Understanding Ecological Response to Disturbance: Mechanisms and Management Strategies in a Changing World

by

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B.Sc., University of Texas, Austin, 2008

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Abstract

Ecosystems in the modern world face a vast array of disturbances, from globally shifting abiotic conditions, to increasingly variable extreme natural events, to high intensity discrete human-caused disturbances. Well-developed, applicable theoretical frameworks on how ecosystems can respond to and withstand these disturbances are needed for adequate management of valued ecological systems. To date, the most promising theoretical development for understanding ecological response to complex sets of disturbances is resilience. Ecological resilience acknowledges non-linear ecosystem behavior, incorporates the role of slowly changing environmental parameters in ecological dynamics, and offers one of the few potential methods to predict, and avoid, impending ecological collapse. However, as ecological resilience has evolved conceptually to include social, political, and economic fields, it has become increasingly difficult to clearly define in, and apply to, managed ecosystems. This dissertation pairs ecological resilience with other, well-established attributes of ecological response to disturbance, namely resistance, persistence, and recovery. By doing so, we can clearly define and quantify each attribute in a range of ecosystem types and over a variety of ecological scales. In Chapter 1, we use microcosm communities to test the relationship between one potential mechanism, landscape connectivity, and multiple attributes of ecological response to disturbance including resistance, resilience, and recovery. We find that each attribute responds uniquely to connectivity, and that generalizing the role of connectivity over all three may give an inaccurate prediction of how ecosystems may respond to individual disturbances. In Chapter 2, we experimentally investigate the presence of early warning indicators of approaching critical thresholds. Using water table drawdown treatments in bog, we test for critical slowing and increased autocorrelation as the bog approaches a transition to forest. We find that critical slowing is clear in composition and moss cover, but that autocorrelation is not apparent. The decoupling of critical slowing and increased autocorrelation could be due to a number of complex ecosystem dynamics, all of which are common in ecosystem management globally. Thus, early warning indicators likely need further development if they are to become applicable. In Chapter 3, we observationally study how conservation management actions may increase or decrease ecological resilience. In particular, we explore how invasive species management intensity correlates with changes in functional redundancy, response diversity, and spatial occurrence of regime shifts in Garry oak meadows. We find that more intense management correlates with less area lost to woody encroachment and increases in functional redundancy through time. However, the relationship was strongly mediated by individual landscape settings. Finally, in Chapter 4, we scale up to a provincial study, investigating persistence of ecosystems and large mammal species in the face of the continuous pressures of land use change. In the results from all four chapters, it is clear that individual attributes of ecological response to disturbance, *i.e.* resistance, persistence, resilience, or recovery, all play unique roles in ecosystem dynamics. Additionally, the metric chosen to quantify each attribute can play a pivotal role in how we interpret observed dynamics. The work in this dissertation highlights that we cannot understand or predict ecological response to disturbance without clear, measurable concepts. Around a single state of interest, resilience is only one among a suite of attributes that are important to understand. Its additional strength, of potentially predicting the occurrence of ecological thresholds, is still being developed as we explore methods of quantification and application in individual ecosystems.

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Glossary

Alternative stable states (adapted from May 1977) – systems that are capable of persisting in multiple unique configurations and structures given a single set of environmental conditions; small perturbations result in a return to the current configuration, where large perturbations can result in shifts to an alternative configuration

Autocorrelation (Scheffer 2009) – correlation between sequential observations in a time series; described by lag times (lag-1 is correlation with itself in the previous year, lag-2 two years previous, *etc.*)

Basin of attraction (adapted from Beisner *et al.* 2003) – range of parameters within which ecosystems will return to a particular equilibrium state after perturbation

Bifurcation (Andersen *et al.* 2009) – a qualitative change in the behavior of a dynamical system resulting from a small change in a system parameter

> *Saddle-node/folded bifurcation* (Scheffer 2009) – type of bifurcation that is characterized by hysteresis; involves two alternative stable states with an unstable state between them (see **Figure 2.1**, **panel c**)

Critical slowing (van Nes & Scheffer 2007) – slowed rate of recovery after small perturbations in ecosystems as the approach a threshold

Disturbance (Lake 2000) – potentially damaging forces are applied to habitat space occupied by a population, community, or ecosystem

> *Pulse disturbance* – short-term and sharply delineated disturbances (*e.g.* fire)
>
> *Press disturbance* – disturbances that may arise sharply and then reach a constant level that is maintained (*e.g.* isolation)
>
> *Ramp disturbance* – disturbances with steadily increasing strength over time. Ramp disturbances may have no endpoint, or reach an asymptote after an extended period (*e.g.* nutrient deposition)

Ecological resilience; shortened in subsequent use to **resilience** (Holling 1973) – magnitude of disturbance that can be absorbed before the system changes its structure by changing the variables and processes that control behavior

Engineering resilience; shortened in subsequent use to **recovery** (Pimm 1984) – speed at which variables return towards their equilibrium following a disturbance

Equilibrium (adapted from Beisner *et al.* 2003) – ecological state that persists through time and to which the ecosystem will return after small perturbations

Functional trait (McGill *et al.* 2006) – a well-defined, measurable property of organisms that strongly influences organismal performance; usually measured at the individual level and used comparatively across species

> *Effect trait* (Lavorel & Garnier 2002) – functional traits that impact biogeochemical processes in the system
>
> *Response trait* (Lavorel & Garnier 2002) – functional traits that shape a species response to disturbance

Hysteresis (Andersen *et al.* 2009) – a property of systems that can follow different paths under an increasing disturbance than it will once the disturbance begins to decrease; *i.e.* an overlap in the environmental conditions underlying two alternative stable states

Persistence (adapted from Grimm & Wissel 1997) – continued existence through time of an ecological system or value

Perturbation (Lake 2000) – combination of disturbance and resulting response in community

Recovery – see definition for **engineering resilience**

Regime shift (Kinzig *et al.* 2006) – change from one state to another in an ecosystem, accompanied by alterations in the internal controls and feedbacks in the ecosystem

Resilience – see definition for **ecological resilience**

Resistance (Pimm 1984) – the degree to which a variable is changed after a disturbance

State [of an ecosystem]; used here interchangeably with **community** and **ecosystem** (Levin *et al.* 2009) – the conditions of an ecosystem at a given point in time and space, especially as defined by either the dominant species or composition of species and associated processes

Threshold; used here interchangeably with **tipping point** (Andersen *et al.* 2009) – the critical value of an environmental driver for which small changes can produce an ecological regime shift

Acknowledgements

When I first started, I was told that finishing a PhD is 80% persistence. Persistence, as defined in my very own dissertation here, is simply ‘continued existence through time’. It is strange to get to this point and realize that most of the reason I am here, that I finished, is simply because I just kept going. In writing my acknowledgements, then, I need to start with why I could keep going.

At the lowest dips, and at the highest peaks, I had my husband. He’s a warm, silly, source of stability who doesn’t care to understand the inner-workings of academia, and he always, always reminds me that this is a job, not a life, and that he is deeply proud of me. On the other end of my phone I have had my mother, who sighs and laughs at all the right moments, regardless of how she is feeling that day. At every ping of WhatsApp, I had my Roomie, who sent me endless photos of my growing nephew in all his joy and curiosity, his stumbles and his triumphs. He feels each of those far more than I can ever feel the success of a published paper or the frustration of a rejection.

Why I kept going was the sway of the boat on anchor, King Boogie’s pattering footfalls on the deck, the challenge of a new project to shout about with Adam until it all came together, and the loving support of the Bluewater Cruising Association talking about how wide the world is. Oh, and Darrell sneaking over the cinnamon buns just when I needed them.

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You guys are awesome!

General Introduction

Since the scope and breadth of human effects on the globe have become more apparent, our concepts and definitions within ecology have had to expand to incorporate new concepts on disturbance and ecological dynamics. As late as the mid-1980s, for example, a disturbance to an ecosystem was regarded as a discrete event in time causing an ecological response (Pickett & White 1985). Some definitions were even more limited, with disturbance only encompassing mortality-inducing events in ecosystems (Sousa 1984). Yet only a few years before, Charles Keeling and his colleagues had published his now infamous graph of CO_2 records from Mauna Loa, Hawaii (Keeling *et al.* 1976). By 1990, the Intergovernmental Panel on Climate Change released their first global Assessment Report (Houghton *et al.* 1990), and ecologists were faced with an undeniably changing world. Some of the most relevant questions became about how ecosystems will respond to continuously increasing global changes. The accepted definition of disturbance broadened, gradually including long term pressures on ecosystems that may have no foreseeable end (Lake 2000).

In parallel, ecologists' understanding of ecological dynamics was going through its own evolution. The traditional view of deterministic climax communities (Clements 1916; Horn 1974) and ecological stability (see Goh 1975) was coming under criticism (e.g. Whittaker 1967; May 1973). In 1969, Lewontin first proposed that ecosystems may have multiple stable states in any given location (Lewontin 1969). Years later, C.S. 'Buzz' Holling (1973) situated Lewontin's ideas into a framework that would change ecology. He separated ecological stability through time from the ability of an ecosystem to maintain a particular state through disturbance. An ecosystem lacked resilience when a disturbance led to a fundamental change in its identity, *i.e.*

when a disturbance tipped the ecosystem into another stable state. The underlying tenet was that ecosystems may have multiple stable states, an idea that gained initial traction in ecosystem modeling (e.g. Lewontin 1969; May 1977; Wissel 1984). In years since, research on the theory and application of ecological resilience has grown exponentially, linking fields of disturbance ecology, system dynamics, and social sciences to create a broad field of its own (Curtin & Parker 2014).

Questions about ecological response to disturbance have gained in importance since most ecosystems now face a variety of disturbances in tandem. Climate shifts are paired with harvest pressure, increasingly extreme natural events, and human land use change. Multiple disturbances can lead to synergisms (Crain *et al.* 2008) and unexpected outcomes (Darling & Côté 2008). The rise and expansion of conservation biology (Soulé 1985; Kareiva & Marvier 2012) and more recently ecological restoration (SER 2004; Suding 2011; Miller *et al.* 2017), has enriched ecological theory. At the same time, increasing recognition of the complex socio-ecological systems that frame ecological dynamics as one small part of a larger whole has led to a systems approach to resilience research and management (Folke *et al.* 2002; Walker *et al.* 2004). Thus, resilience, once defined as a single aspect of ecosystem response to disturbance (Holling 1973), became a broad concept that spans ecological, mathematical, social, political, and economic disciplines (Brand & Jax 2007).

The rapid expansion of resilience theory is driven by the seemingly intractable questions and problems that many ecosystem researchers and managers face. The benefits of a broad, overarching framework, however, are potentially offset by a lack of clarity. An evolving definition of resilience has created a crowd of quantitative, qualitative, and normative interpretations of the term (Grimm & Wissel 1997; Brand & Jax 2007). Even at its inception, suggestions on how to measure ecological resilience were relatively vague and largely mathematical (Holling 1973). With the added complexity and confusion of definition, clearly quantifying resilience as a system attribute can be prohibitively difficult (Standish *et al.* 2014). Its relevance to individual ecosystems is also an open question. The theoretical foundations of resilience concepts still rest on alternative stable states, yet whether that is the rare exception or the undiscovered norm in ecological communities is still unknown (Schröder *et al.* 2005).

It is no coincidence that the major thinkers behind resilience are the original developers of adaptive management techniques (e.g. Holling 1978; Gunderson 1999). Both focus on the ecological unknown, the surprises and dramatic changes that can occur in an ecosystem (Walters 1986; Walters & Holling 1990; Walker 2008). The lessons of unpredicted population collapse (e.g. Myers *et al.* 1997; Lever *et al.* 2014) and sudden, devastating of loss entire ecosystems (e.g. Darkoh 1998; Lambers 2003) reinforce the importance of continued research in resilience. For ecosystem managers, however, resilience may be most useful when clearly defined as one attribute of ecological response to disturbance and paired with other key aspects. Ultimately, ecosystem researchers and managers are interested in whether ecological communities can withstand disturbance, how much change an ecological community can absorb, and how ecological communities recover from discrete disturbances.

The research in this dissertation focuses on ecological resilience as originally conceived, as the amount of disturbance or change that an ecosystem can absorb before transition to an alternative stable state. We focused on this definition because it is a potentially measurable attribute of an ecological community. However, by narrowing our definition, we risk excluding other important aspects of ecological response to disturbance. Thus, this work gives weight to other attributes of ecological response to disturbance, notably resistance (Pimm 1984), recovery (Pimm 1984), and persistence (Grimm & Wissel 1997). These aspects of disturbance response focus on how ecosystems behave around a single equilibrium during and after a disturbance event. Clearly delineating each aspect of response allows flexibility in the types of disturbances we consider as well as in the ecological communities, and their underlying dynamics, that we study.

Each chapter investigates different aspects of ecological response to disturbance. The first chapter assesses connectivity as a mechanism facilitating the ability of an ecosystem to withstand and recover from disturbance. By experimentally testing its role in resistance, resilience, and recovery, the study begins to parse apart whether different attributes of ecological response are driven by the same manageable landscape characteristic. The second chapter investigates whether early warning indicators of ecological collapse are detectable in a field setting. Most managed ecosystems are poorly understood yet face continuous, slow changes in environmental conditions (Gunderson 1999; Zalasiewicz *et al.* 2010). The ability to detect potential thresholds in how the ecosystem responds to environmental changes may be key to managing and mitigating the impacts of climate change, land use change, nutrient shifts, and other global disturbances. The third chapter focuses on how we can measure resilience in managed ecosystems. Conservation management techniques may, or may not, positively influence the resilience of ecological communities to local and global disturbances. By outlining quantitative metrics of resilience, we can track how resilience changes through time and corresponds with differing management intensities. Finally, the fourth chapter is a cumulative effects assessment of British Columbia and impacts to large mammal ranges in the province. Land use change, the largest threat to global biodiversity (Millennium Ecosystem Assessment 2005), is a constant disturbance on ecosystems and individual species' populations, generally of increasing intensity. To plan and manage land use on large scales, there is a great need to understand how particular species can persist in the face of differing land use types, scales, and intensities.

Every chapter deals explicitly with how ecological systems respond to disturbance. In chapters one and two, resilience concepts are combined with recovery dynamics around a single state. In chapters three and four, the two observational pieces, we focus more closely on resilience dynamics, investigating potential drivers of resilience or ecological collapse. In each case, theoretical concepts are applied to real communities at different scales, with the ultimate goal of understanding whether and how each concept can be applicable to ecological management. We use experimental, observational, and statistical methods in tandem, finding trends that cross methodologies and scales to help generalize our findings. Predicting ecological dynamics, pinpointing manageable mechanisms, accurately monitoring resilience in field settings, and laying the foundation for predictive models of species persistence all deeply reflect management interests in the burgeoning field of resilience research. By using resilience as only one attribute of ecological response to disturbance, flexibility and clarity in understanding ecological response to disturbance are made more achievable.

Chapter 1 : The role of landscape connectivity in resistance, resilience, and recovery of multi-trophic microarthropod communities

with Rachel J. Standish, Zoë Lindo, and Brian M. Starzomski

Abstract

There is a need to find generalizable mechanisms supporting ecological resilience, resistance, and recovery. One hypothesized mechanism is landscape connectivity, a habitat configuration that allows movement of biotic and abiotic resources between local patches. Whether connectivity increases all or only one of resistance, resilience, and recovery has not been teased apart, however, and has been difficult to test at large scales and for complex trophic webs. Natural microcosms offer a complex system that can be manipulated to test questions at a landscape-scale relative to the community of study. Here, we test the role of connectivity in altering resistance, resilience, and recovery to a gradient of heating disturbance in moss microcosms. To test across trophic levels, we focused on community composition as our metric of response and applied three connectivity treatments – isolation, connected to an equally disturbed patch, and connected to an undisturbed patch. We found that connectivity between equally disturbed patches boosted resistance of communities to disturbance. Additionally, recovery was linear and rapid in communities connected to undisturbed landscapes, hump shaped when connected to equally disturbed landscapes, and linear but slow in isolated communities. We did not find thresholds on the disturbance gradient at which disturbed communities exhibited zero or increasing dissimilarity to controls through time, so were unable to draw conclusions on the role of connectivity in ecological resilience. Ultimately, isolated communities exhibited increasingly variable composition and slow recovery patterns even in control communities when compared with connected treatments.

Metric Details

State – community composition of a single experimental unit; no assumptions are made about stability or natural variability of individual states

Reference state –the compositional centroid of all control communities within a certain treatment at a certain time point

Resistance – the compositional dissimilarity between disturbed communities immediately post-disturbance and the reference community

Resilience – disturbance intensity at which long-term recovery trends significantly change; *i.e.* the tipping point on the disturbance gradient at which compositional dissimilarity from the reference community significantly increases

Recovery – rate of decrease through time in compositional dissimilarity between disturbed communities and the reference community

Introduction

Effective management of ecological communities requires that we understand how, and by what mechanisms, communities are able to absorb and recover from disturbance. The response of a community to disturbance can be conceptualized as a multi-staged process. Given a discrete disturbance event, a community will often experience an immediate change in abundance, diversity, and/or composition typically followed by recovery to its pre-disturbance trajectory (e.g. Peterson & Stevenson 1992; Hershkovitz & Gasith 2013). The resistance of a community determines how large the initial change is; higher resistance implies that less change occurs (Pimm 1984). As time passes post-disturbance, a community may return to its pre-disturbance state (state here meaning community composition and structure within a range of variation (Westoby *et al.* 1989)) along a recovery trajectory. In some cases, communities are not able to recover to the pre-disturbance trajectory. This can occur, for example, if positive feedbacks are broken or shifted (Suding & Hobbs 2009), if keystone species are lost from the system (Peterson *et al.* 1998), or if altered *in situ* resources (*e.g.* soil seedbanks) prevent recovery (Cramer *et al.* 2008). Ecological resilience is the amount of disturbance an ecosystem can absorb before it loses its ability to recover to a pre-disturbance state; *i.e.* the amount of disturbance an ecosystem can withstand without undergoing a state change (Holling 1973).

Though each of these three concepts (resistance, resilience, and recovery) is theoretically unique, they have proven difficult to quantify and disentangle in studies of community response to disturbance. This situation arises in part because the same mechanisms and processes that increase one may also lead to increases in the others (Nimmo *et al.* 2015). For example, species diversity has been proposed as a driver of recovery and resilience (McCann 2000), allowing a community to maintain and recover ecological function post-disturbance as multiple species respond in diverse manners (Elmqvist *et al.* 2003). Similarly, connectivity is thought to increase the ability of a community to resist and recover from disturbance (Standish *et al.* 2014). Ecological resilience can be increased through connections with specialized habitat and external populations. For example, coral reef systems have been shown to benefit from connectivity to mangrove islands that act as nursery habitats for coral reef grazers and increase resilience to bleaching by preventing coral collapse into an alternative algal state (Mumby & Hastings 2008). Additionally, recovery speed can be increased through propagule dispersal from connected patches. For example, macrobenthic recovery after experimental smothering was significantly accelerated by connectivity to regional species pools (Thrush *et al.* 2013). Resistance, though less understood in the context of connectivity, may be influenced by increased connections to refugia. Forest patch connectivity with moist granite outcrops has been shown to provide refuge potential for mammal communities during fire, increasing resistance to that disturbance (Keith *et al.* 2002). Thus, diversity and connectivity are likely mechanisms supporting all three components of community response: resistance, resilience and recovery.

Though much of the literature has focused on connectivity as a positive aspect of landscape configuration, connections between two habitat patches may also facilitate transmission of a disturbance event. For example, mountain pine beetle outbreaks move through connected patches of Canadian forest (Raffa *et al.* 2008), while fire follows connected vegetation patches (Miller & Urban 2000). When a disturbance moves through connected landscapes without leaving undisturbed areas, benefits of connectivity such as the rescue effect, abiotic resource exchange, and refugia availability (Turner *et al.* 1998) may no longer be relevant. Thus, connectivity may shape community response to disturbance only when the disturbance is heterogeneous among patches (Chapin *et al.* 2002), and specifically, when at least one patch acts as a source of biotic and abiotic resources. Whether these source-sink dynamics are the main mechanism behind the influential role of connectivity in promoting resistance, resilience, and recovery is unknown.

In this experiment, we used microarthopod communities in moss patches subjected to extreme heat to test how connectivity impacts community response to disturbance. Moss cover found on granitic outcrops is simple to collect and to manipulate, and contains abundant microarthropod communities (Starzomski & Srivastava 2007),which are predominantly composed of mites (Acari) and springtails (four orders in Subclass Collembola). Mites are a diverse group of organisms, with estimated global richness exceeding 500,000 species (Krantz & Walter 2009). They are classified into six orders and seven suborders, a subset of which encompasses the majority of microarthropods found in these moss communities. Broadly, this subset includes prostigmatids (order Trombidiformes, suborder Prostigmata), mesostigmatids (order Mesostigmata), and oribatids (order Sarcoptiformes, suborder Oribatida), each of which represents an approximate functional role in the community. Soil-dwelling mesostigmatid and large-bodied prostigmatid mites tend to be carnivores (Klarner *et al.* 2013), while oribatids tend to be generalists, feeding on fungi, but also scavenging on detritus and other dead organisms (Maraun *et al.* 2011). Springtails also tend to be generalists (Scheu 2002) and can be highly mobile (e.g. Bengtsson *et al.* 2004). Together, these communities are complex and dynamic, and can be encompassed at experimental scales to represent an entire landscape. By using these moss-microarthropod communities, we were able to investigate the individual relationships between connectivity and resistance, resilience, and recovery across a disturbance gradient, at a landscape-scale relevant to the organisms under study, and over several generations for the shortest-lived species and one full generation for all but the longest-lived.

We included two connectivity treatments and one isolation treatment. First, we connected a disturbed patch with an undisturbed patch, allowing the undisturbed patch to act as a potential resource. In our second treatment, we simulated transmission of disturbance through a connection by equally disturbing both patches, interrupting the potential for one to act as a source. This design allowed us to investigate mechanisms of connectivity in greater detail. Our final treatment was to fully isolate patches. We further differentiated between stages of community response by separating measures of resistance, resilience, and recovery. We measured resistance as the change immediately post-disturbance and recovery as the rate of return to undisturbed community composition. To measure resilience, defined as the disturbance intensity at which community collapse occurs, we implemented a gradient of disturbance intensities and assessed community response to identify this threshold. As connectivity is a potential driver of all three components, we aim to tease apart its role at each stage of community response to disturbance and understand how connectivity influences the post-disturbance behavior of ecological communities with a view to applying this knowledge to conservation and management.

Methods

Experimental methods

Intact moss (*Racomitrium* spp.) carpets (averaging 1×0.5m) were collected from rock faces within a 10km radius of Victoria, British Columbia, Canada. In the lab, moss carpets were cut into 360 circular mats, each 25cm in diameter, and placed in 5cm deep plastic dishes under a forest canopy of Garry Oak (*Quercus garryiana*) and Douglas fir (*Pseudotsuga menziesii*). Landscapes in ecology are often scaled by the perspective of the study organism (Wiens & Milne 1989; Turner *et al.* 1995) and focus on areas that encompass process and function of the organism (Addicott *et al.* 1987). Our patch size was over 600,000 times the size of the largest species, an area we deemed adequate to cover the full process and function of all organisms.

Dishes had holes in the bottom for drainage and were installed on wooden platforms. Every mat was isolated from other mats for four weeks to allow the microarthropod communities to settle after being disturbed by fragmentation and relocation. The experiment consisted of three treatments: isolated plots (I), plots connected to a disturbed plot (P–D), and plots connected to an undisturbed plot (P–U). Excess moss carpets were stored on a concrete patio adjacent to the experimental area and covered with tarp. To minimize risk of external colonization, tarp was used under and over the moss, with an empty tarp border of approximately a meter on all sides. These were used in the fifth week to create bridges (connectivity) between mats in the P–D and P–U treatments. Dishes with connecting bridges were linked prior to the experiment with plastic, U-shaped connectors, 5cm wide. These were taped closed for the first four weeks, and then opened and filled with moss on the fifth week. We allowed two more weeks for mobile species to begin movement between connected patches after the moss bridges were installed, before experimental disturbance. We had five disturbance intensities (described below) plus an undisturbed control in each connectivity treatment. Communities were destructively sampled over four sampling times with three replicates per time and treatment. In total, 288 moss mats were connected by a bridge, creating 144 experimental units, and 72 moss mats (experimental units) were isolated (**Figure 1.1**).

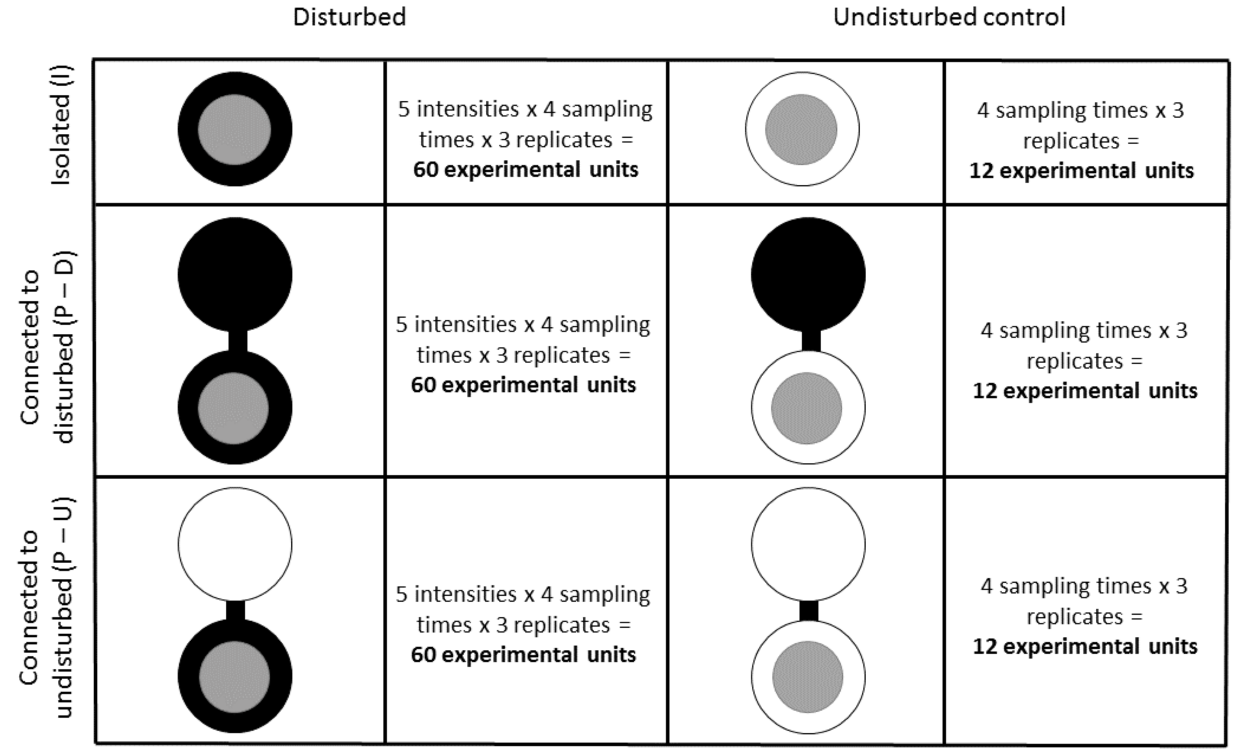


Figure 1.1: Experimental treatments and comparisons

Black circles represent disturbed mats, and white represent undisturbed mats. The grey middle circles represent the moss plug destructively harvested during post-disturbance sampling periods. The number of experimental units are listed in the column to the right of each treatment figure.

Our disturbance gradient was a range of temperatures to induce drying. Southeastern Vancouver Island, where the moss was collected, experiences wet-dry cycles, with cool, wet winters and dry, warm summers (Government of Canada 2017). The lowest end of the disturbance gradient represented a short warm, dry period, while the highest end represented heat not found naturally. At week seven, all experimental units were brought indoors and placed beneath a cardboard tunnel. At the top of the tunnel, we placed a halogen bulb on a rheostat and a cap of aluminum foil. The gradient was established by five rheostat settings (representing low, medium low, medium, medium high, and high disturbance) for 48 hours. Absolute temperatures experienced by the communities varied between and within treatments, but steadily increased according along the expected gradient (rheostat setting of Low = 25.3±6.1°C; Med-Low = 27.2±7.9°C; Med = 31.1±11.8°C; Med-High = 31.1±13.6°C; High = 33.8±11.9°C).. Controls for each treatment were placed under tunnels with no light source (average temperature 21.4±5.7°C). For the P–U treatment, one randomly selected side of the paired plots was left without a light source. We tracked temperature in all tunnels with iButtons for the full disturbance period and used average temperature as a continuous variable to describe disturbance intensity. At the end of the disturbance, we returned the experimental units to their outdoor location.

