University of Alberta

Human disturbance and boreal vascular plant biodiversity in Alberta, Canada

by

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Dedication

To the disturbed ecologist

Abstract

The worldwide biodiversity crisis has intensified the need to better understand how biodiversity and human disturbance are related. Yet this relationship lacks both consensus in theoretical expectations and consistency in observed empirical patterns. I present one of the largest extent studies of human impacts on boreal plant biodiversity to date, in the boreal ecoregion of Alberta, where disturbance in sites range ranged from 0 – 100 % area disturbed by varying land use types including agricultural fields, forestry cut-blocks, and petroleum extraction.

The 'intermediate disturbance hypothesis' (IDH) suggests that disturbance regimes generate predictable non-linear patterns in species richness. But evidence often contradicts IDH at small scales and is generally lacking at large regional scales. I show that across a broad region species richness peaked in communities with intermediate anthropogenic disturbance, as predicted by IDH, even when accounting for many environmental covariates. IDH was consistently supported across trees, shrubs, forbs, and grasses and with temporary and perpetual disturbances. However, only native species fit this pattern; exotic species richness increased linearly with disturbance.

A fundamental impediment to understanding the diversity-disturbance relationship is that both diversity and disturbance can depend on the scales at which they are sampled. To test the dependence of species richness on disturbance scale and the scale-dependence of the intermediate disturbance hypothesis, I hold the area over which species richness is measured constant and instead manipulate the area over which human disturbance is measured. I show the shape of richness-disturbance relationship is consistent across scales, but predictions of richness depend on the scale at which disturbance was measured.

I also explore impacts of human disturbance on community composition and structure to both identify the risks facing communities and to assess the potential utility of these metrics for monitoring applications. In particular, I explore ranked species occupancy curves, species functional trait dispersion, and species specialization in relation to anthropogenic disturbance extent. Disturbed communities differed in functional traits, particularly in fruit and seed characteristics, but community structure was similar across communities regardless of disturbance class, and both species specialization and functional dispersion of traits were not strongly related to disturbance.

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TABLE OF CONTENTS

List of Figures

List of Tables

Chapter 1: Introduction

General background to disturbance in ecology

If species were to exist at equilibrium, never gaining nor losing substantially in abundance, living on a homogeneous and uniform surface, then only a few species would likely exist. Competition would have driven the rest to extinction, leaving the remaining few to dominate that hypothetical world (Gause, 1934; Grace & Tilman, 1990). The real world, however, is heterogeneous in space and time. Under heterogeneous conditions various species may gain an evolutionary advantage; that is, species may specialize on different resources or conditions (Hutchinson, 1959; Futuyma & Moreno, 1988). The various possible conditions available for specialization present an ecological trade-off. Further, generalist species may succeed under many conditions, but may not thrive as well as a specialist in any given one (Levins, 1968; MacArthur, 1972). The continuum of specialism to generalism, niche width, represents a second trade-off that can facilitate co-existence. Whether patchily distributed resources or fluctuating climate, variability often begets diversity.

One of the key processes that can prevent competitive exclusion and thereby facilitate coexistence is disturbance. Disturbances are relatively discrete events in time that disrupt the ecosystem, community, or population structure and bring about a change in resources, substrate availability, or the physical environment (Pickett & White, 1985). Disturbance can be both a generator and destroyer of diversity. As a destroyer, it removes biomass (Grime, 1977), while as a generator, it can either create environmental heterogeneity as discussed, or 'reset' succession. Johnson & Miyanishi (2007) defined succession (Cooper, 1923) as "an orderly unidirectional process of community change in which communities replace each other sequentially until a stable community is reached." Thus succession itself is change in composition, not necessarily diversity. However, the eventual end of succession, the supposed 'climax community' is often thought to be lower in species diversity because of competitive exclusion. A third trade-off I need to consider is that between competition, which is thought to be favoured late in succession, and colonization, favoured early in succession.

The intermediate disturbance hypothesis

The intermediate disturbance hypothesis (hereafter 'IDH'; Connell, 1978; Grime, 1973) suggests that species coexistence is facilitated by moderate levels of disturbance. At low disturbance (or late succession), species richness is expected to be low because of competitively dominant species exclude those which are inferior. Likewise, at high disturbance, species richness is expected to be low but because only weedy species quickly able to colonize and establish themselves are likely to be present. At intermediate disturbance levels, a sort of ecological ‘goldilocks’ level, species richness is maximized as both colonizers and competitors may persist and co-exist. Sousa (1979) famously showed support for IDH studying algae growing on boulders in the marine intertidal zone which were overturned by tidal action in proportion to their size. He controlled for boulder size by stabilizing smaller boulders and observed that boulders disturbed moderately frequently harboured greater algal species than either frequently or infrequently disturbed boulders. IDH has been applied to a wide variety of disturbance types and ‘levels’, be they frequency (or time since last), duration, magnitude, intensity, or extent (Roxburgh et al., 2004). Over several decades, IDH became widely accepted, but its generality has more recently been questioned (Mackey & Currie, 2001; Sheil & Burslem, 2003; Shea et al., 2004). Sheil and Burslem (2003:24) suggest that the IDH is ‘‘an elegant but oversimplified representation of a complex knot of concepts” and extensive work has been conducted attempting to decipher ecological mechanisms behind the IDH. Recently, Fox (2012) attempted to debunk the IDH, mechanism by mechanism, but stopped short of a critical blow to the most commonly cited driver of the IDH, the colonization-competition trade-off. In this thesis I do not seek to test mechanisms behind the intermediate disturbance hypothesis, I aim simply to test if it and other patterns are supported in this system. A first step in understanding a pattern is to see if it exists.

Conservation and management

Despite the limited generality of IDH, management of land use and forestry resources has often imposed intermediate and varied disturbance regimes.

Management often seeks to emulate natural disturbance (Bergeron et al., 1999; Landres et al., 1999; Seymour et al., 2002; Long, 2009) and natural disturbances tend to be distributed on a continuum of large and infrequent, to small and frequent. The resulting consequence for the landscape is an intermediately disturbed mosaic.

In the boreal forest of Alberta, the case for emulating natural disturbance like fire arguably fits reasonably well with forest resource management, the analogy is more strained for petroleum development, linear features, and agriculture. It may seem inappropriate to treat features like croplands, pastures or well pads as disturbances at all. They are in fact perpetual, nearly permanent features, entirely unlike the effects of fire, pest outbreaks, or storms. However, natural disturbances can be of even greater permanence, like volcanic eruptions or glacial erosion, and of higher frequency, such as repeated tidal action. Relative to these natural disturbances, semi-annual tilling by farm equipment, intensive grazing by livestock, and even built structures and parking lots are appropriately considered disturbances. However similar to natural disturbance, anthropogenic land use is expanding rapidly in this region, prompting the need to better understand the possible ecological changes taking place.

Boreal plant disturbance ecology

The boreal forest biome makes up 25 % of the world's closed-canopy forest area, and half of the forest undisturbed by modern humanity (Potapov et al., 2008). Over half of Canada's land is in the boreal biome. However, much of the southern boreal forest has faced heavy pressures for natural resource extraction, and especially in Alberta, these pressures are intensifying. The major natural disturbance in the boreal ecoregion of Alberta is fire, though mountain pine beetle (*Dendroctonus ponderosae*) has recently become a significant agent of disturbance, particularly for lodgepole pine (*Pinus contorta)*.

Boreal forests have long been characterized as relatively homogeneous stands in repetitious recovery from fire, progressing from a common set of post-fire colonizing species again toward simple old growth stands with few species, but more often than not burning again. However, recent insights and observations paint a far more complex picture, articulated by Bergeron & Fenton (2012). Indeed, old growth often progresses past initial even aged stands to mixed age forests supporting a wide variety of understory species. A variety of non-fire, smaller scale disturbances like wind, localized insect pest and disease mortality can operate simultaneously. Bergeron & Fenton (2012) suggested vascular plant understory species were richest in boreal stands aged 150 to 200 years, but also showed stands aged 100 to 150 years old were less rich than younger 50 to 100 year old stands.

What is biodiversity?

Biodiversity is a broad and vague term invoking all the variability in life, be it at genetic, species, or broader community or ecosystem levels. Countless indices to describe biodiversity components have been developed, each capturing various aspects of biodiversity in different ways, but the most common metric is still the simplest: species richness (Buckland, 2005; Lamb et al., 2009). Many indices, especially those seeking to capture species evenness across sites, require known relative abundances of species. This information is valuable but often costly and difficult to collect. Occupancy data is usually more efficiently collected, and recent work suggests it can be more strongly linked to environmental conditions (Lawrence Lodge et al., 2007; Wilson, 2012). The Alberta Biodiversity Monitoring Institute (ABMI; Nielsen, Bayne, Schieck, Herbers, & Boutin, 2007) developed a metric called ‘biodiversity intactness’ which compares current occupancy to reference (minimally disturbed conditions). While ‘intactness’ serves ABMI’s purpose, it is rarely utilized externally, so any comparison to other studies and systems, or testing for patterns and processes observed elsewhere would be limited.

A new scale for boreal biodiversity ecology

This thesis is uses a large, robust data set provided by the Alberta Biodiversity Monitoring Institute describing vascular plant species occupancy in systematically sampled sites across boreal Alberta (Boutin et al., 2009). I supplemented this data with additional field collection, with a particular focus on sites of high human footprint, which were sparsely available. Chapter 2 uses a more limited data set than Chapters 3 and 4 because available data were more limited when Chapter 2 was completed.

To this occupancy data, ABMI added human land use data based on aerial photography and satellite imagery. From these layers, several ‘plot sizes’ were used as scales for assessing land use. In Chapter 2 and 4, I used 150 m radius circles, whereas in Chapter 3 I used 1 ha square (the same scale as the vascular plant data) and 3 x 6 km rectangles. The differences in shape are an unfortunate lack of control due simply to availability of data from ABMI.

ABMI’s data provided the basis for the study of human impacts on boreal biodiversity at an unprecedented extent and resolution. I had the good fortune to be among the first to ask independent scientific questions with the data. Admittedly, knowing where to begin was a daunting challenge. Starting with a test of one of the simplest, oldest, and controversial ideas relating biodiversity to disturbance, the IDH, was a logical starting point.

Data and study limitations

Note that ABMI sampling design and data collection were not specifically intended for the research presented in this thesis, but part of a much broader biodiversity monitoring initiative. While these data are an enormous wealth of information, the types of analyses that could be conducted were limited to this sampling scheme developed for other purposes. For instance, in Chapter 3 I examine impacts of human disturbance on biodiversity at multiple scales of disturbance, but was unable to examine these impacts at multiple scales of biodiversity. The sites were also located without stratifying by environmental conditions or ecotype, so sites could include multiple habitats.

Further, ABMI’s collection of data was incomplete in that only a portion of sites intended to be sampled at 20 km grid spacing throughout the study region had been sampled. Thus, the data collection sites were sparsely distributed throughout the region. The sites for which data was available were not selected randomly for reasons related to field sampling logistics. The sample of sites was not necessarily a true random sample of the region.

Aims and structure of the thesis

This thesis is made up of three data chapters. Chapter 2 provides a test of the IDH in this large regional system. It is significant in that it provided one of the first tests of IDH at a large regional scale other than in tropical forests, the system for which it was first proposed by Connell (1978). It also was the first at a large regional scale to test anthropogenic rather than natural disturbance and the first to explicitly distinguish native and exotic species. It overcame major criticisms in study design of earlier high profile investigations into IDH, and employed a complete 0 – 100 % disturbance continuum.

Chapter 3 somewhat repeats Chapter 2, but at two different scales to assess the scale dependency of the pattern. Rather than merely an exercise in redundancy, however, Chapter 2 breaks new ground in providing a new perspective on the diversity-disturbance relationship. The scale dependence of the diversity-disturbance relationship has received decades of attention in the form of the species area relationship, island biogeography, and habitat fragmentation. In these studies, the area over which species richness is measured is altered. Instead, I examine the scale dependence of the other side of the diversity-disturbance relationship, disturbance, by holding the area of richness estimation constant and examining multiple scales of disturbance. In this way, I not only test the robustness of the IDH across scales, but distinguish local from landscape scale influences of disturbance on species richness.

Chapter 4 widens the scope to explore a variety of community characteristics to assess their sensitivity to disturbance. The aim was two-fold: to assess the utility of these metrics for monitoring and to identify risks facing communities in this region. A variety of community characteristics were examined, but I test the unifying hypothesis communities impacted by land use disturbance are ecologically impoverished, compositionally and functionally homogeneous, and composed of less desirable species.

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Chapter 2: Regional boreal biodiversity peaks at intermediate human disturbance

Abstract

The worldwide biodiversity crisis has intensified the need to better understand how biodiversity and human disturbance are related. The 'intermediate disturbance hypothesis' (IDH) suggests that disturbance regimes generate predictable non-linear patterns in species richness. Evidence often contradicts IDH at small scales, and is generally lacking at large regional scales. I present the largest extent study of human impacts on boreal plant biodiversity to date. Disturbance extent ranged from 0 – 100 % disturbed in vascular plant communities, varying from intact forest to agricultural fields, forestry cut-blocks, and oil sands. I show for the first time that across a broad region species richness peaked in communities with intermediate anthropogenic disturbance, as predicted by IDH, even when accounting for many environmental covariates. IDH was consistently supported across trees, shrubs, forbs, and grasses and with temporary and perpetual disturbances. However, only native species fit this pattern; exotic species richness increased linearly with disturbance.

Introduction

The ongoing human-caused global biodiversity decline and continuing expansion of human land use have deepened the need to better understand the relationship of biodiversity to anthropogenic disturbance(Barnosky et al., 2011). The 'intermediate disturbance hypothesis' (IDH), a foundational idea in community ecology, suggests that differences in disturbance among local communities can explain broad patterns in diversity throughout a region(Connell, 1978, Grime, 1973). In communities with moderate disturbance levels, species richness should be higher than in those with low or high disturbance(Connell, 1978, Grime, 1973). After nearly 40 years of research, most studies have found little or no empirical evidence to support the IDH (Mackey and Currie, 2001). Support has been even slimmer with anthropogenic than with natural disturbances(Mackey and Currie, 2001, Shea et al., 2004), and our ability to predict changes in community diversity patterns following human disturbance is still extremely limited(Mackey and Currie, 2001, Shea et al., 2004). Further, studies of the IDH have rarely differentiated native and exotic species, a puzzling oversight given concerns of exotic species invasions, particularly in disturbed environments(Hobbs and Huenneke, 1992).

One reason implicated for the scarcity of empirical support for IDH(Mackey and Currie, 2001, Shea et al., 2004) is that most investigations of diversity-disturbance relationships have been conducted at insufficiently small spatial scales(Bongers et al., 2009, Sheil and Burslem, 2003). Species richness varies nonlinearly with spatial scale(MacArthur and Wilson, 1967, Preston, 1962, Whittaker et al., 2001) and processes thought to generate IDH vary with scale(Cadotte, 2007), so support for the IDH may itself depend on the scale at which it is tested(Bongers et al., 2009, Mackey and Currie, 2001, Sheil and Burslem, 2003). Testing the IDH might best be accomplished by matching the scales of investigation to the scales at which those processes generating the IDH operate. Our understanding of the IDH is poorest at regional extents(Mackey and Currie, 2001, Shea et al., 2004) (i.e. across multiple landscapes), where it has been mostly limited to the system to which IDH was first applied, tropical forest trees. Further, at regional extents – those at which land use planning and management are often conducted – the IDH has generally been tested only with natural, not anthropogenic disturbances(Mackey and Currie, 2001, Shea et al., 2004).

I tested the specific prediction of the IDH that a non-linear unimodal relationship exists between species richness and anthropogenic disturbance extent, with the greatest number of species present at intermediate disturbance. I conducted this test by examining local communities across the largest spatial extent to date: the 381,047 km^2 boreal ecoregion of Alberta, Canada, an area comparable to Germany. Within this region, vascular plant species richness was sampled with 1 ha surveys of 242 local communities (SI, Fig. 2-1). I used a direct measure of anthropogenic disturbance: area of land altered by human land use (hereafter 'extent') as assessed with aerial and satellite imagery of 150 m radius circular areas (SI). The sample plots exhibited a complete gradient (0 – 100 %) in human disturbance extent: disturbances varied vastly in intensity, area, and type among communities ranging from intact wilderness of one of the world's largest national parks (Wood Buffalo N.P.) to human-dominated landscapes of towns, forestry, agriculture, linear features, conventional oil and gas, and oil sands extraction. I found that species richness of boreal vascular plants showed a unimodal relationship with human disturbance. Richness peaked at intermediate disturbance, with or without accounting for numerous environmental factors, supporting the IDH. Also consistent with the IDH, communities at low and high human disturbance were composed of different sets of species, while communities with intermediate disturbance overlapped with those of low and high disturbance. However I also tested the consistency of the IDH among native and exotic species individually and show that while native species exhibited the predicted peaked relationship of richness to human disturbance, exotic species instead increased linearly.

Methods

Study design

Vascular plant richness was surveyed in the boreal ecoregion of the province of Alberta, Canada by the Alberta Biodiversity Monitoring Institute, using standardized protocols(ABMI, 2009). Vascular plant species occupancy was surveyed within 1 ha for 25 min at 242 sites, a subset of 959 sites of the Canadian National Forestry Inventory grid with grid centre spacing of 20 km (Fig. 2-1). All surveys were conducted Jun 26 – Aug 18 of 2003 – 2009. Human disturbance extent (% land area converted by humans) was assessed by manual interpretation of 1:30 000 aerial photos and SPOT satellite imagery within circles of 150 m radius (7.07 ha) at each site. Disturbance extent was assessed within a larger area than that at which richness was surveyed because both direct local disturbances and those in the surrounding landscape may potentially affect local richness (Turner, 2010). I distinguished native and exotic species according to (ACIMS, 2011).

To determine the best fit shape of the richness-disturbance relationship, I performed linear and polynomial regression analyses. Polynomial (quadratic and cubic) models required additional model parameters not included in simple linear regression, so I adopted those models only when they were both significant (reported as "$p < 0.05$") and when they fit significantly better by explaining significantly more variation than the simpler model of fewer parameters, as diagnosed with an ANOVA of candidate models (reported as "p of increase in r^2 over linear model"). In all cases, that frequentist model selection protocol resulted in the same adopted model as with model selection by AIC (highest model likelihood, AIC weight > 0.5).

Disturbance types

Human disturbance only described spatial extent of disturbance; it was not a measure of 'area removed' (as in some theoretical models) and I did not quantify intensity, frequency or time since disturbance, which varied greatly within and among disturbance types. Anthropogenic disturbances included agricultural pasture and croplands, forestry cut areas of variable ages, linear features (including pipelines, powerlines, roads, railways, and cutlines primarily for oil/gas seismic exploration), industrial/commercial disturbances (including coal and mineral surface mines, oil and gas well pads, communication towers, gravel pits, heavy oil sands development, and spoil piles), and both urban and rural settlements. Natural disturbances such as fire and insect damage were not correlated to anthropogenic disturbance.

Species composition

To determine if species composition of communities was consistent with proposed mechanisms for the IDH, I tested for differences in species composition among communities varying in human footprint. I classified sites as <33.3, 33.4 – 66.6, and > 66.7 human footprint and used a Multi-Response Permutation Procedure (MRPP) using a Euclidean distance measure and rank transformed distance matrix to make pairwise comparisons of species composition across sites grouped by human footprint class. I performed non-metric multidimensional scaling (NMDS) analysis, an ordination technique which graphically presents the overlap in composition across sites, then classified each site by disturbance level (Fig. 2-3).

Species origin and growth form

I used a common non-taxonomic categorization of plant species – ‘growth form’ – to explore the consistency of the IDH among species of different functional types(USDA, 2011). Vascular plant species in boreal Alberta vary from small herbaceous forbs to tall woody canopy trees and because these different growth forms have different functional roles, they could be expected to respond differently to disturbance (Lavorel et al., 1997).

Environmental covariates

To determine the best fit shape of the richness-disturbance relationship while accounting for potentially confounding variables, I constructed multiple regression models and selected model shapes as above. For human disturbance and each environmental covariate, I selected the best fitting linear or polynomial form. I used a subset of 146 sites for which data was available for 18 potentially confounding variables. I included in the models human disturbance plus the following: natural subregion type, latitude, longitude, elevation, topographic heterogeneity, growing degree days, mean annual temperature, mean annual precipitation, terrain wetness, site wetness, solar flux, canopy closure, oldest tree age, organic depth, soil type, surficial geology, slope position, and landform classification (Supplementary Table S4). Too few data were available to include natural disturbance (year of last fire and natural disturbance extent) in the models. Details of environmental variable observation and estimation are available at abmi.ca.

Temporary anthropogenic disturbance

To investigate the relationship of richness to temporary disturbance, I categorized forestry cut areas, cutlines, pipelines, powerlines as temporary, and all other disturbances as perpetual. I first excluded all sites with any perpetual disturbance at the 1 ha scale where vascular plants were sampled. I then subtracted any perpetually disturbed area in the 150 m radius circle plot and calculated the proportion of temporary disturbance in the remaining area.

Results

Richness-disturbance relationship

A simple unimodal model with peak at 47.7 % disturbance best explained vascular plant species richness in relation to human disturbance extent: species richness peaked at intermediate disturbance (Fig. 2-2), supporting the intermediate disturbance hypothesis. That simple quadratic curve ($r^2 = 0.135$, $p < 0.001$, p of increase in r^2 over linear model < 0.001) fit significantly better than other model shapes, whereas the linear regression model was not statistically significant (r^2 = 0.007, p = 0. 202, Table S1).

Species composition

The IDH also predicts that composition of species should differ among communities depending on level of disturbance(Connell, 1978, Grime, 1973). Mechanisms thought to drive the peaked disturbance-richness relationship, such as trade-offs in species traits associated with disturbance, suggest that communities with intermediate disturbance are more species rich because they are composed of species associated with both low and high disturbance levels(Connell, 1978, Grime, 1973). Consistent with the IDH, I observed that communities with low (< 33.3 %) and high (> 66.7 %) disturbance were composed of significantly different sets of species ($p < 0.001$), with species composition overlapping least among communities of low and high disturbance (A = 0.028, Fig. 2-3). Also consistent with the IDH, species composition of communities with intermediate (33.4 – 66.6 %) disturbance overlapped with composition of communities with low (A= 0.027) or high (A = 0.017) disturbance (Fig. 2-3). The difference in composition between intermediate and low disturbance communities was statistically significant (p < 0.001), whereas the difference between intermediate and high disturbance communities was less clear: it was not significantly more different in species composition than would be expected by chance ($p = 0.085$), but the higher p-value may be due in part to fewer sites in that comparison. Although a high proportion of sites sampled exhibited low disturbance, 30.7 % of species were found only at sites with < 33.3 % human disturbance.

Species origin and growth form

One possible difference in species composition along the disturbance gradient is the proportion of native and exotic species. These groups are often managed differently: exotic species are traditionally considered of lesser conservation priority than native species and detrimental exotics (‘invasive species’) are often targets for control(Davis, 2009). I therefore tested the IDH with native and exotic species separately. I found that while native species richness peaked at intermediate extent of human disturbance ($r^2 = 0.104$, $p < 0.001$), exotic species richness increased linearly ($r^2 = 0.371$, $p < 0.001$, p of increase in r^2 for quadratic model over linear = 0.082, Fig. 2-4A, Table S2). Because native and exotic species showed different shaped functions, I compared the changes in native and exotic richness at ranges in disturbance extent less than or greater than ‘intermediate disturbance’, where native richness peaked, to better understand relative changes in these species groups. At < 47.7 % disturbance extent, native species increased (linear regression slope = 0.503) more steeply (*p* = 0.001, ANCOVA) with extent than exotic species (slope = 0.119). However, at > 47.7 % disturbance extent, native species decreased (slope = - 0.693, SE = 0.172) significantly more steeply than exotic species increased (slope = 0.022, SE = 0.038) with disturbance, as indicated by the standard errors of the absolute values of the slopes which were less than the gap between those errors. Anthropogenic disturbance was a more accurate predictor of richness of exotic species than of natives; disturbance extent explained 3.6 times the variance in exotics than in natives (Fig. 2-4A).

