

**COMMUNITY ASSEMBLY ALONG SUB-ARCTIC ROADSIDES:
THE ROLE OF PLANT FUNCTIONAL TRAITS
IN NATIVE AND EXOTIC SPECIES**

by

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Abstract

Much is known about plant-environment associations, but we are far from able to predict community species composition under a given set of environmental conditions. Recent research using functional traits suggests niche-based processes are vital in structuring communities, though the generality of results across different ecosystems is unknown. I investigated community trait distribution along environmental gradients in sub-Arctic roadsides-- communities which represent novel ecosystems in which to apply trait-based analysis, and which allow for the comparison of ecological strategies and trait distribution of native and exotic species. While these environments have features specific to northern latitudes, they also broadly represent global roadside environments and their important role in the establishment and spread of exotic species. Invasive exotic species present a pervasive threat to global diversity, and understanding mechanisms of assembly, coexistence and strategies of native and exotic roadside communities can improve our ability to predict invasive species behaviour. I measured species abundance and three functional traits in 42 roadside plots in the Yukon Territory and compared community traits across elevation, latitude and age of road. Across all species, abundance-weighted community height was negatively correlated with elevation and positively correlated to latitude. Native and exotic species tracked environment differently, however, and exotic species showed correlations between height and road age as well as between specific leaf area (SLA) and latitude that were not present among native species. A comparison of mean trait values of native and exotic species irrespective of environment revealed specific leaf area (SLA) was greater in exotic species than native species. In addition, I used three null models to test for habitat filtering and competitive exclusion, two important niche-based assembly processes. Ranges of trait values

across plots were smaller than expected and trait values more evenly spaced compared to random samples from the regional species pool, suggesting both habitat filtering and competitive exclusion (limiting similarity) shape these disturbance communities. Both processes were found to also affect both presence/absence and abundance of species. Understanding mechanisms of community assembly along roadsides and the characterisation of native and exotic community constituents will have important implications for development of conservation management strategies.

Preface

This thesis is original, unpublished, independent work by the author, Jamie A. Leathem.

Project design was developed with help from Nathan Kraft, and analysis of habitat filtering and limiting similarity data was done with an adaptation of methods used by Nathan Kraft, Will Cornwell and Maude Bernard-Verdier.

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For my dad

1. Introduction

Understanding the processes involved in community assembly remains a central question in ecology. It is key to understanding both ecosystem functioning and the maintenance of biodiversity (Cavender-Bares et al. 2004, Ejrnæs et al. 2006, Gjerde et al. 2011, Allan et al. 2013). Much is known about plant-environment associations and patterns, but we are far from able to predict the composition of species occurring in a community under a given set of environmental conditions. Global vegetation is currently facing unprecedented rates of anthropogenic disturbance, exotic species introductions and shifts in climate, thus it is increasingly important to understand the forces involved in structuring communities to anticipate consequences and trends of vegetation change.

1.1 Roadside environments

My research uses several approaches to examine the structure of disturbed roadside plant communities in sub-Arctic Yukon Territory, and the ecological strategies of their native and exotic constituents. These ecosystems are a research priority for several reasons. Roadsides themselves are one of the most widespread anthropogenic disturbance types worldwide (Forman and Alexander 1998, Fahrig and Rytwinski 2009, Meunier and Lavoie 2012) and have been described by some ecologists as the “sleeping giant” of ecology, due to the relative lack of knowledge about their functioning and impacts on surrounding ecosystems (Forman and Alexander 1998, Schaffers and Sýkora 2002, Matesanz et al. 2006, Coffin 2007). They are novel and/or emerging ecosystems because they contain species in combinations and relative abundances with no historical precedence in a given biome (Hobbs et al. 2006), and while they are constantly increasing in area, they remain an understudied ecosystem type. Roadside habitats

are global in scope and despite huge variation in environments, share many similarities across biomes. Thus, while our research is focused on northern roadsides, it is likely relevant to roadside habitats worldwide.

Typical roadside conditions include high light availability, ongoing physical disturbance and changes in physical and chemical soil properties relative to surrounding areas (Auerbach et al. 1997, Coffin 2007). They typically favour disturbance-adapted plants including weeds and exotic species (Spellerberg 1998, Forman and Alexander 1998, Jones et al. 2000, Trombulak and Frissell 2000), and in cases where adjacent vegetation is relatively undisturbed the differences between roadside and natural areas can be great (Johnston and Johnston 2004). Initial removal of vegetation and topsoil, the addition of mineral soil or gravel/sand, and other construction processes make roadside soil more compacted, with more coarse grained materials and fewer fine-grained particles than natural areas (Forman and Alexander 1998, Johnston and Johnston 2004). These soils typically have lower organic matter content and, at least initially, lower nutrient content than surrounding areas because of the importation of mineral soil and gravel. In some cases the low nutrient state persists (Walker and Everett 1987). More commonly, however, nitrogen builds up in soil over time from both vehicle exhaust deposition (Gilbert et al. 2003, Cape et al. 2004, Truscott et al. 2005) and successional processes (Inouye et al. 1987, Knops and Tilman 2000). Leachates in storm water runoff also contribute to nutrient accumulation, rendering roadsides higher in available nutrients than surrounding areas (Truscott et al. 2005). Soil pH is made higher due to initial mineral soil addition and accumulation of potential leachates such as salt and other alkalinizing cations (Angold 1997, Trombulak and Frissell 2000). Higher pH values increase availability of nitrogen to plants making road edges suitable

for nutriphilic and disturbance-tolerant ruderals (Huenneke et al. 1990). The combination of disturbance and eutrophication has been shown to reduce native plant cover and diversity and increase cover of exotic species (Humphries et al. 1991, Kolb et al. 2002). Along gravel roads, road dust can influence community structure by changing soil pH and nutrient profile, blocking photosynthesis and clogging stomata (Walker and Everett 1987, Farmer 1993, Myers-Smith et al. 2006). Effects of nitrogen deposition and other roadside features have been detected at up to 200 m away from roads (Angold 1997, Forman et al. 1997, Forman and Deblinger 1998, Gilbert et al. 2003); however, they are most pronounced along a gradient within the first 5-10 metres, and begin to decline sharply after the first 1 or 2 metres (Angold 1997, Johnston and Johnston 2004).

Roadsides are also known to be sites of exotic species establishment. The often weedy, disturbance-adapted species commonly thrive in these low-competition, high nutrient environments. Especially in areas where nitrogen is strongly limiting, such as the sub-Arctic, nitrification from vehicle exhaust and runoff can have a large impact on plant communities, increasing abundance of exotic species over native species (Huenneke et al. 1990, Trombulak and Frissell 2000, Davis et al. 2000, Thomsen et al. 2006). Roads and surrounding environments also facilitate spread of exotics through direct transportation of propagules by human or animal traffic, or by air movement created by traffic or just the open space a road cut provides (Forman and Alexander 1998, Gelbard and Belnap 2003, Christen and Matlack 2006, Wurtz et al. 2010, Gieselman et al. 2013). This can also allow spread of exotic species into “natural” areas such as streambanks, which can in turn increase spread by transporting propagules via waterways (Parendes and Jones 2000, Bennett and Mulder 2008).

1.2 Northern roadsides

Northern roadsides are similar to roadsides worldwide, with a few exceptions. Salt is not commonly used due to extreme cold temperatures, but gravel and grit used for winter traction are still likely to increase pH (Truscott et al. 2005). Heat islands may be created when paved roads absorb heat through the day and release it slowly at night (Farmer 1993). This causes ground ice to thaw earlier and to a greater depth near roads (Auerbach et al. 1997). Ground that is bare in continually disturbed areas has decreased albedo in summer, which can further warm the area (Walker and Everett 1987). These conditions allow for earlier growth of some roadside species (Farmer 1993).

These roadsides are a research priority for several reasons. Northern regions are currently facing unprecedented development pressures from petroleum and mineral exploration and development (Prowse et al. 2009). To understand potential impacts of disturbances associated with these types of development, existing roadsides need to be characterized. Northern regions are more affected by current climate warming than lower latitudes (Parry et al. 2007) and are already experiencing some dramatic ecological consequences (Post et al. 2009), such as increased forest fire frequency and intensity (Johnstone et al. 2010) expansion of tree- and shrub-lines (Danby and Hik 2007, Harsch et al. 2009, Myers-Smith et al. 2011), and plant community shifts (Post et al. 2009, Elmendorf et al. 2012, Pearson et al. 2013). Characterization of disturbed communities can provide essential baseline data for assessing future responses to climate change.

Northern roadsides, as elsewhere, are sites where non-native plants can establish, some of which can become problematic (Conn et al. 2008, Villano 2008, Vilà et al. 2011, Pyšek et al. 2012,

Sanderson et al. 2012). Until the early 1990s, little was known about the impacts of exotic plants in northern North America (Bennett and Mulder 2008, Conn et al. 2008). However, in recent decades they have garnered attention as their numbers and spread have increased rapidly and they begin to have measurable impacts on habitat and hydrology (Carlson and Shephard 2007, Spellman 2008, Line et al. 2008, Wurtz et al. 2010). While these impacts are not necessarily negative, some non-native plants at northern latitudes have been shown to cause a decrease in biodiversity and to threaten native species, and have thus been labelled invasive. This term usually refers to non-native species that are likely to cause economic, environmental or societal harm (US Department of Agriculture 1999, Environment Canada 2012), and is the definition we use here. Northern Canada is undergoing increasing resource development disturbance, which, along with accompanying roads and other similar disturbance types increases the potential spread of exotic species, and thus some invasive exotic species.

So far in Yukon, where this research is focussed, exotic species remain mostly associated with areas of human disturbance (Conn and Beattie 2004, Bennett and Mulder 2008), though a few species have colonized natural riparian areas (Conn et al. 2008) and the boreal forest may be susceptible as well (Sanderson et al. 2012). While exotic species establishment can be a consequence of human-driven ecosystem change, i.e., exotic species can act as “passengers” benefitting from disturbance (MacDougall and Turkington 2005), they can in many cases drive change themselves. For example, white sweetclover (*Melilotus albus*) is able to colonize pristine river banks in Alaska and Yukon and outcompete lower-growing native seedlings (Spellman 2008), forming dense stands that alter river geomorphology via channelization (Conn et al. 2008). The majority of Yukon plant communities are still relatively free from exotic species,

which tend to be restricted to areas of disturbance and development. This makes it an ideal time to identify and study the invaded environments and to characterize the potentially aggressive exotics in order to predict future invasions. Spread of exotic plants is projected to increase with global change (Dukes and Mooney 1999), and to understand how their spread may change with increased disturbance through development and climate change, it is necessary to understand the forces shaping the communities they thrive in and the characteristics of the species themselves.

1.3 Functional-trait based approaches

Recent advances in trait-based approaches have made them a powerful tool in investigating plant community structure and function. While trait-based analysis of communities is not new, the past decade has seen the identification of cohesive suites of functional traits representing key axes of plant variation and ecological strategy (Westoby et al. 2002, Wright et al. 2004, McGill et al. 2006). Functional traits (hereafter referred to as “traits”) are measurable plant characteristics that are indicative of overall plant performance and ecological strategy (McGill et al. 2006, Violle et al. 2012). Key traits represent multiple dimensions of plant performance and because they are quantifiable, provide a measurable common currency with which to compare diverse species or groups of species. They allow direct comparison of plants from vastly different environments; for example, the leaf traits of a desert rose can be numerically compared to those of a coastal lily to quantify functional differences indicative of level of drought tolerance.

Analysis of plant traits is useful in examining many aspect of plant communities and their constituent species or species groups. For example, characterizing patterns of community trait change along environmental gradients is an effective way to identify ecological strategies across

species and communities (Lavorel and Garnier 2002, Bernard-Verdier et al. 2012). Trait analysis also allows the quantitative functional comparison of exotic and native species, which may be important in attempts to predict invasiveness and invasibility of communities (Tilman 1997, Symstad 2000, Tecco et al. 2010, van Kleunen et al. 2010). Furthermore, analysis of trait distributions can reveal patterns of community organization, such as trait overdispersion linked to assembly processes, which provide insight into forces that shape given communities (Shipley et al. 2006, McGill et al. 2006). I discuss each of these trait-based analyses in turn below.

1.4 Community traits along environmental gradients

While the association between environmental gradients and plant community composition has long been recognized (Schimper 1898, Dachnowski 1911, Day and Monk 1974, Vitousek et al. 2009), the importance of this coupling relative to other factors that structure communities is still debated. For instance, it has been proposed that stochastic events may be more important than deterministic, niche-based processes (resource competition, for example) in shaping communities in a given environment (Hubbell 2001, Lavorel and Garnier 2002). There is some evidence that stochastic factors may be especially important in shaping communities in highly disturbed environments (Lepori and Malmqvist 2009). Examining how traits change along environmental gradients is one way to test for evidence of deterministic vs. stochastic processes underlying community assembly. One of the fundamental insights in community ecology is that different types of plants are successful in different environments (Schimper 1898), and the analysis of functional traits across environments can reveal which traits allow plant species to track changes in abiotic variables (Weiher et al. 1998, Cornwell and Ackerly 2009, Jung et al. 2010, Bernard-Verdier et al. 2012). This can ultimately lead to prediction of potential community

membership. Trait-environment relationships have been shown in various environments such as grasslands (Pillar et al. 2009, Bernard-Verdier et al. 2012) and wetlands (Weiher et al. 1998) but little work has specifically targeted roadsides or compared native and exotic species therein (but see Ullmann et al. 1995, Arévalo et al. 2005). My analysis tests whether different community trait values are associated with different environmental conditions in order to quantify the degree to which roadside assembly is influenced by abiotic factors associated with various environmental gradients.

In the analysis of functional traits along environmental gradients, I also consider the often-overlooked *within*-species change as well as among-species change. Most trait-gradient studies use single trait values for each species, with trait-environment relationships reflecting turnover of species membership under different environmental conditions (Wright et al. 2001, Cavender-Bares et al. 2004). However, intraspecific variation along environmental gradients has been shown to be an important factor creating community-level trait-environment relationships (Jung et al. 2010, Violle et al. 2012). Intraspecific variation, whether from phenotypic plasticity or genetic variation (e.g., local ecotypes), can account for a large proportion of community-level trait change along gradients (Ackerly and Cornwell 2007, Cornwell and Ackerly 2009). For instance, Cornwell and Ackerly (2009) found that, along a soil moisture gradient, intraspecific variation was responsible for between 14 and 21% of the variation in specific leaf area (leaf area divided by leaf mass, SLA), an important leaf trait. That is, while change in species identity at different moisture levels was responsible for some of the correlation with environment, variation in SLA *within species* was also an important component of this response. They also found it was in the same direction as interspecific variation in SLA among these environments, strengthening

the relationship of SLA with environment. Nonetheless, they found that species turnover consistently made a greater contribution to the relationship than intraspecific variation, i.e., that species turnover was a stronger force than intraspecific variation. I quantified intraspecific trait change in my analyses and tested its influence on trait/environment relationships, as it is an important part of how traits track environmental change.