Sampling occurred two weeks after the disturbance (time 0) to allow moss rehydration and recovery of typical life history habits of surviving organisms. Subsequent sampling occurred at 3, 6, and 9 months after the disturbance. Three mats in each treatment at each disturbance level were destructively sampled at each time point. We cut 5 cm diameter moss plugs (1/5th the size of the patch) from the mats and placed them under Tullgren funnels for 48 hours, increasing the temperature after 24 hours to encourage microarthropod migration into the alcohol mixture (70% ethanol, 30% water) below. Oribatid mites were identified to either genus or species using keys (Krantz & Walter 2009; unpublished keys provided by the Ohio State University Acarology Summer Program). Mesostigmata mites, Prostigmata mites, and springtails were classified into ordinal groups based on morphology. Other microarthropods were broadly identified as: thrips (order Thysanoptera), booklice (order Psocoptera), earwigs (order Dermaptera), beetles (order Coleoptera), spiders (order Araneae), pseudoscorpions (order Pseudoscorpionida), and 'other microarthropods'.

Disturbance response metrics

To measure community response, we focused on Bray-Curtis compositional dissimilarity of disturbed communities to their relative control communities within the same time period. Community dissimilarity was calculated on abundance matrices. However, abundance data were based on counts of species or ordinal groups and did not allow us to consider functional composition. For instance, two communities with 80 mesostigmatid mites each are functionally more similar that two communities in which one has 80 mestigmatid mites and one has 80 oribatid mites. To capture this dynamic, we added four extra columns to the composition matrix, one for the total number of mesostigmatid mites in each plug, one for the total number of prostigmatid mites in each plug, one for the total number of oribatid mites in each plug, and one for the total number of springtails in each plug. Thus, each individual was included in the abundance matrix twice, excluding the 3% of individuals that were insects, spiders, pseudoscorpions, or 'other'. The effect of this weighting structure was to shift the response variable, *i.e.* community dissimilarity, to decrease dissimilarity between communities with similar higher-order structures. Additionally, populations in our communities had wide fluctuations in population abundance, up to three orders of magnitude difference in a single experimental unit. To deal with such variability, we square root transformed the abundance data, including the four totals.

We used the vegan package (Oksanen *et al.* 2013) in R (R Core Team 2014) to calculate the dissimilarity of each plot to the average control community, measured as the compositional centroid of the control community within connectivity treatments. Thus, we calculated the dissimilarity of disturbed isolated (I) communities to undisturbed isolated communities (*i.e.*, row one of **Figure 1.1**), P–D communities to undisturbed communities that were linked with a disturbed community (*i.e.*, row two of **Figure 1.1**), and P–U communities to undisturbed communities that were linked to undisturbed communities (*i.e.*, row three of **Figure 1.1**). To quantify the impact of our higher-order weighting columns, we checked the Pearson's correlation coefficient between the non-weighted dissimilarity calculations and the weighted dissimilarity calculations and found high correlation ($\rho = 0.95$). Thus, the response variable including the weighting columns was retained, as it corresponded with the unweighted response variable but allowed us to consider higher-order structure in each community comparison.

The focus of this investigation was on dynamics of the whole multi-trophic community. However, given the likely contribution of major lifeforms to community response to disturbance, we also assessed each of the disturbance response metrics for the four major lifeform groups (springtails and oribatid, mesostigmatid, and prostigmatid mites).

Resistance

Resistance is the amount of change in a community following a disturbance (Pimm 1984).We measured resistance as the compositional dissimilarity between disturbed and undisturbed mats immediately post-disturbance (*i.e.*, time 0). We ran a linear model of resistance by disturbance intensity (average temperature), connectivity, and their interaction to test whether connectivity alters resistance to disturbance. Checks of this model were concerning due to a nonlinear relationship between the response variable and disturbance intensity. We thus adopted a generalized additive model (GAM) and used a smoothing function on average temperature (disturbance) using the mgcv package (Wood 2016).

Resilience

Ecological resilience can be defined as the amount of disturbance that an ecosystem can absorb before changing states (Holling 1973). It is most easily understood in ecosystems with known multiple stable states and quantifiable thresholds between them (e.g. Carpenter *et al.* 2011). In cryptic ecosystems such as moss-microarthropod systems, we have little information on ecosystem states and thresholds. However, theory suggests it is possible to identify a threshold associated according to the disturbance intensity at which fundamental changes in community composition persist despite time allowing opportunity for recovery. We tested for thresholds using segmented linear models of compositional dissimilarity by disturbance intensity. Segmented linear models are continuous piecewise linear models that identify breakpoints in the relationship between the response and covariate (Muggeo 2003). The segmented package (Muggeo 2015) in R uses maximum likelihood to determine whether the threshold point is statistically significant. Separate models were run for each connectivity treatment using data only from the last time point in the study under the assumption that nine months is adequate time for population turnover of the microarthropods and therefore community recovery.

Recovery

Recovery is defined as the time taken for recovery of an ecosystem to a pre-disturbance state after disturbance (Pimm 1984). In our case, temporal comparisons reflected seasonal rather than treatment differences because pre-disturbance coincided with microarthropod dormancy (late February prior to spring) and post-disturbance coincided with peak microarthropod activity. Instead, full recovery was defined as a statistically non-significant difference between community composition of disturbed and the control treatments at the same time point. None of our treatments reached full recovery under this definition. To measure recovery, we estimated speed to full recovery by modeling compositional dissimilarity through time for each connectivity treatment. Given that recovery is often a non-linear process (see Shackelford *et al.* 2016 for an overview), we used GAMs to allow flexibility in the relationship between composition and time since disturbance. Each connectivity treatment composition was modeled against disturbance intensity and a smoothed function of time. If the smoother returned a linear result (edf = 1), we reverted to a linear term for ease of interpretation. The resulting model was used to estimate recovery rate by calculating the slope of response against time at the last time point.

Because the response variable in all models was compositional dissimilarity (between 0 and 1), we used generalized linear models with a Gamma distribution and log link function (Crawley 2007). We validated each model using a Shapiro-Wilks test for residual normality (Shapiro & Wilk 1965) and visual exploration of residuals against predicted values and each covariate.

Results

Microarthropod richness and abundance

Overall, we counted 43,380 microarthropods, including 10,697 oribatid mites, 1,731 mesostigmatid mites, 7,898 prostigmatid mites, and 17,910 collembola. Average total abundance in each of the connectivity treatments were similar; isolated mats averaged 183.3

microarthropods per plug extraction, mats connected to a disturbed mat averaged 200.0 microarthropods, and mats connected to an undisturbed mat averaged 210.4 microarthropods. We found a total of 65 oribatid species or genera (**Appendix 1.A**); richness was lowest just after the disturbance (average 3.7 species per sample) and peaked at 6 months (average 6.3 species per sample). For most treatments, there was a burst of springtail abundance at 3 months post-disturbance (June 2014) followed by a decline at 6 months (September 2014). Exceptions to this trend were isolated, disturbed mats which had a peak springtail abundance at the 6-month time point, and undisturbed mats connected to a disturbed mat, which showed a linear increase in average springtail abundance. The highest abundance of springtails in these plots was at 9 months (December 2014) and was matched by a decline of oribatid mites and predatory mites (mesostigmatid and prostigmatid mites), between 3 and 9 months, and 6 and 9 months, respectively.

Oribatid population dynamics were largely driven by populations of *Autogneta* nr. *longilamellata* (Michael, 1885), *Trihypochthonius tectorum* (Berlese, 1896), *Quadroppia quadricarinata* (Michael 1885), and immatures, which each experienced an average increase of 915% from 6 months to 9 months in the isolated, undisturbed mats (**Appendix 1.A**). These mats had the same pattern of increases and decreases through time for all three microarthropod groups, where average abundance of all organisms increased from 0 to 3 months, decreased from 3 to 6, and increased from 6 to 9 month (**Appendix 1.B**).

Disturbance response metrics

Connectivity was a significant driver of resistance (**Table 1.1**) and recovery (**Figure 1.4**). We modeled recovery trajectories separately for each of the connectivity treatments, and each was found to have a unique trajectory through time. By contrast, disturbance intensity (*i.e.*, temperature gradient) was not significant for any of the three measures of response.

Table 1.1: Model results for resistance, resilience, and recovery
Resistance was modeled as a single generalized additive model with a smoother function applied to temperature (represented as s(Temperature)). Resilience was modeled for each connectivity treatment as a segmented linear model. If no segmentation point was found, it returned a simple linear model. If a segmentation point was found, the breakpoint is presented as indices. The breakpoint found (in the P–D treatment) was not statistically significant. Finally, recovery was modeled for each individual connectivity treatment, first as a generalized additive model with a smoother applied to time, then again without the smoother if it was found to be linear.

Response	**Model**	**Significant covariates**	**Deviance explained**
Resistance	Dissimilarity$_0$ ~ s(Temperature) + Connectivity	Connected to disturbed (estimate = - 0.19; p = 0.02)	0.2
Resilience			
Connected with undisturbed (P – U)	Dissimilarity$_9$ ~ Temperature	None	0.001
Connected with disturbed (P – D)	Dissimilarity$_9$ ~ Temperature$_{[24.0 – 37.2]}$ + Temperature$_{[37.2 - 44.9]}$	None	0.22
Isolated (I)	Dissimilarity$_9$ ~ Temperature	None	0.04
Recovery			
Connected with undisturbed (P – U)	Dissimilarity$_{0-9}$ ~ Temperature + Time	Time (estimate = -0.06; $p < 0.001$)	0.54
Connected with disturbed (P – D)	Dissimilarity$_{0-9}$ ~ Temperature + s(Time)	Time (edf = 2.78; $p < 0.001$)	0.44

Isolated (I)	Dissimilarity$_{0\text{-}9}$ ~ Temperature + Time	Time (estimate = -0.02; p = 0.02)	0.09

Resistance

We found that immediately after a disturbance, treatments connected to an equally disturbed community (P–D) were significantly more resistant, *i.e.* had higher similarity between disturbed and undisturbed P–D communities, compared with P–U and isolated treatments (**Table 1.1**). The effect size for isolated communities was negative (coefficient estimate = -0.08) but not statistically significant (**Figure 1.2**). The model explained relatively little variation in the data (deviance explained = 0.2).

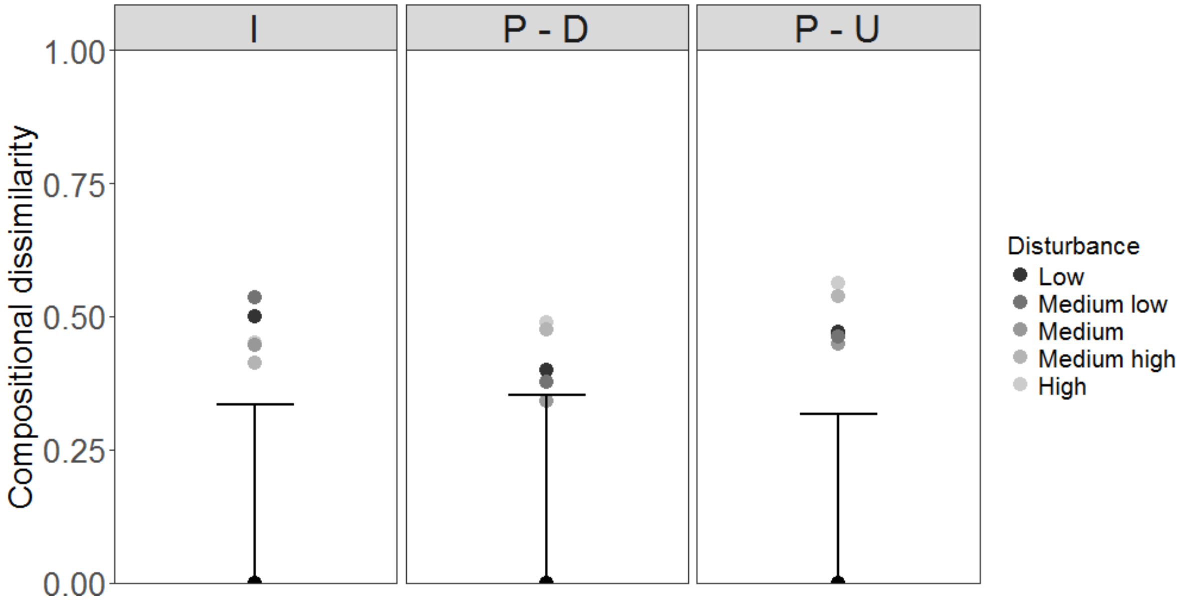


Figure 1.2: Average compositional dissimilarity immediately after the disturbance

Average compositional dissimilarity (Bray-Curtis dissimilarity, ranging from 0 -1) of each disturbance intensity level immediately after the disturbance split by connectivity treatment (from left to right: isolated, connected to a disturbed community, connected to an undisturbed community). The error bars represent the average range of variation within the controls, with the 0-value x-axis representing the compositional centroid of the controls.

Resilience

We found no significant threshold points along the disturbance gradient and dissimilarity after 9 months was not explained by disturbance intensity under any connectivity treatment (**Table 1.1** and **Figure 1.3**).

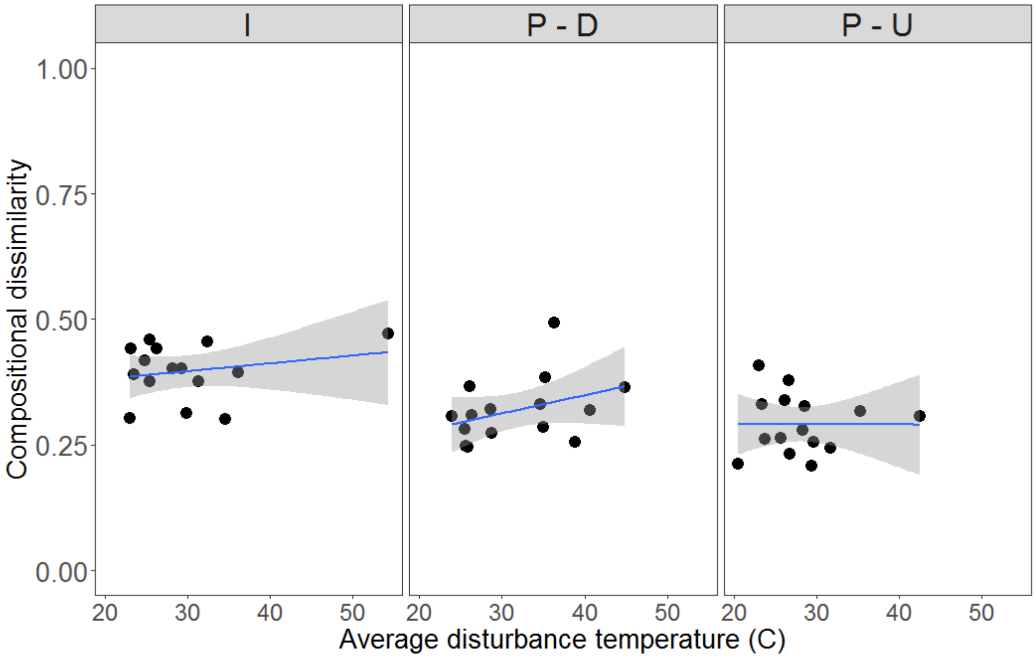


Figure 1.3: Compositional dissimilarity to controls at nine months

Compositional dissimilarity to controls in the same connectivity treatment by average disturbance temperature (for, from left to right: isolated, connected to a disturbed community, connected to an undisturbed community) and smoothed lines with 95% confidence bands. Average temperature was determined by the rheostat setting to represent the low – high disturbance categories. Predictions for each connectivity treatment do not extend past the maximum average temperature experienced by an individual mat within that treatment.

Recovery

Estimated time to recovery and the relationship between time and recovery differed amongst connectivity treatments (**Figure 1.4**). In communities connected to undisturbed communities (P–U), 0 to 9 months showed linear, constant change towards full recovery (*i.e.*, non-significant differences in community similarity between controls and disturbed communities). According to estimated model parameters, at 9 months post-disturbance, compositional dissimilarity was decreasing at a rate of 0.02 per month; *i.e.* the disturbed mats were becoming 6% more similar to the undisturbed mats each month. The linear model had high explanatory power (deviance explained = 0.54). In communities connected to disturbed communities (P–D), there was a sharp increase in dissimilarity between 0 and 3 months, then a recovery process that led to estimated dissimilarity decrease of 0.03 per month. Again, the model had high explanatory power compared with the other models (deviance explained = 0.44). In isolated mats, there was a significant relationship between time and recovery, with the rate of recovery estimated to be a decrease in dissimilarity of 0.007 per month.

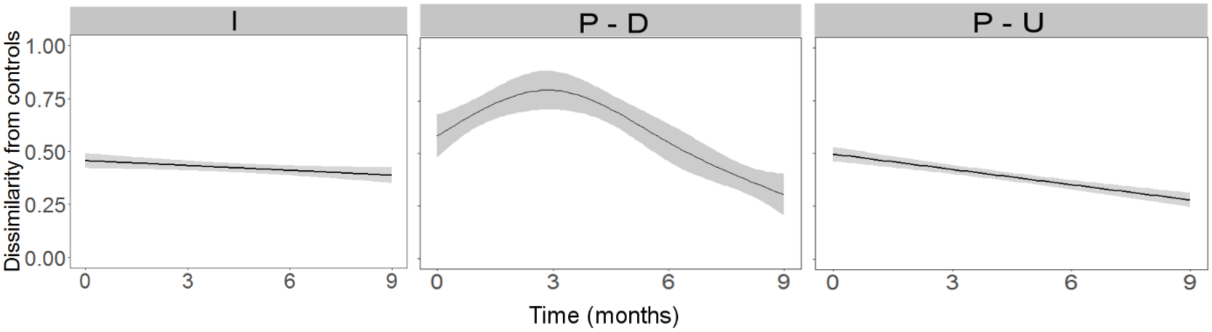


Figure 1.4: Modeled recovery through time
Relationship of recovery through time for mats connected to undisturbed mats (left), mats connected to disturbed mats (middle), and isolated mats (right).

Discussion

Current resilience-based management recommendations focus on articulating feedbacks, identifying thresholds, and mapping specific threats for an individual community (e.g. Cumming *et al.* 2005; Briske *et al.* 2008). Yet many communities remain relatively little known, with knowledge gaps around even major drivers of ecological dynamics in extensively managed systems like forests (Reyer *et al.* 2015). There is still a need, therefore, for generalizable mechanisms that support more resilient and resistant communities, and communities that are better able to recover from a discrete disturbance. Landscape connectivity is one promising hypothesized mechanism. Here, using a model experimental system we show that connectivity facilitates the resistance and recovery of communities after a discrete disturbance, but its effect changed between differing attributes of ecological response to disturbance.

We found that disturbed microarthropod communities connected to a disturbed landscape (P–D) had higher resistance, *i.e.* were more similar post-disturbance to an undisturbed community connected to a disturbed landscape. We hypothesized that connectivity to another landscape, even when both are disturbed, provides increased opportunities for refugia such as deeper, moister soil patches. The presence of refugia has often been found to increase biotic resistance of communities (e.g. Schmalholz & Hylander 2011; Selwood *et al.* 2015), and connecting two patches in this study could have doubled the potential refugia availability. If this were the case, the isolated treatment should have had the least resistance, and connectivity benefits should be reflected in the most mobile species, commonly large-bodied predators (Harestad & Bunnell 1979). Neither of these patterns was found. Rather, the P–D treatment had the highest resistance, likely because the control landscape that represented the P–D reference was connected to a disturbed community. That disturbed community may have been a sink for mobile organisms immediately post-disturbance, leading to population fluctuations in the P–D reference as a response and thus increased similarity between the reference and the disturbed communities. In the P–U treatment, the disturbance led to an influx of predators, potentially from the connected undisturbed community (**Appendix 1.B**). As a result, compositional dissimilarity was higher in the P–U treatment than the P–D for both predator groups (**Appendix 1.C**), and the community as a whole.

Springtails, in contrast, had the lowest resistance in the P–D treatment (**Appendix 1.C**) which may be linked to the source-sink dynamics, as the control plugs in the P–D treatment were almost absent of springtails. Springtails are mobile foragers and were potentially moving into the adjacent post-disturbance landscape to take advantage of available resources. Across all treatments, however, there was consistently low abundance of springtails at our first sampling point followed by a large increase at three months, with larger increases in disturbed plots than undisturbed controls. Short generation times (Irmler 2004) may have allowed rapid reproduction and predator release in disturbed plots may have emphasized these trends. The low abundance at time 0 highlights that a late-winter, early-spring disturbance may not impact springtail populations at seasonally low abundance. The timing of disturbance is well-known to influence overall impact in ecological communities (e.g. Pakeman & Small 2005; Wright & Clarke 2007), and springtail response highlighted the potential importance of disturbance timing in these systems.

Recovery towards control trajectories was, however, strongly linked with connectivity treatment. Those connected to undisturbed communities, the P–U treatment, showed steadily decreasing dissimilarity with the controls at each time point. This mirrors the traditional secondary succession trajectory (Pimm 1984) that has been found in communities elsewhere (e.g. Mack *et al.* 2008; Jones 2010). Succession theory, however, has also proposed a hump-shaped trajectory, where a suite of opportunistic species creates a highly dissimilar community that is slowly outcompeted by the climax community species (Connell 1978; Huston & Smith 1987). In the P–D treatment, oribatid communities were on average 1/3 as abundant as in the controls at 3 months, while springtails were 16 times more abundant in the disturbed communities than in the controls. Oribatid life histories contrast with springtails in that their generation time can be relatively slow, and thus their response time delayed compared to springtails. The large increase in springtails and slower recovery of oribatids lead to high dissimilarity in disturbed P–D communities at 3 months, followed by linear recovery.

Isolated community recovery was linear but much slower than in the connected treatments. The disturbed isolated communities fluctuated from lower than average community abundance (over all treatments) at 3 months, to higher than average at 6 months, and back to well below lower than average at 9 months. In parallel, the controls had low abundance at 6 months and a huge increase in immatures and oribatid species at 9 months, leading to a large deviation between controls and disturbed communities in oribatid communities (**Appendix 1.D**) as well as in the full community dynamics. The isolated control dynamics were notably different than those found in the P–U and P–D control communities. Recovery studies tend to rely on a climax community framework whereby the pre-disturbance state is often considered synonymous with the climax state (Holling 1996). Given the variable and cryptic nature of these systems, we relied on compositional trends towards control communities to estimate recovery. The erratic abundance dynamics of the isolated controls made it difficult to measure a reference state, suggesting that changes induced by isolation may have pushed the controls out of their stable state dynamics. In a global condition that involves constant environmental changes coupled with expanding landscape fragmentation (Fahrig 2003; Ellis & Ramankutty 2007), stable reference states may be increasingly less abundant or relevant.

We defined resilience as the disturbance intensity at which a community no longer trended towards the control; *i.e.* the disturbance intensity at which the microarthropod community was pushed towards another state (Holling 1973). If resilience was overcome, we would expect to see no discernible pattern of increasing similarity between disturbed and undisturbed community composition within each connectivity treatment. According to that standard, these communities were resilient despite being subjected to temperatures up to 70°C for 48 hours. In addition to disturbance intensity, other disturbance attributes like timing or frequency could potentially lead to transitions to alternative stable states. It has been suggested that large, but infrequent disturbances yield little long term changes, while compounded effects from multiple disturbances are more likely to result in nonlinear ecological behavior (Paine *et al.* 1998). Thus, the role of connectivity in increasing resilience may be more apparent under a periodic or repeated disturbance regime.

Previous work in moss-microarthropod communities has found links between composition and area. Species richness and abundance in these communities have been found to decrease with decreasing area (e.g. Gonzalez *et al.* 1998; Starzomski & Srivastava 2007). To limit the influence of area on community response, we created mats of equal size for both connected and isolated treatments, only pairing these same-sized mats for the connected treatments after four weeks of isolation. We also statistically tested the relationship between abundance and area, as well as oribatid species richness and area, and found no significant relationship (**Appendix 1.E**). Thus, the experimental design was appropriate for testing connectivity and not area. Indeed, the smallest landscape we created was roughly 600,000 times the size of largest-bodied species in the mite communities, and our sampling area was consistent across all treatments.

Microcosms, though excellent experimental communities, do have limitations and drawbacks. Ecological processes often shift as scales change (Peterson *et al.* 1998). This work explores multi-trophic communities on small scales, but it is unclear whether the findings will predictably scale up to human-perceived landscapes. Even when focusing in on life form groups individually, the exact ecological role individual species or groups may play in these systems is unknown. Thus, interpreting group-level responses in microcosm systems has limitations when we begin to scale up to larger-bodied animal communities. Without clear functional analogues, results for individual morphological groups may give little generalizable insight. Additionally, the dynamic nature of these particular communities led to unpredictable behavior and large variability in the controls. Microarthropod communities are cryptic, and defining clear ecological states likely requires better understanding of the overall dynamics. A large suite of controls, over longer time periods, would have given a better view of both the natural dynamics and the likely impact isolation appeared to have on community behavior.

Despite the complexity and cryptic nature of these communities, connectivity in this study stabilized the undisturbed communities and promoted recovery pathways for disturbed communities, though that pattern differed between communities connected to an undisturbed versus an equally disturbed landscape. These results are not unique; connectivity has been found to boost ecological ability to respond to disturbance on large scales and across taxa (Shackelford *et al.* 2016). Here, its importance was found in complex communities that encompass many trophic levels. The consistency of results continues to build the case that landscape configuration is one general concept to support the ability of ecological communities to respond to disturbance.

Chapter 2 : Early warning signals in the face of uncertainty: Field testing critical slowing and autocorrelation in a bog-forest ecosystem

with Rachel J. Standish, Kira M. Hoffman, and Brian M. Starzomski

Abstract

Nonlinear dynamics are an increasing concern for ecological management in the face of slow changing environmental conditions. Thus, a number of early warning signals have been developed to anticipate when ecosystems are approaching a threshold. These early warning signals have key barriers to field application, particularly the long time series needed to detect them adequately, and their limited relevance beyond ecosystems with bifurcated threshold dynamics. Here, we test for the detectability of two early warning signals, critical slowing and increased autocorrelation, in an ecosystem where thresholds are hypothesized but unproven. We focused on the transition between bog and forest on the Central Coast of British Columbia, by experimentally manipulating bog towards transition to forest through water table drawdown. We tracked autocorrelation of vegetation communities through time in control and drawdown communities. To investigate critical slowing, we applied a trampling disturbance and measured recovery speed. We found critical slowing in compositional recovery and recovery of moss cover in drawdown plots relative to recovery in control plots. However, we did not find increased autocorrelation. The decoupling of critical slowing and increased autocorrelation may be due to a number of potential ecosystem dynamics, including the potential presence of multiple stable states and transition types that could characterize these systems. In most management situations, a complex set of alternative stable states is likely to exist, with unknown transition types that may differ from the typical hysteresis-driven threshold dynamics that are the current focus of early warning dynamics. Our study emphasizes the gap between

theory and practical application of early warning signals. Incorporating a wider range of ecosystem states and transitions into field testing of early warning signals will increase their application to ecosystem management.

Metric Details

Autocorrelation – the compositional dissimilarity of a plot and itself in consecutive time steps. Three time distances are used:

lag-1 autocorrelation – the dissimilarity between a plot and itself one year prior

lag-2 autocorrelation – the dissimilarity between a plot and itself two years prior

lag-3 autocorrelation – the dissimilarity between a plot and itself three years prior

Recovery – the difference between vegetation metrics in a plot post-trampling and the average value of the metric in untrampled plots in the same year; split by treatment, where trampled drawdown plots are compared to the average of untrampled drawdown plots and trampled control plots are compared to the average of untrampled control plots

Critical slowing – slower rates of recovery based on distance to a bifurcated ecological threshold

Introduction

Ecological collapse is becoming an increasingly common theme of modern ecosystem management. Collapses can devastate economic or ecological values and include fisheries collapse on the east coast of North America (Hutchings & Myers 1994), abrupt desertification in arid zones of Africa (Darkoh 1998), and sudden landscape-scale salinization in heath of Western Australia (Lambers 2003). Even when the alternative state is characterized by new ecological function and value, it is often economically and ecologically disruptive. For example, North American woodland systems have replaced large expanses that were previously prairie (Van Auken 2009), causing a shift in available rangeland resources and a loss of biodiverse herbaceous ecosystems (Ratajczak *et al.* 2012). With abiotic conditions such as climate and nutrient availability shifting globally, managers worldwide face the concern that small additional changes will lead to a disproportionate ecological response and sudden collapse of current states. In most systems, collapse is associated with the presence of thresholds. Ecosystem management requires signs that ecosystems are approaching critical thresholds before these are crossed, especially where collapse is difficult or impossible to reverse (Hughes *et al.* 2013).