The ratio of native to exotic species declined linearly with human-disturbed area (slope = -0.247, r^2 = 0.203, $p < 0.001$, Fig. 2-4B). The IDH was conceived without apparent consideration of invasive species, and the non-conformance of exotics implies the hypothesis may only apply to regional metacommunities with a 'closed' species pool. The correlation of exotic species and human disturbance is consistent with previous studies(Davis, 2009), and suggests that fundamentally different responses to disturbance exist among some groups. However, when I categorized species by 'growth form'(USDA, 2011), another common ecological categorization and indicator of functional role, richness of each type of vascular plant species (including forbs, graminoids, shrubs, and trees) peaked at intermediate disturbance extent (Supplementary Table S3). The generality of the IDH among types of species requires greater scrutiny.

Environmental covariates

Total species richness varied considerably along the disturbance gradient, an expected result shared by other related observational studies[4, 5, 35] due to effects of numerous other factors including climate, topography, stand age, soil and other environmental conditions. I accounted for many such factors by constructing multiple regression models that included 19 environmental variables (SI, Table S4) including human disturbance, and again compared possible shapes of the relationship between richness and human disturbance. Consistent with the IDH, a quadratic curve with maximum species richness at intermediate disturbance fit best ($p < 0.001$, Table S5). As expected, including the environmental variables in the model better explained species richness across sites ($r^2 = 0.709$) than did the simple quadratic model of human disturbance in response to richness ($r^2 = 0.137$, $p = 0.780$, Table S5). However, accounting for these variables did not qualitatively change the shape of the relationship between richness and disturbance.

Anthropogenic disturbance types

Anthropogenic disturbance varied greatly in intensity, frequency, permanence, and spatial characteristics, so different types of disturbance might be expected to drive different disturbance-diversity relationships as a result. Agricultural disturbance is often so frequent and intensive (e.g. annual cultivation) such that successional processes are minimal, and primary roads plus urban and industrial sites are virtually permanent landscape changes. I classified those disturbances as ‘perpetual’. By contrast, vegetation on forestry cut blocks, pipelines and seismic lines usually exhibit dynamic and successional changes in species composition following initial disturbance, classified here as ‘temporary’. To investigate the relationship of richness to proportion of temporary human footprint, I excluded perpetual human footprint (SI). In areas not perpetually disturbed, richness again peaked at intermediate temporary disturbance extent. The simple quadratic model with peak at 55.3 % temporary disturbance fit significantly better than other model shapes ($r^2 = 0.1136$, $p < 0.001$, p of increase in r^2 over linear model < 0.001, Table S6); the linear model had a likelihood of 0.011 (ΔAIC = 9.05, AIC weight = 0.008). Thus, the IDH was supported both for total disturbance (including perpetual disturbance) and for temporary disturbance alone, suggesting the hypothesis is robust to disturbance permanence.

Discussion

Our results for native species in anthropogenically disturbed communities lend support to the IDH, in contrast to more than 80% of other studies which did not exhibit the predicted unimodal relationship(Mackey and Currie, 2001, Shea et al., 2004). I attribute support for IDH found in this study but not many others to several aspects of study design. First, this study was conducted at a large regional extent. Reviews of IDH concluded many tests of IDH have been inadequately small scaled(Bongers et al., 2009, Mackey and Currie, 2001, Shea et al., 2004); few tests have approached the regional extents at which the IDH was intended to apply (e.g. the 35,000 ha Budongo rainforest(Connell, 1978)). Connell, who advanced the IDH, was specific in stating this hypothesis applied to "variation in diversity among local stands [i.e. communities]", not among sites within small communities, nor among large biomes(Connell, 1978). Diversity-disturbance relationships at either local (e.g. within a single community) or interregional scales are generated by different processes and tend to exhibit different diversity patterns(Sax and Gaines, 2003). Our study was truly regional because I observed consistent results among widely separated communities sampled across a large geographic range. Second, I utilized a direct measure of disturbance: area altered by human land use. Data-rich studies of tropical forest trees(Bongers et al., 2009, Hubbell et al., 1999, Molino and Sabatier, 2001) have used indirect proxies for disturbance such as % pioneer species or canopy height, which may have contributed to their opposing conclusions and which have been criticized for their poor interpretability(Sheil and Burslem, 2003). Third, the communities under investigation varied on a full gradient of 0 – 100% disturbance extent. Many studies may have encompassed a narrow range of disturbance levels, thereby risking missing any 'intermediate' peak in richness (Bongers et al., 2009, Mackey and Currie, 2001, Shea et al., 2004).

Our results have important implications for prominent theories of species invasion which predict a strong link between richness of native and exotic species. Communities richer in native species may be more resistant to invasion of exotics due to competition among species, thereby producing a negative relationship between native and exotic richness(Elton, 1958, Kennedy et al., 2002, Tilman, 2004). A contrasting idea suggests native and exotic species richness should be positively related because the key environmental factors driving richness are shared by native and exotic species(Levine et al., 2004, Stohlgren et al., 2003). I found little support for either of these conflicting predictions: native species (x) weakly explained exotic (y) richness ($y = 0.030x + 1.440$, $r^2 = 0.033$, $p = 0.005$). By contrast, human disturbance was a relatively good predictor of exotic richness ($r^2 = 0.371$, $p < 0.001$), supporting the view that exotic species are not independent drivers of native biodiversity declines, but ‘passengers’ simply accompanying community change in disturbed environments (MacDougall and Turkington, 2005).

Considerations of biodiversity conservation in regional land use planning decisions usually focus on preservation of species which are at risk or have particular economic or cultural value. However, biodiversity is increasingly being more broadly considered in land use planning decisions(Boutin et al., 2009), species richness is considered in conservation prioritization(Myers et al., 2000), and ecological theory is being called upon to aid conservation oriented land use decisions (Bestelmeyer et al., 2003). I show that the IDH can partially explain the variation in species richness found throughout a large region subjected to a diversity of anthropogenic impacts. Although simple, IDH is an enduring idea that may be applicable to land use planning(Sasaki et al., 2009)and along with invasion theories can contribute to understanding changes in native richness expected with human land use(Catford et al., 2012). Our results are generally consistent with both the IDH and the more specific ‘patch mosaic dynamics hypothesis’, which suggests that landscapes with a mosaic of disturbed patches of various intensity, extent, and frequency can host the greatest diversity(Pickett, 1986). However, the findings also suggest that management strategies designed to maximize biodiversity by imposing intermediate human disturbance regimes could result in communities with a) species composition statistically indistinguishable from those at high disturbance (Fig. 2-3), b) exclusion of some species or community types found only at low disturbance, and c) proportionally fewer native species(Catford et al., 2012) (Fig. 2-4B). Thus, I strongly suggest any management application of this work take into consideration the overall species composition across the study area, and not focus solely on species richness levels in individual plots. Because disturbance was more strongly correlated with and better predicted richness of exotics than natives (SI), management efforts aimed exclusively at maximizing species richness could have a greater impact on exotic species than natives. I found that although human disturbance significantly predicted native species richness ($r^2 = 0.104$, $p < 0.001$), the interactive effects of disturbance and exotic species richness explained nearly twice as much variation in native richness as did disturbance alone ($r^2 = 0.206$, $p < 0.001$). Efforts to conserve native species diversity should therefore consider not only management of human disturbance, but also the interactions of land use and exotic species, such as the roles of human disturbance in creating opportunities for exotic species establishment or acting as conduits for exotic dispersal(Catford et al., 2012, Didham et al., 2007). Catford et al.(Catford et al., 2012) suggest a range of management options informed by IDH and invasion patterns. However, the inconsistency in support and possible scale dependence of IDH warrant caution in its application. In the boreal biome, among the world's largest and most intact terrestrial ecoregions, the IDH may serve as a starting point for understanding how continued expansion of human activities may affect local plant communities.

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Figures

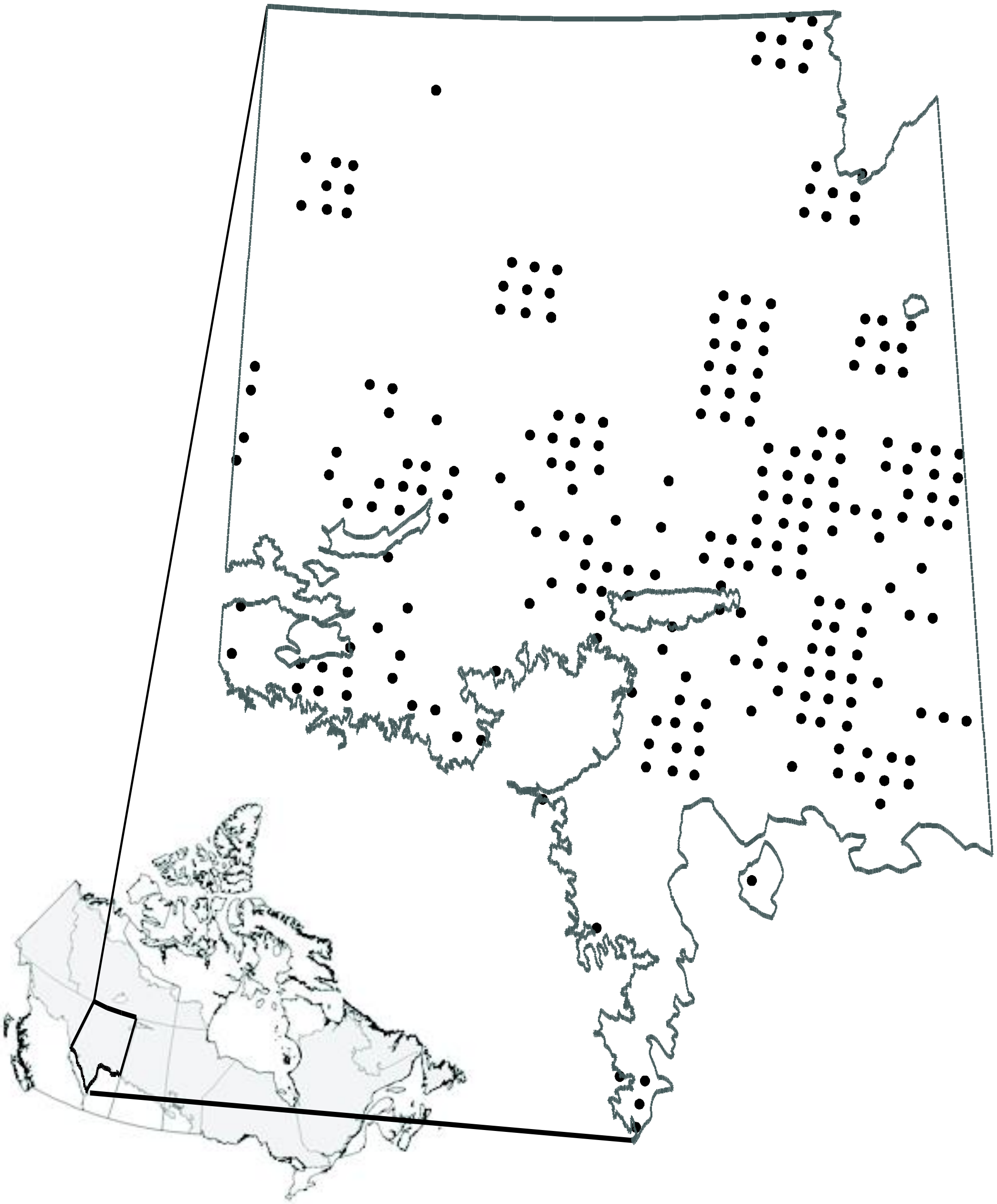

Fig. 2-1. Map of the 242 sampling site locations within boreal ecoregion of Alberta, Canada. Inset map shows Canada with boreal region shaded.

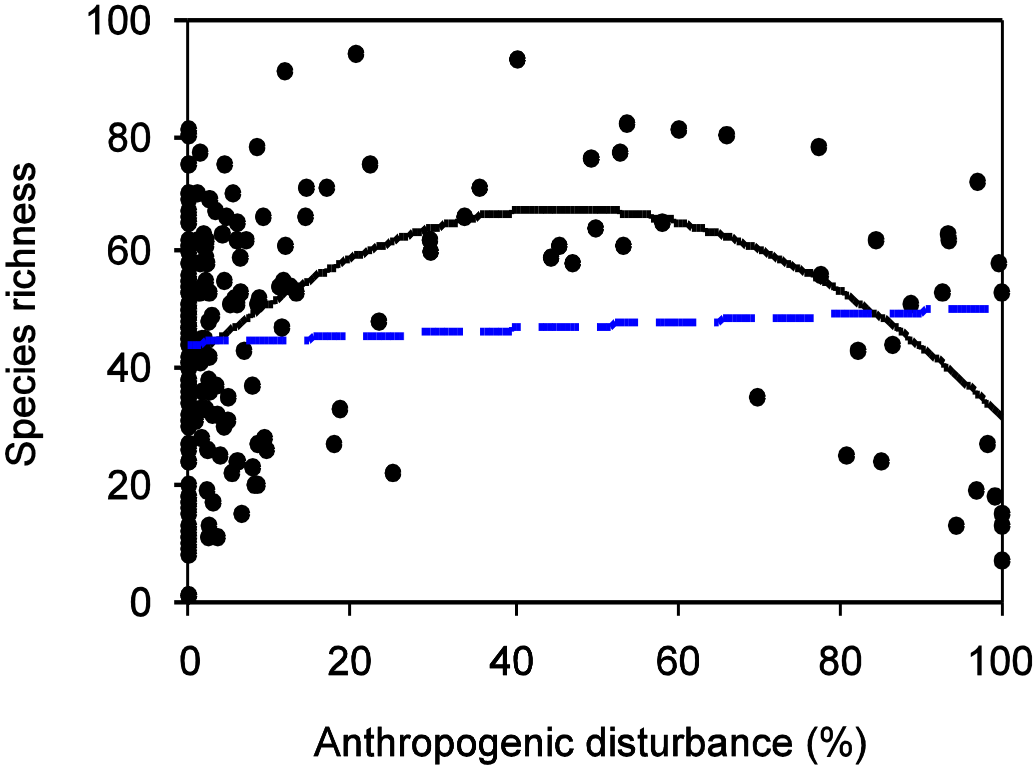

Fig. 2-2. Species richness per ha of boreal vascular plants as a function of percent total anthropogenic disturbance extent. The black solid curve represents the adopted model, a quadratic curve (n = 242, p < 0.001), which supports the intermediate disturbance hypothesis.

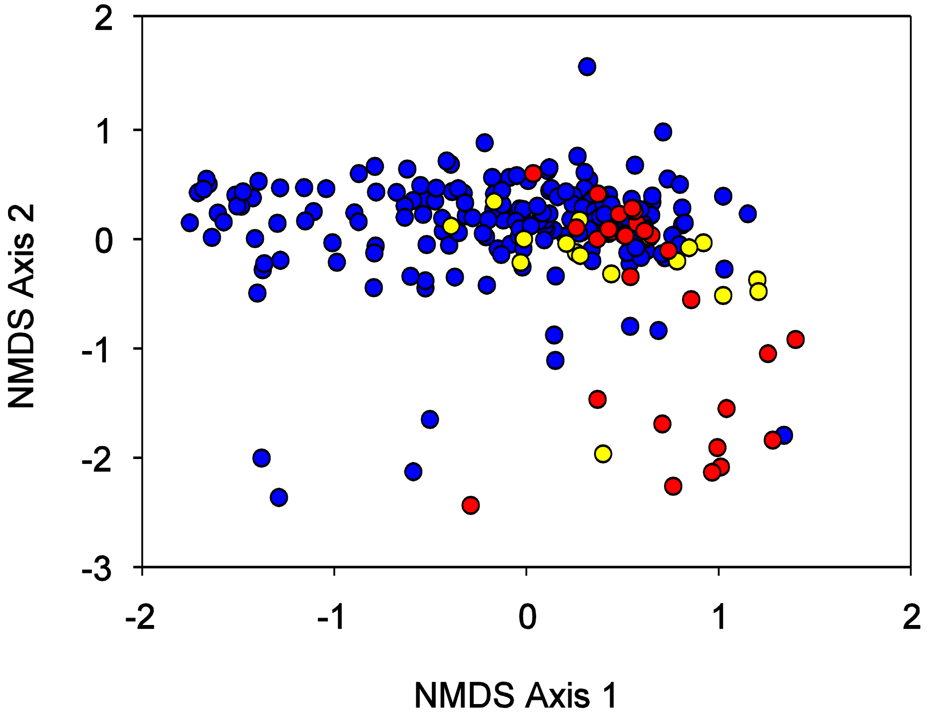

Fig. 2-3. Non-metric multidimensional scaling (NMDS) ordination of species composition across sites. Each point represents a sample site and each site is classified by percent human disturbance (blue: < 33.3 %, yellow: 33.4 – 66.6 %, red: > 66.7 %). Overlap of sites in different disturbance levels indicates similarity in species composition between those levels. The axes are unitless.

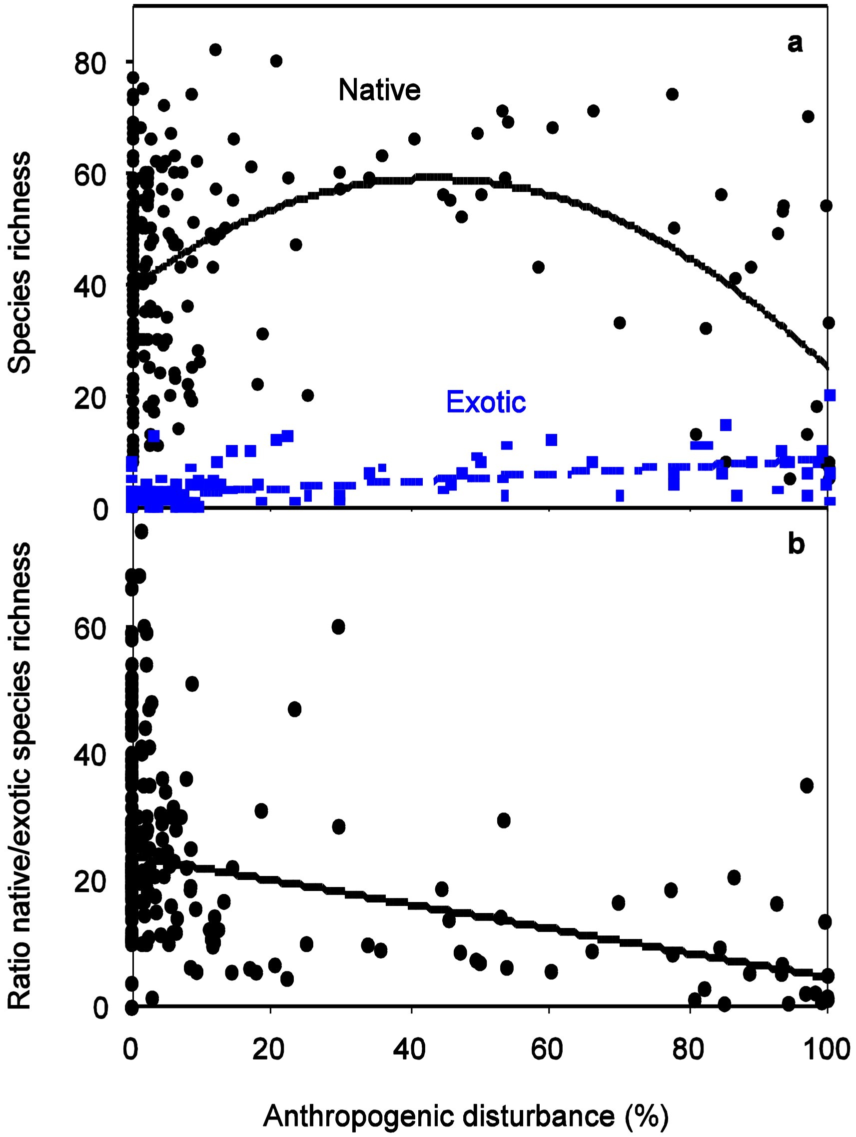

Fig. 2-4. Comparison of species richness per ha of native and exotic boreal vascular plants in relation to percent anthropogenic disturbance extent. **(a)** Native (black circles) and exotic (blue squares) species richness as a function of disturbance extent. A quadratic model fit (solid black curve) native species richness with its peak at intermediate disturbance (n = 237, $p < 0.001$), whereas a linearly increasing model (dashed blue line) fit exotic species richness over human disturbance (n = 237, $p < 0.001$). **(b)** Ratio of native to exotic species richness as a function of disturbance extent decreased linearly.

Supplementary Information

Table 2-S1. Comparison of regression model shapes of the species richness - human disturbance relationship.

Model	Response	Estimate	df	r^2	p	*p* of increase in r^2 of quadratic over linear model	AIC score
Linear	Intercept	44.286	241	0.007	< 0.001*		2149.89
	HD	0.061			0.202		
Quadratic	Intercept	40.989	240	0.135	< 0.001*	< 0.001*	2120.47
	HD	1.145			< 0.001*		
	HD^2	-0.012			< 0.001*		
Cubic	Intercept	41.330	239	0.136	< 0.001*	0.55	2120.22
	HD	0.940			0.017*		
	HD^2	-0.006			0.627		
	HD^3	0.000			0.554		

Table 2-S2. Comparison of model shapes of native and exotic species richness in relation to human disturbance.

	Model	Equation	p	df	p of increase in r^2 of quadratic over linear model	r^2	AIC score
Native species richness	Linear	$y = -0.028x + 42.991$	0.529	236		0.002	2070.863
	Quadratic	$y = -0.010x^2 +0.849x + 40.268$	< 0.001*	235	< 0.001*	0.104	2047.169
	Cubic	$y = 0.539x + 40.790$	<0.001*	234	0.423	0.107	2048.217
Exotic species richness	Linear	$y = 0.067x + 1.821$	< 0.001*	236		0.371	1072.585
	Quadratic	$y = -0.001 + 0.157 + 1.546$	< 0.001*	235	0.082*	0.378	1073.469
	Cubic	$y = -0.002x2 + 0.201x + 1.472$	< 0.001*	234	0.865	0.379	1085.678

Table 2-S3. Comparison of model shapes of species richness of individual plant growth forms in relation to human disturbance.

	Model	Equation	% human disturbance at peak richness	*p*	df	*p* of increase in r^2 of quadratic over linear model	r^2	AIC score
Forb species richness	Linear	$y = 0.063x + 22.670$		0.02*	240		0.023	1831.199
	Quadratic	$y = -0.007x2 + 0.651x + 19.94$	46.50	< 0.001*	239	< 0.001*	0.149	1801.118
	Cubic	$y = -0.013x2 + 0.863x + 1.938$		< 0.001*	238	0.28	0.153	1801.939
Graminoid species richness	Linear	$y = 0.038x + 4.496$		< 0.001*	240		0.069	1332.39
	Quadratic	$y = -0.003x^2 + 0.275x + 3.401$	45.83	< 0.001*	239	< 0.001*	0.234	1289.021
	Cubic	$y = -0.001x2 + 0.0.218x + 3.555$		< 0.001*	238	0.38	0.236	1290.243
Shrub species richness	Linear	$y = -0.035x + 16.969$		0.027*	240		0.021	1582.119
	Quadratic	$y = -0.002x^2 + 0.200x + 15.880$	50.00	< 0.001*	239	< 0.001*	0.080	1569.723
	Cubic	$y = -0.005x2 + 0.268x + 15.700$		< 0.001*	238	0.57	0.081	1571.395
Tree species richness	Linear	$y = -0.007 + 6.719$		0.30	240		0.005	1215.346
	Quadratic	$y = -0.001x^2 + 0.091x + 6.263$	45.5	< 0.001*	239	< 0.001*	0.055	1205.203
	Cubic	$y = -0.001x2 + 0.009x + 6.279$		0.005*	238	0.912	0.055	1207.191

Table 2-S4. Explanatory variables included in this study. All measures observed or estimated at site centre or within entire local 1 ha site, unless otherwise noted. Details are available from the Alberta Biodiversity Monitoring Institute.