1.5 Ecological strategies of native and exotic plants

Exotic species introductions are not inherently harmful. They can increase local biodiversity while providing ecosystem services such as food for humans and habitat for wildlife. In the case of roadsides, they can often provide soil stabilization more reliably and quickly than native species (Matheus and Omtzigt 2012). However, introduction of invasive exotic species can have far-reaching and sometimes harmful consequences. Invasive species are second only to habitat loss in threatening global biodiversity (Sala et al. 2000) and in Canada they are among the top threats to at-risk species (Venter et al. 2006, McCune et al. 2013). Worldwide, they present substantial economic and environmental threats (Vitousek et al. 1996, Brooks et al. 2004, Pimentel et al. 2005) and as such, identification and control of weedy and exotic invasive species is one of the most significant challenges facing land managers worldwide, and is of significant concern in Yukon (Government of Yukon, Department of Environment 2011). The cost of control measures and losses in productivity are estimated at C\$30-40 billion annually in North America, which, coupled with harder to calculate costs of habitat and diversity loss, changes in ecosystem function, loss of culturally valued plants and animals and aesthetic value, makes identifying potential invaders before they become problematic an important task (Wilcove et al. 1998, Hulme 2003, Simberloff 2005). To this end, identification of biological differences

between exotic species and the native species they can displace has become a high priority in conservation biology, with the goal of creating predictive models to determine what species are most likely to become invasive (Rejmánek 2000, Kolar and Lodge 2001, Hayes and Barry 2007). Comparisons of single biological traits have had only limited success to date (Rejmanek and Richardson 1996, Hayes and Barry 2007), but because functional trait analysis allows us to quantitatively compare life strategies between native and exotic species it may prove more useful in predictive models.

Multiple factors may play a role in invasiveness, including as enemy release (Blumenthal et al. 2009, Seastedt 2009), adaptation to disturbance (Grime 1977, Rejmanek and Richardson 1996), and genetic or phenotypic variability. Differences in ecological strategy of exotic species compared to their native neighbours underpins many of these factors (McDowell 2002, Daehler 2003, Lloret et al. 2005, van Kleunen et al. 2010, Ordonez et al. 2010). Invaders are likely to be different than natives as they are often species that have qualities desirable to humans, such as good forage quality or fast growth, or they are adapted to human-disturbed environments through centuries of exposure to agriculture and development in their native regions (Randall and Marinelli 1996, Kitajima et al. 2006, van Kleunen et al. 2010a, Cleland et al. 2011). Many of the native species colonizing Yukon roadsides have come from adjacent forest, which has strongly contrasting environmental conditions: low-light availability, acidic soils and low nutrient availability. Plants in this type of environment are often characterized by low photosynthetic rates, slow growth, and low nutrient uptake capacity (Grime 1977, Chapin 1980). Conversely, the often weedy exotic invaders tend to have high photosynthetic rates, fast growth and high capacity for nutrient uptake (Leishman et al. 2007). By identifying trait differences between the

two groups in Yukon, I hope to increase the knowledge of what makes a species invasive, both locally and more broadly. Additionally, comparing trait change across environmental gradients for both native and exotic species will increase our understanding of community dynamics and response to environmental change from climate shifts and increasing anthropogenic disturbance.

1.6 Null models and community assembly filters at two scales

Analysis of trait distribution patterns in communities can provide insight into community assembly processes. Debate exists about the relative importance of deterministic forces in community assembly, such as a balance between intra- and inter-specific competition predicted by classical community assembly theory (Macarthur and Levins 1967), or stochastic processes, such as local drift and dispersal, as emphasized in neutral assembly models (Hubbell 2001). The importance of both sets of processes has been demonstrated (Fargione et al. 2003, Fukami et al. 2005, Adler et al. 2007, Weiher et al. 2011, de Bello 2012), and indeed recent frameworks conceptualize coexistence as a function of chance, historical patterns, dispersal, and abiotic and biotic habitat processes that combine to define a given community (Vellend 2010, Gotzenberger et al. 2012). However, it is far from predictable how these processes manifest in a given environment.

Previous research using functional trait analysis has found support for deterministic assembly patterns in communities in various ecosystem types, including temperate forests and shrublands (Mouillot et al. 2007, Cornwell and Ackerly 2009, Schamp and Aarssen 2009), tropical forests (Kraft et al. 2008, Swenson and Enquist 2009), and sand dunes (Stubbs and Wilson 2004) (but see Schamp et al. 2008, and Gotzenberger et al. 2012, for example). The northern roadsides that

are the focus of our research represent recently and continually disturbed communities with comparatively novel species combinations—most non-native species have been present in Yukon for less than 120 years and have only become widespread along roads in the past 30 years (Bennett and Mulder 2008). It is possible, then, that niche-based processes are relatively weak in such an environment. Most environments in which deterministic plant community assembly processes have been tested using trait-based approaches have more established vegetation with species combinations that have a much longer history (e.g., Stubbs and Wilson 2004, Ejrnæs et al. 2006, Kraft et al. 2008, Swenson and Enquist 2009, Lebrija-Trejos et al. 2010); there are few such studies aimed at exotic communities (Booth and Swanton 2002). If strong deterministic signals, such as patterns of habitat filtering (reduced range of trait values) or limiting similarity (overdispersion of trait values), were to be found in such disturbed novel ecosystems, it would broaden the range of environments where we may expect these processes to be important, and indicate that these processes develop very early and not just after hundreds of years of co-evolution or in the mature communities of well-established systems. It would also show that community assembly theory is a useful framework for understanding even exotic communities, which is increasingly important with ever-expanding human development and the accompanying inevitable species introductions.

Presence/absence filters. Functional trait analysis typically uses patterns of presence/absence of local species to test predictions about how communities form over time from a regional species pool (Booth and Swanton 2002). These analyses are used to predict the trait patterns we might expect from different assembly processes. The major processes underlying community assembly are conceptualized as nested filters determining what species from a regional species pool are

found in a given local community (Keddy 1992, Weiher and Keddy 1995, Belyea and Lancaster 1999). The two main assembly processes posited are habitat filtering and resource competition. Habitat filtering occurs when environmental conditions restrict the range of trait values “allowed” in a given community, and is expected to result in a pattern of local trait convergence or underdispersion relative to the range of trait values found in the regional species pool. For example, high elevation may restrict community membership to species of low stature. Habitat filtering therefore results in a reduction in the range of trait values present in a local community. The second process, competition for limiting resources, is expected to limit the similarity of coexisting species, preventing taxa from coexisting if their trait values are too similar and thus spreading out trait values and creating a pattern of divergence or overdispersion (Macarthur and Levins 1967, Ricklefs and Travis 1980, Abrams 1983, Pacala and Tilman 1994, Stubbs and Wilson 2004). This limiting similarity results in the trait values of species in a local community being less similar to one another than expected at random (Watkins and Wilson 2003).

Traits and abundance filters. Community assembly processes may be reflected in patterns of local abundance of species in addition to simply their presence/absence. It is important to understand not only which species pass successfully through both filters and are therefore present in the local community, but also whether the species that are present differ in abundance. If so, local abundance may also be affected by the same filters, suggesting the possibility of habitat filtering (convergence) or limiting similarity (divergence) in trait abundance, not just presence or absence. For example, if habitat filtering affects abundance of species in a local community, there could still be a wide range of trait values present, though with most individuals occupying a very narrow range of trait space. We could then infer that trait convergence is taking

place and that habitat favours a specific trait value over others (i.e. there is one optimal trait), even if outlying trait values are not excluded entirely. Conversely, trait abundances may display a divergent pattern with multiple, evenly-spaced values being favoured, suggesting more successful (abundant) species occupy different niches and that limiting similarity is an important determinant of community structure. This is a much less studied facet of community assembly (but see Mouillot 2007, Mason 2011, Cornwell and Ackerly 2010) and investigating abundance patterns can further increase insights into the forces acting on community traits and the levels at which they act (Bernard-Verdier et al. 2012).

While it is common to use null models to test whether observed trait dispersions are significantly different than expected from random patterns, several studies that have failed to find evidence of filtering processes use only one null model to test for both convergent and divergent patterns simultaneously (Watkins and Wilson 2003, Schamp and Aarssen 2009). To increase our ability to detect both patterns, I have used a hierarchical set of null models specifically aimed at testing each filtering process independently (Kraft et al. 2008, Cornwell and Ackerly 2009). This will aid in detection of opposing processes (i.e., convergence and divergence) in the same system.

1.7 Key functional traits

Important work on functional traits in the past decade has identified key axes of functional variation among plant species and the traits that represent them. Light capture strategy and leaf economics/nutrient-use efficiency are two of the most important axes of functional variation. Plant height quantifies light-capture strategy and shade tolerance (Falster and Westoby 2005, Preston et al. 2006) and is an indicator of potential seed dispersal distance (Thomson et al. 2011).

It is also related to Grime's M , a morphology index of the maximum size a plant will attain under advantageous conditions (Grime and Grime 2001). Specific leaf area (leaf area divided by mass, SLA) represents position on the leaf economic spectrum of ecological strategies, an axis which represents the trade-off between cheaply produced (low carbon investment), short-lived, thin leaves and those requiring a high carbon investment that are thicker and more long-lived (Westoby 1998 in Wright 2002). SLA is strongly correlated with photosynthetic rate, nitrogen per unit leaf mass and longevity (Reich et al. 1997, Diemer 1998, Ryser and Urbas 2000) and is related to Grime's R_{\max} , the potential maximum rate of dry matter production grown in a standardized favourable environment (Grime 1974, Grime and Grime 2001). Leaves with high SLA have higher nitrogen and phosphorus concentrations and higher rates of gas exchange so they provide a faster return on carbon investment (Wright et al. 2004). Leaves with low SLA are thicker, longer-lived, slower energy producers (Reich et al. 1997, Wright et al. 2004). However, they are more tolerant to drought and cold stress (Atkin et al. 1996, Thapa et al. 2008, Coopman et al. 2010). A third trait, leaf size or leaf area, is related to both light and heat capture. Small leaves are associated with high light, low nutrient or low moisture conditions (Givnish 1987, Ackerly et al. 1992, Niinemets and Kull 1994). Leaf size is also indicative of photosynthetic capacity, as it partly determines how much area is available for light capture (Westoby 1998). Leaf traits are likely to reveal assembly patterns as well as respond to environmental gradients (Kraft et al. 2008, Cornwell and Ackerly 2009, Bernard-Verdier et al. 2012, Gotzenberger et al. 2012). All three traits are expected to change across environments (McDonald et al. 2003, Moles et al. 2009). Furthermore, there is a large body of evidence demonstrating differences between traits of native and exotic species (Smith and Knapp 2001, Hamilton et al. 2005, Leishman et al. 2007, van Kleunen et al. 2010, Ordonez et al. 2010).

1.8 Research questions

This research addresses the following questions:

Traits along environmental gradients:

1. Do traits in roadside plant communities change predictably along environmental gradients, either through species turnover or intraspecific variation?

Native vs. exotic traits:

2. a) Do native and exotic species traits track environments in the same way?
b) Do native and exotic species exhibit different ecological strategies as measured by average trait values?
3. Are exotic species generally restricted to roadside disturbances, or are they also found in nearby undisturbed vegetation?

Community Structure:

4. Do disturbed roadside communities exhibit non-random trait-distributions suggestive of deterministic community assembly processes?
 - 4a. Specifically, is there evidence of habitat filtering and/or limiting similarity in patterns of species occurrence in plots?
 - 4b. Are these processes evident in patterns of species abundance?

2. Methods

2.1 Study site

The roadside communities investigated are located along the North Klondike Highway (Highway 2) in the south-central Yukon Territory (Fig. 1). The highway runs northwest from 60.71 N to 64.05 N for 532 km and connects the cities of Whitehorse and Dawson. It is constructed on a thick bed of sand and mineral soil and surfaced either with asphalt or bituminous surface treatment (BST), which is a thin asphalt membrane (Precision Research Services 2009). The study area is in the boreal cordillera where the climate is continental sub-Arctic. Winters are long, dark and cold while summers are short, mild and sunny with a few days of nearly constant daylight at higher latitudes (Environment Yukon 2011). Average annual precipitation is 296 mm, with more than half falling as rain in summer and the rest as snow in winter (Environment Canada 2011). Mean annual temperatures range from -0.7°C at the southernmost site to -4.4°C at the northernmost site. Notably, however, summer average temperatures are actually higher at northern sites, which average 13.9°C compared to 12.8°C in southern sites. This is due to the more continental climate to the north where coastal influences decrease (Environment Canada 2011), as well as decreasing elevation moving northward. Along the 500 km stretch of highway containing the sampling area, elevation above sea level (asl) varies between 437 and 854 m.

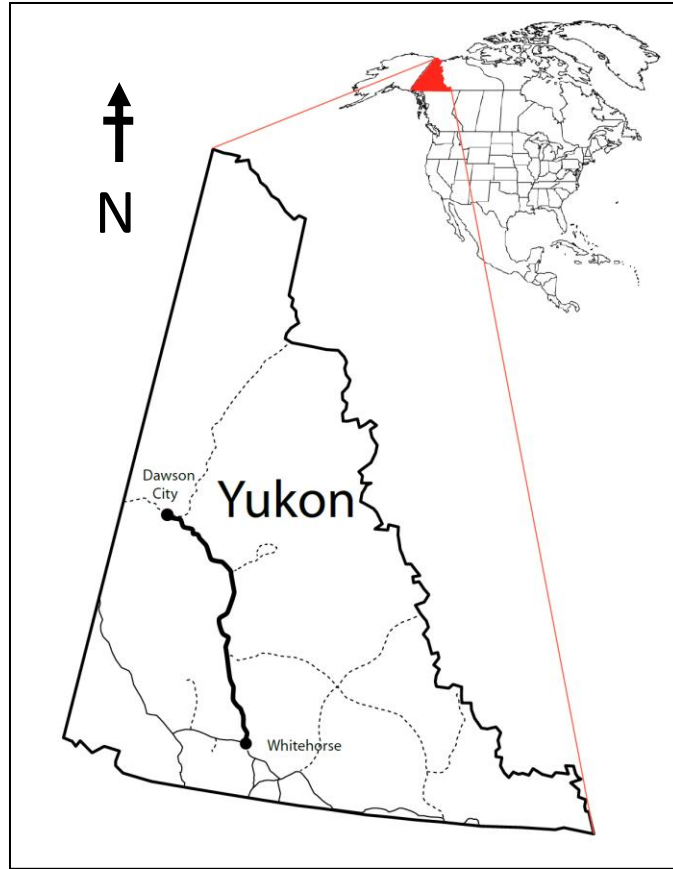


Figure 1: Map of the study area in Yukon Territory, Canada. The thick black line traces the extent of the study area along the North Klondike Highway (Hwy 2). Roadside plots ($n=42$) were located at random locations along the 532 km highway.

2.2 Vegetation types

Common herbaceous roadside species include Yukon's official flower *Chamerion angustifolium* (fireweed), along with *Hedysarum boreale* ssp. *mackenzii* (boreal sweetvetch), three species of *Oxytropis*, as well as seven non-native species: *Taraxacum officinale* (dandelion), *Trifolium hybridum* (alsike clover), and *Melilotus albus* (white sweetclover), *Bromus inermis* (smooth brome), *Crepis tectorum* (narrowleaf hawksbeard), *Medicago sativa* (alfalfa) and *Plantago major* (common plantain). All but one of these species (*Plantago major*) is considered an invasive or aggressive/widespread exotic by the Yukon Department of Environment

(Government of Yukon, Department of Environment 2011). Common grasses include *Elymus trachycaulus* and *Calamagrostis purpurea*. Woody vegetation consists mostly of *Populus balsamifera*, *P. tremuloides*, *Shepherdia canadensis*, *Betula glandulosa* and *Salix glauca*. Vegetation adjacent to disturbed roadside areas is commonly trembling aspen-spruce mixed forests with predominantly white spruce (*Picea glauca*), though forests at the northern end of the system are dominated by black spruce (*Picea mariana*) and *Sphagnum* spp. (Viereck et al. 1992; Fig. 2). Wildfires are common in the area, and several of the sampling plots were located within areas burned between 45 and 11 years ago. Nomenclature follows VASCAN, the Database of Vascular Plants of Canada (Brouillet et al. 2010).