There are three likely dynamics of transition between states (**Figure 2.1**). The first is a smooth, linear change in the equilibrium, where a small change in environmental conditions leads to a correspondingly small change in equilibrium state (**Figure 2.1, panel a**). Though predicting the exact trajectory of the equilibrium might not be possible, no sudden and dramatic changes are expected given small amounts of environmental change. The second two dynamics both exhibit threshold behavior. One is a dramatic ecological response to a small environmental change that can be reversed by returning to previous conditions (**Figure 2.1, panel b**; Suding & Hobbs 2009). A classic example of this is the extinction threshold (Fahrig 2001), where the probability of population extinction is near zero until a small additional habitat loss which tips the probability to near one. The extinction probability can be returned to near zero by reinstating the same amount of additional habitat. The second type of threshold is a dramatic ecological response that cannot be reversed by reinstating the conditions immediately prior to the collapse (Ludwig *et al.* 1997). Rather, the conditions must be reinstated from well before the collapse to return to the original ecological state (**Figure 2.1, panel c**). For example, a small nutrient addition can tip lake ecosystems from a clear to turbid state, but a much larger amount of nutrient removal is required to return a turbid lake to a clear state (Scheffer *et al.* 1993). In this third type of dynamic, there is an overlap of environmental conditions in which both states are able to persist (known as hysteresis: Gunderson & Pritchard 2012). Within that area of overlap, the states are alternative stable states (Scheffer & Carpenter 2003).

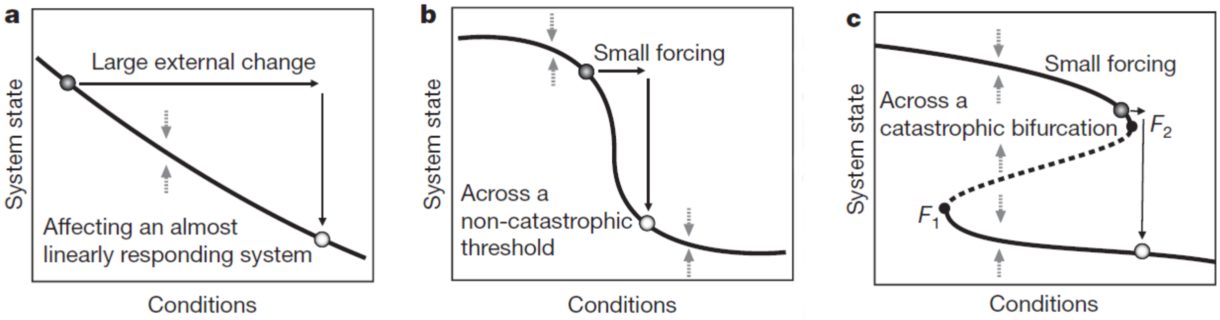


Figure 2.1 Three potential dynamics of ecosystem response to change

The first panel (a) shows a linear response, with the amount of change in environmental conditions directly reflected by the amount of change in the ecosystem. There is no threshold associated with change in ecosystem state because it is incremental. The grey arrows show the trajectory of the ecosystem if it deviates slightly from equilibrium. At all points along the transition, the equilibrium is the same (reflected in the direction of the grey arrows). In the second panel (b), a small change in conditions results in a large ecosystem change, but this dramatic shift is reversible by reversing the change in conditions. Again, only one equilibrium exists at all points along the trajectory. In the final panel (c), a small change in conditions results in a large ecosystem change, and a large reversal in conditions is required before the ecosystem will return. This overlap of environmental conditions is known as hysteresis, and it results in three distinct equilibria, two stable (the solid lines) and one unstable (the dashed line). Figure adapted from Scheffer, et al. (2009).

Ecosystems characterized by alternative stable states and hysteresis (**Figure 2.1, panel c**) have unique mathematical properties. Exploration of these properties, coupled with the need to anticipate critical thresholds, has led to a set of early warning signals for critical collapse to alternative stable states (Scheffer *et al.* 2009, 2012, 2015). These indicators include increasing spatial and temporal correlation in ecosystem dynamics (Ives 1995; Dakos *et al.* 2010), changing frequency spectra in variance patterns (Kleinen *et al.* 2003), increasing skewness in the distribution of ecosystem dynamics through time (Guttal & Jayaprakash 2008), and slowed response to disturbance (critical slowing down: van Nes & Scheffer 2007). Despite their detailed development in modeling literature, there are many barriers to the application of these signals in real world systems. Each requires relatively long-term, high-resolution time series data with high levels of precision (van de Leemput *et al.* 2017). The two most applicable in field settings to date are critical slowing in response to discrete disturbance and increased annual autocorrelation, as both may be possible to detect in time frames feasible for field studies. The term 'critical slowing down' refers to slower recovery back to equilibrium after discrete disturbances in ecosystems close to a threshold (Scheffer *et al.* 2012). As ecosystems undergo stochastic environmental changes and disturbances, slower return rates mean that an ecosystem is more correlated to its past than to the equilibrium state, thus leading to increased autocorrelation between timesteps in ecosystems near a threshold (Dakos *et al.* 2012).

Even if timeframes for measurement are feasible, however, an additional barrier to application is the requirement for alternative stable states and hysteresis dynamics, which have only been clearly established in a subset of global ecosystems. Proof of alternative stable states usually requires large spatial and temporal data on ecosystem dynamics that is generally unavailable

(Beisner *et al.* 2003). However, the presence of positive feedbacks between biotic and abiotic processes is one of the underlying drivers of abrupt shifts between alternative stable states (Scheffer *et al.* 2012). Once a critical point has been passed, the positive feedbacks may switch and accelerate the rate of transition to the alternative state. Strong positive feedbacks of this kind often lead to spatial partitioning of resources, with discontinuous vegetation patterns in response to small environmental changes linked to the feedback processes (Eppinga *et al.* 2009). Thus, historical records of nonlinear transitions can be coupled with spatial patterning and known feedbacks to provide evidence of past alternative stable states and more critically, transition signals that could be used to forecast transitional change in the future.

To date, there are only two examples of empirically derived data of early warning detection; one in a closed-system environment of freshwater lakes (Carpenter *et al.* 2011), and one using a 30-year dataset in marsh ecosystems (van Belzen *et al.* 2017). In the first example, the ecosystem was well-studied, well-modeled, and closed. The indicator used in early warning signal detection was chlorophyll-*a*, a metric that can be sampled at extremely small time steps with high precision. In the second example of the marsh ecosystems, the two alternative stable states were dense *Spartina* or *Schoenoplectus* marshes and bare tidal flats. The indicator used in early warning signal detection was marsh biomass, a rapid response metric that can be measured with high precision. In many management scenarios, however, appropriate metrics may respond on considerably longer time scales (*e.g.* woody cover in prairie), may involve full compositional shifts (*e.g.* native annual California grassland versus exotic perennial herbaceous systems), or may have high natural variability and low measurement precision that masks potential signals (*e.g.* salmon fishery populations in the Pacific Northwest). Therefore, it's an open question as to whether early warning signals could be identified in other ecosystems.

Here, we test whether early warning signals are detectable in a bog-forest ecosystem in British Columbia (BC). Similar to most management scenarios, the ecosystem under study has only hypothesized, not proven, alternative stable states and potentially slow response variables. In BC, paleoecology and current evidence support the presence of alternative stable states between bog and forest, with the primary indicator metric likely to be either tree or peat cover. We experimentally applied a slow environmental change, manipulating bog away from its existing equilibrium and towards a hypothesized critical threshold leading to a forest equilibrium. We applied a discrete disturbance and looked for critical slowing down and increased annual autocorrelation over a range of commonly measured vegetation metrics, including percentage cover of key lifeforms and vegetation composition. Given that the presence of or proximity to thresholds is unknown in many managed ecosystems, there is a pressing need for applicable indicators of regime shifts. To be useful, however, early warning signals must be detectable in complex ecological settings with limited time series data over the span of potential regime shifts. In testing for their presence here, we aim to help close the gap between long-standing ecological theory and potential management application.

Methods

Ecosystem description

Bog-forest mosaics exhibit a number of characteristics that imply potential bistability. Paleoecological studies have shown long persistence (thousands of years) of a variety of bog types, including hollows, hummocks, and a mosaic of the two, where hollows are typically wet depressions dominated by *Sphagnum*, and hummocks are typically drier raised areas dominated by vascular plants coexisting with *Sphagnum* species (Wallén *et al.* 1988). At certain levels of environmental change, ecosystem collapse into alternative stable states has been observed, with hollow-dominated landscapes shifting to open forb- and shrub-dominated systems and hummock-dominated landscapes shifting to woodland (e.g. Alexandrov & Logofet 1994; Jukaine 1995; Ohlson *et al.* 2001; Talbot *et al.* 2010). These transitions have also been found in the other direction, with woodland and open mires shifting to hummock- and hollow-dominated bog systems (van Breemen 1995a; Frankl & Schmeidl 2000). These relatively rapid transitions driven by small environmental changes are one of the strongest indicators of ecological bistability (Scheffer & Carpenter 2003). Therefore, the possibility of early warning signals exists for this system.

One known driver of bistability is the presence of positive feedbacks between biotic and abiotic conditions in each basin of attraction (Scheffer *et al.* 2001). Regardless of the type of bog, biotic and abiotic conditions create positive feedbacks linking water table level with biotic process like transpiration (**Figure 2.2**). High water table levels and high organic matter content in the soil lead to saturated, anoxic conditions (Sahrawat 2003) that hamper the establishment of tree species. Slow decomposition leads to low available nutrient levels (van Breemen 1995b) and further increases soil organic matter. With few tree and overstory species, transpiration is low, the water table remains high, and saturation levels are maintained (Rietkerk *et al.* 2004). However, as tree cover increases, these conditions may change. Higher tree cover may lead to drier conditions through precipitation interception and higher levels of transpiration (Waddington *et al.* 2015), increased nutrients through litter fall (Aerts *et al.* 1999; Ohlson *et al.*

2001), and altered microclimate through shading and wind shelter. Drier areas with higher nutrients and lower environmental pressures are likely to further increase woody establishment and growth (Rietkerk *et al.* 2004; Eppinga *et al.* 2009).

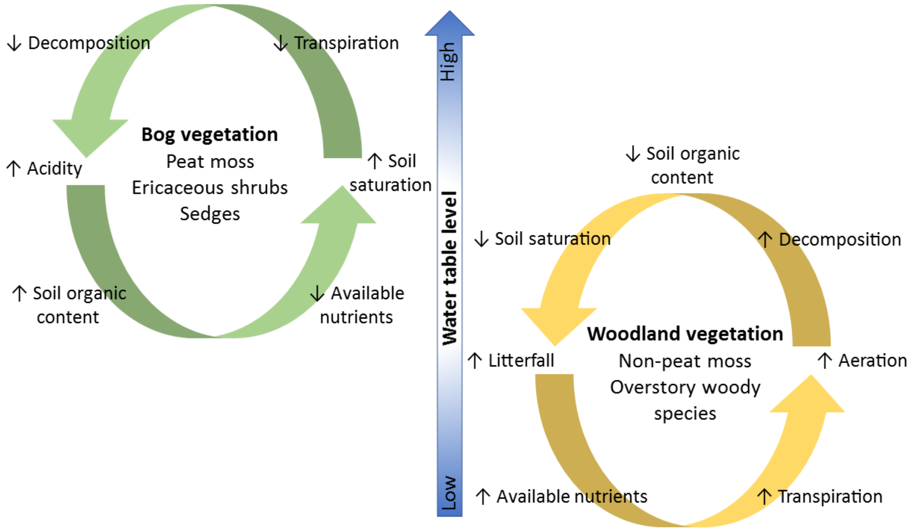


Figure 2.2 Positive feedbacks between water table level and vegetation type
High water tables lead to saturated environments with low decomposition, high organic content, and low soil oxygen levels that create poor environmental conditions for many vascular plants like trees. Moss and sedge-dominated vegetation systems maintain the high water table through low transpiration and nutrient-poor and low volume leaf litterfall. When trees begin establishing, however, high transpiration leads to drops in the water table which increases aeration and decomposition. This condition, in turn, encourages more tree establishment, and increased quality leaf litterfall and soil nutrients.

On the coast of British Columbia (BC), there are historical and contemporary data to support the hypothesis that bog and forest are alternative stable states. Paleoecological evidence from the northern tip of Vancouver Island shows changes from woodland state in drier eras to the existing open bog state in wetter, cooler periods, with potentially rapid transitions between the two (Hebda 1983). The distribution of bog and woodland along the coast is spatially patchy, with open bog abruptly transitioning to woodland or bog-woodland. Though the bog to woodland transition has not been recorded recently, there is strong evidence of bog encroachment in previously productive forests (known as paludification: Joosten & Clarke 2002). Post-logging, the pioneer appearance of *Sphagnum* has altered moisture and growth conditions so dramatically that a trajectory towards bog rather than back to forest is expected (Banner *et al.* 2005). Historical abrupt changes, spatial coexistence and patterning, and priority-effect induced state changes all support the idea that bog and forest are alternative stable states on the BC coast.

Study Site

The study site was located on Calvert Island in the Hakai Lúxvbálís Conservancy on the central coast of British Columbia, Canada. Calvert Island is located in the Very Wet Hypermaritime subzone (Pojar *et al.* 1987), an ecological variant of the Coastal Western Hemlock biogeoclimatic zone that receives an average annual rainfall of 2682 (1555-4387) mm and has a mean temperature of the warmest month of 16.3 (13.8-18.8)°C (Green & Klinka 1994). Soils in flat or low-lying areas are characterized by surplus moisture due to high rainfall and low evapotranspiration, leading to anaerobic conditions that promote moss growth and reduce decomposition of organic matter (Banner *et al.* 2005). We chose a sedge-dominated peat bog, where total *Sphagnum* cover is often low, organic levels in soil are high, and there is no connection with a permanent groundwater source. Vegetation cover was characterized by sedge (*e.g. Trichophorum cespitosum* (L.) Hartm. and *Rhynchospora alba* (L.) Vahl.) and herbaceous perennials (*e.g. Fauria crista-galli* (Menzies ex Hook.) Mak. and *Dodecatheon jeffreyi* van Houtte), with an understory of moss (primarily *Racomitrium lanuginosum* (Hedw.) Brid. and *Sphagnum* sp.) and an overstory of ericaceous shrubs (*e.g. Empetrum nigrum* (L.) and *Vaccinium uliginosum* (L.)). Thus, the study site most strongly resembled the vegetation community of hummock-dominated bog with the expected alternative stable state of woodland (Eppinga *et al.* 2009). The sedge-dominated bog type on the BC central coast is embedded in a matrix of *Sphagnum*-dominated bog (hollow), sedge-dominated bog (hummock), bog-woodland, and woodland.

Experimental manipulation towards a threshold

The transition from bog to forest has been linked to water table drawdown and warming temperatures (Heijmans *et al.* 2013). We focused on water table drawdown, as there is a larger body of evidence to support its role in bog state change (see references in: Jukaine 1995; Talbot *et al.* 2010). We used a stratified random sampling design in two, one-hectare areas encompassing a hummock-hollow bog with soils that were approximately 20cm deep. We chose one relatively flat patch within the bog upslope, and one steeper patch downslope to capture the natural range of drainage conditions. At each patch, we created ten drawdown replicates and ten control replicates (**Figure 2.3**) by cutting 20 soil pieces randomly distributed across the patches. Sod pieces incorporated the rhizosphere (*i.e.*, soil immediately surrounding plant roots), and the soil horizons beneath the rhizosphere. In each treatment, we cut 30cm × 50cm pieces of sod. For the drawdown treatment, sod pieces were transplanted to rubber containers 61cm × 40.6cm × 31.8cm lined with granodiorite rocks from the site to mimic the parent material. Approximately fifty, 3cm diameter drainage holes were drilled in each container to create aerobic and unsaturated soil conditions in each microcosm. Control pieces were lifted up and then replaced to ensure similar amounts of root disturbance between treatments. Plant survival was high throughout the experimental period (May 2013 – July 2017).

To track abiotic changes due to the drawdown treatment, we focused on changes in soil chemical composition, soil temperature, and soil moisture. For soil chemical composition, we collected soil samples in 2013, just prior to applying the drawdown treatment. We tested total C and N, organic matter, and moisture content. In 2017, four years after the treatment was applied, we repeated the same analyses on a second set of soil samples. For soil temperature, we took hourly measurements for the last year of the treatment (June 2016 – June 2017) using Hobo dataloggers. Finally, for soil moisture, we took measurements in 2014, one year post-treatment and again in 2015 after the application of the discrete disturbance event (see below for details).

Vegetation changes approaching a threshold

To track vegetation changes, we monitored annually in mid-July from 2013 to 2017 (*i.e.*, four monitoring events). We used a point-framing monitoring technique because it collects accurate percentage cover data and measures plant height (Bonham 2013). A 30cm × 30cm PVC frame was placed above the tallest vegetation in each plot. The frame had a 10 × 10 fishing line grid with cells that were 3cm × 3cm. One datapoint was taken in the bottom right corner of each grid cell by lowering a point rod straight down and recording each plant species touched, as well as the height above ground of each species. All vascular plants and mosses were identified to species where possible. *Sphagnum* mosses were not identified to species as they were difficult to reliably key in the field.

Given that we were interested in bog state change to forest, we did not analyze vegetation at a species-scale. Rather, we focused on the major life history groups of woody vegetation, sedges, grasses, other herbaceous forbs, and mosses. To track whether significant changes were occurring through time, we fit linear mixed effects models of total lifeform cover against year within the drawdown plots. Because these data were repeated measures, we included a random effect for plot (Crawley 2007), and because the up- and downslope patches had different local environmental conditions and lifeform composition, we modeled them separately. To compare the trends in the drawdown treatment with the trends in the control treatment, we fit the same structured models to control plots in each patch.

Additionally, we included a test of the potential positive feedback of tree growth in bog. In the downslope patch only, we planted half of the plots (five drawdown plots and five controls plots) with eight western red cedar (*Thuja plicata*) seedlings in October 2014. In July of each year, we tracked seedling survival and seedling height to test whether survival and growth were higher in plots undergoing drawdown. For survival, we fit a generalized linear mixed effects model (Bolker *et al.* 2009) using a binomial distribution for the response (0/1 survival in 2017) and plot as the random effect. For height, we fit a mixed effects model with change in height as the response, year as the fixed effect, and plot as the random effect. We also tested whether shifts in lifeform changed based on the introduction of tree seedlings. To do so, we fit linear mixed effects models of total lifeform cover against year within the planted plots, split by treatment.

Autocorrelation

As per previous work on early warning signals, we hypothesized that drawdown plots would exhibit increased autocorrelation. In other words, on average each drawdown plot would be more similar to itself in the previous time steps than each control plot would be to itself in previous time steps. We measured autocorrelation by calculating the compositional dissimilarity of each plot to itself in previous time steps. We were not interested in major shifts, but rather subtle annual changes in the full community. Thus, we calculated the Bray-Curtis distance on cover values for all species. The primary signal of concern was lag-1 autocorrelation; *i.e.* the correlation between a time step and the time immediately prior. In a single plot, we calculated lag-1 autocorrelation in each year. Thus, each plot had a correlation value for the similarity between years 2 and 1, years 3 and 2, years 4 and 3, and years 5 and 4. Additionally, we calculated lag-2 autocorrelation (the similarity between a plot and itself two years prior) and lag-3 autocorrelation (the similarity between a plot and itself three years prior). Though lag-1 has been primarily used for identifying early warning signals, lag-2 and lag-3 autocorrelation will indicate longer term dynamics.

For each level of autocorrelation, we fit linear mixed effects models of the autocorrelation values against treatment (drawdown or control) with plot as a random effect. Given that these were within-plot comparisons, we did not separate the data by patch but grouped them together to increase replicates. To check for within-patch dependence, we assessed residuals against patch identity and found no evidence to support including patch as an additional random component.

Discrete disturbance and critical slowing

To investigate the presence of critical slowing, we applied a secondary, discrete disturbance event and tracked recovery from that event. We applied trampling as our discrete event in 2014, one year after the drawdown treatment was applied. Trampling is a relatively common and impactful disturbance in bog (Lindsay *et al.* 2014), but sites with low intensity trampling have been known to recover within a few years (e.g. Slater & Agnew 1977; Studlar 1983). To standardize the treatment, we filled two rubber boots with approximately 20kg of concrete and 'walked' 300 steps per day for two days on half of the plots in the upslope patch (five drawdown plots and five controls plots; **Figure 2.3**).

We monitored recovery for three years post-trampling. We measured recovery of all vegetation metrics, including each of the five lifeform groups as well as compositional dissimilarity. Because we expected annual community shifts in at least the drawdown plots, we based our calculations of recovery against the untrampled plots within the same time step. Thus, recovery of each lifeform was the difference between the lifeform cover of each plot in that year, and the mean of that lifeform cover in that year for all corresponding untrampled plots:

$$recovery_{LP_y} = mean\left(untrampled\ cover_{Ly_t}\right) - cover_{LP_y}$$

where *L* represents each individual lifeform, *P* represents plot, *y* represents year, and *t* represents the treatment of plot *P*.

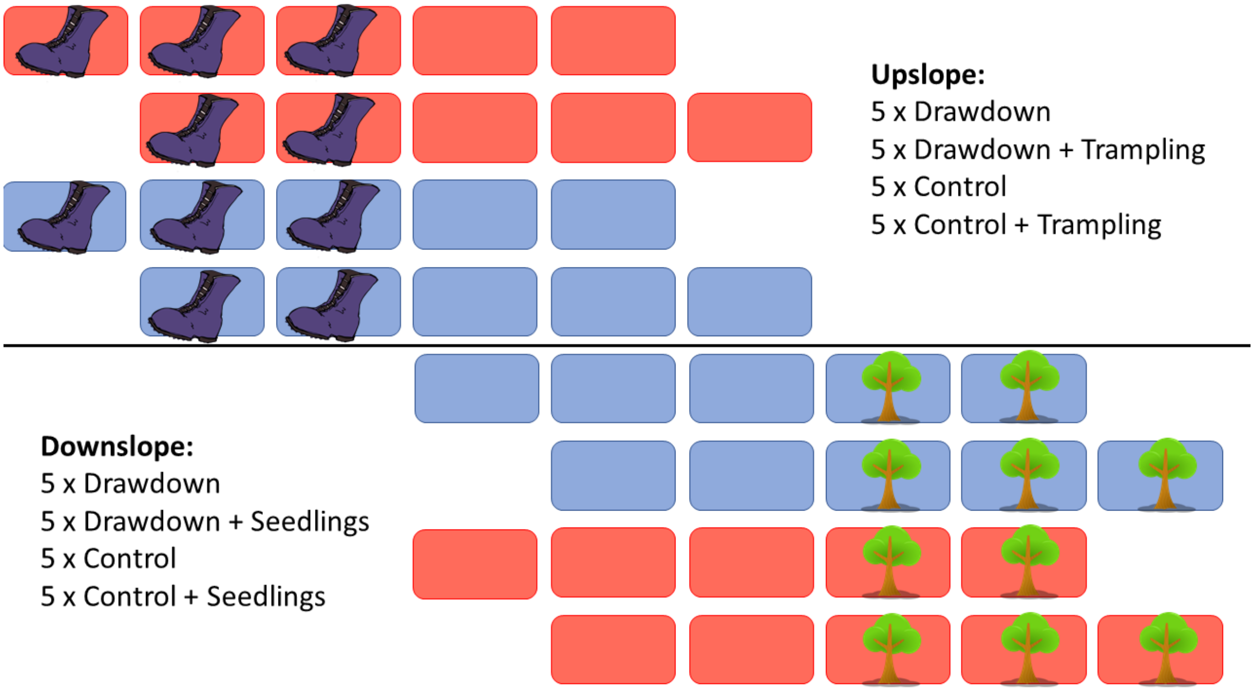


Figure 2.3 Experimental design

Experimental design over the two patches (upslope and downslope). Both patches had twenty plots in total, ten drawdown (red) and ten control (blue) treatments. Half of each treatment in each patch also underwent a secondary treatment. In the upslope patch, five drawdown and five controls were trampled to investigate critical slowing. In the downslope patch, five drawdown and five controls were planted with eight cedar seedlings to investigate positive feedbacks.

Compositional recovery of each year was calculated as the Bray-Curtis distance of each plot to the compositional centroid of the untrampled plots undergoing the same treatment (drawdown or control) in the same year. We fit linear mixed effects models of recovery metrics against year, with a random effect for plot. Models were fit for control and drawdown recovery separately. We used the resulting estimated coefficient for recovery against year as the estimate of recovery speed. Critical slow down would occur in this case if the estimated coefficient of annual recovery for the drawdown treatment was less positive than the coefficient of annual recovery for the control treatment. In some cases, patterns in the residuals showed non-linear relationships with time. To address the issue, we added smoothers through a generalized additive mixed effects structure (gamm: Zuur *et al.* 2009) to a subset of the models.

For all models fit in this study (see **Table 2.1** for full list and **Supplementary Material 2.A** for more details), we calculated marginal and conditional R^2 using the technique outlined in Nakagawa and Schielzeth (2013). We checked models by assessing the residuals for normality and for patterns against the response values and random effects (Zuur *et al.* 2009). All statistical analyses were performed using the R Statistical Software (R Core Team 2014) including the nlme package (Pinheiro *et al.* 2014) and lme4 package (Bates *et al.* 2014).

Table 2.1 Model list and hypotheses

List of models fit in the study including the response variable, the predictor variables, the details of the data used in each, and the hypothesis being tested. Recovery was fit with a nonlinear relationship between recovery and year (s(Year)) when model checking showed nonrandom residuals patterns against year.

Response		Predictor	Data	Hypothesis
Cover	Moss Woody species	~ Year	Fit on four datasets: five untrampled drawdown plots upslope; five	Cover of woody vegetation will incrementally increase and sedges and mosses

	Herbaceous Forbs Grasses Sedges		untrampled control plots upslope; five drawdown plots with no seedlings downslope; five control plots with no seedlings downslope	will decrease in drawdown plots, indicating approach towards a threshold
Cover	Moss Woody species Herbaceous Forbs Grasses Sedges	~ Year	Fit on two datasets: five drawdown plots with seedlings downslope and five control plots with seedlings downslope	Cover of woody vegetation will incrementally increase and sedges and mosses will decrease in control plots with seedlings and more rapidly in drawdown plots with seedlings, indicating a feedback between trees and drawdown impacts
Compositional autocorrelation	First-order Second-order Third-order	~ Treatment (drawdown/control)	Fit on one dataset including all drawdown and control plots without an additional treatment (trampling or cedar seedlings); note that all available years are used for all plots	Autocorrelation will be greater between years in drawdown plots, indicating an early warning of critical collapse
Cover recovery	Moss Woody species Herbaceous Forbs Grasses Sedges	~ Year [or ~ s(Year)]	Fit on two datasets: five drawdown plots upslope post-trampling and five control plots upslope post-trampling	Recovery would occur more slowly in drawdown plots, indicating an early warning of critical collapse
Compositional recovery		~ Year [or ~ s(Year)]	Fit on two datasets: five drawdown plots upslope post-trampling and five control plots upslope post-trampling	Recovery would occur more slowly in drawdown plots, indicating an early warning of critical collapse

Results

Impacts of experimental manipulation towards a threshold

Environmental shifts

Plots undergoing the drawdown treatment were significantly drier ($p < 0.001$; Adjusted-R^2 = 0.8) and cooler ($p = 0.04$; Adjusted-R^2 = 0.17). Soil nutrients did not significantly shift at any point in the experiment post-drawdown.

Vegetation shifts

Vegetation communities changed when subjected to drawdown conditions. Both patches showed some similar trends, with grass cover significantly increasing and moss, woody, and sedge cover significantly decreasing through time (**Figure 2.4: top panels**). Forb cover did not show consistent changes.

