantly in only one case: at south-facing ecotones where the abundance was lower than in adjacent forests

(Table 2.8). Some studies have cited higher diversity of bird-dispersed species (Kollmann 2000) and greater abundance of animal seed dispersers (Burgess et al. 2006) at forest edges. Animal-dispersed seeds can move great distances both inside and outside forest patches (Bossuyt et al. 1999), which might explain why there was very little difference found in richness of this functional group. However, wind dispersed species may be influenced by the structure of a forest canopy and edge (Devlaeminck et al. 2005; Kumar et al. 2006) and this is supported by the data; at both north and south transects there was a significant decrease in the richness of wind dispersed species in adjacent forest habitats (Table 2.7). Likewise, Baldwin and Bradfield (2005) noted that disturbance-associated bryophytes which have a high wind-dispersal capacity have higher richness in forest edges.

The final *a priori* hypothesis suggests the increased richness and abundance of exotic species within ecotones may explain expected patterns. In this study, this was supported only at north-facing transects where there was an increased richness of exotic species within ecotonal belts when compared with forested belts (Table 2.7). If a link between aspect, moisture and productivity is assumed this result correlates with the findings of Stohlgren et al. (1998) who found that riparian zones (a type of ecotone) contained an increase in exotic species compared to adjacent habitats. The authors of this study suggested that because riparian zones are highly productive, they are easily invaded by opportunistic exotics. However, the abundance of exotic species did not contribute to significant differences in species composition within these ecotones when compared to adjacent belt types; this agrees with the findings of both Senft (2009) and Walker et al. (2003).

INFLUENCE OF ASPECT

Based on the results of this study, the influence of aspect varied with the habitat type with which ecotones were compared. When ecotones were compared to adjacent forest, the majority of significant comparisons (15 out of 18 across both north- and south-facing aspects) indicated that ecotones contained a higher species richness of each functional group. Aspect was more important in the ecotone-grassland comparisons where significant comparisons indicated ecotones had higher species richness within functional groups on north-facing ecotones and lower species richness within functional groups on south-facing ecotones. A lack of aspect influence on the ecotone forest comparisons may be explained by the moderating effect of the forest canopy on solar radiation, drought and temperature (Rhoades 1997). But, in contrast, Hylander (2005) observed a strong influence of aspect on bryophyte community characteristics at forest edges. Some studies have found that edge zones between forest and meadow are wider on edges with higher solar exposure i.e., south aspects (Fraver 1994; Murcia 1995; Orczewska & Glista 2005).

CONCLUSION

Overall, the ecotones in this study were not more species rich than the adjacent grasslands and aspen stands, when considered using the moving window method to define boundaries. There were very few significant differences in species richness and functional group richness or abundance. In general, differences in functional group richness between ecotones and adjacent habitats did not support the four *a priori* hypotheses, with one exception; dispersal mode played a role in the difference in species richness between ecotones and forests. It would seem, that at least in this aspen-grassland matrix, assumptions about increased richness and abundance within ecotones are not supported.

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CHAPTER 3 TESTING THE METHODS: COMPARING STRUCTURAL AND STATISTICAL APPROACHES IN ECOTONE ANALYSIS

INTRODUCTION

It is increasingly clear that, in science, how we ask and answer questions influences the nature of our conclusions. Bogen (2014) argued that all aspects of research – experimental design, methods and data production – are strongly influenced by background assumptions about the subject under investigation. In ecology, differing assumptions have led to contradictory definitions even of such fundamental terms as “competition” and “interference”; these definitions took years of extensive debate to achieve consensus (Connolly et al. 2001). Beyond definitions, aspects of experimental design such as the choice of predictor and response variables, scale, and methods of ecosystem simplification can lead to conflicting conclusions from studies testing similar hypotheses even within the same communities (Gosz 1993; Murcia 1995; Pausas & Austin 2001; Erdős et al. 2011). Finally, competing statistical approaches can also lead to variable results.

An additional issue related to ecotones, specifically, is that they have been analyzed both as discrete blocks and as gradients between the surrounding habitats (Gosz 1993; Fortin et al. 2000). This difference in approach is not unlike the historic controversy between Gleason and Clements regarding plant communities (Clements 1916; Gleason 1926; Callaway 1997). Within ecotones, some species may respond to an ecotone as a discrete boundary (or a block), whereas some may respond as if it is a gradient (Harper & MacDonald 2001). With this in mind, it is important to examine the data from a gradient as well as a blocked approach.

In science we often strive to clearly categorize and simplify systems, but natural systems often do not fit within such discrete definitions (Erdős et al. 2011). With this in mind, this chapter will compare the analysis of Chapter Two (a blocked approach) with a gradient approach. This chapter will also compare the results when ecotones are defined subjectively to the results when ecotones are defined statistically as in Chapter Two. Although repeated analysis of the same dataset will increase the likelihood of finding significant results, in this case it was necessary to compare methods of ecotone definition.

The objective of this chapter is to address how ecotone definition and experimental approach affect observed patterns by asking these questions:

1) How does species richness and abundance of functional groups (taxonomic, shade tolerance, growth form, dispersal method, status, drought tolerance and habitat indicator species) vary over grassland-aspen ecotones? 2) How do the observed patterns vary across north- and south-facing ecotones in the same system?

METHODS

Methods follow Chapter Two for site selection, vegetation sampling, functional group classification and statistical identification of ecotones. The same dataset that was used in Chapter 2 is used here. This chapter compares alternative methods of ecotone definition and analysis, where ecotones have been defined either statistically as the location of the greatest species turnover, or structurally as the location of aspen patch treeline, and were analyzed either with a blocked approach similar to that used in Chapter 2 or with a gradient approach. When the data was analyzed as a gradient distance from treeline into forest or grassland was included as a continuous variable in the generalized linear models and the belts were not blocked together. Data was compared from the treeline outwards into the forested

belts or grassland belts for this approach.

BLOCKED APPROACH - STRUCTURALLY-DEFINED ECOTONES

The centres of structurally-defined ecotones were located at the treeline edge of aspen stands as defined by the presence of mature aspen boles. To allow for comparison of structurally-defined ecotones with the statistically defined ecotones in Chapter Two, I used the mean ecotone width identified by the moving window analysis (7 m) centred on the treeline. All belts falling within the ecotone boundaries were categorized as ecotone belts, while those on the forest side and grassland sides of the ecotone were categorized respectively as forest and grassland belts. To evaluate the relationship between belt type and functional group richness and abundance, I used normal linear regression with functional group richness and abundance logarithmically transformed (where necessary) and belt type entered as a categorical variable in the model. As the overall intent of this chapter is to compare the results that are found when ecotones are defined statistically or structurally, I limited the analysis of transects to those fifteen “acceptable” transects with clearly defined ecotone centers and boundaries (Chapter 2, page 34). However, results from the analysis of all sampled transects can be found in Appendix A (Tables A.4, A.5, A.6, A.7, A.8, A.9 and A.10).

GRADIENT APPROACH - STATISTICAL AND STRUCTURAL DEFINITIONS

The data was also analyzed from a gradient approach, in order to compare the effect of increasing distance from the centre of the ecotone. Each variable was compared using linear regression from the centre outwards. This analysis was repeated using both the statistically- and structurally-defined ecotone centres. In the case of the statistically-defined ecotone, the belt identified as the peak in species turnover was used as the ecotone centre and data was analyzed outward

into either the forest or the grassland. For the structurally-defined ecotone, the treeline created by the mature boles of the aspen trees was used to identify the centre. Again, all data was analyzed outwards into the forest or grassland. To evaluate the relationship between distance from ecotone centre and functional group richness and abundance, I used normal linear regression with functional group richness and abundance logarithmically transformed where necessary.

RESULTS

BLOCKED APPROACH, STRUCTURALLY-DEFINED ECOTONES

Canopy cover and Soil Data

As might be expected, canopy cover was significantly higher in structurally-defined ecotone belts when compared to grassland belts on both north- and south-facing aspect (Table 3.1). In comparison soil moisture and soil pH in ecotones did not differ significantly from that found in either forest or grassland belts.

Functional Group Richness and Abundance: Blocked Approach, Structurally-Defined Ecotones

As in Chapter Two, the results from this analysis did not find general support for the assumption that ecotones are more species rich than adjacent habitats (Table 3.2); however, statistically significant differences in total species richness were found in the comparison of south-facing structurally-defined ecotonal and grassland belts.

Overall, comparison of individual plant functional group richness between ecotone and grassland belts varied with aspect (Table 3.2). This pattern is consistent with that observed in Chapter Two (p. 34). On south-facing transects, ecotone belts had lower total richness than adjacent grassland belts as well as lower richness in functional groups expected to be associated with grasslands: shade intolerants,

Table 3.1 Results from generalized linear models comparing canopy cover, soil moisture and soil pH in structurally-defined ecotone belts versus forested or grassland belts, with transect as a blocking variable and belt type as a categorical variable in each model (lm=variable~belt.type+transect).¹

Variable	North-facing Ecotone				South-facing Ecotone			
	Forest-Ecotone		Grassland-Ecotone		Forest-Ecotone		Grassland-Ecotone	
	Δ in intercept	<i>p</i> value	Δ in intercept	<i>p</i> value	Δ in intercept	<i>p</i> value	Δ in intercept	<i>p</i> value
Canopy cover								
Tree	pos	0.360	pos	<0.000	neg	0.008	pos	<0.000
Intermediate	neg	0.265	pos	0.495	pos	0.555	pos	0.008
Shrub	pos	0.682	pos	0.564	pos	0.653	pos	0.307
Soil moisture	pos	0.902	neg	0.075	neg	0.307	pos	0.171
Soil pH	neg	0.104	neg	0.298	pos	0.898	pos	0.627

¹Change in intercept indicates the direction of change in the variable between belt types (i.e., at north-facing aspects there is significant more tree canopy cover in ecotone belts compared to grassland belts). North and south transects are analyzed separately and *p* values in bold are statistically significant ($p < 0.05$).

wind dispersers and grassland indicator species. Ecotonal belts in this comparison also had significantly fewer rare species and forbs. Only one functional group, shrubs, showed higher richness at south-facing structurally-defined ecotone belts when compared to grassland belts. In comparison, on north-facing transects, structurally-defined ecotonal belts, as compared to grassland belts, had significant increases in the richness of four functional groups (shrubs, animal-dispersed species, species with no clear dispersal method and aspen indicators, Table 3.2).

When ecotone belts were compared with adjacent forest belts, aspect influenced the results far less. For both north- and south-facing ecotones, nearly all statistically significant comparisons of plant functional groups found higher species richness in the ecotone as compared to the adjacent forest (with the exception of aspen-indicator species in south-facing ecotones, Table 3.2).