2.3 Study design

Forty-two, 30 m x 5 m plots were randomly located adjacent to the road between kilometres 192 and 710 of the North Klondike Highway (kilometers 0-192 are part of the South Klondike Highway and were not part of the study area). Forty-two off-road plots were also located parallel to the roadside plots but 50 m away from the road. The Yukon Mining and Lands Viewer online mapping tool (Government of Yukon, Dept. of Energy, Mines and Resources 2008) and Google Earth (Google Inc. 2009) were used to make sure locations did not occur within any other large disturbances. Plots were between 1 km and 53 km apart and spanned 487 km (see Appendix A for plot co-ordinates).



a.



b.

Figure 2. Typical roadside vegetation and adjacent forest. a) North Klondike Highway km 419, July 2, 2009. The purple flowers are *Oxytropis deflexa*. b) North Klondike Highway km 649, July 31, 2009. The background forest is mostly white and black spruce (*Picea glauca* and *P. mariana*).

In this study system, slight changes in latitude have large effects on day length and average temperature. In summer, hours of daylight and average temperatures actually increase with latitude. Average summer temperature is 13.9°C at the northernmost site and 12.8°C at the southernmost site (Environment Canada 2011). Elevation change also produces non-trivial temperature differences and may be partially responsible for the higher temperatures at the northern sites, since they tended to be at lower elevations. For this reason, these are especially important variables to consider in characterizing community associations in the sub-Arctic. Elevation and latitude were recorded at each plot using a Garmin eTrex GPS receiver, to ± 6 m error. Plot age (time since latest roadside construction) is also an important factor because different trait values are expected in long-established communities relative to recently established ones (McIntyre et al. 1999, Mason et al. 2012). Historical highway records were consulted to determine the age of each plot (Yukon Highways and Public Works 1998, Jeffries 2010), defined as number of years since last major renovation/construction or fire.

2.5 Species composition

From June 17th - July 4th, 2010 the herbaceous vegetation in each plot was surveyed. Ten 1m² quadrats were placed in each 30 m \times 5 m plot using the same randomly determined placement pattern, and percent cover of all herbaceous species present was estimated visually. Very rare species (less than 0.5% cover in a 1m² quadrat) were given a value of 0.25%. To eliminate potential confounding of plot location and survey date (relative to the growing season), vegetation surveys were conducted in three separate trips over the 17 days of sampling. During the first sampling we travelled from south to north sampling every third plot, then went south again sampling the second plot in each set of three plots. In the third pass the remaining plots were sampled. Plots that had been surveyed earliest in the growing season were re-visited to

confirm and (rarely) adjust abundance estimations of late-emerging species. While herbaceous species were the focus, low shrubs *Arctostaphylos uva-ursi* and *Linnaea borealis* were included as they are functionally part of the herbaceous layer. Several grasses were unidentified and grouped into a single taxon representing <1% of cover. Three herb types were only identified to genus (*Arabis* spp., *Carex* spp., and some *Juncus* spp.).

2.6 Off-road species

To test the hypothesis that exotic species do not persist away from human disturbance, a survey was conducted 50 m away from each roadside plot in adjacent undisturbed forest. After walking 50 m perpendicular to the road, a 30 m x 5 m plot was established parallel to the road. Two observers each performed a 20 minute visual survey for exotic species. Any exotic species present were identified and the number of individuals recorded. Six of the off-road plots were within areas that had been burned by wildfire, three of them in a 1995 fire and three in a 1998 fire.

2.7 Trait measurement

Traits were selected to represent two key axes of plant strategy indicative of resource use by established individuals. The first axis is light capture strategy, represented here by plant height. The second, leaf economics, or rate of photosynthetic return on leaf tissue investment, is represented by two traits, specific leaf area (SLA, leaf surface area per unit dry mass) and absolute leaf area (lamina area). Between July 5th and Aug 2nd, 2010, traits were measured for the 48 most abundant species cumulatively representing at least 80% of the cover in the study area (Garnier et al. 2007). As with species cover data, trait data were collected in three separate trips

to minimize confounding sampling time and latitudinal position on trait values. Both inter- and intra-specific trait variation were recorded in the sampling to differentiate between overall community trait change resulting from *only* species turnover from community trait change resulting from species turnover *plus* within-species plasticity/local adaptation. Following standardized procedures, maximum height of 48 species (41 native, 7 exotic) was measured by taking the shortest distance from the ground to the uppermost leaf or photosynthetic structure on the ten tallest individuals of each species in each plot (Cornelissen et al. 2003, Pérez-Harguindeguy et al. 2013). Leaf trait data were gathered from 44 species (38 native, 6 exotic) by collecting entire plants or branches from five healthy individuals growing in full sun with young but fully developed and undamaged leaves (Cornelissen et al. 2003, Pérez-Harguindeguy et al. 2013). These were immediately stored in plastic bags with moist paper towels and placed in a cooler. Two leaves from each individual were scanned using a CanoScan LiDE 210 scanner (Lake Success, New York). ImageJ software (Rasband 1997) was used to calculate leaf area from scanned images for each species as the mean across two leaves per five individuals. Leaves were dried at 70 °C for 4 days and then weighed in the lab (Pérez-Harguindeguy et al. 2013). All trait values were log-transformed to improve normality. SLA was calculated by dividing individual fresh, one-sided leaf areas by the dry weight of the leaf.

2.8 Data analysis

Community context. In order to examine general vegetation-environment relationships and provide context for trait-based analyses, canonical correspondence analysis (CCA) was performed using species composition and three important environmental variables: latitude, elevation, and plot age (i.e., time since major disturbance) (Legendre and Legendre 1998).

Trait change along environmental gradients. To test for trends in community-level trait values along environmental gradients, community weighted mean trait values (CWM) were calculated for each plot. The trait value of each species in a plot was weighted by its relative abundance in that plot. Pearson's r was used to test for correlations between CWM and latitude, elevation, and age of plot for all species in each plot together, as well as for native and exotic species separately. Testing for significant correlations was performed, first with species-level trait means (one mean value per species for each trait—where a correlation with environment indicates species turnover), and then with plot-level means (42 mean values per species, one calculated for each plot— where a correlation with environment indicates the influence of both intraspecific variation *and* species turnover). To determine what proportion of any observed relationship was due to turnover vs. intraspecific variation, the slope of the log-log relationship between plot-level trait means and environment was calculated first (accounting for both turnover and intraspecific variation). Then, slope of the same relationship between species-wide trait means and environment was calculated (accounting for turnover alone), and the reduction in slope when only turnover was accounted for was determined.

Native vs. exotic traits: Students t tests were used to test for differences in each of the three traits between native and exotic species, using mean trait values across all individuals of a given species. Trait values were log-transformed to improve normality.

Species pools and null models. Random assembly null models were used to test for non-random patterns in community assembly. The use of this type of null model is based on community assembly theory, which posits that local communities are formed from a regional pool of

available species. The local community was defined as all species observed in a given 30 m x 5 m plot, while the regional species pool was designated as all species observed over all plots combined (Zobel et al. 1998). Separate null models were used to test for the effects of habitat filtering and limiting similarity in the same communities, as outlined below (Kraft et al. 2008, Cornwell and Ackerly 2009, Bernard-Verdier et al. 2012).

Habitat filtering of species occurrence, null model 1(NM1). To test for habitat filtering, the observed trait range and variance was compared to null expectations for these metrics (Fig. 3) (Weiher et al. 1998, Cornwell and Ackerly 2009). A null model (NM1a) was used to draw repeated samples of R species from the regional pool, with the probability of each selection for each species proportional to the number of plots where it was observed (i.e., weighted by frequency of occurrence). Because species richness varied among plots and can be correlated with test statistics, we used 99,999 random draws of each level of species richness to form null communities (Lawlor 1980, Gotelli and Graves 1996, Cornwell and Ackerly 2009). In addition, because range is particularly sensitive to extreme values, variance of observed and null trait distributions were also compared, with the expectation that variance should be low when environmental filtering is important. Wilcoxon signed-ranks test was used to determine whether observed trait range and variance was significantly different from values calculated for randomly assembled communities (Kraft and Ackerly 2010). One-tailed tests were used to test the hypothesis that observed values were smaller than the values predicted from the null distribution of values.

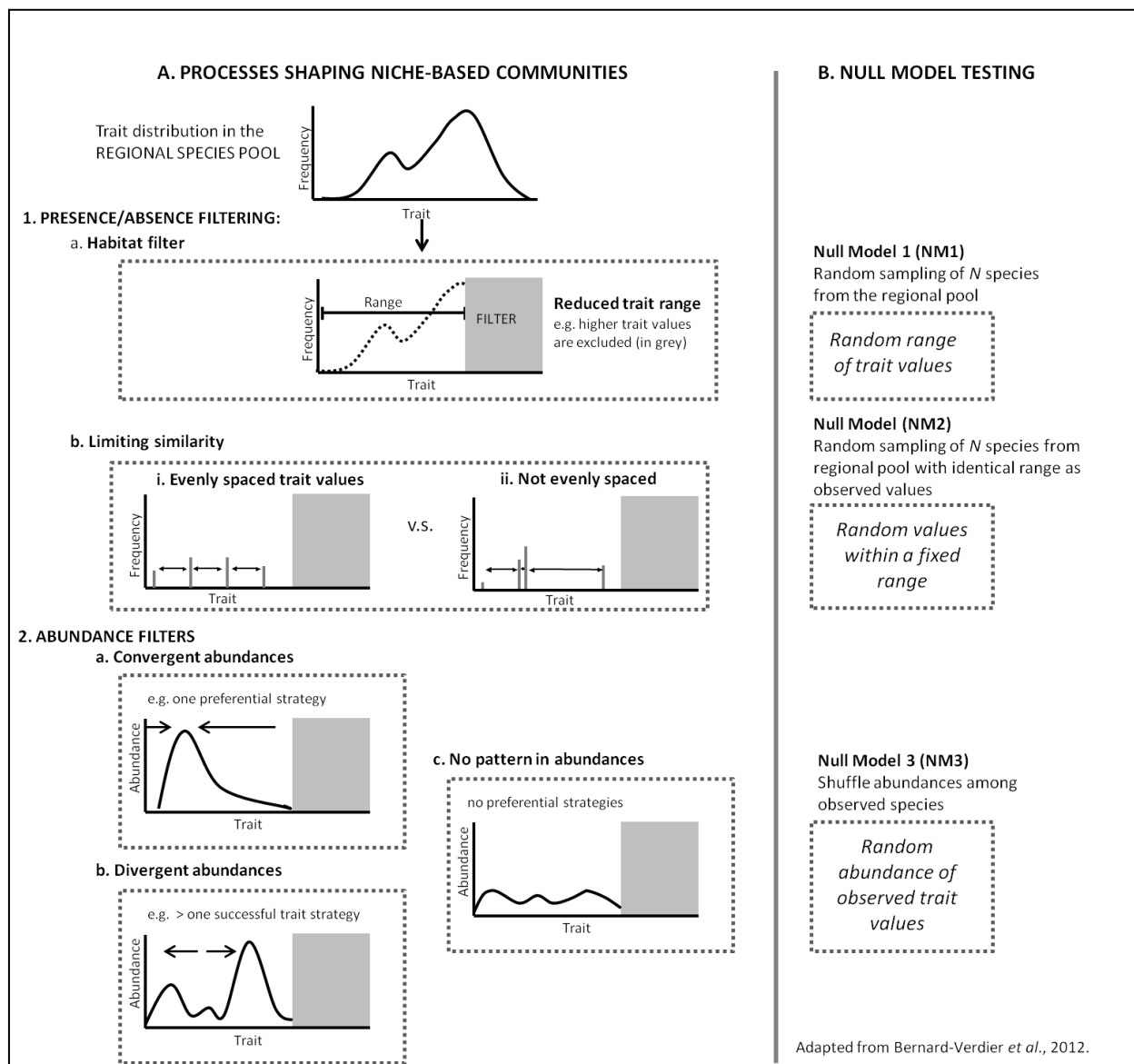
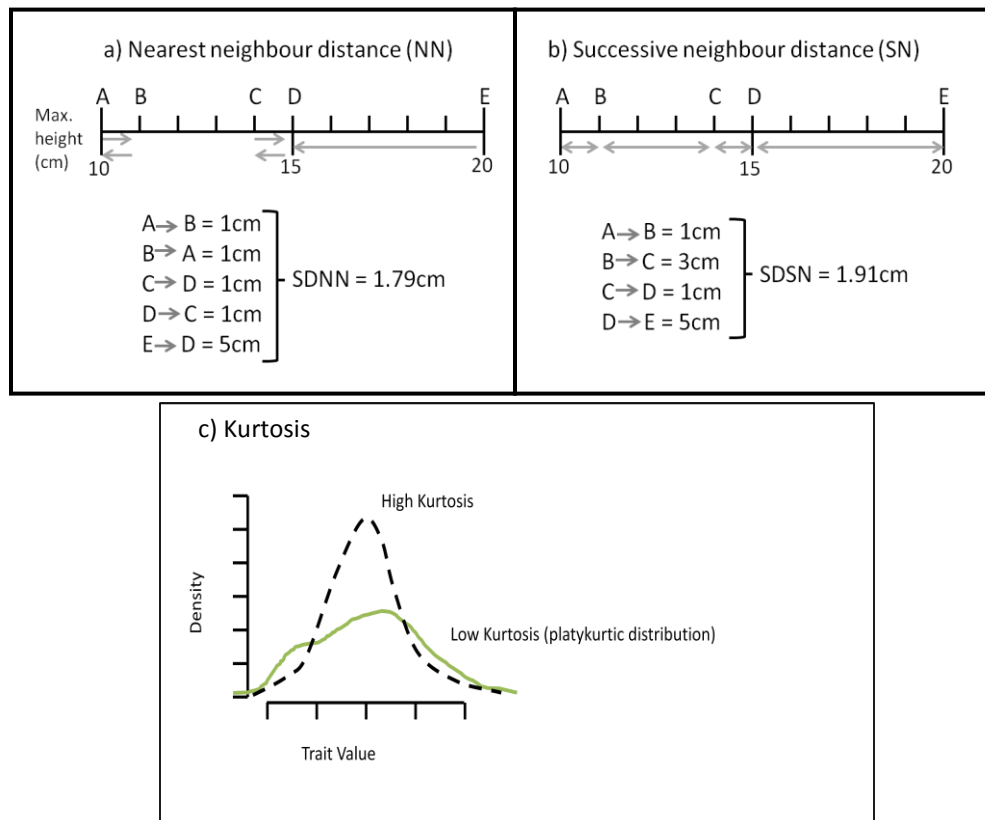


Figure 3. A framework for the niche-based assembly of local communities from regional species pools and the null models used to test for them. **A1.) Processes shaping niche-based communities: Presence/absence filters.** Habitat filtering limits occurrence of certain traits through abiotic or biotic conditions, resulting in a smaller range of trait values than expected if assembly were random with respect to traits (1a). Limiting similarity restricts occurrence through interactive processes such as competitive exclusion or resource partitioning and results in more evenly spaced traits than expected at random (1b). **A2.) Abundance filters.** The above processes may also affect abundance among species whose traits allow them to be present in the community. For example, abundances may converge on one trait value (2a), indicating an optimal trait value exists (like “soft”-habitat filtering), e.g., one height confers abundance and all the species with that height tend to be more abundant than the others. Conversely, there may be several trait values that confer abundance, as in the case of divergence (2b). In this case having complementary traits confers abundance, and can be thought of as “soft” limiting similarity, where too-similar traits are not necessarily absent, but are less abundant. **B) Null model testing.** The three null models used to test for non-random patterns in observed communities corresponding to the processes of assembly in A. NM1 is a general null model that randomly samples species from the regional pool to create random communities at each species richness. NM2 is a restricted null model that tailors each regional pool to include identical maximum and minimum trait values to the corresponding observed community. It tests for evenness of spacing within that same range, thereby able to detect patterns of biotic filtering against a background of environmental filtering. NM3 shuffles abundances (frequencies) among species in observed plots creating a random trait frequency distribution against which to test for convergence or divergence of traits using community weighted variance (CWV).