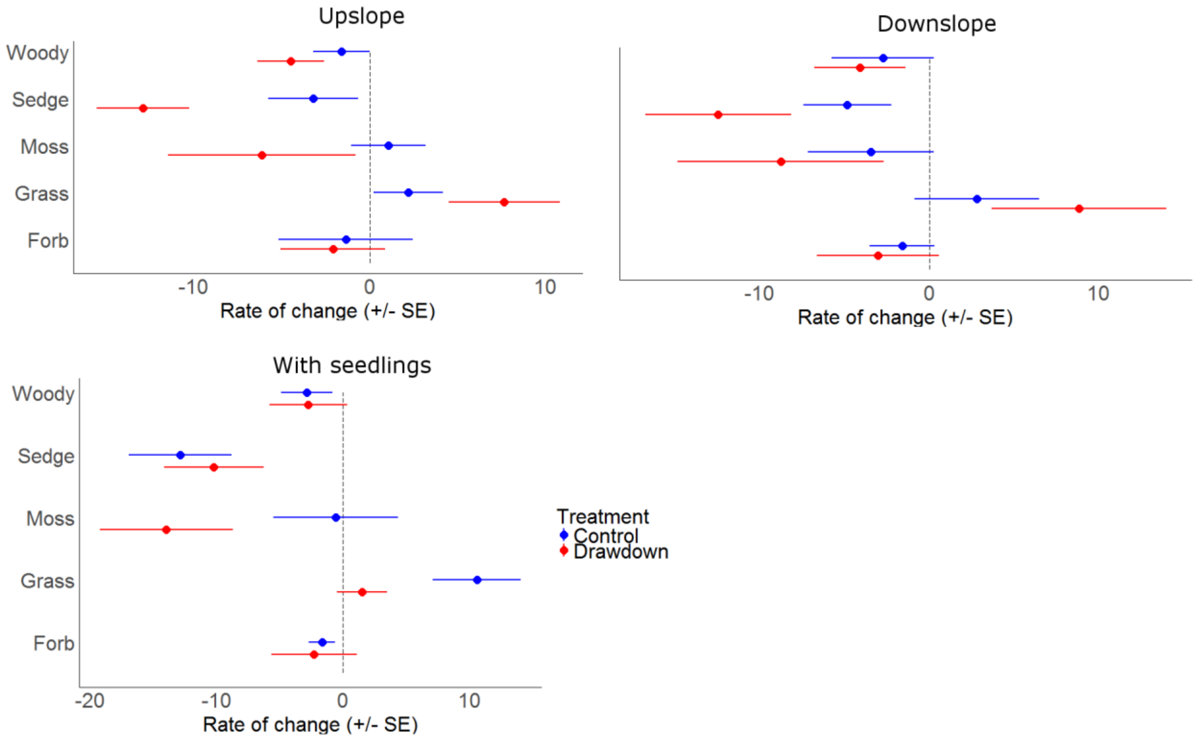


Figure 2.4 Model coefficient estimates for vegetation changes through time

Coefficient estimates for annual changes in each major lifeform group based on drawdown treatment (all panels) and cedar seedling planting (lower panel). The points represent estimated annual changes; i.e. grass cover under the upslope drawdown treatment increased at an estimated 7.6% cover per year. The lines represent 95% confidence intervals around each estimate. The panel on the left shows results for the patch upslope, while the center panel shows results for the patch downslope. Colors represent estimates for each of the two treatments (blue for controls, red for drawdown). The far-right panel shows changes in vegetation communities when cedar seedlings were planted.

Potential feedbacks

Trees that were planted in drawdown conditions had higher overall survival (36/40 as opposed to 31/40; non-significant). However, the number of replicates that experienced seedling mortality was the same for controls and for drawdown treatments: two of five replicates in each treatment had at least one seedling death. Overall growth was significantly higher in drawdown conditions ($p = 0.04$; marginal-$R^2 = 0.09$). Control vegetation communities with planted seedlings showed significant increases in grasses and significant decreases in sedges through time (**Figure 2.4: right panel**). The presence of seedlings in vegetation communities undergoing drawdown, however, corresponded with negligible grass increase and slower rates of sedge decrease.

Early-warnings of regime shift

Auto-correlation

Contrary to our hypothesis, lag-1 auto-correlation was significantly higher in control pots compared with plots undergoing the drawdown treatment, *i.e.* the similarity was greater between each year in the control plots. For second-order and third-order auto-correlation in both patches, the drawdown plots were increasingly less correlated compared to control plots. Full model results can be found in **Supplementary Material 2.B**.

Critical slowing

On average, the trampling disturbance decreased cover in all life forms for both treatments with the exception of a mean change of +1% cover of grasses in the drawdown treated-plots. The median change was more negative in the drawdown treated-plots across all lifeforms (**Supplementary Material 2.B**). Additionally, median compositional change was greater in the drawdown-treated plots. The only statistically significant difference between changes in control and drawdown-treated plots, however, was the greater decrease in sedge cover found in the drawdown-treated plots ($p = 0.02$; Adjusted-$R^2 = 0.43$).

Two lifeforms showed a consistent trend of increase post-trampling in the control plots. The difference between post-trampled moss cover and the untrampled plot cover decreased through time in the controls, until recovery was achieved by year three (average difference near 0). Moss continued to decline post-trampling in the drawdown plots. The second lifeform that showed consistent increases was grass, and the increase rate was only significant in the control plots. However, grass cover in the trampled control plots overshot the untrampled control plots by year two and continued increasing into year three (**Figure 2.5**).

We found that forb cover in the trampled drawdown plots exhibited non-linear patterns through time, increasing in the first year and stabilizing by year two at levels slightly lower than the untrampled drawdown-treated plots. Compositional dissimilarity significantly increased through time in the control plots until the third year, which showed a decrease in dissimilarity (**Figure 2.5**). There was no change in compositional distance to untrampled plots in the trampled drawdown-treated plots. The only statistically significant trends were grass increases ($p = 0.02$) and compositional changes through time ($p < 0.001$) in the controls.

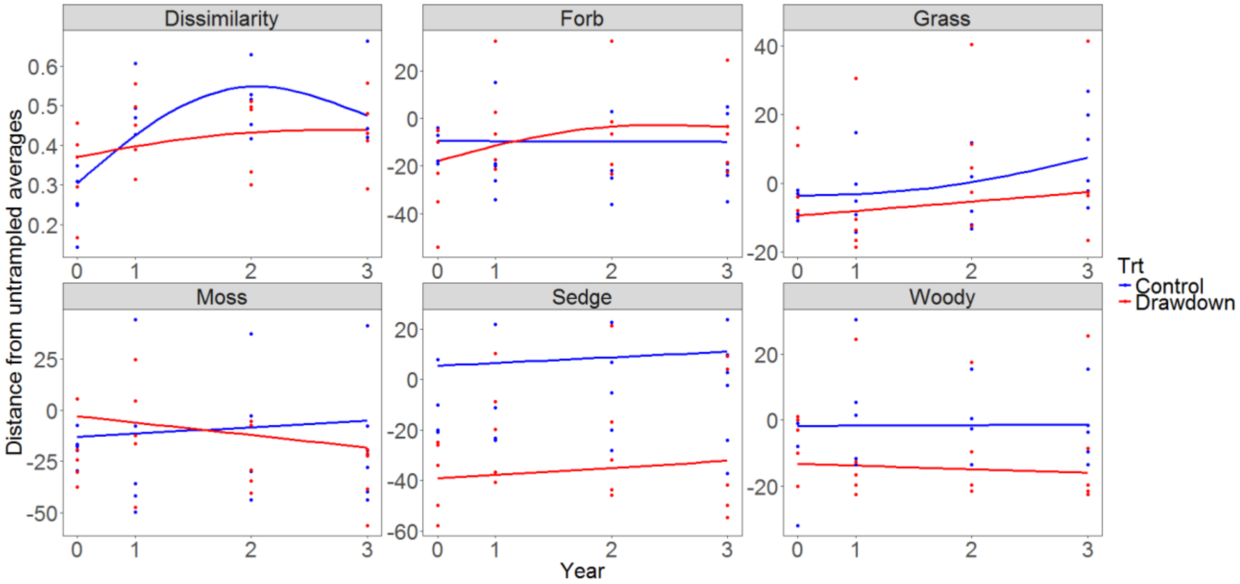


Figure 2.5 Recovery trajectories post-trampling

Trajectories through time of drawdown-treated (red) and control (blue) communities from immediately after a trampling disturbance (time = 0 on the x-axis) through three years after the disturbance (time = 3 on the x-axis). The top left panel shows trends in compositional dissimilarity to untrampled plots at the same time step. The remaining panels show the difference between cover of each life form in the trampled plots and cover at the same time step in untrampled plots through time.

Discussion

In ecological management, there is a clear need to have well-understood, consistent, and measurable early warning signals of imminent regime shift. To date, critical slowing and increased autocorrelation may have the most promise for field use. Both can be measured in discrete time intervals and have been repeatedly found in models (e.g. van Nes & Scheffer 2007; Dakos *et al.* 2012; van de Leemput *et al.* 2017), lab experiments (e.g. Veraart *et al.* 2012), and in the field (Carpenter *et al.* 2011; van Belzen *et al.* 2017). We did find evidence of critical slowing in bog undergoing transition to forest though slower rates of compositional recovery and total absence of moss recovery. However, we found no signal of the expected increase in annual autocorrelation, highlighting both the potential utility of early warning signals and underscoring their potential limitations.

Compositional recovery in the trampled control plots was found by year three, with a sharp decrease in average dissimilarity between trampled and untrampled plots in that year. In contrast, compositional recovery in the drawdown plots was zero. Similar trends were found in moss cover, mirroring previous studies where recovery rates in ecosystems approaching a threshold approached zero. Yet, other metrics did not have the same patterns. In previous examples of laboratory or field studies, the relevant univariate measure of ecosystem dynamics has been fairly clear; *e.g.* single-species biomass in yeast or marshland (Veraart *et al.* 2012; van Belzen *et al.* 2017). Here, the most relevant metric is probably woody cover. However, our measures of woody cover suggest its slow response will limit its use as a field indicator over short time scales such as this study. In our case, root death from the experimental setup may have altered results, and woody growth is likely to change over decades rather than years. The paucity of rapid response metrics for bog-forest ecosystems inhibit the ability to demonstrate local alternative stable states and there is a reliance on long-term observations, paleoecological data and lab experiments to populate models rather than actual time series (similar to woodland-prairie models. e.g. Twidwell *et al.* 2013a). Metric choice is key to detecting early warning signals, yet knowing which metric to use where and when is an open question for most ecosystems. Thus, pinpointing an appropriate indicator, on tractable time scales, with limited error or variability is a considerable obstacle to implementing these techniques in the field (Scheffer *et al.* 2001; Dakos *et al.* 2012).

We did not find increased autocorrelation as the drawdown treatments moved away from the bog state. Control plots showed signs of being at compositional equilibrium, with year-to-year dissimilarity averaging only around 0.16 and significant changes only in sedge cover, which showed small decreases through time. In contrast, drawdown plots showed strong directional changes, which drove significantly larger year-to-year compositional differences that increased in strength for longer lag times. Increased autocorrelation is a direct derivative of critical slowing (Dakos *et al.* 2012), where slowed response to small, stochastic environmental changes leads to increasingly correlated annual dynamics compared to ecosystems rapidly returning to equilibrium. In our case, the ambient environmental conditions are relatively stable (Pojar *et al.* 1987; Banner *et al.* 2005), and may not disturb communities enough to lead to increased autocorrelation. The applicability, therefore, of autocorrelation may be clearer in areas with higher annual variation in species composition.

The lack of increased autocorrelation may also indicate ecosystem behavior that differs from the alternative stable state and hysteresis-driven dynamics that are the assumption of these early warning signals. The drawdown treatment significantly changed the temperature and moisture of the soil, likely shifted key mycorrhizal communities, and may have caused the drawdown plots to immediately cross a threshold in the equilibrium state rather than simply moving closer to a threshold. If that were the case, ecosystem patterns recorded here would likely reflect transitional rather than equilibrium dynamics. Little is known on how to differentiate transitional dynamics as opposed to equilibrium dynamics, despite their likely prevalence in current global ecosystems (Hughes *et al.* 2013). Alternatively, the tree planting results indicate that, rather than simple bistability, there may be multiple potential ecosystem states based on feedbacks between biotic and abiotic processes as well as competitive interactions between lifeforms. In drawdown plots where seedlings were planted, there was almost no increase in grass cover, contrasting sharply with drawdown plots that had no seedling addition. Thus, there are likely competitive interactions between grasses and trees. Without propagule inputs from surrounding woodland, grassland may be an additional potential state, as it is often found interspersed with bog ecosystems in treeless landscapes (e.g. Ratcliffe 1959; Wahren *et al.* 2001).

The situation where there are multiple potential states rather than two, with many potential transition types, is common in ecological management (e.g. Westoby *et al.* 1989; Bestelmeyer *et al.* 2003; Briske *et al.* 2005). Even in ecosystems with known alternative stable states, the presence of hysteresis may change based on individual location or a single driving environmental variable (Loehle 1985). Thresholds characterized by hysteresis remain little shown in most natural ecosystems (Schröder *et al.* 2005), and the limited application of early warning signals to situations characterized by a bifurcated threshold may restrict their usefulness. This is particularly true in situations with multiple possible transitions that are complicated by other external environmental drivers.

Both the temporal and spatial scale of this study may present additional barriers to detecting early warning signals in ecological dynamics. Mesocosms of the size used, though easy to manipulate abiotically, are likely too small to undergo independent state changes towards woodland. Whether and how this spatial scale impacts expected community response to disturbances is unknown. Additionally, though moss showed full recovery over three years in the control communities, compositional recovery had just begun in the last years of sampling. Perennial herbaceous and woody communities may take considerably longer to recovery to pre-disturbance composition; thus, continued monitoring may have yielded full recovery patterns more indicative of long-term dynamics.

Finally, the decoupling of autocorrelation and critical slowing may imply that the critical slowing found here is a false positive. False positives can occur when the perturbation is large and the ecosystem immediately crosses a critical threshold, as may have occurred given the drawdown intensity, or when the transition towards the threshold is not a gradual, monotonic process but is rapid or highly nonlinear transition (Boettiger & Hastings 2012). The overall aim of this study was to investigate whether pushing an ecosystem towards a likely, but only hypothesized, threshold in a field setting would allow detection of early warning signals of regime shifts. Though there was a promising signal of critical slowing, it is difficult to determine whether this is a true or false positive given the potential for multiple stable states, unique transition types, and unknown transitional dynamics. Managers face many of the same challenges, where alternative stable states are unproven and complex (Schröder *et al.* 2005) and ideal metrics are unknown or logistically infeasible (Allen *et al.* 2011; Rist *et al.* 2013). Thus, early warning signals will be most useful in a management setting when there are clearer guidelines to their use, and applicable tools to fill in the gaps; *i.e.* to test for thresholds without bifurcations and to identify transitional dynamics. The continued exploration of ecological models coupled with on-ground field testing could lead to broad tools for understanding dynamics of changing ecosystems in a changing global environment.

Chapter 3 : The impact of reactive management on ecological resilience: Invasive species control contributes to resilience of urban Garry Oak savannahs

with Sean M. Murray, Joseph R. Bennett, Patrick L. Lilley, Brian M. Starzomski, and Rachel J. Standish

Abstract

Ecosystem management is moving towards proactive decision-making, yet reactive decision-making is still the norm. Beyond the singular goal motivating reactive management, we have little understanding of how reactive management impacts broader goals like ecological resilience. Here, we assessed how ten years of invasive species removal, a common reactive management tool, impacted Garry oak savanna resilience, measured as response diversity, functional redundancy, and sustained boundaries of the savanna state. We tested how management intensity impacted patch-level resilience and benchmarked results against the influence of other human impact measures like road density and connectivity. We found that management increased functional redundancy and patch area retention of Garry oak sites. However, the relationship shifted based on road density, with remote areas showing greater patch area retention but also neutral to negative changes in redundancy at high management intensities. Connectivity between Garry oak patches was also positively linked with functional redundancy and patch area retention. Taken together, our results imply that reactive management can contribute to resilience, but that management effectiveness depends on the resilience metric and the landscape context.

Metric Details

Resilience *(of Garry oak savanna to woody encroachment)* – measured as the amount of patch area that has been lost to woody encroachment and canopy closure

Relative resilience – using resilience proxies (below), we measured whether each proxy had decreased or increased over a ten-year time; not a direct quantification of resilience, but of relative resilience between two time steps. Measured as changes in:

Functional redundancy within groups

The number of species in each functional group within a patch

Average functional redundancy within the patch

Average functional redundancy within quadrats surveyed in a patch calculated as species diversity minus functional diversity

Response diversity within groups

The response diversity in each functional group within a patch

Average response diversity within the patch

Average response diversity within quadrats surveyed in a patch

Introduction

Though protected areas remain one of the primary methods of biodiversity conservation globally (Margules & Pressey 2000a), they often face a number of ecological stressors, including altered disturbance regimes, invasive species, and surrounding land use changes (Pressey *et al.* 2007). Thus, management decisions in protected areas are often forced to reactively plan for existing pressures using current or historical data. The need for proactive planning, where predicted future scenarios drive much of the decision-making process (Liu & Heino 2013), is increasing as climate effects and impacts of other global trends become likely. Despite concerted moves to shift conservation management toward proactive decision-making rather than reactive (Heller & Zavaleta 2009), reactive decision-making is often the primary management tactic where resources are limited and there is an abundance of local-scale crises (Allen *et al.* 2011).

Existing stressors on protected areas are enhanced in the pockets of conservation land scattered through urban landscapes. Urban parks and green spaces are increasingly essential for biodiversity conservation, yet are also particularly beset by issues requiring reactive management such as intense pressure from non-indigenous and invasive species. The benefit of an urban setting, however, is that volunteer engagement and community stewardship become useful resources for achieving conservation goals (Svendsen & Campbell 2008). Thus, achievable, reactive activities such as invasive species removal become the dominant management tactic in urban areas, both because there is an unusually high invasive pressure, and because community-based volunteers can be effectively harnessed for these activities (Asah 2008).

The assumption of continuous invasive species removal is that by reactively dealing with problematic species, management increases an ecosystem's ability to respond to other pressures (Carwardine *et al.* 2012), effectively creating proactive outcomes. For example, many invasive species are known to outcompete native species, alter ecological function, and shift disturbance regimes (Mack *et al.* 2000; Shackelford *et al.* 2013). The expected outcome of invasive species control is that biodiversity and ecological function are maintained, both of which are thought to increase ecological resilience (Timpane-Padgham *et al.* 2017), *i.e.* the ability of the ecosystem to withstand other, future disturbances without undergoing a regime shift (Holling 1973). Effective monitoring of these additional conservation outcomes, however, is rare (Lindenmayer & Likens 2009), leaving the indirect benefits of invasive species management largely unknown.

One challenge of monitoring outcomes like ecological resilience is choosing which metrics to measure (Duelli & Obrist 2003). Resilience is an abstract ecosystem characteristic that is notoriously difficult to quantify (Standish *et al.* 2014). One common practice is to monitor proxies of resilience – concrete attributes thought to correlate closely with resilience (Bennett *et al.* 2005). Functional redundancy (Walker 1992) and response diversity (Elmqvist *et al.* 2003) are two such proxies. Current theory suggests that a resilient ecosystem will have many species within primary ecological functions (functional redundancy), enabling fluctuations in one population to be compensated by another (Pillar *et al.* 2013). As a resilience proxy, functional redundancy is necessarily paired with response diversity – the diversity of response types among species within a functional group. If redundancy is high but all species respond negatively to disturbance, the compensatory dynamics are lost (Mori *et al.* 2013). Thus, the combination of high functional redundancy and high response diversity within a single function is hypothesized to make that function resilient to disturbance and change (Elmqvist *et al.* 2003; Mori *et al.* 2013).

Here, we investigate the relationship between reactive management of invasive species in an urban landscape and resilience metrics. We chose protected Garry oak savannas in a highly developed matrix of urban and peri-urban activity. Garry oak savannas in Canada are found in a restricted range in southwest British Columbia, yet house among the highest number of endangered species in the nation (COSEWIC, *pers. comm.*). Many remaining patches of savanna are urban parks, which undergo pressure from recreational use and landscape fragmentation, as well as a suite of invasive species and less invasive non-indigenous species (NIS). We estimated the amount of invasive species management in each park through qualitative data provided by local managers. To capture landscape fragmentation, we also estimated connectivity among Garry oak patches, as connectivity has consistently been linked with ecological resilience (Suding *et al.* 2004; Mumby & Hastings 2008; Shackelford *et al.* 2017). As a proxy for human pressure, we used road density within a 1km buffer surrounding each patch. Roads are linked to increased invasion pressure, impaired ecological function, and increased compositional change in adjacent ecosystems (Forman & Alexander 1998a; Sanderson *et al.* 2002; Coffin 2007a). Finally, we considered the proportional presence of non-invasive NIS. Representing a large proportion of Garry oak savanna diversity (Bennett *et al.* 2013), NIS may play an important role in shifting resilience by increasing local species richness and functional diversity (e.g. Thomas & Palmer 2015) or by outcompeting native species and suppressing diversity (e.g. Hejda *et al.* 2009).

Building on previous work in these parks (Lilley & Vellend 2009; Bennett *et al.* 2013), we measured the change in functional redundancy and response diversity in the vegetation communities from 2006 to 2017. Our primary goal is to understand how invasive species control, mediated by landscape configuration and human density, can influence resilience in urban parks of high conservation value.

Methods

Site description

Garry oak savannas are a threatened ecological community in the northwest region of North America. They are highly diverse, forb-dominated communities with a sparse overstory of Garry oak (*Quercus garryana*) and Douglas fir (*Pseudotsuga menziesii*). Climate is sub-Mediterranean, with wet winters and significant summer drought (MacDougall 2005). The range is limited from southern California to southern British Columbia (Fuchs 2001), and less than 10% of the historical extent is thought to remain (Bjorkman & Vellend 2010). Much of the remaining savanna fragments are scattered in a matrix of urban and rural development, secondary coastal Douglas Fir forests, and agricultural areas (Fuchs 2001). This study was conducted at the northern tip of the savanna range on Vancouver Island, British Columbia. Given the pressure of climate shifts globally, resilience may be particularly important at the northern end of range distributions as suites of species track their shifting climatic envelope (Gibson *et al.* 2009; Renton *et al.* 2012).

Other than land use change, the largest threat to Garry oak savanna communities in this region is the diverse suite of NIS, a subset of which can become invasive if not managed. Invasive species such as Scotch broom (*Cytisus scoparius*), Himalayan blackberry (*Rubus armeniacus*), and laurel-leaved daphne (*Daphne laureola*) are managed almost exclusively by hand-pulling. Additionally, fire management in the region by First Nations communities is thought to have maintained the open savanna structure (Bjorkman & Vellend 2010). With the loss of traditional management, canopy closure of savanna by Douglas Fir has occurred in some areas (Bjorkman & Vellend 2010), with additional evidence of savanna loss to native shrub invasion (e.g. *Symphoriocarpos albus*: MacDougall 2005).

We chose 23 parks with historical data on plant species composition and abundance (Lilley & Vellend 2009; Bennett *et al.* 2013). Garry oak savannas are naturally patchy, and few parks are entirely of savanna. Within parks, we focused on savanna patches less than 10ha, as patches larger than 10ha are rare and tend to be dramatically larger. Seven parks had multiple patches within our size limit; in these parks, we surveyed two randomly selected patches each for a total of 30 individual patches.

Vegetation surveys

For patch-level surveys, we repeated the 2006 surveys of Lilley and Vellend (2009). We ran parallel transects 25m apart across the patch extent, along which we recorded all vascular plant species. Garry oak savannas undergo dramatic compositional shifts between seasons. To capture the full suite of plant species, we conducted two surveys in 2017, one in spring (10 Apr – 4 May) and a second in summer (29 May – 24 Jun). The previous patch-level surveys were conducted in spring and summer 2006.

We also conducted quadrat-based surveys in each patch, repeating the 2007/8 surveys of Bennett *et al.* (2013). Quadrats, 1m × 1m in size, were established previously based on a stratified-random sampling protocol at the patch scale, with the number of quadrats scaled by the patch area. We used GPS coordinates to locate the original quadrat locations as closely as possible. Error in GPS readings (up to 10m) means that relocation was only approximate. Thus, we did not compare individual quadrats; rather, our metrics were expressed as quadrat-based averages for each patch for times one and two (the original and repeat surveys). In 2017, we surveyed 222 quadrats, recording all species and cover for each. In a few cases, species in a single genus would be nearly identical in appearance and habitat, and we were only able to ID to taxonomic group (*e.g. Luzula comosa/multiflorum*).

Plant functional traits

Defining functional redundancy and response diversity requires specifying relevant plant functional traits, in our case with respect to resilience, and distinction between response and effect traits. We defined effect traits as those traits that impact biogeochemical processes in the system, such as growth rates or lifeform which shape overall community productivity and structure (Lavorel & Garnier 2002; Cornelissen *et al.* 2003). Response traits are traits that shape a species response to disturbance (Lavorel & Garnier 2002; Suding *et al.* 2008). Predominantly, response traits are captured by regeneration habits like dispersal or seed size, both of which influence the conditions and locations that will lead to successful species establishment. We also included environmental tolerances, estimated by key databases, to capture the window of environmental conditions within which each species could respond neutrally or positively. We collected 22 traits over 304 species. We were missing more than three traits for only 4% of species. See **Appendix 3.A** for trait details and primary data collection sources.

Resilience metrics

Given a long history of refining and redefining the term ‘resilience’ (e.g. see Grimm & Wissel 1997), difficulty in measurement (e.g. see Standish *et al.* 2014), and overall complexity, we narrow our consideration of resilience using the suggested question, “Resilience of what to what?” (Carpenter *et al.* 2001). The ‘of what’ is relatively straightforward. We are interested in the identity and structure of Garry oak savanna as open canopy communities with a diverse herbaceous understory. The ‘to what’ is more complex. On a patch-scale, the immediate pressure is often the loss of fire disturbance and propagule pressure by woody species, both native and invasive. However, the focus of this study was patches on the northern tip of the Garry oak savanna range, and resilience to slowly shifting global conditions (*i.e.* changing climate) and long-term pressures (*i.e.* fragmentation) may be pivotal for overall persistence of the Garry oak savanna system. To get at these multiple pressures, we measured resilience in multiple ways.

Woody encroachment

The open canopy savanna and understory can be lost when woodland species encroach along the boundaries, or when invasive shrubs become dominant. Patch area lost to woody encroachment through time can be used to measure how resilient that patch has been to woody encroachment. Less loss implies higher resilience; more loss implies lower resilience. Using 2016 aerial photographs, we estimated patch boundaries based on vegetation density. We ground-truthed the boundaries during field surveys, using a GPS to mark necessary adjustments based on canopy cover and characteristic species. Patch area lost to woody encroachment was estimated by comparing these boundaries to the boundaries estimated in 2006 using the same methods (Lilley & Vellend 2009).

Changing conditions

Beyond woody encroachment, impacts of existing fragmentation and changing environmental conditions are likely to vary, from increasing summer drought and climatic warming (Hamann & Wang 2006), to ongoing NIS propagule inputs. Thus, savanna patch resilience will depend on the ability of species within the patch to cope with multiple continuous changes. We used functional redundancy and response diversity to capture a more general metric of resilience and focused on how each has changed within a patch over the course of this study. We aimed to estimate the impact of our predictor variables on resilience through time.

We included two scales of functional redundancy and response diversity. Redundancy and response diversity were initially proposed in the context of resilience in individual ecological functions (Elmqvist *et al.* 2003). Thus, our first measure of redundancy and response diversity was at the scale of individual ecological functions. Using the patch-level surveys, we assessed functional redundancy and response diversity for each functional group in a savanna patch.

To define functional groups, we used the FD package (Laliberté *et al.* 2014) in R (R Core Team 2014). Functional group classifications were created using Ward’s minimum variance clustering on the trait dissimilarity matrix (Legendre & Legendre 2012). Because we had mixed classes of variables (continuous, categorical, and ordinal) as well as some missing values, distance matrices were computed as a Gower dissimilarity matrix (Podani 1999). Ward’s clustering of Gower dissimilarities tends to result in roughly equally-sized functional groups if the species are evenly distributed within the trait space (Legendre & Legendre 2012). We defined the number of groups based on a visual inspection of the clustering dendogram (Aubin *et al.* 2009). Clusters were computed using Principal Coordinates Analysis (PCoA), a method requiring Euclidean distance matrices. Thus, we corrected our Gower's distance matrix using the Cailliez correction method (Cailliez 1983).

Once the classification was complete, we recorded the functional group for each species. A few of the groups were composed either entirely of NIS or of NIS and one native species. We considered these groups as functional groups not indigenous to the historical Garry oak savanna system and excluded them from subsequent calculations.

For each functional group in each patch, functional redundancy was measured as the total number of recorded species (Walker 1992; Laliberté *et al.* 2010). Response diversity for each functional group in each patch was measured as the multivariate functional dispersion of represented species in response trait space (Laliberté & Legendre 2010). The functional dispersion is an average distance to the centroid of the response trait space, meaning that it is little influenced by the number of species, ensuring independence of response diversity from redundancy. Gower dissimilarity matrices were used and corrections for non-Euclidean distances were made prior to dispersion calculations based on Anderson's (2006) methods.

We were also interested in extending the idea of functional redundancy and response diversity beyond individual functions to overall redundancy and response diversity of the understory communities. In general, these understory communities are the main structural component of the Garry oak savanna system most under threat. Thus, our second scale was community-level.