Specifically, on south-facing aspects, ecotones had significantly higher richness of shade intolerants, graminoids, wind dispersers, generalists, intermediate drought

tolerants, grassland indicators, and aspen indicator species. The only functional group to show decreased richness in the ecotone as compared to the forest was the aspen-indicator group. Likewise comparison of north-facing structurally-defined ecotones with adjacent forest indicated ecotones had significantly higher richness of grassland-associated groups (shade intolerants, graminoids, wind dispersers, high and intermediate drought tolerant species and grassland indicators) as well as non-grassland associated groups (forbs, generalist dispersers, native and exotic species).

Overall, analysis of functional group abundance yielded fewer significant results than the richness analysis (Table 3.3). Unlike the analysis of functional group richness, significant differences in functional group abundance across the ecotone did not vary with aspect in an obvious pattern. At south facing sites there was an increase in rarely occurring species in structurally-defined ecotone belts compared to both grassland and forest belts. South-facing ecotone belts, when compared to adjacent grassland belts, had a decrease in the abundance of grassland indicator species. Compared to adjacent forest belts, south-facing structurally-defined ecotone belts showed a significant decrease in the abundance of shrubs and animal-dispersed species and an increase in the abundance of aspen indicator species, generalist dispersers and grassland indicators.

North-facing structurally-defined ecotone belts exhibited a significant decrease in native species abundance when compared to both forest belts and grassland belts (Table 3.3). North-facing ecotonal belts compared to grassland belts exhibited a significant increase in the abundance of aspen indicator species and a decrease in shade intolerant abundance. There was a decrease in shrub and an increase in exotic species abundance within north-facing structurally-defined ecotonal belts compared to forested belt.

Table 3.2 Results from linear models comparing functional group richness in structurally-defined ecotone belts versus forested and grassland belts, with transect as a blocking variable and belt type as a categorical variable in each model (lm=Variable~Belt.type+Transect).¹

Variable	North-facing Ecotone				South-facing Ecotone			
	Forest-Ecotone		Grassland-Ecotone		Forest-Ecotone		Grassland-Ecotone	
	Δ in intercept	<i>p</i> value						
Mean species richness	pos	0.055	pos	0.758	pos	0.767	neg	0.097
Total species richness	neg	0.406	neg	0.303	neg	0.062	neg	0.021
Rare species	pos	0.093	neg	0.836	pos	0.227	neg	0.029
Shade Tolerant Groups								
Tolerant	pos	0.214	pos	0.348	neg	0.469	neg	0.831
Intermediate	pos	0.090	pos	0.203	neg	0.444	pos	0.871
Intolerant	pos	0.005	neg	0.053	pos	0.011	neg	0.007
Growth Form Groups								
Forb	pos	0.007	pos	0.456	pos	0.392	neg	0.038
Graminoid	pos	0.004	neg	0.870	pos	0.022	neg	0.338
Shrub	neg	0.188	pos	0.054	neg	0.066	pos	0.041
Tree sapling	pos	0.190	neg	0.809	pos	0.446	neg	0.102
Dispersal Method Groups								
None	pos	0.127	pos	0.034	neg	0.719	neg	0.106
Wind	pos	0.047	neg	0.693	pos	0.040	neg	0.010
Animal	pos	0.157	pos	0.039	neg	0.207	neg	0.623
Generalist	pos	0.028	neg	0.197	pos	0.005	neg	0.528
Status Groups								
Native	pos	0.021	pos	0.521	pos	0.256	neg	0.145
Exotic	pos	0.003	pos	0.438	pos	0.337	neg	0.167
Drought Tolerant Groups								
Tolerant	pos	0.049	pos	0.489	neg	0.224	neg	0.103
Intermediate	pos	0.009	pos	0.554	pos	0.023	neg	0.374
Intolerant	pos	0.103	pos	0.986	neg	0.136	neg	0.072
Indicator Species Groups								
Aspen stands	pos	0.403	pos	0.003	neg	0.004	pos	0.279
Grassland	pos	0.019	neg	0.170	pos	0.011	neg	0.010

¹Change in intercept indicates the direction of change in the variable in structurally-defined ecotonal belts compared to either the forested or grassland belts (i.e., at south-facing aspects total species richness is significantly lower in ecotonal belts than in grassland belts). North and south are analyzed separately and p values in bold are statistically significant (p<0.05).

Table 3.3 Results from linear models comparing abundance of functional groups in structurally-defined ecotone belts versus forested and grassland belts, with transect as a blocking variable and belt type as a categorical variable in each (lm=Variable~Belt.type+Transect).¹

Variable	North-facing Ecotone				South-facing Ecotone			
	Forest-Ecotone		Grassland-Ecotone		Forest-Ecotone		Grassland-Ecotone	
	Δ in intercept	<i>p</i> value	Δ in intercept	<i>p</i> value	Δ in intercept	<i>p</i> value	Δ in intercept	<i>p</i> value
Rare species	neg	0.889	pos	0.072	pos	0.054	pos	0.005
Shade Tolerant Groups								
Tolerant	neg	0.178	pos	0.594	neg	0.605	pos	0.304
Intermediate	pos	0.386	pos	0.127	neg	0.090	neg	0.760
Intolerant	neg	0.290	neg	<0.000	pos	0.888	pos	0.690
Growth Form Groups								
Forb	pos	0.354	pos	0.437	neg	0.894	neg	0.594
Graminoid	pos	0.090	neg	0.099	pos	0.087	pos	0.514
Shrub	neg	0.010	pos	0.267	neg	0.002	neg	0.984
Tree sapling	pos	0.192	neg	0.179	pos	0.396	neg	0.070
Dispersal Method Groups								
None	neg	0.808	pos	0.225	neg	0.053	neg	0.409
Wind	pos	0.151	pos	0.942	pos	0.892	neg	0.485
Animal	neg	0.172	pos	0.921	neg	0.009	pos	0.751
Generalist	pos	0.129	neg	0.276	pos	0.030	pos	0.623
Status Groups								
Native	neg	0.026	neg	0.015	neg	0.316	neg	0.689
Exotic	pos	0.032	pos	0.295	pos	0.820	pos	0.550
Drought Tolerant Groups								
Tolerant	pos	0.226	neg	0.652	pos	0.731	pos	0.138
Intermediate	neg	0.467	neg	0.151	pos	0.534	neg	0.084
Intolerant	pos	0.336	pos	0.772	pos	0.551	neg	0.653
Indicator species Groups								
Aspen stands	pos	0.507	pos	0.003	pos	0.003	pos	0.609
Grassland	pos	0.079	neg	0.229	pos	0.011	neg	0.008

¹Change in intercept indicates the direction of change in the variable in structurally-defined ecotonal belts compared to either the forested or grassland belts (i.e., at south-facing aspects there is significantly greater abundance of rare species ecotonal belts than in grassland belts). North and south are analyzed separately and p values in bold are statistically significant (p<0.05).

GRADIENT APPROACH, STRUCTURALLY-DEFINED ECOTONES

Canopy Cover and Soil Data

Both north- and south-facing grassland belts exhibited a significant increase in canopy cover with increasing proximity to the structurally-defined ecotone (Table 3.4). In addition, north-facing forest belts also displayed a significant increase in tree canopy cover with proximity to the structurally-defined ecotone centre. This agrees with personal observations of diminished forest canopy in the patch center where it appeared old trees were dying (M. Ross, personal observation). On north-facing grassland belts, soil moisture was positively associated with increased proximity to the structurally-defined ecotone. Soil pH increased with proximity to the structural edge on north-facing grassland belts and decreased with proximity on south-facing belts. With one exception (south-facing grassland belts) non-vascular plant abundance decreased with proximity to the structural ecotone across both north- and south-facing aspects (Table 3.4).

Species Richness and Abundance: Gradient Approach

In this study, the gradient approach analysis of ecotones produced more significant differences in species richness (Table 3.5) than when the same ecotones were analyzed with a blocked approach (Tables 3.2). However, like the blocked approach, results varied with the ecotone aspect. At north-facing structurally-defined ecotones, both grassland and forest belts exhibited a positive association between mean species richness and proximity to the structurally-defined ecotone (Table 3.5). In contrast, within south-facing ecotones, mean richness in grassland-belts significantly decreased with proximity to structurally-defined ecotone and forested belts showed no significant association with mean species richness and

proximity to the structurally-defined ecotone (Table 3.5).

Table 3.4 Summaries of generalized linear models comparing canopy cover, soil moisture and soil pH for both forested and grassland transects with increasing proximity to the structurally-defined ecotone centre (treeline). Distance included as a continuous variable. lm= variable~distance towards treeline.¹

Variable	North-facing Ecotones		South-facing Ecotones	
	p value	slope	p value	slope
Canopy cover				
Grassland				
Tree	0.000	pos	0.000	pos
Tree sapling	0.005	pos	0.000	pos
Shrub	0.428	neg	0.157	pos
Forested				
Tree	0.000	pos	0.316	pos
Tree sapling	0.002	neg	0.301	neg
Shrub	0.119	pos	0.157	pos
Soil Moisture				
Grassland	<0.000	pos	0.481	neg
Forested	0.434	neg	0.062	pos
Soil pH				
Grassland	0.020	pos	0.002	neg
Forested	0.156	pos	0.598	neg
Non-vascular Plants				
Grassland	0.042	neg	0.003	neg
Forested	0.002	neg	0.003	pos

¹North and south transects are analyzed separately and p value in bold are statistically significant ($p < 0.05$). Slope indicates the change in variable values with increasing proximity to the ecotone, defined here as the structural treeline (i.e. for north-facing aspects, there is a significant increase in tree canopy cover with increasing proximity to the structural ecotone).

The significant association between mean species richness and ecotone proximity found in north-facing grassland and forest belts was driven by the large number of significantly positive associations between individual functional groups and proximity to the structural edge. In grassland-belts, the richness of groups expected to be associated with aspen habitats (high- and medium-shade

tolerants, shrubs, drought-intolerants, medium drought-tolerants and aspen indicators) as well as nitrogen and non-nitrogen-fixers, animal-dispersed species and species with no obvious dispersal method all increased significantly with proximity to the structural ecotone (Table 3.5). Likewise forest belts on north-facing ecotones were characterized by significantly positive associations between the proximity from the structural ecotone and the richness of groups associated with grasslands (shade-intolerant species and graminoids) as well as the richness of exotic species, forbs, medium- and drought-intolerants, non nitrogen-fixers, wind-, animal-, and generalist-dispersers. On north-facing ecotones, those functional groups that exhibited a negative association between richness and proximity to the structural edge differed between grassland and forest belts. On forested belts, the richness of shrubs and aspen-indicators showed negative association with proximity to the structural edge, whereas on grassland-belts, the richness of shade intolerants, drought-tolerants, grassland indicators (all groups expected to increase in grasslands) as well as generalist dispersers displayed significant negative associations with proximity (Table 3.5).