Limiting similarity of species occurrence, null model 2 (NM2). To test for limiting similarity, a second null model (NM2) was used. Adapted from recently developed approaches using nearest neighbour distances along trait axes (Cornwell and Ackerly 2009, Kraft and Ackerly 2010), this model is tailored to detect evenness of spacing while controlling for effects of habitat filtering. The regional pool for each observed plot was restricted so that it contained only species with trait values between the maximum and minimum values of the observed community. Null communities for each plot were made to have the same maximum and minimum trait values as the corresponding observed community by forcing the two local extreme trait values to be present. Species were weighted by relative abundance across all plots and randomly chosen for null communities.

Combining the strengths of recent work, three different metrics of spacing were employed in the range-restricted model, NM2 (Figs. 3B, 4a) (Kraft et al. 2008, Cornwell and Ackerly 2009, Kraft and Ackerly 2010). The first metric, standard deviation of nearest neighbour distance (SDNN), represents limiting similarity by quantifying the standard deviation of trait distance from each species to the *species closest in value*, i.e. the most similar along a given trait dimension (Fig. 4a). A different measure is based on successive neighbour distances (Fig. 4b). The standard deviation of successive neighbour distances (SDSN) is based on the *successive set of distances* between species aligned along the same trait axis in order of increasing or decreasing value (see Fig. 4b). SDSN reflects the regularity of spacing across the range of trait values in a given plot expected if limiting similarity is occurring (Ricklefs and Travis 1980, Stubbs and Wilson 2004, Cornwell and Ackerly 2009, Kraft and Ackerly 2010). Another expected result of even spacing is a platykurtic distribution of trait values (low kurtosis) so kurtosis, or “peakedness” of a trait

distribution, was also examined (Stubbs and Wilson 2004, Cornwell and Ackerly 2009). Again, Wilcoxon signed-ranks tests were used to identify significant deviations from the null.



After Kraft and Ackerly 2010, Kraft et al. 2008.

Figure 4. Schematic illustrating the three metrics used to measure limiting similarity and evenness of spacing among trait values, using height (cm) as an example. In (a) and (b), A-E represent five theoretical species. Each tick denotes 1cm in height. (a) Nearest neighbour distance (NN) measures the distance along the trait axis (spread of height values) between each species and the one to which it is closest in value. (b) Successive neighbour distance (SN) measures the distance between each species and the species with the next greatest trait value. While conceptually similar, standard deviations of each measure (SDNN and SDSN) represent two slightly different aspects of spacing, the former more indicative of limiting similarity and the latter, evenness of spacing (See Kraft 2008 for a discussion of the differences). (c) Illustrates distributions with both high and low kurtosis. Low kurtosis occurs in a platykurtic distribution and is characteristic of evenly spaced values.

Patterns of species abundance: divergence vs. convergence (NM3). To determine whether filters also act on trait abundance, not just presence or absence in a community, patterns of species abundance within each plot were examined. Evidence of habitat filtering or limiting similarity occurring at the level of abundance would indicate these filters not only affect what trait values “get in to” a community, but also their abundances once there. Convergence toward a single abundant trait value or range would suggest habitat filtering may create one optimal trait value. Divergence in abundances would suggest many successful trait values, or multiple trait optima. A third null model, NM3, was designed to test this. The null communities for NM3 were created for each plot out of the same list of species present in that plot, but abundances were shuffled across species (Bernard-Verdier et al. 2012). In contrast to NM1, which tests the trait range of co-occurring species and uses the number of plots in which a species occurs to weight the probability of selection, in NM3 (Fig. 3B), null community members were the same species as those observed in a given plot, but their relative abundances (estimated cover in that plot) were included and randomly shuffled among members. In this way it was possible to test for non-random patterns in abundance with respect to trait values. A community weighted variance was then calculated for each plot (trait variance weighted by the relative abundance of each species; CWV) and compared between observed and null communities (Sonnier et al. 2010, Bernard-Verdier et al. 2012). Lower than expected CWV values indicate convergent trait values (one optimal strategy) (Fig. 3A2a). In effect it represents habitat filtering (or at least influence) at the level of abundance, rather than occurrence. Higher than expected CWV indicates trait divergence, a sign that limiting similarity influences abundance of present species (Fig. 3A2b). In this case multiple dissimilar trait values may permit high abundance.

All statistical analyses were performed in R (R Development Core Team 2009), using the “vegan” package for CCA (Oksanen et al. 2011) and modifications of scripts from Kraft and Ackerly (2010), Kraft et al. (2008) and Bernard-Verdier et al. (2012) for null models.

3. Results

3.1 Site and environmental variables

Elevation of plots varied from 437 m to 854 m above sea level. Age of sites (time since last major highway construction) was between 11 and 61 years (Yukon Highways and Public Works 1998). Elevation and latitude were strongly negatively correlated ($r = -0.63$; Table 1), that is, more northerly plots tended to be at lower elevations than more southerly plots. No other pair of abiotic variables was significantly correlated (Table 1).

Table 1. Correlations among abiotic variables in roadside plots along the North Klondike Highway.

	Age		Elevation	
	r	P	r	P
Latitude	0.18	0.25	-0.63	<0.00001
Age	-	-	-0.12	0.45
Elevation	-	-	-	-

3.2 Vegetation surveys and trait measurements

Across all plots, we identified and estimated percent cover of 70 herbaceous taxa. A total of seven exotic species were identified. Each plot contained between one and four exotic species and the mean per plot was 2.6. Total species richness in individual plots ranged from 7- 26 species. Trait data were collected on the most abundant species by cover in the system, totalling 95% of the total cover across all sites. Appendix B contains a list of species and their trait means.

3.3 Off-road surveys

Forty of the 42 possible interior plots were surveyed. Two were not surveyed because they had unexpected disturbances at or near 50 m from the road. Exotic species were uncommon in the 40 surveyed plots: we found two exotic species (*Crepis tectorum* and *Taraxacum officinale*) in just three of the 40 off-road plots. These three plots were in areas burned in wildfires within twenty years prior to the surveys: two were burned in 1998 and the other in 1995. The three other plots burned during this time period contained no exotic species.

3.4 Community composition

Canonical correspondence analysis (CCA): In the CCA of species composition by environmental variables, axes 1 and 2 accounted for significant variation in species composition among plots (34.7% and 26.8%, respectively; Fig. 5). Two variables, elevation and latitude, loaded significantly on the axes ($P = 0.009$ (elevation) and $P = 0.008$ (latitude) using 999 permutations each; Table 2). Partial CCA analyses with elevation and latitude showed that they contribute roughly equally to the variation in species composition (43.6% and 50.6%, respectively), and that 5.8% of the variation was accounted for by both variables jointly. The cover of sixteen species was significantly correlated with either latitude or elevation. Six species' abundances were significantly correlated with elevation: *Oxytropis campestris* ($r = 0.31$, $P = 0.045$), *Oxytropis deflexa* ($r = 0.51$, $P < 0.001$) and *Solidago simplex* ($r = 0.36$, $P = 0.019$) were more abundant at higher elevation sites, while *Eurybia sibiricus* ($r = -0.38$, $P = 0.012$), *Calamagrostis purpurea* ($r = -0.35$, $P = 0.022$) and *Equisetum arvense* ($r = -0.31$, $P = 0.041$) were more abundant at lower elevations. Ten species were significantly correlated with latitude: *Arnica angustifolia* ($r = 0.35$, $P = 0.023$), *Equisetum arvense* ($r = 0.36$, $P = 0.020$), *Plantago*

major ($r = 0.38$, $P = 0.012$), *Polemonium pulcherrimum* ($r = 0.46$, $P = 0.002$), and *Potentilla litoralis* ($r = 0.37$, $P = 0.017$) were more abundant in more northern plots; the abundance of *Bromus inermis* ($r = -0.40$, $P = 0.008$), *Hordeum jubatum* ($r = 0.38$, $P = 0.012$) *Linum lewisii* ($r = -0.32$, $P = 0.036$), and *Oxytropis campestris* ($r = -0.32$, $P = 0.036$) and *Oxytropis deflexa* ($r = -0.39$, $P = 0.010$) was greater to the south. No significant relationship was found between species composition and plot age. Plot richness increased with latitude ($r = 0.51$, $P < 0.001$), though the number of exotic species did not.

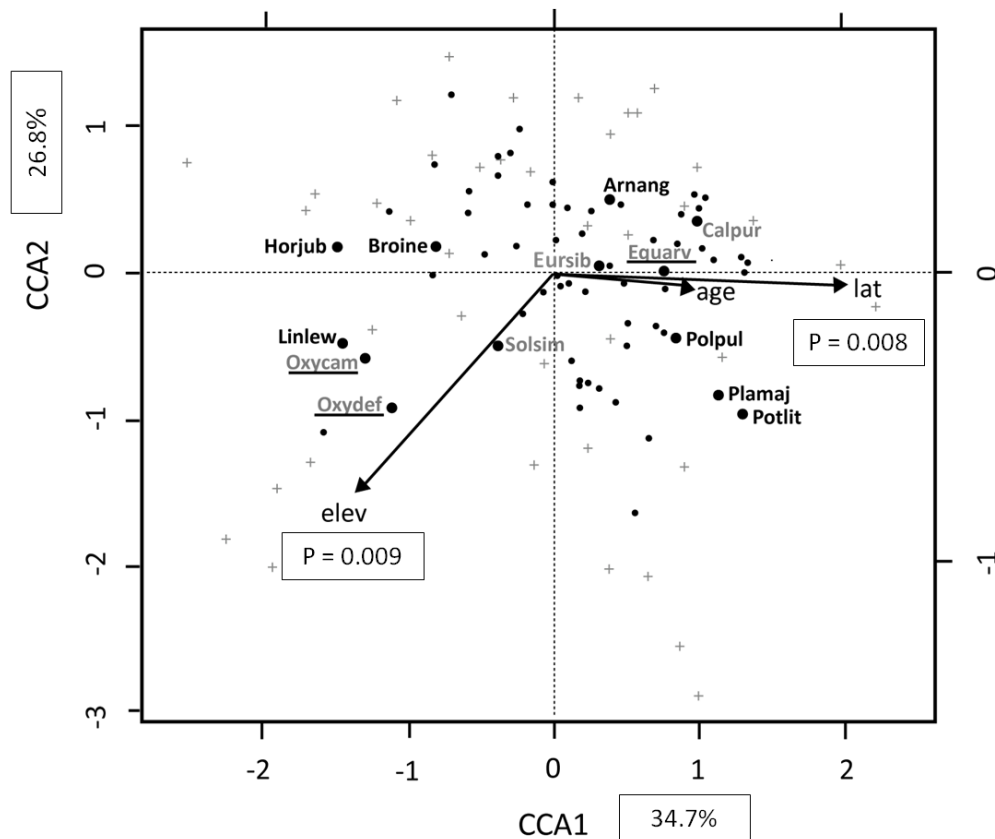


Figure 5. CCA triplot of species composition constrained by three abiotic variables: elevation (elev), latitude (lat), and plot age or time since last major disturbance (age). Grey crosses represent plots and black dots represent species. Elevation and latitude both significantly influenced species composition ($P = 0.009$ and 0.008 , respectively), but age did not. Thirteen species, labelled with six-letter species codes, are significant drivers of the association with elevation and/or latitude: *Arnica angustifolia* (Arnang), *Bromus inermis* (Broine), *Calamagrostis purpurascens* (Calpur), *Equisetum arvense* (Equarv), *Eurybia siberica* (Eursib), *Hordeum jubatum* (Horjub), *Linum lewisii* (Linlew), *Oxytropis campestris* (Oxycam), *Oxytropis deflexa* (Oxydef), *Plantago major* (Plamaj), *Polemonium pulcherrimum* (Polpul), *Potentilla litoralis* (Potlit), *Solidago simplex* (Solsim). Species in grey text are correlated with elevation and those in black are correlated with latitude. *Oxytropis campestris*, *O. deflexa* and *Equisetum arvense* (underlined) are strong predictors of both.

Table 2. CCA permutation test results showing significant influence of elevation and latitude on species composition.

	Df	Chi Square	F	No. Perm.	Pr(>F)
Elevation	1	0.2680	1.7852	999	0.009
Latitude	1	0.2873	1.9137	999	0.008
Age	1	0.1615	1.0759	999	0.469

3.5 Community traits across environments

All species together. Using only species-level trait means, there were no significant trait-environment relationships. However, using plot level community means, plant height was significantly related to both latitude and elevation. Plants were taller at lower elevations ($r = -0.37$, $P = 0.015$) and shorter at lower latitudes ($r = 0.38$, $P = 0.013$, Table 3). Plot-level community means include trait values calculated separately *for each species in each plot* and uses these plot-specific values to calculate *plot-level* community means (thereby incorporating within-species trait changes across environments in addition to turnover).