We calculated redundancy and response diversity over all species within a quadrat, regardless of functional group, using relative cover to weight our metrics.

To capture abundance-weighted functional redundancy for quadrats, we used an alternative definition that focuses on community saturation by particular traits; *i.e.* redundancy is the difference between potential and actual functional diversity of plants (de Bello *et al.* 2007; Pillar *et al.* 2013). Rao's quadratic entropy is often used to measure actual functional diversity, as it captures the dissimilarity between species, weighted by relative abundance (Botta-Dukát 2005):

$$FD = \sum_{i=1}^{s}\sum_{j=1}^{s} d_{ij}p_i p_j$$

where d_{ij} is the trait-based distance between species i and species j, p_i is the proportion of the total abundance represented by species i, and p_j is the proportion of the total abundance represented by species j. In a situation where all species are the same abundance ($p_i = p_j$ for all i and j) and all species are fully functionally different ($d_{ij} = 1$ for all i and j), Rao's quadratic entropy equals the Simpson diversity metric (*SD*):

$$SD = \sum_{i=1}^{s} p_i^2$$

The Simpson diversity index maximizes at the lowest diversity (one species at p = 1), so the highest possible diversity can be represented as 1 – SD. Thus, our final equation for functional redundancy (*FR*) in each quadrat was:

$$FR = \left(1 - \sum_{i=1}^{s} p_i^2\right) - \sum_{i=1}^{s}\sum_{j=1}^{s} d_{ij}p_i p_j$$

Response diversity was measured as the multivariate functional dispersion in response trait space of all species in the quadrat. Again, Gower dissimilarity was used with Anderson's (2006) correction for non-Euclidean representation applied. In this instance, dissimilarity calculations included relative cover. Both quadrat-level functional redundancy and quadrat-level response diversity were averaged over all quadrats in each patch to give a single, patch-level value for each.

Predictor variables

Management in Garry oak savanna is primarily focused on invasive species control. We met with managers at each of the 23 parks and discussed the amount of time and resources invested in each patch for the last 10 years. We categorized management effort as one of four levels – none, low, medium, and high. A patch had no management if the organization did none and we found no evidence of community intervention, low management if the organization did no formal management, but we found management evidence (*e.g.* old piles of pulled plants), medium if the organization applied irregular invasive species control, and high if consistent, annual invasive species removal occurred.

We had three other predictor variables: non-indigenous species (NIS) presence in the 2006 surveys, connectivity, and surrounding road density. For woody encroachment and quadrat-based functional redundancy and response diversity, we used the proportion of NIS found in the patch. For redundancy and response diversity within functional groups, we used the proportion of species within that group in that patch. The highest proportion of NIS in these systems are herbaceous, so we expected little impact to resilience to woody encroachment. However, the presence of non-invasive NIS has been shown to have a variety of impacts to native diversity, including positive, negative, and neutral (Shackelford *et al.* 2013). In Garry oak savannas, species like orchard grass (*Dactylis glomerata*) may create thick monoculture stands that reduce overall diversity and thus negatively impact metrics like functional redundancy and response diversity. Given the sheer variety of NIS, we therefore predicted neutral or slightly negative impacts of NIS presence to functional redundancy and response diversity.

Connectivity and road density were also determined previously (Lilley & Vellend 2009). Road density was calculated as the length of roads per unit area within a 1km radius of the patch edge. Connectivity (C_i) was calculated as a distance-weighted sum of surrounding savanna patches:

$$C_i = \sum_{i \neq j} \exp\left(-\alpha d_{ij}\right) A_j$$

where A_j is the area of patch *j* (in m^2), d_{ij} is the minimum edge-edge distances between patches *i* and *j*, and α represents the influence of distance on biotic connectivity (Moilanen & Nieminen 2002), *i.e.* species' distance-dependent dispersal rate. For grassland species, α = 0.002 is likely a realistic estimate of migration range (Verheyen *et al.* 2004), representing migration in which medium-long distance dispersal events are not rare.

With the exception of the ordinal variable management level, we standardized all predictor variables by subtracting the mean and dividing by the standard deviation to easily compare effect-sizes.

Statistical analysis

We fit multiple linear models of each response variable against the predictors. We fit a full model, a full model minus the interaction term, models against each of the individual predictors, and a model against the two interacting terms (**Table 3.1**). For group-level analyses, we also fit a null model against the fixed effect of group identity, and group was included as a fixed effect in all models. Using AIC-scores, we averaged the best model and any within ΔAIC of approximately two of the best model's AIC-score. Averaged models were calculated using individual model parameter estimates and the model Akaike weight (Anderson 2008), producing a single model per response. All responses had non-normal distributions; area change, changes in average redundancy and response diversity within quadrats, and changes in functional group response diversity were between 0 and 1, while changes in functional group redundancy were integers. For each averaged model, we visually checked residuals for normality and for random distribution against each of the predictor variables. All calculations and analyses were conducted in R (R Core Team 2014).

Table 3.1 Details of statistical model set
List of models used in model selection methods. The response variables are listed in the left column, the number of replicates in the center, and the model set in the right. All predictors were continuous. Management level was a continuous ordinal variable.

Response	N	Model Set
Patch-level:	30	~ NIS presence + Road density:Management level + Connectivity
Proportion area lost		~ NIS presence + Road density + Management level + Connectivity
Avg change in FR		~ Road density:Management level
Avg change in RD		~ NIS presence
		~ Road density
		~ Management level
		~ Connectivity

Functional group-level:	750	~ NIS presence + Road density:Management level + Connectivity + Group
Change in FR		~ NIS presence + Road density + Management level + Connectivity + Group
Change in RD		~ Road density:Management level + Group
		~ NIS presence + Group
		~ Road density + Group
		~ Management level + Group
		~ Connectivity + Group
		~ Group

Results

Average patch species richness was 89 in 2006 and 98 in 2017 (**Appendix 3.B**). Both additional and missing species were evenly divided between native species and NIS. We found 25 functional groups that characterize Garry oak savannas (**Appendix 3.C**).

Woody encroachment

The average area lost to woody encroachment was 13%, with only six patches maintaining the 2006 extent (**Appendix 3.B**). Woody encroachment was predominantly shrub growth, with expansions in native snowberry (*Symphoricarpos albus*) and invasive Scotch broom and Himalayan blackberry. Some increases in overstory species like Douglas fir were observed in areas near woodlands.

The two top models to explain the amount of area lost to woody encroachment were the full models with and without the interaction term. We found that proportional area lost to woody encroachment was significantly related to management and connectivity, where higher levels of management and higher relative connectivity were linked with lower area lost (**Figure 3.1; Table 3.2**).

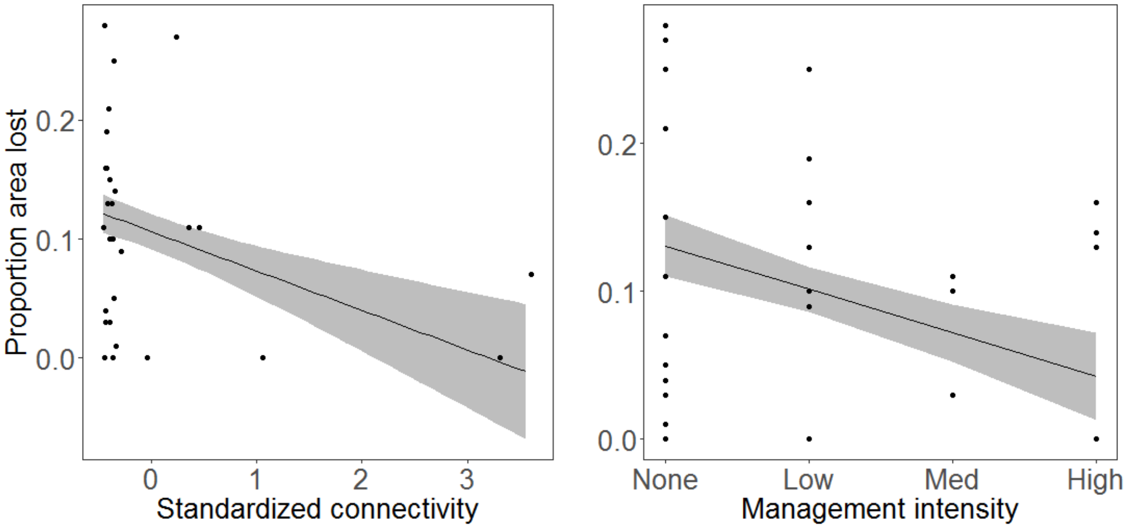


Figure 3.1 Area lost plotted against significant predictors

Patch area lost to woody encroachment as a proportion of 2006 area against connectivity (standardized) and management level, where points represent real data and lines represent relationships predicted by the best model. Standard error bars are shown in grey; both predictors were significant at α = 0.05.

Functional redundancy

Patch functional redundancy and group redundancy both responded positively to management. On average, patch redundancy decreased from 0.55 to 0.48. The top model was change in patch redundancy against road density, management, and their interaction (**Table 3.2**), where management in areas with lower road density was associated with negative changes in redundancy, while management in areas with higher road density was associated with positive changes (**Figure 3.2**). The only significant relationship was between functional redundancy and the interaction term.

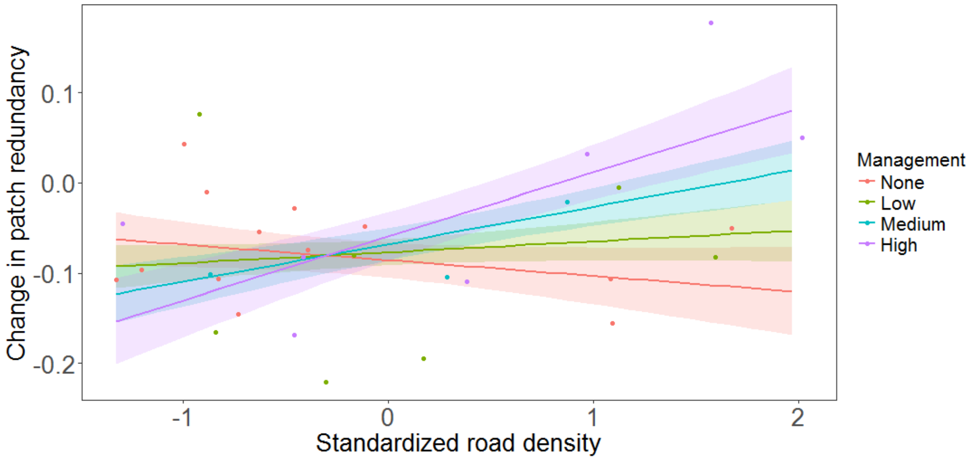


Figure 3.2 Changes in patch redundancy based on road density and management

Average change in patch functional redundancy based on surrounding road density (standardized), with points representing real data for each patch and lines representing relationships predicted by the best model. Each colored line and band represents the predicted effect and standard error of road density at differing levels of management intensity.

Within functional groups, redundancy increased on average by 0.28 species from 2006 to 2017. In our single best model, the largest effect size was a positive relationship between higher levels of connectivity and increasing redundancy within groups (**Figure 3.3**; **Table 3.2**). We also found significant positive relationships between increasing redundancy and management effort, and with NIS proportion in each group (**Figure 3.3**).

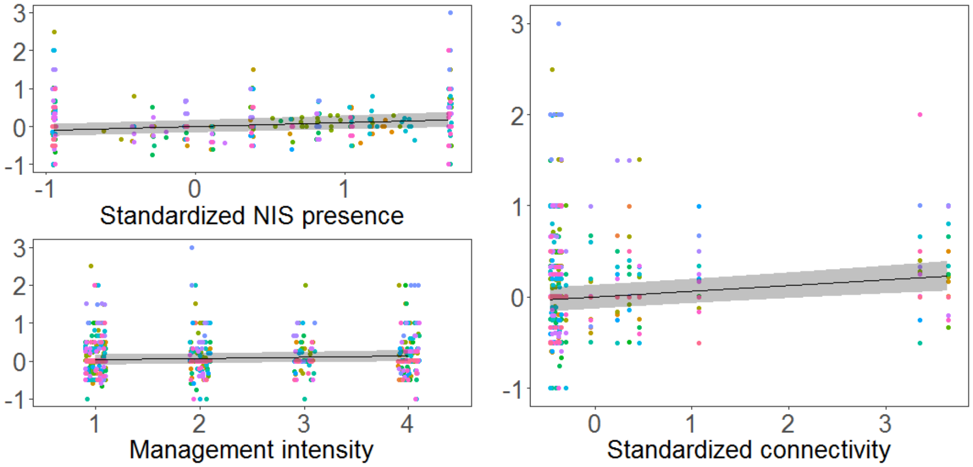


Figure 3.3 Model results for changes in group redundancy

Changes in functional redundancy within individual functional groups against level of connectivity (c), management effort (b), and the proportion of NIS in each group, in each site, in 2006 (a). Lines represent the coefficient estimates from models and grey bars represent the standard error around those coefficients

Response diversity

We found no significant predictors of response diversity changes at either scale. Patch response diversity decreased on average by 0.003 between 2006 and 2017. No one model was better than others. The final averaged model had no significant predictors (**Table 3.2**). Within functional groups, response diversity calculation required at least three species, which excluded 42% of groups over all patches. Relative to redundancy in those groups, response diversity was largely unchanged, increasing on average by 0.02 between 2006 and 2017. All but the full models were within two of the lowest AIC-score and were used in the averaged model. No predictors were found to be significant other than group identity (**Table 3.2**), where the appearance of native rose species increased the response diversity in a woody shrub group.

Table 3.2 Averaged model results
Model results for each averaged model, where numbers represent the estimated coefficients for each predictor. Because predictors were standardized, coefficients capture relative effect sizes. Bolded predictors were significant at the α = 0.05 level.

Resilience metric	Averaged model
Proportion area lost	~ 0.16 + 0.02 x NIS richness - 0.04 x Road density - **0.03 x Management** - **0.03 x Connectivity** + 0.02 x Road density:Management
Change in functional redundancy (group)	~ 0.17 + **0.24 x NIS proportion** + 0.07 x Road density + **0.08 x Management** + **0.18 x Connectivity** - 0.003 x Road density:Management + **Group**
Change in response diversity (group)	~ 0.01 + 0.003 x NIS proportion + 0.001 x Road density + **Group***
Change in functional redundancy (patch)	~ -0.09 + 0.04 x Road density + 0.008 x Management + **0.03 x Road density:Management**
Change in response diversity (patch)	~ -0.005 - 0.005 x NIS richness + 0.003 x Road density + 0.003 x Management + 0.002 x Connectivity + 0.003 x Road density:Management

Discussion

Management issues like fragmentation and non-indigenous species are particularly heightened in urban parks, (Murphy 1988), limiting resources available for proactive management decisions. There is often a suite of invasive species that must be managed, as invasive species are known to fundamentally shift the composition, structure, and function of ecological communities (Hejda *et al.* 2009; Vilà *et al.* 2011). The implicit expectation is that by controlling the dominant invasive species, biological and functional diversity can be maintained (Pyšek & Richardson 2010), thus enhancing ecological resilience (Standish *et al.* 2014). Here, we assessed the impact of invasive species management over ten years and found that management coupled with other anthropogenic factors has played a varied yet important role in maintaining ecological resilience in urban parks.

Woody encroachment was significantly lower in heavily managed parks. Much of the canopy closure observed was driven by invasive woody shrubs like Scotch broom (*Cytisus scoparius*). This result was mediated somewhat by landscape context, however. Though not significant in the final averaged model, the largest effect size in the model was estimated to be against road density, where higher road density was related to larger losses in patch area, and the model included an interaction between road density and management, where the effect of management was more important in remote areas. Even in remote patches, invasive woody species are present, having presumably dispersed along roads or power lines. Without invasive species control, these patches are losing area to the combined effects of native and invasive shrub encroachment. Many ecosystems undergoing woody encroachment evolved under different fire and grazing regimes than they currently experience (e.g. Twidwell et al. 2013b; Parr et al. 2014). Similarly, First People actively managed Garry oak savannas with fire to maintain open canopies (Bjorkman & Vellend 2010). After massive losses in extent over the past 150 years, the urban setting may benefit remaining Garry oak savannas by eliminating encroachment pressure from native forest while encouraging local community control of invasive woody species.

Average patch functional redundancy was strongly related to the interaction between management and road density. Relative to unmanaged remote areas, highly managed remote areas underwent more negative shifts in redundancy, with species losses evenly spread across native species and non-indigenous species (NIS). The implication is that for redundancy, less management in remote areas may be beneficial. Remote areas may thus present a trade-off, where management prevents regime shifts to woodland, but reduces some attributes supporting resilience to other pressures like climate change. Conservation management has been known to act as a disruptive event (e.g. Menakis *et al.* 2003; Müller *et al.* 2010). Here, trampling and soil disturbance from invasive species removal may favor some species, reducing small-scale diversity and negatively impacting redundancy at that scale. This supports the calls to specify resilience 'of what to what' (Carpenter *et al.* 2001), and may undercut the utility of 'general' resilience proxies.

Within functional groups, changes in redundancy were most strongly related to the proportion of NIS. Groups with more NIS tended to have no change, or increases, in redundancy and tended to have higher response diversity (**Appendix 3.C**). NIS evolved separately from the native species and environment. They are more likely to have response traits adapted to human activities and dispersal modes, and functional traits that differ from local specialist species (Buckley & Catford 2016). Functional traits chosen for this study focused on growth form, habit, rate, and life history. From a purely functional perspective, the presence of NIS may increase the likelihood that a function will be resilient to change and disturbance through increases in the redundancy and response diversity of that function. However, given the unknown interactions between changing conditions and each NIS, as well as the potential for NIS to become invasive long after introduction (Simberloff 2014), the ultimate role of NIS in ecological resilience is difficult to predict.

As a compositional suite, however, NIS tend to have more homogenous traits than their native counterparts (Catford *et al.* 2014). Should they become dominant by outcompeting natives, NIS may reduce the redundancy and diversity within individual functions and thus lead to reductions in ecological resilience (Buckley & Catford 2016). However, the suite of NIS in our study was more diverse in both effect and response traits than the native suite of species (data not shown). Additionally, the average NIS proportion within these patches has remained relatively unchanged over the last ten years, and the composition may be fairly stable. Given that controlling the entire suite of NIS is difficult to impossible (Shackelford *et al.* 2013), particularly in urban settings surrounded by gardens and cultivated green space (Goddard *et al.* 2010), the presence of non-invasive NIS may not be a pressing concern in urban Garry oak patches. Indeed, our data suggest that management goals that focus on the control of woody encroachment over the management of non-invasive NIS may be more effective at sustaining existing values in these landscapes. There must be awareness, however, that some NIS may become invasive in the future (Williamson & Fitter 1996; Bennett *et al.* 2013).

Both within-group functional redundancy as well as area lost to woody encroachment showed positive relationships with the degree of connectivity between patches, making it the most consistently positive predictor of resilience after management intensity. Connectivity has been found to maintain native species populations (Damschen *et al.* 2006), enable biotic and abiotic flow between patches (Lundberg & Moberg 2003), and ensure access to refugia and specialized habitat (e.g. Keith *et al.* 2002; Dorenbosch *et al.* 2007). The connectivity considered here is a distance-weighted sum of surrounding area that is Garry oak savanna. Higher levels of nearby savanna likely encourage propagule dispersal between patches (Rudnick *et al.* 2012). As NIS tend to be better dispersers, connectivity may eventually favor NIS populations. Within this study, however, recruitment, loss, and retention of species was evenly spread between NIS and native species (**Appendix 3.B**). As a manageable landscape attribute, connectivity seems to be one of the most generalizable resilience mechanisms, both in this study and in others (Shackelford *et al.* 2017).

The variation in connectivity among surveyed Garry oak patches was limited by the landscape context. More connected patches tended to be in parks with multiple savannas, and isolated patches tended to be in highly urbanized areas. Ideally, more patches over a wider range of conditions would strengthen the relationships found, as well as highlight the potential generalizability of these results. For example, mechanisms like connectivity and invasive species management may be most important in urban and rural areas, but decline in importance in remote settings. Additionally, reactive management of invasive species may be beneficial primarily in these specialized circumstances, where the invader fundamentally changes the structure and function of the ecosystem and is relatively easy to control with annual hand-pulling. Further research on the mechanisms explored here in a wider range of ecosystems and settings is needed.

We found some limitations in the applicability of response diversity, which was difficult to measure and difficult to explain with the chosen predictor set. Group-level response diversity needed at least three species for calculation; only 58% of the functions had three or more species in a single patch (data not shown). For those groups with three or more species in a patch, response diversity variation was small, and the final model had only weak relationships with predictors. This particular proxy of resilience may be difficult to apply unless ecological functional groups are composed of very diverse species. Though its theoretical importance has been stressed (Mori *et al.* 2013), and its applicability in certain ecosystems is clear (e.g. Nash *et al.* 2016), managers may find more usefulness in functional redundancy or other resilience proxies in systems with low levels of diversity.

In an urban environment, long-term reactive management of invasive species generally had the benefit of boosting ecological resilience of Garry oak savannas, measured as patch area retention against woody encroachment and increased functional redundancy. In this way, reactive management had both expected direct benefits (*i.e.*, invasive species control) and additional proactive outcomes (*i.e.*, maintaining resilience to other disturbances). Yet management effect was influenced by human pressure as measured by surrounding road density. Results in remote areas highlighted that there may be trade-offs to management, where resilience to woody encroachment was positively related to management, but patch functional redundancy was negatively related to management. Thus, reactive management decisions should be contextualized in the framework of long-term goals, with an outline of particularly concerning pressures and state changes. Where possible, indirect and assumed benefits such as increased diversity or resilience should be monitored to allow adaptive management strategies.

Chapter 4 : Cumulative impacts of human activity threaten biodiversity conservation in one of North America's last wildlife frontiers

with Rachel J. Standish, William Ripple, and Brian M. Starzomski

Abstract

Land-use change is the largest proximate threat to biodiversity, yet remains one of the most complex to manage. In British Columbia (BC), where large mammals roam extensive tracts of intact habitat, continued land-use development is of global concern. Extant mammal diversity in BC is unrivalled in North America owing, in part, to its unique position at the intersection of alpine, boreal and temperate biomes. Despite high conservation values, understanding of cumulative ecological impacts from human development is limited. Using cumulative effects assessments (CEAs) methodologies, we assess the current human footprint over 16 regional ecosystems and seven large mammal species. Using historical and current range estimates of the mammals, we investigated impacts of human land-use on species persistence. For ecosystems, we found that Bunchgrass, Coastal Douglas Fir and Ponderosa Pine have experienced over 50% land-use conversion; over 85% of their spatial extent has undergone either direct or estimated indirect impacts. Of the mammals we considered, wolves were the least impacted yet all species have reduced ranges compared with historical estimates. We found evidence for a hard trade-off between development and conservation, most clearly for mammals with large distributions and ecosystems that have experienced high levels of conversion. Rather than serve as a platform to monitor species decline, we strongly advocate these data be used to inform land-use planning and to assess current conservation efforts. More generally, CEAs offer a robust tool to inform wildlife and habitat conservation at scale.

Metric Details

Human footprint – the spatial extent of direct land-use plus indirect impacts estimated as a range of buffer distances around physical infrastructure

Persistence – the continued presence of animal populations in their historical range, where either a population is persistent or not

Introduction

Conservation management aims to prevent species and ecosystem loss (Soulé 1985) while still managing human uses of environmental resources (Kareiva & Marvier 2012). Yet land-use change is the single largest threat to biodiversity (Millennium Ecosystem Assessment 2005; Turner *et al.* 2007) and planning efforts to manage it have failed to slow development or resulting biodiversity impacts (Butchart *et al.* 2010; Newbold *et al.* 2016). The variety of land-use activities, from agriculture to land clearing for settlement or resource extraction (Foley *et al.* 2005), make tracking and managing cumulative use challenging (Raiter *et al.* 2014). Systematic conservation planning has emerged to address this challenge (Margules & Pressey 2000b) and frameworks like cumulative effects assessment (CEA: Halpern & Fujita 2013) are gaining traction.

CEAs contextualize local development in a regional setting, assessing large-scale land-use impacts to inform small-scale planning (Baxter *et al.* 2001). Typically, CEAs have three primary steps focused around pre-defined ecological values (Spaling & Smit 1993). The first is quantifying the total regional human footprint. The chosen ecological values determine the spatial boundaries of the assessment (Therivel & Ross 2007). Thus, footprints may shift depending on species' ranges or ecosystem distributions. The second step is estimating the impact of that footprint on ecological values. Estimating impacts is based on quantitative predictions that are refined by monitoring ecological values through time (Burton *et al.* 2014). The final step of a CEA is outlining future development scenarios. Using calculated footprints, estimated impacts, and future scenarios, CEAs can advise strategies that minimize risks to ecological values. CEAs aim to bridge multiple scales and land-uses, protecting conservation values while allowing sustainable development (Duinker & Greig 2006). In practice, examples of comprehensive CEAs are rare, even where they are increasingly needed.

British Columbia (BC) represents an area of high global conservation value, yet it has undergone little provincial-level CEA and planning. Habitat diversity in BC is high, with elevations ranging from 0 to over 4000 m and climate regimes ranging from the very wet hypermaritime to the semi-arid grasslands (Meidinger & Pojar 1991). In continental North America, range contractions of over 20% have occurred for seventeen mammals since Euro-American settlement. BC plays a prominent role in habitat provision for these dwindling populations (Laliberte & Ripple 2004), containing large tracts of globally significant untouched habitat. Land-use in BC is recent because much of the natural resource base is remote and inaccessible. Pressures on the landscape are increasing as technology opens previously inaccessible areas, and terrestrial species populations are declining across the province (BC Ministry of Environment 2014). Nowadays, there is significant economic reliance on natural resources, especially natural gas and lumber (BC Ministry of Finance 2016), and agriculture is prominent in the central, south, and northeast regions. This situation creates a pressing need for comprehensive land-use planning.

CEAs start with mapping the human footprint (Connelly 2011), often represented by the spatial extent of land-use (Toews 2016). Here, we map the current footprint provincially, focusing on its distribution across ecosystems and select mammal ranges. Given BC's accessibility issues, and the spatial distribution of resources, we expect that particular land-use types will be isolated within certain ecosystems. However, some development types like roads are likely diffuse, impacting all provincial ecosystem types. When narrowed to individual species' ranges, the footprint will likely shift, with wide-ranging species such as large carnivores experiencing higher impacts.

Once mapped, the next step is estimating land-use impacts on ecological values. We used historic range estimates of mammal species to investigate local species extirpations based on individual activities, cumulative effects, and indirect effects. Range boundaries are notoriously coarse (Hurlbert & Jetz 2007) and comparing to historical estimates is difficult (Tingley & Beissinger 2009). We acknowledge these pitfalls; yet range estimates provide a critical foundation for future species monitoring and for monitoring the effectiveness of land-use planning for conservation outcomes, of which species persistence is a key performance indicator.

By creating quantitative models of land-use relationships to range loss, we are building foundations for refined, predictive knowledge of land-use impacts on these mammals. In the final step of the CEA process, future scenarios are outlined and paired with predicted ecological impacts (Smit & Spaling 1995). From this, recommendations on sustainable development can be made. This study does not extend into scenario predictions. Assessing cumulative impacts for multiple species is essential for understanding trade-offs and for identifying both idiosyncratic and consistent impacts. This study aims to take the first major steps towards a comprehensive CEA in a globally important region by a) calculating the total human footprint for a set of ecological values; b) assessing the status of those values based on land-use cover and range loss; and c) creating preliminary predictive models of land-use impacts on those values.

Methods

Study Area

British Columbia (BC) covers 945,000 km^2 and is the western-most province of Canada. Vegetation communities have been comprehensively described and classified by the Ministry of Forests (Pojar *et al.* 1987) using a system known as the Biogeoclimatic Ecosystem Classification (BEC). The BEC zones are determined primarily by climate, vegetation, and soil data (Pojar *et al.* 1987). Originally established to map forest types and commercial tree occurrence, BEC zones house differing levels of extractable resources and biodiversity. There are 16 BEC zones in BC (**Figure 4.2** and **Table 4.3**), and each zone was treated as an individual ecosystem. Wildlife use of zones tends to have high overlap, with only 12% of terrestrial vertebrate species thought to be zone-specific (Bunnell 1995). Thus, ecosystem analysis based on the BEC zones captures climate, soils, and vegetation rather than habitat and range size of individual species.

Data collection

We collected spatial data on land-use and mammal range estimates (historic and current). For land-use information, we utilized data publicly available through GeoBC (http://geobc.gov.bc.ca/), a subset of the BC Integrated Resource Operations Division that oversees baseline spatial data and Provincial Crown Registries on land development. Details of all impact shapefiles can be found in **Appendix 4.A**. Species ranges were mapped previously (Laliberte & Ripple 2004) and details on historic and current range estimate creation can be found in **Appendix 4.B**.