Variable	Description
Human disturbance	Proportion of area altered by human land use as assessed with aerial and satellite imagery of 150 m radius circular areas
Temporary human disturbance	Proportion of area altered by temporary human land use (e.g. forestry, pipelines, seismic lines) relative to area with no human land use, within 150 m radius circular areas.
Natural subregion	Ecological classification of geographic units within the boreal ecoregion based on landscape patterns in climate, physiographic features, vegetation, soil, wildlife and land use attributes(Natural Regions Committee, 2006)
Latitude	
Longitude	
Elevation	
Topographic heterogeneity	Index of topographic ruggedness, expresses spatial variation in elevation(Riley et al., 1999)
Growing degree days	Heat accumulation, or annual sum of mean daily temperature degrees > 5 °C
Mean annual temperature	Estimated by Alberta Climate Model(Alberta Environment, 2005) based on climatological records of Environment Canada
Mean annual precipitation	Estimated by Alberta Climate Model(Alberta Environment, 2005) based on climatological records of Environment Canada
Terrain wetness	Terrain based site wetness derived from digital elevation model using moisture flows and retention(Gessler et al., 2000)
Site wetness	Observed proportion of 1 ha area in wetland
Solar flux	Estimated annual solar irradiance (MJ/cm^2)(McCune, 2007)
Canopy closure	Mean amount of sky obscured by canopy using densitometer at 8 specific points in local site
Oldest tree age	Age of oldest tree determined by tree core/growth ring analysis
Organic depth	Mean depth of organic soil layer (cm)
Soil type	Dominant soil sub-order classification in local site
Surficial geology	Dominant geological classification of surficial materials in local site
Slope position	Index of topographic position on slope based on elevation(Jenness, 2006)
Landform classification	General shape of landscape feature, such as upland drainage or local ridge (Jenness, 2006)

Table 2-S5. Comparison of quadratic and linear model shapes of the species richness-human disturbance relationship when controlling for environmental variables. Models are saturated forms of negative binomial generalized linear models with log link. Simple quadratic model with no control for environmental variables shown for comparison. Variables described in Table 2-S4.

Model	Response	Estimate	df	r^2	p	AIC score
Linear	Intercept	1121.000	96	0.658	0.014*	1220.943
	Human Disturbance	-0.017			0.780	
	Natural sub-region [Central Mixedwood]	14.050			0.231	
	Natural sub-region [Dry Mixedwood]	1.443			0.916	
	Natural sub-region [Lower Boreal Highlands]	19.190			0.150	
	Natural sub-region [Northern Mixedwood]	-13.480			0.627	
	Natural sub-region [Upper Boreal Highlands]	31.960			0.058	
	Latitude	-11.050			0.071	
	Longitude	-0.192			0.872	
	Elevation	-0.059			0.207	
	Topographic heterogeneity	3.541			0.004*	
	Topographic heterogeneity ^{2}	-0.218			0.005*	
	Topographic heterogeneity ^{3}	0.003			0.011*	
	Growing Degree Days > 5°C	-0.040			0.613	
	Mean Annual Temperature	1.275			0.890	
	Mean Annual Temperature ^{2}	-0.800			0.593	
	Mean Annual Precipitation	-1.880			0.023*	
	Mean Annual Precipitation ^{2}	0.002			0.031*	
	Terrain Wetness	0.596			0.562	
	Site Wetness	0.155			0.390	
	Site Wetness ^{2}	-0.002			0.382	
	Solar Flux	84.140			0.559	
	Canopy Closure	0.755			0.003*	
	Canopy Closure ^{2}	-0.009			0.000*	
	Tree Age	0.030			0.454	
	Organic Depth	-0.094			0.017*	
	Soil Type [Brunisolic Gray Luvisol]	33.740			0.122	
	Soil Type [Cryosols]	8.866			0.652	

	Soil Type [Dark Gray Chernozemic Luvisol]	26.530			0.080	
	Soil Type [Dystric Brunisol]	15.500			0.141	
	Soil Type [Eutric Brunisol]	12.020			0.519	
	Soil Type [Gleysol]	18.840			0.112	
	Soil Type [Gray Luvisolic Solonetz]	29.550			0.006*	
	Soil Type [Organic]	24.020			0.025*	
	Soil Type [Regosols]	36.830			0.094	
	Geology [Eolian]	5.626			0.863	
	Geology [Glaciofluvial Plain]	-5.057			0.875	
	Geology [Lacustrine Coarse]	8.319			0.799	
	Geology [Lacustrine Fine]	-5.224			0.871	
	Geology [Organic]	2.165			0.947	
	Geology [Till Blanket]	2.232			0.945	
	Geology [Till Veneer]	-6.146			0.858	
	Slope Position [Midslope]	5.396			0.876	
	Slope Position [Toe Slope]	-9.530			0.242	
	Slope Position [Upper Slope]	-2.746			0.744	
	Slope Position [Valley]	-269.700			0.136	
	Landform Class [Mountain Ridge Top]	7.557			0.697	
	Landform Class [Open Slope]	2.188			0.952	
	Landform Class [Plain]	-9.549			0.516	
	Landform Class [Upper Slope]	-7.722			0.606	
	Landform Class [U-shaped Valley]	-8.970			0.529	
Quadratic	Intercept	729.100	95	0.709	0.091	1199.271
	Human Disturbance	0.774			< 0.001*	
	(Human Disturbance)^2	-0.009			< 0.001*	
	Natural sub-region [Central Mixedwood]	8.268			0.451	
	Natural sub-region [Dry Mixedwood]	-2.933			0.817	
	Natural sub-region [Lower Boreal Highlands]	13.480			0.277	
	Natural sub-region [Northern Mixedwood]	-9.594			0.709	
	Natural sub-region [Upper Boreal Highlands]	30.270			0.053	
	Latitude	-4.339			0.460	
	Longitude	0.594			0.597	
	Elevation	-0.035			0.419	
	Topographic heterogeneity	3.760			0.001*	

Topographic heterogeneity ^{2}	-0.237	0.001*
Topographic heterogeneity ^{3}	0.003	0.002*
Growing Degree Days > 5^{o}C	-0.011	0.884
Mean Annual Temperature	5.104	0.552
Mean Annual Temperature ^{2}	-1.698	0.229
Mean Annual Precipitation	-1.956	0.011*
Mean Annual Precipitation ^{2}	0.002	0.015*
Terrain Wetness	0.700	0.463
Site Wetness	0.127	0.449
Site Wetness ^{2}	-0.001	0.435
Solar Flux	189.900	0.165
Canopy Closure	0.625	0.009*
Canopy Closure ^{2}	-0.007	0.001*
Tree Age	0.027	0.467
Organic Depth	-0.097	0.009*
Soil Type [Brunisolic Gray Luvisol]	24.040	0.237
Soil Type [Cryosols]	11.140	0.541
Soil Type [Dark Gray Chernozemic Luvisol]	29.340	0.038*
Soil Type [Dystric Brunisol]	17.590	0.073
Soil Type [Eutric Brunisol]	15.280	0.377
Soil Type [Gleysol]	17.970	0.103
Soil Type [Gray Luvisolic Solonetz]	29.000	0.004*
Soil Type [Organic]	24.820	0.013*
Soil Type [Regosols]	39.490	0.054
Geology [Eolian]	17.720	0.560
Geology [Glaciofluvial Plain]	0.507	0.986
Geology [Lacustrine Coarse]	19.240	0.528
Geology [Lacustrine Fine]	8.472	0.779
Geology [Organic]	14.290	0.639
Geology [Till Blanket]	14.070	0.643
Geology [Till Veneer]	7.645	0.812
Slope Position [Midslope]	-6.369	0.843
Slope Position [Toe Slope]	-6.636	0.381
Slope Position [Upper Slope]	-1.464	0.851
Slope Position [Valley]	-366.500	0.031*
Landform Class [Mountain Ridge Top]	13.160	0.466
Landform Class [Open Slope]	23.540	0.489
Landform Class [Plain]	-7.202	0.598
Landform Class [Upper Slope]	-5.849	0.674

	Landform Class [U-shaped Valley]	-6.963			0.598	
Quadratic	(Intercept)	40.417	144	0.137	< 0.001*	1260.995
	Human Disturbance	1.001			< 0.001*	
	(Human Disturbance)^2	-0.011			< 0.001*	

Table 2-S6. Comparison of model shapes of the species richness - temporary human disturbance relationship.

Model	Equation	df	r^2	*p*	*p* of increase in r^2 of quadratic over linear model	AIC score
Linear	$y = 0.063x + 22.670$	235	0.071	< 0.001*		2065.13
Quadratic	$y = -0.008x^2 + 0.885x + 41.936$	234	0.114	< 0.001*	< 0.001*	2056.08
Cubic	$y = -0.014x^2 + 1.065x + 14.670$	233	0.115	< 0.001*	0.630	2057.85

Chapter 3: Scaling disturbance instead of richness to better understand anthropogenic impacts on biodiversity

Abstract

Rising concern of decreasing global biodiversity driven by human activity merits a better understanding of how species diversity and anthropogenic disturbance are related. A primary impediment to this understanding is that both diversity and disturbance can depend on the scales at which they are sampled. While the scale dependence of diversity estimation has received substantial attention, the scale dependence of disturbance estimation has been essentially overlooked. Here, I break from conventional examination of the diversity-disturbance relationship by holding the area over which species richness is estimated constant and instead manipulating the area over which human disturbance is measured. I test the dependence of species richness on disturbance scale, the scale-dependence of the intermediate disturbance hypothesis, and the consistency of these patterns in native versus exotic species and among human disturbance types. I investigate boreal vascular plant communities in the boreal forest ecoregion of Alberta, Canada (381 047 km^2). I employ generalized linear models relating field estimates of species richness in 1 ha surveys of 372 boreal vascular plant communities to remotely sensed measures of human disturbance extent at two survey scales: local (1 ha) and landscape (18 km^2). Species richness-disturbance relationships were quadratic at local and landscape scales of disturbance measurement. However, predicted species richness varied significantly at moderate to high disturbance extents. In the extreme, richness could be twice as great when estimated from high local disturbance as from high landscape disturbance. Richness-disturbance relationships were also contingent on disturbance types, and native and exotic species showed different patterns. The shapes of richness-disturbance relationships were generally consistent across scales, supporting the intermediate disturbance hypothesis. However, predictions of species richness depended on scale of disturbance measurement. The observed dependence of species richness on disturbance at multiple scales suggests that

indirect landscape-level processes (e.g. dispersal) influenced by disturbance and direct disturbance of local conditions can both impact biodiversity of local communities.

Introduction

The ongoing decline of global biodiversity must be met with a greater understanding of how species diversity and human disturbance are related. A primary impediment to this understanding is that assessments of both diversity and disturbance can depend on scale. Neither diversity nor disturbance are uniformly or randomly distributed in space, so scale dependency of both these variables are predictable features of most systems (Greig-Smith, 1979, Lindenmayer and Fischer, 2006). The concept of scale is thus a cornerstone in many areas of biodiversity theory and conservation (Table 1).

Scale dependence of species richness has long been recognised and has received extensive attention over many decades (Austin and Greig-Smith, 1968, De Candolle, 1855, Desmet and Cowling, 2004, Gleason, 1925, Goodall, 1952, Greig-Smith, 1964, Jaccard, 1902). Perceptions of the species-area relationship (SAR) have ranged from a "statistical artefact" (Connor and McCoy, 1979), a "useful tool for exploring other patterns of biological diversity" (Lomolino, 2005), p.2), to a "fundamental pattern of nature" (Lomolino and Weiser, 2001) that is "one of community ecology's few general laws" (Schoener, 1976), p. 629). The SAR was a central concept incorporated into theories like Island Biogeography (MacArthur and Wilson, 1967) and in our understanding of processes such as habitat fragmentation (Fahrig, 2003). Research on SAR and IBT has been fueled in part by their application to conservation problems. These ideas have formed the foundation of global extinction rate estimation (He and Hubbell, 2011, Pimm and Raven, 2000), biodiversity hotspot identification (Myers et al., 2000), and protected area design (Soule and Simberloff, 1986, Wilcox and Murphy, 1985)

Despite these many applications of the scale dependence of richness to conservation biology, I offer a new approach unlike those presented in Table 1. Why? Investigation of the scale dependence of the diversity-disturbance relationship has been highly skewed to one side of the diversity-disturbance equation: the focus has been on scale dependence of diversity, while the scale dependence of disturbance has been largely overlooked. Investigations have manipulated either the scale at which species richness is measured, or the scales of richness and disturbance are manipulated together. But the scale at which disturbance is measured is rarely manipulated alone, so the potential influence of variation in disturbance across scales on species richness is largely unknown. Here, I control the scale at which I measure species richness while manipulating the scale at which I measure disturbance. I anticipate new insights from this novel perspective on examining the fundamental relationship of between richness and disturbance.

The relationship of diversity to the *scale of disturbance estimation or measurement* (e.g. sample extent, temporal range, range of intensities, etc.) should not be confused with the relationship of diversity to the *scale of disturbance itself* (e.g. spatial extent, duration, frequency, intensity, etc., Fig. 3-1). The latter has garnered much attention, but my focus here is on the former. Among the most prominent theories of the response of richness to disturbance is the intermediate disturbance hypothesis (IDH). The IDH predicts that species richness should show a unimodal relationship to disturbance, such that richness is maximal at moderate extents of disturbance (Connell, 1978). By contrast, habitat loss and fragmentation studies typically predict declines in richness within remaining patches as disturbance increases (Fahrig, 2003) and positive richness-disturbance relationships have also been observed (Mackey and Currie, 2001).

In these cases, the possible dependence of species richness on scale at which disturbance is evaluated is rarely considered. The same is true in many areas of biodiversity research: the measurement scale of disturbance (as opposed to extent of disturbance itself) is neglected or given little attention (Table 1). It is therefore unclear how the richness-disturbance relationship should vary with scales of disturbance. However, because many ecological processes influenced by disturbance vary with scale (Blackburn and Gaston, 2002, Levin, 1992), I predict that species richness will be sensitive to disturbance scale. For example, if human disturbance impacts environmental filtering of species, I expect species richness to be related to local disturbance of environmental conditions. But if disturbance alters dispersal or connectivity, I expect disturbance in the broader landscape to be related to species richness.

Here, I determine the relationship between species richness of boreal vascular plants and human disturbance extent where disturbance is measured at two spatial scales: local and landscape. My study provides a test of the IDH at multiple disturbance scales. I recently showed that species richness can exhibit a hump shaped relationship to disturbance extent (Mayor et al., 2012), but little is understood of how this relationship may depend on the scale at which disturbance is measured. Following that study, I used samples of richness and human disturbance in 371 sites throughout the 381,047 km^2 boreal ecoregion of Alberta, Canada. IDH is rarely tested in relation to human disturbances in sites representing such a large region (Mayor et al., 2012, Shea et al., 2004). This region exhibited a large variety of human disturbance types, and disturbance varied from 0 to 100 percent at both local and landscape scales. I then compare the relative power of disturbance at each scale in explaining richness, and discuss possible mechanisms driving these results.

Methods

Vascular plant richness was surveyed in the boreal ecoregion of Alberta, Canada. I used data and the standardized protocols of Alberta Biodiversity Monitoring Institute (ABMI, 2009), and collected supplementary data at additional sites. Vascular plant species occupancy was surveyed within 1 ha for 90 min at a total of 372 sites (see Fig. 3-S1 in Supporting Information). I distinguished native and exotic species according to (ACIMS, 2011). Surveys were conducted between Jun 26 and Aug 18 of 2003 and 2011. Human disturbance extent was defined as proportion of land area converted by humans, and was assessed by manual interpretation of 1:30 000 aerial photos and SPOT satellite imagery at each site (ABMI, 2007). For each site, human disturbance extent was measured at two scales: 'local scale', the 1 ha square on which plant species were measured; and 'landscape scale', a 3 km x 6 km rectangle surrounding the 1 ha site (18 km^2, minus the central 1 ha; ABMI, 2007). Landscape scale disturbance excluded disturbance measured at the local scale (the 1 ha site); the local scale sample was not nested within the landscape scale. One can imagine schematically that the landscape scale sample was like a thick donut or ring with an empty centre, whereas the local scale sample was like a donut "hole" (or colloquially, like a "timbit"). Only the spatial extent of human disturbance was measured, not its intensity, frequency, or time since disturbance, all of which varied greatly within and among disturbance types. Disturbance types were categorized as agricultural (which included pasture and croplands), forestry cut areas (of varying age), hard linear features (permanent and intense; roads and railways), soft linear features (temporary disturbances which allow successional processes; pipelines, powerlines, and cutlines primarily for oil/gas exploration), and urban/industrial (urban and rural settlements, coal and mineral surface mines, oil and gas well pads, communication towers, gravel pits, spoil pads, and heavy oil sands development; (ABMI, 2007).

In interpreting the scale dependence of the species richness-disturbance relationship, I distinguished between two components of the relationship: a) *shape of model*, the difference in number of regression model parameters across local and landscape scales (e.g. linear versus quadratic) b) *predicted richness* of the model along the disturbance gradient (e.g. 20 versus 40 species with 75% disturbance at local and landscape scales, respectively). I used 95% confidence ellipses to determine if differences existed between predicted richness across scales.

To determine the best fit shape of the richness-disturbance relationships, I constructed generalized linear models (GLMs). Although richness-disturbance relationships are sometimes represented by simple regressions, the GLMs took the form of negative binomial regressions because the species richness data are counts and were overdispersed. Individual GLMs were constructed for local and landscape scales individually. I tested GLMs with one (linear), two (quadratic) and three (cubic) parameters. I only adopted higher parameter polynomial models when they were both significant (reported as "$p < 0.05$") and when they fit significantly better (by explaining significantly more variation) than the simpler model of fewer parameters, as diagnosed with an ANOVA of candidate models (reported as "p of increase in r^2 over linear model"). In all cases, that frequentist model selection protocol resulted in the same adopted model as with model selection by AIC (highest model likelihood, AIC weight > 0.5). Cubic models were never selected, so aren't reported. In Figs. 2-4, I exponentiated the (log-linear) negative binomial models so that they could be plotted on axes comparable to linear models, as they are customarily plotted.

To determine the best fit shape of richness-disturbance relationships while accounting for potentially confounding variables, I constructed GLMs and selected model shapes as above but included additional parameters. For human disturbance and each environmental covariate, I selected the best fitting linear or polynomial form. I used a subset of 192 sites for which data was available for 18 potentially confounding variables. I included in the models human disturbance plus the following: natural subregion type, latitude, longitude, elevation, topographic heterogeneity, growing degree days, mean annual temperature, mean annual precipitation, terrain wetness, site wetness, solar flux, canopy closure, oldest tree age, organic depth, soil type, surficial geology, slope position, and landform classification (see Table S2). Too few data were available to include natural disturbance (year of last fire and natural disturbance extent) in the models. Details of environmental variable observation and estimation are available at abmi.ca.

To determine if richness-disturbance relationships depended on disturbance types, I first determined the best fitting shape richness-disturbance GLM for each disturbance type at the local scale. I then used stepwise selection functions to assess the significance of each disturbance variable. I repeated this procedure for disturbance at the landscape scale (Fig. 3-4, Table S6). Next, I determined the best multi-scaled model of species richness in relation to disturbance by using stepwise selection functions with each disturbance type at each scale as candidate variables for inclusion (Table S7).

Results

Species richness of boreal vascular plants depended on the extent of human disturbance at multiple spatial scales (Fig. 3-2, Table S1). I observed statistically significant relationships ($p < 0.001$) when human disturbance was measured at local and landscape scales. Thus, species richness was not only affected by direct, local disturbance of vegetation, but by distant disturbances in the broader landscape (which excluded local disturbance). As expected, human disturbance was correlated across scales ($R = 0.465$), however the consistent dependence of richness on disturbance extent at each scale could not be explained by this relationship. A model including disturbance at both scales explained significantly more variation in richness ($R^2 = 0.226$, $p < 0.001$) than models of disturbance at either local ($R^2 = 0.108$) or landscape scale disturbance ($R^2 = 0.122$) individually.

The shape of the richness-disturbance relationship was also consistent across scales (Fig. 3-2, Table S1). When linear, quadratic, and cubic models were compared, quadratic relationships best fit species richness relative to disturbance extent regardless of the scale at which disturbance was measured. At each disturbance scale, species richness peaked at intermediate human disturbance extent (Fig. 3-2, Table S1). Both frequentist (p-values) and AIC approaches resulted in the same model being selected in all cases.

Species richness was influenced by many factors besides disturbance, and many of these factors were correlated (Table S3). When I accounted for these potentially confounding variables, the percentage total human disturbance extent at the local scale was still significantly related to richness by a quadratic function ($p = 0.032$) which fit significantly better than a linear model ($p = 0.032$, Table S4). At the landscape scale however, total human disturbance was unrelated to richness ($p = 0.120$). There are several reasons however, why the effects of disturbance were lower than without accounting for those variables and why disturbance impacts may be underestimated. First, by accounting for these variables, I effectively assumed that disturbance was driven by those variables. Variables such as latitude, natural subregion, soil type, and climate related variables may influence where humans use land. However, several variables such as canopy cover, depth of organic soil, terrain wetness may instead have been effects of disturbance, so factoring them out could have masked those effects. Second, human disturbance was only considered as a total percentage of any type of disturbance, but disturbance types differed in intensity, frequency, permanence, and other characteristics. Models which included all environmental covariates explained more variability in richness when disturbance types were categorized and treated as individual parameters (R^2 =0.768) than when disturbance was considered a total (R^2 = 0.738). Third, because environmental data were unavailable for 176 sites (of 367 sites), I excluded those sites from analyses using environmental covariates.

Unlike the *shape* of the richness-disturbance relationships, the *number of species* predicted by richness-human disturbance extent relationships depended strongly on the scale at which disturbance was measured (Fig. 3-2). At low to moderate human disturbance (< 45 %), species richness predictions were statistically indistinguishable across scales of disturbance. However, at moderate to high disturbance, predicted richness was higher when disturbance was measured at the local scale than at the landscape scale (Fig. 3-2). Species richness was predicted to be 44 species at 100 % local disturbance, but only 21 at 100 % landscape disturbance, a two-fold difference. Species richness varied most with disturbance extent at the landscape scale, where predicted richness ranged from 21 to 57 species. Predicted species richness ranged from 44 to 68 depending on local disturbance.

Native and exotic species differed in their response to disturbance in several ways. Native species richness was quadratically related to human disturbance extent at all scales (Fig. 3-3, Table S5). However with landscape disturbance—which explained more variation in native species richness than did local disturbance ($p < 0.001$)—richness decreased significantly more at greater disturbance extent and approached zero species at 100 % landscape disturbance. Native species richness peaked at 46.1 % local disturbance but only 28.7 % landscape disturbance (Fig. 3-3). Native richness predicted by 100 % disturbance at the local scale was 35.9 species, very close to the 42.0 native species expected with no disturbance, but with 100% disturbance at the landscape scale only 1.4 species were predicted (Table S5).

Exotic species richness by comparison showed different shaped richness-disturbance relationships at local and landscape scales (Fig. 3-3, Table S5). With locally measured disturbance, the relationship was concave down, but with landscape level disturbance the exotic richness-disturbance relationship was concave up (Fig. 3-3). Despite the curvilinear shapes of these relationships, they both tended to increase with disturbance extent and never peaked. Predicted exotic richness at 100 % disturbance extent was 6.7 with local disturbance, nearly half the 13.2 exotic species expected with landscape disturbance (Table S5).

Species richness-disturbance relationships also varied by disturbance type (Fig. 3-4, Table S6-S7). Agricultural disturbance explained the most variation in richness among disturbance types, regardless of whether that disturbance was local or at the landscape scale. Species richness was locally affected significantly by all anthropogenic disturbance types. At the landscape scale, the only anthropogenic disturbance type significantly explaining species richness was agriculture, with the exception of roads and rail, which covered a very small area of the landscape. Although species richness appeared to linearly increase with non-agricultural local disturbances, too few sites exhibited high disturbance extent of these types for the relationship to be considered reliable at high disturbance.

The complete saturated model, accounting for environmental variables and considering disturbance types individually, explained more than three quarters of the variation in species richness ($R^2 = 0.768$, $p < 0.001$).

Discussion

Local richness depended on disturbance extent at multiple scales

The results show that species richness can depend on multiple spatial scales of anthropogenic disturbance. Richness of boreal vascular plants was partly explained by direct local disturbance and disturbance in the broader landscape up to 3 km away. These multi-scaled effects of disturbance on species richness were evident when local and landscape areas of disturbance estimation were non-overlapping, non-nested, and with relatively low correlation in disturbance across scales. Because the two scales at which disturbance was measured offered quantitatively different information, the similarity in shapes of richness-disturbance relationships between scales of disturbance cannot be attributed simply to propagation of patterns at the local scale to the landscape scale or vice versa (sensu Wiens, 1989). Including disturbance at both scales explained nearly double the variation in richness ($R^2 = 0.226$) as did either scale individually.

Local human disturbance may alter species richness by a combination of factors: i) direct removal of individuals; ii) direct and indirect alteration of abiotic environmental conditions like sunlight, moisture, and soil characteristics; iii) prevention or inhibition of successional processes by permanent structures or frequent disturbances (e.g. semi-annual tilling, mowing, or brush clearing); iv) indirect alteration of biotic interactions (e.g. herbivory, pollination, competition).