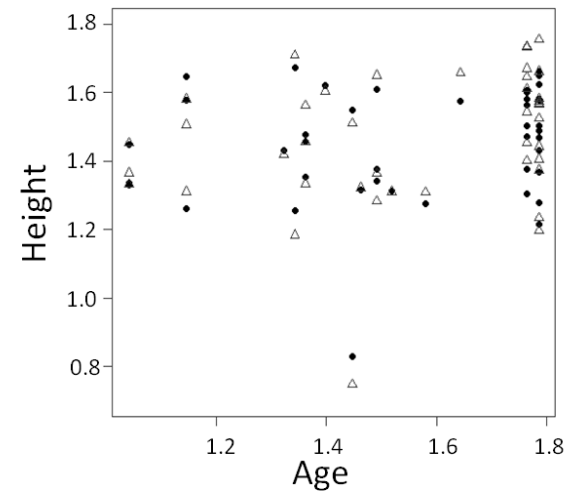
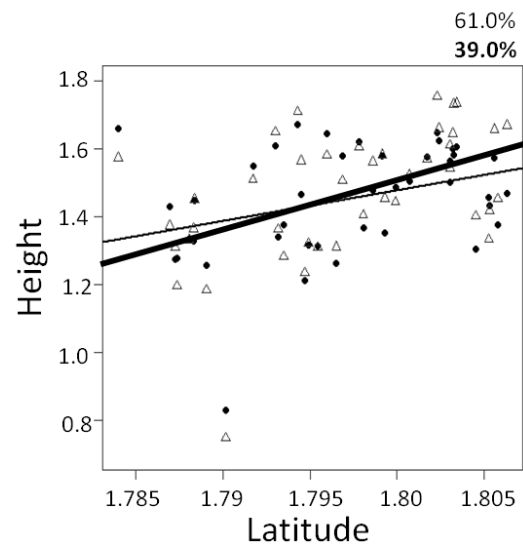
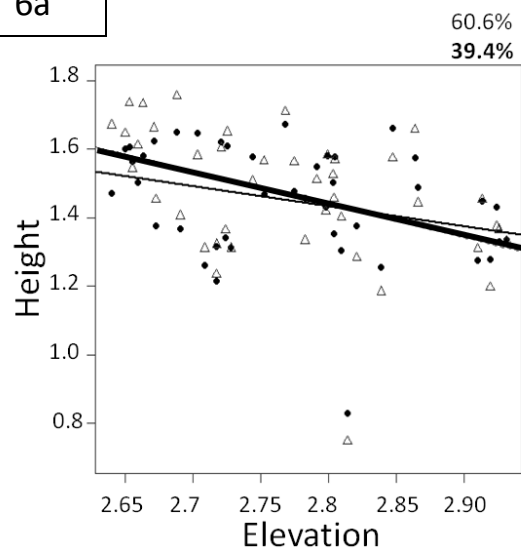
Native and exotic species as separate groups. Using only species level traits, the height of native species was negatively correlated with elevation and positively correlated with latitude. That is, taller plants were found at lower elevations ($r = -0.31$, $P = 0.043$; Table 3, Fig. 6a) and higher latitudes ($r = 0.35$, $P = 0.024$; Table 3, Fig. 6a) (though it must be noted that elevation and latitude were themselves negatively correlated). Both associations were non-significant among exotic species. Several additional significant relationships were identified when using plot-level means. The relationships between native plants and both elevation and latitude were still significant and greater in strength. Plot-level native height was correlated with elevation with an

r value of -0.42 ($P = 0.015$) and with latitude with an r value of 0.47 ($P = 0.002$). Among exotic species, plot-level mean height was positively correlated with plot age, i.e., older sections of highway tended to have taller exotic plants than younger sections ($r = 0.37$, $P = 0.015$; Fig. 7a). Plot-mean exotic SLA was correlated with latitude, with northern plots tending to have exotic plants with thicker leaves ($r = 0.45$, $P = 0.003$; Table 3, Fig. 7b). No correction was made for multiple P values in this analysis so inferences are made based on the full set of results rather than individual p values (Perneger 1998).

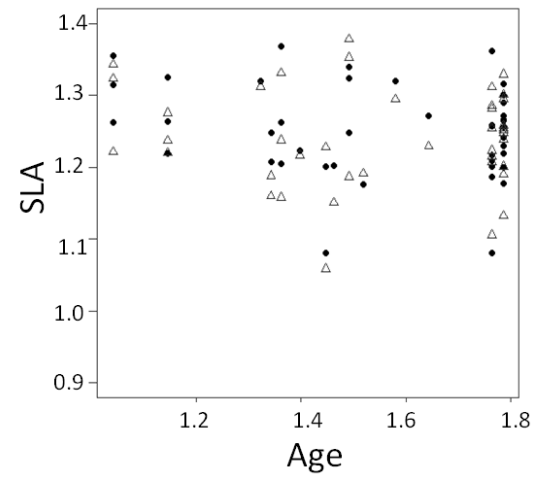
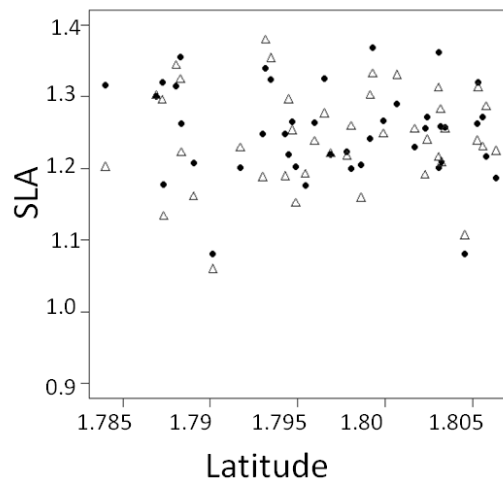
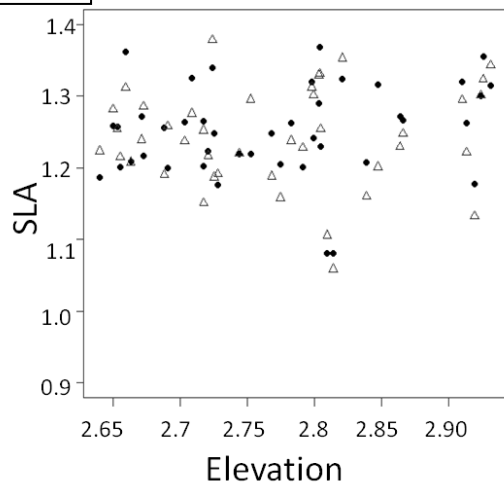
Table 3. Inter- and intra-specific correlations of community mean trait values for three traits and three abiotic variables, grouped by native and exotic species or all species together. Bolded values indicate significant correlations.

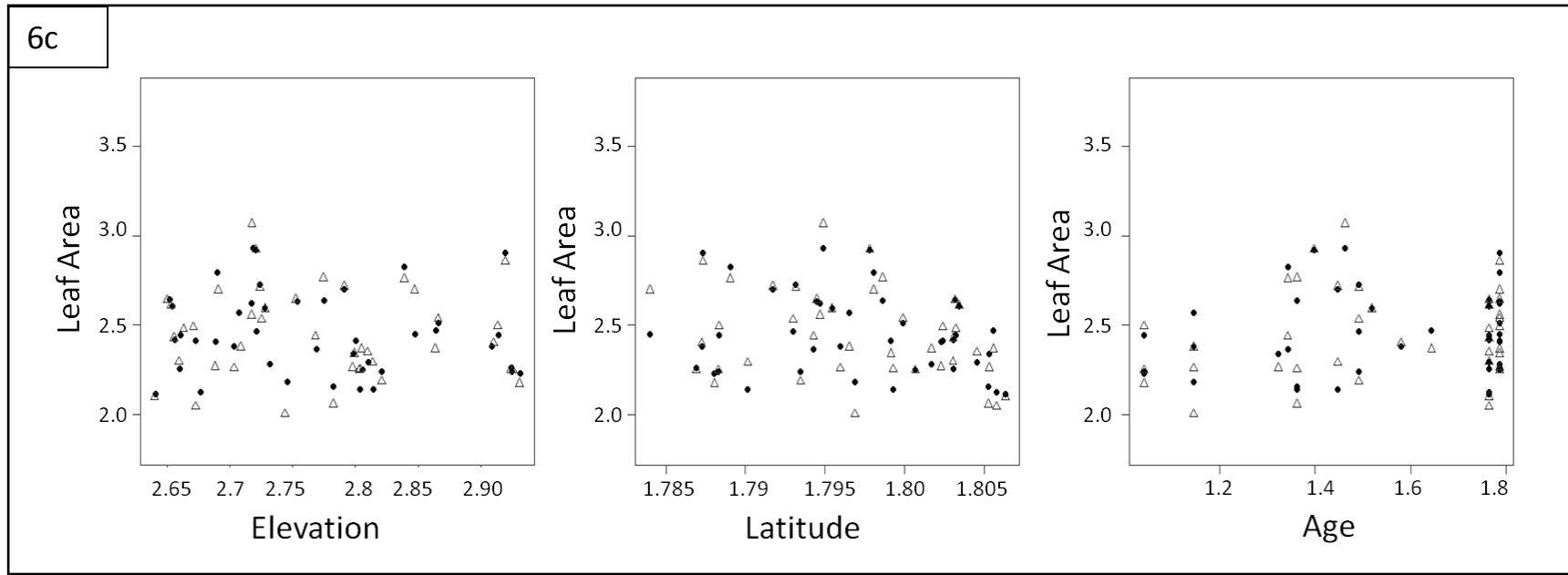
Trait	Abiotic variable	Group	Species turnover		Intra-specific variation + species turnover	
			r	P	r	P
Height	Age	All	0.22	0.155	0.30	0.056
Height	Age	Native	0.18	0.249	0.28	0.073
Height	Age	Exotic	0.17	0.2972	0.37	0.015
Height	Elevation	All	-0.22	0.152	-0.37	0.015
Height	Elevation	Native	-0.31	0.043	-0.42	0.005
Height	Elevation	Exotic	-0.11	0.503	-0.17	0.279
Height	Latitude	All	0.21	0.190	0.38	0.013
Height	Latitude	Native	0.35	0.024	0.47	0.002
Height	Latitude	Exotic	-0.30	0.054	0.12	0.430
Leaf Area	Age	All	-0.05	0.761	-0.03	0.818
Leaf Area	Age	Native	0.09	0.570	0.15	0.358
Leaf Area	Age	Exotic	-0.05	0.736	-0.01	0.932
Leaf Area	Elevation	All	-0.04	0.795	0.05	0.731
Leaf Area	Elevation	Native	-0.11	0.506	-0.07	0.681
Leaf Area	Elevation	Exotic	-0.01	0.960	-0.17	0.286
Leaf Area	Latitude	All	-0.17	0.275	-0.24	0.118
Leaf Area	Latitude	Native	-0.23	0.147	-0.29	0.059
Leaf Area	Latitude	Exotic	-0.01	0.927	0.12	0.473
SLA	Age	All	-0.15	0.330	-0.13	0.426
SLA	Age	Native	-0.23	0.146	0.03	0.872
SLA	Age	Exotic	-0.04	0.799	0.04	0.827
SLA	Elevation	All	0.22	0.154	0.24	0.129
SLA	Elevation	Native	0.18	0.245	0.06	0.719
SLA	Elevation	Exotic	-0.06	0.689	-0.26	0.106
SLA	Latitude	All	-0.10	0.531	0.00	0.999
SLA	Latitude	Native	-0.14	0.388	0.05	0.756
SLA	Latitude	Exotic	0.19	0.229	0.45	0.003

6a



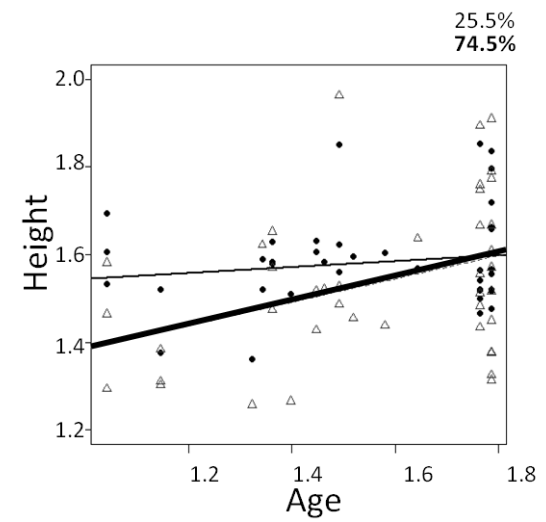
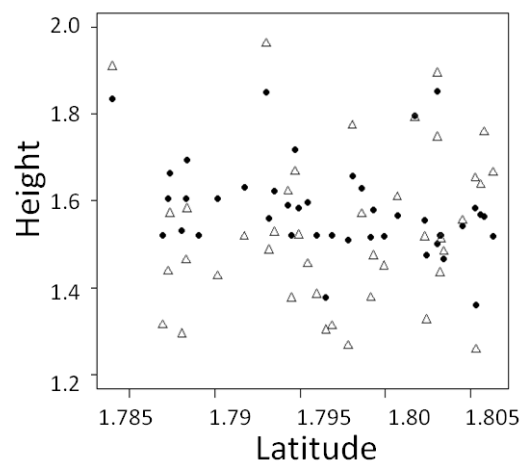
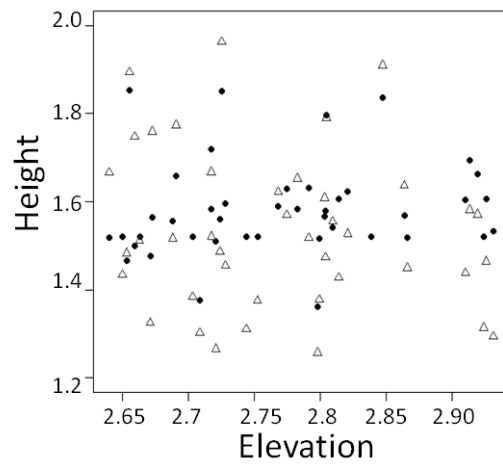
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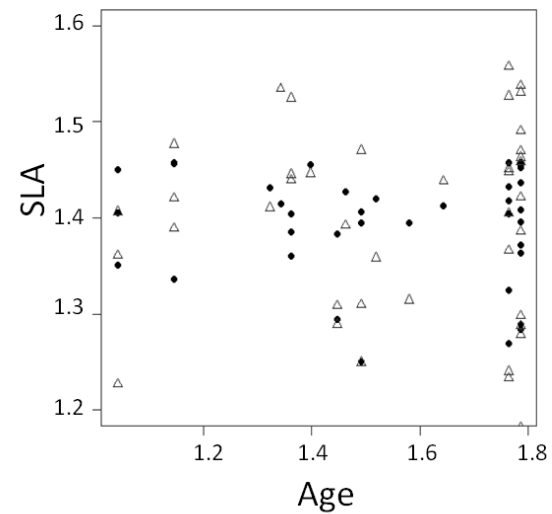
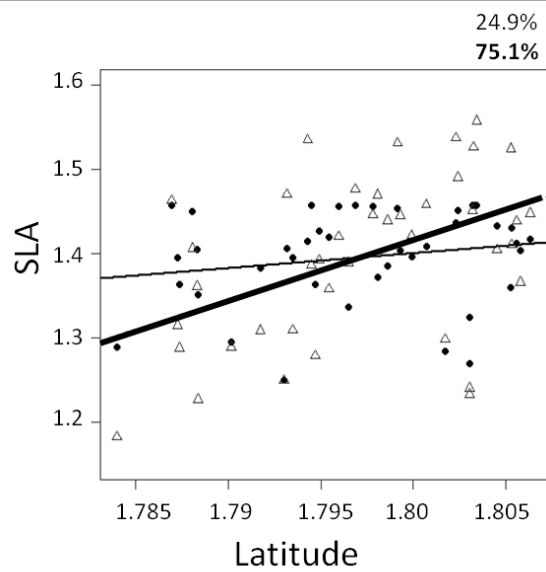
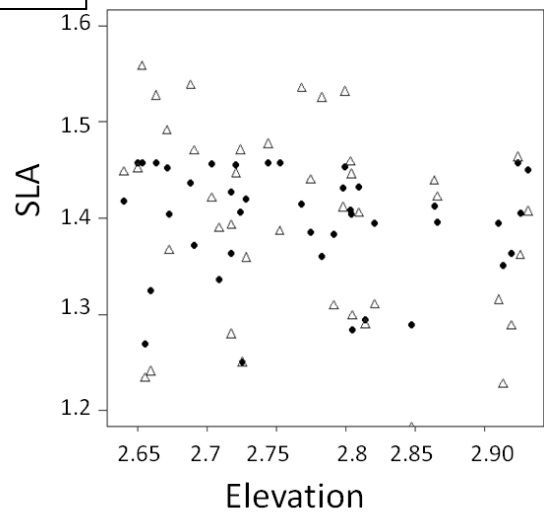