We transformed all shapefiles into rasters. Each raster was approximately 35 million cells at 250 m × 250 m. This resolution is significantly finer than the typical management scale (Halpern & Fujita 2013) and allowed detailed analysis over the study area.

Land-use

We separated land-use into categories (**Table 4.1**), within which impacts will generally be of a similar type but vary in intensity. Infrastructure covered urban and residential development, with a small area converted for mining. These impacts are diffuse and require large amounts of clearing. Roads were analyzed independently, as they dissect landscapes on large scales and are linked to compositional changes, abiotic shifts, and vertebrate mortality (Forman & Alexander 1998b; Coffin 2007b). Oil and gas in BC is isolated physical structures associated with extraction (*e.g.*, drills) connected by a network of access roads and development lines. Agriculture and rangeland were grouped together.

Our last category was logging, a primary source of BC economic revenue (BC Ministry of Finance 2016). In the first 10 years post-logging, vegetation tends to be open with high forage. Through time, vegetation thickens and dense stands offer grazer protection (Fisher & Wilkinson 2005). Gradually stands thin, and achieve ‘old growth’ designation according to their species, with the minimum ‘old growth’ forest age at 120 years (Ministry of Forests, Lands, and Natural Resources 2003). We thus considered different times since last logging as different impact levels – 0-10 years (as of December, 2016), 11-60 years, 61-120 years, and then all areas that have been logged plus all land under logging tenure. Tenured land in BC is licensed to private companies for active management and exploration of timber resources (Zhang & Pearse 1996). Though tenured land may also represent future human impacts, human presence and activities are heightened compared with untenured forested land. Thus, we considered it current land-use.

Table 4.1: Land use types and classifications

Land use and individual impacts used in this analysis from the most impactful decreasing to indirect effects calculated as buffers of varying distance

Land use	Individual impacts and ranges in estimated spatial extent
Infrastructure	Urban areas, residential areas, and mining
Roads	Roads
Oil and gas	Facility sites, pipelines, development and access roads, seismic lines, well sites, disposal sites, sump locations
Agriculture	Agricultural Land Reserves, other agriculture and rangeland development
Logging: Recent	Land logged within the last 10 years, 60 years, and 120 years
Logging: Sites of activity, no time limit	All tenured logging land
Indirect effects: Oil and gas	All land within 250 m, 500 m, 1000 m, or 2000 m of oil and gas development
Indirect effects: Roads	All land within 250 m, 500 m, 1000 m, or 2000 m of roads

Human development has effects beyond the physical footprint. We estimated indirect impacts around a subset of land-uses, with a focus on roads and oil and gas development. Both are structures on the landscape that have known impacts beyond their physical presence. Because the impact to wildlife varies between and within species (Toews 2016), we estimated indirect impacts for increasing distances based on mammal avoidance data. Data collected in BC on avoidance behavior has often focused on caribou, whose avoidance patterns range from 250 m (Dyer *et al.* 2001) to 2,000 m (Polfus *et al.* 2011). We used these 250 m and 2,000 m endpoints and intermediate distances of 500 m and 1,000 m to represent a range of discrete buffer widths around direct impacts.

We did not estimate indirect impacts around other land-uses. Activities like urban and residential development or agriculture are diffuse rather than singular structures. Reflecting this, data on these land-uses were available as large polygons with smoothed boundaries likely incorporating the indirect buffer distances we chose. For logging, we chose the time-since-logged classification to represent different levels of direct-to-indirect impact. In addition to the temporal component, the tenured land boundaries include the majority of indirect spatial buffers that would have been calculated around recently logged land.

Ecosystem-level indicators

Within a BEC zone, we calculated proportional area lost to each of the impacts and calculated fragmentation patterns based on direct land-use: infrastructure, roads, oil and gas, agriculture, and logging within the last 120 years. In each zone, we calculated average mean patch area (km^2), total edge of all patches (m), average perimeter-area ratio (PAR), aggregation (the number of like adjacencies divided by maximum possible number), and the number of patches. We calculated metrics in Fragstats (McGarigal *et al.* 2002).

Population-level indicators

Current distributions for seven ungulates and carnivores were estimated: bighorn sheep (*Ovis canadensis*), caribou (*Rangifer tarandus caribou*), elk (*Cervus canadensis*), fisher (*Pekania pennanti*), mountain goat (*Oreamnos americanus*), grizzly bears (*Ursus arctos*), and wolves (*Canis lupus*). British Columbia has 32 native terrestrial carnivore and ungulate species (Eder & Pattie 2001). We did not consider wildlife that are known to respond neutrally or positively to land-use (cougars: Carter & Linnell 2016; e.g. white-tailed deer and coyote: Toews 2016), mimicking management prioritizations that consider sensitive species first. Additionally, we were not able to consider species with too little data to confirm range loss despite recorded declines in abundance. Please see **Appendix 4.B** for further details on species selection.

We calculated the range extent impacted by land-use and indirect effects and assessed fragmentation patterns due to cumulative direct effects.

Population-level impacts

We compared current ranges with historic range estimates. Distribution maps are known to overestimate suitable habitat by smoothing edges and excluding small-scale extirpation (Hurlbert & Jetz 2007), leading to optimistic estimates of species occurrence (Rondinini *et al.* 2005). In our case, the scale of a provincial-study on multiple species makes finding smaller-scale range data difficult. The distribution maps used here were made at a provincial scale and likely provide the appropriate level of detail.

Scale also drove our choice of presence-absence rather than abundance data. Only caribou and grizzly bears have abundance data across the province. The smaller-bodied species are far more difficult to count and consequently have less available data. The temporal scale of this study is large, with historic range estimates from the 18th century compared against those of the 20th century. Presence-absence data capture the current outcome of that extended period for each species. In the case of delayed response to recent development (*e.g.* oil and gas), presence-absence data may not be adequate. Each individual species result was assessed in that light.

To enable statistical modeling of species persistence, we divided the landscape into 25km x 25km non-overlapping landscape parcels. Each of the resulting 1,714 parcels had a present, absent, or extirpated designation for each species as well as amount of habitat loss and fragmentation. Additionally, we classified each parcel as either having experienced local extirpation of any species, or having maintained all known populations. We modeled persistence using a series of generalized linear models with a binomial response (0/1 for extirpated/persistent). To incorporate spatial dependency between parcels, we used an autocovariate regression (Dormann *et al.* 2007). We calculated an autocovariation metric (Augustin *et al.* 1996) with the spdep package (Bivand & Piras 2015) that was a weighted average of the 'successes' (here, persistence) amongst all parcel neighbors. The autocovariation was included as a fixed effect in models.

The candidate set totaled nineteen models for each species: a null model with only the spatial covariation, proportion of habitat loss to individual categories, proportion total loss, proportion total loss plus differing levels of indirect effects, and each fragmentation metric. Total loss did not differentiate between land-uses. Overlap and spatial distribution of land-uses led to high correlation between each use that left them inappropriate for separate predictors in a single model. We recorded coefficient estimates and the Akaike Information Criterion (AIC) to assess support for each model. All analyses were completed in R (R Core Team 2014).

We used caution in interpreting model results. Provincial data lack details of land-uses like mining or non-governmental development like private logging. Thus, our collected land-use data and coarse range estimates are conservative, likely underestimating total impacts and range contraction. Additionally, we do not have access to historical land-use data, limiting our analysis to a temporal snapshot potentially underestimating historical impacts.

Results

Land-use

Approximately 13% of BC has been directly modified (**Figure 4.1**). When indirect effects of a 2 km buffer are included, 35% of the landscape has been impacted. The most wide-spread use is logging, with 7% of the total landscape under logging tenure. Agricultural development has occurred over 5% of the province, and oil and gas development over 2.5%. The spatial distribution of some impacts is limited (*e.g.*, oil and gas), though collectively the impacts are widespread. Human land-use has reduced the average intact patch size in each zone by 62%.

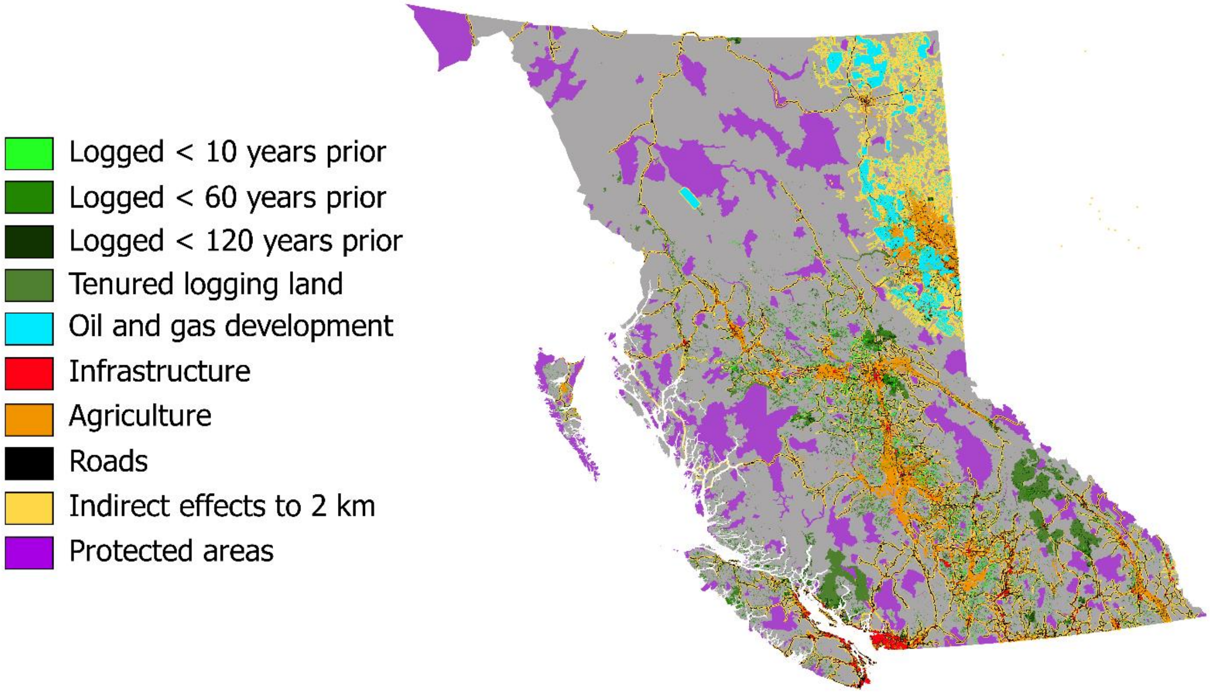


Figure 4.1: Land use change and protected areas across British Columbia
Land use change and protected areas across British Columbia, including infrastructure, roads, oil and gas, agriculture, logging, tenured logging lands, and indirect buffers up to 2 km.

Ecosystem-level indicators

The distribution of land-use was as we predicted, with some land-uses, like logging, diffuse across the province. Logging tenures are present in every zone, and active logging has occurred in 12/16 of the zones within the last 10 years. In contrast, other land-uses were concentrated in relatively small areas. Agriculture and infrastructure occurred largely in a subset of the BEC zones, resulting in three zones (Bunchgrass, Ponderosa Pine, and Coastal Douglas Fir) that have experienced 58 – 74% land conversion (**Figure 4.2**). Some impacts were even more localized, with almost 90% of oil and gas development in the Boreal White and Black Spruce. Indirect effects further emphasize these patterns, with the three zones under pressure from agriculture and infrastructure all exceeding 85% of their area under direct + indirect effects, and 24% of the landscape covered by oil and gas direct + indirect effects in the Boreal White and Black Spruce.

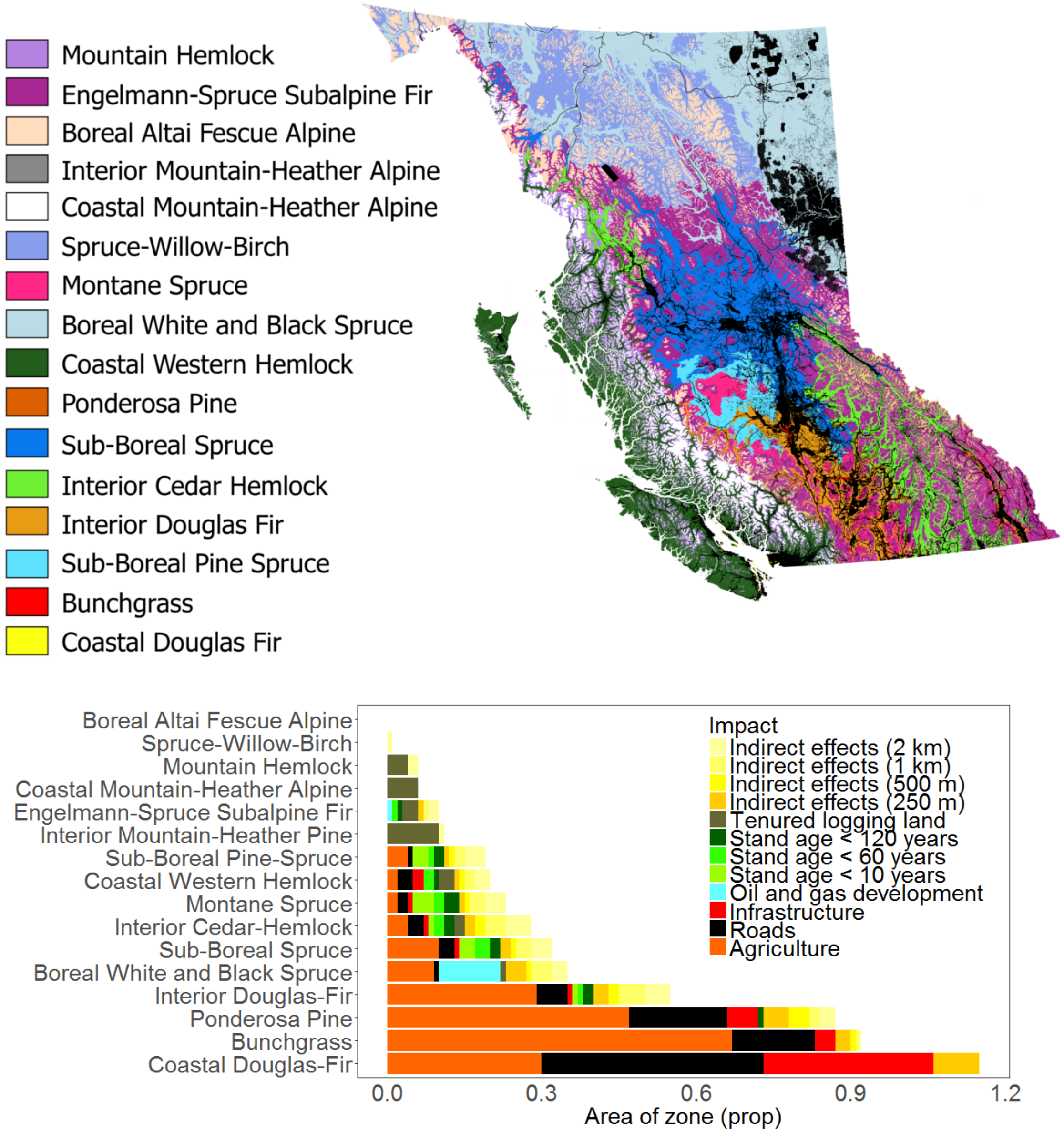


Figure 4.2: BEC Zones with land use impacts and a breakdown of impacts by zone

BEC zones with all direct impacts overlaid (in black; top), including infrastructure, roads, oil and gas, agriculture, and logging (time since logging < 120 years). The bottom panel shows the breakdown of impacts within each zone.

Given the spatial distribution of land-uses, it was unsurprising that a subset of zones was relatively intact. The eight zones with the least amount of total impacts were all remote or difficult access. Predominantly, the eight were alpine and high-altitude zones. Coastal Western Hemlock was one exception, which has a relatively low footprint and is lower altitude. Large portions are away from population centers and generally surrounded by either ocean to the west or mountains to the east, making access difficult for most activities.

Despite the often localized distribution of land-use, there was dramatic habitat fragmentation over most of the province. On average, land-use has increased the number of patches within a single zone by 13 times (**Table 4.2**). Increased patch numbers were strongly correlated with increased road cover. Total edge either stayed the same or decreased once impacts were considered, with the largest decreases occurring in zones with the highest impacts. In contrast, the perimeter-to-area ratio (PAR) increased for all zones due to consistent decreases in mean patch area. For 7/16 zones, the mean patch area was reduced by 90%. Aggregation remained relatively unchanged.

Table 4.2: Spatial changes due to land use by zone

Spatial changes of each BEC zone before / after direct impacts are removed from the landscape where direct impacts include infrastructure, roads, oil and gas, agriculture, and logging (logged < 120 years ago).

Zone	Mean patch area change	Total edge change	PAR change	Aggregation change	Number of patches change
Boreal Altai Fescue Alpine	-2.8%	-0.7%	5.0%	0.0%	2.6%
Spruce-Willow-Birch	-5.5%	-0.3%	9.1%	-0.1%	5.6%
Boreal White and Black Spruce	-98.4%	-4.4%	9.0%	-3.9%	4,904.6%
Engelmann-Spruce Subalpine Fir	-71.0%	-3.6%	205.7%	-1.0%	237.0%
Coastal Mountain-Heather Alpine	-0.2%	-0.0%	0.1%	0.0%	0.2%
Sub-Boreal Spruce	-93.8%	-10.2%	26.9%	-5.8%	1,205.4%
Mountain Hemlock	-2.0%	-0.4%	1.7%	-0.1%	1.8%
Coastal Western Hemlock	-69.3%	-1.5%	55.6%	-2.8%	201.7%

Interior Cedar-Hemlock	-82.6%	-7.8%	80.5%	-4.6%	416.8%
Interior Mountain-Heather Alpine	-0.1%	-0.2%	0.1%	0.0%	0.1%
Sub-Boreal Pine-Spruce	-91.4%	-12.9%	25.8%	-4.3%	956.5%
Montane Spruce	-73.3%	-9.2%	101.2%	-5.2%	239.2%
Interior Douglas-Fir	-97.5%	-21.7%	105.0%	-8.6%	2,557.1%
Bunchgrass	-99.4%	-73.2%	152.6%	-24.1%	4,600%
Ponderosa Pine	-98.2%	-50.2%	236.1%	-19.3%	2,212.5%
Coastal Douglas Fir	-97.5%	-57.7%	90.6%	-35.0%	1,224.1%

Population-level indicators

We found up to 18% direct impact within a single species range (bighorn sheep) and 45% direct and indirect impact (**Table 4.3**). Bighorn sheep had both the smallest range, and the highest proportional impact. Direct land-use was linked to considerable spatial change within species' ranges. Each distribution has been heavily fragmented, ranging from 1,001 individual patches within the bighorn sheep range to 15,299 for wolf (**Figure 4.3**). Mean intact patch area has been reduced by an average of 97% across species.

Table 4.3: Range size of each species and land use impacts within each

Range size of each species, and percentage of that range impacted by agriculture; built-up impacts (infrastructure + roads + oil and gas; grouped for simplicity); recently logged land (within 120 years); total direct use (all the previous minus overlap); land under any governmental logging tenure; indirect effects up to 2 km; and all effects (direct, tenured land, and indirect effects up to 2 km).

Animal	Range size (thousand km^2)	Agriculture	Built up land	Recently logged	Total direct use	Tenured land	Indirect effects up to 2 km	All effects
Bighorn sheep	1150	11%	5%	5%	18%	11.54%	20%	45%
Caribou	4540	2%	5%	1%	7%	3.81%	15%	25%
Elk	3620	9%	7%	4%	18%	9.58%	21%	44%
Fisher	4090	8%	7%	3%	16%	7.08%	21%	41%
Mountain Goat	6210	2%	3%	2%	5%	5.16%	9%	18%
Grizzly	7650	2%	4%	2%	7%	5.73%	13%	25%
Wolf	9090	5%	4%	3%	11%	6.79%	15%	30%

Population-level impacts

Estimated range losses span from 1% of the historic range for wolves to 42% for fisher (**Figure 4.3**). In all cases, models of persistence ignoring land-use – the null models – were not within the top models (**Table 4.4**). When we modeled the probability of all species persisting, the null model was the worst and all relationships with land-use were negative.

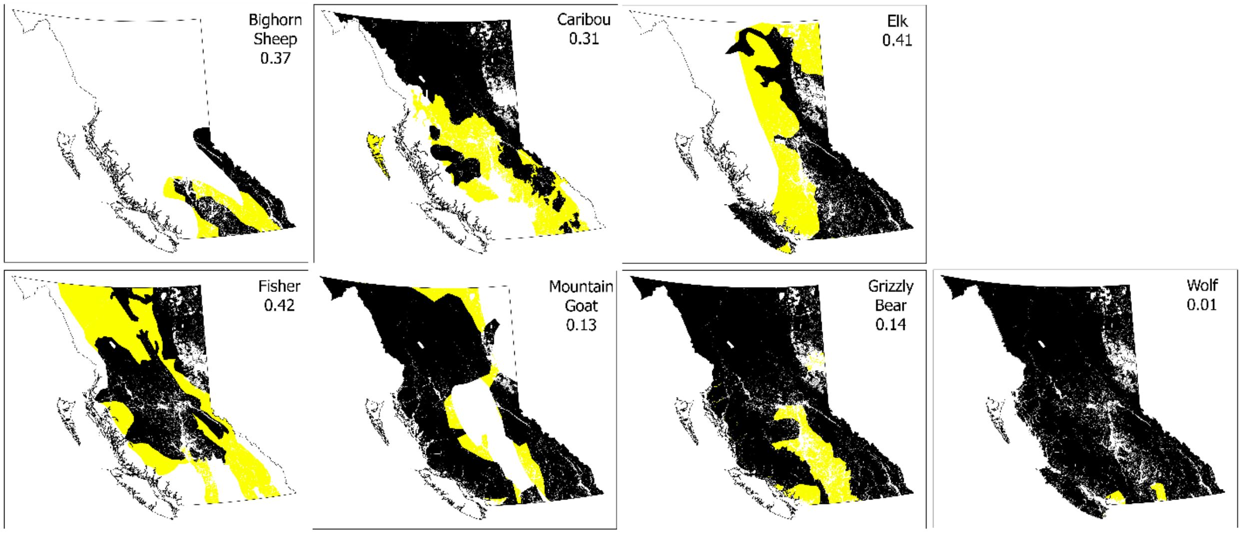


Figure 4.3: Historical and current estimated ranges for mammal species
Historical and current estimated ranges for all seven mammals. Black areas are the current estimated ranges, yellow are the historical estimated ranges in which local extinction has likely occurred, and the white areas represent either locations in BC never thought to have been within the ranges, or human impacts that have been removed from the ranges. The number in each box is the proportion of the estimated historic range from which extirpation is thought to have occurred.

Oil and gas development was the only land-use with a consistently neutral or positive relationship with species persistence. It is also the most recent form of development, so effects on measured species may be forthcoming. All other impacts tended to have neutral or negative relationships with persistence, often at great improvement to the null model. Only one species, fisher, was found to have consistent positive trends between persistence and land-use. Models including total cumulative use were worse than the null for bighorn sheep, caribou, and elk, and better than the null for mountain goat, grizzly, and wolf.

Beyond these larger patterns, species varied in their apparent response to land-use. Bighorn sheep persistence was related only to recent logging. In contrast, caribou persistence related negatively to all but agriculture and oil and gas on an individual basis, but showed no relation with total effects; models with the lowest AIC values all involved logging. Mountain goat and grizzly persistence was found to relate negatively with all human land-uses except oil and gas development. Wolf persistence was negatively related to all human uses except oil and gas, and logging that occurred less than 60 years ago.

Including indirect effects did not improve models for any species. In general, species persistence was positively related to mean patch area and negatively related to PAR. These variables were the only improvements on the null for elk. For those species linked to cumulative habitat loss (mountain goat, grizzly, wolf, and all species), we also found positive relationships with aggregation and total edge. Fisher persistence was the opposite – negatively related to mean patch area, total edge, and aggregation, and positively to PAR.

Table 4.4: Model results for species persistence

Model results for species persistence. The species is listed on the far left; the top model according to the lowest AIC score is listed next; the right portion of the table is all other models for each species that had significant co-variates but were not in the top models (within 2 of the lowest AIC score). The AIC for each model is included.

Species	Top Model(s)	AIC	Model(s) with significant predictors	AIC
Bighorn Sheep	~ -0.8 * Logging (0 - 10 yrs + 11 - 60 yrs + 61 - 120 yrs)	74.3	~ 0.1 * Mean patch area	77.51
	~ -1.7 * Logging (0 - 10 yrs)	74.43	~ - 0.01 * Perimeter-area-ratio	76.21
	~ -1.1 * Logging (0 - 10 yrs + 11 - 60 yrs)	74.78		
Caribou	~ -1.5 * Logging (0 - 10 yrs + 11 - 60 yrs)	51.7	~ -2.3 * Infrastructure	77.27
			~ -1.4 * Roads	68.41
			~ 0.2 * Oil and gas	75.48

			~ -2.2 * Logging (0 - 10 yrs)	60.68
			~ -1.0 * Logging (0 - 10 yrs + 11 - 60 yrs + 61 - 120 yrs)	55.32
			~ -0.3 * Logging (0 - 10 yrs + 11 - 60 yrs + 61 - 120 yrs + tenured land)	69.84
			~ 0.1 * Mean patch area	78.95
			~ - 0.01 * Perimeter-area-ratio	79.58
Elk	~ 0.03 * Mean patch area	-223.59	~ - 0.01 * Perimeter-area-ratio	-231
Fisher	~ 0.1 * Total impacts (direct + 2 km indirect)	3.31	~ 0.1 * Agriculture	24.63
			~ 0.7 * Roads	21.53
			~ 0.3 * Oil and gas	22.33
			~ 0.1 * Total impacts (direct)	18.85
			~ 0.1 * Total impacts (direct + 250 m indirect)	15.96
			~ 0.1 * Total impacts (direct + 500 m indirect)	12.46
			~ 0.1 * Total impacts (direct + 1 km indirect)	7.3
			~ -0.1 * Mean patch area	12.32
			~ -0.1 * Total edge	16.78
			~ 0.01 * Perimeter-area-ratio	19.12
			~ -0.5 * Aggregation	12.72
Mountain Goat	~ -3.4 * Logging (0 - 10 yrs) ~ - 0.01 * Perimeter-area-ratio~ - 0.01	-149.04 -148.64	~ -0.3 * Agriculture	-138.72
			~ -0.5 * Infrastructure	-130.89
			~ -0.5 * Roads	-133.08
			~ -1.1 * Logging (0 - 10 yrs + 11 - 60 yrs)	-135.1
			~ -0.5 * Logging (0 - 10 yrs + 11 - 60 yrs + 61 - 120 yrs)	-128.57
			~ -0.3 * Logging (0 - 10 yrs + 11 - 60 yrs + 61 - 120 yrs + tenured land)	-124.6
			~ -0.2 * Total impacts (direct)	-138.16
			~ -0.1 * Total impacts (direct + 250 m indirect)	-133.14
			~ -0.1 * Total impacts (direct + 500 m indirect)	-132.61
			~ -0.1 * Total impacts (direct + 1 km indirect)	-131.53
			~ -0.1 * Total impacts (direct + 2 km indirect)	-130.69
			~ 0.1 * Mean patch area	-137.77

			~ 0.2 * Total edge	-135.61
			~ 0.4 * Aggregation	-123.94
Grizzly bear	~ -0.3 * Agriculture	-508.74	~ -0.5 * Infrastructure	-452.37
			~ -1.1 * Roads	-506.49
			~ 0.1 * Oil and gas	-440.28
			~ -2.0 * Logging (0 - 10 yrs)	-483.21
			~ -1.3 * Logging (0 - 10 yrs + 11 - 60 yrs)	-492.96
			~ -0.9 * Logging (0 - 10 yrs + 11 - 60 yrs + 61 - 120 yrs)	-489.91
			~ -0.1 * Logging (0 - 10 yrs + 11 - 60 yrs + 61 - 120 yrs + tenured land)	-447.65
			~ -0.3 * Total impacts (direct)	-505.71
			~ -0.2 * Total impacts (direct + 250 m indirect)	-483.02
			~ -0.2 * Total impacts (direct + 500 m indirect)	-480.11
			~ -0.1 * Total impacts (direct + 1 km indirect)	-470.09
			~ -0.1 * Total impacts (direct + 2 km indirect)	-462.73
			~ 0.1 * Mean patch area	-485.34
			~ 0.2 * Total edge	-501.94
			~ -0.01 * Perimeter-area-ratio	-471.61
			~ 0.6 * Aggregation	-474.54
Wolf	~ -0.7 * Infrastructure	-2,896.53	~ -0.1 * Agriculture	-2,732.57
			~ -0.6 * Roads	-2,893.43
			~ 0.1 * Oil and gas	-2,715.49
			~ -0.1 * Logging (0 - 10 yrs + 11 - 60 yrs + 61 - 120 yrs)	-2,717.58
			~ -0.03 * Logging (0 - 10 yrs + 11 - 60 yrs + 61 - 120 yrs + tenured land)	-2,714.56
			~ -0.1 * Total impacts (direct)	-2,746.57
			~ -0.1 * Total impacts (direct + 250 m indirect)	-2,736.14
			~ -0.1 * Total impacts (direct + 500 m indirect)	-2,735.99
			~ -0.1 * Total impacts (direct + 1 km indirect)	-2,732.98
			~ -0.04 * Total impacts (direct + 2 km indirect)	-2,729.15
			~ 0.03 * Mean patch area	-2,730.13

			~ 0.1 * Total edge	-2,744.99
			~ -0.01 * Perimeter-area-ratio	-2,718.94
			~ 0.2 * Aggregation	-2,735.12
All species	~ 0.1 * Mean patch area	-106.73	~ -0.3 * Agriculture	-96.77
			~ -0.3 * Infrastructure	-57.97
			~ -0.5 * Roads	-76.03
			~ -1.9 * Logging (0 - 10 yrs)	-84
			~ -1.1 * Logging (0 - 10 yrs + 11 - 60 yrs)	-88.72
			~ -0.8 * Logging (0 - 10 yrs + 11 - 60 yrs + 61 - 120 yrs)	-93.49
			~ -0.2 * Logging (0 - 10 yrs + 11 - 60 yrs + 61 - 120 yrs + tenured land)	-68.94
			~ -0.2 * Total impacts (direct)	-98.96
			~ -0.2 * Total impacts (direct + 250 m indirect)	-79.28
			~ -0.2 * Total impacts (direct + 500 m indirect)	-79.32
			~ -0.1 * Total impacts (direct + 1 km indirect)	-76.44
			~ -0.1 * Total impacts (direct + 2 km indirect)	-77.04
			~ 0.2 * Total edge	-95.43
			~ -0.01 * Perimeter-area-ratio	-101.79
			~ 0.5 * Aggregation	-76.11

Discussion

The scale and extent of global land-use change is staggering (Wilcove *et al.* 1998; Pimm *et al.* 2014), and managers at all scales are struggling to plan for it. In areas like British Columbia, where rapid and relatively recent land-use threatens larger continental-scale values, regional-scale CEAs can inform land-use and conservation policies. Our analysis supports recent claims (Auditor General of British Columbia 2015) that current land-use planning has not prevented substantial losses to ecological values in BC. The ongoing impact of habitat conversion on conservation is consistent worldwide (Foley *et al.* 2005), and more effective methods must be implemented to achieve global conservation goals. This study lays the groundwork for a full CEA for a region critical to North American mammal and habitat diversity. Future steps require refinement of the predictive models presented here, scenario creation across the province, and application to land-use decisions at all scales.