On south-facing grassland-belts, the negative association between mean species richness and proximity to the structural ecotone was likely driven by the large number of functional groups that displayed a significant negative association between richness and proximity to the structural edge (i.e., shade intolerants, forbs, graminoids, drought tolerant and drought intolerants, non-nitrogen fixers, nitrogen fixers, grassland-indicators, wind and species with no dispersal mechanism (Table 3.5)). The only functional groups to show a significant positive association with proximity to the structural edge in south-facing grassland-belts were shrubs and aspen indicators. In south-facing forest belts, groups associated with grasslands such low shade-tolerants, graminoids, as well as medium

drought-tolerants, non-nitrogen fixers, exotics, and generalist dispersers all displayed significant negative associations with increasing proximity to the structurally-defined ecotone. In comparison, shrubs, low drought-tolerants, aspen indicators and animal-dispersed species) exhibited positive associations with proximity (Table 3.5). In most cases in forested belts, grassland-associated functional group richness showed positive associations with proximity to the structural ecotone and negative association with proximity in grassland-belts. Aspen-associated groups, in general, exhibited the opposite trend.

When functional group abundance was analyzed, fewer functional groups showed significant associations with proximity to the structurally-defined ecotone (Table 3.6). Within north-facing grassland-belts, the abundance of some forest-associated species (shade tolerants, forbs, shrubs and aspen indicators) was positively associated with proximity to the structurally-defined ecotone, whereas the abundance of grassland-associated groups (shade intolerants, graminoids, drought tolerants and grassland indicators) were negatively associated with proximity to the structural ecotone. South-facing grassland-belts exhibited the same general trend although the fewer functional groups had significant associations between abundance and proximity (Table 3.6). In these belts, the abundance of one forest-associated group (aspen indicator species) was positively associated with proximity to the structural ecotone and one grassland-associated group (drought tolerants) was negatively associated with proximity to the structural edge.

Within north-facing forested belts, the abundance of aspen-associated groups (forbs, shrubs and aspen indicators) was positively associated with proximity to the structural edge. On south-facing forest belts, the abundance of grassland-associated groups (graminoids, drought tolerants and grassland

indicators) was positively associated with proximity to the structurally-defined ecotone (Table 3.6).

Table 3.5 Summaries of generalized linear models comparing plant functional group richness for both forested and grassland transects with increasing distance from the structurally-defined ecotone centre (treeline), with distance included as a continuous variable. $lm = \text{variable} \sim \text{distance from treeline}$.¹

Variable	North-facing Ecotone		South-facing Ecotone	
	p value	slope	p value	slope
Mean Species Richness				
Grassland	0.002	pos	0.008	neg
Forested	<0.000	pos	0.973	pos
Exotic Species				
Grassland	0.327	neg	0.454	neg
Forested	0.030	pos	0.001	pos
Shade Tolerant Groups				
Grassland				
Tolerant	0.001	pos	0.588	pos
Intermediate	<0.000	pos	0.459	neg
Intolerant	0.003	neg	<0.000	neg
Forested				
Tolerant	0.534	pos	0.003	neg
Intermediate	0.056	pos	0.323	neg
Intolerant	<0.000	pos	<0.000	pos
Growth Form Groups				
Grassland				
Forb	0.002	pos	0.002	neg
Graminoid	0.731	neg	0.026	neg
Shrub	<0.000	pos	0.002	pos
Tree sapling	0.895	pos	0.100	neg
Forested				
Forb	0.001	pos	0.169	neg
Graminoid	0.002	pos	<0.000	pos
Shrub	0.007	neg	0.005	neg
Tree sapling	0.033	pos	0.332	pos
Drought Tolerance				
Grassland				
Tolerant	0.125	neg	0.023	neg
Intermediate	0.001	pos	0.261	neg
Intolerant	<0.000	pos	0.005	neg
Forested				

	Tolerant	0.775	pos	0.064	pos
	Intermediate	<0.000	pos	<0.000	pos
	Intolerant	0.001	pos	0.004	neg
Nitrogen fixation					
Grassland					
	Fixation	0.004	pos	0.002	neg
	None	0.015	pos	0.004	neg
Forested					
	Fixation	0.068	pos	<0.000	neg
	None	0.001	pos	0.001	pos
Indicator Groups					
Grassland					
	Aspen	<0.000	pos	0.001	pos
	Grassland	<0.000	neg	<0.000	neg
Forested					
	Aspen	<0.000	neg	<0.000	neg
	Grassland	0.367	pos	0.027	pos
Dispersal method					
Grassland					
	None	0.022	pos	0.001	neg
	Wind	0.542	pos	0.007	neg
	Animal	<0.000	pos	0.450	neg
	Generalist	0.002	neg	0.585	neg
Forested					
	None	0.061	pos	0.365	neg
	Wind	<0.000	pos	0.090	pos
	Animal	0.036	pos	0.006	neg
	Generalist	0.003	pos	<0.000	pos

¹North- and south-facing are analyzed separately and p values in bold are statistically significant (p<0.05). Slope indicates the change in the variable over the distance gradient (i.e., on north-facing grassland belts there is a significant increase in mean species richness with increasing proximity to the ecotone).

Table 3.6 Summaries of generalized linear models comparing abundance of plant functional groups for both forested and grassland transects along a distance gradient from the structural ecotone (treeline). $lm=variable\sim distance\ from\ treeline.$ ¹

Variable		North-facing Ecotones		South-facing Ecotones		
		p value	slope	p value	slope	
Exotic Species						
	Grassland	0.212	pos	0.040	pos	
	Forest	0.404	pos	0.024	pos	
Shade Tolerance						
	Grassland					
		Tolerant	<0.000	pos	0.091	pos
		Intermediate	<0.000	pos	0.131	pos
		Intolerant	<0.000	neg	0.225	neg
	Forested					
		Tolerant	0.171	neg	0.697	neg
		Intermediate	0.874	neg	<0.000	neg
		Intolerant	0.062	neg	0.279	pos
Growth Form						
	Grassland					
		Forb	0.021	pos	0.791	neg
		Graminoid	<0.000	neg	0.666	neg
		Shrub	0.001	pos	0.005	pos
		Tree sapling	0.948	pos	0.182	neg
	Forested					
		Forb	0.888	pos	<0.000	neg
		Graminoid	0.001	pos	<0.000	pos
		Shrub	<0.000	neg	<0.000	neg
		Tree sapling	0.117	pos	0.294	pos
Drought Tolerance						
	Grassland					
		Tolerant	0.007	neg	<0.000	neg
		Intermediate	0.007	neg	<0.000	pos
		Intolerant	0.056	neg	<0.000	neg
	Forested					
		Tolerant	0.055	pos	<0.000	pos
		Intermediate	0.409	neg	0.064	pos
		Intolerant	0.091	pos	0.015	pos
Nitrogen Fixation						
	Grassland					
		Fixation	0.038	pos	0.676	pos
		None	<0.000	neg	0.594	neg
	Forested					
		Fixation	0.624	pos	<0.000	neg
		None	0.002	neg	0.194	neg
Indicator Species						
	Grassland					
		Aspen	<0.000	pos	0.001	pos
		Grassland	0.001	neg	<0.000	neg
	Forested					
		Aspen	<0.000	neg	<0.000	neg
		Grassland	0.208	pos	0.027	pos
Dispersal Method						

Grassland	None	0.006	pos	0.600	neg
	Wind	0.273	pos	0.831	pos
	Animal	0.315	pos	0.681	neg
	Generalist	<0.000	neg	0.936	neg
Forested	None	0.357	pos	0.001	neg
	Wind	0.888	neg	0.010	neg
	Animal	<0.000	neg	<0.000	neg
	Generalist	0.005	pos	<0.000	pos

¹North- and south-facing aspects are analyzed separately and p values in bold are statistically significant ($p < 0.05$). Slope indicates the change in the variable over the distance gradient (i.e., for south-facing grasslands there is a significant increase in abundance of exotic species with increasing proximity to the ecotone).

GRADIENT APPROACH, STATISTICALLY-DEFINED ECOTONES

Gradient analysis was also completed using distance from the statistically defined ecotone centre rather than the structurally-defined ecotone centre (treeline). Due to the fact that statistically defined ecotone centres were located primarily within the grassland-belts of each section, it was only feasible to analyze the data from the ecotone center toward the forest. Thus, all the following results are only one-sided: examining the richness and abundance from the ecotone center towards the forest belts.

With this approach, mean species richness within south-facing ecotones was positively associated with increasing proximity to the statistically-defined ecotone centres (Table 3.7). This increase in mean richness on these south-facing transects was likely driven by the positive association of both grassland-associated groups (graminoids, drought tolerant species and wind dispersers) and aspen-associated groups (forbs, juvenile trees) in addition to animal and generalist dispersers.

Within north-facing ecotones, the richness of grassland-associated groups (shade intolerants, graminoids, drought-tolerants and grassland indicators) and

two aspen-associated groups (forbs and understory trees), as well as exotics, nitrogen fixers, and animal and generalist dispersers all showed a significant positive association with increasing proximity to the ecotone center. On north-facing ecotones the only plant functional groups with significant negative associations with proximity to the statistical ecotone were non-nitrogen fixers and two aspen-associated groups (shrubs and aspen indicator species).

When plant abundance is considered the results are quite similar with a few exceptions (Table 3.8). At both north- and south-facing transects, the abundance of animal-dispersed species was negatively associated with increasing proximity to the ecotone center, even though the richness of this functional group showed the opposite trend. Furthermore, on south-facing ecotones, the abundance of two grassland-associated groups (shade intolerants and grassland indicators) was negatively associated with increasing proximity and the abundance of drought intolerants was positively associated with increasing proximity. In general, the gradient approach, using the statistically-defined ecotone centre, showed even more significant associations between plant functional group richness and abundance with increasing distance from the ecotone center than was found using a gradient approach from the structural ecotone.

Table 3.7 Summaries of generalized linear models comparing plant functional group richness for forested belts with increasing distance from the statistically-defined ecotone centre, with distance included as a continuous variable.

lm=variable~distance from ecotone centre.¹

Acceptable Ecotones	North-facing Ecotone		South-facing Ecotone	
	p value	slope	p value	slope
Mean Species Richness	0.859	pos	0.004	pos
Exotic Species	<0.000	pos	0.425	neg
Shade Tolerant Groups				
Tolerant	0.064	pos	0.515	pos
Intermediate	0.001	pos	0.692	pos
Intolerant	<0.000	pos	<0.000	pos
Growth Form Groups				
Forb	<0.000	pos	<0.000	pos
Graminoid	<0.000	pos	<0.000	pos
Shrub	<0.000	neg	<0.000	neg
Tree sapling	0.016	pos	0.002	pos
Drought Tolerance				
Tolerant	<0.000	pos	0.003	pos
Intermediate	<0.000	pos	<0.000	pos
Intolerant	0.001	pos	<0.000	neg
Nitrogen Fixation				
Fixation	<0.000	pos	0.459	pos
None	0.001	neg	<0.000	neg
Indicator Species				
Aspen	<0.000	neg	<0.000	neg
Grassland	<0.000	pos	<0.000	pos
Dispersal Method				
None	0.573	pos	0.716	pos
Wind	0.233	pos	0.026	pos
Animal	<0.000	pos	<0.000	pos
Generalist	<0.000	pos	<0.000	pos

¹North and south are analyzed separately and p values in bold are statistically significant (<0.05). Slope indicates the change in the variable over the distance gradient (i.e., for south-facing aspects there is a significant increase in mean species richness with increasing proximity to the ecotone centre).

Table 3.8 Summaries of generalized linear models comparing plant functional group abundance for forested belts with increasing distance from the statistically-defined ecotone centre, with distance included as a continuous variable.

lm=variable~distance from statistically-defined ecotone centre.¹

Acceptable Ecotones	North-facing Ecotone		South-facing Ecotones	
	p value	slope	p value	slope
Exotic species	<0.000	pos	0.004	neg
Shade Tolerant Groups				
Tolerant	0.048	neg	0.009	neg
Intermediate	<0.000	pos	0.001	neg
Intolerant	0.001	neg	0.001	neg
Form				
Forb	<0.000	pos	0.673	neg
Graminoid	<0.000	pos	0.606	pos
Shrub	<0.000	neg	<0.000	neg
Tree sapling	0.023	pos	<0.000	pos
Drought Tolerance				
Tolerant	0.001	pos	0.004	neg
Intermediate	0.827	neg	0.001	pos
Intolerant	<0.000	pos	<0.000	pos
Nitrogen fixation				
Fixation	<0.000	pos	0.327	pos
None	<0.000	neg	<0.000	neg
Indicator Species				
Aspen	<0.000	neg	0.459	pos
Grassland	<0.000	pos	<0.000	neg
Dispersal method				
None	0.007	pos	0.268	neg
Wind	<0.000	pos	0.473	neg
Animal	<0.000	neg	<0.000	neg
Generalist	<0.000	pos	0.330	pos

¹North and south are analyzed separately and p values in bold are statistically significant (p<0.05). Slope indicates the change in the variable over the distance gradient (i.e., for north-facing aspects there is a significant increase in abundance of exotic species with increasing proximity the ecotone centre).

DISCUSSION

STRUCTURALLY-DEFINED ECOTONES: CONTRASTING THE BLOCKED AND GRADIENT APPROACH

Treelines, such as those forming the center of the structurally-defined ecotones analyzed in this chapter, are conspicuous features of the landscape and are often assumed to indicate the location of abrupt changes in species composition and/or diversity (Grytnes et al. 2006). Whereas the results of Chapter Two clearly indicated that structurally-defined ecotones were not the location of the most rapid compositional change in understory plants, the results of this chapter indicate that our understanding of structurally-defined ecotones as sites of increased plant richness depends upon whether the ecotone was analyzed as a block or as a gradient. Regardless of aspect, the blocked approach found little evidence for increased richness, as compared to adjacent belt types, in ecotonal belts. The gradient approach, in comparison, demonstrated the species richness declined with increasing distance from the structurally-defined ecotone for both grassland and forest belts, but only for north-facing transects. This result concurs with that of Gelhausen et al. (2000) who found a similar decrease in species diversity with increasing distance from treeline in their aspen stand surveys.

Fundamentally, the decision to adopt a blocked or gradient approach to analyzing ecotones depends upon whether the entire ecotone is viewed as distinct from adjacent communities or as an assemblage of individual species distributed across an ecotonal gradient—a difference of opinion that dates back to the debate between Gleason and Clements in the first half of the twentieth century (Clements 1916; Gleason 1926). While numerous studies (Walker et al. 2003; Senft 2009; Hennenberg et al. 2005; Harper & MacDonald 2001; Jules et al. 2010; Kark 2013) have taken a blocked approach to describing patterns of species richness at edges

and ecotones, however some functional groups may respond to environmental variation as a gradient rather than an abrupt change (Harper & MacDonald, 2001). This “lumping” of belts found at different distances from the structurally-defined ecotones may mask difference between the blocks and may explain why, in this study, blocked analysis of the ecotones found fewer significant differences and the gradient approach found more.

The first of the four *a priori* hypothesis considered in Chapter Two suggested that increased environmental heterogeneity found in ecotones could lead to increased species packing, which in turn would be associated with increased species richness. In Chapter Two, high rates of species composition change were used as a proxy for increased species packing and found no correlation with increased species richness. In this chapter, the presence of an abrupt treeline, would, nearly by definition, imply increased environmental heterogeneity at the structurally-defined ecotone (Camarero et al. 2006; Peltzer & Wilson 2006). However, the results of this study, as stated above, indicate support for this specific hypothesis only when the north-facing ecotones are analyzed with a gradient approach. In contrast, Camarero et al. (2006) found some evidence in favour of the impact of environmental heterogeneity on increased species diversity at a small scale. A study on old growth forest edges found that increased environmental heterogeneity lead to increased species richness as compared to forest interiors (Brothers & Spingarn 1992). Kumar et al. (2006) found environmental heterogeneity influenced native and nonnative species differently and also varied between spatial scales.

The second hypothesis suggests that ecotones will be species-rich due to the influx of propagules (spatial mass effect) from adjacent habitats. In this chapter, both the blocked and gradient approach provided support for this hypothesis as, in general, the richness and abundance of aspen indicators were

higher in ecotones than in grasslands. Likewise, as would be expected with spatial mass effects, the richness and abundance of grassland indicators were higher in ecotone belts when compared to forest belts. In a study of altitudinal gradients Grytnes et al. (2008) found support for mass effects at a finer scale (0.5x0.5 m² plots), but no evidence when they examined the gradient at a coarser scale (5x5 m² plots). However, Walker et al. (2003) found little evidence for the impact of spatial mass effect on ecotone species composition. A study of a large number of transects found mixed evidence for the influence of mass effects on species composition at edges (Kunin 1998).

The third hypothesis predicts animal seed dispersal and/or predation as potential drivers of richness within ecotones. In this chapter, I found evidence supporting this hypothesis (i.e., higher richness of animal-dispersed species in ecotones compared to adjacent habitats) only in the north-facing structurally-defined ecotone-grassland comparison. Previously, Jones et al. (2015) working in the same area of Lac du Bois found that no animal-dispersed species occurred within the grassland matrix. As many of the animal-dispersed species in this study are bird-dispersed, the increased richness found at the ecotones could have arisen as birds used edge trees as perches. North-facing slopes are moister than south-facing ecotones and moisture levels have been shown to affect the occurrence of animal-dispersed seeds (Herault & Honnay 2007). Likewise, a Belgian study found the occurrence of animal-dispersed seeds in the seed bank increased as they moved from the clearings into forest interiors (Devlaeminck et al. 2005). Interestingly, one study found that the structure of forest edges can influence seed dispersal through the structure of the stand edge; that is, if the forest edge is densely vegetated wind dispersed seed interception will be high, however, if the forest edge is relatively open wind dispersed seed can reach deeper into the forest (Cadenasso et al. 2003). This could be a factor influencing observed seed dispersal

patterns across these aspen-grassland ecotones, where the vegetation density at the treeline was variable when compared between forest patches (M. Ross, personal observation). Additionally, although Baker et al. (2011) found no evidence for ecotone-specific birds in their study, they did find significantly more bird species within the forest than in an adjacent heathland. This increased bird activity within the forest could also explain why an increase in animal dispersers was found only within forest belts.

The final *a priori* hypothesis suggests that increased ecotone richness might arise through an influx of exotic species. In this chapter, I did find both increased richness and abundance of exotic species in north-facing structurally-defined ecotones as compared to north-facing forested belts. Likewise, Chapter Two found an increase in richness of exotic species in north-facing, statistically-defined ecotones, when compared to adjacent forest belts. These results support Risser's (1995) contention that ecotones allow exotic species invasion, in contrast to the other studies such as Walker et al. 2003 which failed to find any such evidence. Lloyd et al. (2000) found no clear pattern of higher exotic species richness within ecotones and suggested that an increased richness of exotics is not an intrinsic characteristic of ecotones. In comparison, Stohlgren et al. (1998) argued that riparian ecotones were particularly susceptible to invasion by exotic species, furthering the argument that ecotone characteristics differ based on ecological conditions and generalization about ecotones as a whole are problematic.

COMPARING THE GRADIENT APPROACH WITH PREVIOUS METHODS: STATISTICALLY-DEFINED ECOTONE RESULTS

Of the different definitional and analytic approaches used in this study, the results of the gradient analysis of species richness patterns from the center of the statistically-defined ecotone towards the aspen stands was, perhaps

unsurprisingly, most similar to the results found with the structurally-defined ecotone, gradient approach. It is important, however, to emphasize that these two approaches are not analyzing the exact data as the structurally-defined and statistically-defined ecotones rarely overlapped on any given transects. Perhaps the most surprising result of this study is that overall, a blocked approach showed more significant differences in the richness of plant functional groups on south-facing ecotones, whereas the gradient approach showed more significant differences within north-facing ecotones.

Overall, it is clear that both the method of defining ecotones and the analytical approach have a significant impact on the nature of the results when patterns of species richness in ecotones are assessed. Walker et al. (2003) and Senft (2009) also came to a similar conclusion. Not only does overall significant difference in species richness alter, but which plant functional group changes in either richness or abundance also varies with ecotone definition and analytical approach. Based on this study, there appears to be few universal attributes of ecotones related to species richness, although the richness and/or abundance of functional groups such as seed-dispersal methods, shade and drought tolerance and as well as indicator status were repeatedly found to vary within multiple analyses. This research went a step further than Walker et al. (2003) and Senft (2009) in that it explicitly considered the influence of aspect on the patterns of species richness. This is particularly important as patterns of change in species richness were often reversed on north- versus south-facing ecotones.

This study makes apparent that using a standardized method is important to allow comparison across different systems and scales. Furthermore, this study highlights the importance of not relying on composite response variables such as species richness but evaluating the response of individual plant functional groups.

Future studies in this system could also develop a functional group analysis which could allow for comparisons of ecotone functional characteristics between flora and fauna (Garnier & Navas 2012). This comparison may help create a more holistic understanding of natural systems and their underlying processes.

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CHAPTER 4 IMPLICATIONS, FUTURE RESEARCH AND CONCLUSIONS

BROAD CONTEXT

This study contributes to a further understanding of functional group richness and abundance patterns, as well as the influence of aspect on ecotones in general and at aspen-grassland ecotones specifically. By using a standardized approach, the moving window method, this study is directly relatable to other studies, regardless of the specific system examined. The observed patterns can be compared to other types of ecotones like riparian edges, mangroves or even animal boundaries for example. As with any study, choices need to be made regarding site location, methods and analysis. As this is an observational study, it comes with both limitations and strengths (Dunne et al. 2004). Short term manipulative studies can yield poor predictions of long term responses, so it is important to use both manipulative and natural experiments (Saleska et al. 2002). In the Lac du Bois area the grassland-aspen ecotones are naturally occurring and are not perfect replicates. However, this type of observational study does provide baseline data upon which future manipulative studies could be based.

Using the moving window analysis, one peak in the first ordination score was used to define the ecotone centres. Many of the transects, however, have multiple minor peaks. Those transects with multiple similar sized peaks were not used in the analysis of acceptable transects, however many of the acceptable transects also had minor, secondary peaks. Further investigation into these secondary peaks may yield some interesting results. In most cases the secondary peak was within the aspen stand and there were also in some cases more than one secondary peak. Based on my understanding of the moving window method, I chose the highest peak to

identify the main ecotone (Walker et al. 2003). It is possible, however, that I should have chosen the one closest to the structural edge (physiognomic change) in order to better compare like variables. This study looked at ecotone locations relative to grassland-aspen treeline. I found a few ecotones located within or near the treeline; but more often they were not associated with the treeline at all, occurring within the grassland or forested belts. This study contradicts any assumption that peaks in species richness or species turnover will occur at a visually obvious boundary such as a treeline. Given ecologists long reliance on visually obvious breaks in vegetation, the results of this study suggest that managing for biodiversity along ecosystem gradients may be more complicated than initially assumed.

Choice of analysis within this research followed a standardized approach to ecotone definition (Walker et al. 2003). Using a standardized approach allows for the comparison between studies where ecotone types may vary. Non-metric multidimensional scaling ordination was used with a Bray-Curtis dissimilarity measure. Many possible measures of dissimilarity can be used, but Bray-Curtis is a widely used dissimilarity for ecological abundance data (Warton et al. 2001). Bray-Curtis can be sensitive to outliers (McCune et al. 2002), and this was addressed in this research by first removing species with very low abundance (less than 1%) before running the ordinations. However, by using the raw (as opposed to relativized abundance data), the Bray-Curtis dissimilarity index also weights abundant species more heavily than less common species. In the future, it would be interesting to compare the ordinations obtained with a dissimilarity index that relativized abundance across all species.

A further factor that needs to be considered is the local topography of the study site. Although the grasslands in this area are have a rolling topography, they also have an overall south-facing exposure. Due to this specific geographic feature, north-facing ecotones tended to occur on the upslope side of the aspen patches. This

could have implication for plant functional richness and abundance patterns across the ecotones, as slope locations may impact soil moisture regimes.

A final consideration for this study involves language used in the definition of ecotones in general. The lack of increased species richness in this paper found in statistically defined ecotones contributes to the definition of ecotones as areas of tension rather than areas of mixing. Van der Maarel (1990) argued that there should be a distinction in the classification of edge environments as either ecoclines (areas with typically higher species richness) or ecotones (areas with similar or lesser species richness). I am inclined to agree with this at least in the broad sense; there is no simple way to generalize characteristics of ecotones universally. As demonstrated in this study, the greatest change in species composition was not correlated with the greatest change in structure. This suggests that boundaries are more subtle than we might first approximate.

ECOTONES AND CLIMATE CHANGE

Given that the impacts of environmental shifts are expected to show at ecosystem margins first, ecotones are generally viewed as being at the frontline of climate change, and (Hampe & Petit 2005). Hebda (2007) specifically predicts that treeline ecotones will move northward or to higher elevations as climate change increases environmental pressures. It has been suggested that species in ecotones may already be adapted to frequent change, which would help to mitigate climate change impacts (Gayton 2008).

However, one study found that alpine treeline ecotones are slow to respond to change and are often broken up, rather than advancing as a front (Noble 1993). Such a treeline ecotone would not be ideal for climate change monitoring as one needs high resiliency and stability within an ecotone in order to detect potential climate change impacts (Noble 1993). Van der Maarel (1990)

cautions that although it might be convenient to think of ecotones as good predictors of climate change impacts, it is important to understand which features to measure, which features are being influenced and which are influencing others.

Changing climate also has a strong impact on aspen stands specifically; many aspen populations are in decline around North America, much of this attributed to climate change and land use practices (Wooley et al. 2008; Michaelian et al. 2010; Worrall et al. 2010). This is concerning to researchers because aspen stands are cited as the second most biodiverse ecosystem in western North America (Wooley et al. 2008).

MANAGEMENT

Management of ecotones is problematic – due, at least in part, to the lack of consensus around the definition of ecotone boundaries, study designs, low sample size and analysis methods (objectively or subjectively defined). “Ecotone” is a very broad term and is therefore not a useful management unit unless the specific ecotone type is noted. For example, riparian ecotones are often very dynamic (Naiman & Décamps 1990) whereas alpine treeline ecotones tend to be more static and slow to change (Noble 1993). Broad references and generalizations about ecotones in general should be avoided as no intrinsic properties of ecotones have been identified (Lloyd et al. 2000; Walker et al. 2003). Adding to this difficulty, most management decisions do not consider boundaries, but focus solely on the uniform habitats in isolation (Naiman & Décamps 1990). Overall, within this study, ecotones were not more species rich than adjacent habitat types. However, aspen forests were more species rich than grasslands in many cases and the ecotones were generally found to contain similar species richness as the forest patches. This helps highlight the importance of aspen stands for increased species richness within the grassland matrix. Management of grazing may consider the impact on aspen stands rather

than just the impact on the grassland. Carlson et al. (2014) found a reduction in grassland habitat due to changes in land use practices and due to a management focus on the preservation of forested land. The pattern of species richness differs somewhat when the gradient approach was considered (species richness decreases away from edge/ecotone centre) in this study. This serves to support the point that definition of the ecotone (using a blocked or gradient approach) matters for management decisions. When monitoring changes for future management decisions, it is important to consider the approach taken.

FURTHER STUDIES

In future ecotone studies, it would be interesting to examine site specific functional traits to study how characteristics such as leaf area, plant height and seed size differ over the ecotones. Functional characteristics used in this paper were relatively general and gleaned from the literature, and it would be informative to observe if ecotonal habitats have any effect on the functional traits of individual species. These site specific traits could tell us more about the impact of the ecotone on resource acquisition, dispersal and fecundity, for example (Lavorel et al. 2007).

This research focused on vascular plant species in the grasslands and forest understory. Non-vascular plant richness and abundance data was not specifically examined; this would be an interesting project for future work in this area as these organisms may respond to environmental gradients differently.

Underlying soils and other substrates are invisible factors that impact plant survival and site preference (McLean 1970; Ryswyk & McLean 1989; Kunin 1998). Future ecotone research in the Lac Du Bois area should consider the underlying soil type or even aspen stand age, to observe if these have an impact on the position, boundaries and characteristics of ecotones. Additionally, it would be

informative to investigate grassland-aspen ecotone importance for other species – insects, rodents or ungulates, for example.

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APPENDIX

Table A.1 Results from generalized linear models of all transects comparing canopy cover, soil moisture, soil pH and non-vascular plant species abundance in statistically-defined ecotonal belts versus forested or grassland belts, with transect as a blocking variable and belt type as a categorical variable in each model (lm=variable~belt.type+transect).¹

Variable	North-facing Ecotone				South-facing Ecotone			
	Forest-Ecotone		Grassland-Ecotone		Forest-Ecotone		Grassland-Ecotone	
	Δ in intercept	<i>p</i> value						
Canopy cover								
Tree	neg	0.020	pos	0.027	neg	0.002	pos	0.089
Intermediate	neg	0.326	pos	0.148	neg	0.096	pos	0.737
Shrub	pos	0.196	pos	0.226	neg	0.279	pos	0.856
Soil moisture	pos	0.897	neg	0.064	pos	0.897	neg	0.064
Soil pH	neg	0.142	neg	0.533	neg	0.654	neg	0.856
Non-vascular plants	neg	0.299	neg	0.133	pos	0.319	neg	0.169

¹Change in intercept indicates the direction of change in the variable from ecotonal to adjacent belts (i.e., at north-facing aspects there is significant less tree canopy cover in ecotone belts than forest belts). North- and south-facing ecotones are analyzed separately and *p* values in bold are statistically significant ($p < 0.05$).

Table A.2 Results from generalized linear models, of all transects, comparing richness of functional groups in statistically defined ecotone belts versus forested and grassland belts, with transect as a blocking variable and belt type as a categorical variable in each model (lm=Variable~Belt.type+Transect).¹

Variable	North-facing Ecotones				South-facing Ecotones			
	Forest-Ecotone		Grassland-Ecotone		Forest-Ecotone		Grassland-Ecotone	
	Δ in intercept	<i>p</i> value	Δ in intercept	<i>p</i> value	Δ in intercept	<i>p</i> value	Δ in intercept	<i>p</i> value
Mean species richness	neg	0.700	pos	0.155	pos	0.291	pos	0.021
Total species richness	neg	0.742	pos	0.338	pos	0.133	neg	0.962
Rare species	pos	0.412	neg	0.308	pos	0.346	neg	0.061
Shade tolerance Group								
Tolerant	neg	0.970	pos	0.536	neg	0.407	neg	0.956
Intermediate	pos	0.828	pos	0.595	pos	0.224	pos	0.590
Intolerant	pos	<0.000	pos	0.063	pos	<0.000	neg	0.028
Form								
Forb	pos	0.092	pos	0.832	pos	0.074	neg	0.089
Graminoid	pos	0.023	pos	0.189	pos	0.002	neg	0.238
Shrub	pos	0.070	pos	0.013	pos	0.013	pos	0.018
Tree sapling	pos	0.031	pos	0.577	pos	0.089	neg	0.686
Dispersal								
None	neg	0.643	pos	0.585	pos	0.250	neg	0.848
Wind	pos	0.010	neg	0.741	pos	0.007	neg	0.062
Animal	neg	0.584	pos	0.302	neg	0.084	pos	0.731
Generalist	pos	0.006	neg	0.049	pos	0.005	neg	0.255
Status								
Native	pos	0.195	pos	0.863	pos	0.019	neg	0.654
Exotic	pos	0.004	neg	0.987	pos	0.521	neg	0.049
Drought tolerance								
Tolerant	pos	0.301	pos	0.305	pos	0.360	pos	0.606
Intermediate	pos	0.197	neg	0.178	pos	0.029	neg	0.454
Intolerant	pos	0.047	neg	0.814	neg	0.025	neg	0.063
Indicator species								
Aspen stands	neg	0.073	pos	0.362	neg	0.001	pos	0.334
Grassland	pos	0.018	neg	0.074	pos	<0.000	neg	0.244

¹Change in intercept indicates the direction of change in the variable in ecotonal belts compared to either the forested or grassland belts (i.e., at south-facing aspects, there is a significantly greater mean species richness in ecotone belts than grassland belts). North and south transects are analyzed separately and *p* values in bold are statistically significant (*p*<0.05).

Table A.3 Results from generalized linear models, of all transects, comparing abundance of functional groups in statistically defined ecotone belts versus forested and grassland belts, with transect as a blocking variable and belt type as a categorical variable and belt type as a categorical variable in each model (lm=variable~belt.type+transect).¹

Variable	North-facing Ecotones				South-facing Ecotones			
	Forest-Ecotone Δ in intercept	<i>p</i> value	Grassland-Ecotone Δ in intercept	<i>p</i> value	Forest-Ecotone Δ in intercept	<i>p</i> value	Grassland-Ecotone Δ in intercept	<i>p</i> value
Rare species	pos	0.528	pos	0.744	pos	0.050	pos	0.004
Shade tolerance								
Tolerant	neg	0.276	pos	0.152	neg	0.067	neg	0.970
Intermediate	pos	0.585	pos	0.053	neg	0.514	pos	0.241
Intolerant	pos	0.110	neg	0.006	pos	0.826	neg	0.396
Form								
Forb	pos	0.641	pos	0.286	pos	0.842	pos	0.684
Graminoid	pos	0.100	neg	0.048	pos	0.024	neg	0.112
Shrub	neg	0.015	pos	0.274	neg	0.001	pos	0.218
Tree sapling	pos	0.107	neg	0.132	pos	0.287	neg	0.067
Dispersal								
None	neg	0.671	pos	0.102	neg	0.815	pos	0.270
Wind	pos	0.100	pos	0.099	pos	0.532	neg	0.466
Animal	neg	0.140	pos	0.681	neg	0.002	pos	0.923
Generalist	pos	0.161	neg	0.026	pos	0.035	neg	0.269
Status								
Native	neg	0.495	neg	0.066	neg	0.613	pos	0.810
Exotic	pos	0.219	pos	0.393	neg	0.890	neg	0.800
Drought tolerance								
Tolerant	neg	0.812	neg	0.507	neg	0.864	pos	0.459
Intermediate	neg	0.233	neg	0.009	pos	0.737	neg	0.379
Intolerant	pos	0.073	neg	0.728	pos	0.233	pos	0.881
Indicator species								
Aspen stands	neg	0.073	pos	0.362	neg	0.001	pos	0.334
Grassland	pos	0.018	neg	0.074	pos	<0.000	neg	0.244

¹Change in intercept indicates the direction of change in the variable in ecotonal belts compared to either the forested or grassland belts (i.e., at north-facing aspects, there is a significantly less abundance of intermediately shade tolerant species in grassland belts than in ecotonal belts). North and are analyzed separately and *p* values in bold are statistically significant.

Table A.4 Results from generalized linear models comparing canopy cover, soil moisture and soil pH in structurally-defined ecotone belts versus forested or grassland belts, with transect as a blocking variable and belt type as a categorical variable in each model (lm=variable~belt.type+transect). ¹

Variable	North-facing Ecotones				South-facing Ecotones			
	Forest-Ecotone		Grassland-Ecotone		Forest-Ecotone		Grassland-Ecotone	
	Δ in intercept	<i>p</i> value	Δ in intercept	<i>p</i> value	Δ in intercept	<i>p</i> value	Δ in intercept	<i>p</i> value
Canopy cover								
Tree	pos	0.194	pos	<0.000	neg	0.069	pos	<0.000
Intermediate	neg	0.043	pos	0.897	pos	0.653	pos	0.004
Shrub	pos	0.880	neg	0.661	neg	0.820	pos	0.422
Soil moisture	pos	0.896	neg	0.050	pos	0.898	pos	0.627
Soil pH	neg	0.056	neg	0.555	pos	0.831	pos	0.266

¹Change in intercept indicates the direction of change in the variable between belt types (i.e., at north-facing aspects there is significant greater tree canopy cover in ecotonal belts than grassland belts). North and south transects are analyzed separately and *p* values in bold are statistically significant ($p < 0.05$).

Table A.5 Results from linear models, from all transects, comparing functional group richness in structurally-defined ecotone belts versus forested and grassland belts, with transect as a blocking variable and belt type as a categorical variable in each model (lm=Variable~Belt.type+Transect).¹

Variable	North-facing Ecotones				South-facing Ecotones			
	Forest-Ecotone		Grassland-Ecotone		Forest-Ecotone		Grassland-Ecotone	
	Δ in intercept	<i>p</i> value	Δ in intercept	<i>p</i> value	Δ in intercept	<i>p</i> value	Δ in intercept	<i>p</i> value
Mean species								
Richness	pos	0.062	neg	0.756	pos	0.526	neg	0.157
Total species								
Richness	neg	0.145	neg	0.103	neg	0.033	neg	0.087
Rare species	pos	0.079	neg	0.326	pos	0.194	neg	0.076
Shade Tolerant Groups								
Tolerant	pos	0.564	pos	0.221	neg	0.280	neg	0.900
Intermediate	pos	0.162	pos	0.701	neg	0.217	pos	0.930
Intolerant	pos	<0.000	neg	<0.000	pos	0.001	neg	0.001
Growth Form Group								
Forb	pos	0.011	neg	0.868	pos	0.488	neg	0.020
Graminoid	pos	<0.000	neg	0.383	pos	0.020	neg	0.061
Shrub	neg	0.023	pos	0.210	neg	0.017	pos	0.011
Tree sapling	pos	0.018	neg	0.282	pos	0.505	neg	0.059
Dispersal Method Group								
None	pos	0.182	pos	0.043	neg	0.447	neg	0.007
Wind	pos	0.011	neg	0.022	pos	0.007	neg	0.003
Animal	pos	0.319	pos	<0.000	neg	0.064	pos	0.934
Generalist	pos	0.002	neg	<0.000	pos	0.007	neg	0.024
Status Groups								
Native	pos	0.011	neg	0.736	pos	0.265	neg	0.062
Exotic	pos	0.001	pos	0.584	pos	0.478	neg	0.137
Drought Tolerant Groups								
Tolerant	pos	0.134	pos	0.860	neg	0.395	neg	0.314
Intermediate	pos	0.003	neg	0.834	pos	0.054	neg	0.301
Intolerant	pos	0.114	neg	0.891	neg	0.068	neg	0.234
Indicator Groups								
Aspen stands	pos	0.799	pos	0.004	neg	0.008	pos	0.346
Grassland	pos	0.021	neg	0.010	pos	0.005	neg	0.006

¹North and are analyzed separately and p values in bold are statistically significant ($p < 0.05$). Change in intercept indicates the direction of change in the variable in ecotonal belts compared to either the forested or grassland belts (i.e., at south-facing aspects total species richness is significantly lower in ecotonal belts than in forest belts).

Table A.6 Results from linear models comparing abundance of functional groups in structurally-defined ecotone belts versus forested and grassland belts, with transect as a blocking variable and belt type as a categorical variable in each (lm= variable~belt.type+transect).¹

Variable	North-facing Ecotones				South-facing Ecotones			
	Forest-Ecotone		Grassland-Ecotone		Forest-Ecotone		Grassland-Ecotone	
	Δ in intercept	<i>p</i> value	Δ in intercept	<i>p</i> value	Δ in intercept	<i>p</i> value	Δ in intercept	<i>p</i> value
Rare species	pos	0.740	neg	0.017	pos	0.062	pos	0.002
Shade Tolerant Groups								
Tolerant	neg	0.052	pos	0.863	neg	0.313	pos	0.327
Intermediate	pos	0.602	pos	0.039	neg	0.048	pos	0.959
Intolerant	pos	0.576	neg	0.005	pos	0.704	neg	0.615
Growth Form Groups								
Forb	pos	0.842	pos	0.684	neg	0.379	neg	0.399
Graminoid	pos	0.024	neg	0.112	pos	0.022	neg	0.926
Shrub	neg	0.001	pos	0.218	neg	0.005	pos	0.421
Tree sapling	pos	0.287	pos	0.067	pos	0.636	neg	0.037
Dispersal Method Groups								
None	neg	0.788	pos	0.001	neg	0.010	pos	0.965
Wind	pos	0.177	pos	0.050	pos	0.531	pos	0.072
Animal	neg	0.070	pos	0.201	neg	0.006	pos	0.442
Generalist	pos	0.037	neg	<0.000	pos	0.015	pos	0.984
Status Groups								
Native	neg	0.047	neg	0.011	neg	0.218	neg	0.522
Exotic	pos	0.054	pos	0.117	pos	0.780	pos	0.580
Drought Tolerant Groups								
Tolerant	pos	0.251	pos	0.924	pos	0.736	pos	0.121
Intermediate	neg	0.710	neg	0.017	pos	0.734	neg	0.285
Intolerant	pos	0.221	pos	0.130	pos	0.269	neg	0.849
Indicator Groups								
Aspen stands	pos	0.893	pos	0.005	neg	<0.000	pos	0.464
Grassland	pos	0.009	neg	0.046	pos	0.001	neg	0.010

¹North and south are analyzed separately and *p* values in bold are statistically significant (*p*<0.05). Change in intercept indicates the direction of change in the variable in ecotonal belts compared to either the forested or grassland belts (i.e., at north-facing aspects rare species abundance is significantly lower in ecotone belts than in grassland belts).

Table A.7 Summaries of generalized linear models comparing plant functional group richness for forested belts with increasing distance from the statistically-defined ecotone centre, with distance included as a continuous variable. lm=variable~distance from statistically-defined ecotone centre.¹

Variable	North-facing Ecotone		South-facing Ecotones	
	p value	slope	p value	slope
Mean Species Richness	0.468	pos	0.001	pos
Exotic Species	<0.000	pos	0.439	neg
Shade Tolerant Groups				
Tolerant	0.016	pos	0.430	neg
Intermediate	0.002	pos	0.167	neg
Intolerant	<0.000	pos	<0.000	pos
Growth Form Groups				
Forb	<0.000	pos	<0.000	pos
Graminoid	<0.000	pos	<0.000	pos
Shrub	0.001	neg	0.002	neg
Tree sapling	0.020	pos	<0.000	pos
Drought Tolerant Groups				
Tolerant	<0.000	pos	<0.000	pos
Intermediate	<0.000	pos	<0.000	pos
Intolerant	0.001	pos	<0.000	neg
Nitrogen Fixation Groups				
Fixation	0.051	pos	0.892	pos
None	0.136	neg	<0.000	neg
Indicator Species Groups				
Aspen	<0.000	neg	<0.000	neg
Grassland	<0.000	pos	<0.000	pos
Dispersal Method Groups				
None	0.227	pos	0.101	neg
Wind	0.246	pos	0.050	pos
Animal	<0.000	pos	<0.000	pos
Generalist	<0.000	pos	<0.000	pos

¹North and south are analyzed separately and p values in bold are statistically significant (p<0.05). Slope indicates the change in the variable over the distance gradient (i.e., at south-facing aspects there is a significant increase in mean species richness with increasing proximity to the ecotone centre).

Table A.8 Summaries of generalized linear models comparing plant functional group abundance for forested belts with increasing distance from the statistically-defined ecotone centre, with distance included as a continuous variable. lm=variable~distance from statistically-defined ecotone centre.¹

Variable	North-facing Ecotone		South-facing Ecotones	
	p value	slope	p value	slope
Exotic Species	0.114	pos	0.734	neg
Shade Tolerant Groups				
Tolerant	0.592	neg	0.014	neg
Intermediate	0.001	pos	0.003	neg
Intolerant	0.015	neg	0.096	neg
Growth Form Groups				
Forb	0.323	neg	0.312	pos
Graminoid	0.263	neg	0.499	pos
Shrub	0.060	neg	0.972	pos
Tree sapling	0.247	pos	0.058	neg
Drought Tolerant Groups				
Tolerant	0.001	pos	0.004	neg
Intermediate	0.692	pos	0.034	pos
Intolerant	<0.000	pos	0.001	pos
Nitrogen Fixation Groups				
Fixation	0.446	pos	0.812	pos
None	0.198	neg	<0.000	neg
Indicator Species Groups				
Aspen	<0.000	neg	<0.000	neg
Grassland	<0.000	pos	<0.000	pos
Dispersal Method Groups				
None	0.005	pos	0.002	neg
Wind	<0.000	pos	0.014	pos
Animal	<0.000	neg	<0.000	neg
Generalist	<0.000	pos	0.027	pos

¹North and south are analyzed separately and p values in bold are statistically significant (p<0.05). Slope indicates the change in the variable over the distance gradient (i.e., at north-facing aspects there is a significant increase in abundance of intermediate shade tolerant species with increasing proximity to the ecotone centre).

Table A.9 Summaries of generalized linear models comparing plant functional group richness for both forested and grassland transects with increasing distance from the structural ecotone (treeline), with distance included as a continuous variable.

lm=variable~distance from treeline.¹

Variable	North-facing Ecotone		South-facing Ecotones	
	p value	slope	p value	slope
Mean Species richness				
Grassland	0.053	pos	0.026	neg
Forested	<0.000	pos	0.246	pos
Exotic species				
Grassland	0.817	pos	0.035	neg
Forested	<0.000	pos	0.001	pos
Shade Tolerant Groups				
Grassland				
Tolerant	0.248	pos	0.221	pos
Intermediate	0.003	pos	0.701	pos
Intolerant	0.001	pos	<0.000	neg
Forested				
Tolerant	0.044	neg	0.002	neg
Intermediate	0.182	pos	0.027	neg
Intolerant	<0.000	pos	<0.000	pos
Growth Form Groups				
Grassland				
Forb	0.184	pos	0.002	neg
Graminoid	0.032	neg	0.255	neg
Shrub	<0.000	pos	0.002	pos
Tree sapling	0.416	neg	0.100	neg
Forested				
Forb	<0.000	pos	0.169	neg
Graminoid	<0.000	pos	<0.000	pos
Shrub	<0.000	neg	0.005	neg
Tree sapling	0.029	pos	0.332	pos
Drought Tolerant Groups				
Grassland				
Tolerant	0.008	neg	0.001	neg
Intermediate	0.060	neg	0.648	neg
Intolerant	<0.000	pos	0.059	neg
Forested				

	Tolerant	<0.000	pos	0.169	pos
	Intermediate	<0.000	pos	0.000	pos
	Intolerant	0.251	neg	0.243	neg
Nitrogen Fixation Groups					
Grassland					
	Fixation	0.003	pos	0.062	neg
	None	0.991	neg	0.003	neg
Forested					
	Fixation	<0.000	pos	<0.000	neg
	None	0.002	pos	0.003	pos
Indicator Species Groups					
Grassland					
	Aspen	<0.000	pos	0.277	pos
	Grassland	<0.000	neg	0.013	neg
Forested					
	Aspen	0.723	pos	<0.000	neg
	Grassland	<0.000	pos	<0.000	pos
Dispersal Method Groups					
Grassland					
	None	0.043	neg	0.007	pos
	Wind	0.022	pos	0.003	pos
	Animal	<0.000	neg	0.933	neg
	Generalist	<0.000	pos	0.024	pos
Forested					
	None	0.013	neg	0.318	pos
	Wind	<0.000	neg	0.023	neg
	Animal	0.253	pos	<0.000	pos
	Generalist	<0.000	neg	<0.000	neg

¹North and south are analyzed separately and p values in bold are statistically significant (<0.05). Slope indicates the change in the variable over the distance gradient (i.e., at north-facing grasslands there is a significant increase in mean species richness with increasing proximity to the ecotone centre).

Table A.10 Summaries of generalized linear models comparing abundance of plant functional groups for both forested and grassland transects along a distance gradient from the structurally-defined ecotone (treeline). lm=variable~distance from treeline.¹

Variable	North-facing Ecotone		South-facing Ecotones	
	p value	slope	p value	slope
Exotic species				
Grassland	0.001	pos	0.927	neg
Forest	0.073	pos	0.002	pos
Shade Tolerant Groups				
Grassland				
Tolerant	0.010	pos	0.011	pos
Intermediate	< 0.000	pos	0.026	neg
Intolerant	< 0.000	neg	0.091	neg
Forested				
Tolerant	< 0.000	neg	0.586	pos
Intermediate	0.058	pos	< 0.000	neg
Intolerant	0.802	neg	0.622	pos
Growth Form Groups				
Grassland				
Forb	0.002	pos	0.867	neg
Graminoid	< 0.000	neg	0.808	pos
Shrub	0.002	pos	0.017	pos
Tree sapling	0.521	neg	0.191	neg
Forested				
Forb	0.296	neg	< 0.000	neg
Graminoid	0.163	pos	< 0.000	pos
Shrub	0.050	neg	< 0.000	neg
Tree sapling	0.176	pos	0.668	pos
Drought Tolerant Groups				
Grassland				
Tolerant	0.151	pos	< 0.000	pos
Intermediate	0.003	neg	< 0.000	neg
Intolerant	0.410	pos	0.052	pos
Forested				
Tolerant	< 0.000	pos	< 0.000	pos
Intermediate	0.298	neg	0.898	neg
Intolerant	0.086	pos	0.052	pos
Nitrogen Fixation Groups				
Grassland				
Fixation	0.114	pos	0.390	pos
None	< 0.000	neg	0.716	pos
Forested				

	Fixation	0.034	pos	<0.000	neg
	None	0.012	neg	0.228	neg
Indicator Species Groups					
Grassland					
	Aspen	<0.000	pos	0.001	pos
	Grassland	<0.000	neg	<0.000	neg
Forested					
	Aspen	<0.000	neg	<0.000	neg
	Grassland	<0.000	pos	0.060	pos
Dispersal method Groups					
Grassland					
	None	0.001	neg	0.965	neg
	Wind	0.050	neg	0.072	neg
	Animal	0.201	neg	0.442	pos
	Generalist	<0.000	pos	0.984	pos
Forested					
	None	0.930	pos	0.930	neg
	Wind	0.281	neg	0.281	pos
	Animal	<0.000	pos	<0.000	neg
	Generalist	<0.000	neg	<0.000	pos

¹North and south are analyzed separately and p values in bold are statistically significant ($p < 0.05$). Slope indicates the change in the variable over the distance gradient (i.e., at north-facing aspects there is a significant increase in abundance of exotic species with increasing proximity to the ecotone centre into the grassland).

Table A.11. Species identified in this study and functional groupings.

Scientific names	Status	Growth form	Shade tolerance	Seed distribution	Nitrogen fixation	Drought tolerance	Indicator
<i>Acer glabrum</i>	native	shrub	intermediate	wind	none	intermediate	unkn
<i>Achillea millefolium</i>	native	forb	tolerant	wind	none	intermediate	grassland
<i>Achnatherum occidentale</i>	native	graminoid	intermediate	wind/animal	none	tolerant	grassland
<i>Achnatherum richardsonii</i>	native	graminoid	intermediate	wind/animal	none	unkn	grassland
<i>Agoseris glauca</i>	native	forb	intolerant	wind	none	intermediate	none
<i>Agoseris grandiflora</i>	native	forb	intolerant	wind	none	intermediate	none
<i>Agrostis scabra</i>	native	graminoid	intolerant	none	none	intolerant	unkn
<i>Allium cernuum</i>	native	forb	intermediate	none	none	intermediate	none
<i>Allium geeyeri</i> var. <i>Tenerum</i>	native	forb	unkn	none	none	unkn	none
<i>Alnus incana</i> subsp. <i>tenuifolia</i>	native	forb	intermediate	animal	intermediate	intolerant	unkn
<i>Alyssum alyssoides</i>	exotic	forb	unkn	none	none	unkn	unkn
<i>Amelanchier alnifolia</i>	native	forb	intermediate	animal	none	intolerant	aspen
<i>Anemone multifida</i> var. <i>multifida</i>	native	forb	intermediate	wind	none	intermediate	none
<i>Antennaria microphylla</i>	native	forb	intolerant	wind	none	intermediate	grassland
<i>Arabis holboellii</i>	native	forb	intermediate	wind	none	intermediate	none
<i>Arctium minus</i>	exotic	forb	unkn	animal	none	unkn	unkn
<i>Arenaria serpyllifolia</i>	exotic	forb	unkn	none	none	unkn	none
<i>Arnica fulgens</i>	native	forb	tolerant	wind	none	intolerant	none
<i>Artemisia dracunculus</i>	native	forb	intermediate	wind	none	tolerant	unkn
<i>Astragalus collinus</i>	native	forb	intolerant	animal	none	unkn	none
<i>Astragalus miser</i>	native	forb	intolerant	animal	none	unkn	unkn
<i>Balsamorhiza sagittata</i>	native	forb	intermediate	wind	none	tolerant	none
<i>Bromus ciliatus</i>	native	graminoid	tolerant	wind	none	intolerant	unkn
<i>Bromus inermis</i>	exotic	graminoid	intolerant	wind/animal	none	intermediate	none
<i>Bromus pumpellianus</i>	native	graminoid	unkn	none	none	unkn	unkn
<i>Bromus tectorum</i>	exotic	graminoid	intolerant	wind/animal	none	tolerant	none
<i>Calamagrostis rubescens</i>	native	graminoid	tolerant	wind	none	intolerant	none
<i>Calochortus macrocarpus</i>	native	forb	intolerant	none	none	tolerant	grassland

<i>Camelina microcarpa</i>	exotic	forb	unkn	none	none	unkn	none
<i>Campanula rotundifolia</i>	native	forb	intolerant	wind	none	tolerant	none
<i>Carex aurea</i>	native	forb	intermediate	none	none	intolerant	none
<i>Carex disperma</i>	native	forb	intermediate	wind	none	intolerant	none
<i>Carex petasata</i>	native	graminoid	unkn	none	none	unkn	none
<i>Castilleja thompsonii</i>	native	forb	intolerant	none	none	intermediate	none
<i>Centaurea stoebe</i>	exotic	forb	intolerant	wind	none	tolerant	unkn
<i>Cerastium arvense</i>	native	forb	intermediate	animal	none	tolerant	grassland
<i>Chenopodium album</i>	exotic	forb	intolerant	none	none	intermediate	none
<i>Chimaphila umbellata</i>	native	forb	tolerant	none	none	intermediate	unkn
<i>Cichorium intybus</i>	exotic	forb	intolerant	animal	none	intermediate	none
<i>Collinsia parviflora</i>	native	forb	tolerant	none	none	intolerant	none
<i>Collomia linearis</i>	native	forb	intolerant	animal	none	tolerant	grassland
<i>Comandra umbellata</i>	native	forb	intolerant	animal	none	tolerant	grassland
<i>Conyza canadensis</i>	exotic	forb	intolerant	wind	none	intolerant	unkn
<i>Crataegus monogyna</i>	exotic	tree	intolerant	animal	none	tolerant	unkn
<i>Crepis atribarba</i>	native	forb	intermediate	wind	none	intermediate	none
<i>Crepis tectorum</i>	exotic	forb	intolerant	wind	none	intermediate	unkn
<i>Cynoglossum officinale</i>	exotic	forb	intolerant	animal	none	unkn	none
<i>Dactylis glomerata</i>	exotic	graminoid	tolerant	animal	none	intermediate	none
<i>Danthonia intermedia</i>	native	graminoid	intermediate	wind/animal	none	intermediate	unkn
<i>Delphinium nuttallianum</i>	native	forb	tolerant	none	none	tolerant	none
<i>Descurainia sophia</i>	exotic	forb	intolerant	animal	none	intermediate	none
<i>Elymus glaucus</i>	native	graminoid	tolerant	none	none	tolerant	aspen
<i>Elymus repens</i>	exotic	graminoid	intolerant	none	none	intolerant	none
<i>Epilobium angustifolium</i>	native	forb	tolerant	wind	none	intermediate	unkn
<i>Eremogone capillaris</i> var. <i>americana</i>	native	forb	tolerant	none	none	tolerant	unkn
<i>Erigeron corymbosus</i>	native	forb	tolerant	wind	none	intermediate	none
<i>Erigeron filifolius</i> var. <i>filifolius</i>	native	forb	intolerant	wind	none	tolerant	none
<i>Erigeron flagellaris</i>	native	forb	unkn	wind	none	unkn	none

<i>Erigeron linearis</i>	native	forb	intolerant	wind	none	tolerant	unkn
<i>Erigeron pumilus</i> <i>var. Intermedius</i>	native	forb	unkn	wind	none	unkn	unkn
<i>Eriogonum</i> <i>heracleoides</i>	native	forb	intolerant	wind	none	unkn	grassland
<i>Eurybia conspicua</i>	native	forb	unkn	wind	none	unkn	none
<i>Festuca campestris</i>	native	graminoid	intolerant	wind/animal	none	intermediate	grassland
<i>Fragaria</i> <i>virginiana</i>	native	forb	tolerant	animal	none	intolerant	aspen
<i>Fritillaria affinis</i>	native	forb	intermediate	wind	none	unkn	unkn
<i>Fritillaria pudica</i>	native	forb	intermediate	wind	none	intermediate	grassland
<i>Gaillardia</i> <i>aristata</i>	native	forb	intolerant	wind	none	intermediate	none
<i>Galium boreale</i>	native	forb	intermediate	animal	none	intermediate	aspen
<i>Gentianella</i> <i>amarella</i>	native	forb	intermediate	wind	none	unkn	none
<i>Geranium</i> <i>viscosissimum</i>	native	forb	tolerant	none	none	intolerant	none
<i>Geum triflorum</i>	native	forb	intermediate	wind	none	tolerant	none
<i>Hesperostipa</i> <i>comata</i>	native	graminoid	intolerant	wind/animal	none	tolerant	none
<i>Heuchera</i> <i>cylindrica</i>	native	forb	intermediate	none	none	tolerant	none
<i>Juncus balticus</i>	native	graminoid	tolerant	wind/animal	none	intermediate	grassland
<i>Juniperus</i> <i>communis</i>	native	shrub	intolerant	animal	none	tolerant	none
<i>Juniperus</i> <i>scopulorum</i>	native	shrub	intolerant	animal	none	tolerant	none
<i>Koeleria</i> <i>macrantha</i>	native	graminoid	tolerant	none	none	tolerant	unkn
<i>Lathyrus</i> <i>nevadensis</i>	native	forb	intermediate	none	none	unkn	unkn
<i>Lathyrus</i> <i>ochroleucus</i>	native	forb	intermediate	none	none	unkn	aspen
<i>Lilium</i> <i>columbianum</i>	native	forb	intermediate	wind	none	unkn	none
<i>Linnaea borealis</i>	native	forb	tolerant	none	none	unkn	none
<i>Lithospermum</i> <i>ruderae</i>	native	forb	intolerant	none	none	intermediate	grassland
<i>Lomatium</i> <i>dissectum</i>	native	forb	intermediate	wind	none	tolerant	none
<i>Lomatium</i> <i>macrocarpum</i>	native	forb	intolerant	wind	none	tolerant	none
<i>Lomatium</i> <i>triternatum</i>	native	forb	intermediate	wind	none	intolerant	unkn
<i>Lotus denticulatus</i>	native	forb	intolerant	none	none	unkn	grassland
<i>Mahonia</i> <i>aquifolium</i>	native	shrub	tolerant	animal	none	tolerant	aspen
<i>Maianthemum</i> <i>racemosum</i>	native	forb	tolerant	animal	none	unkn	none
<i>Maianthemum</i>	native	forb	tolerant	animal	none	unkn	aspen

<i>stellatum</i>							
<i>Medicago lupulina</i>	exotic	forb	intolerant	animal	intermediate	intolerant	none
<i>Medicago sativa</i>	exotic	forb	intolerant	animal	tolerant	tolerant	none
<i>Melilotus alba</i>	exotic	forb	intolerant	wind/animal	intermediate	tolerant	none
<i>Moehringia lateriflora</i>	native	forb	tolerant	animal	none	unkn	aspen
<i>Muhlenbergia richardsonis</i>	native	graminoid	intolerant	none	none	intolerant	none
<i>Myosotis stricta</i>	exotic	forb	intolerant	animal	none	unkn	grassland
<i>Orthocarpus luteus</i>	native	forb	intolerant	none	none	tolerant	none
<i>Osmorhiza berteroi</i>	native	forb	intermediate	animal	none	unkn	aspen
<i>Penstemon procerus</i>	native	forb	intolerant	none	none	unkn	grassland
<i>Perideridia gairdneri</i>	native	forb	intolerant	wind/animal	none	intolerant	unkn
<i>Phacelia linearis</i>	native	forb	intermediate	none	none	unkn	unkn
<i>Phleum pratense</i>	native	graminoid	intermediate	wind/animal	none	intolerant	none
<i>Piperia unalascensis</i>	native	forb	tolerant	wind	none	unkn	unkn
<i>Poa compressa</i>	exotic	graminoid	tolerant	wind/animal	none	intermediate	unkn
<i>Poa pratensis</i>	exotic	graminoid	intolerant	wind/animal	none	unkn	none
<i>Poa secunda</i>	native	graminoid	intermediate	wind/animal	none	tolerant	grassland
<i>Polygonum douglasii</i>	native	forb	intolerant	wind	none	unkn	grassland
<i>Populus tremuloides</i>	native	tree	intolerant	wind	none	intolerant	aspen
<i>Potentilla glandulosa</i>	native	forb	unkn	none	none	unkn	none
<i>Potentilla gracilis</i>	native	forb	intolerant	none	none	intermediate	none
<i>Prosartes trachycarpa</i>	native	forb	tolerant	animal	none	unkn	none
<i>Prunus virginiana</i>	native	shrub	intolerant	animal	none	intermediate	none
<i>Pseudoroegneria spicata</i>	native	graminoid	intolerant	wind/animal	none	tolerant	grassland
<i>Pseudotsuga menziesii</i>	native	tree	intermediate	wind	none	intolerant	none
<i>Rhinanthus minor</i>	native	forb	intolerant	wind	none	unkn	grassland
<i>Ribes lacustre</i>	native	shrub	tolerant	animal	none	intolerant	none
<i>Rosa acicularis</i>	native	shrub	tolerant	animal	none	intolerant	none
<i>Silene menziesii</i>	native	forb	intermediate	wind	none	unkn	aspen
<i>Sisyrinchium idahoense</i>	native	forb	tolerant	none	none	intolerant	none
<i>Solidago simplex</i>	native	forb	tolerant	wind	none	unkn	none

<i>Sonchus arvensis</i>	exotic	forb	intolerant	wind	none	unkn	none
<i>Spartina gracilis</i>	native	graminoid	intolerant	wind	none	intermediate	none
<i>Spiraea betulifolia</i>	native	shrub	tolerant	wind/animal	none	intolerant	unkn
<i>Spiranthes romanzoffiana</i>	native	forb	intermediate	wind	none	intolerant	unkn
<i>Sporobolus cryptandrus</i>	native	graminoid	intolerant	wind	none	tolerant	unkn
<i>Streptopus lanceolatus</i>	native	forb	tolerant	animal	none	unkn	unkn
<i>Symphoricarpos albus</i>	native	shrub	intolerant	animal	none	tolerant	aspen
<i>Symphiotrichum ericoides var. pansum</i>	native	forb	intermediate	wind	none	unkn	unkn
<i>Symphiotrichum foliaceum</i>	native	forb	intermediate	wind	none	unkn	unkn
<i>Symphiotrichum subspicatum</i>	native	forb	intermediate	wind	none	intolerant	unkn
<i>Taraxacum officinale</i>	exotic	forb	intermediate	wind	none	intermediate	aspen
<i>Thalictrum occidentale</i>	native	forb	intermediate	wind	none	unkn	unkn
<i>Tragopogon dubius</i>	exotic	forb	intolerant	wind	none	tolerant	grassland
<i>Trifolium pratense</i>	exotic	forb	intermediate	animal	intermediate	unkn	none
<i>Trifolium repens</i>	exotic	forb	intermediate	animal	tolerant	unkn	unkn
<i>Verbascum thapsus</i>	exotic	forb	intermediate	none	none	unkn	none
<i>Vicia americana</i>	native	forb	intermediate	none	intolerant	tolerant	aspen
<i>Viola adunca</i>	native	forb	intolerant	animal	none	intolerant	none
<i>Viola canadensis</i>	native	forb	tolerant	animal	none	intolerant	none
<i>Vulpia octoflora</i>	native	graminoid	intolerant	wind	none	unkn	unkn
<i>Zigadenus venenosus</i>	native	forb	intolerant	none	none	unkn	grassland