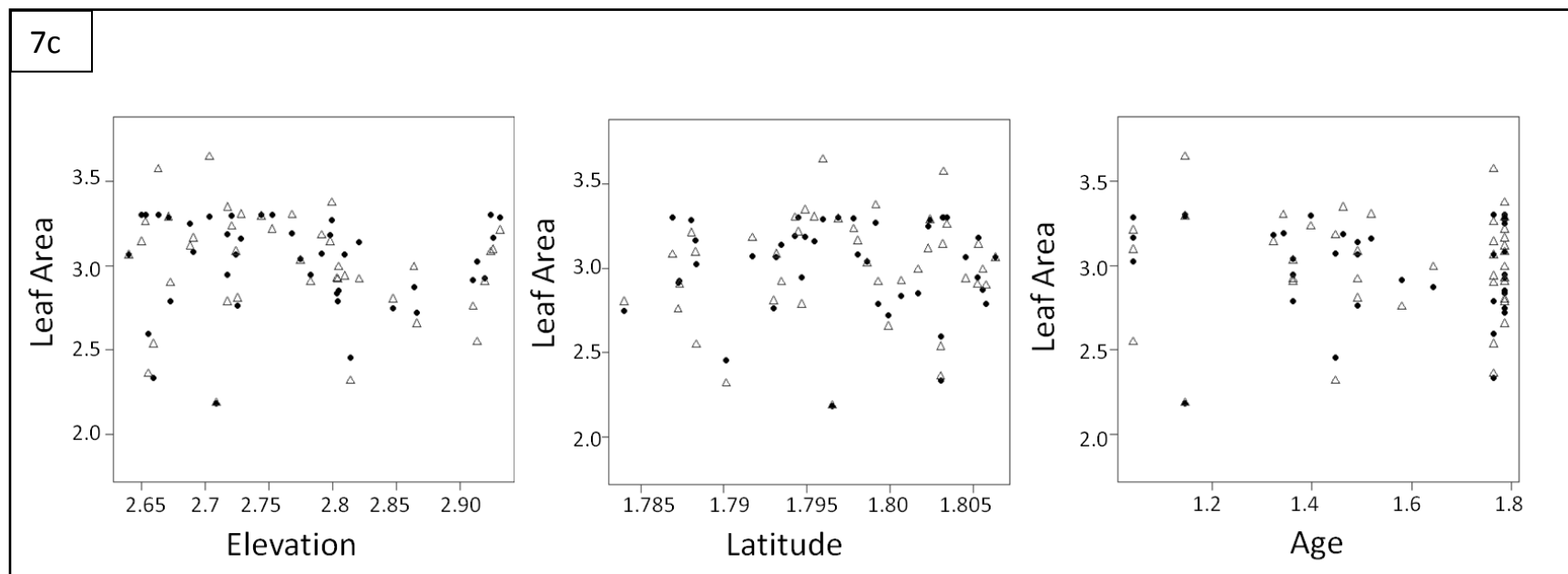
Figures 6a-c. Native species community weighted trait means (CWM) across elevation, latitude and age. Both trait change due to species turnover (solid dots) and trait change due to turnover + intraspecific change (triangles) are plotted. Significant trait-environment correlations are indicated by regression lines, with thin lines showing turnover and bold lines showing turnover + intraspecific variation. Panel A illustrates the negative correlation between native plant height and elevation and the positive correlation between native plant height and latitude. Panels B and C show that no significant relationships exist between SLA or leaf area and the environmental gradients. In all cases where significant relationships exist, intraspecific change occurs in the same direction as turnover and strengthens the trait-environment relationship. Percentages at the upper right corner of graphs of correlated pairs show the amount of slope contributed to by species turnover vs. intraspecific variation (bolded). See Table 3 for all Pearson's r values, only those significant to $P < 0.05$ are shown here. All trait values are logged to improve normality. Units of measurement along y-axes are as follows: Height = $\log(\text{cm})$, SLA = $\log(\text{mm}^2/\text{mg})$, leaf area = $\log(\text{mm}^2)$.

7a



7b





Figures 7 a-c. Invasive species community weighted trait means (CWM) across elevation, latitude and plot age. Both trait change due to species turnover (solid dots) and trait change due to turnover + intraspecific change (triangles) are plotted. Significant trait-environment correlations are indicated by regression lines, with thin lines showing turnover and bold lines showing turnover + intraspecific variation. comparing trait change due to species turnover vs. trait change due to turnover + intraspecific change. Panel A illustrates the positive correlation between invasive plant height and plot age, while panel B illustrates the positive correlation between invasive plant SLA and latitude. Panel C shows leaf area across environmental gradients, where we observed no significant relationships. As with native species, intraspecific change occurs in the same direction as turnover and strengthens the trait-environment relationship. Percentages on upper right corner of correlated pairs show the amount of slope contributed to by species turnover vs. intraspecific variation (bolded). See Table 3 for all Pearson's R values, only those significant to $P < 0.05$ are illustrated here. All trait values are logged to improve normality. Units of measurement along y-axes are as follows: Height = log(cm), SLA = log(mm²/mg), leaf area = log(mm²).

Relative contributions of intraspecific change and species turnover. For all significant relationships, intraspecific variation in trait values increased the slope of the regression line, as it was in the same direction as species turnover. In the negative relationship between native plant height and elevation, 60.6% of the slope was due to turnover and the remaining 39.4% due to intraspecific variation (Fig. 6a, Table 4). In the positive relationship between native height and latitude, 61.0% and 39.0% of the slope was due to turnover and intraspecific variation, respectively. Turnover contributed 24.9% of the slope of exotic SLA x latitude, while intraspecific variation accounted for the remaining 75.1%. Similarly, turnover accounted for 25.5% of the slope in the relationship between height of exotic species and plot age, while intraspecific variation was responsible for the remaining 74.5% (Fig. 7a, Table 4). However, in one case, intraspecific variation occurred in the opposite direction from turnover, though neither relationship was significant. A negative relationship between turnover in community mean exotic height and latitude was nearly significant ($r = -0.30$, $P = 0.054$), but when intraspecific change was factored in this trend disappeared ($r = 0.12$, $P = 0.430$).

Table 4. Relative contributions of species turnover and intra-specific variation to slopes of trait change across environment for significantly correlated trait-environment combinations identified in Table 3a. Percent contributions are obtained by calculating the reduction in total slope (intra-specific change + turnover, bold lines in Figures 6 and 7) when only species means (turnover) are considered. Trait and abiotic variables were logged (log10) to improve normality.

Trait	Abiotic Variable	Group	Slope of turnover alone	Slope of intra-specific change + turnover	Percentage of slope from turnover	Percentage of slope from intra-specific change
Height	Elevation	Native	-0.584	-0.963	60.6%	39.4%
Height	Latitude	Native	8.976	14.725	61.0%	39.0%
Height	Age	Exotic	0.067	0.264	25.5%	74.5%
SLA	Latitude	Exotic	1.766	7.095	24.9%	75.1%

3.6 Traits of native and exotic species compared

Mean SLA per species was significantly greater in exotic species than native species, that is, exotic species had thinner leaves ($P = 0.036$; Table 5, Fig. 8). Leaf area was not significantly different between groups, but showed a weak trend toward larger leaves in exotic species ($P = 0.052$). There was no difference in height between the two groups ($P = 0.15$). None of the pairs of traits was significantly correlated ($P > 0.20$ for all trait combinations).

Table 5. Results of a t-test comparing average trait values of three traits between native and exotic species. SLA of exotic plants is significantly greater than that of native plants, meaning exotic plants tend to have thinner, shorter-lived leaves. No other means are significantly different, though leaf area shows a trend toward larger areas among exotic species than native species. All trait values were logged (log10) to improve normality.

Trait	t	P	Native Trait Mean (log10)	Exotic Trait Mean (log10)
Height	-1.58	0.15	1.37	1.55
SLA	-2.36	0.036	1.25	1.35
Leaf Area	-2.37	0.052	2.38	2.79

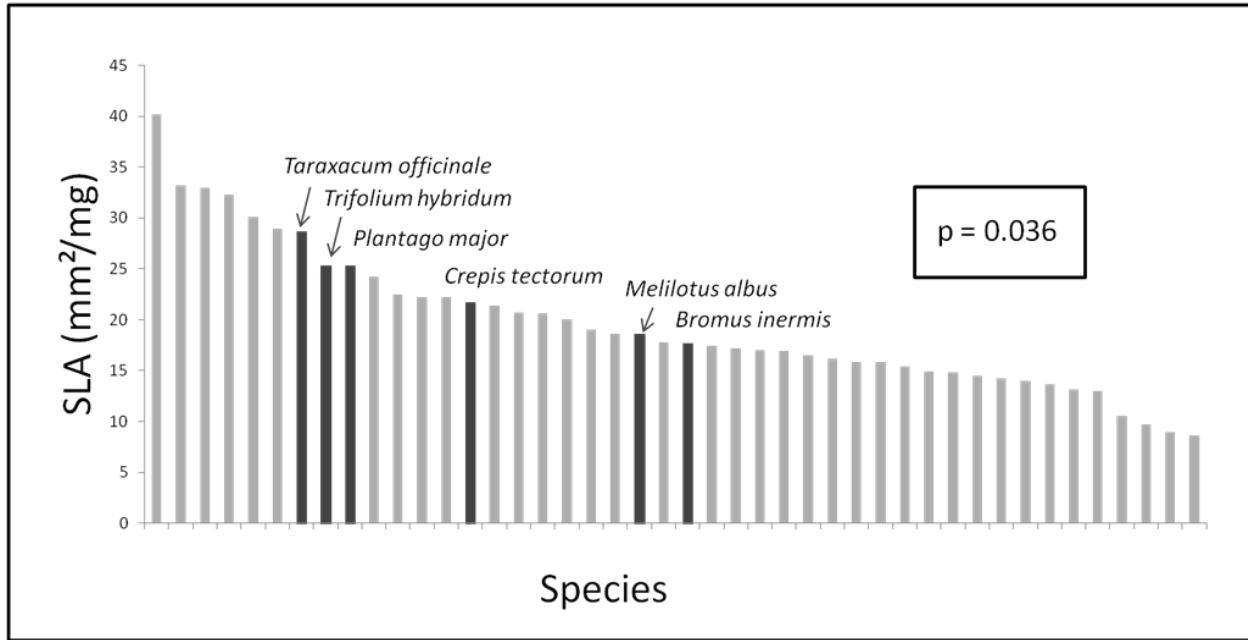


Figure 8. Specific leaf area of 44 species measured. Black bars represent exotic species and grey bars represent native species. Mean SLA is significantly higher in exotic species than native species. No other traits were significantly different between groups, however leaf area shows a tendency toward being greater in exotic species (see Table 5).

3.7 Testing for assembly filters with three null models

Habitat filtering (presence/absence, NM1). On average, the ranges of height and SLA were smaller than expected compared to NM1, suggesting that habitat filtering was occurring (both Wilcoxon $P < 0.0001$; Table 6, Fig. 9). In contrast, the range of leaf area values was not significantly different from NM1, in fact, a 2-tailed test revealed a greater range of leaf area values than expected by chance (Wilcoxon $P < 0.0001$). Results were similar for tests on the variance of trait values, which was smaller across all plots for height and SLA (both Wilcoxon $P < 0.001$) but not leaf area, which was again greater than expected, though borderline in significance (Wilcoxon $P = 0.0496$, Fig.9).

Limiting similarity (presence/absence, NM2). SDNN was significantly smaller than expected compared to NM2 for SLA and leaf area (Wilcoxon $P < 0.001$ and $P < 0.0001$, respectively; Table 6, Fig. 10) but not for height (Wilcoxon $P = 0.062$). SDSN was significantly smaller than expected for all three traits (Wilcoxon $P < 0.001$). Kurtosis was lower than expected (i.e. more platykurtic distribution) only in SLA (Wilcoxon $P < 0.0001$) but not height or leaf area (Wilcoxon $P = 0.16$ and 0.34 , respectively, Table 6, Fig. 10).

Trait abundance distribution (convergence/divergence, NM3). Using plot-level trait values (accounting for intraspecific changes *and* species turnover across plots), height CWV was significantly smaller than expected (Wilcoxon $P = 0.003$, Table 7) revealing convergence toward higher values, i.e. taller plants were more abundant overall. Neither SLA nor leaf area CWV was significantly different from random (Wilcoxon $P = 0.45$ and $P = 0.44$, respectively, Table 7).

Table 6. Cumulative significance testing of observed vs. null community trait distributions using Wilcoxon signed-ranks tests. P values and standardized effect sizes (SES, in units of standard deviations) are shown for differences between observed measures and null model expectations. SDNN is standard deviation of nearest neighbour distance, SDSN is standard deviation of successive neighbour distance. All tests are one-tailed and trait values are logged to improve normality.

	Habitat Filtering				Limiting Similarity					
	Range		Variance		SDNN		SDSN		Kurtosis	
	P	SES	P	SES	P	SES	P	SES	P	SES
Height	<0.0001	-0.82	<0.0001	-0.83	0.062	-0.24	0.004	-0.33	0.16	-0.06
SLA	<0.0001	-0.93	<0.0001	-0.72	0.0003	-0.60	<0.0001	-0.64	<0.0001	-0.58
Leaf Area	1.00	0.85	0.95	0.17	<0.0001	-0.60	<0.0001	-0.57	0.34	-0.04

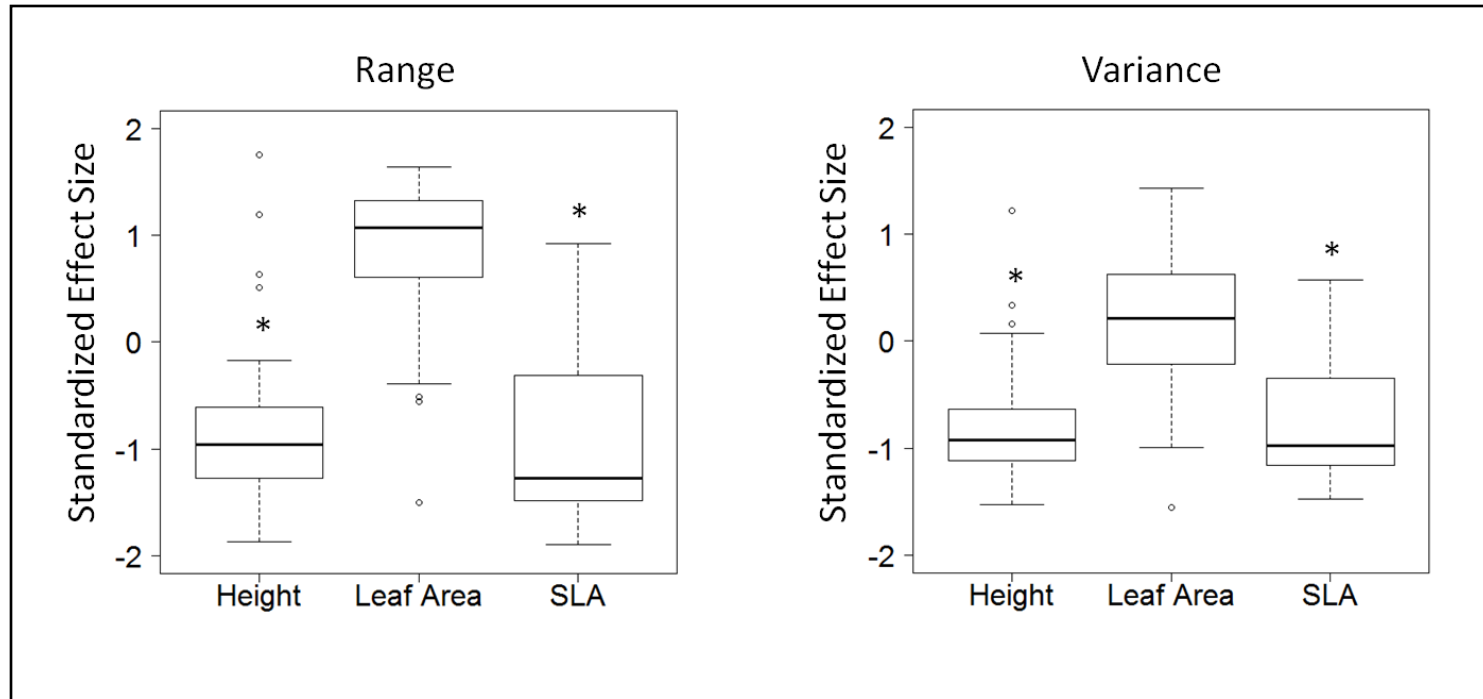


Figure 9. Observed standardized effect sizes of habitat filtering metrics for three functional traits. Boxplots of standardized effect sizes (SES) of range and variance for height, leaf area and SLA. Wilcoxon’s signed rank was used to test whether, across all plots, range or variance was smaller than expected for a given trait. Traits with range or variance significantly lower than expected (negative values with $P < 0.05$) are denoted with an asterisk and are indicative of habitat filtering. See Table 6 for P values.