As predicted, some land-uses were clustered in particular zones, leading to high losses in individual ecosystems. Lower elevation zones have undergone the largest changes. All three of the most impacted zones occur between 0 and 1,000 m. In contrast, five of the six least impacted zones occur at 1,000 m and higher. This is unsurprising, given that lower elevation sites are more accessible for agriculture, resource extraction, and urbanization. Importantly in BC, these are often the zones along the southern border, where some high and low latitude species' range limits intersect (Swenson & Howard 2005)**.** These zones are generally the most diverse in the province with the highest numbers of threatened or rare species (Gibson *et al.* 2009; Fraser *et al.* 2011) . Continuing on the same development trajectory in the worst impacted zones may lead to substantial losses in provincial-level diversity.

Despite only 13% total direct impact, high fragmentation has occurred. Large spatial changes were not always linked with total land-use cover; *e.g.* oil and gas development typically covers a small total area, but is comprised of scattered linear features. Boreal White and Black Spruce, the zone most developed for oil and gas, has around 20% total direct land-use, but a 98% decrease in average patch area and a 4,900% increase in the total number of patches. In general, larger ecosystem patches are expected to house higher species richness than smaller patches and be exposed to fewer edge effects such as microclimate shifts and altered nutrient cycles (Saunders *et al.* 1991; Haddad *et al.* 2015). For individual species, it is likely that fragmentation interacts with habitat loss, potentially compounding the singular effect of habitat loss (Andrén 1994). Here, the strong correlation between fragmentation and habitat loss made statistically teasing apart the role of each, and their interactions, impossible. Though the experienced levels of fragmentation will differ depending on species, *e.g.* some species may experience roads as corridors rather than barriers (Toews 2016), such dramatic changes in spatial configuration are broadly concerning for ecological diversity and ecosystem functioning.

Total human footprint was largest in the distributions of bighorn sheep, elk, fisher, and wolf. Yet wolves have lost the least amount of range, and models of species response found fisher to be positively related to many land-uses, elk to be neutrally related to all land-uses, and bighorn sheep negatively related only to logging. All three species have experienced local extirpation, but these areas do not align with intense land-use. Thus, they may be more able to adapt to land-use than other species. Alternatively, these species may be better explained by impacts not captured here or at different scales than those considered. For example, fisher populations have declined historically due to trapping (Weir 2003) and are still experiencing trapping pressure (Weir & Corbould 2006). It is unknown whether pressure from human behavior like trapping is intense enough to cause recorded range losses. Fisher also function in smaller-scale home ranges than species like caribou and grizzly bears, and so fisher responses to land-use may be reflected in smaller-scale models. The type of footprint calculated and the relevant scale at which it is modeled is likely to shift on a species-by-species basis.

Caribou offer an excellent case study for interpreting these data, as they have been extensively researched and there are well-supported hypotheses on local extinction drivers. Caribou experience indirect land-use impacts linked to inter-specific competition. Moose (*Alces alces*) often move into early seral logging sites near caribou herd ranges (Potvin *et al.* 2005). Their presence provides prey year-round for wolves, whose populations spike due to winter resource limitation release (Seip 1992). When summer caribou ranges overlap with moose ranges, predator-induced mortality reaches up to 30% of adult females and 100% of herd calves (Seip 1992). In our models, we found that wolves were negatively related with all human land-use except forest logged within the last 60 years (**Table 4.4**), while the best caribou extirpation model was against forest logged within the last 60 years, and the largest effect size against stands logged within the last 10 years. Our models effectively highlighted these complex ecological relationships, implying that other models presented here may accurately reflect natural processes. For instance, we did not find a relationship between elk or fisher and land-use; managing these species may need to focus on other threats like over-exploitation that may play a larger role in range contraction.

There are also known links between caribou decline and oil and gas development (Hebblewhite 2017) that did not appear in our results. Rather, oil and gas development was positively linked to caribou persistence because much of the remaining caribou territory is being developed for petroleum. Though herd numbers across Canada have been reduced dramatically (Wittmer *et al.* 2005; Johnson *et al.* 2015), population management in BC has been active and extirpation has not occurred, despite precipitous declines. All quantitative models must be complemented by detailed ecological knowledge and monitoring-based refinement of hypotheses (Burton *et al.* 2014), particularly given that observational models such as this do not test causality. For application in future scenario planning, models presented here would benefit from data such as abundance, historical land-use, and other forms of human impact.

This study emphasizes the presence of threatened ecosystems and species. Ecosystems such as Coastal Douglas Fir, Bunchgrass, and Ponderosa Pine have been largely developed for human use and are vulnerable to further change. Beyond the heavily managed caribou, there is evidence to suggest that large carnivores are particularly sensitive to land-use. Grizzly bears lost an estimated 14% of their historic range, and persistence was negatively related to all land-uses. Wolf persistence had similar trends, despite low range loss. It is well known that large predators are sensitive to land-use change and fragmentation (Crooks 2002; Crooks *et al.* 2011) because they require large tracts of habitat, large-bodied prey, massive quantities of forage (grizzlies), and protection from conflict with humans (Prugh *et al.* 2009; Ripple *et al.* 2014).

Additionally, particular types of impact featured in our analysis. Logging tenures were found in every BEC zone. Five of the seven species' persistence patterns had negative relationships with logging, including bighorn sheep, a species not found to have relationships with any other land-use type. Though we found that logging has recently occurred on less than 10% of BC, total impacts are likely underreported (**Figure 4.4**). The difference between public information on logging and the on-ground reality underscores the amount of data that may be missing from our calculations. Thus, our footprint estimations may be conservative to varying degrees. A more accurate assessment would likely shift model results and provide stronger hypotheses for management planning.

The amount of error likely to be present in data measured at provincial scales is of concern for interpreting our results, or any results over large landscapes. Though this was most clearly seen in the incomplete nature of the human footprint data, provincial information on species presence is also error-prone. Beyond the spatial consideration, there is also a large temporal scale captured by both the historic-to-current range estimates and the total accumulated human footprint. Thus, conclusions drawn on how any one ecological value is likely to respond to additional land use should be viewed with caution and tested thoroughly in the future through targeted monitoring. This method would also confront the issue with lagged response, where long-lived species such as caribou may not have shown the full impacts of newer land uses like oil and gas development. Targeted monitoring may also guide a deeper understanding of how the human footprint impacts ecosystems, exploring the gradient of ecosystem degradation based on differing land uses and the implications for ecosystem persistence in future.

More generally, this analysis emphasizes that the resources and tools are available for comprehensive CEAs. Land-use data such as those used here are readily available for many regions, and the methods applied accessible to any manager. Yet CEAs that create future forecasts and assess cumulative impacts regionally, rather than make decisions on a project-by-project basis, are extremely rare (Baxter *et al.* 2001; Duinker & Greig 2006; Halpern & Fujita 2013). CEAs offer a robust land-use planning tool in changing landscapes, but only if they inform decisions at early stages of project development, a process that involves establishing stakeholder-driven ecological values, highlighting areas for conservation or sustainable use, and bridging decision-making across regulatory agencies (Johnson 2011). History shows that species in decline have an elevated probability of extinction (Woinarski et al. 2017), and methodically applying available tools is critical for preventing other species from sharing the same fate. This study begins that process for an area of high conservation concern in North America, by generating quantitative relationships between land-use and probability of extinction that can be applied to future cumulative effects assessments.

General Discussion

Current global conditions have led to a myriad of disturbances impacting ecological communities. Ecologists studying the dynamics of natural ecosystems must consider slow environmental changes from global climate shifts interacting with both human disturbances like land use or resource extraction, and discrete natural disturbances like extreme fires or hurricanes. Exploring questions of how ecosystems will respond to this complex set of disturbances is both theoretically interesting and fundamentally necessary to manage and conserve ecological values in the modern age (Sala *et al.* 2000; Zalasiewicz *et al.* 2010). The study of ecological resilience has a history of tackling complex inquiries into how ecosystems respond to disturbance (Nelson *et al.* 2007; Walker & Salt 2012). Yet, resilience is only one measure of how an ecosystem may respond to or recover from a disturbance. Clearly defining and measuring resilience, while considering other aspects of ecological response like resistance, persistence, and recovery, may provide the best set of tools to understand and potentially predict how disturbances will impact communities in the short and long term.

As resilience theory has developed, key authors have reviewed and clarified concepts in ways that strongly influence the work in this dissertation. Pimm (1984) laid out essential definitions for considering ecological stability, *i.e.* the important attributes shaping behavior of ecosystems around a single stable state. He was so precise that he gave specific units to resistance, persistence, and resilience (now known as ‘engineering resilience’ and referred to as ‘recovery’ in this work). In all chapters of this dissertation, behavior around a stable state is measured by these same three attributes of response. Though the exact units have been informed by a variety of other sources, we have aspired to the same clarity, providing both conceptual and specific measurement details on each attribute for each individual chapter. In order to maintain such specificity in regards to ecological resilience, we have forgone the more complex definitions of resilience that have evolved in the literature. Work that reviews the complexity of ecological resilience theory (key influences in this dissertation include but are not limited to: Grimm & Wissel 1997; Brand & Jax 2007; Standish *et al.* 2014) highlight that without a measurable definition, resilience is difficult to implement or utilize in ecological management. We thus attempted to focus our definition of resilience to something quantifiable within each project context.

This process of clarifying definitions within each project allows us to better refine our understanding of mechanisms that may increase an ecosystem's ability to respond to, or recover from, disturbance. Often, when theory supports a driver of one attribute of ecological response to disturbance, it is assumed to drive multiple attributes of ecological response. For example, refugia is discussed in the context of resistance, resilience, and recovery in the same ecological communities (e.g. Noss 2001; Magoulick & Kobza 2003). Similarly, connectivity has been proposed as a driver of multiple aspects of ecological response to disturbance (e.g. Taylor *et al.* 1993; Starzomski & Srivastava 2007; Staddon *et al.* 2010). However, findings in this thesis, for example in Chapter 1, emphasize that each attribute responds uniquely to connectivity, and thus generalizing one mechanism over multiple attributes may inaccurately predict community response. Even within one particular attribute, different metrics may respond differently to the same potential driver. For example, in Chapter 3 we found that Garry Oak savanna resilience responded positively to management when resilience was measured as patch area lost to woody encroachment, but that signal weakened or was lost when resilience was measured as functional redundancy. Even within species, the ability to persist shifts between land use types, and genotypic differences can lead to differing disturbance responses (Ehlers *et al.* 2008). Thus, understanding individual attributes of ecological response to disturbance requires choosing the most relevant, accurate indicator metrics for specific ecological states.

As an example, in Chapter 2, we investigated early warning signals of impending regime shifts; *i.e.* signals of decreasing resilience. In the bog-forest ecosystem, there is no single community metric known to provide an accurate measure of ecosystem-level resilience. Woody cover and *Sphagnum* sp. cover are likely to cause the strongest feedbacks (van Breemen 1995a; Rietkerk *et al.* 2004; Waddington *et al.* 2015), but both operate on intractably long temporal scales, and woody cover operates on larger spatial scales than captured in the mesocosm experiment. We thus chose to measure all major lifeforms as well as total community composition, and found that composition and moss cover gave relatively clear signs of critical slowing. In management application, however, measuring a variety of nonspecific community metrics is likely to increase the chance of false positives, and decrease the efficient use of limited monitoring resources. Appropriate metrics should likely be defined *a priori*, based on the dominant drivers of feedbacks and of ecosystem structure or function (e.g. King *et al.* 2012), tempered by the need for accuracy (Scheffer *et al.* 2009) and feasible temporal and spatial scales.

Given the increasing frequency and intensity of extreme events (Planton *et al.* 2008), there is still a heavy focus on pulse disturbances in ecological communities. The immediate, and dramatic, response of communities to destructive pulse disturbances is a compelling dynamic to study. Additionally, there is justified concern that pulse events may interact with long term disturbances that have altered the underlying ecosystem dynamics, pushing an ecosystem over a tipping point through the discrete disturbance event. This has been classically shown in coral communities in the Caribbean, where herbivore declines slowly erode the resilience of the coral ecosystem (Mumby *et al.* 2007). It is then an intense pulse event that can lead to an abrupt change into an algal-dominated state. The work in this dissertation, however, highlighted that long-term changes can have profound impacts that overpower signals from discrete changes. In Chapter 1, isolation caused significant changes in reference communities after a year in microarthropod communities that dominated dynamics over the initial heat disturbance; in Chapter 2, drawdown in bog led to linear changes and likely loss of equilibrium dynamics much more strongly than the discrete trampling disturbance, and in Chapter 3, the lost fire disturbance regime and long-term woody invasion seem to represent the largest issues for remnant Garry Oak savannas.

The majority of global ecosystems evolved with some level of discrete disturbance, creating high potential for recovery to stable states even after extreme events. Traditional succession studies focused on intense events such as volcanic eruption (e.g. Tagawa *et al.* 1985) and land clearing (e.g. Letcher & Chazdon 2009), with the implicit assumption that vegetation slowly approaches the historical composition. The introduction of long term disturbances, however, potentially alters the equilibrium state, shifting composition and processes in novel and disruptive ways. In addition to posing the likely largest threat to managed ecological values, shifting states creates a problem of the 'moving target' (e.g. García-Valdés *et al.* 2013). Thus, spatial references may be undergoing transitional or unstable dynamics, and temporal references may no longer represent the state to which a disturbed community would return. This was clearly seen in the bog study of Chapter 2, where the pre-trampled drawdown plots were not appropriate references for post-disturbance recovery, as the drawdown treatment directionally altered community composition with each passing year. Additionally, the changing untrampled drawdown references may not represent the final stable equilibria community that will establish in the drier conditions. This not only complicates research objectives, but trickles down to have significant implications for management, because the altered conditions make the goal to return to a previous community difficult or impossible to achieve (Hiers *et al.* 2012; Hobbs *et al.* 2014).

By considering a suite of ecological response attributes, *e.g.* resistance, resilience, recovery, and persistence, researchers can increase our understanding of and ability to predict ecosystem response to disturbance. However, only resilience considers shifting equilibria as the primary dynamic of concern (Hughes *et al.* 2013). The remaining attributes all refer to the behavior of an ecosystem around a single equilibrium of interest (Holling 1996). Yet, theoretical developments around resilience also have great limitations. The implicit focus of resilience concepts on bifurcated dynamics (**Figure 2.1**, **panel c**) makes resilience applicable only along one potential pathway that ecosystem stable states might follow (Boettiger & Hastings 2012). Thus, there is a gap in our disturbance theory. We have a suite of tools for predicting behavior when disturbance has moved an ecosystem away from a stable state to which it will return. We have resilience to frame and understand bifurcation dynamics, where a threshold is irreversible along much of the parameter extent (*i.e.*, the ecosystem exhibits hysteresis). However, we lack a framework that predicts theoretically reversible, but often pragmatically irreversible, thresholds. We also have few tools to identify and understand transitional dynamics as ecosystems move around or between states.

For those attributes of ecological response to disturbance that are more developed in the literature, the work in this dissertation highlights that each is likely unique in its drivers and ecological role. When considering a single ecological state of interest, it is pivotal to parse apart each attribute as much as possible. Ecosystem management is generally aimed at conservation of particular ecological values. In other words, maintaining existing ecological states. Thus, increasing resistance, recovery, persistence, and resilience are all equally valuable. Resistance and persistence address immediate ecological responses to disturbance or change, recovery addresses patterns of return after disturbance, and resilience addresses the amount of disturbance or change that can be absorbed by an ecosystem. The additional contribution of resilience is that it may offer prediction strategies. Through tools like early warning signals and measurement of resilience in existing ecosystems, managers may be able to estimate how far an ecosystem is from a threshold. This type of application, however, requires further clarity in metric definition, measurement, and analysis. Additionally, the lack of broader application to ecosystems without bifurcated thresholds is an obstacle to wider use. Though resilience offers promise, its current applicability in ecosystem management is more limited than its potential.

References

Addicott, J.F., Aho, J.M., Antolin, M.F., Padilla, D.K., Richardson, J.S. & Soluk, D.A. (1987). Ecological neighborhoods: Scaling environmental patterns. *Oikos*, 49, 340–346.

Aerts, R., Verhoeven, J.T.A. & Whigham, D.F. (1999). Plant-mediated controls on nutrient cycling in temperate fens and bogs. *Ecology*, 80, 2170–2181.

Alexandrov, G.A. & Logofet, D.O. (1994). Raised mire succession as modelled by multiple equilibria and dissipative structures. In: *Global Wetlands: Old World and New* (ed. Mitsch, W.J.). Elsevier, Amsterdam, pp. 585–592.

Allen, C.R., Fontaine, J.J., Pope, K.L. & Garmestani, A.S. (2011). Adaptive management for a turbulent future. *J. Environ. Manage.*, Adaptive management for Natural Resources, 92, 1339–1345.

Andersen, T., Carstensen, J., Hernández-García, E. & Duarte, C.M. (2009). Ecological thresholds and regime shifts: Approaches to identification. *Trends Ecol. Evol.*, 24, 49–57.

Anderson, D.R. (2008). *Model Based Inference in the Life Sciences: A Primer on Evidence*. Springer.

Anderson, M.J. (2006). Distance-based tests for homogeneity of multivariate dispersions. *Biometrics*, 62, 245–253.

Andrén, H. (1994). Effects of habitat fragmentation on birds and mammals in lanscapes with different proportions of suitable habitat: A review. *Oikos*, 71, 355–366.

Asah, S.T. (2008). Empirical social-ecological system analysis: From theoretical framework to latent variable structural equation model. *Environ. Manage.*, 42, 1077–1090.

Aubin, I., Ouellette, M.-H., Legendre, P., Messier, C. & Bouchard, A. (2009). Comparison of two plant functional approaches to evaluate natural restoration along an old-field – deciduous forest chronosequence. *J. Veg. Sci.*, 20, 185–198.

Auditor General of British Columbia. (2015). *Managing the cumulative effects of natural resource development in British Columbia*.

Augustin, N.H., Mugglestone, M.A. & Buckland, S.T. (1996). An autologistic model for the spatial distribution of wildlife. *J. Appl. Ecol.*, 33, 339–347.

Banner, A., LePage, P., Moran, J. & de Groot, A. (2005). *The Hyp3 Project: Pattern, process, and productivity in hypermaritime forests of coastal British Columbia. A synthesis of 7-year results* (No. Special Report 10). BC Ministry of Forests: Forest Science Program, British Columbia.

Bates, D., Maechler, M., Bolker, B. & Walker, S. (2014). *Fitting linear mixed-effects models using lme4* (No. R package version 1.1-7).

Baxter, W., Ross, W.A. & Spaling, H. (2001). Improving the practice of cumulative effects assessment in Canada. *Impact Assess. Proj. Apprais.*, 19, 253–262.

BC Ministry of Environment. (2014). *Trends of Native Vertebrate Species (1992-2012)*. Environmental Reporting BC.

BC Ministry of Finance. (2016). *British Columbia Financial and Economic Review*.

Bee, J.N., Kunstler, G. & Coomes, D.A. (2007). Resistance and resilience of New Zealand tree species to browsing. *J. Ecol.*, 95, 1014–1026.

Beisner, B.E., Haydon, D.T. & Cuddington, K. (2003). Alternative stable states in ecology. *Front. Ecol. Environ.*, 1, 376–382.

de Bello, F., Lepš, J., Lavorel, S. & Moretti, M. (2007). Importance of species abundance for assessment of trait composition: An example based on pollinator communities. *Community Ecol.*, 8, 163–170.

van Belzen, J., van de Koppel, J., Kirwan, M.L., van der Wal, D., Herman, P.M.J., Dakos, V., *et al.* (2017). Vegetation recovery in tidal marshes reveals critical slowing down under increased inundation. *Nat. Commun.*, 8, 15811.

Bennett, E.M., Cumming, G.S. & Peterson, G.D. (2005). A systems model approach to determining resilience surrogates for case studies. *Ecosystems*, 8, 945–957.

Bennett, J.R., Vellend, M., Lilley, P.L., Cornwell, W.K. & Arcese, P. (2013). Abundance, rarity and invasion debt among exotic species in a patchy ecosystem. *Biol. Invasions*, 15, 707–716.

Bestelmeyer, B.T., Brown, J.R., Havstad, K.M., Alexander, R., Chavez, G. & Herrick, J.E. (2003). Development and use of state-and-transition models for rangelands. *J. Range Manag.*, 56, 114–126.

Bivand, R. & Piras, G. (2015). Comparing implementations of estimation methods for spatial econometrics. *J. Stat. Softw.*, 63, 1–36.

Bjorkman, A.D. & Vellend, M. (2010). Defining historical baselines for conservation: Ecological changes since European settlement on Vancouver Island, Canada. *Conserv. Biol.*, 24, 1559–1568.

Blood, D. (2000a). *Bighorn Sheep in British Columbia: Ecology, conservation, and management*. British Columbia, Ministry of Environment, Lands, and Parks, Province of British Columbia.

Blood, D. (2000b). *Elk in British Columbia: Ecology, conservation, and management*. British Columbia, Ministry of Environment, Lands, and Parks, Province of British Columbia.

Boettiger, C. & Hastings, A. (2012). Quantifying limits to detection of early warning for critical transitions. *J. R. Soc. Interface*, rsif20120125.

Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H., *et al.* (2009). Generalized linear mixed models: A practical guide for ecology and evolution. *Trends Ecol. Evol.*, 24, 127–135.

Bonham, C.D. (2013). *Measurements for Terrestrial Vegetation*. John Wiley & Sons.

Botta-Dukát, Z. (2005). Rao's quadratic entropy as a measure of functional diversity based on multiple traits. *J. Veg. Sci.*, 16, 533–540.

Brand, F.S. & Jax, K. (2007). Focusing the meaning(s) of resilience: Resilience as a descriptive concept and a boundary object. *Ecol. Soc.*, 12, 23.

van Breemen, N. (1995a). How Sphagnum bogs down other plants. *Trends Ecol. Evol.*, 10, 270–275.

van Breemen, N. (1995b). Nutrient cycling strategies. In: *Nutrient Uptake and Cycling in Forest Ecosystems*, Developments in Plant and Soil Sciences. Springer, Dordrecht, pp. 321–326.

Briske, D.D., Bestelmeyer, B.T., Stringham, T.K. & Shaver, P.L. (2008). Recommendations for development of resilience-based state-and-transition models. *Rangel. Ecol. Manag.*, 61, 359–367.

Briske, D.D., Fuhlendorf, S.D. & Smeins, F.E. (2005). State-and-transition models, thresholds, and rangeland health: A synthesis of ecological concepts and perspectives. *Rangel. Ecol. Manag.*, 58, 1–10.

Buckley, Y.M. & Catford, J. (2016). Does the biogeographic origin of species matter? Ecological effects of native and non-native species and the use of origin to guide management. *J. Ecol.*, 104, 4–17.

Bunnell, F.L. (1995). Forest-dwelling vertebrate faunas and natural fire regimes in British Columbia: Patterns and implications for conservation. *Conserv. Biol.*, 9, 636–644.

Burton, A.C., Huggard, D., Bayne, E., Schieck, J., Sólymos, P., Muhly, T., *et al.* (2014). A framework for adaptive monitoring of the cumulative effects of human footprint on biodiversity. *Environ. Monit. Assess.*, 186, 3605–3617.

Butchart, S.H.M., Walpole, M., Collen, B., Strien, A. van, Scharlemann, J.P.W., Almond, R.E.A., *et al.* (2010). Global biodiversity: Indicators of recent declines. *Science*, 328, 1164–1168.

Cailliez, F. (1983). The analytical solution of the additive constant problem. *Psychometrika*, 48, 305–308.

Carpenter, S., Walker, B.H., Anderies, J.M. & Abel, N. (2001). From metaphor to measurement: Resilience of what to what? *Ecosystems*, 4, 765–781.

Carpenter, S.R., Cole, J.J., Pace, M.L., Batt, R., Brock, W.A., Cline, T., *et al.* (2011). Early warnings of regime shifts: A whole-ecosystem experiment. *Science*, 332, 1079–1082.

Carter, N.H. & Linnell, J.D.C. (2016). Co-adaptation is key to coexisting with large carnivores. *Trends Ecol. Evol.*, 31, 575–578.

Carwardine, J., O'Connor, T., Legge, S., Mackey, B., Possingham, H.P. & Martin, T.G. (2012). Prioritizing threat management for biodiversity conservation. *Conserv. Lett.*, 5, 196–204.

Catford, J.A., Morris, W.K., Vesk, P.A., Gippel, C.J. & Downes, B.J. (2014). Species and environmental characteristics point to flow regulation and drought as drivers of riparian plant invasion. *Divers. Distrib.*, 20, 1084–1096.

Chapin, F.S., Matson, P.A. & Mooney, H.A. (2002). Landscape Heterogeneity and Ecosystem Dynamics. In: *Principles of Terrestrial Ecosystem Ecology*. Springer New York, pp. 305–331.

Clements, F.E. (1916). Plant succession: An analysis of the development of vegetation. *Carnegie Inst. Wash.*

Coffin, A.W. (2007a). From roadkill to road ecology: A review of the ecological effects of roads. *J. Transp. Geogr.*, 15, 396–406.

Coffin, A.W. (2007b). From roadkill to road ecology: A review of the ecological effects of roads. *J. Transp. Geogr.*, 15, 396–406.

Connell, J.H. (1978). Diversity in tropical rain forests and coral reefs. *Science*, 199, 1302–1310.

Connelly, R. (Bob). (2011). Canadian and international EIA frameworks as they apply to cumulative effects. *Environ. Impact Assess. Rev.*, 31, 453–456.

Cornelissen, J.H.C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D.E., *et al.* (2003). A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Aust. J. Bot.*, 51, 335–380.

Crain, C.M., Kroeker, K. & Halpern, B.S. (2008). Interactive and cumulative effects of multiple human stressors in marine systems. *Ecol. Lett.*, 11, 1304–1315.

Cramer, V.A., Hobbs, R.J. & Standish, R.J. (2008). What's new about old fields? Land abandonment and ecosystem assembly. *Trends Ecol. Evol.*, 23, 104–112.

Crawley, M.J. (2007). *The R Book*. Wiley, Chichester, England; Hoboken, N.J.

Crooks, K.R. (2002). Relative sensitivities of mammalian carnivores to habitat fragmentation. *Conserv. Biol.*, 16, 488–502.

Crooks, K.R., Burdett, C.L., Theobald, D.M., Rondinini, C. & Boitani, L. (2011). Global patterns of fragmentation and connectivity of mammalian carnivore habitat. *Philos. Trans. R. Soc. B Biol. Sci.*, 366, 2642–2651.

Cumming, G.S., Barnes, G.G., Perz, S., Schmink, M., Sieving, K.E., Southworth, J., *et al.* (2005). An exploratory framework for the empirical measurement of resilience. *Ecosystems*, 8, 975–987.

Curtin, C.G. & Parker, J.P. (2014). Foundations of resilience thinking. *Conserv. Biol.*, 28, 912–923.

Dakos, V., van Nes, E.H., D'Odorico, P. & Scheffer, M. (2012). Robustness of variance and autocorrelation as indicators of critical slowing down. *Ecology*, 93, 264–271.

Dakos, V., van Nes, E.H., Donangelo, R., Fort, H. & Scheffer, M. (2010). Spatial correlation as leading indicator of catastrophic shifts. *Theor. Ecol.*, 3, 163–174.

Damschen, E.I., Haddad, N.M., Orrock, J.L., Tewksbury, J.J. & Levey, D.J. (2006). Corridors increase plant species richness at large scales. *Science*, 313, 1284–1286.

Darkoh, M.B.K. (1998). The nature, causes and consequences of desertification in the drylands of Africa. *Land Degrad. Dev.*, 9, 1–20.

Darling, E.S. & Côté, I.M. (2008). Quantifying the evidence for ecological synergies. *Ecol. Lett.*, 11, 1278–1286.

Dearborn, D.C. & Kark, S. (2010). Motivations for conserving urban biodiversity. *Conserv. Biol.*, 24, 432–440.

Dorenbosch, M., Verberk, W., Nagelkerken, I. & van der Velde, G. (2007). Influence of habitat configuration on connectivity between fish assemblages of Caribbean seagrass beds, mangroves and coral reefs. *Mar. Ecol. Prog. Ser.*, 334, 103–116.

Dormann, C.F., McPherson, J.M., Araújo, M.B., Bivand, R., Bolliger, J., Carl, G., *et al.* (2007). Methods to account for spatial autocorrelation in the analysis of species distributional data: A review. *Ecography*, 30, 609–628.

Duelli, P. & Obrist, M.K. (2003). Biodiversity indicators: The choice of values and measures. *Agric. Ecosyst. Environ.*, Biotic Indicators for Biodiversity and Sustainable Agriculture, 98, 87–98.

Duinker, P.N. & Greig, L.A. (2006). The impotence of cumulative effects assessment in Canada: Ailments and ideas for redeployment. *Environ. Manage.*, 37, 153–161.

Dyer, S.J., O'Neill, J.P., Wasel, S.M. & Boutin, S. (2001). Avoidance of industrial development by woodland caribou. *J. Wildl. Manag.*, 65, 531–542.

Eder, T. & Pattie, D. (2001). *Mammals of British Columbia*. Lone Pine Publishing.

Ehlers, A., Worm, B. & Reusch, T.B.H. (2008). Importance of genetic diversity in eelgrass Zostera marina for its resilience to global warming. *Mar. Ecol. Prog. Ser.*, 355, 1–7.

Ellis, E.C. & Ramankutty, N. (2007). Putting people in the map: Anthropogenic biomes of the world. *Front. Ecol. Environ.*, 6, 439–447.

Elmqvist, T., Folke, C., Nyström, M., Peterson, G., Bengtsson, J., Walker, B.H., *et al.* (2003). Response diversity, ecosystem change, and resilience. *Front. Ecol. Environ.*, 1, 488–494.

Eppinga, M.B., Rietkerk, M., Wassen, M.J. & Ruiter, P.C.D. (2009). Linking habitat modification to catastrophic shifts and vegetation patterns in bogs. *Plant Ecol.*, 200, 53–68.

Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., *et al.* (2011). Trophic downgrading of planet Earth. *Science*, 333, 301–306.

Fahrig, L. (2001). How much habitat is enough? *Biol. Conserv.*, 100, 65–74.

Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annu. Rev. Ecol. Evol. Syst.*, 34, 487–515.

Fisher, J.T. & Wilkinson, L. (2005). The response of mammals to forest fire and timber harvest in the North American boreal forest. *Mammal Rev.*, 35, 51–81.

Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., *et al.* (2005). Global consequences of land use. *Science*, 309, 570–574.

Folke, C., Carpenter, S.R., Elmqvist, T., Gunderson, L.H., Holling, C.S. & Walker, B. (2002). Resilience and sustainable development: Building adaptive capacity in a world of transformations. *AMBIO J. Hum. Environ.*, 31, 437–440.

Forman, R.T.T. & Alexander, and L.E. (1998a). Roads and their major ecological effects. *Annu. Rev. Ecol. Syst.*, 29, 207–231.

Forman, R.T.T. & Alexander, L.E. (1998b). Roads and their major ecological effects. *Annu. Rev. Ecol. Syst.*, 29, 207-C2.

Frankl, R. & Schmeidl, H. (2000). Vegetation change in a South German raised bog: Ecosystem engineering by plant species, vegetation switch or ecosystem level feedback mechanisms? *Flora*, 195, 267–276.

Fraser, B., Arnold, M., Gratton, P., Guichon, J., Hatler, D., Hebert, D., *et al.* (2011). *Report of the British Columbia Task Force on Species at Risk*. British Columbia Task Force on Species at Risk.

Fuchs, M.A. (2001). *Towards a recovery strategy for Garry Oak and associated ecosystems in Canada: Ecological assessment and literature review* (No. Technical Report GBEI/EC-00-030). Environment Canada, Canadian Wildlife Service, Pacific and Yukon Region.

García-Valdés, R., Zavala, M.A., Araújo, M.B. & Purves, D.W. (2013). Chasing a moving target: Projecting climate change-induced shifts in non-equilibrial tree species distributions. *J. Ecol.*, 101, 441–453.

Gibson, S.Y., Van Der Marel, R.C. & Starzomski, B.M. (2009). Climate change and conservation of leading-edge peripheral populations. *Conserv. Biol.*, 23, 1369–1373.

Goddard, M.A., Dougill, A.J. & Benton, T.G. (2010). Scaling up from gardens: Biodiversity conservation in urban environments. *Trends Ecol. Evol.*, 25, 90–98.

Goh, B.S. (1975). Stability, vulnerability and persistence of complex ecosystems. *Ecol. Model.*, 1, 105–116.

Gonzalez, A., Lawton, J.H., Gilbert, F.S., Blackburn, T.M. & Evans-Freke, I. (1998). Metapopulation dynamics, abundance, and distribution in a microecosystem. *Science*, 281, 2045–2047.

Government of Canada. (2017). *Canadian Climate Normals 1981-2010*. Ministry of Environment and Natural Resources.

Green, R.N. & Klinka, K. (1994). *A field guide to site identification and interpretation for the Vancouver Forest Region*. British Columbia Ministry of Forests Research Branch, Burnaby, B.C.

Grimm, V. & Wissel, C. (1997). Babel, or the ecological stability discussions: An inventory and analysis of terminology and a guide for avoiding confusion. *Oecologia*, 109, 323–334.

Gunderson, L.H. (1999). Resilience, flexibility, and adaptive management: Antidotes for spurious certitude? *Ecol. Soc.*, 3.

Gunderson, L.H. (2000). Ecological resilience -- In theory and application. *Annu. Rev. Ecol. Syst.*, 31, 425–439.

Gunderson, L.H. & Pritchard, L. (Eds.). (2012). *Resilience and the Behavior of Large-Scale Systems*. Island Press.

Guttal, V. & Jayaprakash, C. (2008). Changing skewness: An early warning signal of regime shifts in ecosystems. *Ecol. Lett.*, 11, 450–460.

Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., *et al.* (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. *Sci. Adv.*, 1, e1500052.

Hall, E.R. & Kelson, K.R. (1959). *The Mammals of North America*. Ronald Press Co.

Halpern, B.S. & Fujita, R. (2013). Assumptions, challenges, and future directions in cumulative impact analysis. *Ecosphere*, 4, 1–11.

Hamann, A. & Wang, T. (2006). Potential effects of climate change on ecosystem and tree species distribution in British Columbia. *Ecology*, 87, 2773–2786.

Harestad, A.S. & Bunnell, F.L. (1979). Home range and body weight -- A re-evaluation. *Ecology*, 60, 389–402.

Hebblewhite, M. (2017). Billion dollar boreal woodland caribou and the biodiversity impacts of the global oil and gas industry. *Biol. Conserv.*, 206, 102–111.

Hebda, R.J. (1983). Late-glacial and postglacial vegetation history at Bear Cove Bog, northeast Vancouver Island, British Columbia. *Can. J. Bot.*, 61, 3172–3192.

Heijmans, M.M.P.D., van der Knaap, Y.A.M., Holmgren, M. & Limpens, J. (2013). Persistent versus transient tree encroachment of temperate peat bogs: Effects of climate warming and drought events. *Glob. Change Biol.*, 19, 2240–2250.

Hejda, M., Pyšek, P. & Jarošík, V. (2009). Impact of invasive plants on the species richness, diversity and composition of invaded communities. *J. Ecol.*, 97, 393–403.

Heller, N.E. & Zavaleta, E.S. (2009). Biodiversity management in the face of climate change: A review of 22 years of recommendations. *Biol. Conserv.*, 142, 14–32.

Hershkovitz, Y. & Gasith, A. (2013). Resistance, resilience, and community dynamics in mediterranean-climate streams. *Hydrobiologia*, 719, 59–75.

Hiers, J.K., Mitchell, R.J., Barnett, A., Walters, J.R., Mack, M., Williams, B., *et al.* (2012). The dynamic reference concept: Measuring restoration success in a rapidly changing no-analogue future. *Ecol. Restor.*, 30, 27–36.

Hobbs, R.J., Higgs, E., Hall, C.M., Bridgewater, P., Chapin, F.S., Ellis, E.C., *et al.* (2014). Managing the whole landscape: Historical, hybrid, and novel ecosystems. *Front. Ecol. Environ.*, 12, 557–564.

Holling, C.S. (1973). Resilience and stability of ecological systems. *Annu. Rev. Ecol. Syst.*, 4, 1–23.

Holling, C.S. (1978). *Adaptive Environmental Assessment and Management*.

Holling, C.S. (1996). Engineering resilience versus ecological resilience. In: *Engineering within Ecological Constraints*. pp. 31–44.

Horn, H.S. (1974). The ecology of secondary succession. *Annu. Rev. Ecol. Syst.*, 5, 25–37.

Houghton, J.T., Jenkins, G.J. & Ephraums, J.J. (Eds.). (1990). *Climate Change: The IPCC Scientific Assessment*. Cambridge University Press, Cambridge, Greate Britain.

Hughes, T.P., Linares, C., Dakos, V., van de Leemput, I.A. & van Nes, E.H. (2013). Living dangerously on borrowed time during slow, unrecognized regime shifts. *Trends Ecol. Evol.*, 28, 149–155.

Hurlbert, A.H. & Jetz, W. (2007). Species richness, hotspots, and the scale dependence of range maps in ecology and conservation. *Proc. Natl. Acad. Sci.*, 104, 13384–13389.

Huston, M. & Smith, T. (1987). Plant succession: Life history and competition. *Am. Nat.*, 130, 168–198.

Hutchings, J.A. & Myers, R.A. (1994). What can be learned from the collapse of a renewable resource? Atlantic Cod, Gadus morhua, of Newfoundland and Labrador. *Can. J. Fish. Aquat. Sci.*, 51, 2126–2146.

Irmler, U. (2004). Long-term fluctuation of the soil fauna (Collembola and Oribatida) at groundwater-near sites in an alder wood. *Pedobiologia*, 48, 349–363.

Ives, A.R. (1995). Measuring resilience in stochastic systems. *Ecol. Monogr.*, 65, 217–233.

Johnson, C.J. (2011). Regulating and planning for cumulative effects: The Canadian experience. In: *Cumulative Effects in Wildlife Management: Impact Mitigation*. CRC Press.

Johnson, C.J., Ehlers, L.P.W. & Seip, D.R. (2015). Witnessing extinction – Cumulative impacts across landscapes and the future loss of an evolutionarily significant unit of woodland caribou in Canada. *Biol. Conserv.*, 186, 176–186.

Jones, H.P. (2010). Seabird islands take mere decades to recover following rat eradication. *Ecol. Appl.*, 20, 2075–2080.

Joosten, H. & Clarke, D. (2002). *Wise use of mires and peatlands: Background and principles including a framework for decision-making*. International Mire Conservation Group and International Peat Society, Jyväskylä, Finland.

Jukaine. (1995). Long-term effects of water level drawdown on the vegetation of drained pine mires in southern Finland. *J. Appl. Ecol.*, 32, 785–802.

Kareiva, P. & Marvier, M. (2012). What is conservation science? *BioScience*, 62, 962–969.

Kays, R.W. & Wilson, D.E. (2009). *Mammals of North America*. 2nd edn. Princeton University Press.

Keeling, C.D., Bacastow, R.B., Bainbridge, A.E., Jr, C.A.E., Guenther, P.R., Waterman, L.S., *et al.* (1976). Atmospheric carbon dioxide variations at Mauna Loa Observatory, Hawaii. *Tellus*, 28, 538–551.

Keith, D.A., McCaw, W.L. & Whelan, R.J. (2002). Fire regimes in Australian heathlands and their effects on plants and animals. In: *Flammable Australia: the fire regimes and biodiversity of a continent*. Cambridge University Press, Cambridge, pp. 199–237.

King, E.G., Franz, T.E. & Caylor, K.K. (2012). Ecohydrological interactions in a degraded two-phase mosaic dryland: Implications for regime shifts, resilience, and restoration. *Ecohydrology*, 5, 733–745.

Kinzig, A., Ryan, P., Etienne, M., Allison, H., Elmqvist, T. & Walker, B. (2006). Resilience and regime shifts: Assessing cascading effects. *Ecol. Soc.*, 11.

Klarner, B., Maraun, M. & Scheu, S. (2013). Trophic diversity and niche partitioning in a species rich predator guild: Natural variations in stable isotope ratios (13C/12C, 15N/14N) of mesostigmatid mites (Acari, Mesostigmata) from Central European beech forests. *Soil Biol. Biochem.*, 57, 327–333.

Kleinen, T., Held, H. & Petschel-Held, G. (2003). The potential role of spectral properties in detecting thresholds in the Earth system: Application to the thermohaline circulation. *Ocean Dyn.*, 53, 53–63.

Krantz, G.W. & Walter, D.E. (2009). *A Manual of Acarology*. 3rd edn. Texas Tech University Press, Lubbock, Texas.

Lake, P.S. (2000). Disturbance, patchiness, and diversity in streams. *J. North Am. Benthol. Soc.*, 19, 573–592.

Laliberte, A.S. & Ripple, W.J. (2004). Range contractions of North American carnivores and ungulates. *BioScience*, 54, 123–138.

Laliberté, E. & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, 91, 299–305.

Laliberté, E., Legendre, P. & Shipley, B. (2014). *FD: Measuring functional diversity (FD) from multiple traits, and other tools for functional ecology*.

Laliberté, E., Wells, J.A., Declerck, F., Metcalfe, D.J., Catterall, C.P., Queiroz, C., *et al.* (2010). Land-use intensification reduces functional redundancy and response diversity in plant communities. *Ecol. Lett.*, 13, 76–86.

Lambers, H. (2003). Introduction, dryland salinity: A key environmental issue in southern Australia. *Plant Soil*, 257, 5–7.

Lavorel, S. & Garnier, E. (2002). Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Funct. Ecol.*, 16, 545–556.

van de Leemput, I.A., Dakos, V., Scheffer, M. & van Nes, E.H. (2017). Slow recovery from local disturbances as an indicator for loss of ecosystem resilience. *Ecosystems*, 1–12.

Legendre, P. & Legendre, L.F.J. (2012). *Numerical Ecology*. Elsevier.

Letcher, S.G. & Chazdon, R.L. (2009). Rapid recovery of biomass, species richness, and species composition in a forest chronosequence in northeastern Costa Rica. *Biotropica*, 41, 608–617.

Lever, J.J., van Nes, E.H., Scheffer, M. & Bascompte, J. (2014). The sudden collapse of pollinator communities. *Ecol. Lett.*, 17, 350–359.

Levin, S.A., Carpenter, S.R., Godfray, H.C.J., Kinzig, A.P., Loreau, M., Losos, J.B., *et al.* (2009). *The Princeton Guide to Ecology*. Princeton University Press.

Lewontin, R.C. (1969). The meaning of stability. *Brookhaven Symp. Biol.*, 13–23.

Lilley, P.L. & Vellend, M. (2009). Negative native–exotic diversity relationship in oak savannas explained by human influence and climate. *Oikos*, 118, 1373–1382.

Lindenmayer, D.B. & Likens, G.E. (2009). Adaptive monitoring: A new paradigm for long-term research and monitoring. *Trends Ecol. Evol.*, 24, 482–486.

Lindo, Z. & Winchester, N.N. (2006). A comparison of microarthropod assemblages with emphasis on oribatid mites in canopy suspended soils and forest floors associated with ancient western redcedar trees. *Pedobiologia*, 50, 31–41.

Lindsay, R., Birnie, R. & Clough, J. (2014). *Grazing and trampling* (No. Briefing Note No 7). IUCN UK Committee Peatland Programme.

Loehle, C. (1985). Optimal stocking for semi-desert range: a catastrophe theory model. *Ecol. Model.*, v. 27, 285–297.

Ludwig, D., Walker, B.H. & Holling, C.S. (1997). Sustainability, stability, and resilience. *Conserv. Ecol.*, 1.

Lundberg, J. & Moberg, F. (2003). Mobile link organisms and ecosystem functioning: Implications for ecosystem resilience and management. *Ecosystems*, 6, 0087–0098.

MacDougall, A.S. (2005). Responses of diversity and invasibility to burning in a northern oak savanna. *Ecology*, 86, 3354–3363.

Mack, M.C., Treseder, K.K., Manies, K.L., Harden, J.W., Schuur, E.A.G., Vogel, J.G., *et al.* (2008). Recovery of aboveground plant biomass and productivity after fire in mesic and dry black spruce forests of interior Alaska. *Ecosystems*, 11, 209–225.

Mack, R.N., Simberloff, D., Mark Lonsdale, W., Evans, H., Clout, M. & Bazzaz, F.A. (2000). Biotic invasions: Causes, epidemiology, global consequences, and control. *Ecol. Appl.*, 10, 689–710.

Magoulick, D.D. & Kobza, R.M. (2003). The role of refugia for fishes during drought: A review and synthesis. *Freshw. Biol.*, 48, 1186–1198.

Margules, C.R. & Pressey, R.L. (2000). Systematic conservation planning. *Nature*, 405, 243–253.

May, R.M. (1973). *Stability and Complexity in Model Ecosystems*. Princeton.

May, R.M. (1977). Thresholds and breakpoints in ecosystems with a multiplicity of stable states. *Nature*, 269, 471–477.

McCann, K.S. (2000). The diversity–stability debate. *Nature*, 405, 228–233.

McGarigal, K., Cushman, S.A., Neel, M.C. & Ene, E. (2002). FRAGSTATS: Spatial pattern analysis program for categorical maps.

McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends Ecol. Evol.*, 21, 178–185.

Meidinger, D.V. & Pojar, J. (1991). Ecosystems of British Columbia. In: *Special Report Series No. 6. British Columbia Ministry of Forests*.

Menakis, J.P., Osborne, D. & Miller, M. (2003). Mapping the cheatgrass-caused departure from historical natural fire regimes in the Great Basin, USA. *USDA For. Serv. Proc.*, 281–288.

Millennium Ecosystem Assessment. (2005). *Millennium Ecosystem Assessment Findings*. Millennium Ecosystem Assessment.

Miller, A.D., Chesson, P., Mazancourt, A.E.C. de & DeAngelis, E.D.L. (2009). Coexistence in disturbance-prone communities: How a resistance-resilience trade-off generates coexistence via the storage effect. *Am. Nat.*, 173, E30–E43.

Miller, B.P., Sinclair, E.A., Menz, M.H.M., Elliott, C.P., Bunn, E., Commander, L.E., *et al.* (2017). A framework for the practical science necessary to restore sustainable, resilient, and biodiverse ecosystems. *Restor. Ecol.*, 25, 605–617.

Miller, C. & Urban, D.L. (2000). Connectivity of forest fuels and surface fire regimes. *Landsc. Ecol.*, 15, 145–154.

Ministry of Forests, Lands and Natural Resource Operations. (2014). *Management plan for the grey wolf (Canis lupus) in British Columbia*. Ministry of Forests, Lands and Natural Resource Operations, Province of British Columbia.

Ministry of Forests, Lands, and Natural Resources. (2003). *British Columbia's forests: A geographical snapshot*.

Moilanen, A. & Nieminen, M. (2002). Simple connectivity measures in spatial ecology. *Ecology*, 83, 1131–1145.

Mori, A.S., Furukawa, T. & Sasaki, T. (2013). Response diversity determines the resilience of ecosystems to environmental change. *Biol. Rev.*, 88, 349–364.

Muggeo, V.M.R. (2003). Estimating regression models with unknown break-points. *Stat. Med.*, 22, 3055–3071.

Muggeo, V.M.R. (2015). *segmented: Regression Models with Breakpoints/Changepoints Estimation*.

Müller, J., Noss, R.F., Bussler, H. & Brandl, R. (2010). Learning from a "benign neglect strategy" in a national park: Response of saproxylic beetles to dead wood accumulation. *Biol. Conserv.*, 143, 2559–2569.

Mumby, P.J. & Hastings, A. (2008). The impact of ecosystem connectivity on coral reef resilience. *J. Appl. Ecol.*, 45, 854–862.

Mumby, P.J., Hastings, A. & Edwards, H.J. (2007). Thresholds and the resilience of Caribbean coral reefs. *Nature*, 450, 98–101.

Murphy, D.D. (1988). Challenges to biological diversity in urban areas. In: *Biodiversity*, National Academy of Sciences/Smithsonian Institution, Division on Earth and Life Studies, Commission on Life Sciences, E.O. Wilson. National Academies Press.

Myers, R.A., Hutchings, J.A. & Barrowman, N.J. (1997). Why do fish stocks collapse? The example of cod in Atlantic Canada. *Ecol. Appl.*, 7, 91–106.

Nakagawa, S. & Schielzeth, H. (2013). A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods Ecol. Evol.*, 4, 133–142.

Nash, K.L., Graham, N.A.J., Jennings, S., Wilson, S.K. & Bellwood, D.R. (2016). Herbivore cross-scale redundancy supports response diversity and promotes coral reef resilience. *J. Appl. Ecol.*, 53, 646–655.

Nelson, D.R., Adger, W.N. & Brown, K. (2007). Adaptation to environmental change: Contributions of a resilience framework. *Annu. Rev. Environ. Resour.*, 32, 395–419.

van Nes, E.H. & Scheffer, M. (2007). Slow recovery from perturbations as a generic indicator of a nearby catastrophic shift. *Am. Nat.*, 169, 738–747.

Newbold, T., Hudson, L.N., Arnell, A.P., Contu, S., Palma, A.D., Ferrier, S., *et al.* (2016). Has land use pushed terrestrial biodiversity beyond the planetary boundary? A global assessment. *Science*, 353, 288–291.

Nimmo, D.G., Mac Nally, R., Cunningham, S.C., Haslem, A. & Bennett, A.F. (2015). Vive la résistance: Reviving resistance for 21st century conservation. *Trends Ecol. Evol.*, 30, 516–523.

Noss, R.F. (2001). Beyond Kyoto: Forest management in a time of rapid climate change. *Conserv. Biol.*, 15, 578–590.

Ohlson, M., Økland, R.H., Nordbakken, J.-F. & Dahlberg, B. (2001). Fatal interactions between Scots pine and Sphagnum mosses in bog ecosystems. *Oikos*, 94, 425–432.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., *et al.* (2013). *vegan: Community Ecology Package*.

Parr, C.L., Lehmann, C.E.R., Bond, W.J., Hoffmann, W.A. & Andersen, A.N. (2014). Tropical grassy biomes: Misunderstood, neglected, and under threat. *Trends Ecol. Evol.*, 29, 205–213.

Peschel, K., Norton, R.A., Scheu, S. & Maraun, M. (2006). Do oribatid mites live in enemy-free space? Evidence from feeding experiments with the predatory mite Pergamasus septentrionalis. *Soil Biol. Biochem.*, 38, 2985–2989.

Petersen, H. & Luxton, M. (1982). A comparative analysis of soil fauna populations and their role in decomposition processes. *Oikos*, 39, 288–388.

Peterson, C.G. & Stevenson, R.J. (1992). Resistance and resilience of lotic algal communities: Importance of disturbance timing and current. *Ecology*, 73, 1445–1461.

Pickett, S.T. & White, P.S. (1985). *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press.

Pillar, V.D., Blanco, C.C., Müller, S.C., Sosinski, E.E., Joner, F. & Duarte, L.D.S. (2013). Functional redundancy and stability in plant communities. *J. Veg. Sci.*, 24, 963–974.

Pimm, S.L. (1984). The complexity and stability of ecosystems. *Nature*, 307, 321–326.

Pimm, S.L., Jenkins, C.N., Abell, R., Brooks, T.M., Gittleman, J.L., Joppa, L.N., *et al.* (2014). The biodiversity of species and their rates of extinction, distribution, and protection. *Science*, 344, 1246752.

Pinheiro, J., Bates, D., DebRoy, S. & Sarkar, D. (2014). *nlme: Linear and Nonlinear Mixed Effects Models*.

Planton, S., Déqué, M., Chauvin, F. & Terray, L. (2008). Expected impacts of climate change on extreme climate events. *Comptes Rendus Geosci.*, Ecosystèmes et événements climatiques extrêmes Ecosystems and extreme climatic events, 340, 564–574.

Podani, J. (1999). Extending Gower's general coefficient of similarity to ordinal characters. *Taxon*, 48, 331–340.

Pojar, J., Klinka, K. & Meidinger, D.V. (1987). Biogeoclimatic ecosystem classification in British Columbia. *For. Ecol. Manag.*, 22, 119–154.

Polfus, J.L., Hebblewhite, M. & Heinemeyer, K. (2011). Identifying indirect habitat loss and avoidance of human infrastructure by northern mountain woodland caribou. *Biol. Conserv.*, 144, 2637–2646.

Potvin, F., Breton, L. & Courtois, R. (2005). Response of beaver, moose, and snowshoe hare to clear-cutting in a Quebec boreal forest: a reassessment 10 years after cut. *Can. J. For. Res.*, 35, 151–160.

Pressey, R.L., Cabeza, M., Watts, M.E., Cowling, R.M. & Wilson, K.A. (2007). Conservation planning in a changing world. *Trends Ecol. Evol.*, 22, 583–592.

Prugh, L.R., Stoner, C.J., Epps, C.W., Bean, W.T., Ripple, W.J., Laliberte, A.S., *et al.* (2009). The rise of the mesopredator. *BioScience*, 59, 779–791.

Pyšek, P. & Richardson, D.M. (2010). Invasive species, environmental change and management, and health. *Annu. Rev. Environ. Resour.*, 35, 25–55.

R Core Team. (2014). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Raffa, K.F., Aukema, B.H., Bentz, B.J., Carroll, A.L., Hicke, J.A., Turner, M.G., *et al.* (2008). Cross-scale drivers of natural disturbances prone to anthropogenic amplification: The dynamics of bark beetle eruptions. *BioScience*, 58, 501–517.

Raiter, K.G., Possingham, H.P., Prober, S.M. & Hobbs, R.J. (2014). Under the radar: Mitigating enigmatic ecological impacts. *Trends Ecol. Evol.*, 29, 635–644.

Ratajczak, Z., Nippert, J.B. & Collins, S.L. (2012). Woody encroachment decreases diversity across North American grasslands and savannas. *Ecology*, 93, 697–703.

Ratcliffe, D.A. (1959). The vegetation of the Carneddau, North Wales: I. Grasslands, heaths and bogs. *J. Ecol.*, 47, 371–413.

Renton, M., Shackelford, N. & Standish, R.J. (2012). