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Long-term Changes in Four Plant Communities Along an Elevational Gradient in the
Front Range of Colorado

A Thesis

Presented to

The Faculty of Natural Sciences and Mathematics

University of Denver

In Partial Fulfillment

of the Requirements for the Degree

Masters of Biological Sciences

by

Gregory J. Sproull

June 2014

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Title: Long-term Changes in Four Plant Communities Along an Elevational Gradient in the Front Range of Colorado
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ABSTRACT

We surveyed four plant communities along an elevational gradient in the Front Range of the Colorado Rocky Mountains for long-term overstory and understory changes. Our results were compared to those found in 1981 and 1996. We evaluated changes in succession, elevational species migration and range expansion, community diversity, and composition. We related temporal floristic shifts to prior literature on disturbance history at each site. Over time, all communities changed significantly, though in different manners. This analysis shows that plant communities are changing in dynamic and idiosyncratic ways that correspond to individualistic distribution shifts. Moreover, we exhibit the necessity of comprehensively investigating long-term community change using multiple approaches, incorporating plant guild relationships, and concentrating efforts to further understand the interplay between climate effects and disturbance.

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CHAPTER ONE: LITERATURE REVIEW

Introduction

Plant communities can be transient systems that may change with elevational gradients. Community composition is dictated by a complex suite of biotic and abiotic interactions and the stochastic events that act upon them (Botkin 1980). Ecological research has elucidated many of the underlying mechanisms driving these relationships but predictive power has been only loosely applicable to specific communities (McCook 1994, Van Bogaert et al. 2011). It is imperative that our understanding of floristic dynamics continues to progress because ecosystem services, the benefits provided by the ecosystem that enable humanity to thrive and persist, are directly affected by the function, structure, and diversity of these interactions and the communities that they comprise (Díaz et al. 2006).

Not only are plant communities remarkably interconnected, but many of them are differentially sensitive to abiotic and biotic change (Körner 2003, Lesica and McCune 2004). Small compositional changes can have extensive effects on community function (Parmesan 2003). Reductions in species richness and functional groups can affect ecological processes such as primary production, nutrient cycling, and decomposition, and can alter community organization and ecosystem function (Díaz et al. 2006, Cardinale et al. 2012). Species range expansions or contractions can disrupt niche

stability and can change the natural trajectory of post-disturbance processes and successional pathways (le Roux and McGeoch 2008, Kullman 2010).

In the last four decades, increased anthropogenic stressors have altered plant community composition and diversity across the world (Butchart et al. 2010). During this time, global biodiversity has been reduced with little evidence of slowing, while pressures on biodiversity, such as non-native organismal invasion, atmospheric nitrogen deposition, and resource exploitation by humans have increased (Butchart et al. 2010). These pressures, in concert with increased climatic warming and disturbance regime changes, have had synergistic effects (Folke et al. 2004) that are thought to be responsible for a multitude of landscape mosaic and species interaction changes (Vitousek et al. 1997, Hooper et al. 2005). In fact, a meta-study by Root et al. (2003) found an increase in geographic range for 80% of the species surveyed over a span of 30 years.

Tracking these changes in community composition is optimized by integrating accurate spatio-temporal modeling with long-term floristic survey data analysis (Ferrier and Guisan 2006). The need for long-term data is especially important in high-elevation systems, unique with plant species that are highly sensitive to weather and perturbation (Körner 1999). Though long-term studies have elucidated plant community shifts in recent years (Ebersole 2002, Klanderud and Birks 2003, Smith and Smith 2005, le Roux and McGeoch 2008, Coop et al. 2010, Johnson et al. 2011), most experiments occur over shorter timespans that offer only snapshots of community change (Connell and Slatyer 1977, Drake 1991). Lengthier studies can limit confounding environmental factors (Whipple and Dix 1979, MacMahon 1980, Klanderud and Birks 2003) and can more

comprehensively evaluate community organization (Drake 1991) and temporal stability (Hooper et al. 2005).

Secondary successional patterns and processes, in particular, are best demonstrated and interpreted via long-term resurveys on historical plots. The secondary successional pathway or temporal pattern of change in a disturbed community (Pickett et al. 1987) can be traced through fluxes in biomass, productivity, and composition (O'Neill and Reichle 1980). Each pathway consists of a continuum of indeterminate states (Gleason 1926, Tansley 1935) that reflect the stability and composition of the system relative to its previous forms (Holling 1973, O'Neill and Reichle 1980). Long-term data can provide more accurate accounts of these stressors responses. Studies of dynamics in secondary succession forests (Billings 1969, Whipple and Dix 1979, Peet 1981, Veblen 1986, Whitmore 1989, Hadley 1994, Smith and Smith 2005, Johnson et al. 2011, Worrall et al. 2013) can be especially useful for forest management, conservation assessment, and theoretical modeling. They provide site-specific floristic data, evaluating community resilience and response to disturbance regimes shifts and anthropogenic pressures, such as human resource exploitation, pollution, and land-use change that ultimately affect ecosystem services, including plant biomass production, soil formation, water quality regulation, pollination and seed dispersal of highly-valued plants, community resistance to invasive species, and climate and disease regulation (Folke et al. 2004, Díaz et al. 2006).

Geographic range expansion along elevational gradients is another measure of community change that can be elucidated through long-term floristic analysis.

Geographic ranges for arctic plants have contracted (Lesica and McCune 2004), while lowland and mid-elevation plants have expanded upward in elevation and have shown phenological shifts precipitated by global climate change (Parmesan and Yohe 2003). Models suggest that alpine tree-lines will likely move to higher elevations (Chauchard et al. 2010), decoupling certain species from their known communities (Iverson and Prasad 1998). Though the specific environmental drivers facilitating geographic expansion have often been generalized (Stephenson 1990, Stephenson 1998, Woodward and Beerling 2013), it is clear that climatic/weather and edaphic changes affect floristic distribution (Dolezal and Srutek 2002, Root et al. 2003, Parmesan and Yohe 2003, Lesica and McCune 2004).

Long-term assessments of elevational range shifts in floristics are important because they can describe changes in community resilience and biodiversity (Klanderud and Birks 2003) that may have far-reaching effects on community function, productivity, and ecosystem services (Folke et al. 2004). Rates and ranges of elevational migration differ from species to species and from guild to guild (Huntley 1996, le Roux and McGeoch 2008) due to disparities in response to abiotic factors such as solar radiation, soil moisture and structure, and ambient air temperature, and biotic factors such as competition, predation, and symbiosis (Gleason 1926, Tansley 1935, MacMahon 1980, Huntley 1996, Dolezal and Srutek 2002, le Roux and McGeoch 2008). Therefore, a firmer understanding of geographic range shifts may assist ecologists and conservationists in determining which species and community configurations are most likely to impact ecosystem processes and function (Root et al. 2003).

Succession

Historical Perspective

First conceived in 1825 (Dureau de la Malle) and formally demonstrated in 1899 (Cowles), ecological succession is broadly characterized as the continual sequence of compositional changes in plant communities (Tansley 1935) that occur over a wide range of spatial and temporal scales (MacMahon 1980, McCook 1994). It is a process measured through time (Davis 1899). Nearly all communities are considered to be in secondary successional phases, having been altered previously by some form of disturbance.

Early ecologists, including Cowles (1899) and Clements (1916, 1928, 1936), viewed succession patterns as deterministic and directional, climaxing in single stable, or unchanging, climate-driven community states. This idea, coined as the ‘Monoclimax Theory,’ relates to the community as a whole, ostensibly proving plant communities to be autonomous ‘superorganisms’ that behave as units unto themselves (Clements 1928). Though these seminal concepts would come under heavy assault (Gleason 1926, Whittaker 1953), they provided an empirical framework for successional theory.

Gleason’s individualistic concept of succession (1926) and Tansley’s ecosystem equilibrium concepts (1935) viewed plant association as a continuum of plastic species interactions largely governed by stochastic environmental events. Their studies provided ample evidence for the existence of multiple secondary successional “climax” states alternative to those relating to climate/weather, such as edaphic, physiographic, and biotic climaxes—an idea commonly known as the ‘Polyclimax Theory.’ Theories on secondary

successional pattern and community association evolved in myriad trajectories in the decades that followed. Watt (1947) provided a context for community pattern as a measurable unit in a space-time mosaic of species and proposed the concept of cyclical succession that refuted the notion of stable state climax communities. Egler (1954) attributed “vegetation development,” a term he preferred over succession (McCook 1994), to floristic growth rate differences.

Theories relating to monoclimax and polyclimax communities came under scrutiny as being too subjective and abstract in Whittaker’s ‘Pattern Climax Hypothesis’ (1953). Whittaker argued that plant communities have no inherent fixed endpoint or overarching rules. This concept was further expanded by Horn (1974), who focused on diversity in secondary succession and the limitless potential of climax patterns, and by Lewontin’s ‘Alternative Stable State Hypothesis’ (1969), which questioned previous ideas of stability and equilibrium, and described community composition states as derivatives of ecosystem change. Sutherland’s (1974) work on multiple stable points in the context of historical events aligned with Lewontin’s (1969) ideas on analyzing community succession from a historical perspective, and provided a theoretical basis for modeling autogenic secondary successional pathways (Connell and Slatyer 1977, Pickett 1987), alternative stable states (May 1977, Law and Morton 1993), and life history traits of species as predictors of successional pattern (Grime 1977, Chapin et al. 1994).

Plant community resilience, or the degree to which plant systems can withstand short-term environmental perturbations without having long-term changes in process or structure, was first demonstrated in the context of ecological succession by Holling

(1973). Holling expanded on this concept in his 'Ball-in-cup' model of resistance, which now serves as a heuristic explanation of community thresholds and state shifts (Holling et al. 1995).

In more recent times, secondary successional research has focused on disturbance hypotheses (Roxburgh et al. 2004, Fox 2013) and regime shifts in the context of biodiversity, resilience, and hysteresis, the condition of physical property lags in response to perturbation (Scheffer et al. 2001, Scheffer and Carpenter 2003, Beisner et al. 2003, Folke et al. 2004, Schmitz 2004). These factors are thought to have synergistic effects on ecosystem function (Folke et al. 2004). Gradual environmental changes may abruptly shift communities to alternative stable states (Schmitz 2004, Folke et al. 2004), causing large ecological and economic losses (Scheffer et al. 2001). Much of the terminology surrounding these ideas has been scrutinized (McCook 1994, Grimm and Wissel 1997, Beisner et al. 2003) in hopes of clarifying ambiguities and controversies that persist.

Ecological theory can be further convoluted by differing perspectives— an issue intrinsically difficult to assess (Beisner et al. 2003). Most successional theory can be separated into two paradigms: the ecosystem perspective and the community perspective. The ecosystem perspective is a school of thought, focused on the effects of environmental change on community states, that views ecological resilience as dynamic (Scheffer et al. 2001). The community perspective is concerned with community configurations and interactions, regarding the environment as somewhat fixed and ecological resilience as static (Drake 1991, Law and Morton 1993). Though both perspectives are widely valued, a comprehensive synthesis of approaches will be required to advance our understanding

of the complex continuum of plant community state shifts, patterns, and drivers amidst continued anthropogenic disturbance (Beisner et al. 2003).

High-altitude Temperate Forest as a Model System

Though the first physiological characterization of alpine systems was not published until 1968 (Billings and Mooney), alpine experimentation can be traced back to Kerner's reciprocal transplant work in the Tyrol (1869), and perhaps even farther back to work performed in the Alps by Naegeli in the mid-19th century (Körner 1999). Since then, alpine research has been largely focused on temperate zone forest interactions, thought to be governed by a combination of adaptive traits and climatic limitations (Körner 1999). The unique compression of life zones in mountain forest communities (Körner 1999), categorized by elevation (Ramaley 1907), are useful models for describing the interplay between environmental gradients and plant community dynamics (Whittaker 1953).

In North America, John Marr's secondary succession research in the Central Rocky Mountains of Colorado (1961) paved the way for field studies associating floristic dynamics with climatic variables. His work included detailed descriptions of elevational ecosystem types and floristic indicators of terrestrial ecological units (Marr 1961). Whittaker (1967) and Peet (1981) advanced the study of forest succession gradient analysis by classifying vegetation types as distinct entities within an environment, defined by elevation and exposure. Peet's research on post-disturbance floristic patterns (1981) remains a cornerstone of alpine secondary succession pattern theory.

Other contributions to temperate forest secondary succession research in North America include Daly and Shankman's tree-line work (Daly and Shankman 1985) that

showed exposure to wind to be a big determinant of local ranges of plants. This was supplemented by Whipple and Dix's study using age structures of populations to delineate successional phases (1979), Veblen's subalpine age and size structure work (1986), Hadley's post-disturbance successional research demonstrating the importance of aspect, elevation, and topography in determining landscape mosaics (1994), and Whitmore's canopy studies that differentiated pioneer from climax species (1989).

In the Rocky Mountains in particular, large-scale periodic disturbance has always been an important driver of community health and maintenance (Billings 1969). However, over the past century anthropogenic fires, logging, and mining have altered disturbance regimes and have influenced successional pathways in most forest communities in this region (Peet 1981). Such changes are known to have profound effects on ecologic processes such as nutrient cycling, evapotranspiration, ecologic resistance, resilience, and primary and secondary productivity (Díaz et al. 2006). Fire regime shifts (Billings 1969, Hadley 1994, Veblen et al. 2000, Coop et al. 2010, Keith et al. 2010, Williams and Baker 2012.), logging (Marr 1961, Peet 1981), insect infestation (Merrill and Hawksworth 1987, Hadley 1994, Robertson et al. 2009), herbivory (Sherrod and Seastedt 2001, Worrall et al. 2013), human recreation (Willard et al. 2007), anthropogenic nitrogen deposition (Bowman et al. 2006), nonnative invasions (Byrne et al. 2010), and increased atmospheric warming (Villalba et al. 1994, McGuire et al. 2012) have influenced secondary successional trajectories in these forests (Körner 1999).

Though some anthropogenic stressors, such as climate warming, nitrogen deposition, herbivory, and recreation may expedite secondary successional rates by

increasing resource availability and nutrient cycling (Körner 1999, Klanderud and Birks 2003), alterations to any disturbance regime can ultimately decrease community resilience. This may cause irreversible alternative states, or dynamic regime shifts (Scheffer et al. 2001, Folke et al. 2004, Schmitz 2004).

Research conducted in high-elevation temperate forests is especially relevant to understanding general successional patterns and processes. Long-term studies on post-disturbance recovery, a process known in high-elevation systems to progress at slower rates (Ives 1941, Körner 1999, Ebersole 2002) and show less distinguished secondary successional states (MacMahon 1980), provide land managers and conservationists with valuable resilience and diversity data that may rely on the transformation of undesirable community states into more amenable configurations (Folke et al. 2004). Furthermore, these studies can be analyzed in combination with floristic models as a means of assessing predictive accuracy (Ferrier and Guisan 2006) and ecologic theory, such as alternative stable states (Scheffer and Carpenter 2003). Lastly, since high-altitude communities are especially sensitive to environmental change, such as increased warming or decreased precipitation (Lesica and Steele 1996), changes in the composition, diversity, and function of these systems can serve as proxies for anthropogenic disturbance effects that should be more apparent at high elevations (Price and Waser 2000).

Geographic Range Expansion

Mechanisms of Control and Evidence of Elevational Shifts

Most plant species are distributed along environmental gradients. Their ranges are bounded by relative environmental tolerance (Gleason 1926) and biotic interactions (Dobzhansky 1950, MacArthur 1972, Dolezal and Srutek 2002, le Roux et al. 2012). Biogeographic research investigates the spatio-temporal processes that determine the shape, size, and boundary of these distributions (Brown et al. 1996). Species are generally most fit in the centers of their geographic range, and become increasingly stressed as they reach their outer boundaries (Angert and Schemske 2005). However, as species respond to environmental changes, invasions into new communities can cause wholesale shifts in community assemblage (le Roux and McGeoch 2008).

Though most historical studies have focused on associating elevational range boundaries with environmental factors, it was Dobzhansky (1950) and MacArthur (1972) who first differentiated the effects of abiotic and biotic factors in relation to elevational range limitations (Brown et al. 1996). They posited that biotic factors tend to limit distribution in lower elevations whereas abiotic factors are more likely to limit distribution in higher elevations. It has also been shown that higher elevation species generally have broader elevational ranges than lower elevation species (Brown et al. 1996). In the case of higher-elevation systems, abiotic limitations can include climatic factors of temperature and precipitation, as well as physiographic factors such as topography, edaphic agents, evapotranspiration, freezing and melting regimes, and erosion (Nichols 1923). If abiotic restrictions are prolonged, susceptibility to invasion from lower-elevation communities can ensue, increasing stress on species native to those ranges (Körner 1999). Migration in response to abiotic change has clear-cut winners and

losers in the community context, with species richness increasing at higher elevations (Grabherr 1994, Klanderud and Birks 2003) at the expense of alpine plants (Lesica and McCune 2004, Pauli et al. 2007, Kullman 2010).

The specific abiotic predictor variables of range expansion are still contested. Traditional climatic controls are often loosely correlated to floristic distribution (Stephenson 1990). In North America for instance, the best indicator of geographic range capacity is water balance, or the interaction between energy and water in plants (Stephenson 1990). Though some ecologists have shown correlations between elevational range expansion and abiotic parameters, such as wind exposure (Daly and Shankman 1985), temperature, nitrogen deposition (Johnson et al. 2011), snow duration, soil, and humidity (Dolezal and Srutek 2002), others have expressed concern in attributing species distributions to common meteorological variables, such as temperature (Stephenson 1998, Körner 1999, Woodward and Beerling 2013).

Regardless of the specific mechanisms driving elevational range distributions, empirical evidence points to upward elevational expansion in plant communities (Iverson and Prasad 1998, Parmesan and Yohe 2003, Root et al. 2003, Klanderud and Birks 2003, Pauli et al. 2007, le Roux and McGeoch 2008, Chauchard et al. 2010, Kullman 2010). Tree-lines (Iverson and Prasad 1998, Van Bogaert et al. 2011) and lower-elevation species (Root et al. 2003, Klanderud and Birks 2003, Pauli et al. 2007, Kullman 2010) have shown upward advancements, while most cold-adapted species have declined in abundance (Lesica and McCune 2004, Pauli et al. 2007). This trend is further illustrated by Parmesan and Yohe's global meta-analysis of 1,700 species, showing an average

upward range shift of 6.1 km per decade in conjunction with a 2.3 day advancement of spring phenology. The underlying causes of this shift are attributed to anthropogenic stressors, such as global warming (Iverson and Prasad 1998, Parmesan and Yohe 2003, Root et al. 2003, le Roux and McGeoch 2008, Kullman 2010), increased nitrogen deposition (Korb and Ranker 2001, Klanderud and Birks 2003, Bowman et al. 2006, Johnson et al. 2011), disturbance regime alteration (Van Bogaert et al. 2011), and changing biotic interactions (le Roux et al. 2012). These factors should be viewed synergistically (Peet 1978) and their effects should be gauged over long periods to account for hysteresis (Woodward 1987, Scheffer et al. 2001).

Individual Species Migration vs. Community Migration

The concept of community migration is nested in the work of Cowles (1899) but was championed most rigorously by Clements (1928, 1936), who viewed communities as autonomous units of vegetation that he termed ‘superorganisms.’ Though this concept is much more sophisticated than was originally interpreted (MacMahon 1980, McCook 1994), inspiring valuable works on ecosystem changes over time (Watt 1947, Odum 1969), it was diametrically opposed by individual species migration theorists, beginning with Gleason (1926). Gleason viewed plant communities as relics of species distribution configurations and range boundaries as dynamic continua. In the years that followed, community migration theory came under much scrutiny and was generally thought to have been disproven (Tansley 1935, Horn 1974, Pickett 1976, Connell and Slatyer 1977, Grime 1977).

More recently, individual species migration has been further demonstrated by studies relating community response to anthropogenic stressors. Models have been developed to evaluate individual tree species shifts (Iverson and Prasad 1998). Huntley's work in quaternary paleoecology (1996) showed differing migration rates among species, predicating new community compositions, and Dolezal and Srutek's (2002) case study in the Carpathians, involving altitudinal species migration, suggested no evidence of species aggregations at elevational boundary limits and instead demonstrated unique composite assemblages along elevational gradients. Le Roux and McGeoch's work (2008) also showed Gleasonian migration patterns, evidenced by shifts in plant species richness and composition that contrasted with migration rates, as did Kullman (2010) in his review of plant cover change correlating to warming in the Scandes, and Johnson et al. (2011) in their floristic resurvey along Niwot Ridge in Colorado that illustrated a decoupling of high-altitude mesic and xeric species.

Individual species' migration rates must be accounted for when examining community composition and species richness alterations. In mountain systems in particular, where diversity is enhanced by small-scale microclimates and perturbations coinciding with relief-influenced edaphic patterns such as slope and aspect, altitudinal migration can cause significant changes in community composition and diversity that greatly influence ecosystem function (Körner 1999). As anthropogenic pressures continue to build and global warming rates persist (Butchart et al. 2010), individual species migration rate studies will be of paramount significance in evaluating community

change because they provide tangible evidence of anthropogenic influence and can improve the capacity to manage ecosystems in the future (Root et al. 2003).

Gaps in Research

Many plant community patterns have been elucidated along elevational gradients over the past century, but few sites have been subjected to long-term observation. Long-term floristic analyses provide unique data on community patterns and processes (Woodward and Beerling 2013). Such studies offer rare glimpses into the continua of change that are often confounded by short-lived experiments that require bold extrapolation (Connell and Slatyer 1977, Drake 1991). Continuous processes, such as secondary succession and range expansion, merit prolonged observation that most studies cannot afford (Whipple and Dix 1979). Alternative state shifts and other dynamic successional patterns correlating to anthropogenic pressures may have nonlinear or lag responses that warrant extended analysis (Woodward 1987, Scheffer et al. 2001). Moreover, a firmer understanding of long-term plant community change can increase predictive modeling accuracy in the fields of restoration and conservation (Sardinero 2000, Ferrier and Guisan 2006). With this knowledge, future conservation and restoration projects relating to post-disturbance succession and species range expansion will be better informed (Parmesan and Yohe 2003, Root et al. 2003, Butchart et al. 2010).