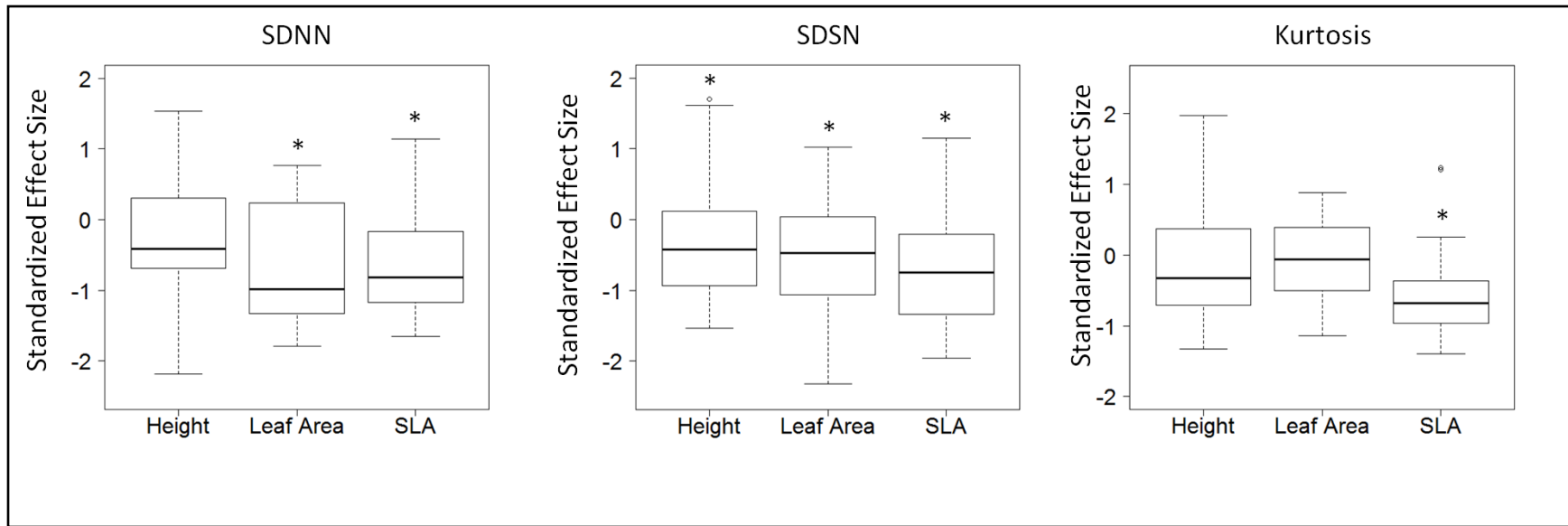


Figure 10. Observed standardized effect sizes of limiting similarity metrics for three functional traits. Boxplots of standardized effect sizes (SES) of standard deviation of nearest neighbour distance (SDNN), standard deviation of successive neighbour distance (SDSN) and kurtosis for each trait. Wilcoxon's signed rank test was used to test whether, across all plots, metrics of limiting similarity were smaller than expected for a given trait (expressed here as negative values). Significant values to $P < 0.05$ are denoted with an asterisk and indicate limiting similarity. See Table 6 for P values.

Table 7. Significance and effect size of deviation from the null of community weighted variance (CWV), calculated by shuffling abundances of species in a given plot and testing whether observed abundances are significantly convergent or divergent from the null generated with NM3. The significant negative effect size in height represents lower than expected CWV values, suggesting a convergent distribution where similar trait values confer abundance (also see Fig. 3.A.2a for schematic). Neither SLA nor leaf area showed any significant difference from the null expectation.

Trait	P	Effect Size
(a) Height	0.003	-0.388
(b) SLA	0.79	0.128
(c) Leaf area	0.86	0.0760

4. Discussion

The goal of this research was to investigate functional trait distribution patterns to better understand the processes underlying roadside plant community structure. Overall, we found that traits change predictably with environment, but that native and exotic species respond differently. Native and exotic species also differ in ecological strategy as quantified by average trait values. Additionally, we found patterns suggesting that roadside plant communities, despite their relatively recent establishment, are shaped by deterministic assembly processes affecting both community membership and patterns of abundance.

4.1 Native and exotic species across environmental gradients

As expected, community-level trait values changed with environmental variables, supporting the idea that different traits are adaptive in different habitats (Schimper 1898). Interestingly, native and exotic species appear sensitive to different environmental gradients. While the small number of exotic species makes our conclusions tentative, a discussion of possible explanations for observed relationships is warranted as it highlights important potential differences in behaviour and strategy between exotic and native species. These differences can provide hypotheses for further experimental testing.

Firstly, the height of exotic species increased with plot age: older, more established plots had taller exotic species than more recently established plots. Height is indicative of initial growth rate, shade tolerance and light-capture strategy (Westoby 1998, McGill et al. 2006) and involves tradeoffs between maintenance costs and the ability to intercept sunlight (Thomas and Bazzaz 1999). Taller structures require more investment in stem tissue and have increased costs of

longer-distance water transport (Givnish 1995, Falster and Westoby 2005). Most of the species are perennial, so in older plots they would have had more time to develop root systems that could support this investment and enable them to grow taller. The relationship is consistent with data showing plant height increases along successional gradients due to higher light competition and greater available nitrogen (Gleeson and Tilman 1990, Olff et al. 1993, Kahmen et al. 2004).

Older plots in the study system are likely to have higher nutrient availability for a number of reasons. Nutrient concentrations in recently constructed roadsides are likely to be low due to the use of sandy materials with low organic matter used in road berm construction (Reimchen et al. 2009). Older plots, some of them 60 years old, should have increased nutrients after years of organic matter deposition by resident plants. Nitrogen, especially, should be higher given the presence of several nitrogen fixing species (e.g., *Oxytropis* spp., *Hedysarum* spp., *Astragalus* spp., *Lupinus arcticus*, *Melilotus albus*, *Medicago sativa*, and *Trifolium hybridum* – 11 of the 51 species are legumes. In addition, nitrogen dioxide deposition from vehicle traffic builds up over time on roadsides (Cape et al. 2004) and the North Klondike Highway is well-travelled in summer with 400-700 vehicles daily (Yukon Highways and Public Works 2011). While much of the increase in nutrients is sequestered in plant tissues, the available nutrient concentrations are still likely higher (Vitousek and Walker 1987). Nitrogen is a strong limiting resource in northern systems (Matheus and Omtzigt 2012), and greater N availability in can increase plant height (Tilman 1987). It is also likely these more mature soils with more organic matter have greater moisture retention than quick-draining sands, contributing to greater growth and height.

That there was no similar height increase in native species in older plots could suggest that exotic species are better able to capitalize on increased resources than native species. There is evidence that exotic plants in general have higher growth rates and SLA than their native neighbours, making them better able to capture available resources than the often slower-growing, lower SLA natives (Baruch 1996, Daehler 2003, Funk and Vitousek 2007). Native roadside species in boreal Yukon tend to be adapted to the nutrient-poor, low-light conditions of the forest understory, being stress-tolerant (*sensu* Grime (1977) and slow-growing with thick-leaves (low SLA) (Chapin 1980, Wedin and Tilman 1996, Dukes and Mooney 1999, Grime and Grime 2001, Lee and Power 2013). It is important to note that the majority of the height increase in older plots was due to within-species variation, not turnover, although we are unlikely to detect strong turnover effects from a pool of only seven exotic species. Intraspecific change is consistent with the idea that exotic species are able to respond to resource increases, either through plasticity or local adaptation (Funk 2008).

We also found that SLA of exotic species increased at higher latitudes, again likely due to the combination of lower elevation and warmer summers, but native species SLA did not. Increase in SLA is associated with relative growth rate (Lambers and Poorter 1992, Cornelissen et al. 1996, Reich et al. 1997) and is an indicator of ability to respond to favourable conditions (Grime 1977, Chapin et al. 1993, Grelet et al. 2001). It is associated with increased growth rate because it allows a greater photosynthetic rate, providing a faster return on unit of carbon invested (Poorter 1994). Whether the observed pattern is due to plasticity or genetic variation, it suggests a mechanism by which exotic species can capitalize on higher resource availability, in this case light (Milford and Lenton 1976, Carlen et al. 1999): greater day length during the growing

season at high latitudes can be turned into greater growth if SLA increases. That native plants do not show the same shift across latitudes suggests native and exotic plants may not respond in the same way to changes in climate.

Height of native species decreased with elevation and increased with latitude. It was expected that height would covary positively with latitude, as longer days during the growing season often translates to greater growth rate and plant size (Garner and Allard 1920, Grime and Grime 2001). That we did not see the same trend in exotic species could be because the exotic pool is so small. Certainly there are not enough exotic species to make detection of turnover effects likely, though the native trend was also due in large part to intraspecific change (39%). Exotic heights did show a non-significant trend of increase with latitude, but unlike with natives, accounting for intraspecific variation did not strengthen the trend (see Table 3). That is, taller exotic species are more abundant in southern plots, but individuals within species get taller as plots get farther north.

Native plant height was also negatively correlated with elevation. Latitude and elevation are negatively correlated, so part of the effect is likely due to covariates of latitude like summer temperatures (counterintuitively higher to the north) and day-length. Elevation is a strong predictor of height in woody species and in annuals above treeline (Smiley and Rank 1991, Bhattarai and Vetaas 2003), and even in the moderate elevation gains in my study system (437-854 m asl), it is expected that shorter species would be more abundant at higher elevations.

4.2 Intraspecific trait variation

It is clear that intraspecific variation plays a key role in community trait change along environmental gradients, since it strengthened all observed trait-environment relationships and was responsible for 39-75% of relationship slopes. When we account for intraspecific variation in the analysis, more relationships became significant, underscoring the importance of capturing plot-specific trait means (Jung et al. 2010, Violle et al. 2012). As in previous studies, most within-species trait variability paralleled the trends seen with turnover (Ackerly et al. 2002, Cornwell and Ackerly 2009). However, this was not true for height of exotic species and latitude. Though not significant, there was a trend toward a negative relationship between height and latitude in the turnover of exotic species. Intraspecific change appeared to occur in the opposite direction, however, decreasing the slope of the regression. This contradicts previous research (Cornwell and Ackerly 2009) and the expectation that change in trait values among individuals of a species will mirror change due to turnover in the community as a whole along the same gradient (i.e. if tall species are replaced by shorter species as elevation increases (turnover), individuals of species present along the gradient should also decrease in height with increasing elevation (intraspecific variation). It is also notable that the trend between turnover of exotic heights and latitude is also directly opposite the significant positive relationship between native height and latitude. The most likely explanation is that distribution of exotic species has more to do with dispersal opportunities than sorting over time due to environmental conditions. The tallest species, *Melilotus albus*, is thought to have become established on roadsides as an agricultural escapee, and farmland is more common around the more populous and climatically-suitable Whitehorse at the southern end of the study system (pers. obsv). The second tallest species, *Bromus inermis*, was planted for roadside revegetation as late as the 1980's (Matheus

and Omtzigt 2012). Since native species turnover showed the opposite relationship (that mean community height of native species increased with latitude), over time we may expect exotic species to exhibit trends in community height that are more affected by environmental filters than dispersal history.

Results comparing relative contributions of turnover vs. intraspecific change among native species were consistent with previous findings that species turnover was the main force in trait change across environment, since intraspecific change accounted for relatively less of the slope of the regression. Quantifying relative contributions of within-species variation and turnover is important in understanding how communities may behave in future climate change scenarios, and our findings are consistent with others in suggesting that shifts in community member identity will be a bigger part of the response than shifts in phenotypes or ecotypes (Cornwell and Ackerly 2009). However, for exotic species as a group, intraspecific variation was responsible for a greater proportion of the resulting slopes than species turnover. While tempting to think this means exotic species are more phenotypically or genetically variable than natives -- afterall greater phenotypic plasticity is often cited as a reason for invasion success (Milberg et al. 1999, Daehler 2003, Leishman and Thomson 2005, Davidson et al. 2011)-- it is more likely due to the small pool of exotic species. A small sample makes it unlikely for turnover of exotic species to be substantial, and more likely that any relationship reflects within-species change.

4.3 Trait differences between native and exotic species

Previous studies have shown substantial differences in the ecological strategies of native and widespread or invasive exotic species (for example, Rejmanek and Richardson 1996, Daehler

2003, Pysek and Richardson 2007, van Kleunen et al. 2010, Davidson et al. 2011, Matzek 2012). Because six of the seven exotic species we sampled are considered invasive or aggressive exotic species (Government of Yukon, Department of Environment 2011) we expected that at least some of their traits would be statistically different from native species. SLA of exotic species was greater than that of native species, consistent with much of the literature showing SLA as a predictor of invasiveness (e.g., Baruch and Goldstein 1999, Grotkopp et al. 2002, Lake and Leishman 2004, Leishman et al. 2007, Feng et al. 2008, Sandel and Dangremond 2012). While the small sample size of exotic species precludes generalization, our results suggest SLA may be an important predictor of invasiveness in northern roadside environments, as elsewhere. High SLA is associated with high relative growth rate, high photosynthetic rate and short-lived, thin leaves. This suite of traits is thought to be adaptive in the high-light and high-nutrient conditions of disturbed sites (Grime 1974, Davis et al. 2000, Grotkopp and Rejmánek 2007). While Yukon roadsides have the available light associated with disturbance, they may be nitrogen-limited, since the sand and gravel used in their construction are low in organic matter (at least at first, before nutrient runoff from roads and vehicles has time to build up) (Matheus and Omtzigt 2012). However, invasive species with high SLA have been shown to be successful in both high- and low-nutrient conditions (Funk and Vitousek 2007), so this strategy could be successful on these roadsides whether nutrient limited or not. Additionally, high SLA is associated with the ability to attain resources opportunistically: rapid leaf growth can increase photosynthetic surface area in response to light availability, thus allowing individuals to capitalize on favourable conditions (Donald 1958, Campbell et al. 1991, Grime 1993). This opportunistic resource capture is also a key feature of many invasive exotics (Davis et al. 2000, Shea and Chesson 2002) and suggests they may have greater plasticity in response to favourable

conditions than native species with lower SLA (Richards et al. 2006, Funk 2008, Davidson et al. 2011). This could provide exotic species with an advantage on roadsides and other frequently-disturbed situations.

The fact that native roadside species show lower overall SLA than exotic species suggests they did not evolve in conditions where high SLA is adaptive, such as high available light. Native roadside species are mostly adapted to the forest understory where both nitrogen and light are limited. Shady, established understory conditions favour the slow-growth and long-lived leaves characteristic of species with low SLA (Reich et al. 1992). Widespread human disturbance has only occurred in Yukon during the past 150 years in the form of road construction and town sites and it is likely that continuous high light availability on roadsides represents to a novel environment where high SLA is advantageous. While natural large-scale disturbance from wildfires is common in the boreal forest, fire damage historically provided only temporary high-light conditions for forest herbs, as forest almost always regenerated post-fire (Brown and Johnstone 2012). However, increasingly frequent and severe fires resulting from climate change might make forests less likely to regenerate and more likely to be replaced by open grassland communities (Brown and Johnstone 2012). This will likely provide more open habitat favouring the establishment of exotic species. As the number of roads and other large scale disturbances increase through mineral and petroleum exploration, and as the forest seedbank is depleted through changing fire regimes, we might expect an increasing number of areas to be colonized by exotic species in the sub-Arctic.

4.4 Off-road species

Results from off-road findings suggest that fire makes the boreal forest vulnerable to exotic species that are close enough to disperse into these patches. We expect increasing fire frequency with climate change and know that shorter fire return intervals decrease the forest's ability to regenerate (Brown and Johnstone 2012). Thus, we could start to see more disturbance situations that would increase the spread of aggressive exotic species beyond roadsides and other human-disturbed environments.

4.5 Community structure

We found clear evidence of non-random trait distributions in Yukon roadside plant communities, suggesting deterministic processes of community assembly operate even on these relatively young and disturbed communities. As measured by presence/absence across communities, all three traits showed evidence of limiting similarity, and two traits showed effects of habitat filtering.

Habitat filtering appears to be underlain in part by the latitude/elevation gradient across the study region. Height showed strong evidence of habitat filtering, and given the relationships we found between community weighted mean heights across gradients of latitude and elevation, one or both of these variables likely represents or is strongly correlated with an important filter.

Community weighted mean heights were positively correlated with latitude and negatively correlated with elevation. As noted above, summer day length increases with latitude in our system and is a well-established predictor of plant performance (Garner and Allard 1920, Allard and Garner 1940, Grime and Grime 2001).

It is less clear what aspect of the environment might filter plants based on SLA. This trait was positively related to latitude but only for exotic species ($n=6$). This relationship did not hold for all species together ($n=46$), and is unlikely to explain habitat filtering across all species. Values of leaf mass per area (LMA, the inverse of SLA) have been shown to converge toward higher values (thicker leaves, lower SLA) in dry and nutrient poor environments (Wright et al. 2002) and thick leaves tend also to be wilt-resistant due to thick cuticles and thick-walled cells (Cunningham et al. 1999, Niinemets 2001). SLA is also strongly correlated with leaf lifespan, and the thickness and material investment in thick leaves are thought to better withstand herbivory and wear-and-tear than thinner leaves. Conversely, low SLA leaves require more carbon investment, a trade-off with fast growth. Sites with high nutrients or light levels may support higher SLA, but lower resource sites may require species that can produce strong, hardy leaves that can survive the slow turnover of nutrients. The next step would be to test for correlations with environmental variables we did not measure such as available soil nutrient concentrations, insolation and soil moisture.

An important aspect of our community assembly findings is that we were able to detect evidence of both habitat filtering and limiting similarity in the same system— SLA showed effects of both convergence and divergence in trait values. Compared to a null model of SLA distributions, observed values were restricted in range, and, within that restricted range, more evenly spaced than expected. Overdispersed SLA values across all plots suggest that niche differences contribute to coexistence. Much of the previous work in this area has only used one null model to test for convergence or divergence simultaneously, precluding detection of both processes co-

occurring (Watkins and Wilson 2003, Schamp and Aarssen 2009). However, our research shows that these processes are not mutually exclusive. By demonstrating their co-occurrence in roadside systems, we increase our understanding of the complex forces at work in these, and likely other, plant communities and underscore the utility of using separate null models to test for each effect separately (Bernard-Verdier et al. 2012).

By demonstrating that even when convergence (habitat filtering) is happening, patterns of abundance within species that did make it past the filter can provide another layer of insight into community processes. We showed that habitat filtering occurs by both determining community member identity as well as members' relative abundance. Species may have a range of conditions in which they are able to persist, and another, smaller range of conditions within which they are able to be abundant. Demonstrating these patterns adds greater detail to our understanding of how habitat filters affect community composition, and brings us closer to being able to predict community patterns based on environmental conditions.

5. Conclusions

This research contributed several key findings to the study of community assembly. First, we showed that exotic and native species respond to different aspects of the environment. This has implications as climate change accelerates, suggesting native and exotic plant communities react differently to changing conditions, and exotic species may be differentially favoured. For example, the increasing SLA in exotic plants with latitude (and thus day length) could signal that, like other human-disturbance adapted plants, exotic species will be better able to capitalize on changing conditions. Furthermore, identifying some of the differences between native and exotic strategies suggest there may be quantifiable differences in life strategies that could be used to predict the potential of non-native species to become invasive. Exotic species with relatively high SLA may be especially likely to colonize disturbed areas and emphasis should be placed on monitoring these species.

While most studies using functional traits to explain community assembly have focused on mature vegetation with species that have coexisted historically, we focused on a disturbed habitat with novel species combinations. This has implications for the time-scale at which assembly processes can function, suggesting assembly processes begin to act soon after disturbance, given that they are detectable in these relatively young plots. Understanding the structure of disturbed communities is especially important in this regard because it is an increasing habitat type where invaders usually first establish.

Finally, we found evidence of non-random processes structuring our target communities. Our choice of communities was both novel and relevant to conservation and management practices.

By addressing roadside communities in the sub-Arctic we have presented evidence that disturbed communities in a northern climate show the same signature of habitat filtering and limiting similarity, despite being higher in disturbance than communities previously investigated and despite an extreme climate. Our results thus broaden the generality of these processes of community assembly, adding to the growing body of literature identifying these processes in a range of habitats and climates. As well, we investigated the effects of habitat filtering on abundance. To date this has been seldom considered separately from presence/absence. It is becoming more common to weight species by their abundance in null models testing for limiting similarity, thereby including abundance in presence/absence filters. However, directly testing patterns of trait abundance on their own has thus far received limited treatment (Bernard-Verdier et al. 2012), as has any test of whether traits directly predict abundance (but see Cornwell and Ackerly 2010). In showing effects for four different processes, we have come closer to being able to predict community composition based on habitat. Understanding how communities work is important in advancing our understanding of how communities might react under anthropogenic influence including environmental change due to climate change and/or human disturbance.

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Appendices

Appendix A. Plot coordinates along the North Klondike Highway, Yukon Territory.

Kilometre 192 is the start of the North Klondike highway and is located at the junction with the Alaska Highway (kilometres 0 through 191 make up the South Klondike Highway connecting Skagway, AK and Whitehorse, YK).

Plot no.	Km	Latitude	Longitude	Elevation (masl)	
1	192	60.812	-135.205	704	
2	245	61.224	-135.435	839	
3	251	61.270	-135.497	811	
4	253	61.283	-135.519	830	
5	268	61.385	-135.674	854	
6	273	61.418	-135.724	841	
7	274	61.425	-135.735	820	
8	286	61.523	-135.806	690	
9	305	61.681	-135.914	652	
10	333	61.903	-136.140	618	
11	356	62.088	-136.286	526	
12	358	62.111	-136.269	530	
13	365	62.156	-136.283	663	
14	380	62.273	-136.342	587	
15	385	62.300	-136.284	568	
16	390	62.330	-136.349	521	
17	395	62.358	-136.423	523	
18	409	62.436	-136.627	535	
19	419	62.511	-136.728	505	
20	430	62.591	-136.848	510	
21	437	62.643	-136.830	557	
22	458	62.781	-136.581	525	
23	462	62.813	-136.582	490	
24	474	62.894	-136.506	596	
25	483	62.973	-136.504	631	
26	485	62.991	-136.505	636	
27	497	63.082	-136.455	735	
28	511	63.197	-136.527	640	
29	530	63.344	-136.644	539	
30	546	63.429	-136.864	489	cont'd...

Appendix A cont'd...

Plot no.	Km	Latitude	Longitude	Elevation (masl)
32	572	63.541	-137.258	453
33	576	63.541	-137.336	457
34	581	63.560	-137.418	449
35	582	63.568	-137.430	458
36	587	63.597	-137.495	451
37	610	63.759	-137.691	646
38	635	63.868	-138.105	606
39	636	63.872	-138.122	629
40	649	63.915	-138.354	732
41	664	63.942	-138.597	475
42	679	64.022	-138.803	437

Appendix B. List of all species measured and their corresponding mean trait values.
Naming follows VASCAN (2010)

	Family	Species	Species Code	SLA	Leaf Area	Height
				mm ² /mg	mm ²	cm
1	Apiaceae	<i>Cnidium cnidiifolium</i>	Cnicni	17.15	809.78	-
2	Asteraceae	<i>Achillea millefolium</i>	Achmil	-	-	41.16
3	Asteraceae	<i>Achillea alpina</i>	Achalp	-	-	54.84
4	Asteraceae	<i>Arnica angustifolia</i>	Arnang	19.03	609.43	27.27
5	Asteraceae	<i>Artemisia campestris</i>	Artcam	14.01	141.91	39.06
6	Asteraceae	<i>Crepis tectorum</i>	Cretec	21.70	151.54	23.81
7	Asteraceae	<i>Erigeron compositus</i>	Ericom	9.70	128.28	3.74
8	Asteraceae	<i>Eurybia sibirica</i>	Eursib	21.39	552.07	22.79
9	Asteraceae	<i>Solidago simplex</i>	Solsim	14.50	319.62	35.19
		<i>Taraxacum</i>				
10	Asteraceae	<i>ceratophorum</i>	Tarcer	24.20	732.58	13.88
		<i>Taraxacum</i>				
11	Asteraceae	<i>officinale</i>	Taroff	28.65	2005.30	33.19
12	Boraginaceae	<i>Lappula occidentalis</i>	Lapocc	17.43	70.29	19.92
		<i>Mertensia</i>				
13	Boraginaceae	<i>paniculata</i>	Merpan	20.02	1298.47	39.03
14	Caprifoliaceae	<i>Linnaea borealis</i>	Linbor	17.02	70.78	4.06
16	Equisetaceae	<i>Equisetum arvense</i>	Equarv	14.95	92.01	25.67
		<i>Equisetum</i>				
17	Equisetaceae	<i>sylvaticum</i>	Equsyl	18.59	72.95	27.30
		<i>Arctostaphylos uva-</i>				
18	Ericaceae	<i>ursi</i>	Arcuva	8.63	94.31	10.61
19	Fabaceae	<i>Astragalus alpinus</i>	Astalp	33.00	282.31	13.41
20	Fabaceae	<i>Astragalus tenellus</i>	Astten	15.82	86.99	29.61
21	Fabaceae	<i>Hedysarum alpinum</i>	Hedalp	16.47	194.09	49.86

cont'd...

Appendix B, cont'd.

		Species		SLA mm ² /mg	Leaf Area mm ²	Height cm
Family	Species	Code				
	<i>Hedysarum boreale</i>					
22	Fabaceae	<i>ssp. mackenziei</i>	Hedbor	17.74	218.97	48.95
23	Fabaceae	<i>Lupinus arcticus</i>	Luparc	15.45	504.98	28.97
24	Fabaceae	<i>Medicago sativa</i>	Medsat	-	-	33.86
25	Fabaceae	<i>Melilotus albus</i>	Melalb	18.57	392.15	82.50
26	Fabaceae	<i>Oxytropis campestris</i>	Oxycam	22.20	126.96	16.32
27	Fabaceae	<i>Oxytropis deflexa</i>	Oxydef	30.08	108.87	14.01
28	Fabaceae	<i>Oxytropis splendens</i>	Oxyspl	22.19	214.04	15.96
29	Fabaceae	<i>Trifolium hybridum</i>	Trihyb	25.35	617.76	37.98
30	Linaceae	<i>Linum lewisii</i>	Linlew	15.87	84.07	30.69
	<i>Chamerion</i>					
31	Onagraceae	<i>angustifolium</i>	Chaang	14.78	556.66	43.97
	<i>Platanthera</i>					
32	Orchidaceae	<i>hyperborea</i>	Plahyp	32.27	368.57	13.72
33	Plantaginaceae	<i>Plantago major</i>	Plamaj	25.33	1366.65	12.07
34	Poaceae	<i>Agrostis scabra</i>	Agrsca	33.18	80.04	37.58
35	Poaceae	<i>Bromus inermis</i>	Broine	17.66	581.70	72.38
	<i>Calamagrostis</i>					
36	Poaceae	<i>canadensis</i>	Calcan	-	-	64.67
	<i>Calamagrostis</i>					
37	Poaceae	<i>purpurascens</i>	Calpur	13.00	287.60	45.99
38	Poaceae	<i>Elymus trachycaulus</i>	Elytra	20.7	284.41	48.02
39	Poaceae	<i>Hordeum jubatum</i>	Horjub	20.59	218.63	43.22
	<i>Polemonium</i>					
40	Polemoniaceae	<i>pulcherrimum</i>	Polpul	28.95	76.25	19.61
41	Pyrolaceae	<i>Pyrola asarifolia</i>	Pyrasa	13.15	532.11	5.64
42	Ranunculaceae	<i>Anemone multifida</i>	Anemul	13.69	925.22	26.09
43	Rosaceae	<i>Fragaria virginiana</i>	Fravir	14.21	1414.22	12.77
44	Rosaceae	<i>Potentilla litoralis</i>	Potlit	10.58	637.56	45.05
45	Rosaceae	<i>Potentilla norvegica</i>	Potnor	22.44	288.55	35.62

cont'd...

Appendix B cont'd.

		Species				
Family		Species	Code	SLA	Leaf Area	Height
				mm ² /mg	mm ²	cm
		<i>Potentilla</i>				
46	Rosaceae	<i>pensylvanica</i>	Potpen	16.18	664.18	37.82
47	Rubiaceae	<i>Galium boreale</i>	Galbor	16.89	89.09	34.90
49	Saxifragaceae	<i>Parnassia palustris</i>	Parpal	40.15	229.27	11.63
50	Scrophulariaceae	<i>Euphrasia subarctica</i>	Eupsub	-	-	12.81
51	Scrophulariaceae	<i>Penstemon gormanii</i>	Pengor	8.91	128.34	8.78