The importance of landscape disturbance outside or surrounding communities or areas of interest has long been recognised and is a hallmark of habitat loss and fragmentation studies. Over 50 years of study have revealed that species richness in habitat patches depends on: i) patch area; ii) edge effects, which alter area of 'interior' habitat; iii) biological area effects, such as when patches are too small to support species with large ranges; iv) extirpation cascades, due to impacts on species interactions or extirpation of keystone species; v) patch isolation, due to limitations on dispersal (Debinski and Holt, 2001, Fahrig, 2003, Harrison and Bruna, 1999). Despite these lessons, which often make use of the 'scale' concept, habitat loss and fragmentation studies have not yet provided a basis for predicting richness-disturbance relationships across scales.

Metacommunity theory (Holyoak et al., 2005, Leibold et al., 2004, Wilson, 1992) and its progenitors like island biogeography (Harris, 1984, MacArthur and Wilson, 1967, Simberloff, 1974), fragmentation (Fahrig, 2003) and source-sink dynamics (Dias, 1996, Eriksson, 1996, Pulliam, 1988), invasion ecology (Elton, 1958, Levine and D'Antonio, 1999, Lockwood et al., 2007), and the intermediate disturbance hypothesis (Connell, 1978) help explain conceptually why species richness is affected by disturbance at broader (e.g. landscape) scales. Ecological processes that connect these ideas, like dispersal and isolation, seed rain and propagule supply (Blackburn and Duncan, 2001, Lockwood et al., 2005, Wagner, 1965), succession(Clements, 1916, Connell and Slatyer, 1977, Denslow, 1980, Glenn-Lewin et al., 1992), and the role of environmental heterogeneity (Ricklefs, 1977) and 'matrix habitat' may all contribute to observed relationships.

The concept of disturbance, which is a process but measured here as a proportion of spatial area, is strongly related in practice to environmental heterogeneity. For example, if one considers disturbed area and non-disturbed area as separate "environments" with different sets of species, then 50 % disturbance added to an intact landscape necessarily would maximize heterogeneity, all else being equal, and in turn maximize species richness. Viewing disturbance as a generator of heterogeneity of environmental conditions is a key part of Connell's (1978) IDH. What this leaves out is the underlying mechanism driving IDH, how disturbance creates multiple environments conducive to different sets of species. A commonly invoked mechanism is a trade-off between competitive species traits and colonization-oriented traits, which are favoured in different environmental conditions, with disturbance facilitating species with colonization-oriented traits (Connell, 1978). I did not test this mechanism against others directly, but species trait diversity is explored further in Chapter 4.

Human disturbance was correlated with many abiotic environmental variables (Table S3) and accounting for these variables significantly reduced the proportion of variance explained by disturbance to $R^2 = 0.027$ (Table S4). One might conclude that abiotic variables, not disturbance, drove the observed richness patterns. This situation could result if human disturbances depended on abiotic variables such as latitude. However, I suggest instead that disturbance may also reasonably be expected to alter abiotic environmental variables.

Scale invariant shape of richness-disturbance relationships supports intermediate disturbance hypothesis

The richness-disturbance relationships fit quadratic models at each scale of disturbance, suggesting that the unimodal shaped pattern is robust to sampling scale (Fig. 3-2). I also previously found a unimodal richness-disturbance relationship with disturbance measured at a scale between the local and landscape

(150 m radius circle, (Mayor et al., 2012). The consistent shape of the richness disturbance relationships provides strong multi-scale support for the IDH in this system.

Support for IDH across studies has been limited, with approximately 80% of empirical studies failing to support the hypothesis of peaked richness at intermediate disturbance (Mackey and Currie, 2001, Shea et al., 2004). Theoretical support based on a variety of ecological mechanisms has been stronger (Roxburgh et al., 2004, Shea et al., 2004), but these models have also been criticized (Fox, 2012). (Shea et al., 2004) suggested that the varying support for IDH may be related to study scale. Most previous studies of IDH have been conducted at relatively small spatial extents and small sampling grains. I previously showed support for IDH in this system (estimating disturbance extent at a scale of a 150m radius circle) and suggested that the unusually large regional extent of the study area may have contributed to this unusual finding (Mayor et al., 2012). The consistent support for IDH across scales in this boreal system, but inconsistent findings across other studies conducted at various scales highlight the complexity of scaling biodiversity and disturbance and the limitations of simple models.

Scales of ecological processes

The cross-scale similarity in shape of richness-disturbance relationships is surprising given my expectation of how local and landscape disturbances would affect richness differently. I expected scale-dependence because ecological processes potentially impacted by disturbance vary in the scales at which they operate. For instance, (Garcia and Chacoff, 2006) showed that different scales of decreases in forest cover drove changes in different functional processes such as pollination, frugivory, and seed predation. Similarly, direct habitat loss has a greater effect on species than does habitat fragmentation per se (Fahrig, 2003), but the effects of fragmentation increase with proportion of disturbed area (Andren, 1994). Even the local-regional relationship is dependent on sampling scale: it can appear saturated or not depending on the scale it is evaluated (He et al., 2005).

Can the scale at which disturbance is measured in richness-disturbance relationships help elucidate the processes structuring local plant communities? In the current study, dispersal of propagules may occur over very large distances across landscapes, whereas competition is most likely strongest at small, local scales (Menge and Olson, 1990). Coarse scale disturbance in the landscape therefore likely affects processes related to dispersal like external propagule supply and isolation of communities whereas fine scale local disturbance directly removes vegetation and alters environmental and soil conditions, acting as an environmental filter (Ozinga et al., 2005, Zobel et al., 2000).

Scale dependent predictions of richness from disturbance

Despite the qualitative similarity in shapes of richness-disturbance curves, I found contrasting results when these relationships were used to predict species richness. Predictions of species richness from disturbance extent depended strongly on the scale at which disturbance was measured (Fig. 3-2).

More than double the number of species (44) were predicted from 100 % local disturbance extent as from 100 % landscape disturbance (21 species, Fig. 3-2). The range in predicted species richness with landscape disturbance far exceeded the range predicted with local disturbance. This seems counterintuitive because I expected species richness to be more sensitive to direct, local disturbances of the local vascular plant community than to indirect disturbances surrounding or distant from the local community. The greater sensitivity of richness to landscape scale disturbance could reflect that a given percentage disturbance at that scale represents a much larger disturbed area than the same percentage at the local scale. In addition, only agricultural disturbances (which are intensive and perpetual) were proportionately extensive at the landscape scale, whereas more compact disturbances such as cutblocks or well pads contributed higher percentages of disturbance at the smaller local scale. The varying effects of disturbance types are elaborated upon below.

Native and exotic species

Native species and exotic species differed dramatically in their responses to disturbance (Fig. 3-3, Table 5). While native species richness showed a quadratic relationship to human disturbance extent at each scale, supporting the IDH at both scales, exotic richness increased with landscape scale disturbance without peaking, a pattern inconsistent with the IDH. Those differences in shape of response of native and exotics to disturbance were consistently observed across scales, but were more pronounced with landscape disturbance.

Predicted richness of each of these two groups both strongly depended on the scale at which disturbance was measured. Native species decreased to only 1.4 species with 100% landscape disturbance while maintaining 35.9 species with 100% local disturbance. Exotics, by contrast, rose from near zero species at 0 % disturbance at any scale to 6.7 species at 100 % local disturbance or 13.2 species at 100 % landscape disturbance. Where disturbance was high at either local or landscape scales, native species declined while exotic species richness increased (Fig. 3-3).

Disturbance type

Disturbance varied dramatically across study sites, both in extent and in type. When I separated the effects of various disturbance types, these models explained significantly more variation in richness ($R^2 = 0.307$, Fig. 3-4, Table S6-S7) than when considering the sum extent of disturbance ($R^2 = 0.226$). I observed that the disturbance types significantly impacting total species richness across sites depended on the scale at which disturbance was measured.

With landscape disturbance, only agriculture explained richness significantly, apart from some influence of roads and rail lines at < 9% disturbance extent. By contrast, richness was significantly explained by all observed disturbance types when measured locally, including forestry, soft and hard linear disturbances, and urban/industrial disturbance. Even at the local scale, however, most disturbance types only covered a small percentage of the sample areas of most sites, likely driving the linearly increasing, rather than quadratic, patterns of richness-disturbance relationships in Fig. 3-4. It should not be assumed from these data that species richness continually increases linearly with non-agricultural disturbance.

I suggest that the greater decreases in species richness with total landscape disturbance can be at least partially attributed to the intensive nature of agricultural land use relative to other disturbances such as forestry cut blocks or seismic lines, which more typically allow successional processes to take place. Had I measured disturbance at only the local scale, I would have overestimated the impact of temporary disturbances on richness, demonstrating the valuable insight gained by measurement of disturbance at multiple rather than single scales.

Implications for biodiversity management and conservation

One could argue that scales of the effect of disturbance on richness matter little to conservation practitioners because conservation decisions are rarely made on the basis of richness alone. However, (Hartley and Kunin, 2003) report that extinction risk of species and their relative priority for conservation are also affected by scale: biological conservation cannot escape the scale dependence of the biology it aims to conserve.

The current study has several lessons for conservation and management. First, the observed cross-scale impacts of human land use in this study suggest that assessments of environmental impacts or extirpation risks focussing only on direct, local human disturbance likely underestimate the cumulative impacts of disturbance at broader scales.

Second, the use of species area relationships as predictors of richness relative to disturbance is inadequate. Gains in disturbance may initially seem equivalent to the loss of area, but the two are not equivalent. Disturbance changes environmental conditions rather than removing the environment altogether. Altering the scale of richness and disturbance estimation together may lead to unexpected or nonlinear results because species richness and human disturbance may depend on scale in different ways.

Third, the consistent shape of richness-disturbance relationships and support for the intermediate disturbance hypothesis suggest that in this system, quadratic richness disturbance models can form a simple base level expectation in the absence of more specific information to guide land use planning and management decisions. However the dependence of predicted biodiversity on scale of disturbance estimation suggests predicting the richness-disturbance relationship is more complicated and may best be achieved by multi-scale models.

Conclusions

Dodds (2009, pg. 168) suggested that a primary impediment to applying the IDH is "how to scale disturbance for effect on communities," concluding that "I have no *a priori* method of scaling disturbance based on first principles." Here, I offer field results showing that biodiversity depends on multiple scales of disturbance with a predictable richness-disturbance shape. Still, the results suggest that richness-disturbance parameters depend on the scale at which they are measured. Just as there is no 'correct' scale at which to measure species richness (Levin, 1992), there is no single 'correct' scale to explore how disturbance affects richness. For example, (Huston, 1999) argued that local processes determine observed regional patterns in diversity, but I show here that landscape scale disturbance affects local diversity independent of local disturbance. The scale dependence of the richness-disturbance relationship is not simply a problem of 'scaling up' richness from sample areas to regions. Because human disturbance influences species richness at multiple scales—including scales much larger than those at which richness is measured—the seemingly arbitrary choice of scale at which to measure disturbance may determine expected values of richness.

I aimed in this study to expand our understanding of the richness-disturbance relationship beyond what could be learned from application of the SAR. An important feature of the SAR is that species richness depends not only on sample area, but that the slope of the SAR itself depends on scale; it varies from local to regional, to continental scales (Crawley and Harral, 2001). Similarly, the results suggest species richness depends on both disturbed area and on the scale over which disturbed area is measured. When scaling biodiversity to better understand impacts of human land use change, predictions may be aided by considering scales of both diversity and land use change.

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Table 3-1. Concepts of 'scale' in biodiversity research and conservation.

Pattern, process, or idea	Use of ‘scale’ concept	Implication for conservation	Key references
Species Area Relationship	Area of richness estimation	Larger areas harbour more species	(Crawley and Harral, 2001, Desmet and Cowling, 2004, Palmer and White, 1994)
Island Biogeography Theory	Area of island, distance to mainland	Larger islands, closer to immigration source, harbour more species	(Losos et al., 2010, MacArthur and Wilson, 1967, Whittaker and Fernández-Palacios, 2007)
Habitat loss and fragmentation	Area and insularity of remaining habitat	Larger and more connected patches harbour more species, landscapes with larger, more connected patches harbour more species	(Fahrig, 2003)
Extinction debt	Area and insularity of remaining habitat	Decline in species delayed following habitat loss or fragmentation	(Halley et al., 2013, Kuussaari et al., 2009, Tilman et al., 1994)
Extinction rate estimation	Area of richness estimation (or endemic richness estimation)	Species extinction is inverse of species area relationship (or endemic-area relationship)	(Kinzig and Harte, 2000, Pimm and Raven, 2000)
Biodiversity hotspots	Area of richness estimation	Areas with high density of species richness should be protected	(Myers et al., 2000)
Protected area design	Area and connectivity of reserve	More area protected with greater connectivity among areas may protect more species	(Wilcox and Murphy, 1985)
Local-regional relationships	Area of richness estimation at local and regional scales	Saturated communities can be more easily ‘represented’ in a protected area	(Caley and Schluter, 1997, Cornell and Lawton, 1992, He et al., 2005)
Intermediate disturbance hypothesis	Extent of disturbance	Areas with intermediate disturbance extent, frequency, or intensity harbour more species	(Connell, 1978)
Metapopulation & metacommunity dynamics	Area and insularity of populations or communities in a region	Regions with larger intact habitats and greater connectivity will harbour more species; Areas from which populations or communities are extirpated may be re-established	(Hanski and Hanski, 1999, Leibold et al., 2004)

Richness-disturbance scale relationship	Area of disturbance extent estimation	Areas with intermediate disturbance extent harbour more species, regardless of disturbance scale estimation; More species expected from locally measured disturbance Richness depends on both local disturbance disturbance in broader landscape	Current study

Figures

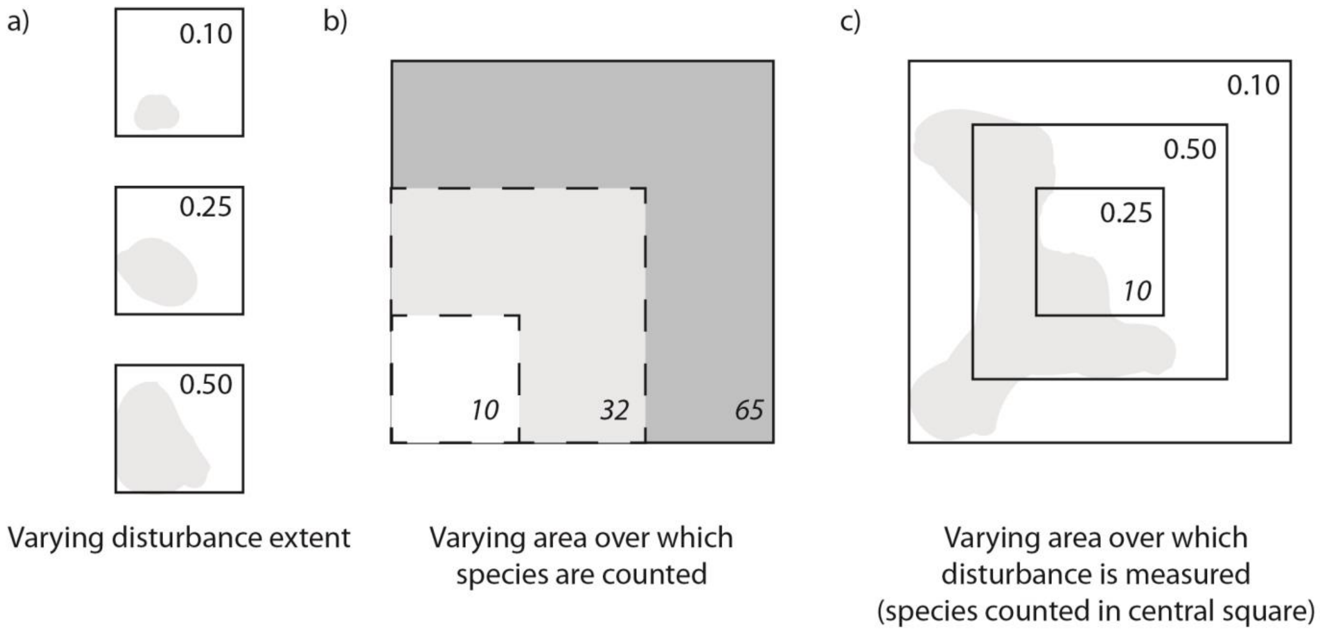

Fig. 3-1. Conceptual approaches to sampling for richness-disturbance relationships. Shading indicates disturbed areas, upper right numbers indicate approximate proportion of area disturbed, and lower right numbers in italics indicate number of species in associated area. In a) the sample area for both disturbance and species richness are identical and do not change, typical of 'habitat loss' studies. In b) the sample area over which species are counted varies, a strategy used to estimate the 'species area relationship'. The largest quadrat is the first sample, in which 65 species were hypothetically found. Dark shading indicates area lost (disturbed) from the first sample, leaving 32 species in the remaining areas. Light shading indicates area lost from the second sample, leaving only the white square area for the third sample, in which 10 species were found. In c) 10 species are counted only in the small central quadrat. Disturbance is first measured in that quadrat, in which a proportion of approximately 0.25 was observed. Disturbance is then measured in multiple larger quadrats, excluding the previous smaller quadrats to minimize dependence of disturbance from one measurement scale to another. This is the sampling approach I followed in the current study, but I measured disturbance at only two scales.

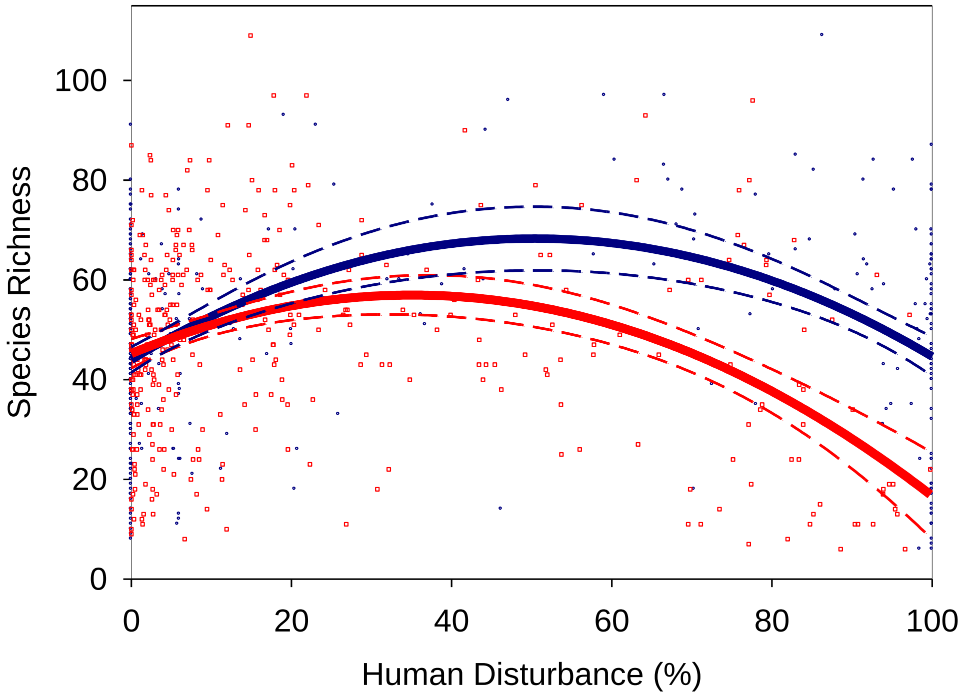

Fig. 3- 2. Vascular plant species richness relative to human disturbance extent measured at two scales. Dark blue circles indicate disturbance measured at local scale, red squares at the landscape scale. Corresponding coloured lines are quadratic regression lines of best fit.

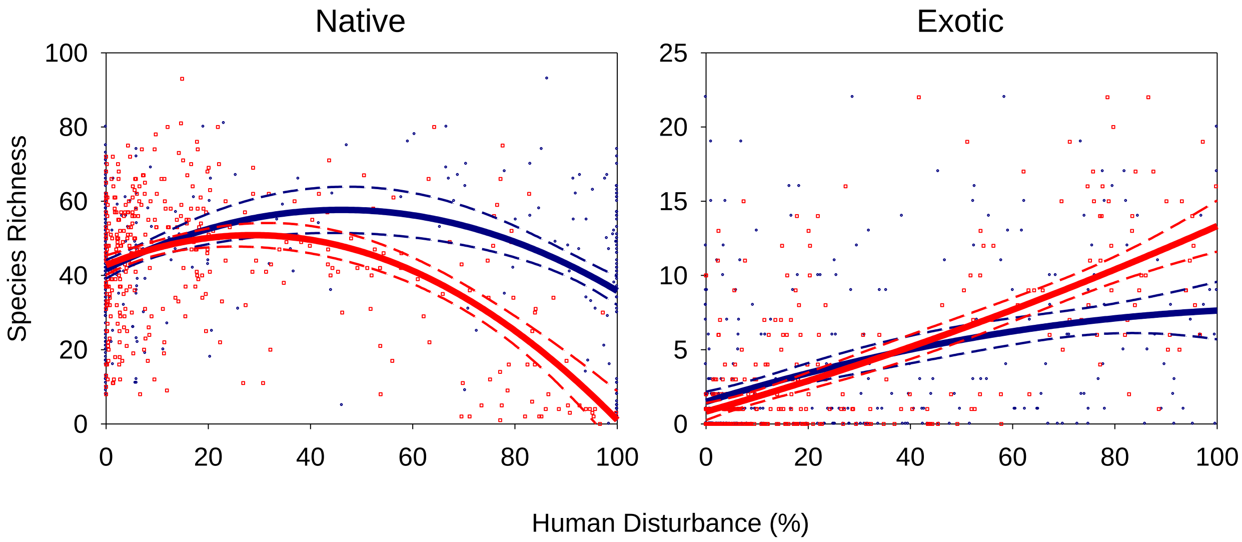

Fig. 3-3. Native and exotic species richness relative to human disturbance extent at two scales. Symbols and lines as in Fig. 3-2.

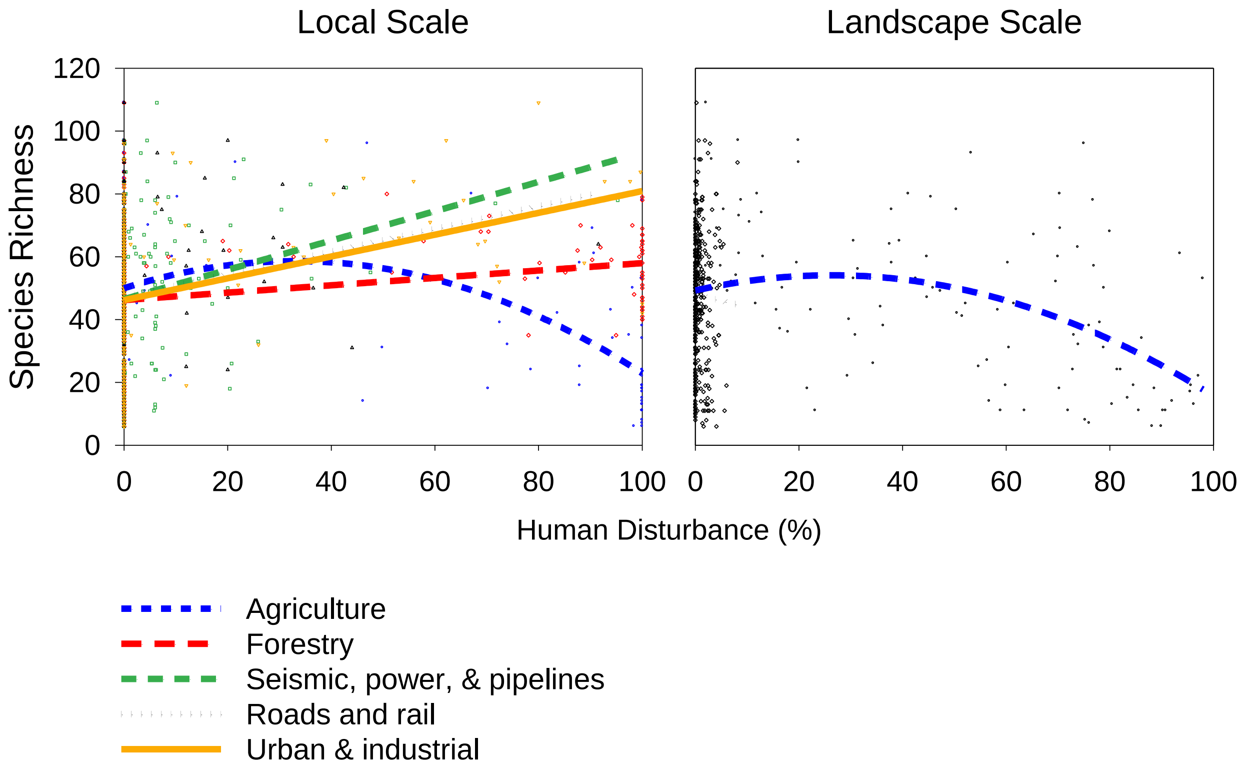

Fig. 3-4. Species richness relative to several types of human disturbance extent, measured at multiple scales. Line colours correspond to point colours.

Supporting Information

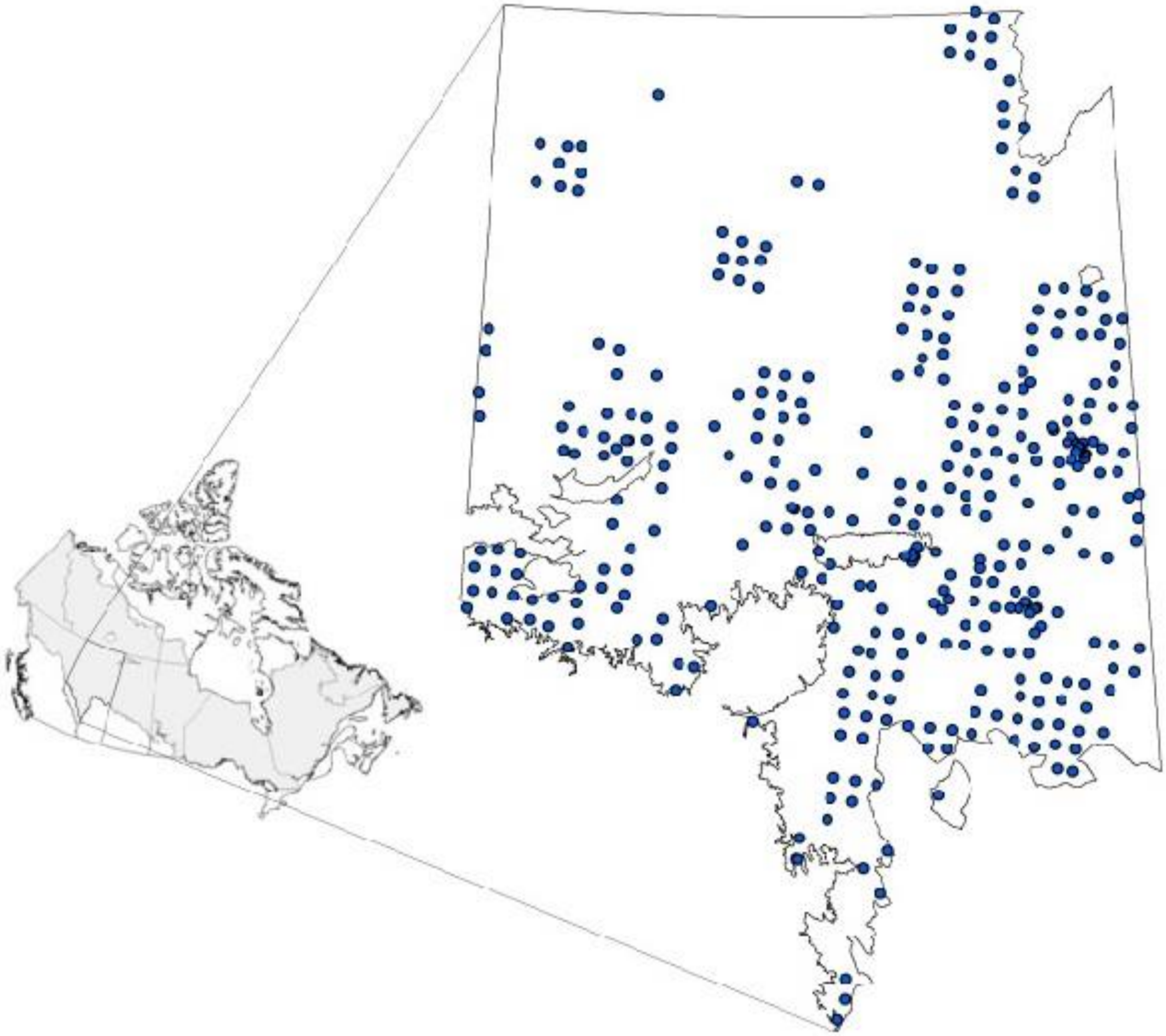

Fig. 3-S1. Map of sample locations in the boreal ecoregion of Alberta. Inset map shows region within Canada, with boreal ecoregion shaded.

Table 3-S1. Comparison of model shapes of species richness-human disturbance relationships at local (1 ha) and landscape (18 km2) scales.

Measurement scale of disturbance	**Model**	**Equation**	**% human disturbance at peak richness**	***p***	**df**	***p* of increase in r^2 of quadratic over linear model**	**r^2**	**AIC score**
1 ha	linear	$y = 0.00068x + 3.84212$		0.229	367		0.004	3296.0
	quadratic	$y = -0.00018x^2 + 0.002x + 3.789$	50.333	< 0.001	366	< 0.001	0.108	3270.7
18 km^2	linear	$y = -0.00300x + 3.92917$		< 0.001	367		0.027	3286.5
	quadratic	$y = -0.00026x^2 + 0.00161x + 3.799$	35.05	< 0.001	366	< 0.001	0.122	3249.6
1 ha & 18km^2	$y = -0.00016x_{local}^2 - 0.00020x_{landscape}^2 + 0.016580x_{local} + 0.01200x_{landscape} + 3.745$		N/A	< 0.001	365	N/A	0.226	3224.6

Table 3-S2. Explanatory variables included in this study. All measures observed or estimated at site centre or within entire local 1 ha site, unless otherwise noted. Details are available from the Alberta Biodiversity Monitoring Institute.

Variable	**Description**
Human disturbance	Proportion of area altered by human land use as assessed with aerial and satellite imagery
Natural subregion	Ecological classification of geographic units within the boreal ecoregion based on landscape patterns in climate, physiographic features, vegetation, soil, wildlife and land use attributes (Natural Regions Committee, 2006)
Latitude	
Longitude	
Elevation	
Topographic heterogeneity	Index of topographic ruggedness, expresses spatial variation in elevation(Riley et al., 1999)
Growing degree days	Heat accumulation, or annual sum of mean daily temperature degrees > 5 °C
Mean annual temperature	Estimated by Alberta Climate Model (Alberta Environment, 2005) based on climatological records of Environment Canada
Mean annual precipitation	Estimated by Alberta Climate Model (Alberta Environment, 2005) based on climatological records of Environment Canada
Terrain wetness	Terrain based site wetness derived from digital elevation model using moisture flows and retention (Gessler et al., 2000)
Site wetness	Observed proportion of 1 ha area in wetland
Solar flux	Estimated annual solar irradiance (MJ/cm^2) (McCune, 2007)
Canopy closure	Mean amount of sky obscured by canopy using densitometer at 8 specific points in local site
Oldest tree age	Age of oldest tree determined by tree core/growth ring analysis
Organic depth	Mean depth of organic soil layer (cm)
Soil type	Dominant soil sub-order classification in local site
Surficial geology	Dominant geological classification of surficial materials in local site
Slope position	Index of topographic position on slope based on elevation (Jenness, 2006)
Landform classification	General shape of landscape feature, such as upland drainage or local ridge (Jenness, 2006)

Table 3-S3. Correlation matrix of human disturbance and continuous environmental covariates. Numbers below the diagonal indicate the correlation. Bold values indicate adjusted $p < 0.05$. Numbers above the diagonal indicate the adjusted p-value.

	Local human disturbance	Landscape human disturbance	Latitude	Longitude	Elevation	Topographic heterogeneity	Growing degree days	Mean annual temperature	Mean annual precipitation	Terrain wetness	Site wetness	Solar flux	Canopy closure	Organic depth
Local human disturbance		0	0.001	1	1	1	0.039	0.001	0.008	0.013	0	0.006	1	0.036
Landscape human disturbance	0.34		0	1	0.012	1	0	0	1	1	0.074	0	0.006	0.076
Latitude	-0.31	-0.53		0	0.391	0	0	0	0.015	0.013	0	1	1	
Longitude	0.1	-0.13	-0.05		0.001	1	0.026	1	1	1	1	1	0.898	1
Elevation	0.15	0.27	-0.68	-0.31		1	0	0	0	0.003	0.001	0	1	1
Topographic heterogeneity	0.11	-0.01	-0.19	-0.07	0.08		0.797	0.124	1	0	0	0.002	0	0.030
Growing degree days	0.24	0.36	-0.39	0.25	-0.34	0.17		0	1	1	1	0.0012	1	1
Mean annual temperature	0.31	0.51	-0.93	-0.11	0.53	0.22	0.56		0	0.220	0.139	0	1	1
Mean annual precipitation	0.27	0.04	-0.66	0.09	0.69	0.13	-0.04	0.58		0	0.797	0	1	1
Terrain wetness	-0.27	0.03	0.26	-0.13	-0.29	-0.47	-0.03	-0.2	-0.33		0	0.014	0.120	0.010
Site wetness	-0.38	-0.23	0.27	0.06	-0.3	-0.36	-0.03	-0.21	-0.17	0.57		0.081	0.276	0
Solar flux	0.28	0.38	-0.74	0.02	0.49	0.3	0.31	0.7	0.48	-0.26	-0.23		1	1
Canopy closure	0.07	0.28	-0.08	0.16	0.04	-0.35	-0.05	-0.02	0.01	0.22	0.2	0.01		0
Organic depth	-0.25	-0.23	0.03	0.06	0.01	-0.25	-0.1	-0.03	0.14	0.27	0.37	-0.04	0.35	

Table 3-S4. Species richness-human disturbance relationships at local and landscape scales, accounting for potentially confounding environmental variables. The negative binomial regression models were constructed using all parameters (saturated) to facilitate comparisons across models.

Measurement scale of disturbance	Model	*p* of disturbance parameter	df	*p* of increase in r^2 of quadratic over linear model	r^2	AIC score
None	N/A	N/A	192	N/A	0.711	1573.9
1 ha	linear	0.015	191		0.722	1573.3
	quadratic	0.032	190	0.032	0.730	1570.7
18 km^2	linear	0.120	191		0.711	1573.9
	quadratic	0.948	190	0.086	0.711	1575.9
1 ha & 18 km^2	N/A	0.019, 0.647	189	N/A	0.738	1535.7

Table 3-S5. Comparison of models of richness-disturbance relationships for native and exotic species.

	Measurement scale of disturbance	Model	Equation	% human disturbance at peak richness	p	df	*p* of increase in r^2 of quadratic over linear model	r^2	AIC score
Native species richness	1 ha	Linear	$y = -0.0009565x + 3.77993$		0.168	367		0.005	3334.990
		quadratic	$y = -0.0001695x^2 + 0.01540x + 3.731$	46.141	< 0.001	366	< 0.001	0.077	3321.361
	18 km^2	linear	$y = -0.0078350x + 3.90660$		< 0.001	367		0.022	3289.817
		quadratic	$y = -0.0003462x^2 + 0.01975x + 3.720$	28.723	< 0.001	366	< 0.001	0.113	3230.435
Exotic species richness	1 ha	linear	$y = 0.019917x + 0.23262$		< 0.001	367		< 0.001	1532.476
		quadratic	$y = -0.0005026x^2 + 0.068829x + 0.013199$	no peak	< 0.001	366	< 0.001	0.047	1507.403
	18 km^2	linear	$y = -0.028812x + 0.190554$		< 0.001	367		0.067	1515.433
		quadratic	$y = -0.0003676x^2 + 0.0600983x - 0.0624855$	no peak	< 0.001	366	0.001	0.026	1507.307

Table 3-S6. Best models (stepwise selected) explaining richness with types of human disturbance.

Measurement scale of disturbance	Human disturbance type	Estimate	df	r^2	p	AIC
1 ha	Forestry	0.002319	363	0.269	< 0.001	3198.41
	Soft linear features	0.007410			0.003	
	Urban and industrial	0.005663			< 0.001	
	Agriculture^2	-0.0001646			< 0.001	
18 km^2	Hard linear features	0.09235	366	0.128	< 0.001	3253.50
	Agriculture^2	-0.0001005			< 0.001	

Table 3-S7. Best multi-scale model of richness explained by human disturbance types at local and landscape scales.

Human disturbance type and scale	Estimate	df	r^2	p	AIC
Forestry (1ha)	0.002271	358	0.307	< 0.001	3192.3
Hard linear features (1 ha)	0.004651			0.128	
Soft linear features (1 ha)	0.006840			0.004	
Urban and industrial (1 ha)	0.005203			< 0.001	
Agriculture^2 (1 ha)	-0.0001887			0.002	
Hard linear features (18 km^2)	0.05066			0.006	
Agriculture^2 (18 km^2)	-0.0001106			0.021	

Chapter 4. Anatomy of biodiversity and community structure change on a human disturbance gradient

Abstract

It is unclear which aspects of biodiversity and community structure are responsive to changes in human land use disturbance. This handicaps our ability to effectively target ecological monitoring efforts and to prepare for or mitigate ecological risks facing communities. I investigate the biodiversity and community structure of 1 ha boreal vascular plant communities in relation to proportion of human land use extent across 371 sites in northern Alberta. Among species increasing or decreasing with disturbance, I analyse changes in proportions of species of various conservation statuses, and with different functional traits. I employ analyses of rank species occupancy curves, an index of specialization based on co-occurrence, and functional trait dispersion. I test the general hypothesis that communities impacted by human land use disturbance are ecologically impoverished, that they are more compositionally and functionally homogeneous, and composed of less desirable species. Although a roughly equal number of species increased with disturbance extent as decreased, most of those that decreased were native species, including many of conservation concern, while those that increased were more likely to be exotic, including some invasive or noxious weeds. Species increasing with disturbance included fewer woody species, but more forbs and grasses. Species which increased also tended to have fewer but more persistent fruits or seeds and a greater ability to resprout, and a higher proportion were caryopses or pods rather than capsules or achenes. However, the dispersion of species functional traits was unrelated to disturbance. Community structure was similar across disturbance classes: site occupancy declined exponentially across ranked species, but intermediately disturbed communities declined with a weaker slope. The degree of species specialization was not strongly related to disturbance, but a co-occurrence based index of specialization suggests all species observed were generalist regardless of disturbance. In general, communities varied in the species they harboured and there were significant patterns in the types and traits of those species, such as fewer native and threatened and more exotic, sometimes detrimental species. But the results do not suggest fundamental changes in the structure of communities with disturbance such as radically greater species dominance, or replacement of varied, specialized communities with homogeneous sets of functionally equivalent generalists.

These results contrast previous findings in more complex or spatially heterogeneous systems and ecological models. I suggest that broad occupancy-based intercommunity patterns are insensitive to human land use extent in boreal vascular plants, perhaps because of underlying systemic characteristics such as ubiquity of generalists, low species richness, and history of disturbance. The poor sensitivity of these metrics to disturbance presents challenges for monitoring and managing impacts to biodiversity and community structure in this region.

Introduction

Rapid human-driven biodiversity changes prompt the need to better understand how communities vary in composition and structure with human land use. The previous chapters focused on the human impacts on biodiversity as expressed by species richness, yet various metrics of biodiversity and community composition can show markedly different responses to disturbance. Many characteristics of community composition and structure that may be of high conservation importance are not well expressed by richness and diversity, and fundamental changes in communities may occur with little impact on richness or diversity (McGill et al., 2006; Devictor & Robert, 2009; Svensson et al., 2012). Motivation to better understand these aspects of biodiversity change with land use is three-fold: i) to identify the ecological risks facing communities; ii) to assess the potential utility of community metrics for ecological monitoring applications; and iii) to test the generality of conceptual ideas of disturbance driven biodiversity change.

In northern Alberta, the rapid expansion of human footprint, ongoing regional land use planning and heightened interest in broad scale environmental monitoring have deepened the importance of effective evaluation of how biodiversity changes with human footprint at a regional scale. Here, I investigate biodiversity at the level of boreal vascular plant communities, exploring how the structure, organization, and composition of these communities change with human disturbance. I test the general hypothesis that communities impacted by human land use disturbance are ecologically impoverished, that they are more homogeneous and composed of less desirable species. Specifically, I compare how human disturbance extent is related to proportions and traits of species, species occupancies across sites, prevalence of specialists and generalists, and the similarity in species traits within sites.

Among the most basic questions to be asked in biological conservation is what proportion of species increase or decrease with human disturbance. However, species vary in their value to society. Apart from obvious benefits of agricultural or otherwise economically important species, the conservation value of a species varies depending largely on their geographic origin (being native or not), their range and abundance, their demographic trend or likelihood of persistence, and their environmental impacts (Davis et al., 2011; Schlaepfer et al., 2011; IUCN, 2012). I compare the probability of species occurrence according to their conservation status, expecting that those species of conservation concern will be less likely to occur in areas of extensive human impact.

Beyond conservation status, species are expected to vary in their response to human disturbance based on individual species traits. Ecologists have long studied the variation in species traits in relation to disturbance (Levins & Culver, 1971; Connell, 1978; Grime, 1979; Hastings, 1980; Huston & Smith, 1987; Halpern, 1989; Nee & May, 1992; McIntyre et al., 1995; Prach et al., 1997). Among the general conclusions of this body of work is that trade-offs exist among traits, especially those associated, with growth, reproduction, and dispersal, and that disturbance alters the relative benefit of species traits. Here, I evaluate the functional and environmental response traits exhibited by species relative to the likelihood of species change with disturbance.

Among the most fundamental characteristics of community structure is the relative abundance or occupancy of species. Akin to species abundance distributions, rank species occupancy curves (RSOC)s provide detailed descriptions of the prevalence and rarity of species where abundance data are lacking (Jenkins, 2011). RSOC's also retain species identity information and avoid arbitrary frequency binning characteristic of occupancy frequency distributions (Jenkins, 2011). Jenkins (2011) built on the intermediate disturbance hypothesis (Connell, 1978) and studies of species occupancy (McGeoch & Gaston, 2002; MacKenzie et al., 2006; Kammer & Vonlanthen, 2009; Gaston et al., 2010) to develop hypotheses for RSOC shapes, suggesting those shapes should vary along a successional gradient, and as a result, on a spatial gradient in disturbance. He suggested that with high disturbance, recruitment limitation should cause an exponential RSOC where some disturbance-adapted species are prevalent but most others rare. At intermediate disturbance, Jenkins predicted a sigmoidal (S-shaped) RSOC, where moderate regional recruitment limitation is accompanied by moderate local niche-based filtering. In this intermediate scenario, many more species are expected to be widespread. With little disturbance, competitive species are expected to be dominant and widespread, while other species exhibit low occupancy. In Chapters 2 and 3, I demonstrated that communities in the study region were richest in species at intermediate disturbance, so in the current study I adopt Jenkins' (2011) predictions for sigmoidal RSOCs among intermediately disturbed communities, and exponential RSOCs among either low or high disturbed communities.

The shapes of RSOC's described above (with some species widespread and others rarely occurring) imply that species vary in the range of conditions under which they may occur. That is, they imply that some species are specialists, and other generalist. Many studies have suggested that human disturbance and invasive species are more likely to negatively affect specialist than generalist species (Devictor et al., 2008a, 2008b; Christian et al., 2009; Clavel et al., 2010), including plants (Fischer & Stöcklin, 1997; Rooney et al., 2004; Brückmann, 2010). Hanski (2000) warned the boreal faces an "imminent wave of extinctions of specialist forest species". Indeed, specialist species have declined globally at a greater pace than other species (Clavel et al., 2010). 'Weedy', 'invasive', 'generalist' species are expanding in some areas such that even with declines in specialists, richness may be maintained, if not greater than in the past (Christian et al. 2009). Further, success of introduction and establishment by exotic species is strongly related to generalism (Fisher & Owens, 2004).

Niche evolution theory predicts that with less heterogeneity across space, and more stable conditions over time, specialists should be favored (Levins, 1968; Futuyma & Moreno, 1988; Tienderen, 1991; Kassen, 2002; Marvier et al., 2004). In contrast, , with greater spatial and temporal variation, generalists are thought to benefit. Marvier et al. (2004) showed this expectation holds despite lower competitive abilities of generalists in any given environment than specialists under the same conditions. These theoretical expectation are explained in part because specialists are thought to be more temporally variable in abundance due to the changing environment (MacArthur, 1955) and variability in abundance can contribute to extinction (Pimm et al., 1988).

In metacommunity simulations comparing indices of biodiversity, specialists declined rapidly with disturbance intensity while species richness and diversity were far less sensitive to changes in disturbance (Devictor & Robert, 2009). Thus, disturbance is expected to act as an environmental filter for specialist rather than generalist species. However, this hypothesis contrasts expectations from the intermediate disturbance hypothesis, for which generalists are expected to be most prevalent at intermediate, rather than high disturbance. I predicted either that a) with increasing disturbance, specialism of species would decline assuming that disturbance homogenizes conditions toward, for example, more light penetration and drier soils; or b) that the heterogeneity of disturbance itself influences composition, such specialism should be higher at both low and high disturbance, but generalism higher at intermediate disturbance.

Specialization is usually estimated by either i) laboratory based experimentation on species responses under ranging environmental conditions, or ii) field based observation of niche characteristics and generation of habitat suitability models (Clavel et al., 2010). Delineating species as specialist, generalist, or somewhere in between is in practice challenging with field data because it involves defining the niche of each species in an unknown number of dimensions (Fridley et al., 2007). Although, these dimensions can sometimes be reliably estimated, I instead employ a new index of specialization that bypasses the need to determine niche width directly, and instead uses the diversity of co-occurring species as an indicator of habitat specialization (Fridley et al., 2007). Specialists are expected to co-occur with similar sets of species wherever they occur, whereas generalists are expected to co-occur with a diverse array of other species. The index employed is further explained under Methods.

The decline of specialists with disturbance is expected to lead to more homogeneous communities (Olden et al., 2004), both in terms of composition and function. Homogenization is the increase in compositional and functional similarity among ecological communities, often due to human-associated habitat degradation and range expansion of widespread exotic species replacing local biotas (Olden & Rooney, 2006). Devictor et al. (2008a) showed that the mean habitat specialization of birds declined with human disturbance. They concluded that communities were more functionally homogeneous with disturbance '(*sensu* Olden & Rooney, 2006)'. However, the degree of specialization of community members seems to say very little about the *functional* similarity of communities. For instance, 'do communities made up of specialists differ in function from communities made up of generalists?' Investigating similarity in functional traits is an alternative method at testing the relationship between functional homogeneity and disturbance. Indeed, Clavel et al. (2010) argued that functional homogenization is a far greater concern than taxonomic homogenization.

Disturbed communities are often expected to contain species with more similar traits than those in undisturbed communities, because disturbance is thought to impose an environmental filter. Vanderwalle et al. (2010) showed that for a variety of faunal groups, mean community traits were consistently good indicators of land use change and offered complementary information to species and functional diversities. In a meta-analysis of plant community datasets from around the globe, Laliberté et al. (2010) showed that the dispersion of traits tends to decline with land use intensity. However, ecosystems varied widely in this response, and the variation in functional dispersion of traits in the boreal remains incompletely understood. To test the prediction that disturbed communities exhibit more similar traits, I determine the similarity in phenotypic functional traits among communities relative to anthropogenic disturbance extent. I focus analyses on growth traits (e.g. max height, growth habit, growth rate), reproduction traits (e.g. regrowth ability, flower type, pollination vector) and dispersal traits (e.g. seed abundance and mass, fruit type)) relative to anthropogenic disturbance extent.

Methods

Vascular plant richness was surveyed in the boreal ecoregion of Alberta, Canada. I used data and the standardized protocols of Alberta Biodiversity Monitoring Institute (ABMI, 2009), and collected supplementary data at additional sites. Vascular plant species occupancy was surveyed within 1 ha for 90 min at a total of 372 sites. I considered all vascular plant species observed at a sampling site to represent an ecological community. Surveys were conducted between Jun 26 and Aug 18 of 2003 and 2011. Human disturbance extent was defined as proportion of land area converted by humans, and was assessed by manual interpretation of 1:30 000 aerial photos and SPOT satellite imagery at each site (ABMI, 2007). For each site, human disturbance extent was measured at two scales: ‘local scale’, the 1 ha square on which plant species were measured; and ‘landscape scale’, a 3 km x 6 km rectangle surrounding the 1 ha site (18 km^2, excluding the central 1 ha; (ABMI, 2007). Only the spatial extent of human disturbance was measured, not its intensity, frequency, or time since disturbance, all of which varied greatly within and among disturbance types. Disturbance types were categorized as agricultural (which included pasture and croplands), forestry cut areas (of varying age), hard linear features (permanent and intense; roads and railways), soft linear features (temporary disturbances which allow successional processes; pipelines, powerlines, and cutlines primarily for oil/gas exploration), and urban/industrial (urban and rural settlements, coal and mineral surface mines, oil and gas well pads, communication towers, gravel pits, spoil pads, and heavy oil sands development; (ABMI, 2007).

Conservation status and species traits

I assessed species specific relationships to human disturbance extent in two ways. First, I investigated species categorized by their probability of occurrence according to disturbance extent. Second, I investigated the mean change (slope) in occurrence according to disturbance extent.

To determine the probability of occurrence in a site based on human disturbance alone, I determined the best fit linear regression relationship between individual species occupancy and human disturbance extent across sites. Slope significance was assessed at $\alpha = 0.05$, and the number of species increasing, decreasing, or not significantly changing with human disturbance extent were counted.

Next, I compared changes in the conservation status of species composing communities of varying anthropogenic disturbance. Species were ranked by their conservation value, origin, and detrimental impacts according to their “conservation status rank” by ACIMS (2011), and as noxious or invasive species according to (ANPC, 2012). Simple counts of species, and proportions of species in each ranked class were then plotted as stacked bar graphs.

To compare relative occupancy of species by status, I determined the number of sites occupied per species, classified species by rank as above, and plotted the mean number and proportion of sites occupied per species in each class. Contingency table analysis with χ^2 tests were used to determine significant relationships between conservation status and probability of increase. Within each class, I then determined and plotted the mean slope of change in site occupancy of species along the disturbance gradient, for each conservation status class.

To assess the relationship of individual functional traits to disturbance, I determined proportions of species exhibiting each functional trait described in Table 3. I analysed contingency tables with χ^2 tests for categorical trait variables and used single factor ANOVA for continuous variables. I plotted the results for traits significant relationships between proportions of species exhibiting traits and their likelihood of increase with anthropogenic disturbance.

Relative occupancy distributions

To reveal and compare the distribution of species relative occupancy (or ‘dominance’), I created rank species occupancy curves (RSOCs) following Jenkins (2011). An RSOC simply ranks species by the number of sites in which it occupies, and plots that occupancy by its rank. RSOCs are akin to occupancy frequency distributions, but do not require binning species by frequency, and relate to ranked species abundance distributions (MacArthur 1957, Hubbell 2001, McGill et al. 2007) but employ presence-absence data rather than abundance data. RSOCs describe the distribution of occupancy across species, and so reveal how widespread species are relative to others in the region, and also how many widespread versus rarely occurring species there are. The shapes of RSOCs have been used to infer community assembly. RSOCs can be fitted to conventional model families (exponential, normal, sigmoidal, linear) and compared using multimodel inference (Anderson et al. 2000). These models can in principle be used to test hypotheses proposed for occupancy frequency distributions, because RSOCs and OFDs represent the same data (Jenkins 2011). However, Jenkins (2011) cautions against OFD-based hypotheses because inferring species-specific biological mechanisms like dispersal abilities, niche factors, or metapopulation processes for multiple communities (as in an RSOC or OFD) assumes these mechanisms are similar across species. Instead, he offers community based hypotheses such as succession and intermediate disturbance hypothesis as inferences to be derived from RSOCs. In general, an S-shaped (e.g. sigmoidal) curve suggests a group of communities with some very widespread species and some narrowly distributed species, but few moderately widespread species. By contrast, a more even distribution of species occupancy is suggested by a flatter RSOC with a long, low sloped middle section, and random species occupancy is suggested by a linearly decreasing RSOC.

To describe the relative species occupancy of species across boreal Alberta, I plotted the occupancy versus rank across all sites, and then fit candidate non-linear models to the distribution to determine the model of best fit. To compare the relative species occupancy of communities relative to human disturbance, I first classified each site by five 20% ranges in human disturbance extent, determined the occupancy of each species within the subset of sites in each disturbance class, then plotted an RSOC for each class. I compared candidate models to determine the best fit relationship for each RSOC.

Following Jenkins (2011), I fit exponential decay, asymmetric sigmoidal (cumulative Weibull), and symmetric sigmoidal (logistic) models to the RSOCs in R using the functions ‘nls’ and ‘nls2’ (nonlinear models as defined by Tjørve, 2003). By visual inspection, other common model forms appeared unlikely to improve model fit (normal, linear, etc.). I assessed the significance of difference among models by overlap in confidence intervals. I used AIC (Akaike, 1974) analyses to select the best fit model.

Species specialization index

An important characteristic of community composition and structure is the relative occupancy of specialists and generalists, a characteristic which may change with human disturbance if disturbance imposes an environmental filter on species occurrence. I therefore computed an index of specialization for each species and compared composition of specialists and generalists relative to in communities of varying human disturbance extent.

To estimate plant species specialization, I used Fridley et al. (2007)'s specialization index 'theta', which is based on co-occurrence among species, rather than species traits or particular environmental conditions. In using this index, I assume that generalists tend to be found with many diverse species such that species turnover across sites in which they occur is high. Specialists by contrast will typically be found with many of the same species across sites (low turnover). A strength of this method is that niches and their potentially numerous and often unknown axes (*sensu* Hutchinson 1957) need not be defined; co-occurrence acts as an 'assay' for diversity of environmental conditions and niche breadth. Since most methods of estimating species specialization rely on predetermining environmental niche axes, and because these axes are often only available for relatively few and more easily measured variables, Fridley's co-occurrence based specialization can be more practical for large regional datasets (Boulangeat et al. 2012) like the one used here. A specialization metric should not be overly sensitive to the frequency at which it is sampled, because frequency can be influenced not only by specialism, but by sampling design. A common feature among studies, including the current study, is variation in representation of habitat types and species, which can bias co-occurrence measures. This method accounts for the frequency of species across sites and among habitats (Fridley 2007, Manthey et al. 2011).

Beta diversity has many formulations (Anderson et al. 2011), and the choice of metric can be critical to assessment of specialization (Boulangeat et al. 2011, Manthey and Fridley 2009, Zeleny 2008). Here I use a Beta measure based on variation among all possible pairs of sites, rather than site to site turnover along a directional gradient (Anderson et al. 2011). I use a multivariate measure of Beta, that compares pairwise similarities in species composition rather than classical measures such as Whittaker's (1960) measure calculated from local and regional diversity directly. I followed Manthey et al. (2011) and calculated Beta as the mean pairwise Jaccard dissimilarity in species composition of those sites occupied by the focal species, excluding the focal species (Jaccard 1912). Jaccard was calculated with the 'simba' package

(0.3-5) in R by (Jurasinski, G.) as: *a* / (2*a* + *b* + *c*) where *a* = number of shared species, *b* = the number of species only found in one of the compared sites, *c* = the number of species only found in the other compared site. This pairwise method was preferred over multiple plot dissimilarity methods (Baselga et al. 2007) because it is insensitive to compositional nestedness, a condition where changes in species loss (subsetting) across a gradient are not considered a change in beta diversity (Manthey et al. 2011).

In calculating the specialization index, the minimum frequency of occurrence for a species to be included must be set. This somewhat arbitrary parameter value must be small enough so as not to exclude too many uncommon species, but large enough that variance from low sample size is not unreasonably high. I selected species with a minimum occurrence of 10 sites, which accounted for 48.1 % of all species. Because this minimum occurrence is low, I tested the sensitivity of the parameter to number of sites by repeating the analyses with minimum occurrence of five and two, following Manthey et al. (2011). I observed that the density distribution of specialists vs. generalists was not sensitive to low minimum occurrence.

To assess how specialists and generalists relate to disturbance, I plotted richness-disturbance relationships of the 50 species with the highest or lowest Jaccard dissimilarities. I fit linear and quadratic relationships to these plots and selected the models with the lowest AIC values (Akaike, 1974).

I assessed how species specialism relates to disturbance on both species-wise basis and a community-wise basis. First, I assessed species by species specialism relative to mean disturbance extent of occupied sites. I compared each species' specialism index value to the mean human disturbance extent across all sites in which the species occurs. If most species were specialists of say, low disturbance levels, Jaccard similarity would be low (i.e. below 0.5) for most species and they have low mean disturbance extents; in Fig. 7a, they would all be expected to appear in the lower left hand corner. If species were all specialized, but for different levels of disturbance (some specialized on old forests, some specialized on intermediately disturbed areas, and others on extensive disturbance), it would be expected that all species would have low Jaccard dissimilarities, but exhibit a flat linear distribution across the gradient in mean disturbance. If species are specialists for a particular disturbance level, it would be expected that Jaccard similarity would increase or decrease with mean disturbance.

The specialism index should not be sensitive to occupancy because such a result would imply species occurring in fewer sites would be more likely to be specialist. I plotted the relationship between species specialism and site occupancy to test this fundamental assumption of the specialism index; a significant linear relationship would suggest the assumption was violated. In Fig. 7b, species were coloured according to their mean disturbance of occupied sites.

Second, I assessed the relationship of community specialism to anthropogenic disturbance. I defined specialization of a community simply as the mean specialization of the group of species occupying a site. This is a modification of Devictor and Robert's (2009) Community Specialization Index, but the index I use here is based on occupancy rather than abundance. For each site, I plotted the mean Jaccard dissimilarity across occupant species by the human disturbance extent of the site. In Fig. 7c, a linear relationship would be expected if sites tended to host relatively more specialist or generalist species according to the extent of site disturbance. A curvilinear relationship would suggest a tendency for sites with intermediate disturbance levels to host either relatively more specialist (if concave down) or generalist species (if concave up).

Functional trait diversity

To determine if the diversity of species' phenotypic traits vary in relation to the anthropogenic disturbance among sites, I determined trait dispersion of each site based on the species present. I first assembled data describing 31 functional traits and an additional 16 environmental response traits from several sources, shown in Table 2.

I calculated the functional dispersion (FDis) of traits for each site following Laliberte and Legendre (2010). FDis is the average distance to the centroid in multivariate trait spaced (Anderson 2006). FDis is well suited to the current analysis because it is not affected by species richness, allows very large numbers of traits to be considered, is not strongly sensitive to outliers, and allows formal statistical significance testing for differences in functional dispersion among communities. FDis may be computed with any distance or dissimilarity measure (Anderson et al. 2006), but I used the Gower (1971) dissimilarity measure for mixed variables following Podani (1999) to accommodate the variety of binary, categorical, ordered factor, and continuous explanatory variables that make up the trait dataset. Analyses were implemented in R with package "FD" (Laliberté and Legendre 2010). I estimated dispersion (FD) for functional traits alone, then for all traits together.

Results

In 371 sites, 662 species were observed. Of these, 104 species (15.7 %) were significantly more likely to be observed in sites of more extensive human disturbance, 107 species (16.2 %) were more likely to be observed in sites with less human disturbance, and the presence of each of the remaining 450 species (68.0 %) was not significantly related to human disturbance extent (Fig. 1a).

Species at risk were more likely to be observed with less disturbance, while exotic species – particularly noxious weeds – were more likely with extensive disturbance (Fig. 1b). Of the species less likely to be observed with more disturbance, the ‘decreasers’, 17.3% were vulnerable species of rank S1 to S3 (Fig. 2), 40.4% were of rank S4 or S5, and 3.8% were exotic species. Of the species more likely to occupy sites with increasing human disturbance, the ‘increasers’, 1.9 % of species were vulnerable, while 30.8% of species were exotic species (Fig. 1b). Of these exotic species more likely with disturbance, 27.3% were detrimental invasive or noxious species. Contingency table analysis revealed the conservation status of species was significantly related to their probability of occurrence relative to disturbance ($\chi^2 = 253.6$, df = 18, $p < 0.001$). A second contingency table analysis on grouped species categories revealed the proportions vulnerable (S1-S3), secure (S4-S5), and exotic (exotic, invasive, or noxious) species were significantly different among species more, less, or unchanging in likelihood of occupancy with increasing human disturbance ($\chi^2 = 66.51$, df = 4, $p < 0.001$).

The change in likelihood of species occurrence with human disturbance extent varied by conservation status (Fig. 2). The mean decrease in likelihood of occurrence with disturbance was steeper in vulnerable S3 species than secure S5 species, for example. However, large variation in slopes – even signs of slopes – among species within a given status category suggest low predictive ability in degree of change in occurrence with disturbance from conservation status alone. Noxious, invasive and otherwise exotic species were statistically indistinguishable in their mean change with disturbance. No statistically significant slopes were detected in S1 or S2 species, likely due to their low occurrence.

Species more likely to occur with disturbance exhibited significantly different functional traits than those likely to decrease with disturbance (Fig. 3). Notably, shrubs and trees were more likely to be decreasers with disturbance, while forbs and grasses were more likely to be increasers. Relative to increasers, a higher proportion of decreasers had the ability to resprout, or the ability to retain leaves year round, but fewer decreasers were nitrogen fixers. Decreasers tended to have higher fruit or seed abundances but were less likely to have persistent fruits or seeds and had higher fertility requirements. Species which were likely to decrease with disturbance were more likely to have berries, capsules, drupes, or nutlets, while increasers were more likely to have achenes, caryopses, or pods.

Rank occupancy

When all species were ranked by their occupancy and plotted as a ranked species occupancy curve, the curve best fit an exponential decay model. This curve shape shows that a few species occur in very many sites, whereas most species are observed in only very few sites (Fig. 4). The 5 % most widespread species occurred in over 30 % of sites, the 10 % most widespread species occur in at least 12 % of sites, whereas the remaining 90 % of species occur in less than 12 % of sites, and the 50% least widespread species occurred in less than 1 % of sites.

When sites were separated by disturbance class, RSOC distributions in each class fit exponential decay models better than other candidate model shapes (in each case, AIC model weight = 1.00, delta. This indicates several findings: first, that the shape of this fundamental descriptor of community structure is very similar regardless of the extent of disturbance in sites. Second, the evenness of occupancy is low in the most widespread species. In each disturbance class the proportion of sites occupied declined rapidly from the most widespread species to the next 50 to 100 most widespread species. Third, there is an abundance localized and few widespread species in each disturbance class.

RSOC models among disturbance classes tended to converge toward high (> 300) and very low (< 25) ranked species; differences in the model distributiuons were most apparent among ranks of 50 to 300 species (Fig. 4b). This observation indicates that the most substantial differences in community structure across disturbance classes were in the occupancy proportions of moderately widespread species. More species were observed at higher proportions of sites in intermediate disturbance classes than at either high or low disturbance classes. The lowest (0 – 20 % disturbance) and highest (80 – 100 %) disturbance classes overlapped. Likewise, the occupancies of species in the low-mid to middle disturbance classes were overlapping each slightly more even (i.e. less right skewed). The mid-high disturbance class was less even than those but more even than the low and high. In short, species in high and low disturbance extent communities were less even in their occupancy than species in intermediate disturbance classes.

Specialization

The Jaccard dissimilarity index of niche breadth varies from 0 to 1. Low numbers indicate a species which co-occurs with a very small set of other species, a pattern suggesting habitat specialization; I call these species ‘specialist’. The converse, high Jaccard dissimilarity indicates a species which co-occurs with a wide variety of other species, here called ‘generalist’s. ‘Niche breadth’ varied between 0.586 and 0.875, indicating that all species observed exhibited wide co-occurrence based ‘niche breadth’ indices: all species appear to be moderate ‘generalists’ (Fig. 5). Species ‘niche breadth’ index had a mean of 0.755, and a median of 0.757.

Richness of the 50 most generalist species was highest at intermediate human land use (Fig. 6, $y = 0.00199x^2 + 0.232x + 1.855$, $R^2 = 0.242$, $p < 0.001$). The same cannot be concluded for the most ‘specialist’ species. The richness of the 50 most specialist species related to disturbance with borderline statistical significance, but the relationship was very weak and not ecologically significant (Fig. 6, $y = 0.000922x^2 + 0.0970x + 7.177$, $R^2 = 0.010$, $p = 0.050$).

Neither ‘generalism’ of species nor the mean ‘generalism’ of communities were very sensitive to disturbance. First, species ‘generalism’ was not strongly related to mean anthropogenic disturbance extent of sites occupied by a species. Jaccard dissimilarity of co-occurring species was statistically significantly related to mean disturbance (Fig. 7a, $y = 0.780 - 0.00267x + 0.0000449x^2$, $R^2 = 0.106$, $p < 0.001$), but this relationship was weak and sensitive to outliers (at high disturbance) so I consider it ecologically non-significant. ‘Generalism’ was also not substantially related to the number of sites occupied by a species, despite statistical significance (Fig. 7b, $y = 0.774 + 0.000537x$, $R^2 = 0.0382$, $p < 0.001$). This confirms that Jaccard dissimilarity is not very sensitive to occupancy; generalists don’t occupy substantially more sites. Finally, community ‘generalism’ was not strongly related to human disturbance extent (Fig. 7c, $y = 0.746 + 0.000146x$, $R^2 = 0.0373$, $p < 0.001$), noting again the statistical significance. Each of these analyses included only species with at least 10 occurrences to ensure ecologically meaningful assessment of co-occurrence. However, each of these analyses were repeated with all species with at least 2 occurrences, and the results were similarly weak; no conclusions changed.

Trait dispersion

Communities observed varied in species composition, and the distribution of phenotypic traits observed at each site varied as a result. The dispersion of functional trait values increased with anthropogenic disturbance extent but only very weakly (Fig. 8a, $y = 0.224 + 0.000192x$, $R^2 = 0.137$, $p < 0.001$). This suggests little relation between the mean function of species relative to disturbance. Similarly, the dispersion of functional and environmental response traits, like tolerances to certain environmental conditions, did not vary substantially (Fig. 8b, $y = 0.187 + 0.0007x - 0.0000063x^2$, $R^2 = 0.0895$, $p < 0.001$.

Discussion

Declining biodiversity and associated biotic homogenization are among the chief global conservation concerns (McKinney & Lockwood, 1999; Christian et al., 2009). Biodiversity is composed of many interrelated elements which I expected to differ in their sensitivity, response, and risk to human disturbance.

With increasing anthropogenic disturbance, most species (68.0 %) were no more or less likely to occur in a given site. Nearly an equal proportion of species were more likely as were less likely to occur with increasing human disturbance. This balance in ‘increasers’ and ‘decreasers’ with disturbance is consistent with observations in Chapters 2 and 3 supporting the intermediate disturbance hypothesis in that low and high disturbance sites were similar in species richness. It is also consistent with Devictor et al. (2008b), who on a similar regional scale observed that roughly half of bird species throughout France increased with disturbance while half decreased. On the basis of species richness alone, it would appear that human disturbance is benign in this study region.

However, the composition of species changed significantly with disturbance; many species decreasing with disturbance were of conservation concern while a majority of species increasing with disturbance were exotics, including noxious weeds (Fig. 1). Similarly, trends in occurrence of exotic species, including noxious weeds, were positive, while those of conservation concern tended to be negative, though considerable variation was observed among species (Fig. 2). These findings are consistent with decades of research demonstrating the link between disturbance and exotic species in a wide variety of ecosystems (Elton, 1958; Mack & D’Antonio, 1998; Davis, 2009; Hejda et al., 2009). However most exotic species were classified neither as noxious nor invasive. Indeed, exotic species are not necessarily detrimental and may even be beneficial in some circumstances (Davis et al., 2011; Schlaepfer et al., 2011).

The structure of species occupancy in communities was statistically distinguishable among disturbance classes, with species slightly more even in their occupancy of intermediately disturbed sites than among sites of low or high disturbance (Fig. 4). That is, there were more species that were moderately prevalent among intermediately disturbed communities. However, the general structure of communities in these disturbance classes was equivalent in shape; regardless of disturbance extent, species occupancy decayed exponentially from most to least prevalent species. That is, only a few species occurred in a high proportion of communities, regardless of disturbance. This general observation is supported by Peltzer et al. (2000) who reported similar rank species abundance distribution for boreal plants in sivicultural landscapes. However, these findings somewhat contrast the findings of Jenkins (2011) who suggested that RSOCs should exhibit a sigmoidal shape at intermediate disturbance. This suggests that RSOC shapes may not be as consistently predictable across metacommunities as Jenkins (2011) proposed (Hui, 2012), despite the support for the intermediate disturbance hypothesis (Chapters 2, 3) that forms the basis for the predictions. Ranked species occupancy curves may be expected to be more exponential at large spatial scales and more sigmoidal at smaller spatial scales (Jenkins, 2011), which could explain the observed consistency in exponential RSOCs observed in this large scale study. However, the scale dependence of RSOC shape has little empirical support (Jenkins, 2011).

The weak relationship of community occupancy structure to disturbance was mirrored by weak relationships of species specialization to disturbance. Contrasting Devictor et al. (2008a; 2008b) but consistent with Abadie et al. (2011) and Vázquez & Simberloff (2002), community specialization was not strongly related to human disturbance. Specialist species were expected to be among the most sensitive groups to human disturbance (Devictor et al. 2010) following one of two related theoretical approaches. Either specialists should decline with disturbance if disturbance creates spatially and temporally heterogeneous environmental conditions more favorable to generalists (Levins, 1968; Futuyma & Moreno, 1988; Kassen, 2002; Devictor et al., 2008a), or specialists should exhibit greater occupancy at very low and very high disturbance if these areas are unique but internally more homogeneous (Connell & Slatyer, 1977; Connell, 1978).

All the species I observed were identified as generalists according to the co-occurrence based specialization index (Fig. 5). Specifically, this means all species co-occurred with a wide variety of species—none showed fidelity to a small subset of species. The ubiquity of boreal plant species generalism may be due to: i) extreme seasonal variation in climatic conditions, ii) relatively short time duration since glaciation (McGlone, 1996), or iii) failure of this study to capture specialist traits. These findings suggest that in this system, specialization is unlikely a key mechanism of niche differentiation facilitating species coexistence (Chase & Leibold, 2003). This failure to identify specialists might have been an artifact of relatively large 1 ha sample sites, however, the boreal region is large-grained (Levin, 1992) relative to highly specialized systems like tropical forests, suggesting the sampling scheme was appropriate. I had no *a priori* expectation that theoretical frameworks developed in more heterogeneous, highly specialized systems ought not apply to the boreal, even knowing in advance that the boreal is an ecosystem with relatively low specialization, high species turnover, and species with high propensities for dispersal.

A species' degree of specialization was not strongly related to the mean disturbance of the sites it occupied, nor was the mean specialization of species in a community strongly related to observed extent of disturbance (Fig. 7). The richness of even the least generalized species was unrelated to disturbance (Fig. 6). These results are inconsistent with previous studies that have suggested specialist species are increasingly shown to be experiencing higher rates of decline and extinction, part of an emerging pattern of biotic homogenization of communities becoming more similar to each other (McKinney & Lockwood, 1999; Lockwood & McKinney, 2001; McKinney, 2006; Olden & Rooney, 2006; Devictor et al., 2008b; Fortin et al., 2008; Clavel et al., 2010). Christian et al. (2009) observed that over a century-long time series of insular birds, species richness increased while specialist richness decreased. Even paleontological data has shown that specialists were disproportionately prone to extinction in previous mass extinctions (McKinney, 1997; Erwin, 1998).

Reviews show that some categories of traits are better predictors than others of sensitivity of species to habitat loss and fragmentation: population size; population fluctuation and storage effects; traits associated with competitive ability and disturbance sensitivity in plants; high specialization; rarity; mobility, and relative biogeographic position (Henle et al., 2004; Ewers & Didham, 2006). By contrast, the following traits were insensitive to habitat fragmentation: dispersal power; reproductive potential; annual survival; sociality; body size; trophic position. I observed differences in traits among species likely to increase versus decrease with human disturbance (Fig. 3), and these differences were generally consistent with expectations for adaptations to disturbance (Halpern, 1989; Grace & Tilman, 1990; Prach et al., 1997; Henle et al., 2004; Pyšek & Richardson, 2007; Kirmer et al., 2008; Sonnier et al., 2010; Newbold et al., 2013). For instance, species likely to increase in occupancy with disturbance were more likely to be forbs or grasses than trees or shrubs, and they had higher resprout abilities, fruit or seed persistence, and lower fertility requirements.

Surprisingly, increasers tended to have fewer seeds or fruits than decreasers, highlighting the view that species characteristics may be more complex than conventional ideas of binary trade-offs (like competition-colonization abilities) may imply (Seifan et al., 2013). Similarly, Ewers & Didham (2006) showed that individual species traits like dispersal ability and habitat specialization can confound expectations of response to habitat fragmentation. Many traits commonly associated with disturbance adaptation, like growth and vegetative spread rates, height, and reproductive strategy were indistinguishable among species increasing versus decreasing with disturbance. Overall, the functional characteristics of species occupying highly disturbed communities differed in some respects from those of less disturbed communities. Without information on the abundance of species however, estimating the mean functional characteristics of communities is not possible.

The analysis of traits has several limitations. First, it is not clear how trait values used – which were sourced from areas sometimes long distances from the study region – represent the true trait values within the study region. Trait values of species with large interregional trait variation may poorly represent true trait values of those species in the study region. Second, traits of any given species may vary across individuals and survey sites. Third, the phenotypic plasticity of species may permit some traits to vary with environmental conditions such and human disturbance. However, Kazakou et al. (2013) reported that intraspecific traits were relatively consistent among databases from different regions, suggesting previously measured trait values are applicable even distant locations. Although the trait data contained much missing information, and much existing information was of a categorical nature, the observations are probably sound for predicting which traits are more likely to be observed with increasing disturbance. I suggest that monitoring efforts like ABMI, would benefit from improved knowledge of species functional traits across monitoring sites and over time, and their relationship with human disturbance. In particular, direct measurement of traits in the field would greatly improve confidence in conclusions about relationships between traits and disturbance.

Unlike species' functional traits themselves, the dispersion of traits was not strongly related to anthropogenic disturbance. I expected that disturbed communities would exhibit greater similarity in traits within sites, given the strong environmental filter disturbance appears to impose. Laliberté et al. (2010) demonstrated, for example, that trait dispersion declines with human disturbance in many ecosystems. It is unclear why trait dispersion was not more strongly related to disturbance in the boreal region, but one possibility is that the various types of human disturbance in the region favour different species traits, or simply that disturbed communities are highly variable in their environmental characteristics. In any case, it appears that disturbance had little impact on functional dispersion, contrasting other studies warning of functional homogenization traits in disturbed communities (McKinney, 2006; Devictor et al., 2008a; Clavel et al., 2010; Abadie et al., 2011).

Overall, the results of this study imply relatively little sensitivity to even very extensive human land use in the boreal forest vascular plant communities. Are communities truly impacted so little by disturbance, or are these findings idiosyncrasies of this study? Several non-mutually exclusive possibilities exist. First, 'community structure' taken as a broadly defined ecological state, may be resilient or resistent to human disturbance in this boreal region and face little risk. Second, community structure may be sensitive to human disturbance, but in ways not captured by the metrics used in the current study's analyses. Third, community structure may be sensitive to the metrics explored, but depends on alternative sampling strategy.

This study is observational, employing systematic sample sites varying in disturbance extent, rather than utilizing before-after controlled experimentation, or employing stratified sampling to target vulnerable species, environmental conditions, or ecological subregions. The design of ABMI sampling involves a focus on assessing the overall state of biodiversity in an impartial, value-neutral manner, so the data may not be the most appropriate for targeting the most dramatic threats to biodiversity related responses to disturbance. For example, even sampling via systematic grid provides equal weighting across the entire region, but unequal weighting by ecological subregions, which vary in area. Data and potential inference inherently emphasizes common, ubiquitous species over rare localized species. To better assess risks to rare, at-risk, or localized species, or in underrepresented environments, a stratified sampling procedure might provide more disturbance-sensitive information.

All biodiversity indices each have their strengths and weaknesses (Buckland, 2005; Lamb et al., 2009). Many indices require known relative abundances of species, information often expensive and demanding to collect. Fortunately, empirical evidence suggests that simple occupancy is usually more correlated with environmental variables than is abundance, especially for spatially extensive data sets and those with many observations (Lawrence Lodge et al., 2007; Wilson, 2012). This is perhaps counter-intuitive given that occupancy data contains less information than abundance. Although the actual mechanisms behind community assembly are still debated, Wilson (2012) suggests that assembly rules may act more strongly on occupancy than on abundance.

Conclusions

There are clear differences among vascular plant communities with and without extensive human disturbance. Different species with different traits occupy communities depending on the level of disturbance, for instance. Those changes are largely in line with what is expected of community change in anthropogenically disturbed environments: species typically have greater environmental tolerances to light and dry conditions, and tend to have high reproductive outputs, for example. Intact forest is easily distinguishable from that with human disturbance in aerial and satellite imagery, and environmental conditions observed in the field, like canopy cover or soil moisture.

However, defining disturbed communities as more impoverished, homogeneous, or somehow objectively ‘negative’ has proven more difficult. Although theory predicts changes in community structure, particularly in relative occupancies of rare and specialized species, I was unable to detect substantial disturbance driven differences in this system. Although some methodological constraints have been identified, the data are extensive and of high quality. I therefore suggest that the measures of community structure that appear insensitive to disturbance in this study will likely not prove useful as strong sentinels of biodiversity impoverishment in this boreal region, even perhaps with extreme land use changes.

The apparent insensitivity of community structure to disturbance might be explained by the high generalism of most species, particularly relative to highly specialized systems like tropical forests (e.g. Hubbell et al., 1999; Wright, 2002) or along strong environmental gradients such as alpine slopes (Boulangeat et al., 2011). The relative rarity of most species may also have contributed to poor detection of disturbance associated changes in structure.

In general, this study's findings provide a better understanding of how plant communities vary with human disturbance. They are particularly relevant for the boreal ecoregion of Alberta, where the human footprint is rapidly expanding and regional land use planning is ongoing.

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Tables

Table 4-1. Classification of species by origin, rarity, ubiquity, and social impact.

Class	Definition	Source
S1	Known from five or fewer occurrences or especially vulnerable to extirpation because of other factor(s)	(ACIMS, 2011)
S2	Known from twenty or fewer occurrences or vulnerable to extirpation because of other factors	(ACIMS, 2011)
S3	Known from 100 or fewer occurrences, or somewhat vulnerable due to other factors, such as restricted range, relatively small population sizes, or other factors	(ACIMS, 2011)
S4	Apparently secure. Taxon is uncommon but not rare. Potentially some cause for long term concern due to declines or other factors	(ACIMS, 2011)
S5	Secure - taxon is common, widespread, and abundant	(ACIMS, 2011)
Exotic	Not native to Alberta	(ACIMS, 2011)
Invasive	Not native to Alberta, with detrimental environmental impacts	(ANPC, 2012)
Noxious	Not native to Alberta and considered a threat to Alberta's environment, economy and society. Listed under Alberta's Weed Control Act as those species which need to be destroyed or controlled.	(ANPC, 2012)
Unknown	Conservation status of species unknown or not assessed	(ACIMS, 2011; ANPC, 2012)
Other non-invasive	Conservation status of species unknown or not assessed, but known to not be invasive.	(ACIMS, 2011; ANPC, 2012)

Table 4-2. Description of species phenotypic functional and environmental response traits examined and source of data.

Trait	**Description**	**Source**
Functional traits		
Lifespan	Continuous, measured.	USDA (2011)
Duration	Binary categorization as annual/biennial, or perennial	Gerling et al. (1996); USDA (2011)
Growth rate		USDA (2011)
Growth form	Categorical classification as tree, shrub, forb, graminoid, other	Gerling et al. (1996); USDA (2011)
Growth habit	Categorical classification as erect, trailing, solitary, bunch, mat, thicket or sod	Gerling et al. (1996); USDA (2011)
Mycorrhizal	Binary categorization as true or false association	Gerling et al. (1996)
Heterotrophs	Categorical classification as insectivorous, saprophytic, or false	Gerling et al. (1996)
Nitrogen fixers	Binary categorization as true or false	Gerling et al. (1996); USDA (2011)
Moisture use	Ordinal categorization as low, moderate, high	USDA (2011)
Leaf retention	Binary categorization as true or false	USDA (2011)
Minimum root depth	Continuous, measured	USDA (2011)
Minimum height	Continuous, measured	Gerling et al. (1996); USDA (2011)
Maximum height	Continuous, measured	Gerling et al. (1996); USDA (2011)
Mean height	Continuous, measured	Gerling et al. (1996); USDA (2011)
Resprout ability	Binary categorization as true or false	USDA (2011)
High responsibility	Binary categorization as true or false	Moss (1994)
Vegetative spread rate	Ordinal categorization as low, moderate, high	USDA, (2011)
Fruit/seed abundance	Ordinal categorization as low, medium, high	Gerling et al. (1996); USDA (2011)
Fruit/seed period begin	Ordinal categorization as spring, summer, fall	USDA (2011)
Fruit/seed period end	Ordinal categorization as spring, summer, fall.	USDA (2011)
Fruit/seed persistence	Ordinal categorization as low, moderate, high	USDA (2011)
Mean seed mass	Continuous, measured	Gerling et al. (1996)
Reproductive strategy	Categorical classification as rhizome, seed, stolon, tillers	Gerling et al. (1996)

Aggressive reproduction	Binary categorization as true or false	Gerling et al. (1996)
Edible fruit producer	Binary categorization as true or false	Moss (1994)
Fruit type	Categorical classification as achene, berry, capsule, caryopsis, cone, drupe, follicle, hip, nutlet, pod, pome, samara, schizocarp, spore, utricle	Moss (1994)
Fertility requirement	Categorical classification as low, medium, high	Moss (1994)
Nectar producers	Binary categorization as true or false	Moss (1994)
Flower colour	Categorical classification as blue, brown, green, purple, red, white, yellow	USDA (2011)
Flower conspicuous	Binary categorization as true or false	USDA (2011)
Bloom period	Categorical classification as early spring, mid spring, late spring, early summer, mid summer, late summer, indeterminate	USDA (2011)
Environmental response traits		
Soil texture	Categorical classification as fine, medium fine, medium, medium coarse, coarse	Gerling et al. (1996); USDA, (2011)
Soil moisture	Categorical classification as dry, medium dry, medium, medium moist, moist	Gerling et al. (1996)
Anaerobic tolerance	Categorical classification as low, medium, high	USDA (2011)
$CaCO_3$ tolerance	Categorical classification as low, medium, high	USDA (2011)
Minimum temperature	Continuous, measured	USDA (2011)
Minimum frost free days	Count, estimated	USDA (2011)
‘Cool’ or ‘warm’ season plant	Categorical classification	Gerling et al. (1996)
Successional stage	Binary categorization as early or late	Gerling et al. (1996)
Human modified	Binary categorization of adaptation to modified condition as true or false	Moss (1994)
Weedy	Binary categorization of habit as true or false	Moss (1994)
Riparian	Binary categorization of adaptation to condition as true or false	Moss (1994)
Cold stratification requirement	Binary categorization as true or false	USDA
Drought tolerance	Binary categorization as true or false	Gerling et al. (1996); USDA (2011)
Fire tolerance	Binary categorization as true or false	Moss (1994)

Minimum pH	Continuous, measured	Moss (1994)
Maximum pH	Continuous, measured	Moss (1994)
Minimum precipitation	Continuous, measured	Moss (1994)
Maximum precipitation	Continuous, measured	Moss (1994)

Table 4- 3. Functional traits relative to counts of species likely to increase, not change, or decrease with anthropogenic disturbance extent. Contingency table analyses performed with Pearson χ^2 test of significant relationship between categorical variables. Single factor ANOVA employed with F test. * indicates $p < 0.05$.

Trait	**N**	**R^2**	**χ^2 (or F)**	**p**
Lifespan	234	0.014	6.903	0.141
Annual/biennial, or perennial	489	0.086	33.771	< 0.001 *
Growth rate	245	0.031	8.45	0.076
Growth form	551	0.022	18.607	0.046 *
Growth habit	353	0.017	2.167	0.338
Mycorrhizal	266	0.009	0.687	0.430
Heterotrophs	489	0.054	7.487	0.112
Nitrogen fixers	488	0.058	7.111	0.029 *
Moisture Use	236	0.016	7.307	0.121
Leaf Retention	249	0.193	27.16	< 0.001 *
Root Depth	247	0.001	(0.174)	0.840
Minimum height	239	0.005	(0.574)	0.564
Maximum height	265	0.002	(0.302)	0.740
Mean height	265	0.002	(0.206)	0.814
Resprout ability	249	0.027	6.360	0.042 *
High responsibility	489	0.080	3.266	0.195
Vegetative spread rate	240	0.021	11.44	0.076
Fruit/seed abundance	236	0.031	16.668	0.011 *
Fruit/seed period begin	242	0.020	5.504	0.239
Fruit/seed Period end	242	0.019	7.432	0.115
Fruit/seed persistence	249	0.051	13.04	0.002 *
Mean seed mass	556	0.003	(0.178)	0.837
Reproductive strategy	300	0.045	5.047	0.008
Aggressive reproduction	266	0.022	4.420	0.110
Edible fruit producer	489	0.008	2.974	0.226
Fruit type	489	0.040	80.11	< 0.001 *
Fertility requirement	244	0.050	23.49	< 0.001 *
Nectar producers	487	< 0.001	0.281	0.869
Flower colour	240	0.019	11.77	0.464
Flower conspicuousness	249	0.002	0.775	0.679
Bloom period	246	0.015	9.342	0.673

Figures

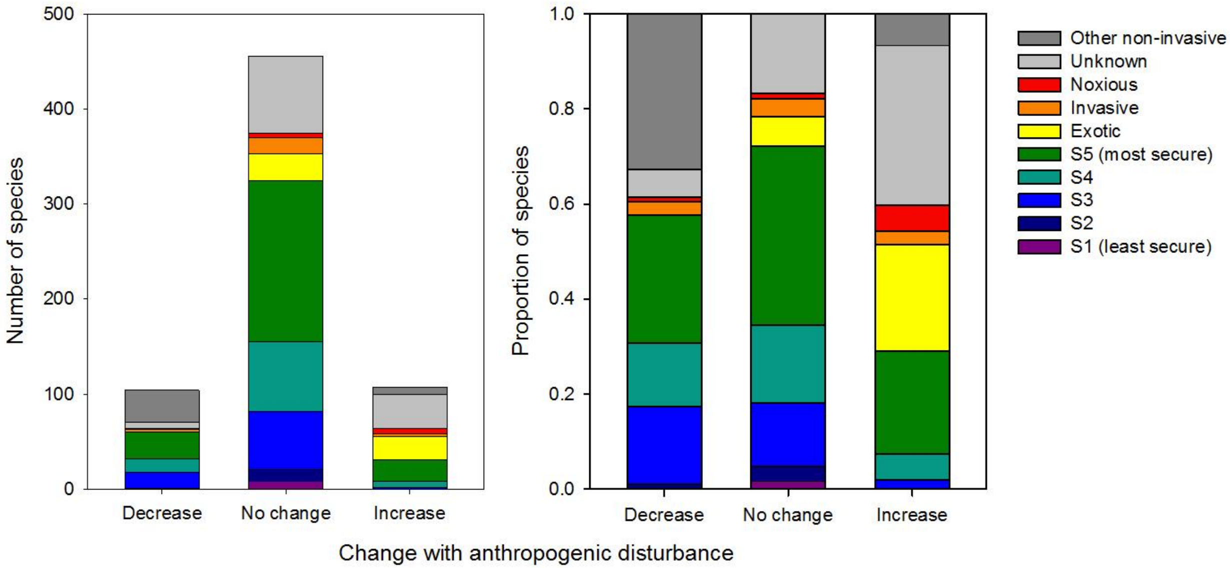

Fig. 4-1. Change in likelihood of species occupancy with anthropogenic disturbance extent. Species' conservation statuses are indicated by colour. S5 to S1 indicate secure to vulnerable; see Table 1 for full conservation status descriptions. **(a)** Count of species with significantly increasing likelihood of occupancy with anthropogenic disturbance extent. **(b)** Proportion of species within groups of significant increase, decrease, or no change in likelihood of occupancy with anthropogenic disturbance extent. Although the number of species increasing and decreasing in likelihood of occupancy with disturbance is nearly equal, the proportions of species in each conservation status varied by change in likelihood of occupancy.

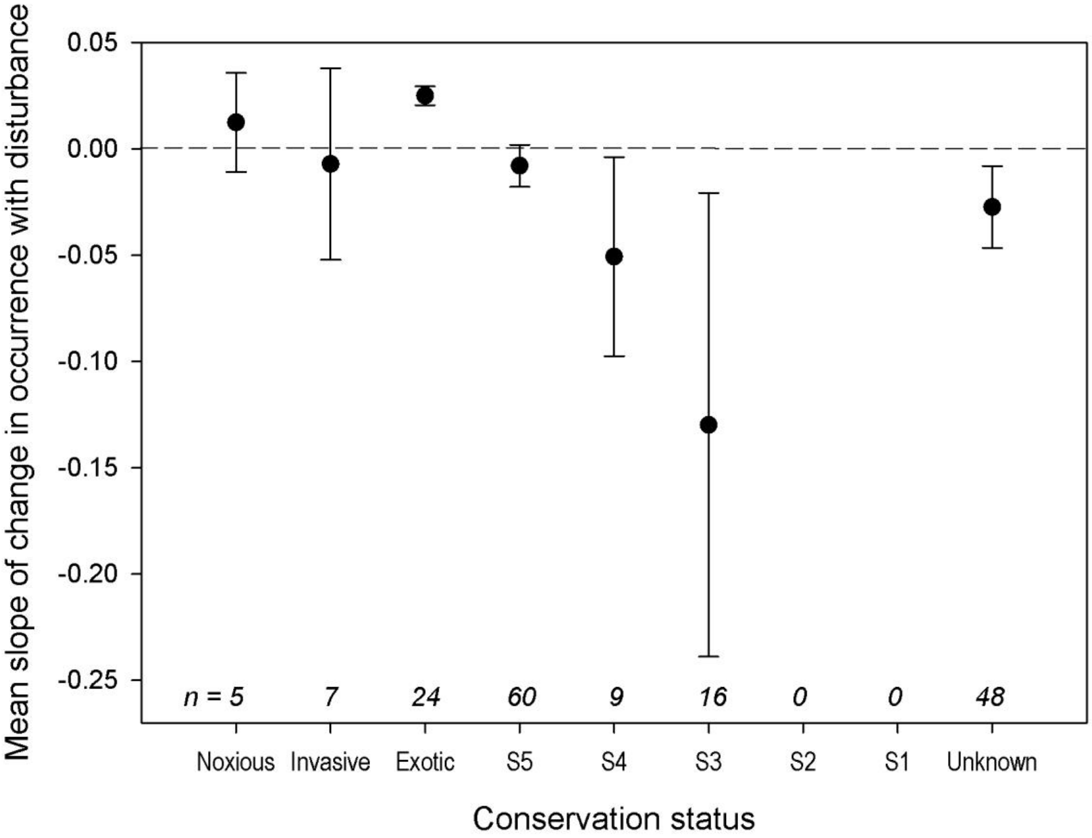

Fig. 4-2. Performance of species by conservation status classification. Dots indicate mean of slopes of change in species-specific probability of occurrence relative to percent anthropogenic disturbance extent. Only statistically significant slopes of species were considered, counts of which are indicated by *n*. Bars indicate 95% confidence intervals. S5 to S1 indicate secure to vulnerable; see Table 1 for full conservation status descriptions.

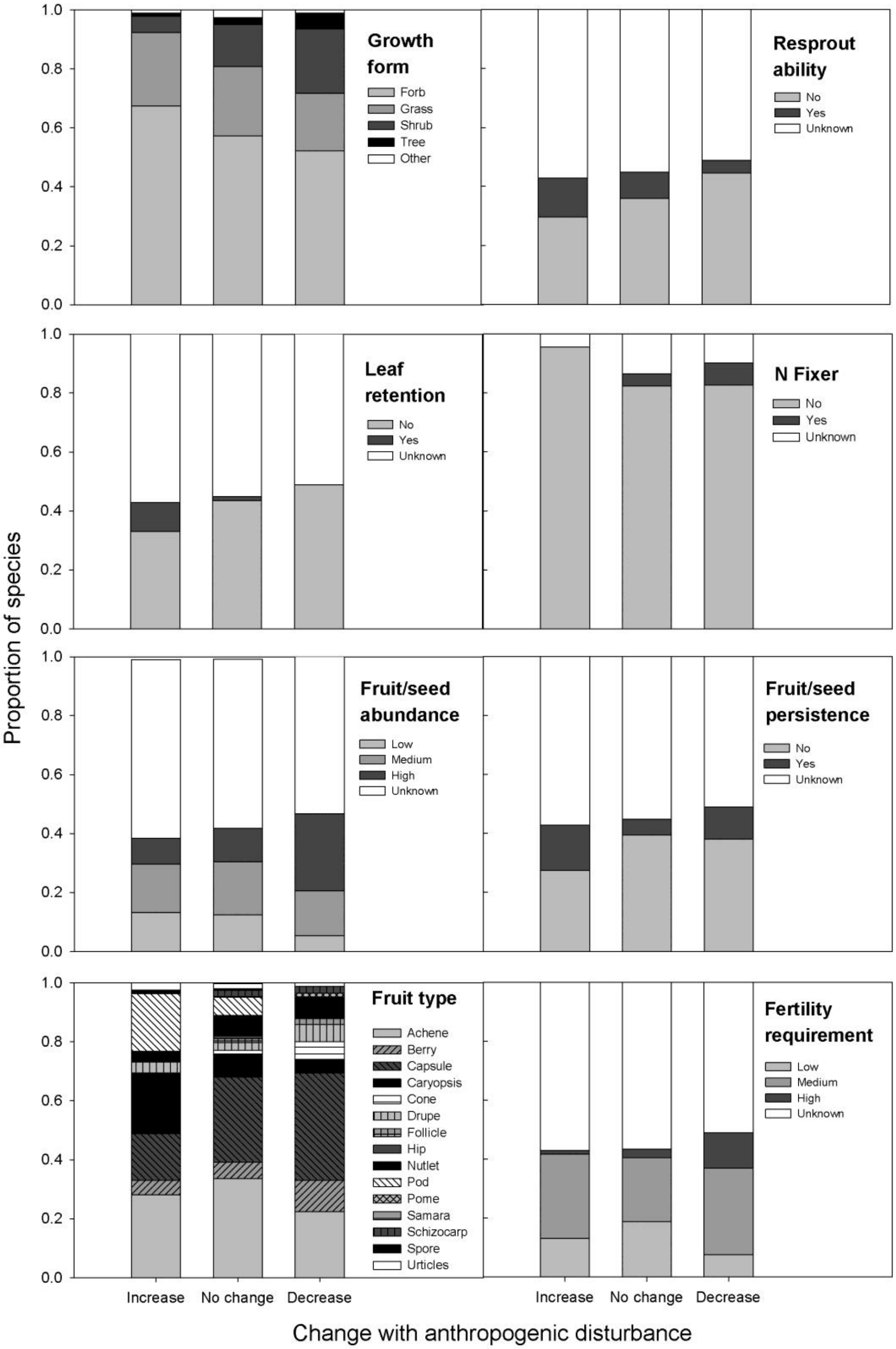

Fig. 4- 3. Proportions of species exhibiting various phenotypic functional traits relative to probability of species increase or decrease with anthropogenic disturbance. Only traits with significantly different proportions among increasers and decreasers shown. Statistics presented in Table 4-1.

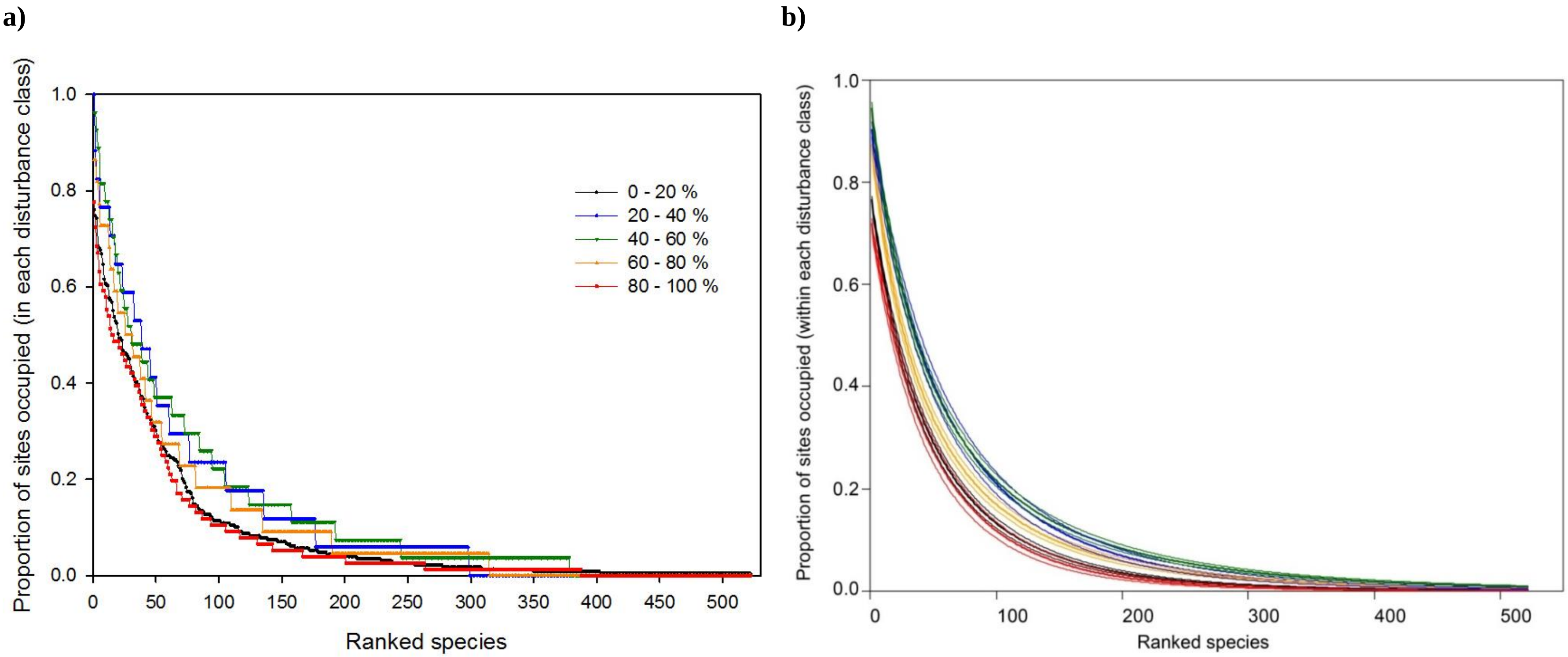

Fig. 4-4. Rank species occupancy curves. **(a)** RSOC data: each site is classified by percent anthropogenic disturbance into one of five ranges. Dots indicate occupancy of each species within each individual land use class. Species are ranked in order of increasing proportion of sites occupied. Occupancy was assessed for each individual disturbance class such that the first ranked species has the greatest occupancy within a given class and may be different across classes. **(b)** Best fit exponential decay models of RSOC distributions in (a). Colours correspond to (a). Thick lines indicate model fit, thin lines indicate 95 % confidence intervals, where lack of overlap in intervals indicates statistically significant difference in model.

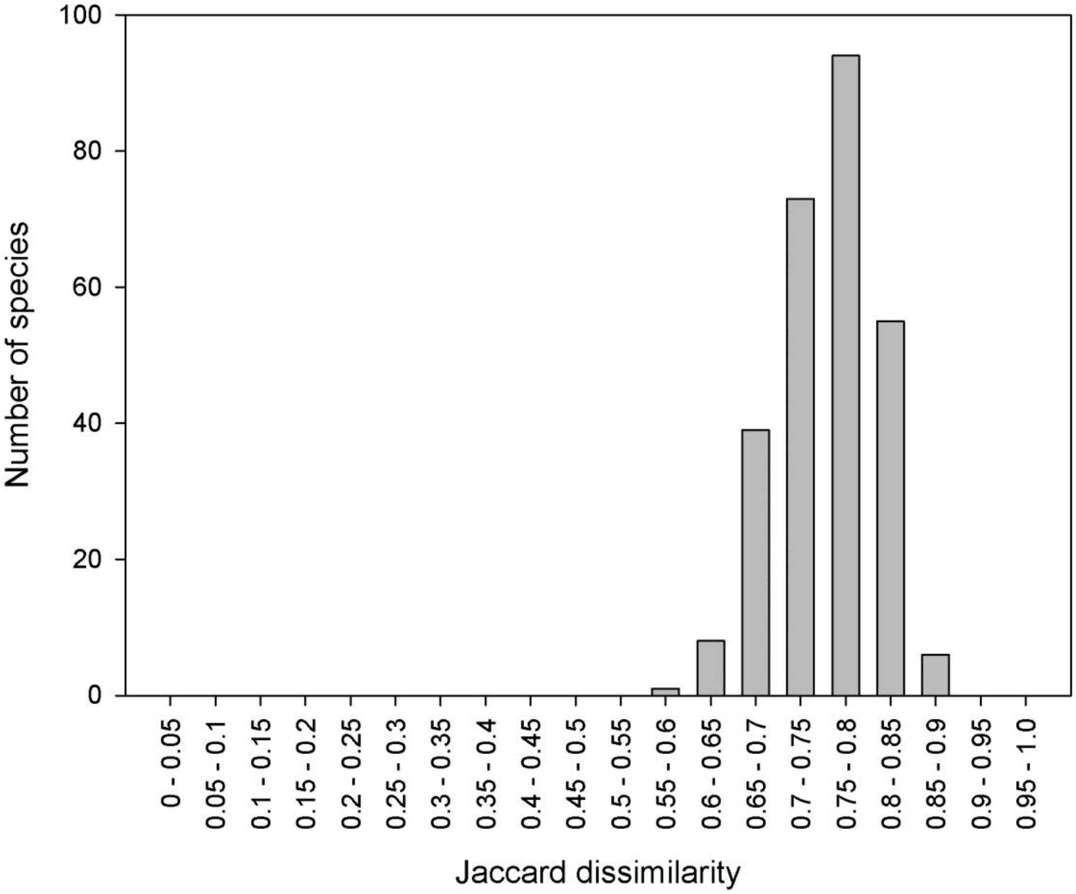

Fig. 4-5. Frequency histogram of Jaccard dissimilarity index of 'niche width'. Species with high dissimilarity co-occur with a wide variety of other species. No species were observed with low dissimilarity, indicating little fidelity to co-occurring species.

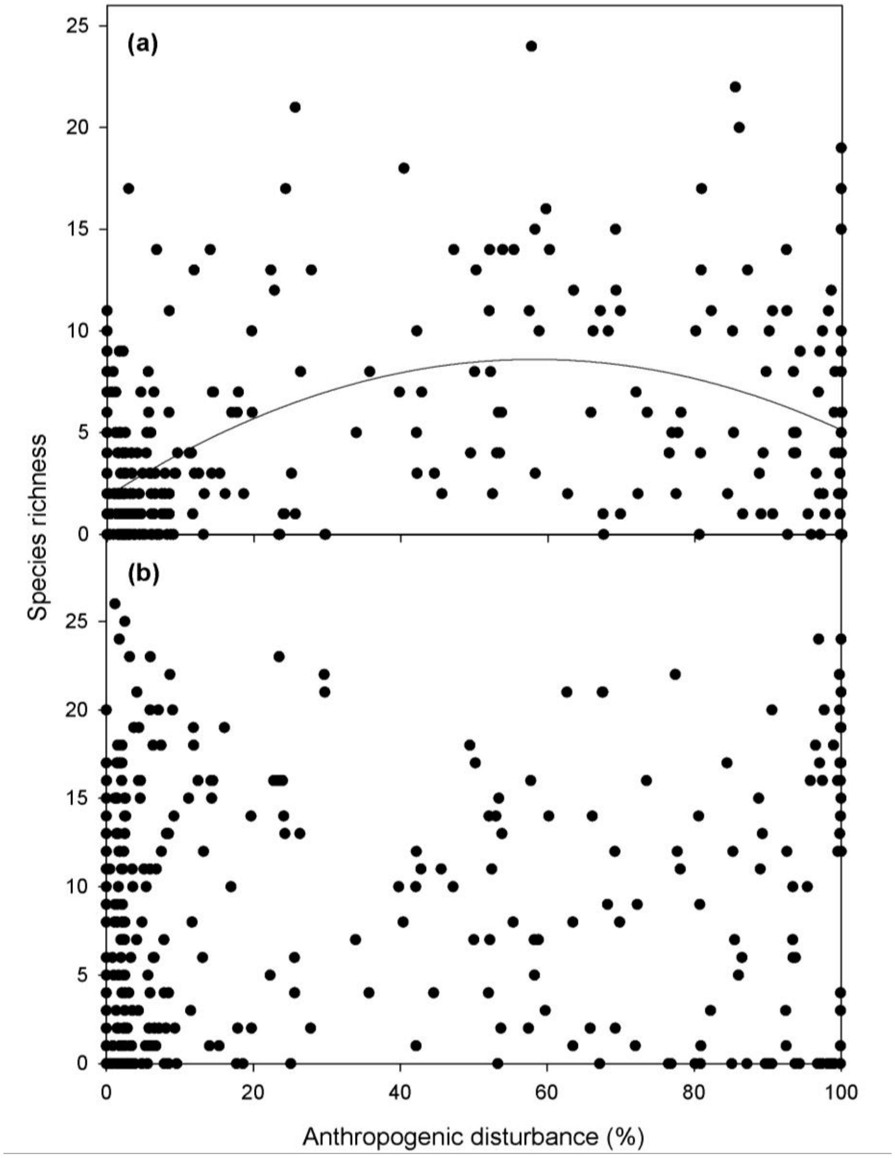

Fig. 4-6. Species richness relative to percent anthropogenic disturbance extent of **(a)** the 50 most 'generalist' species observed ($y = 0.00199x^2 + 0.232x + 1.855$, $R^2 = 0.242$, $p < 0.001$), and **(b)** 50 most 'specialist species ($y = 0.000922x^2 + 0.0970x + 7.177$, $R^2 = 0.010$, $p = 0.050$). Best fit polynomial regression line shown in (a), no ecologically significant trend for (b).

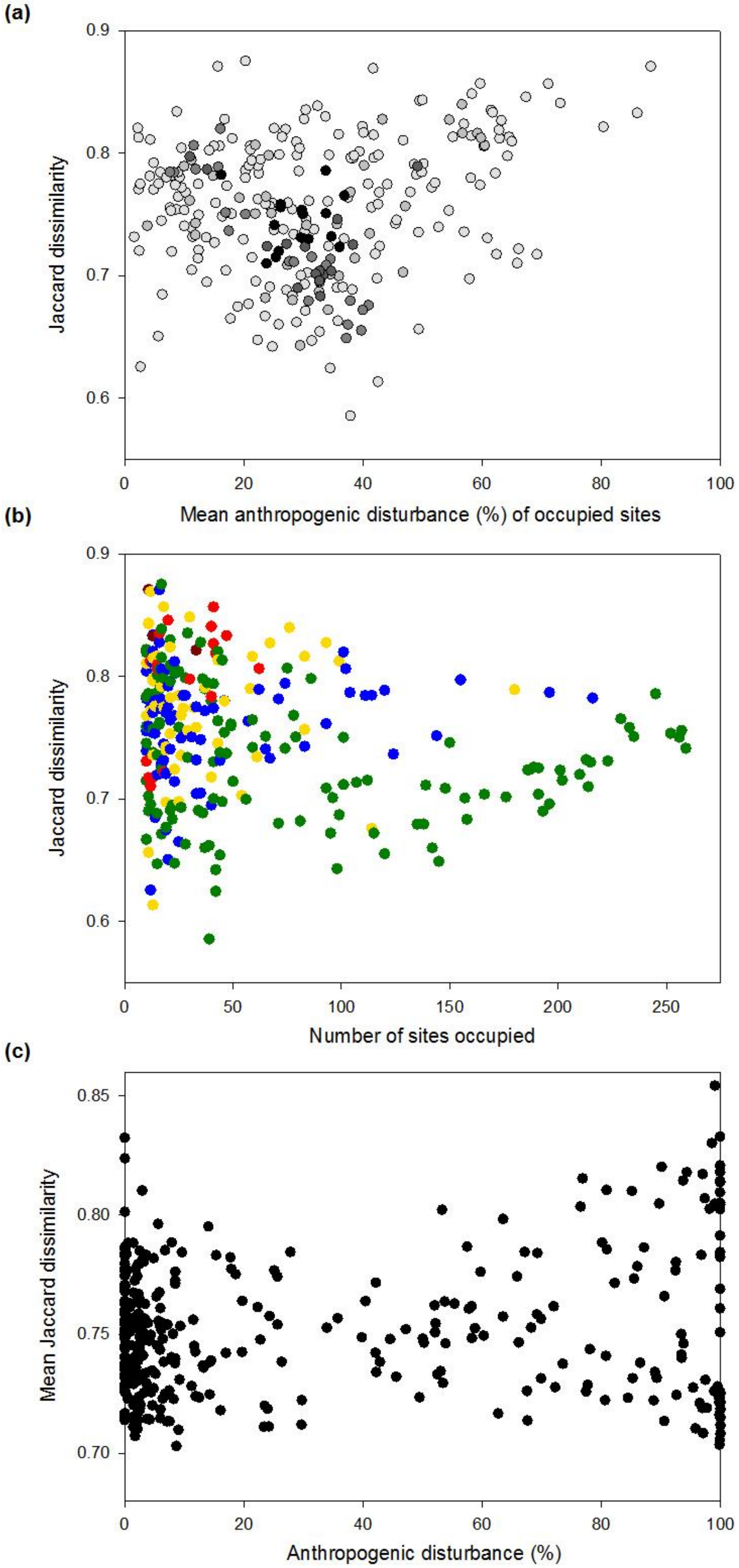

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Fig. 4-7. Vascular plant species specialism and anthropogenic disturbance extent (%). Jaccard dissimilarity is an index of 'specialism' (lower values) to 'generalism' (higher values) ranging from 0 to 1. It is calculated based on species co-occurrence; in effect it measures turnover in co-occupants experienced by the focal species. **(a)** Species generalism as a function of the mean anthropogenic disturbance extent across sites occupied by the focal species. Dots represent individual species and darker shading indicates species occurring in more sites. **(b)** Species generalism relative to site occupancy. Dots represent species, and warmer colours indicate species with higher mean anthropogenic disturbance in occupied sites. **(c)** Community generalism relative to percent anthropogenic disturbance extent. Each dot represents a site, and the mean Jaccard dissimilarity is the average Jaccard index across species occurring at that site.

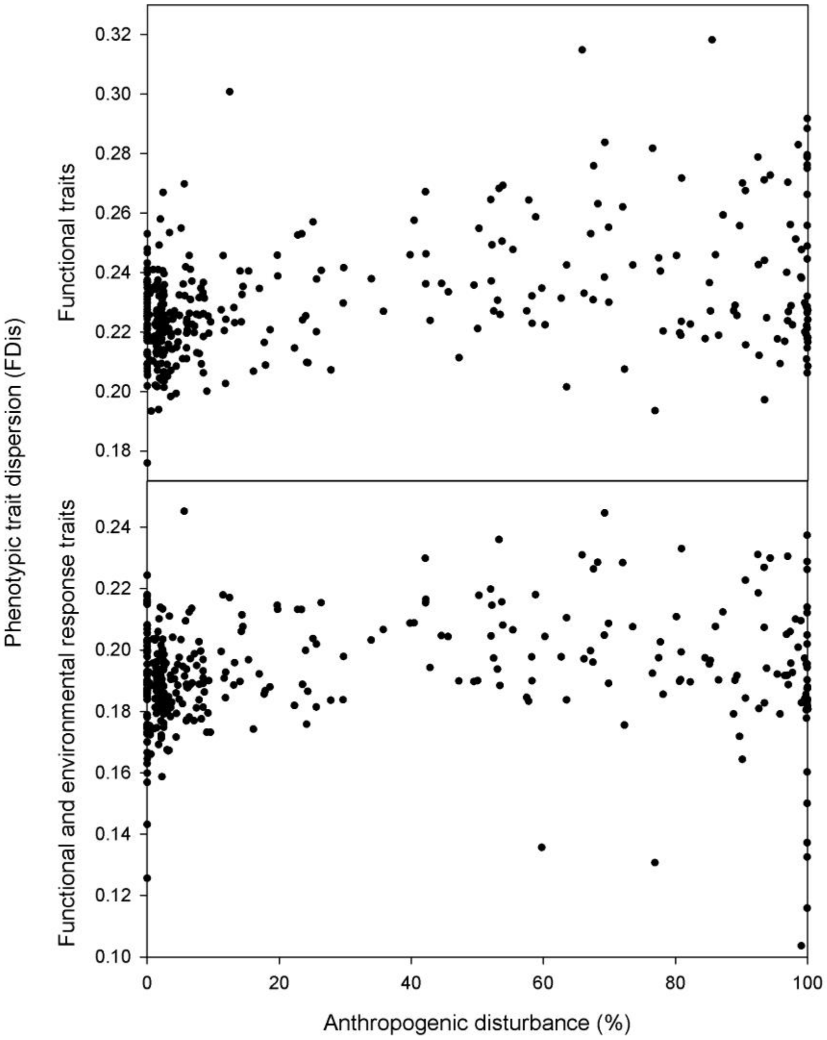

Fig. 4-8. Dispersion of phenotypic traits (FDis) of boreal vascular plants in relation to percent anthropogenic disturbance. FDis is a multidimensional index of trait diversity calculated from a Gower dissimilarity matrix of phenotypic traits (see Table 2 for trait descriptions). **(a)** Dispersion of 30 functional traits (i.e. those related to growth, dispersal, or reproductive) of occupant species relative to the disturbance percentage at each site, i.e. those related to growth, dispersal, or reproductive. **(b)** Dispersion of the functional traits in (a), plus environmental response traits, all relative to percent anthropogenic disturbance.

Chapter 5: Discussion and conclusions

In this study, I began in many ways with only a very broad and general question: "How does human disturbance influence ecological systems at scales relevant to regional land use planning and management." This is undeniably an ecological question, but not one easily answered. Let us consider why it is difficult to answer.

First, controlled experimental manipulation on a large regional scale is generally impossible (Gaston & Blackburn, 2008). This somewhat limits us to biogeographical and observational approaches. To best understand long term responses of plant communities to human land use across a large region, standardized and spatially extensive, frequently repeated surveys over decades are required (Magurran et al., 2010). Unfortunately temporally extensive data of this sort are relatively rare. Lacking widespread temporal sequences of shifts in communities, particularly in this region, I instead use a widespread distribution of standardized sample sites varying in human land use.

One challenge in using field data collected by many different individuals, however well trained, is that not all species present are necessarily observed. This error in detection can impact many types of data sets (MacKenzie et al., 2006). Detectability can be addressed by either repeated sampling or by imposing a correction factor. However, the benefits of repeated sampling to account for detectability may not outweigh the additional costs in time and effort, or in reduced sampling of new location (Kendall & White, 2009; Lele et al., 2012). Greater inference, even if slightly imprecise, may be achieved by sampling more locations than resampling the same ones. Imposing correction factors can also be problematic, because there is inherent uncertainty in the factor itself, so one may be correcting one uncertainty with another—interpretation of such adjusted results may be more strained (Kendall & White, 2009). Overall, detection rate is likely very good for these data as the survey protocols were developed to optimize detection (ABMI, 2009). While never perfect, detection rate of species in ABMI surveys has been studied and considered adequate (Lele et al., 2012), and it is likely better than other surveys of comparable scale by citizen scientists.

Disturbance data

Because I considered only total extent of human land use as the measure of disturbance within each plot, many aspects of anthropogenic disturbance may have been overlooked. Not least of these are spatial pattern of the disturbed and undisturbed components, including connectivity to surrounding the landscape (Fahrig, 2002; Turner, 2010). However, the effects of fragmentation and spatial configuration are usually less pronounced than that of loss per se (Fahrig, 2003).

A shortcoming of this study of disturbance in the boreal is an almost complete lack of analysis of natural disturbance. Areas without human land use were considered ‘undisturbed’ but in reality, landscapes undisturbed by human use consisted of a wide variety of conditions varying not least in natural disturbance. Although analysis in Chapter 2 suggested natural disturbance played an insignificant role in species richness, this finding was probably related to poor detail in data. Although a comparison of natural and anthropogenic disturbances on diversity and community structure would have been ideal, the available natural disturbance data that could be linked to ABMI sites with undisclosed locations was of poor quality. As data availability and quality increases, this line of inquiry could prove very interesting and fruitful.

This thesis explored disturbance throughout a large region, on a 0 – 100 % gradient in human land use. The conclusions drawn for biodiversity and community structure at high land use proportions likely underrepresent potential community level biodiversity changes in response to the *total* land use throughout the region, or at scales much larger than that investigated in Chapter 3. This is because of broad cumulative effects of regional scale land use which are likely not captured in this thesis. For example, my analyses do little to inform us of possible thresholds in metapopulation or metacommunity dynamics, or extinction cascades. Further, the results say very little about the total biodiversity of the region as a whole. They should not be construed as predictive of regional extinctions, for example.

Should the intermediate disturbance hypothesis be abandoned?

IDH is a poorly defined hypothesis with many interpretations (Sheil & Burslem, 2013; Fox, 2013). However, it is most often associated with a trade-off among species adapted to early successional (or high disturbance) environments versus those adapted to late successional (or low disturbance) environments. Disturbance is thought to prevent competitively dominant species from excluding species poorly competitive but disturbance-tolerant species. In a recent opinion piece arguing that the IDH should be abandoned, Fox (2012) rejects a number of mechanistic models that lead to unimodal diversity-disturbance curves, models which Sheil and Burslem (2013) consider satellite ideas to Connell's (1978) original IDH. But Fox skims past the mechanism (the competition-colonization trade-off) which most ecologists widely associate with IDH, that of Connell (1978), accepting it as "a logically valid mechanism which can produce stable coexistence, and peaks in diversity at intermediate disturbance levels" (Fox 2012, pg. 90), and arguing that it shouldn't be confused with the other mechanisms which he rejects. In arguing against 'IDH-like' models for stable co-existence, Fox ironically made Connell's IDH seem more likely due to the elimination of related models – the exact opposite conclusion drawn by Fox.

In light of this debate, the IDH might be better thought of as a predicted pattern rather than a mechanistic model or process. The unimodal richness-disturbance relationship is an observed pattern predicted by IDH, so the observation is *consistent with* and *supports* the hypothesis, but in itself does not necessarily mean the pattern was produced by disturbance or a colonization-competition trade-off. Additional support came from the NMDS in Chapter 2, which showed different communities were present in areas of low versus high disturbance, with much overlap in composition at intermediate disturbance, suggesting a trade-off between disturbance tolerant and disturbance intolerant species, which may imply a colonization-competition trade-off as a generating mechanism. Of course these patterns alone are insufficient to conclude any mechanistic process is occurring in nature. Mechanism is often best elucidated with controlled experiments. IDH has support from some experiments but not others (Mackey & Currie, 2001), suggesting IDH is not universal under all conditions and circumstances, but nonetheless appears to be a mechanistically plausible outcome. In any case, my purpose in this thesis was not to test the mechanics behind the outcomes of disturbance, but to examine the outcomes themselves.

Value judgements in ecology and conservation.

Conservation biology is a value driven science which at its core places value on conserving nature. It is a rare sort of science that accepts a bias as its starting point. In Chapter 4, I tested the general hypothesis that communities impacted by human land use disturbance are ecologically impoverished, that they are more compositionally and functionally homogeneous, and composed of less desirable species. Impoverishment and desirability are clearly not unbiased terms. However, it is reasonable to assume that declines in species at risk are generally undesirable, at the very least if considered in isolation (the values of economic prosperity, human well-being, etc. might modify the isolated value).

But even simple value statements in conservation are fraught with difficulty. Generally, greater biodiversity is valued, for example, so how could higher biodiversity be viewed negatively? Fifty years following Elton's writings on Invasion Ecology, ecologists now question whether exotic species should be controlled or even considered detrimental (Davis et al., 2011). Have I been prejudiced against exotic species? Even if one views "naturalness" as a positive condition (Cole & Yung, 2010), this involves a trade-off between achieving a past (perhaps pre-Colombian or pre-industrial) condition which might involve 'unnatural' active management by humans, and a *laissez faire* approach without active management that permits nature to take its course, even if this means inevitably 'unnatural' conditions like exotic species.

Scope and Conclusions

The results generally support the intermediate disturbance hypothesis (IDH) in this boreal vascular plant system at several scales. Further, several findings of Chapter 4 are consistent with the IDH (though may not offer direct support). A roughly equal number of species increased as decreased with disturbance extent. Species trait characteristics varied along the disturbance gradient. The most generalist species were richer at intermediate disturbance, but overall specialism was unrelated to disturbance. Surprisingly, functional trait dispersion was also unrelated to disturbance.

Given the spatial scope of the underlying data, general patterns observed in this thesis are likely to apply across other boreal vascular plant regions. The poor sensitivity of many community metrics explored was surprising given the extent and intensity of disturbances observed. The results challenge the generality of expected disturbance-dependent trait dispersion and specialism.

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