Plan of Study

Using data from floristic surveys dating back 17, 32, and 60 years, I analyzed the long-term distributional, compositional, and secondary successional patterns of four plant

communities (lower montane, upper montane, subalpine, and alpine) along an elevational gradient. Tree communities were surveyed for density, basal area, and dominance to evaluate long-term secondary successional changes. Herbaceous communities were surveyed for species richness, composition, frequency, diversity, and species presence/absence to track long-term compositional changes and elevational range expansions/contractions. These community changes were compared and correlated to one another, as were survey variables, to show relative extents and rates of change. Results were analyzed from the context of disturbance and climate to elucidate correlations between human-induced influences and community changes.

This research built upon data from resurveys performed in 1981 (Kooiman and Linhart) and 1996 (Korb and Ranker) on plots first established in 1953 by John Marr (1961). In 1951, John Marr established a weather station in each life zone (lower montane, upper montane, subalpine, and alpine) along an elevational gradient on Niwot Ridge, northwest of Boulder, Colorado. In 1953, he performed detailed tree stand and herbaceous understory surveys at plots near his weather stations (Marr 1961). His work was intended to assess plant community composition and to set a baseline for future environmental query. Marr's sites were resurveyed in 1981 for changes in plant species richness, composition, frequency, and community diversity, using different transects and sampling techniques (Kooiman and Linhart 1986). Observed shifts in tree dominance and in the herbaceous understory community were linked to secondary successional changes caused by disturbances, such as logging and fire suppression, that had reshaped the canopy (Kooiman and Linhart 1986). Kooiman and Linhart's transects were

reassessed in 1996 for changes in community composition and richness, and for successional shifts in relative tree density and species dominance (Korb and Ranker 2001). This study provided a third temporal reference point for data relating to the herbaceous community at each site, as well as an additional tree abundance analysis that could be quantitatively compared to Marr's observations in 1953.

My investigation elucidated long-term spatial and temporal plant community shifts along an elevational gradient. It revealed patterns in floristic community dynamics and linked these changes to anthropogenic influence. By tracking various types of community change (distributional, compositional, and successional) in juxtaposed life zones, I determined the rate and manner in which communities have changed over a long period. These data indicated which community types and configurations are most susceptible to change, which species/genera/families are migrating upward in elevation, and which compositional changes and distributional shifts correlate to increased local temperatures and disturbance.

CHAPTER TWO: LONG-TERM SUCCESSIONAL TREE CHANGES

Introduction

Succession is a complex, continuous or intermittent process influenced by myriad biotic and abiotic factors (Tansley 1935, Whittaker 1953, Horn 1974). Secondary successional processes and patterns are thus most accurately evaluated from a long-term perspective, one that encompasses a series of community ‘snapshots’ across a temporal continuum. This method of analysis can better evaluate confounding variables, such as shifts in disturbance regimes and isolated stochastic events that alter successional trajectories and create idiosyncratic community organization. It can provide more robust insights into the environmental factors that drive succession (Drake 1991) and the magnitude of change within a system (Knapp et al. 2012). Elevational gradient analysis facilitates a study of spatial patterns in vegetation (Marr 1961, Whittaker 1967). It has revealed community-level response to elevation-driven physiological stressors and abiotic climatic changes (Sundqvist et al. 2013).

In forest systems, a variety of methods can be used to assess successional change, such as indirect and direct environmental gradient analysis and ordination (Whittaker 1967), age and size structure analysis (Veblen 1986), and canopy gap examination (Whitmore 1989). Here, in three previously disturbed communities along an elevational gradient, we used tree size structure and age demographic metrics to survey for changes in density, basal area per tree, and dominance.

This research was based on previous work by Marr, 1961 (“Ecosystems of the east slope of the Front Range in Colorado”) and Korb and Ranker, 2001 (“Changes in stand composition and structure between 1981 and 1996 in four Front Range plant communities in Colorado”) to examine long-term community changes in the lower montane, upper montane, and subalpine life zones. Our objective was to evaluate the extent and manner of successional change at each of 3 sites over a 17-year span, from 1996 to 2013. Our results were compared to predictions made by Marr in 1953 and Korb/Ranker in 1996 regarding future successional trajectories in each plant community.

The majority of long-term research experiments across the Long Term Ecological Research (LTER) Network were established less than 30 years ago (Knapp et al. 2012). The temporal scope of our analysis (60 years) is unique and elucidates community dynamics that most long-term studies cannot. Our investigation is useful for understanding long-term successional tree patterns in post-disturbance communities, and linking them to disturbance events. Additionally, it provides a third temporal reference point at these sites, for future inquiry into long-term plant community shifts in the Central Rockies.

Study Area

The study area is a field laboratory of the University of Colorado, Boulder, CO, and is comprised of three sites located along an elevational gradient at 40° N. This slope has an eastern aspect, and rises to Niwot Ridge, between the drainage basins of North Boulder Creek and Left Hand Creek in Boulder County, CO (Marr 1961). Each site was located on relatively flat terrain in a distinctly different vegetation zone. The term *site*

refers to a particular tree stand and its environment. Lower montane, upper montane, and subalpine vegetation zones were surveyed in this study (Figure 1). Sites were selected to represent an altitudinal transect that followed one ridge system (from the Plains to the Continental Divide). Transects were situated at intermediate elevations within each vegetation zone, to accurately depict typical tree communities in each zone (Marr 1961). Approximately 850 m in elevation (and 14.5 km in distance) separated the uppermost site from the lowermost site (Figure 2).

Our sites were originally established by John Marr in 1951, where weather stations were erected to measure variables including temperature and precipitation (Marr 1961). Sites were: A1 (lower montane), B1 (upper montane), and C1 (subalpine). In 1953, Marr performed detailed tree stand surveys at each site, to document vegetation and purposefully to create a baseline for future comparison (Marr 1961). Each site was resurveyed in 1996 by Julie Korb and Tom Ranker (Korb 1997, Korb and Ranker 2001).

Site A1 (40.015 N, -105.377 W) is located at an elevation of 2200 m in the lower montane zone on a ridge south of Bummer's Gulch (Appendix 1A). Site B1 (40.023 N, -105.430 W) is located at an elevation of 2600 m in the upper montane zone on the crest of a hill west of Sugarloaf Mountain, near the Switzerland Trail (Appendix 1B). Site C1 (40.036 N, -105.547 W) is located at an elevation of 3050 m in the subalpine zone on Hill's Mill Ridge near Four Mile Creek (Appendix 1C).

Stands

Site A1 (2200 m)

After a period of logging and wildfires in the 1870s, the stand at this site began reassembling (Marr 1961, Kooiman Halford 1983, Kooiman and Linhart 1986). In 1953, Marr recorded many young trees and relatively few mature trees in his plots, which suggested an early successional state (Marr 1961). Marr predicted that this stand would ‘climax’ in the form of an open park-like stand of ponderosa pine (*Pinus ponderosa*) with more space between trees (Marr 1961). Marr’s predictions were based on his knowledge of the processes of succession, ecological publications that investigated similar stand types, and his own survey data. However, shortly after his survey, many of the *P. ponderosa* died, most likely due to a pine beetle (*Dendroctonus ponderosae*) outbreak in 1955 (Kooiman and Linhart 1986). From 1977 to 1980, *P. ponderosa* trees at and around this site were also severely infested with dwarf mistletoe (*Arceuthobium vaginatum*) that killed 75% of the local population (Kooiman and Linhart 1986). Trees that were unaffected by beetles remained susceptible to windthrow; a severe wind storm felled several mature trees in this area in 1982 (Kooiman Halford 1983, Kooiman and Linhart 1986).

These disturbances, coupled with fire suppression, which greatly lowers *P. ponderosa* seedling and sapling establishment (Keane et al. 1990), left this stand dominated by Douglas fir (*Pseudotsuga menziesii*) as of 1996 (Korb and Ranker 2001). Korb and Ranker predicted that, if fire suppression persisted, their plot at this site would continue to be dominated by *P. menziesii*, owing to a lack of surface fires (Hadley 1994, Korb and Ranker 2001). They also predicted that a crown fire could eradicate many of

the trees at this site, shifting the stand's successional trajectory (Peet 1981, Korb 1997, Korb and Ranker 2001).

Site B1 (2600 m)

Before logging in the 1870s, the stand at this site, which is somewhat exposed to wind, had an even distribution of *P. ponderosa* and *P. menziesii* (Kooiman Halford 1983, Kooiman and Linhart 1986). In 1953, this stand had small clusters of individually dispersed *P. ponderosa* and *P. menziesii* (Marr 1961). The oldest *P. menziesii* individuals in Marr's plots were over 300 years old, while the oldest *P. ponderosa* individuals were 122 years old (Marr 1961). Marr described this stand as mid-successional, and he expected it to eventually return to a *P. menziesii/P. ponderosa* mixed stand. From 1977 to 1980, *P. ponderosa* frequency dwindled by 30% due to another ponderosa pine bark beetle outbreak (Kooiman and Linhart 1986). Continued fire suppression in the Central Rockies over the next few years caused many of the *P. menziesii/P. ponderosa* mixed stands in the region to become much more *P. menziesii* dominant, with *P. menziesii* saplings increasing in abundance and *P. ponderosa* saplings declining in abundance (Peet 1981, Hadley 1994).

As of 1996, this site was *P. menziesii* dominant, as was evidenced in Korb and Ranker's plots (Korb and Ranker 2001). Their survey results showed a low regeneration of *P. ponderosa*, most likely due to fire suppression and to dwarf mistletoe infestation. If fire suppression continued, they predicted that their plots would continue to be dominated by *P. menziesii* with little occurrence of *P. ponderosa* or limber pine (*Pinus flexilis*) (Korb and Ranker 2001). This stand may also be susceptible to a stand-clearing crown

fire due to a higher surface area of standing fuel loads (Korb 1997, Korb and Ranker 2001).

Site C1 (3050 m)

Prior to logging in the 1870s, the stand at this site was dominated by conifers (Marr 1961). However, Quaking aspen (*Populus tremuloides*) began establishing after this period, and by 1953 the stand was dominated by *P. tremuloides* ranging between 20 and 52 years of age (Marr 1961). Though seedlings and saplings of Engelmann spruce (*Picea engelmannii*), *P. flexilis*, and lodgepole pine (*Pinus contorta*) were recorded in Marr's plots, their frequencies were comparatively low. Marr considered this stand to be in an early secondary sere. He predicted, in the absence of fire, that it would eventually become a mature *P. engelmannii*/subalpine fir (*Abies lasiocarpa*) stand (Marr 1961). Due to the site's somewhat mesic soils, he hypothesized that the stand would have a larger proportion of *A. lasiocarpa* than that of an average subalpine 'climax' stand (Marr 1961). In 1981, Kooiman and Linhart noted a rise in the mortality of *P. tremuloides*, fewer *P. tremuloides* ramets, and many *P. engelmannii* and *A. lasiocarpa* saplings (Kooiman Halford 1983, Kooiman and Linhart 1986).

This trend continued through 1996, as *P. engelmannii* and *A. lasiocarpa* continued to regenerate and establish in Korb and Ranker's plot, while early successional species, such as *P. contorta* and *P. tremuloides* senesced (Korb and Ranker 2001). Korb and Ranker predicted that *P. tremuloides* and *P. contorta* trees would eventually die out and that *P. engelmannii* and *A. lasiocarpa* would continue to dominate the stand (Korb and Ranker 2001).

Methods

Field Methods

The historical sites were resurveyed for temporal tree community changes along an elevational gradient in the Front Range of Colorado. Resurveys were performed in study plots analyzed by Korb and Ranker (2001) to ensure accurate replication. We used the count-plot sampling method (Mueller-Dombois and Ellenberg 1974) used by Korb and Ranker (2001) to evaluate changes in community structure, age demographics, density, and dominance over the 17 years since 1996. This method required us to record all tree species and size classes of vegetation within a determined sample area, which was represented by our study plots (Mueller-Dombois and Ellenberg 1974).

Plots were located along sampling lines that were permanently marked with iron stakes during an earlier herbaceous resurvey (Kooiman and Linhart 1986). Sites at each elevation measured 100 m x 1 m at each site. Each 1 x 1m plot was located adjacent to the sampling line, at regular 2 m intervals. Plots were not contiguous, but alternated on both sides of the lines. Plot width varied with the tree density at each site. The two sites lowest in elevation (A1 and B1) had sparser tree community populations than did the highest elevation site (C1), and required larger plots to capture overall community composition and density. Plots in A1 and B1 measured 1000 m² (100 m x 10 m) and extended 5 m on either side of the sampling line; the C1 plot measured 400 m² (100 m x 4 m) and extended 2 m on either side of the sampling line. Long narrow plots were chosen by Korb and Ranker (2001), as opposed to Whittaker plots, to most accurately depict successional dynamics and total species richness.

We surveyed each established transect in these plant communities in June of 2013. We identified and counted every tree, sapling, seedling, and stump in each plot, and measured the diameter breast height (dbh) of each living tree over 4 cm dbh. Saplings were categorized as having diameters of less than 4 cm and heights of greater than 1 m. Seedlings were categorized as having heights of < 1 m. Dead and fallen trees were identified and counted but their diameters were not measured.

During our surveys, 1.27 cm by 91.44 cm rebar rods with surveyors' caps were installed with a drilling hammer at both ends of each survey line, to mark plot locations for future work.

Data Analyses

Age demographics were assessed by grouping dbh measurements for all trees into 5 cm increments, to replicate the analysis procedure performed by Korb and Ranker (2001). Basal area and dbh can be useful proxies for biomass (Quigley and Platt 2003). Survey data gathered at each site were used to calculate the absolute density, relative density, basal area, and relative dominance of each tree species present in each plot. Absolute density, the amount of trees/ha, was calculated by dividing tree counts for each species by the total area of the plot. Relative density, the number of individuals for one species as a percentage of the total for all species in an area, was determined by dividing tree counts for each species by the total tree count in each plot. Basal area (cm²), or ba, is the cross-sectional area of the tree trunk, and was computed as

$$ba = \pi \left(\frac{d}{2} \right)^2$$

where d equals the diameter at breast height (Mueller-Dombois and Ellenberg 1974). Relative dominance, the basal area of a species as a percentage of the total basal area of all species, was similarly calculated by dividing the dominance for each species by the total dominance of all species in each plot. Results were compared with those of Korb and Ranker (2001) to determine the extent of temporal change of species and biomass in each plot.

Spatial maps of the sites were created using 30 m resolution 2006 USGS land cover data (US Geological Survey, Gap Analysis Program 2006) and 10 m resolution digital elevation model data (US Geological Survey, National Elevation Dataset 1999). Land classes were separated by geo-referenced and classified configurations as determined by the USGS (2006). Elevation classes were delineated by life zone classifications according to latitude (Kershaw et al. 1998). ESRI's ArcMap and ArcScene were used to compile GIS layer data into presentable formats (ESRI 2013).

Results

Each site changed in different ways over the 17-year span from 1996 to 2013. Site A1 increased in absolute tree density, which was largely facilitated by growth in *P. menziesii* abundance. Site B1 exhibited species loss (*P. ponderosa*) but increased in *P. menziesii* basal area. Site C1 basal area increased for all species and shifted in relative density and relative dominance, from early successional *P. tremuloides* to late successional *P. engelmannii*. Changes at sites A1 and B1 may be attributed to disturbance events (fire suppression and insect/pathogen infestation) that may have altered successional trajectories. However, C1's changes align with successional

pathways that are known to occur at similar sites and high elevations (Marr 1961, Peet 1981).

Site A1 (2200 m)

Though relative dominance shifts from 1996 to 2013 were small in this plot, with continued *P. menziesii* dominance (Figure 3), there were considerable changes in *P. menziesii* size class distribution (Appendix 2). The abundance of mature *P. menziesii* individuals/ha more than doubled over this period (Figure 4). The relative density of *P. menziesii* rose as well (Figure 5). Absolute density for all trees rose by 81.2% (320 trees/ha to 580 trees/ha); the largest absolute density change at any of the sites. *J. scopulorum* basal area changed the most of any species at this site over the 17-year span, increasing 81.0%. Mean basal area per tree for *P. ponderosa* increased 69.1%, while *P. menziesii* basal area per tree showed little change, declining by 2.5% (Figure 6).

In 2013, there were more mature trees and fewer young individuals, those categorized as saplings and seedlings, than in 1996 (Figure 7). In general, both young and dead individual counts were much lower in 2013 than in 1996 (Appendix 3). This lack of young individuals may suggest that the successional rate is slowing at this site; however, this could also be indicative of the short-term growing conditions at this site over the past few years.

These changes align with Korb and Ranker's 1996 prediction that the plot would continue to be heavily *P. menziesii* dominant, with fewer *P. ponderosa* and *J. scopulorum* individuals (Korb and Ranker 2001). However, the increased density and continued dominance of *P. menziesii* at the site does not fit Marr's predictions of an open *P.*

ponderosa stand (Marr 1961). The numerous *P. menziesii* individuals may partially reflect the saplings (7) and seedlings (7) that Korb and Ranker noted in 1996, which likely advanced to maturity. Though several *P. ponderosa* and *J. scopulorum* individuals have persisted in Korb and Ranker's plot, expanding in basal area, the growth of mature *P. menziesii* individuals may create new and difficult resource stresses for the reproductive success of these other species, particularly the shade-intolerant *P. ponderosa* (Peet 1981). Given the increase of *P. menziesii* frequency in nearly every size class (Appendix 1), we expect *P. menziesii* relative dominance to remain high and overall tree density to level off as resource limitation dictates (Table 1).

Site B1 (2600 m)

Site B1's plot remained heavily *P. menziesii* dominant (Figure 3) with modest changes in absolute and relative density (Figure 4 and 5) and overall basal area per tree. However, *P. menziesii* basal area per tree rose 56.3% (Figure 6). Though *P. menziesii* declined 25.0% in absolute density, it rose 7.1% in relative density due to such considerable increases in basal area (Figures 4 and 5). No *P. ponderosa* individuals were observed in 2013, which contrasted with the seven living *P. ponderosa* individuals observed in 1996, indicating a loss of species. Dbh tree class species data from 1996 and 2013 showed no major changes in class distribution frequency for any of the observed species (Appendix 4).

Compared to 1996, in 2013 there were fewer mature and young trees but there were more dead individuals (Figure 7). *P. menziesii* showed the greatest change in young

individuals, declining from 64 to 27. Changes in the number of dead trees were more modest (Appendix 2).

In many cases, species loss can have myriad effects on a plant community (Diaz et al. 2006, Cardinale et al. 2012) and can promote state shifts. However, it is possible that increased basal area per tree for *P. menziesii* may be a better metric of change than is loss of species at this site, due to the confounding effects of the dwarf mistletoe infestation of *P. ponderosa* that was noted in 1996 (Korb and Ranker). Loss of *P. ponderosa* and this shift to a more open plot of larger, more dominant *P. menziesii* individuals fits with Korb and Ranker's predictions (Korb and Ranker 2001). The trajectory of this particular shift matches similar successional changes known to occur in this type of environment under conditions of fire suppression (Peet 1981, Hadley 1994). Marr's prediction of an equal dominance *P. menziesii*/*P. ponderosa* stand remains unfulfilled, due to the effects of fire suppression and dwarf mistletoe infestation. In the absence of a major disturbance event, or disturbance regime shift, we expect this stand to remain highly *P. menziesii* dominant as these individuals continue to grow (Table 1). We also expect little change in absolute and relative density, due to a low total young individual count in 2013 as compared to 1996 (Appendix 3).

Site C1 (3050 m)

This site showed the largest shift in relative tree dominance. *P. tremuloides* dominance declined by 14.6%, while *A. lasiocarpa* rose by 8.6% and *P. engelmannii* rose by 6.1% (Figure 3). *P. engelmannii* is now the dominant tree species in this plot. Total basal area increase per tree was also highest at this site, with an increase of 58.4% (379.2

cm² to 600.7 cm²). *A. lasiocarpa* (179.6%) and *P. contorta* (90.0%) showed significant increases in basal area per tree, *P. engelmannii* (12.1%) and *P. tremuloides* (5.6%) rose only moderately in basal area per tree (Figure 6). Furthermore, density data show a decline in *P. tremuloides* and *P. contorta* individuals/ha and an increase of *A. lasiocarpa*/ha and *P. engelmannii*/ha (Figures 4 and 5), which may reflect effects of resource competition. *P. tremuloides* is shade intolerant and disturbance dependent; therefore a closing canopy coupled with an absence of disturbance may thwart seedling generation and development (Smith and Smith 2005). Dbh class species data from 1996 and 2013 showed no considerable differences in dbh class distribution for any of the observed species over time (Appendix 5).

In Site C, there were fewer mature and young trees, and nearly an equivalent amount of total dead individuals, in 2013 as compared to 1996 (Figure 7). Each species had many more young individuals in 1996. *A. lasiocarpa* showed the largest decline in young individuals, declining from 167 to 64. Dead individual counts were somewhat similar; the greatest disparity was a decline in dead *P. contorta* (20 to 3). Though the total number of young individuals has declined, as has the number of young individuals for each species (Appendix 3), such a change in young individuals favors *P. engelmannii* and *A. lasiocarpa*, which are known to attain larger trunk diameters per tree, once established in such successional communities (Peet 1981), and thus require fewer trees to dominate a community.

Shifts in relative tree dominance indicate successional change (Whittaker 1953, Marr 1961, Peet 1981). Our results support Marr's and Korb/Ranker's predictions that

late successional species *A. lasiocarpa* and *P. engelmannii* would eventually outcompete and overtake early successional species *P. tremuloides* and *P. contorta* (Marr 1961, Korb and Ranker 2001). This is a common successional trajectory for stands in similar high-elevation subalpine environments (Marr 1961, Whipple and Dix 1979, Peet 1981), which are known to undergo state shifts at slower rates (Ives 1941, Körner 1999). It is evident that this community is still shifting from *P. tremuloides* and *P. contorta* to *A. lasiocarpa* and *P. engelmannii*. Shifts in relative density shown in our data reflect this transition (Figure 5). In the absence of major disturbance events, or disturbance regime shifts, we expect this process to continue in the future (Table 1).

Conclusion

Condensation of life zones in mountain forest communities (Körner 1999), categorized by relative elevation (Ramaley 1907), are useful models for analyzing the interplay between plant community dynamics and environmental gradients (Whittaker 1953). A comparison of our survey data to those from previous years shows that a tree community's relative location along an elevational gradient can affect successional rates and trajectories. We found multiple age demographic shifts in size structure that can be used for evaluating successional processes and state shifts along elevational gradients in montane and subalpine systems. Over time, each site exhibited size structure and age/demographic community change in a disparate way, affecting future community structure, function, and composition. Such long-term changes in tree density, dominance, basal area, and size-class distributions can elucidate community patterns that many short-term studies cannot analyze robustly (Connell and Slatyer 1977, Whipple and Dix 1979).

They can also serve as artifacts for herbaceous community changes, which are often more rapid and dramatic, as was evidenced at these sites (Sproull unpublished data).

Major disturbance events and disturbance regime changes can play significant roles in community development and destruction, and may alter a community's successional trajectory (Connell and Slatyer 1977, Peet 1981, Hadley 1994). Short-term studies often cannot account for the scale, frequency, and intensity of these influences. Alternative state shifts and other dynamic successional patterns correlating to anthropogenic pressures may have nonlinear or lag responses that warrant extended analysis (Woodward 1987, Scheffer et al. 2001). Our data show that successional pathways can be largely influenced by disturbance factors such as infestation, fire suppression, and stochastic weather events.

Successional change is an inherently continuous and dynamic process in nearly every plant community (Tansley 1935, Whittaker 1953). Of importance are the extent, rate, and scope of change, from which we can reveal community patterns that improve our understanding of the intrinsic processes underlying nature's vast framework. By studying the manner and direction of long-term secondary successional pathways, we can better inform our scientists, land managers, and conservationists about what community types and configurations are most susceptible to change, how successional change rates can be accelerated or decelerated, and how the effects of rising anthropogenic disturbance can be mitigated.

CHAPTER THREE: LONG-TERM COMMUNITY HERBACEOUS CHANGES

Introduction

In recent decades, communities and ecosystems across the globe have been altered by both the direct and indirect effects of rapid climate change (Root et al. 2003). These stresses, coupled with other anthropogenic disturbances, such as human resource exploitation, pollution, and land-use change, have had combinative effects on landscape compositions and biodiversity (Vitousek et al. 1997, Dale et al. 2000, Folke et al. 2004, Hooper et al. 2005). Many studies on ecological response to anthropogenic influence have focused on deleterious effects at the individual or species level, however, the overlap of spatial and temporal species interactions at the community level may amplify human-induced impacts resulting in a dynamic rippling effect that cascades through ecological networks (Walther 2010).

Changes in community composition can be analyzed through myriad approaches that may serve as proxies for disturbance events and regime shifts (Hooper et al. 2005). Global reductions in biodiversity (Butchart et al. 2010, Pereira et al. 2010, Dawson et al. 2011), upward elevational species migrations and range expansions (Root et al. 2003, Parmesan and Yohe 2003, Kelly and Goulden 2008, le Roux and McGeoch 2008), and vast changes in community composition and species frequencies (Parmesan and Yohe 2003, Pauli et al. 2007, Walther 2010) have all correlated to environmental changes

facilitated by the direct and indirect effects of rapid climate change. Such trends will likely persist since communities are often governed by a lag-response during periods of swift abiotic change (Woodward 1987, Scheffer et al. 2001). These spatial and temporal community shifts may come with steep costs. Ecosystem processes and services, including plant biomass production, soil formation, water quality regulation, pollination and seed dispersal of highly-valued plants, community resistance to invasive species, and disease regulation may be irreparably altered (Folke et al. 2004, Díaz et al. 2006).

In mid to high elevation forests, the effects of human influence have been particularly pronounced (Beniston et al. 1997, Lesica and McCune 2004, Pauli et al. 2007, Randin et al. 2009). At high elevations, heat tolerance thresholds are narrower, acclimation potential is small (Körner 1999), and productivity is limited to a snow-free growing season (Price and Waser 2000). Disturbances such as increased drought, fire, wind storms, insect and pathogen infestations, and invasive species proliferation can often be traced back to increased climatic instability (Dale et al. 2000). Under these environmental stresses, plant communities often change in dynamic ways. Plant guilds in forest systems have complex, entangled relationships that are sensitive to unnatural environmental fluctuation (Villalba et al. 1994, Walther 2010). Moreover, plant species respond dynamically and idiosyncratically to abiotic change (Gleason 1926, le Roux and McGeoch 2008), thus predicting the impact of human influence on plant composition in localized communities can be difficult, especially in the absence of site-specific weather data and disturbance history records (Ferrier and Guisan 2006).

Comprehensive assessment of plant community dynamics requires a pointed long-term approach that offers insight beyond a ‘snapshot’ perspective, or a singular analysis of a community’s structure and composition (Knapp et al. 2012). Most studies cannot afford to observe or investigate long-term plant community changes in this manner. Furthermore, climate modeling may not accurately reflect actual weather shifts at particular sites (McGuire et al. 2012).

Site-specific bias can be minimized by comparing communities across environmental gradients, such as moisture or elevation. Species response to environmental gradients, particularly elevation, is commonly driven by abiotic factors (Sundqvist et al. 2013). Therefore, a robust assessment of plant community change should aim to integrate site-specific weather data and disturbance history records with multiple vegetation surveys performed in replication over time.

This study evaluates long-term plant changes in four communities along an elevational gradient in the Front Range of Colorado. Here, we compare vegetation compositions in 2013 with those from 1981 and 1996 to assess the change that has occurred over both a 17 and 32-year span. In our analysis, we examine shifts in species composition and frequency, alpha and beta diversity, and elevational species ranges. In addition, we investigate the influence of overstory canopy changes and local disturbance events on community change. The fundamental questions addressed by this work are: Have species expanded their ranges upward in elevation? Has local species alpha and beta diversity within each community increased over time? And, have community compositions changed over time, and if so, which plant families are most responsible for

variation, and do these changes correspond to overstory shifts and disturbance events at each site?

Methods

Study Area

The study area comprised four sites located along an elevational gradient (the 40th parallel north), between the drainage basins of North Boulder Creek and Left Hand Creek in Boulder County, Colorado, USA (Marr 1961). Sites were located on ridgetops, each in a different vegetation zone (lower montane, upper montane, subalpine, and alpine) (Figure 8). Sites were originally selected by Marr (1961) to represent an altitudinal transect that followed one ridge system (from the Plains to the Continental Divide). Sites were situated at intermediate elevations within each vegetation zone to accurately depict typical plant communities in each zone (Marr 1961). Approximately 1,550 m in elevation (and 22 km in distance) separated the uppermost site from the lowermost site (Figure 9).

Marr (1961) performed a quantitative analysis of each plant community in 1953. Resurveys of the herbaceous communities at each site were conducted in 1981 (Kooiman and Linhart 1986) and in 1996 (Korb 1997, Korb and Ranker 2001) to determine the extent and manner of plant community changes (Appendix 6). Sites were: A1 (lower montane), B1 (upper montane), C1 (subalpine), and D1 (alpine).

Site A1 (40.015 N, -105.377 W) is located at an elevation of 2200 m in the lower montane zone on a ridge south of Bummer's Gulch. Site B1 (40.023 N, -105.430 W) is located at an elevation of 2600 m in the upper montane zone on the crest of a hill west of

Sugarloaf Mountain, near the Switzerland Trail. Site C1 (40.036 N, -105.547 W) is located at an elevation of 3050 m in the subalpine zone on Hill's Mill Ridge near Four Mile Creek. Site D1 (40.059 N, -105.617 W) is located at an elevation of 3750 m in the alpine zone on Niwot Ridge.

Field Methods

The four historic sites were surveyed for species frequency, richness, and composition by sampling fifty plots at each site. Each plot had an area of 85 x 100 cm. Each plot was divided into 10 cells using nylon string to delineate subplots within each plot. All species that were rooted within the confines of the plot were recorded to determine richness and composition; subplot species presence/absence counts, ranging from 0 to 10, were totaled to determine frequency.

Each site contained a permanently marked survey line that was previously surveyed in 1981 (Kooiman and Linhart 1986) and in 1996 (Korb and Ranker 2001). Survey lines extended 100 x 2 m (200 m²) and comprised 50 plots. Plots were systematically located every two meters alternating to the left and right of the survey line. Plot sizes, plot locations, and sampling methods were the same as those used in 1981 (Kooiman and Linhart 1986) and in 1996 (Korb and Ranker 2001) to ensure accurate survey replication. The sampling method is described as systematic sampling, which requires sampling points to be located at systematic intervals (Kent and Coker 1992). Though plot sizes were similar to those used in 1953 (Marr 1961), plot locations surveyed in 1953 were randomly selected at each site, thus comparisons with 1953 data were not warranted.

Throughout the summer and fall of 2013, the three lower sites were surveyed three times and the alpine site was surveyed two times to account for species with differing life history characteristics (i.e. early bloomers and later bloomers). Progressively later start dates at high elevation sites were due to snow cover constraints. Survey line endpoints were permanently staked with rebar rods at the conclusion of our study to identify plot locations for future surveys. Species composition was determined by identifying all species at each site. Voucher specimens were collected for all species present and were identified by the Denver Botanic Gardens' Herbarium in Denver, Colorado, USA.

Data Analyses

Changes in herbaceous structure were investigated using the same parameters employed by Kooiman and Linhart (1986) and Korb and Ranker (2001) for comparison among the three years of data (1981, 1996, and 2013). We evaluated changes in species richness, presence/absence, frequency, composition, and diversity over time. Using previous species lists (Appendices 7-10), we analyzed species that expanded their ranges upward in elevation or migrated over this period and evaluated the number of new species and lost species that were recorded during each survey.

Species richness was assessed by totaling the number of species within each plant community. Presence/absence was evaluated by recording whether a species was present in a plot. Species frequency was determined by the percentage of subplots an individual was present in within each plot. Frequencies were divided into 10% increments to further analyze species distribution. Alpha species diversity shifts were measured with the

Shannon-Wiener diversity index (H') (Magurran 1988), the Simpson diversity index (D) (Simpson 1949), and the evenness index (J) (Pielou 1966). Beta diversity was measured with Jaccard's similarity index (S_j). Species accumulation curves were used to estimate the validity of our sample sizes (50 samples per site).

Spatial maps of the sites were created using 30 m resolution 2006 USGS land cover data (US Geological Survey, Gap Analysis Program 2006) and 10 m resolution digital elevation model data (US Geological Survey, National Elevation Dataset 1999) to illustrate site locations and elevations. Land classes were separated by geo-referenced and classified configurations as determined by the USGS (2006). Elevation classes were delineated by life zone classifications according to latitude (Kershaw et al. 1998). ESRI's ArcMap and ArcScene were used to compile GIS layer data into presentable formats (ESRI 2013).

Statistical Analyses

We calculated bootstrap and Abundance Cover Estimator (ACE) values via the statistical software program EstimateS (Colwell 2005) using frequency data from 1996 and 2013 to improve the estimation of the population statistic and more accurately gauge our sampling efforts (Gotelli and Ellison 2004). Bootstrap and ACE values were plotted alongside one another to compare species accumulation at each site for 1996 and 2013 survey data. Diversity indices were calculated using EstimateS (Colwell 2005) to accurately compare indices between the 3 survey years. The statistical significance of species composition change over time was established using the critical value of Jaccard's similarity index at the 95% confidence level (Real 1999). We also calculated

95% confidence intervals for individual species presence/absence values for species that were at least 20% present in any of the survey years to evaluate long-term changes (Appendix 11).

We performed a principal component analysis (PCA) using the vegan package (Oksanen et al. 2011) within the statistical software program R (version 2.14.0), to evaluate plant family composition change between 1996 and 2013 at each site and the relative influence of each plant family on community change (R Development Core Team 2011). Frequency data were Hellinger transformed to account for the presence of zeros (Legendre and Gallagher 2001). A non-parametric Wilcoxon matched-pairs test, comparing PCA site scores for 1996 and 2013 data, was used to investigate the statistical significance ($p < 0.05$) of community change over time along the environmental gradients that emerged in the PCA (González et al. 2014). Raw 1981 frequency data were not available, thus our analysis was limited to a 17-year comparison.

Results

Elevational Range Expansion and Migration

From 1996 to 2013, 6 species expanded their ranges upward in elevation to new sites and 2 species migrated upward entirely (Table 2). Only 2 species expanded their ranges downward in elevation during that span, while no species migrated downward. Range expansion was most pronounced at B1, with 5 species moving from the lower montane to the upper montane. Species that exhibited range expansion are broad-distributed throughout North America, particularly those that expanded within the montane zone (USDA, NRCS 2014).

Shifts in Diversity

From 1996 to 2013, every community surveyed along the elevational gradient showed significant ($p < 0.05$) species turnover, evidenced by Jaccard indices (Table 3). This contrasts with the period between 1981 and 1996 when only site C1 (subalpine) changed significantly. Simpson and evenness diversity indices showed negligible changes over time in every community. Simpson indices ranged from (0.05 to 0.07) and evenness indices ranged from (0.83 to 0.90), indicating high levels of sample diversity and low levels of species dominance.

Species richness and Shannon-Wiener diversity indices were more idiosyncratic (Table 3). Site A1 (lower montane) showed a slight Shannon-Wiener diversity increase from 1981 to 2013. Site B1 (upper montane) exhibited consistent Shannon-Wiener diversity in 1981 and 1996 but increased dramatically in 2013. Site C1 (subalpine) fluctuated in Shannon-Wiener diversity over time, as it showed a moderate decrease from 1981 to 1996, followed by a moderate increase from 1996 to 2013. Site D1 (alpine) displayed a moderate decrease in Shannon-Wiener diversity from 1981 to 1996.

The sample size (50) accurately represented the actual species richness of each community in both 1996 and 2013 (Figures 10-13). Percentages of actual sample representation ranged between 89 and 95%.

Community Composition Change

A preliminary PCA using all four sites showed high discrimination. Therefore, in order to better identify vegetation gradients of variability at each site, four different PCAs were implemented; one for each site (Figures 14-17). Wilcoxon tests showed significant

community change ($p < 0.05$) along the main gradient of vegetation variability (PC1) between 1996 and 2013 at each of the four sites. The PC1 integrated a moderate portion of vegetation variability (A1- 32%; B1- 21%; C1- 15%; D1- 36%). Wilcoxon tests performed on PC2 scores displayed significant community change ($p < 0.05$) at sites A1 and C1. Vegetation variability was lower along the PC2 gradient for all sites.

The PC1 gradient of variability for A1, B1, and C1 is most likely shade-tolerance. Shade-tolerant plant families were clustered around the 2013 site score median and shade-intolerant families were clustered around the 1996 median. Plant families that showed contradictory shade-tolerance characteristics at different sites are explained by their specific aggregation of species, which were unique in composition at each site. Site D1's PC1 gradient may either be related to nitrogen uptake capacity and/or growing season length requirements, since species from families clustered around the 2013 median may gain a competitive advantage from the longer growing season conditions (McGuire 2012 et al.) and higher nitrogen levels in snowpack (Bowman 2006 et al.) that are occurring at this site.

Significant shifts in family composition at each site were attributed to increases in new species and lost species from 1996 to 2013 (Figure 18). In general, there were many more new species found at each site in 2013 as compared to 1996, with site B1 exhibiting the most new species over this period. Nearly all of the new species found at each site in 2013 were also not present at those sites in 1981 (A1- 19 of 19; B1- 25 of 28; C1- 14 of 15; D1- 5 of 7). The number of species lost was relatively consistent at each site in 2013,

whereas the number of lost species was more site-dependent in 1996, with the greatest loss of species occurring at site C1.

Discussion

Overstory Influence on Understory Communities

Herbaceous communities are inexorably linked to canopy shifts in overstory communities. Canopy shifts can influence regeneration dynamics that affect understory composition by changing critical abiotic cues such as light, temperature, and moisture (Quigley and Platt 2003). Thus, herbaceous community change analysis must account for successional changes in tree density, dominance, and basal area in the overstory community.

Our sites showed evidence of compositional herbaceous shifts that reflected tree community changes driven by post-disturbance successional processes (Sproull unpublished). In 2013, site A1 (lower montane) was much shadier than in 1996 due to a higher density of trees, particularly Douglas fir (*Pseudotsuga menziesii*). Site B1 (upper montane) was also shadier, increasing in tree basal area over time. Site C1 shifted in dominance from early successional Quaking aspen (*Populus tremuloides*) to late successional subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*), which closed much of the canopy. These changes in shade-tolerance altered herbaceous niches, and provided competitive advantages to select species and families in 2013. This is exhibited by both our PCA on plant family composition changes over time and by the influx of new species, species range expansions, and significant species turnover and that occurred in each community.

Determining Human-induced Drivers of Change

Changes in herbaceous composition and distribution along the elevational gradient align with global trends influenced by climate change, such as upward elevational range expansion (particularly of broadly-distributed species), increased species turnover, and increased rates of compositional change over time (Parmesan and Yohe 2003, Root et al. 2003). However, it is difficult to directly attribute local herbaceous composition or range shifts to climatic influence. Long-term climate trends, using temperature data taken from environmental weather stations located at each site, show that climatic change has not been consistent along the elevational gradient (McGuire 2012 et al.). Though long-term warming has occurred at each site, these changes have been site-specific, varying in intensity based on temporal scale and variable of measure.

Moreover, it is often difficult to extricate direct and indirect climatic influences, such as disturbance (Dale et al. 2000). Our sites are no exception; as A1 and B1 overstory communities have been altered by pathogenic and insect infestations (Kooiman and Linhart 1986) and D1 has been greatly affected by atmospheric nitrogen deposition found in snowpack (Bowman et al. 1993, Bowman et al. 2006). Other anthropogenic disturbances, such as fire suppression (Korb and Ranker 2001) and logging in the 1870s (Marr 1961), have altered the successional trajectories of the overstory in these communities. Thus it is often impractical to ascribe any human-induced influence as the singular driver of vegetation change. Rather, assessments should incorporate the disturbance history and site-specific climatic pressures that have aggregated as one

combinative perturbation effect, and should analyze the probable weight of each component individually relative to the effect as a whole.

Multiple Approaches in Long-term Studies

Long-term floristic analyses provide unique data on community patterns and processes (Woodward and Beerling 2013). Though such analyses have elucidated plant community shifts in recent years (Ebersole 2002, Klanderud and Birks 2003, Smith and Smith 2005, le Roux and McGeoch 2008, Coop et al. 2010, Johnson et al. 2011), most experiments occur over shorter timespans that offer only snapshots of community change (Connell and Slatyer 1977, Drake 1991). The majority of long-term research experiments across the Long Term Ecological Research (LTER) Network were established less than 30 years ago (Knapp et al. 2012). Lengthier studies limit confounding environmental factors (Whipple and Dix 1979, MacMahon 1980, Klanderud and Birks 2003) and can more comprehensively evaluate community organization (Drake 1991) and temporal stability (Hooper et al. 2005).

To further minimize bias, studies should include various methods of approach. In our analysis, species richness and Shannon-Wiener diversity changes over time did not always reflect significant community change. This underscores the importance of analyzing community change from multiple perspectives (Hooper et al. 2005). By incorporating multiple techniques and variables of measure, community insight is more dynamic and robust, and therefore more accurately representative of the manner and extent of change.

Conclusion

Understanding the causal effects and impacts of climate change and anthropogenic disturbance has become a topic of paramount importance over the past several decades (Parmesan and Yohe 2003, Root et al. 2003). In plant communities, the impacts of climate and disturbance have been pronounced, facilitating increased compositional change rates (Klanderud and Birks 2003, Root et al. 2003), elevational species migrations and range expansions (Parmesan and Yohe 2003, Root et al. 2003, Kelly and Goulden 2008, le Roux and McGeoch 2008), and shifts in diversity and composition (Pauli et al. 2007, Walther 2010). Long-term evaluation of these changes, analyzed along environmental gradients, can elucidate patterns in community organization and composition that may correlate to climatic influence and disturbance. As anthropogenic pressures continue to drive landscape composition in new and dynamic trajectories, such studies can link environmental stressors to biotic response, better informing scientists, land managers, and conservationists of the repercussions of ecosystem alteration.

Our study offers a compelling glimpse of various aspects of community change over a broad temporal scale. Over time, each community transformed idiosyncratically and showed significant compositional and diversity shifts. Large shifts in distribution and upward species range expansions were also seen. In some communities, these trends were more obviously indicative of disturbance pressures, such as high levels of nitrogen deposition, while others were more likely driven by overstory canopy changes (some of which may be related to post-disturbance successional processes). Nevertheless, these

changes paralleled global compositional and distributional rate change patterns (Parmesan and Yohe 2003, Root et al. 2003).

Though it is often difficult to disentangle the direct and indirect effects of climate, such as disturbance (Dale et al. 2000), this interplay merits detailed analysis. These results suggest the importance of understanding interactions between climate change and anthropogenic disturbance, and also between different plant guilds within communities, such as trees and herbs, when evaluating community change. Our comprehension of these relationships requires improvement if we wish to mitigate the fingerprint of anthropogenic perturbation on both local and global scales.

Table 1. Comparison of historical successional predictions with current compositional states of three long-term research sites along an elevational gradient in the Front Range of Colorado

Site	Elevation (m)	Vegetation Zone	Historical Successional Predictions	Validity of Predictions in 2013	Future Predictions
A1	2,200	Lower montane	<p>Marr (1961): open stand of Ponderosa pine</p> <p>Korb/Ranker (2001): Douglas-fir steady-state stand with few Ponderosa pines and Rocky Mountain junipers</p>	<p>Marr (1961): <i>False</i>, due to disturbance impacts (fire suppression; dwarf mistletoe/bark beetle infestation of Ponderosa pines)</p> <p>Korb/Ranker (2001): <i>True</i></p>	Continued Douglas-fir dominance; tree density stabilization as resource limitation dictates
B1	2,600	Upper montane	<p>Marr (1961): equal dominance Ponderosa pine/Douglas-fir stand</p> <p>Korb/Ranker (2001): Douglas-fir steady-state stand with few or no Ponderosa pines</p>	<p>Marr (1961): <i>False</i>, due to disturbance impacts (fire suppression; dwarf mistletoe/bark beetle infestation of Ponderosa pines)</p> <p>Korb/Ranker (2001): <i>True</i></p>	Continued Douglas-fir dominance; few changes in density; no new establishment of Ponderosa pines
C1	3,050	Subalpine	<p>Marr (1961): steady-state Engelmann spruce/subalpine fir stand</p> <p>Korb/Ranker (2001): steady-state Engelmann spruce/subalpine fir stand</p>	<p>Marr (1961): <i>True</i></p> <p>Korb/Ranker (2001): <i>True</i></p>	Continued state shift to a spruce and subalpine fir stand; continued loss of quaking aspen and lodgepole pines

Table 2. Elevational species range expansion from 1996 to 2013. Presence/absence values (%) for each species are displayed in parentheses. Species are listed in the new life zone that they have expanded to since 1996. The superscript **M** denotes species that migrated to new life zones.

Study Site	Downward Elevational Expansion	Upward Elevational Expansion
A1 (lower montane)	<i>Astragalus tenellus</i> (22) <i>Pseudocymopterus montanus</i> (12)	
B1 (upper montane)	<i>Pseudocymopterus montanus</i> (64)	<i>Artemisia frigida</i> (2) <i>Elymus canadensis</i> (20) ^M <i>Solidago missouriensis</i> (34) <i>Tragopogon dubius</i> (2) <i>Verbascum thapsus</i> (4)
C1 (subalpine)		<i>Geranium caespitosum</i> (12) <i>Muhlenbergia montana</i> (6) ^M
D1 (alpine)		<i>Antennaria microphylla</i> (2)

Table 3. Species richness and diversity indices for study sites in 1981, 1996, and 2013 were calculated from presence/absence survey data. Jaccard's beta diversity index reflects changes that have occurred since the previous survey year; asterisks denote statistically significant ($p < 0.05$) compositional change, which is represented by a Jaccard index value of less than 0.2 for a sample size of 50. Raw presence/absence data from 1996 were taken from Korb 1997 with permission. Summary data from 1981 were taken from Kooiman and Linhart 1986 with permission.

Location	Year	Species richness (Q)	Shannon-Wiener Diversity (H')	H' min	H' max	Jaccard Diversity (S _j)
Site A1 (lower montane)	1981	36	3.05	2.14	3.58	
	1996	38	3.17	2.22	3.64	0.25
	2013	40	3.16	2.29	3.69	0.13*
Site B1 (upper montane)	1981	40	3.24	2.29	3.69	
	1996	41	3.28	2.30	3.71	0.21
	2013	62	3.53	2.95	4.13	0.13*
Site C1 (subalpine)	1981	45	3.25	2.46	3.81	
	1996	29	2.93	1.85	3.37	0.18*
	2013	38	3.17	2.22	3.64	0.13*
Site D1 (alpine)	1981	41	3.29	2.30	3.71	
	1996	35	3.20	2.10	3.56	0.23
	2013	31	2.84	1.94	3.43	0.19*

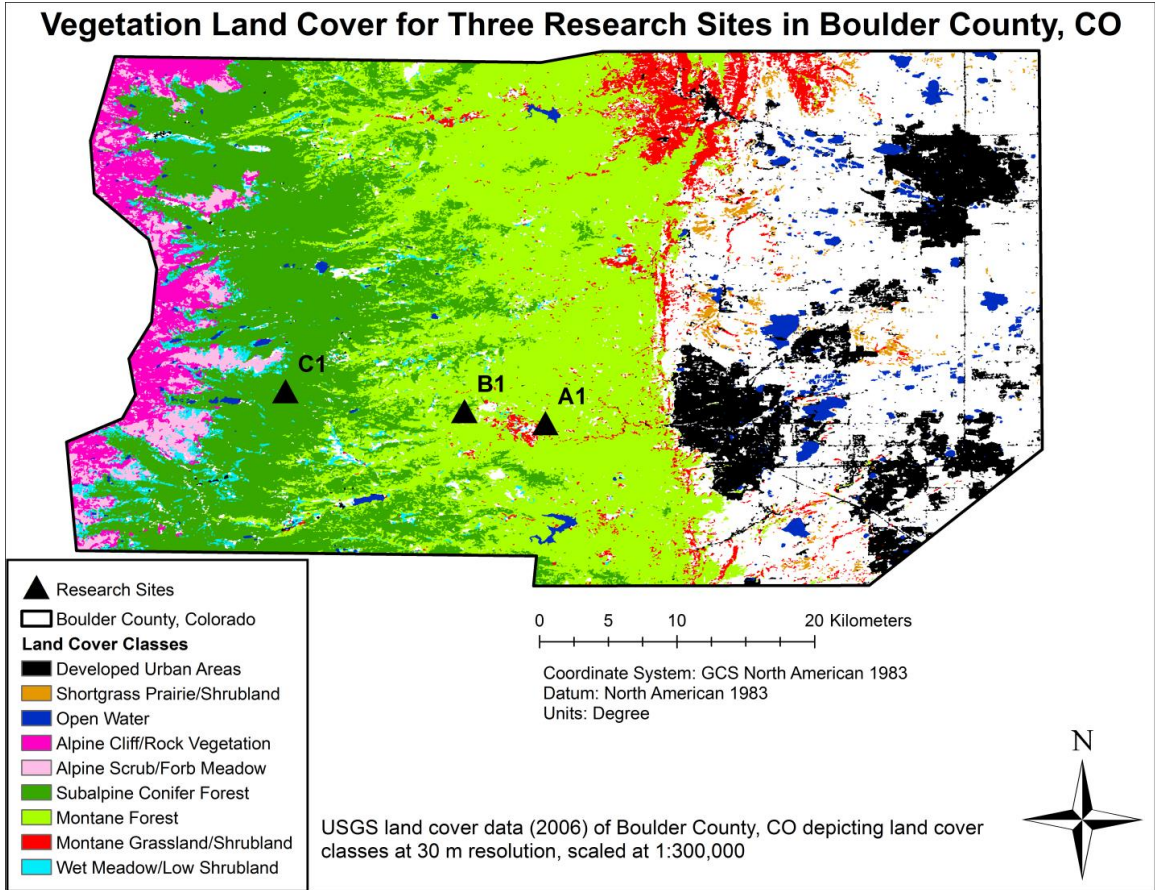


Fig. 1 Land cover at sites A1 (lower montane), B1 (upper montane), and C1 (subalpine) in Boulder County, CO (US Geological Survey, Gap Analysis Program 2006)

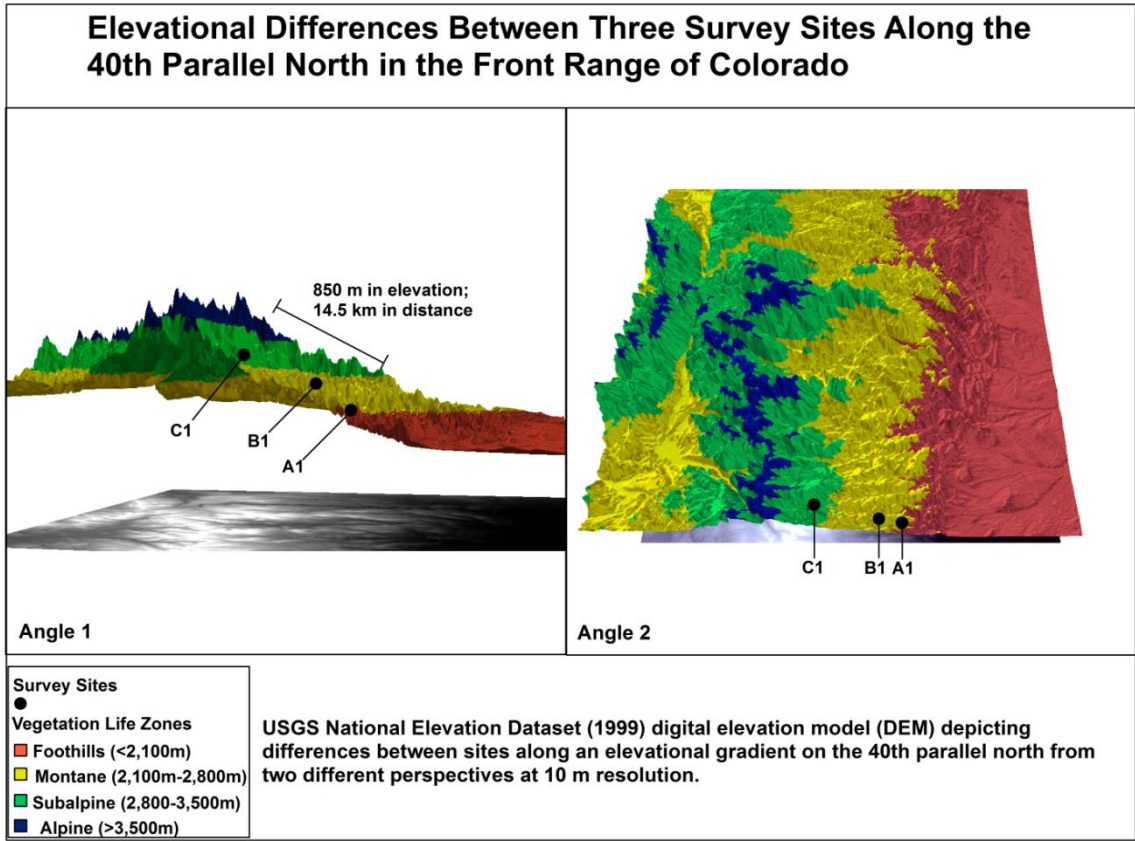


Fig. 2 Digital elevation model (DEM) map of the greater Niwot Ridge area in Boulder County, CO depicting vegetation life zones (US Geological Survey, National Elevation Dataset 1999)

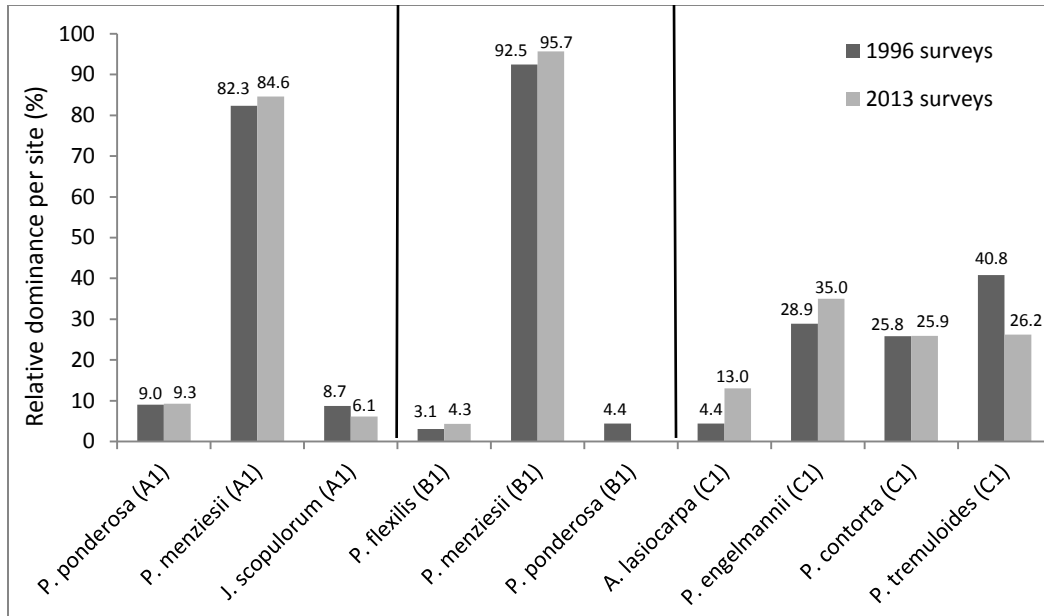


Fig. 3 Relative dominance (%) of tree species in 1996 versus 2013 at sites A1 (lower montane), B1 (upper montane), and C1 (subalpine) (1996 data taken from Korb 1997 with permission)

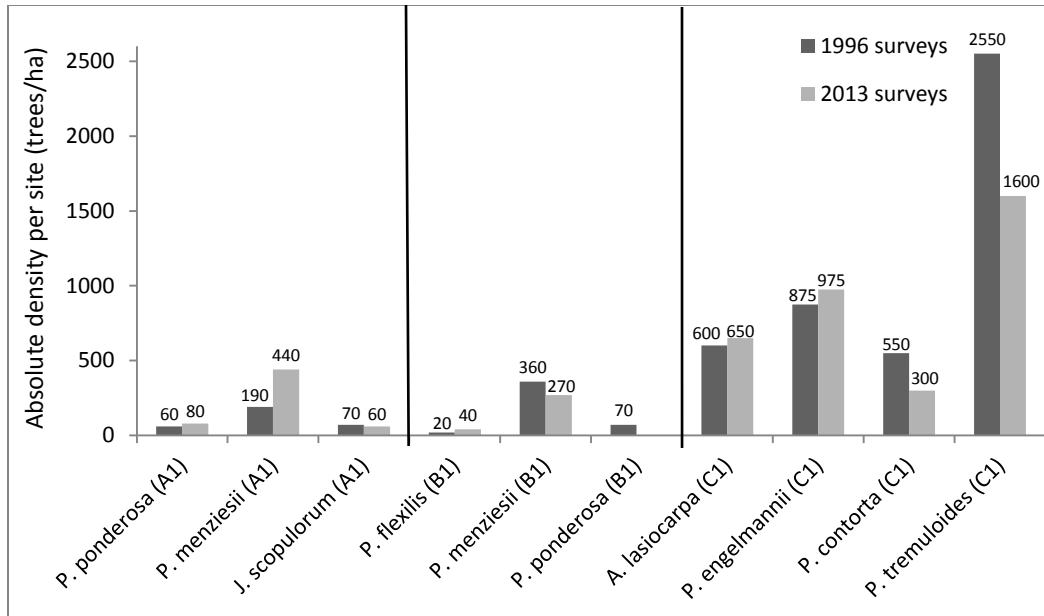


Fig. 4 Absolute density (trees/ha) of tree species in 1996 versus 2013 at sites A1 (lower montane), B1 (upper montane), and C1 (subalpine) (1996 data taken from Korb 1997 with permission)

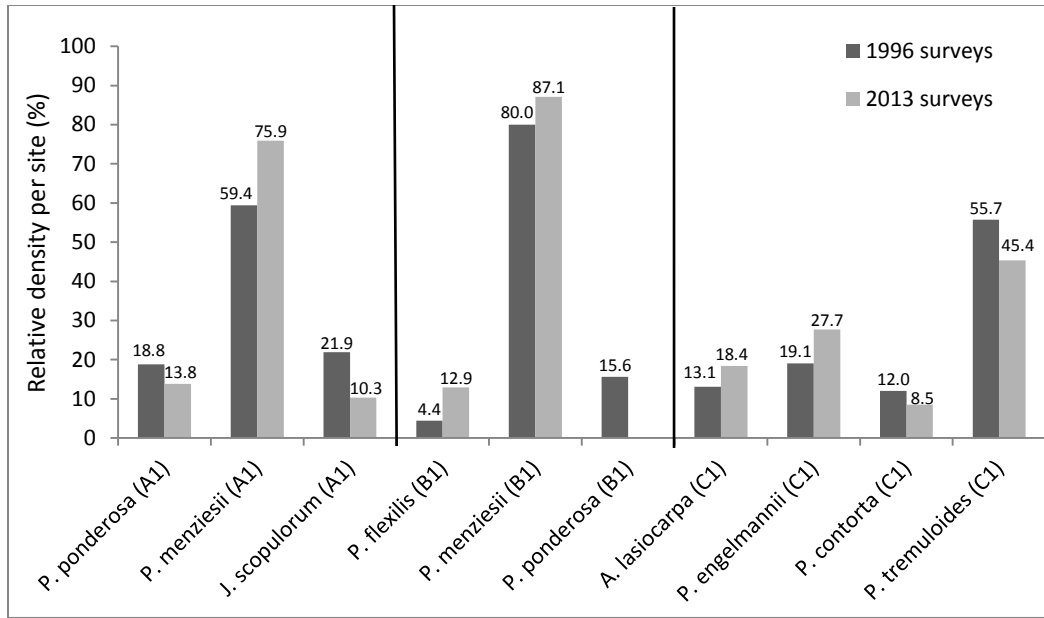


Fig. 5 Relative density (%) of tree species in 1996 versus 2013 at sites A1 (lower montane), B1 (upper montane), C1 (subalpine) (1996 data taken from Korb 1997 with permission)

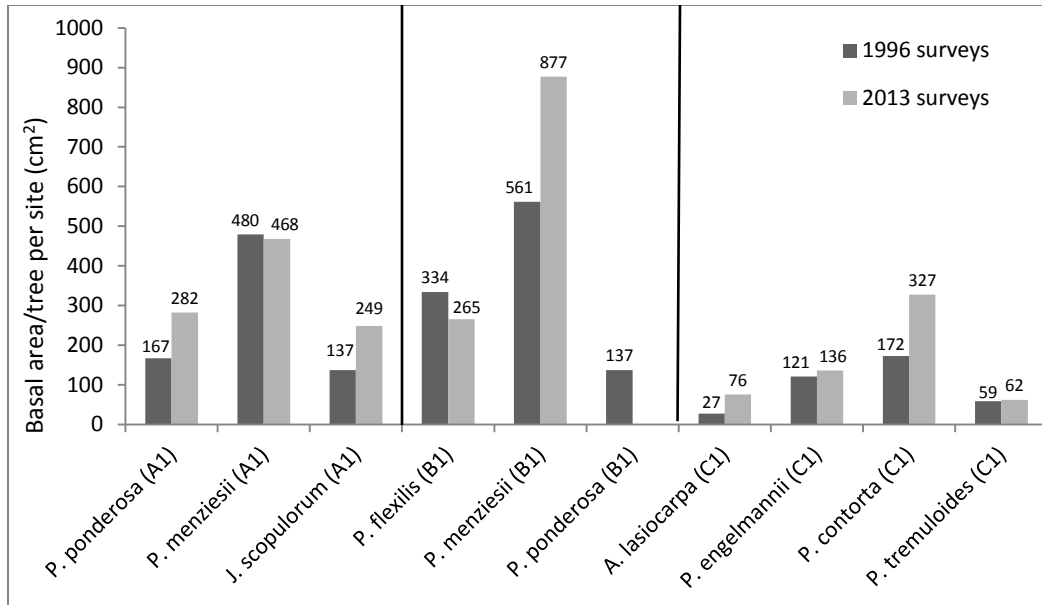


Fig. 6 Basal area/tree (cm²) of tree species in 1996 versus 2013 at sites A1 (lower montane), B1 (upper montane), and C1 (subalpine) (1996 data taken from Korb 1997 with permission)

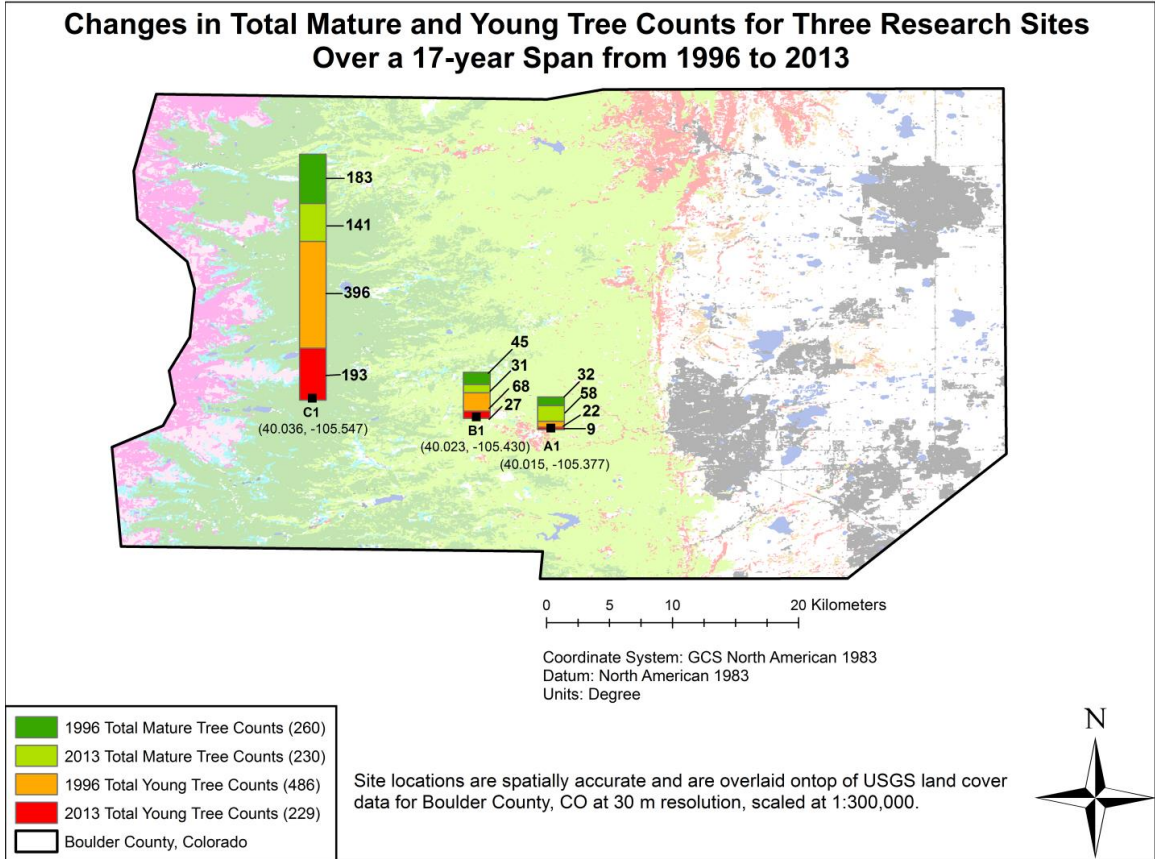


Fig. 7 USGS land cover map of Boulder County, CO comparing total tree counts and young individuals (seedlings and saplings) at each site in 1996 and 2013 (US Geological Survey, Gap Analysis Program 2006)

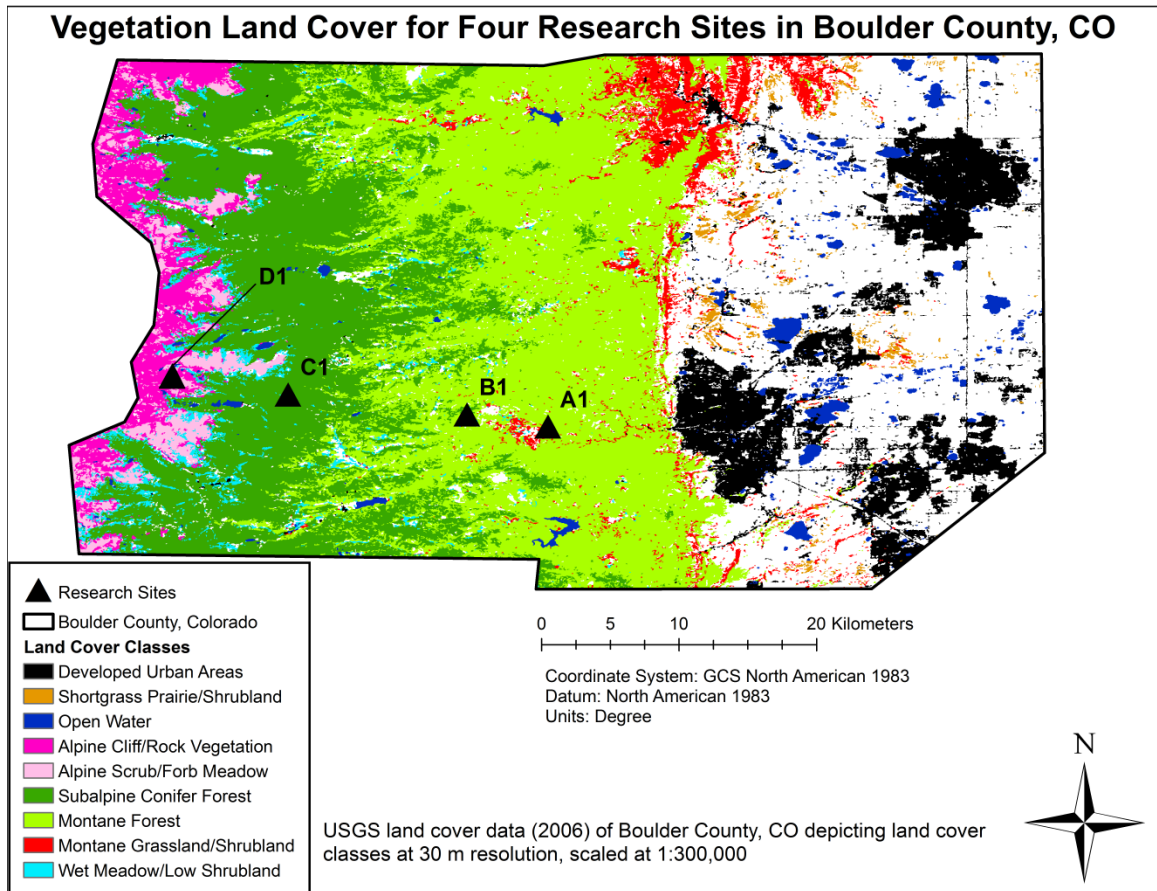


Fig. 8 Land cover at sites A1 (lower montane), B1 (upper montane), C1 (subalpine), and D1 (alpine) in Boulder County, CO, USA (US Geological Survey, Gap Analysis Program 2006)

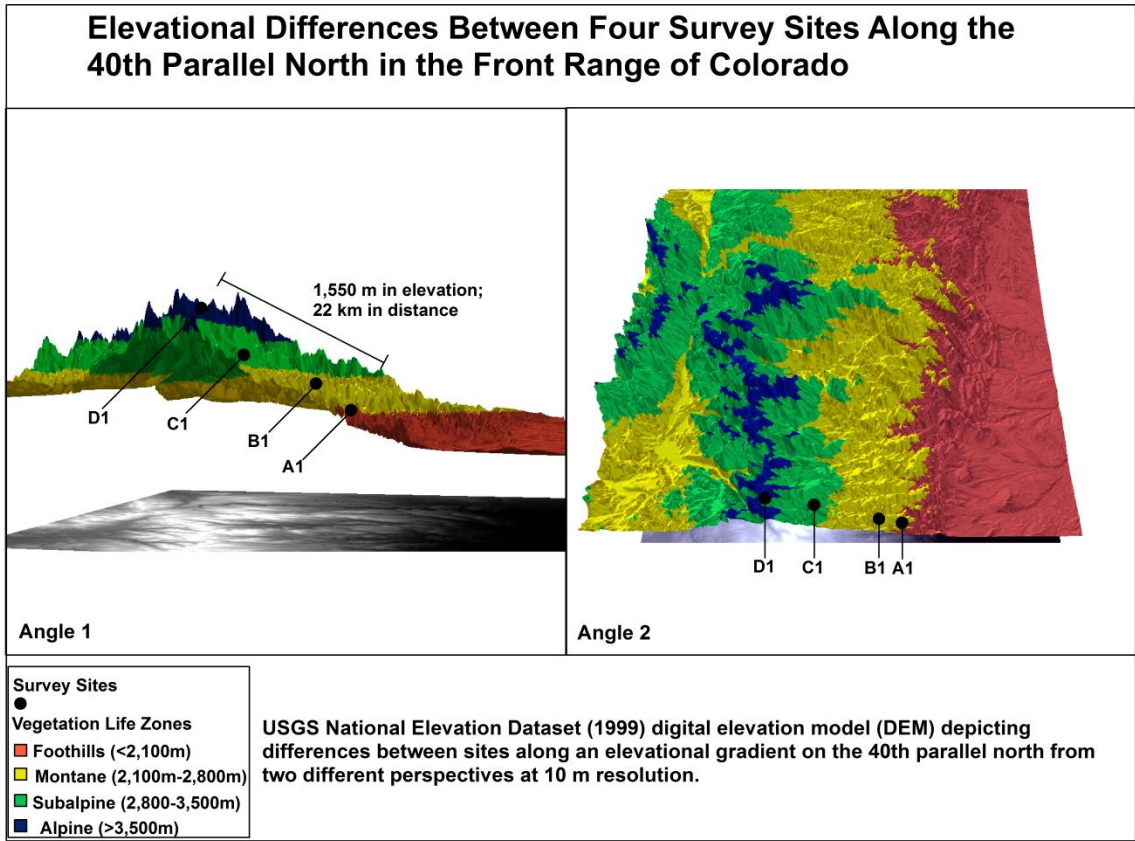


Fig. 9 Digital elevation model (DEM) map of the greater Niwot Ridge area in Boulder County, CO depicting vegetation life zones (US Geological Survey, National Elevation Dataset 1999)

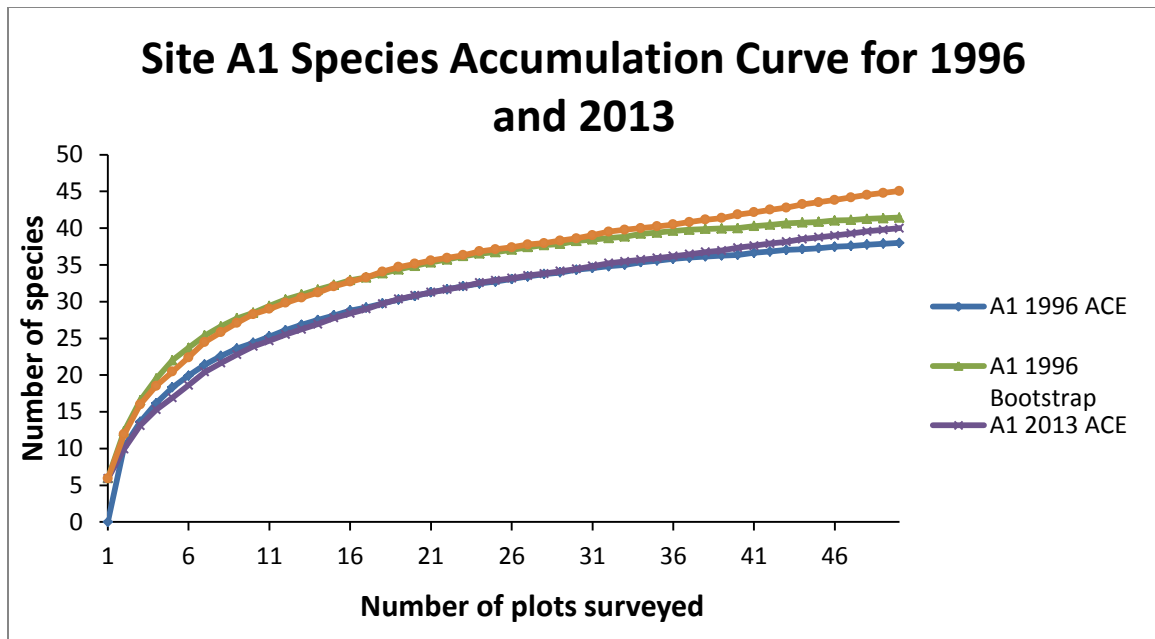


Fig. 10 Site A1 species accumulation curve showing bootstrap and ACE values for 1996 and 2013 survey data (1996 data taken from Korb 1997 with permission)

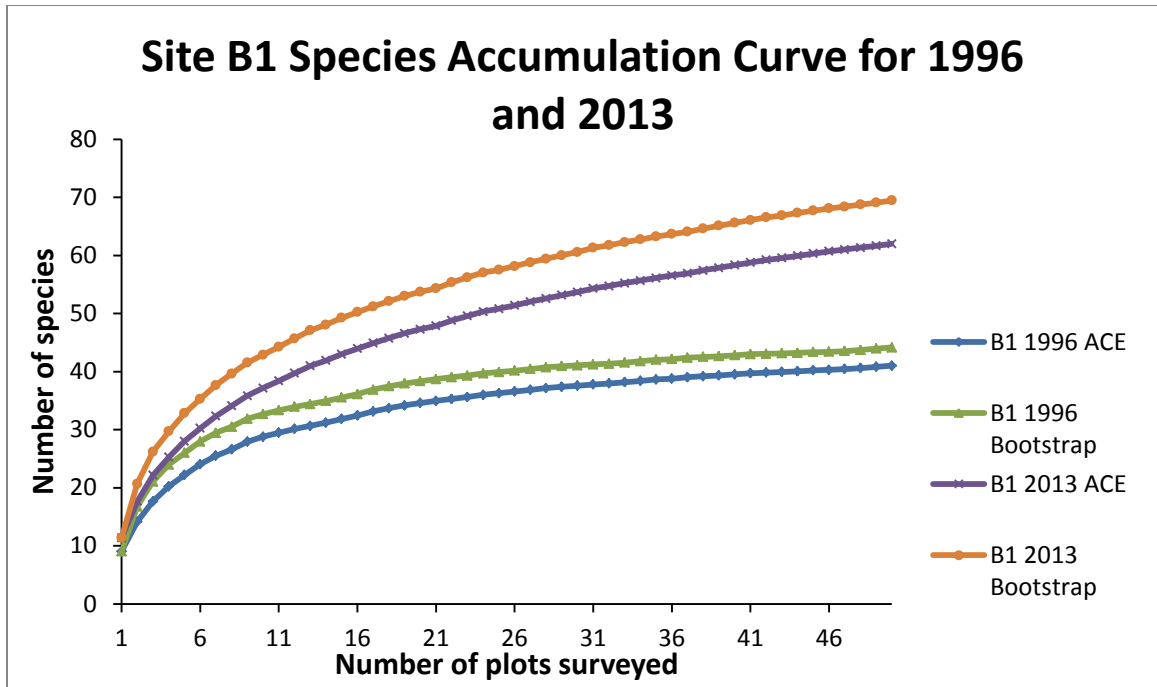


Fig. 11 Site B1 species accumulation curve showing bootstrap and ACE values for 1996 and 2013 survey data (1996 data taken from Korb 1997 with permission)

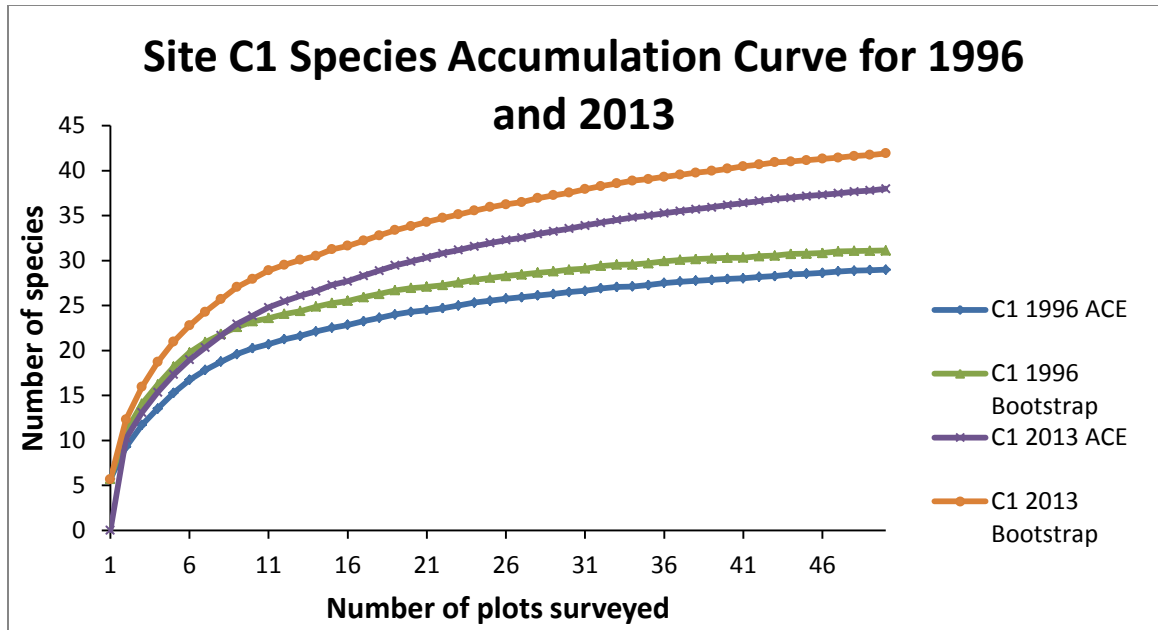


Fig. 12 Site C1 species accumulation curve showing bootstrap and ACE values for 1996 and 2013 survey data (1996 data taken from Korb 1997 with permission)

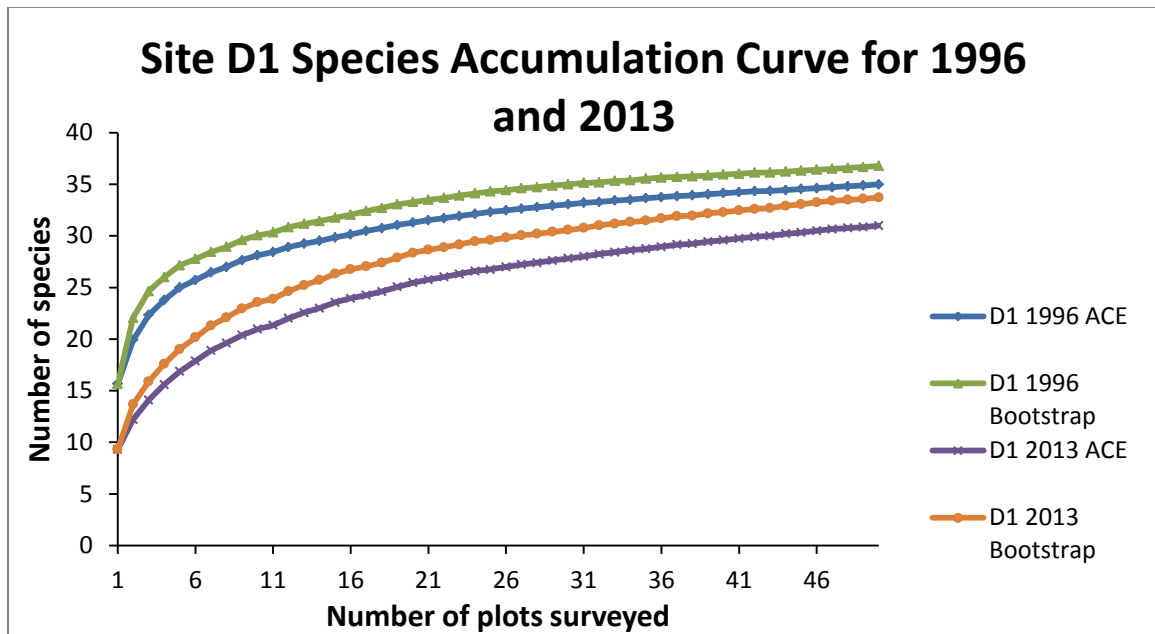


Fig. 13 Site D1 species accumulation curve showing bootstrap and ACE values for 1996 and 2013 survey data (1996 data taken from Korb 1997 with permission)

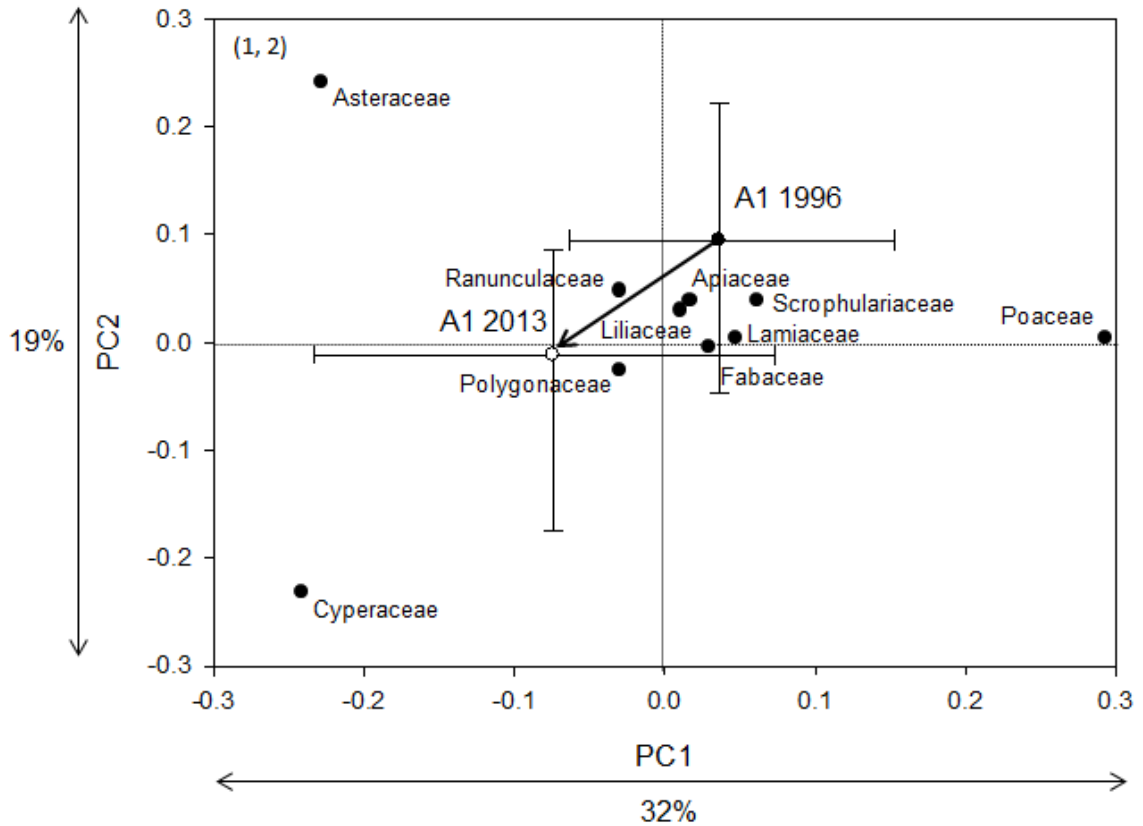


Fig. 14 Principal component analysis (PCA) for site A1 with PC1 and PC2 site and family scores (scaling = 1). To improve the visual clarity of the diagram, only the median site scores and interquartile ranges (1st to 3rd quartiles) for each survey year (filled circles = 1996 and open circles = 2013) were used. Arrows were drawn to link the two survey medians. Percentages corresponding to each axis represent the proportion of data explained by each axis. In the upper left-hand corner, the number 1 denotes a statistically significant ($p < 0.05$) difference between the two years using a Wilcoxon test on PC1 scores; the number 2 denotes a statistically significant ($p < 0.05$) difference between the two years using a Wilcoxon test on PC2 scores. Family scores were scaled by dividing by 3. For simplicity, only the 10 highest family scores are shown on each diagram. Families with the highest scores have the most biological meaning in terms of community change over time. (1996 data taken from Korb 1997 with permission)

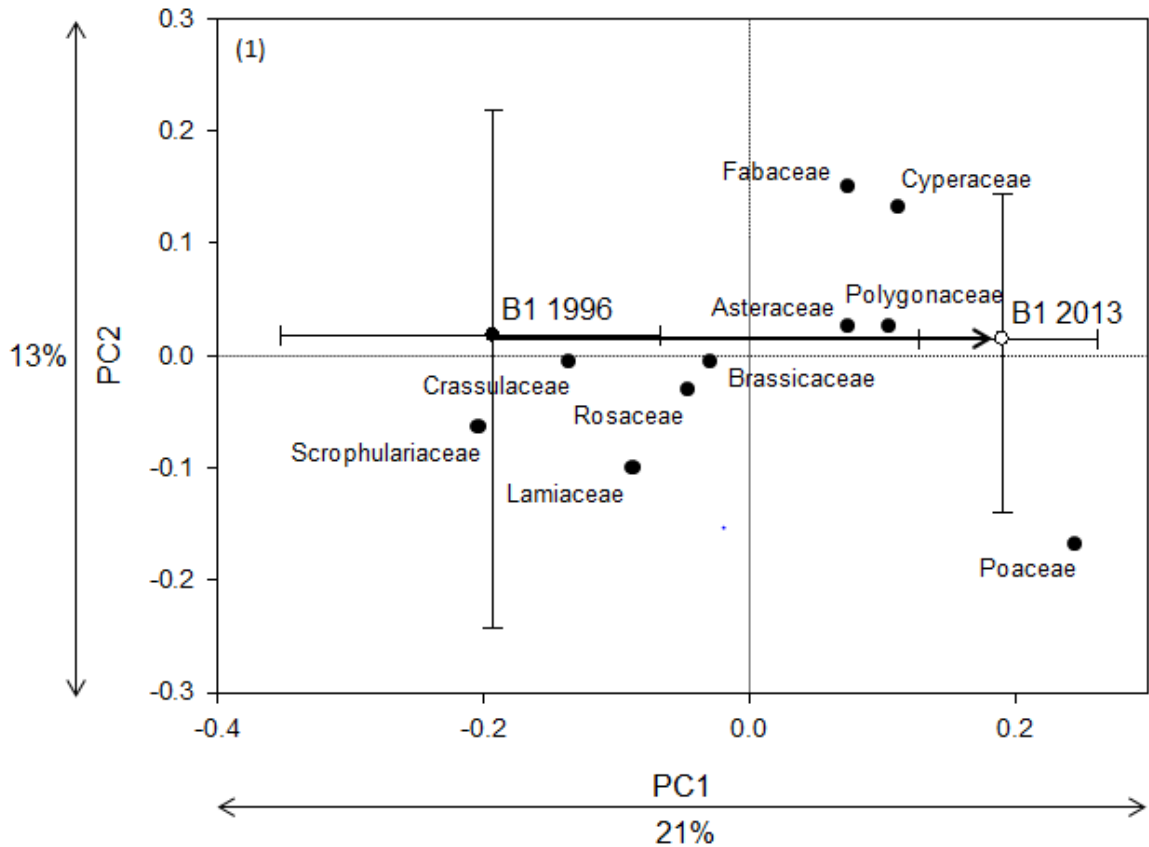


Fig. 15 Principal component analysis (PCA) for site B1 with PC1 and PC2 site and family scores (scaling = 1). To improve the visual clarity of the diagram, only the median site scores and interquartile ranges (1st to 3rd quartiles) for each survey year (filled circles = 1996 and open circles = 2013) were used. Arrows were drawn to link the two survey medians. Percentages corresponding to each axis represent the proportion of data explained by each axis. In the upper left-hand corner, the number 1 denotes a statistically significant ($p < 0.05$) difference between the two years using a Wilcoxon test on PC1 scores; PC2 scores showed no significant difference. Family scores were scaled by dividing by 3. For simplicity, only the 10 highest family scores are shown on each diagram. Families with the highest scores have the most biological meaning in terms of community change over time. (1996 data taken from Korb 1997 with permission)

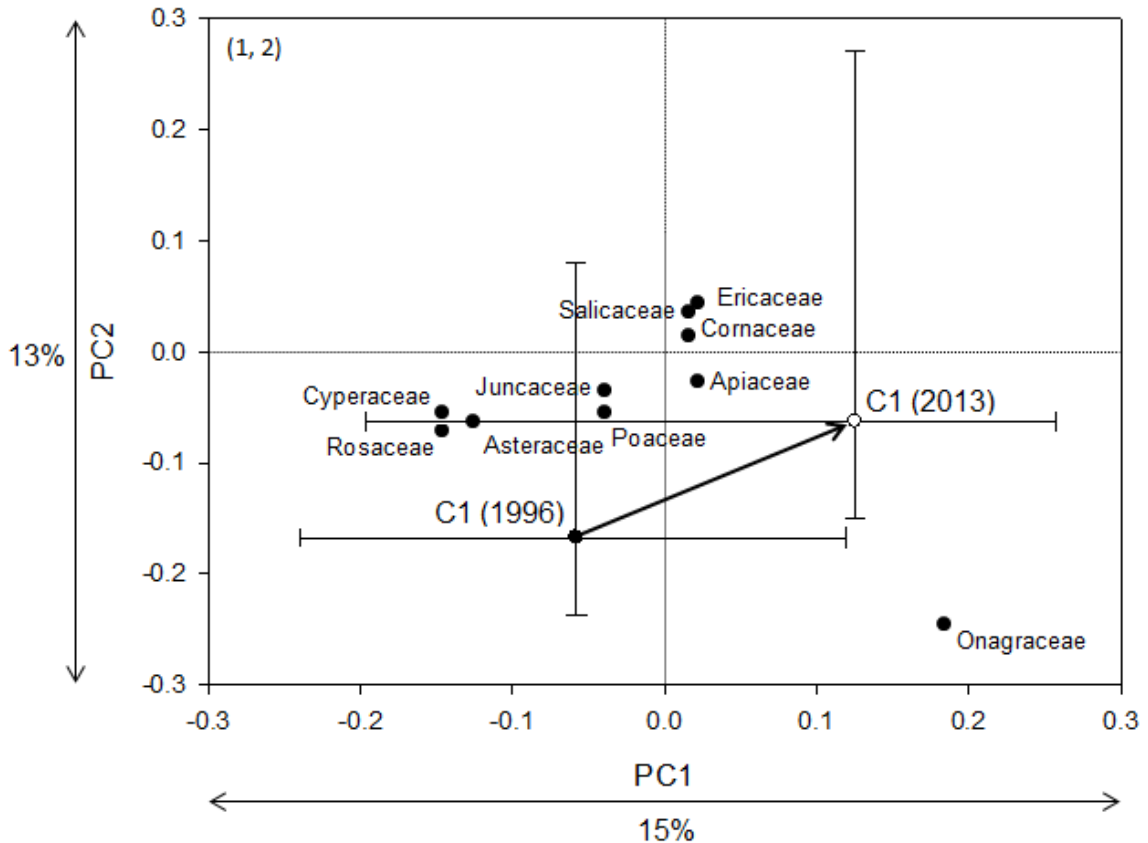


Fig. 16 Principal component analysis (PCA) for site C1 with PC1 and PC2 site and family scores (scaling = 1). To improve the visual clarity of the diagram, only the median site scores and the interquartile ranges (1st to 3rd quartiles) for each survey year (filled circles = 1996 and open circles = 2013) were used. Arrows were drawn to link the two survey medians. Percentages corresponding to each axis represent the proportion of data explained by each axis. In the upper left-hand corner, the number 1 denotes a statistically significant ($p < 0.05$) difference between the two years using a Wilcoxon test on PC1 scores; the number 2 denotes a statistically significant ($p < 0.05$) difference between the two years using a Wilcoxon test on PC2 scores. Family scores were scaled by dividing by 3. For simplicity, only the 10 highest family scores are shown on each diagram. Families with the highest scores have the most biological meaning in terms of community change over time. (1996 data taken from Korb 1997 with permission)

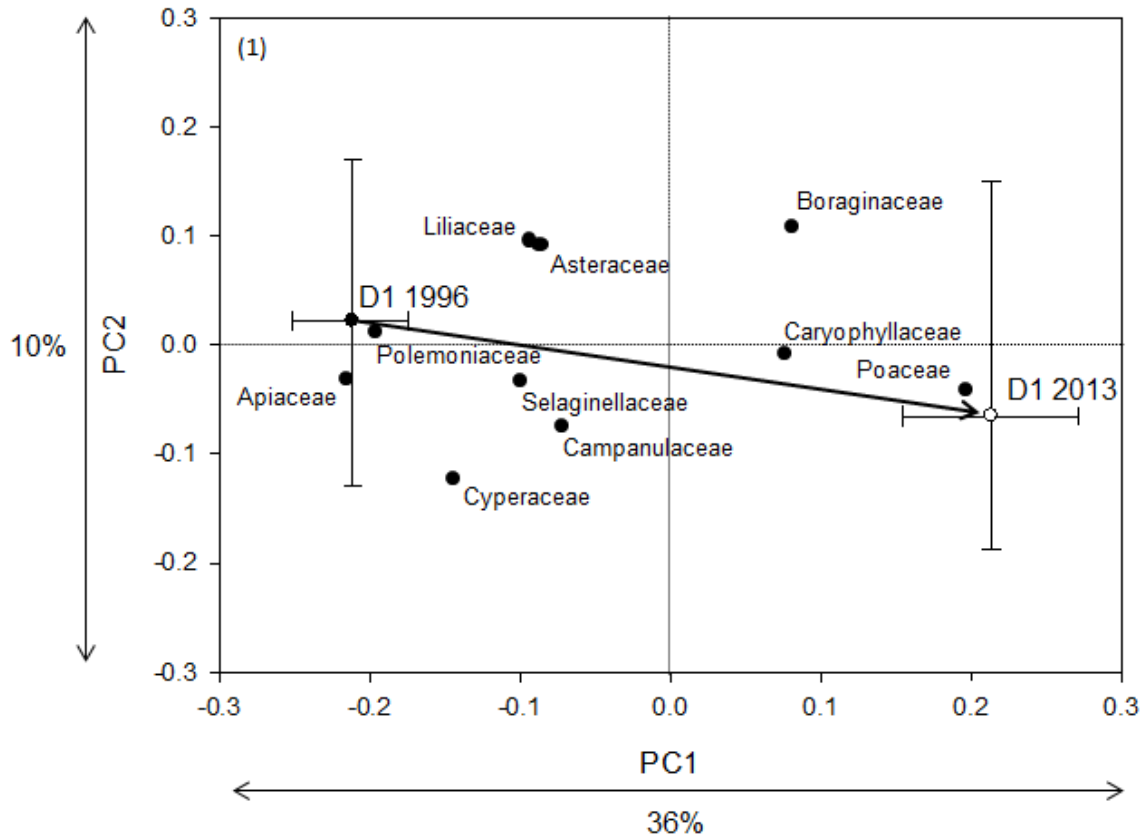


Fig. 17 Principal component analysis (PCA) for site D1 with PC1 and PC2 site and family scores (scaling = 1). To improve the visual clarity of the diagram, only the median site scores and interquartile ranges (1st to 3rd quartiles) for each survey year (filled circles = 1996 and open circles = 2013) were used. Arrows were drawn to link the two survey medians. Percentages corresponding to each axis represent the proportion of data explained by each axis. In the upper left-hand corner, the number 1 denotes a statistically significant ($p < 0.05$) difference between the two years using a Wilcoxon test on PC1 scores; PC2 scores showed no significant difference. Family scores were scaled by dividing by 3. For simplicity, only the 10 highest family scores are shown on each diagram. Families with the highest scores have the most biological meaning in terms of community change over time. (1996 data taken from Korb 1997 with permission)

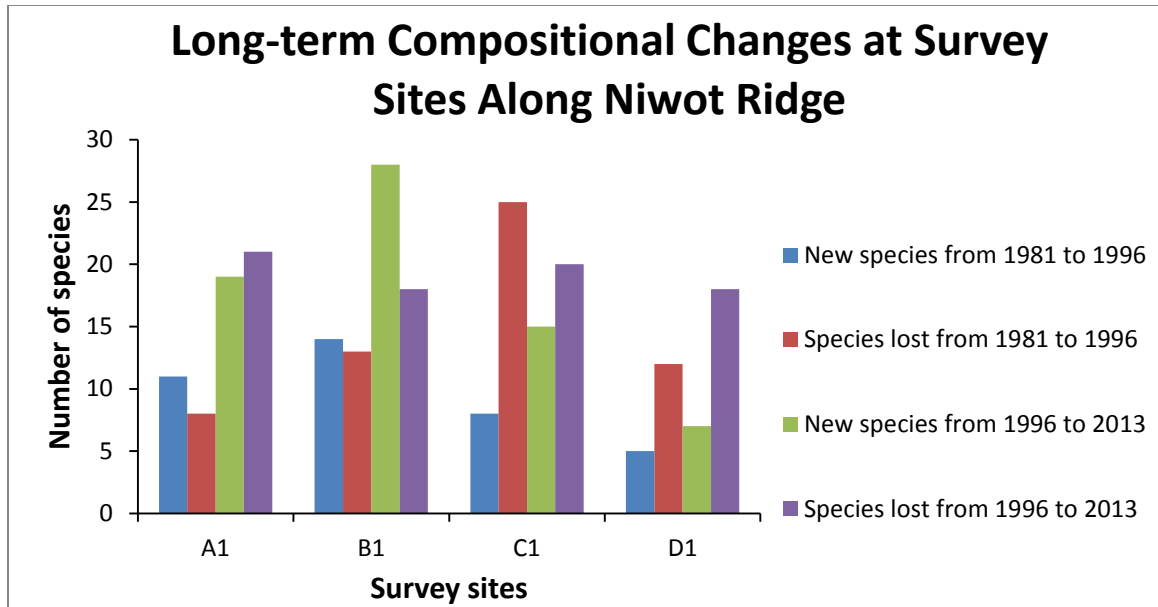


Fig. 18 New and lost species counts for each site in 1996 (compared to 1981) and 2013 (compared to 1996). (1996 data taken from Korb 1997 with permission)

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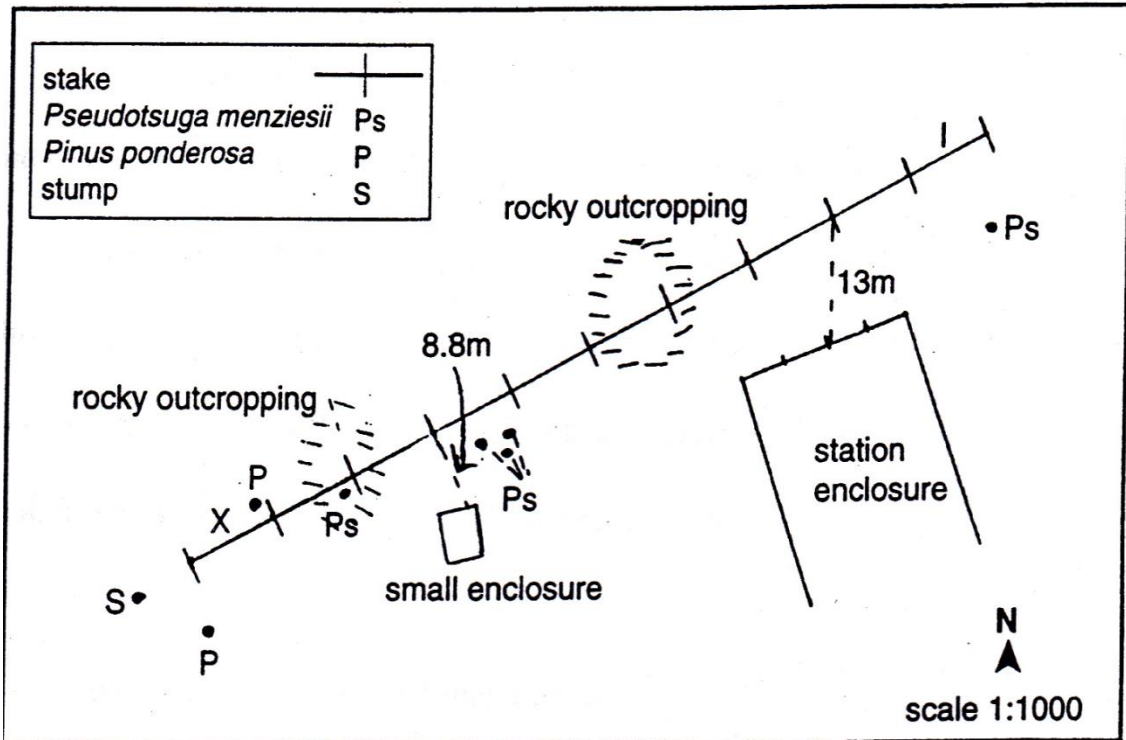
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APPENDICES

Appendix 1 Location of stands (Korb 1997, Korb and Ranker 2001) and survey plots (Kooiman Halford 1983, Kooiman and Linhart 1986)

Site A1 (2200 m)

Take Highway 119 (Canyon Drive) west from Boulder. Follow the road approximately 11.0 km until you reach the Sugarloaf Road turnoff on the right. Take Sugarloaf Road approximately 3.2 km, passing the Sugarloaf District Fire Station. Turn left at the first group of mailboxes on an unnamed dirt road just past Millionaire Road. Take this road approximately 1.5 km, going up and then down a hill. Pull off to the right side of the road on the downslope of the hill where there is an overgrown jeep trail leading uphill to the right. Walk up this trail approximately 0.3 km and take a right through the woods (no trail) until you reach the ridge-top, where there will be a fenced-in weather station. This is the A-1 weather station. The sampling line (Appendix 1A) is marked with 1.27 cm by 91.44 cm rebar rods at either end.

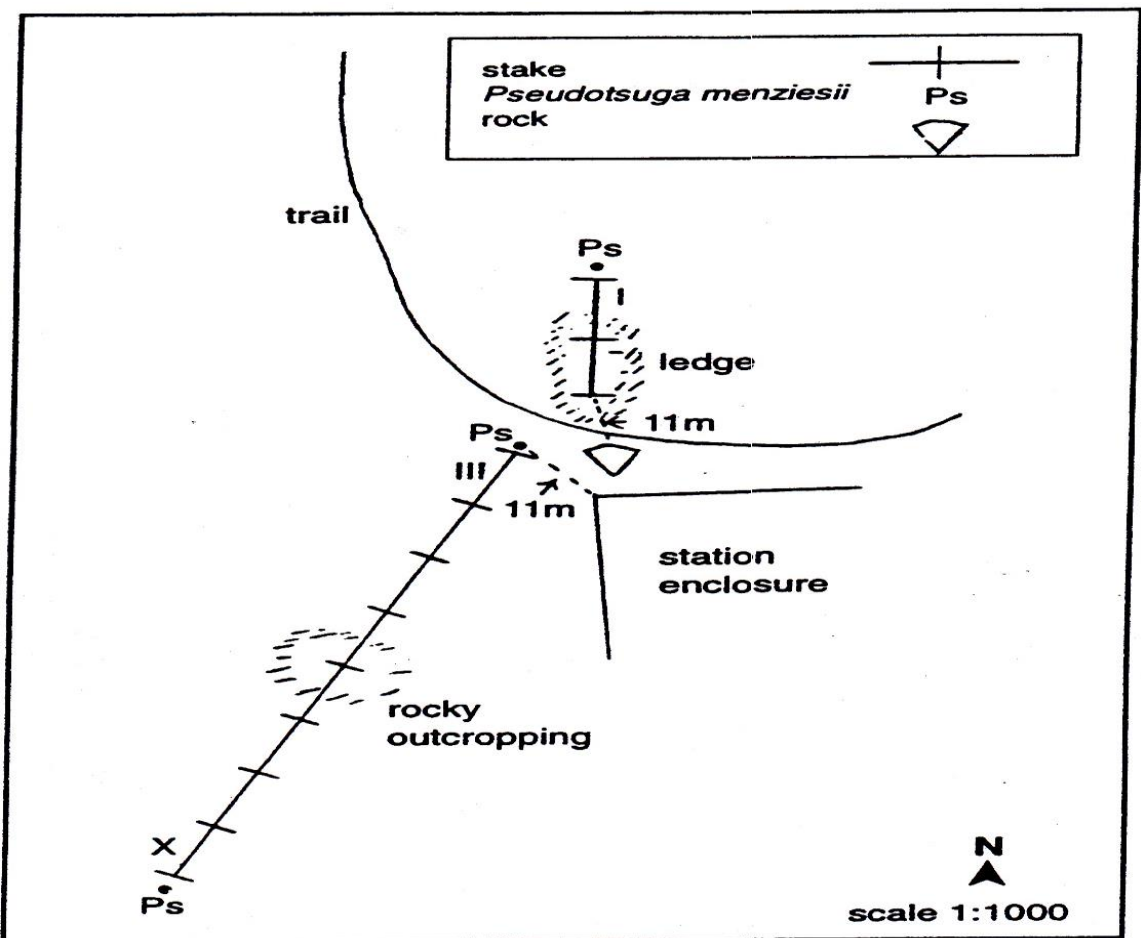


Appendix 1A This is the survey line at site A-1 in Boulder County, CO (taken from Kooiman Halford, 1983 with permission). This line is 100 m long and marks the middle of the survey transect, which extends 5 m on either side of the line to form a 1000 m² sample area (100 m x 10 m). Tick marks intended to represent spots where iron stakes were placed in 1983 are not entirely accurate, as many of the stakes have been uprooted, buried, or moved. Letters representing trees are obsolete.

Site B1 (2600 m)

Follow directions to Site A-1 but instead of turning left at the first group of mailboxes near Millionaire Road continue driving on Sugarloaf Road for an additional 2.4 km. Turn right onto an unnamed gravel road that has a sign pointing towards the Switzerland Trail. Follow this road uphill until you reach an open trailhead parking lot. The road forks directly before the parking lot, where you can continue straight into the parking lot or turn left onto an unnamed dirt jeep road; take this road west approximately 0.8 km until you reach the first jeep trail on your left, which directs you southward. Park in the open

area on the right shortly after the turn (0.1 km). These roads are not well maintained and may require a four-wheel drive vehicle, depending on the conditions. Almost directly across from the small open area is another jeep trail that has been abandoned. Walk up this trail approximately 0.3 km. Near the ridge-top, veer slightly right until you reach the fenced-in B-1 weather station. The sampling line (Appendix 1B) is marked with 1.27 cm by 91.44 cm rebar rods at either end.

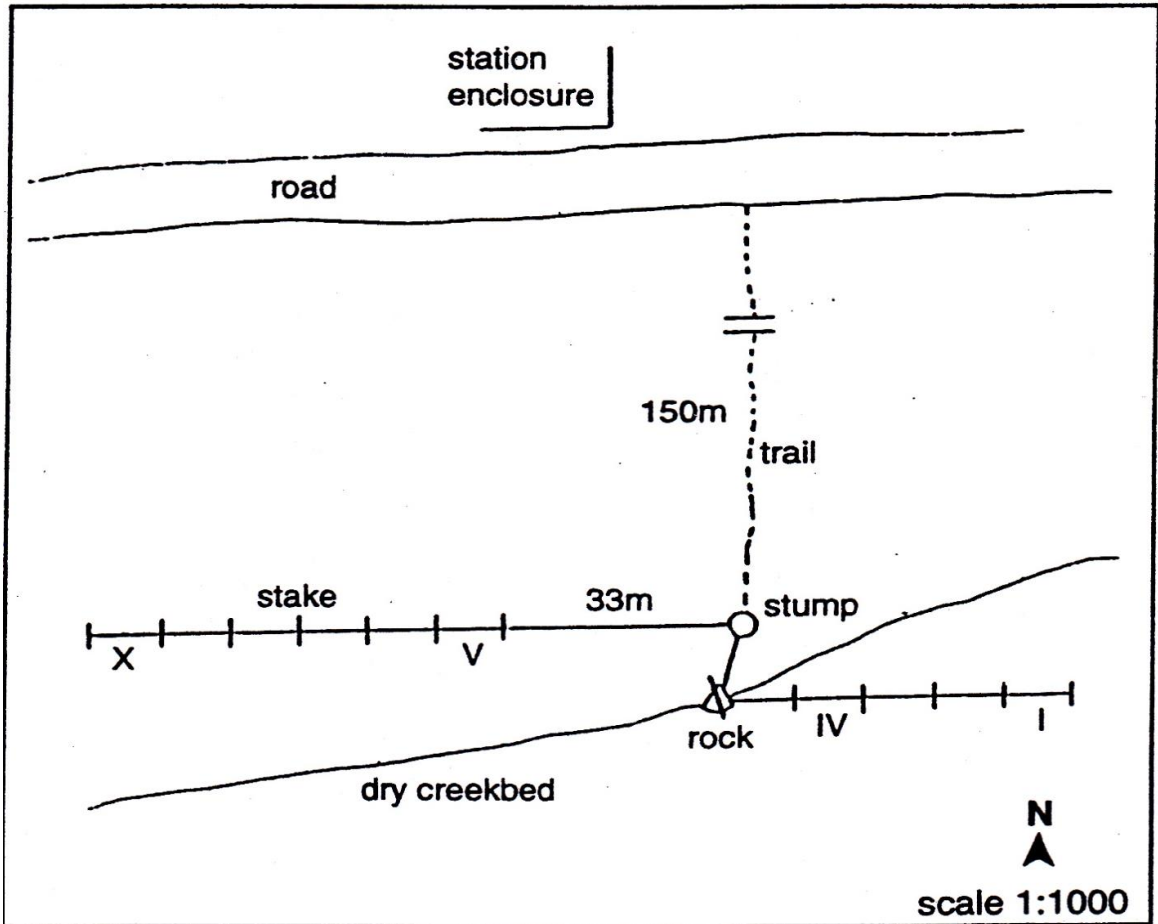


Appendix 1B This is the survey line at site B-1 in Boulder County, CO (taken from Kooiman Halford, 1983 with permission). This line is 100 m long and marks the middle of the survey transect, which extends 5 m on either side of the line to form a 1000 m² sample area (100 m x 10 m). This transect is divided by a jeep trail. The first 20 meters of the survey line are north of the trail and the second 80 m are south of the trail. These

survey areas were treated as two different transects that were totaled together as one. Tick marks intended to represent spots where iron stakes were placed in 1983 are not entirely accurate, as many of the stakes have been uprooted, buried, or moved. Letters representing trees are obsolete.

Site C1 (3050 m)

Follow directions to Site A-1 but instead of turning right onto Sugarloaf Road stay on Highway 119 (Canyon Drive) heading west to Nederland. In Nederland, take Highway 72 (Peak to Peak Highway) north until you see signs for the University of Colorado Boulder's Rocky Mountain Research Station. Turn left on this gravel road and park at the station's headquarters cabin, where a gate blocks a jeep trail heading north. This gate may be locked, and therefore it may be necessary to coordinate with research station employees to acquire keys to the gates on this trail prior to surveying. Take this uphill trail until you reach another gate that will most likely require keys to unlock. Continue driving past the former C-1 weather station on the right until you reach the current C-1 weather station, which should be approximately 2.7 km from the beginning of the trail. Park next to the current weather station and walk approximately 10 m down the trail to the first jeep trail on the left. There are many trails that fork in this area; however, this is the only jeep trail. Follow this trail approximately 150.0 m until you reach an intermittent stream. This stream divides the transect; one part of the transect is on one side of the stream and the second part of the transect is on the other side. The sampling line (Appendix 1C) is marked with 1.27 cm by 91.44 cm rebar rods at either end.



Appendix 1C This is the survey line at site C-1 in Boulder County, CO (taken from Kooiman Halford, 1983 with permission). This line is 100 m long and marks the middle of the survey transect, which extends 2 m on either side of the line to form a 400 m² sample area (100 m x 4 m). This transect is divided by an intermittent creek. The first 40 meters of the survey line are located south of the creek and the second 60 m are north of the creek. These survey areas were treated as two different transects that were totaled together as one. Tick marks intended to represent spots where iron stakes were placed in 1983 are not entirely accurate, as many of the stakes have been uprooted, buried, or moved. Letters representing trees are obsolete.

Appendix 2 Site A1: diameter at breast height (dbh) class distribution frequency counts (1996 data taken from Korb, 1997 with permission)

Mean diameter at breast height (cm)	5	10	15	20	25	30	35	40	45	50
Range (cm)	4-7	8-12	13-17	18-22	23-27	28-32	33-37	38-42	43-47	48-52
<i>P. ponderosa</i> 1996	0	2	3	1	0	0	0	0	0	0
<i>P. ponderosa</i> 2013	0	2	1	3	2	0	0	0	0	0
<i>P. menziesii</i> 1996	3	3	1	2	5	1	3	0	0	1
<i>P. menziesii</i> 2013	4	11	3	7	6	5	1	5	2	0
<i>J. scopulorum</i> 1996	1	4	0	2	0	0	0	0	0	0
<i>J. scopulorum</i> 2013	0	2	2	0	2	0	0	0	0	0

Appendix 3 Survey comparison of the number of seedlings (height < 1 m), saplings (height > 1 m & < 4 cm dbh), stumps, dead trees, total young individuals (seedling + sapling counts), and total dead individuals (stump + dead tree counts) for each species at each of the three survey sites over a 17-year span (1996 data taken from Korb, 1997 with permission)

		Seedlings	Saplings	Stumps	Dead trees	Total young trees	Total dead trees
Site A1	<i>P. ponderosa</i> 1996	2	0	22	3	2	25
	<i>P. ponderosa</i> 2013	0	0	0	0	0	0
	<i>P. menziesii</i> 1996	7	7	2	1	14	3
	<i>P. menziesii</i> 2013	0	6	0	0	6	0
	<i>J. scopulorum</i> 1996	5	1	0	0	6	0
	<i>J. scopulorum</i> 2013	0	3	0	0	3	0
	Total 1996	14	8	24	4	22	28
	Total 2013	0	9	0	0	9	0
Site B1	<i>P. flexilis</i> 1996	0	0	0	0	0	0
	<i>P. flexilis</i> 2013	0	0	1	0	0	1
	<i>P. ponderosa</i> 1996	2	2	0	0	4	0
	<i>P. ponderosa</i> 2013	0	0	0	2	0	2
	<i>P. menziesii</i> 1996	56	8	2	0	64	2
	<i>P. menziesii</i> 2013	23	4	2	2	27	4
	Total 1996	58	10	2	0	68	2
	Total 2013	23	4	3	4	27	7
Site C1	<i>A. lasiocarpa</i> 1996	101	66	0	0	167	0
	<i>A. lasiocarpa</i> 2013	31	33	0	1	64	1
	<i>P. engelmannii</i> 1996	95	50	0	0	145	0
	<i>P. engelmannii</i> 2013	55	47	0	5	102	5
	<i>P. contorta</i> 1996	28	20	2	18	48	20
	<i>P. contorta</i> 2013	12	1	0	3	13	3
	<i>P. tremuloides</i> 1996	5	31	0	55	36	55
	<i>P. tremuloides</i> 2013	3	11	0	56	14	56
	Total 1996	229	167	2	73	396	75
	Total 2013	101	92	0	65	193	65

Appendix 4 Site B1: diameter at breast height (dbh) class distribution frequency counts (1996 data taken from Korb, 1997 with permission)

Mean diameter at breast height (cm)	5	10	15	20	25	30	35	40	45	50	55	60	65
Range (cm)	4-7	8-12	13-17	18-22	23-27	28-32	33-37	38-42	43-47	48-52	53-57	58-62	63-65
<i>P. flexilis</i> 1996	0	0	1	0	1	0	0	0	0	0	0	0	0
<i>P. flexilis</i> 2013	0	1	1	1	1	0	0	0	0	0	0	0	0
<i>P. menziesii</i> 1996	2	4	5	3	11	6	1	2	1	0	0	0	1
<i>P. menziesii</i> 2013	0	0	1	6	5	3	6	2	1	1	1	1	0
<i>P. ponderosa</i> 1996	4	1	0	1	1	0	0	0	0	0	0	0	0
<i>P. ponderosa</i> 2013	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 5 Site C1: diameter at breast height (dbh) class distribution frequency counts (1996 data taken from Korb, 1997 with permission)

Mean diameter at breast height (cm)	5	10	15	20	25	30	35
Range (cm)	4-7	8-12	13-17	18-22	23-27	28-32	33-37
<i>A. lasiocarpa</i> 1996	21	3	0	0	0	0	0
<i>A. lasiocarpa</i> 2013	17	5	3	0	0	1	0
<i>P. engelmannii</i> 1996	21	4	4	2	3	1	0
<i>P. engelmannii</i> 2013	22	9	1	2	2	2	1
<i>P. contorta</i> 1996	9	3	5	1	3	1	0
<i>P. contorta</i> 2013	2	2	2	0	4	2	0
<i>P. tremuloides</i> 1996	56	33	13	0	0	0	0
<i>P. tremuloides</i> 2013	28	30	6	0	0	0	0

Appendix 6. Comparison of study approaches for all four survey years at sites A1, B1, C1 and D1.

	1953	1981	1996	2013
Plots locations replicated?	No	Yes	Yes	Yes
Field Methods	Quadrat Method (random sampling); 12 plots (91 cm x 91 cm)	Systematic Sampling; 50 plots (85 cm x 100 cm)	Same as 1981	Same as 1981/1996
Available Data	Summary data (limited)	Summary data	Raw data	Raw data
Data Analysis Parameters	-Presence and absence	-Richness -Diversity using presence/absence data (Shannon-Wiener index) -Frequency -Distribution of frequency classes -Composition	Same as 1981	-Richness -Diversity using presence/absence data (Shannon-Wiener index, Simpson index, Evenness index, Jaccard index) -Frequency -Composition -New vs. lost species comparison -Species migration/range expansion -Species accumulation using frequency data
Statistical Analyses	None	Kendall's tau and Spearman's rank correlation coefficient analysis (analyzing frequency shifts from 1953 to 1981 for species with frequency	Same as 1981 (analyzing frequency shifts from 1981 to 1996 for species frequency	Principal component analysis (PCA) (analyzing frequency shifts from 1996 to 2013 with raw frequency data from survey plots)

Appendix 7. Species lists for all three survey years at site A1 (lower montane). Species with asterisks were treated as shrubs in 1981 and 1996 and were not included in the PCA. Species with + symbols were new species at A1 in 2013 (not found in 1981 or 1996).

Site A1 2013	Site A1 1996	Site A1 1981
<i>Achillea millefolium</i> var. <i>occidentalis</i> (<i>Achillea lanulosa</i>)	<i>Achillea lanulosa</i>	<i>Achillea lanulosa</i>
<i>Agropyron cristatum</i> +	<i>Aletes acaulis</i>	<i>Amelanchier alnifolia</i> *
<i>Antennaria alpina</i> +	<i>Allium cernuum</i>	<i>Anisantha tectorum</i> (<i>Bromus tectorum</i>)
<i>Antennaria parvifolia</i>	<i>Anisantha tectorum</i> (<i>Bromus tectorum</i>)	<i>Antennaria parvifolia</i>
<i>Antennaria pulcherrima</i> +	<i>Antennaria parvifolia</i>	<i>Arctostaphylos uva-ursi</i> *
<i>Apiaceae</i> sp. 1	<i>Arctostaphylos uva-ursi</i> *	<i>Artemesia ludoviciana</i>
<i>Arctostaphylos uva-ursi</i> *	<i>Artemesia frigida</i>	<i>Aster porter</i>
<i>Artemesia frigida</i>	<i>Artemesia ludoviciana</i>	<i>Campanula rotundifolia</i>
<i>Astragalus tenellus</i> +	<i>Boechera drummondii</i>	<i>Carex pensylvanica</i> ssp. <i>heliophila</i>
<i>Boraginaceae</i> sp. 1	<i>Boechera divaricarpa</i>	<i>Chenopodium atrovirens</i>
<i>Bouteloua gracilis</i> +	<i>Campanula rotundifolia</i>	<i>Collinsia parviflora</i>
<i>Bromus tectorum</i>	<i>Carex pensylvanica</i> ssp. <i>heliophila</i>	<i>Delphinium nuttallianum</i>
<i>Carex pensylvanica</i> ssp. <i>heliophila</i>	<i>Cerastium strictum</i>	<i>Drymocallis fissa</i>
<i>Caryophyllaceae</i> sp. 1	<i>Chenopodium fremontii</i>	<i>Elymus longifolius</i>
<i>Ceanothus fendleri</i> *+	<i>Collinsia parviflora</i>	<i>Eriogonum umbellatum</i>
<i>Cerastium strictum</i>	<i>Delphinium nuttallianum</i>	<i>Gaillardia aristata</i>
<i>Critesion brachyantherum</i> +	<i>Draba streptocarpa</i>	<i>Gayophytum nuttalli</i>
<i>Delphinium nuttallianum</i>	<i>Drymocallis fissa</i>	<i>Geranium caespitosum</i>
<i>Elymus elymoides</i> (<i>Elymus longifolius</i>)	<i>Elymus canadensis</i>	<i>Harbouria trachypleura</i>
<i>Eriogonum umbellatum</i>	<i>Elymus longifolius</i>	<i>Heterotheca villosa</i>
<i>Geranium caespitosum</i>	<i>Eriogonum umbellatum</i>	<i>Juniperus communis</i> *
<i>Geum rossi</i> +	<i>Gaillardia aristata</i>	<i>Lesquerella montana</i>
<i>Hesperostipa comata</i> +	<i>Gayophytum</i> sp.	<i>Leucocrinum montanum</i>

<i>Heterotheca villosa</i>	<i>Geranium caespitosum</i>	<i>Leucopoa kingii</i>
<i>Holodiscus dumosus</i> +	<i>Harbouria trachypyleura</i>	<i>Liatris punctata</i>
<i>Jamesia americana</i> *	<i>Heterotheca villosa</i>	<i>Mertensia lanceolata</i>
<i>Juniperus communis</i> *	<i>Jamesia americana</i> *	<i>Muhlenbergia montana</i>
<i>Linum usitatissimum</i> +	<i>Juniperus communis</i> *	<i>Penstemon virens</i>
<i>Lomatium dissectum</i> var. <i>multifidum</i> +	<i>Leucopoa kingii</i>	<i>Phacelia heterophylla</i>
<i>Mertensia lanceolata</i>	<i>Liatris punctata</i>	<i>Poa agassizensis</i>
<i>Pascopyrum smithii</i> +	<i>Mertensia lanceolata</i>	<i>Poa fendleriana</i>
<i>Penstemon sp. 1</i>	<i>Muhlenbergia montana</i>	<i>Ribes cereum</i> *
<i>Poa compressa</i>	<i>Penstemon virens</i>	<i>Scutellaria brittonii</i>
<i>Poaceae sp. 1</i>	<i>Phacelia heterophylla</i>	<i>Senecio fendleri</i>
<i>Potentilla pensylvanica</i> var. <i>paucijuga</i> +	<i>Poa compressa</i>	<i>Senecio integerrimus</i>
<i>Psathrostachys juncea</i> +	<i>Ribes cereum</i> *	<i>Solidago missouriensis</i>
<i>Pseudocymopterus montanus</i> +	<i>Scutellaria brittonii</i>	<i>Stipa comate</i>
<i>Ribes cereum</i> *	<i>Senecio integerrimus</i>	<i>Tithymalus brachyceras</i>
<i>Rubus parviflorus</i> +	<i>Solidago missouriensis</i>	<i>Tragopogon dubius</i>
<i>Salvia sp. 1</i>	<i>Tithymalus brachyceras</i>	<i>Verbascum thapsus</i>
<i>Solidago missouriensis</i>	<i>Tragopogon dubius</i>	
<i>Stanleya pinnata</i> +	<i>Verbascum thapsus</i>	
<i>Symphotrichum porter</i> +		
<i>Tragopogon dubius</i>		
<i>Verbascum thapsus</i>		

Appendix 8. Species lists for all three survey years at site B1 (upper montane). Species with asterisks were treated as shrubs in 1981 and 1996 and were not included in the PCA. Species with + symbols were new species at B1 in 2013 (not found in 1981 or 1996).

Site B1 2013	Site B1 1996	Site B1 1981
<i>Achillea millefolium</i> <i>var. occidentalis</i> (<i>Achillea lanulosa</i>)	<i>Achillea lanulosa</i>	<i>Achillea lanulosa</i>
<i>Allium cernuum</i>	<i>Aletes acaulis</i>	<i>Aletes acaulis</i>
<i>Antennaria parvifolia</i>	<i>Amerosedum lanceolatum</i>	<i>Allium cernuum</i>
<i>Arctostaphylos uva-ursi</i> *	<i>Androsace septentrionalis</i>	<i>Arabis fendleri</i>
<i>Artemesia frigida</i> +	<i>Anisantha tectorum</i> (<i>Bromus tectorum</i>)	<i>Arctostaphylos uva-ursi</i> *
<i>Artemesia ludoviciana</i>	<i>Antennaria parvifolia</i>	<i>Artemesia ludoviciana</i>
<i>Artemesia sp. 1</i>	<i>Arctostaphylos uva-ursi</i> *	<i>Aster porteri</i>
<i>Artemesia sp. 2</i>	<i>Artemesia ludoviciana</i>	<i>Astragalus adsurgens var. robustior</i>
<i>Asteraceae sp. 2</i>	<i>Astragalus adsurgens var. robustior</i>	<i>Astragalus shortianus</i>
<i>Astragalus adsurgens var. robustior</i>	<i>Astragalus tenellus</i>	<i>Astragalus tenellus</i>
<i>Astragalus alpinus</i> +	<i>Boechera sp.</i>	<i>Bahia dissecta</i>
<i>Astragalus tenellus</i>	<i>Carex pensylvanica ssp. heliophila</i>	<i>Carex pensylvanica ssp. heliophila</i>
<i>Bouteloua gracilis</i> +	<i>Collinsia parviflora</i>	<i>Chenopodium fremontii</i>
<i>Bromus japonicus</i> +	<i>Delphinium nuttallianum</i>	<i>Collinsia parviflora</i>
<i>Bromus tectorum</i>	<i>Draba streptocarpa</i>	<i>Delphinium sp.</i>
<i>Carex concinna</i> +	<i>Drymocallis fissa</i>	<i>Drymocallis fissa</i>
<i>Carex pensylvanica ssp. heliophila</i>	<i>Elymus longifolius</i>	<i>Erigeron compositus</i>
<i>Caryophyllaceae sp. 1</i>	<i>Erigeron colo-mexicanus</i>	<i>Eriogonum umbellatum</i>
<i>Chenopodium fremontii</i>	<i>Eriogonum umbellatum</i>	<i>Erysimum asperum</i>
<i>Critesion brachyantherum</i> +	<i>Erysimum capitatum</i>	<i>Gaillardia aristata</i>
<i>Delphinium nuttallianum</i>	<i>Frasera speciosa</i>	<i>Gayophytum nuttalli</i>
<i>Dryopteris expansa</i> +	<i>Gaillardia aristata</i>	<i>Geranium caespitosum</i>
<i>Elymus canadensis</i> +	<i>Gayophytum sp.</i>	<i>Gilia pinnatifida</i>
<i>Elymus elymoides</i> (<i>Elymus longifolius</i>)	<i>Geranium caespitosum</i>	<i>Harbouria trachypleura</i>

<i>Epilobium branchycarpum+</i>	<i>Gilia pinnatifida</i>	<i>Heterotheca fulcrata</i>
<i>Erigeron colo- mexicanus</i>	<i>Harbouria trachyplerura</i>	<i>Koeleria macrantha</i>
<i>Erigeron compositus</i>	<i>Heterotheca villosa</i>	<i>Lesquerella montana</i>
<i>Eriogonum umbellatum</i>	<i>Juniperus communis*</i>	<i>Leucopoa kingii</i>
<i>Erysimum capitatum</i>	<i>Koeleria macrantha</i>	<i>Lupinus argenteus</i>
<i>Geranium caespitosum</i>	<i>Lesquerella montana</i>	<i>Mertensia lanceolata</i>
<i>Gymnosteris parvula+</i>	<i>Leucopoa kingii</i>	<i>Muhlenbergia montana</i>
<i>Heterotheca villosa</i>	<i>Lupinus argenteus</i>	<i>Packera fendleri</i>
<i>Juniperus communis*</i>	<i>Mertensia lanceolata</i>	<i>Penstemon virens</i>
<i>Linum usitatissimum+</i>	<i>Oreocarya virgata</i>	<i>Phacelia heterophylla</i>
<i>Lomatium dissectum var. multifidum+</i>	<i>Oxytropis multiceps</i>	<i>Poa fendleriana</i>
<i>Lupinus argenteus</i>	<i>Packera fendleri</i>	<i>Pulsatilla patens ssp. multifida</i>
<i>Machaeranthera pattersonii+</i>	<i>Penstemon glaber</i>	<i>Ribes cereum*</i>
<i>Mertensia lanceolata</i>	<i>Penstemon virens</i>	<i>Scutellaria brittonii</i>
<i>Packera fendleri</i>	<i>Phacelia heterophylla</i>	<i>Sedum lanceolatum</i>
<i>Pascopyrum smithii+</i>	<i>Poa compressa</i>	<i>Selaginella densa</i>
<i>Penstemon sp. 1</i>	<i>Ribes cereum*</i>	<i>Solidago multiradiata</i>
<i>Penstemon sp. 2</i>	<i>Scutellaria brittonii</i>	<i>Stipa lettermanii</i>
<i>Phacelia heterophylla</i>	<i>Selaginella densa</i>	
<i>Plantago major+</i>	<i>Solidago multiradiata</i>	
<i>Poa compressa</i>		
<i>Poaceae sp. 1</i>		
<i>Polygonaceae sp. 1</i>		
<i>Psathrostachys juncea+</i>		
<i>Pseudocymopterus montanus+</i>		
<i>Pteridophyta sp. 1</i>		
<i>Ribes cereum*</i>		
<i>Salvia sp. 1</i>		
<i>Sedum lanceolatum</i>		
<i>Solidago</i>		

<i>missouriensis+</i>		
<i>Solidago multiradiata</i>		
<i>Solidago sp. 1</i>		
<i>Stanleya pinnata+</i>		
<i>Symphyotrichum porter+</i>		
<i>Tragopogon dubius+</i>		
<i>Unknown species 1</i>		
<i>Unknown species 2</i>		
<i>Unknown species 3</i>		
<i>Verbascum thapsus+</i>		
<i>Veronica scutellata+</i>		
<i>Woodsia oregana+</i>		
<i>Wyethia amplexicaulis+</i>		

Appendix 9. Species lists for all three survey years at site C1 (subalpine). Species with asterisks were treated as shrubs in 1981 and 1996 and were not included in the PCA. Species with + symbols were new species at C1 in 2013 (not found in 1981 or 1996).

Site C1 2013	Site C1 1996	Site C1 1981
<i>Achillea millefolium</i> var. <i>occidentalis</i> (<i>Achillea lanulosa</i>)	<i>Achillea lanulosa</i>	<i>Achillea lanulosa</i>
<i>Allium</i> sp. 1	<i>Amerosedum lanceolatum</i>	<i>Aletes acaulis</i>
<i>Antennaria microphylla</i> (<i>Antennaria rosea</i>)	<i>Antennaria rosea</i>	<i>Androsace septentrionalis</i>
<i>Anticlea elegans</i>	<i>Anticlea elegans</i>	<i>Antennaria parvifolia</i>
<i>Asteraceae</i> sp. 3	<i>Calamagrostis canadensis</i>	<i>Antennaria rosea</i>
<i>Campanula rotundifolia</i>	<i>Campanula rotundifolia</i>	<i>Anticlea elegans</i>
<i>Carex concinna</i> +	<i>Cardamine cordifolia</i>	<i>Aster foliaceus</i>
<i>Carex foenea</i>	<i>Carex foenea</i>	<i>Bistorta</i> sp.
<i>Chamerion danielsii</i>	<i>Chamerion danielsii</i>	<i>Boechera drummondii</i>
<i>Cornus sericea</i> ssp. <i>sericea</i> +	<i>Distegia involucrata</i> *	<i>Calamagrostis canadensis</i>
<i>Delphinium barbeyi</i> +	<i>Dodecatheon pulchellum</i>	<i>Caltha leptosepala</i>
<i>Distegia involucrata</i> *	<i>Erigeron eximius</i>	<i>Campanula rotundifolia</i>
<i>Fragaria virginiana</i> ssp. <i>glauca</i>	<i>Fragaria virginiana</i> ssp. <i>glauca</i>	<i>Carex occidentalis</i>
<i>Geranium caespitosum</i> +	<i>Hydrophyllum fendleri</i>	<i>Chamerion danielsii</i>
<i>Juncus arcticus</i> ssp. <i>ater</i>	<i>Juncus arcticus</i> ssp. <i>ater</i>	<i>Chenopodium</i> sp.
<i>Lomatium dissectum</i> var. <i>multifidum</i> +	<i>Juniperus communis</i> *	<i>Clementsia rhodantha</i>
<i>Mertensia ciliata</i>	<i>Lupinus argenteus</i>	<i>Cystopteris fragilis</i>
<i>Muhlenbergia montana</i> +	<i>Maianthemum amplexicaule</i>	<i>Danthonia parryi</i>
<i>Paxistma myrsinites</i> +	<i>Orthilla secunda</i> ssp. <i>obtusata</i>	<i>Distegia involucrata</i>
<i>Pedicularis racemosa</i> ssp. <i>alba</i> +	<i>Osmorhiza depauperata</i>	<i>Dodecatheon pulchellum</i>
<i>Penstemon whippleanus</i>	<i>Oxypolis fendleri</i>	<i>Draba streptocarpa</i>
<i>Poaceae</i> sp. 2	<i>Penstemon glaber</i>	<i>Elymus</i> sp.
<i>Potentilla pulcherrima</i>	<i>Penstemon whippleanus</i>	<i>Fragaria ovalis</i>
<i>Pseudocymopterus montanus</i>	<i>Pentaphylloides</i>	<i>Gayophytum nuttalli</i>

	<i>floribunda*</i>	
<i>Pyrola chlorantha+</i>	<i>Potentilla pulcherrima</i>	<i>Harbouria trachypleura</i>
<i>Rosa woodsii</i>	<i>Pseudocymopterus montanus</i>	<i>Juncus arcticus</i>
<i>Rubus idaeus ssp. melanolasius+</i>	<i>Pyrola minor</i>	<i>Juniperus communis*</i>
<i>Salix planifolia+</i>	<i>Rosa woodsii</i>	<i>Lupinus argenteus</i>
<i>Salix reticulata+</i>	<i>Selaginella densa</i>	<i>Mertensia ciliata</i>
<i>Senecio fremontii var. blitoides+</i>	<i>Senecio triangularis</i>	<i>Orthilia secunda</i>
<i>Taraxacum officinale</i>	<i>Solidago multiradiata</i>	<i>Oxypolis fendleri</i>
<i>Unknown species 10</i>	<i>Taraxacum officinale</i>	<i>Rosa acicularis</i>
<i>Unknown species 4</i>	<i>Vaccinium myrtillus ssp. oreophilum*</i>	<i>Penstemon whippleanus</i>
<i>Unknown species 5</i>		<i>Pentaphylloides floribunda*</i>
<i>Unknown species 6</i>		<i>Poa nemoralis ssp. interior</i>
<i>Unknown species 7</i>		<i>Potentilla pulcherrima</i>
<i>Unknown species 8</i>		<i>Pseudocymopterus montanus</i>
<i>Unknown species 9</i>		<i>Pyrola minor</i>
<i>Wyethia amplexicaulis+</i>		<i>Sedum lanceolatum</i>
		<i>Selaginella densa</i>
		<i>Senecio triangularis</i>
		<i>Silene scouleri ssp. hallii</i>
		<i>Smilacina sp.</i>
		<i>Solidago multiradiata</i>
		<i>Taraxacum officinale</i>
		<i>Thermopsis divaricarpa</i>
		<i>Trisetum spicatum</i>
		<i>Vaccinium myrtillus ssp. oreophilum*</i>
		<i>Veronica wormskjoldii</i>

Appendix 10. Species lists for all three survey years at site D1 (alpine). Species with + symbols were new species at D1 in 2013 (not found in 1981 or 1996).

Site D1 2013	Site D1 1996	Site D1 1981
<i>Acomastylis rossii</i> ssp. <i>turbinata</i>	<i>Acetosella vulgaris</i>	<i>Acetosella vulgaris</i>
<i>Antennaria microphylla</i> +	<i>Acomastylis rossii</i> ssp. <i>turbinata</i>	<i>Acomastylis rossii</i> ssp. <i>turbinata</i>
<i>Anticlea elegans</i>	<i>Artemisia scopulorum</i>	<i>Anticlea elegans</i>
<i>Bistorta bistortoides</i>	<i>Besseyia alpine</i>	<i>Arenaria fendleri</i>
<i>Bistorta vivipara</i>	<i>Bistorta bistortoides</i>	<i>Artemisia scopulorum</i>
<i>Campanula uniflora</i>	<i>Campanula uniflora</i>	<i>Besseyia alpina</i>
<i>Carex albonigra</i>	<i>Carex albonigra</i>	<i>Bistorta bistortoides</i>
<i>Castilleja occidentalis</i> +	<i>Carex rupestris</i> ssp. <i>drummondiana</i>	<i>Bistorta vivipara</i>
<i>Erigeron simplex</i> +	<i>Carex scopulorum</i>	<i>Calamagrostis purpurascens</i>
<i>Eritrichum aretoides</i>	<i>Cerastium beeringianum</i> ssp. <i>earlei</i>	<i>Campanula uniflora</i>
<i>Erysimum capitatum</i>	<i>Cystopteris fragilis</i>	<i>Carex albonigra</i>
<i>Fabaceae</i> sp. 1	<i>Eremogone fendleri</i>	<i>Carex arapahoensis</i>
<i>Fabaceae</i> sp. 2	<i>Eritrichum aretoides</i>	<i>Carex norvegica</i>
<i>Fabaceae</i> sp. 3	<i>Erysimum capitatum</i>	<i>Carex norvegica</i> ssp. <i>norvegica</i>
<i>Gentian pneumonanthe</i> +	<i>Helicotrichon mortonianum</i>	<i>Carex rupestris</i>
<i>Kobresia myosuroides</i>	<i>Kobresia myosuroides</i>	<i>Cerastium beeringianum</i> ssp. <i>earlei</i>
<i>Lidia obtusiloba</i>	<i>Lidia obtusiloba</i>	<i>Cystopteris fragilis</i>
<i>Lloydia serotina</i>	<i>Lloydia serotina</i>	<i>Danthonia intermedia</i>
<i>Mertensia lanceolata</i>	<i>Mertensia lanceolata</i>	<i>Eritrichum aretoides</i>
<i>Oreoxis alpina</i>	<i>Oreoxis alpina</i>	<i>Erysimum capitatum</i>
<i>Poa glauca</i> ssp. <i>rupicola</i>	<i>Phlox sibirica</i> ssp. <i>pulvinata</i>	<i>Helicotrichon mortonianum</i>
<i>Potentilla nivea</i>	<i>Poa glauca</i> ssp. <i>rupicola</i>	<i>Kobresia myosuroides</i>
<i>Potentilla rubricaulis</i>	<i>Polemonium viscosum</i>	<i>Lewisia pygmaeae</i>
<i>Rydbergia grandiflora</i>	<i>Potentilla nivea</i>	<i>Lloydia serotina</i>
<i>Stellaria longipes</i> +	<i>Potentilla ovina</i>	<i>Mertensia viridis</i>
<i>Taraxacum ceratophorum</i>	<i>Potentilla rubricaulis</i>	<i>Lidia obtusiloba</i>
<i>Trifolium dasyphyllum</i>	<i>Rhodiola integrifolia</i>	<i>Oreoxis alpina</i>
<i>Trisetum spicatum</i> ssp. <i>congdonii</i>	<i>Rydbergia grandiflora</i>	<i>Phlox sibirica</i> ssp. <i>pulvinata</i>

<i>Unknown species 11</i>	<i>Selaginella densa</i>	<i>Poa glauca</i>
<i>Unknown species 12</i>	<i>Silene acaulis ssp. subacaulescens</i>	<i>Polemonium viscosum</i>
<i>Unknown species 13</i>	<i>Taraxacum ceratophorum</i>	<i>Potentilla nivea</i>
	<i>Tonestus pygmaeus</i>	<i>Potentilla rubricaulis</i>
	<i>Trisetum spicatum ssp. congdonii</i>	<i>Rydbergia grandiflora</i>
	<i>Trifolium dasyphyllum</i>	<i>Saxifraga rhomboidea</i>
	<i>Trifolium nanum</i>	<i>Selaginella densa</i>
		<i>Silene acaulis ssp. subacaulescens</i>
		<i>Taraxacum ceratophorum</i>
		<i>Thlaspi montanum</i>
		<i>Tonestus pygmaeus</i>
		<i>Trifolium dasyphyllum</i>
		<i>Trifolium nanum</i>

Appendix 11. Presence/absence percentages for species having >20% presence in 1981, 1996, or 2013. 95% confidence intervals for binomial distribution are provided in parentheses. Double asterisks refer to species that were present but their frequencies are unknown due to a lack of raw data. Bolded values represent the highest presence values for each site during each year.

Site	Species	1981	1996	2013
A1	<i>Antennaria alpine</i>	0	0	30 (17–43)
	<i>Artemisia ludoviciana</i>	18 (9–31)	28 (16–42)	0
	<i>Artemisia frigida</i>	0	10 (2–18)	44 (30–58)
	<i>Astragalus tenellus</i>	0	0	22 (10–34)
	<i>Bromus tectorum</i>	10 (3–22)	62 (47–75)	14 (4–24)
	<i>Carex pensylvanica</i> ssp. <i>heliophila</i>	72 (58–84)	82 (69–91)	86 (76–96)
	<i>Collinsia parviflora</i>	30 (18–45)	30 (18–45)	0
	<i>Critesion brachyantherum</i>	0	0	20 (9–31)
	<i>Drymocallis fissa</i>	22 (12–36)	16 (7–29)	0
	<i>Elymus elymoides</i>	**	16 (6–26)	62 (48–76)
	<i>Gayophytum nuttallii</i>	30 (18–45)	32 (20–47)	0
	<i>Leucopoa kingie</i>	22 (12–36)	34 (21–49)	0
	<i>Mertensia lanceolatum</i>	16 (7–29)	28 (16–42)	12 (3–21)
	<i>Phacelia heterophylla</i>	24 (13–38)	14 (6–27)	0
	<i>Poa compressa</i>	0	20 (10–34)	38 (24–52)
	<i>Scutellaria brittonii</i>	38 (25–53)	42 (28–57)	0
<i>Senecio integerrimus</i>	28 (16–42)	34 (21–49)	0	
<i>Solidago missouriensis</i>	30 (18–45)	40 (26–55)	38 (24–52)	
B1	<i>Achillea millefolium</i> var. <i>occidentalis</i>	20 (10–36)	34 (21–49)	56 (42–70)
	<i>Aletes acaulis</i>	36 (23–51)	32 (20–47)	0
	<i>Artemisia ludoviciana</i>	54 (39–68)	68 (54–80)	74 (62–86)
	<i>Astragalus adsurgens</i> var. <i>robustior</i>	**	6 (0–13)	30 (17–43)
	<i>Astragalus tenellus</i>	18 (9–31)	28 (15–40)	60 (46–74)
	<i>Boechera</i> sp.	22 (12–36)	4 (0–14)	0
	<i>Carex pensylvanica</i> ssp. <i>heliophila</i>	76 (62–87)	82 (69–91)	96 (91–100)
	<i>Critesion brachyantherum</i>	0	0	52 (38–66)
<i>Drymocallis fissa</i>	36 (23–51)	34 (21–49)	0	

	<i>Elymus Canadensis</i>	0	0	20 (9–31)
	<i>Elymus elymoides</i>	0	4 (0-9)	80 (69–91)
	<i>Eriogonum umbellatum</i>	**	10 (2-18)	68 (55–81)
	<i>Gayophytum sp.</i>	24 (13–38)	18 (9–31)	0
	<i>Geranium caespitosum</i>	**	14 (4-24)	40 (26–54)
	<i>Gilia pinnatifida</i>	12 (5–24)	20 (10–36)	0
	<i>Harbouria trachypleura</i>	34 (21–49)	24 (13–38)	0
	<i>Heterotheca villosa</i>	0	8 (0-16)	32 (19–45)
	<i>Koeleria macrantha</i>	16 (7–29)	28 (16–42)	0
	<i>Leucopoa kingie</i>	50 (36–64)	44 (30–59)	0
	<i>Lupinus argenteus</i>	2 (0–11)	34 (21–49)	12 (3–21)
	<i>Mertensia lanceolatum</i>	**	14 (4-24)	26 (14–38)
	<i>Packera fendleri</i>	28 (16–42)	44 (30–59)	0
	<i>Penstemon virens</i>	72 (58–84)	76 (62–87)	0
	<i>Phacelia heterophylla</i>	24 (13–38)	16 (7–29)	6 (0–13)
	<i>Poa compressa</i>	0	8 (0-16)	28 (15–41)
	<i>Pseudocymopterus montanus</i>	0	0	64 (51–77)
	<i>Scutellaria brittonii</i>	14 (6–27)	28 (16–42)	0
	<i>Sedum lanceolatum</i>	34 (21–49)	54 (39–68)	18 (7–29)
	<i>Solidago missouriensis</i>	0	0	34 (21–47)
	<i>Solidago multiradiata</i>	20 (10–36)	52 (37–66)	54 (40–68)
C1	<i>Achillea millefolium var. occidentalis</i>	74 (60–85)	38 (25–53)	24 (12–36)
	<i>Anticlea elegans</i>	16 (7–29)	20 (10–34)	4 (0–9)
	<i>Antennaria parvifolia</i>	24 (13–38)	2 (0–11)	0
	<i>Aster foliaceus</i>	20 (10–34)	0	0
	<i>Calamagrostis canadensis</i>	6 (1–14)	32 (20–47)	0
	<i>Campanula rotundifolia</i>	28 (16–42)	24 (13–38)	10 (2–18)
	<i>Carex foenea</i>	0	44 (30–59)	32 (19–45)
	<i>Chamerion danielsii</i>	90 (78–97)	78 (65–88)	74 (62–86)
	<i>Fragaria virginiana ssp. glauca</i>	86 (73–94)	84 (72–93)	62 (48–76)
	<i>Juncus arcticus ssp. ater</i>	34 (21–49)	16 (7–29)	18 (7–29)
	<i>Lupinus argenteus</i>	52 (37–66)	6 (0–13)	0
	<i>Mertensia ciliate</i>	0	0	34 (21–47)
	<i>Orthilia secunda ssp. obtusata</i>	18 (9–31)	22 (12–36)	0
	<i>Potentilla pulcherrima</i>	50 (36–64)	36 (23–51)	30 (17–43)

	<i>Pseudocymopterus montanus</i>	34 (20–47)	34 (20–47)	6 (0–13)
	<i>Pyrola chlorantha</i>	0	0	30 (17–43)
	<i>Rosa woodsii</i>	28 (16–42)	14 (6–27)	42 (28–56)
	<i>Salix reticulata</i>	0	0	24 (12–36)
	<i>Selaginella densa</i>	34 (21–49)	28 (16–42)	0
	<i>Solidago multiradiata</i>	32 (20–47)	22 (12–36)	0
	<i>Taraxacum officinale</i>	64 (49–77)	18 (9–31)	14 (4–24)
	<i>Thermopsis divaricarpa</i>	26 (15–40)	0	0
D1	<i>Acomastylis rossii ssp. turbinata</i>	98 (89–100)	98 (89–100)	98 (94–100)
	<i>Bistorta bistortoides</i>	90 (78–97)	98 (89–100)	94 (87–100)
	<i>Bistorta vivipara</i>	26 (15–40)	0	20 (9–31)
	<i>Campanula uniflora</i>	98 (89–100)	90 (78–97)	52 (38–66)
	<i>Carex albonigra</i>	12 (5–24)	58 (43–66)	16 (6–26)
	<i>Carex rupestris ssp. drummondiana</i>	4 (0–14)	24 (13–38)	0
	<i>Eremogone fendleri</i>	34 (21–49)	52 (37–66)	0
	<i>Eritrichum aretiodes</i>	42 (28–57)	12 (5–24)	12 (3–21)
	<i>Erysimum capitatum</i>	38 (25–53)	46 (32–61)	10 (2–18)
	<i>Helicotrichon mortonianum</i>	52 (37–66)	54 (39–68)	0
	<i>Kobresia myosurioides</i>	92 (81–99)	94 (83–100)	70 (57–83)
	<i>Lidia obtusiloba</i>	58 (43–66)	54 (39–68)	76 (64–88)
	<i>Lloydia serotina</i>	92 (81–99)	86 (73–94)	44 (30–58)
	<i>Mertensia lanceolatum</i>	40 (26–55)	56 (41–70)	78 (66–90)
	<i>Oreoxis alpina</i>	98 (89–100)	98 (89–100)	22 (10–34)
	D1	<i>Phlox sibirica ssp. pulvinata</i>	90 (78–97)	86 (73–94)
<i>Poa glauca ssp. rupicola</i>		66 (51–79)	92 (81–99)	100 (100–100)
<i>Polemonium viscosum</i>		34 (21–49)	32 (20–47)	0
<i>Potentilla nivea</i>		40 (26–55)	54 (39–68)	4 (0–9)
<i>Potentilla ovina</i>		0	24 (13–38)	0
<i>Potentilla rubricaulis</i>		38 (25–53)	14 (6–27)	2 (0–6)
<i>Rydbergia grandiflora</i>		8 (2–19)	20 (10–34)	6 (0–13)
<i>Selaginella densa</i>		88 (76–95)	70 (56–82)	0

<i>Silene acaulis</i>	26 (15–40)	6 (1–17)	0
<i>Taraxacum ceratophorum</i>	52 (37–66)	60 (49–77)	28 (15–41)
<i>Thlaspi montanum</i>	22 (12–36)	0	0
<i>Trifolium dasyphyllum</i>	88 (76–95)	98 (89–100)	96 (91–100)
<i>Trifolium nanum</i>	40 (26–55)	6 (1–17)	0
<i>Trisetum spicatum ssp. congdonii</i>	0	0	46 (32–60)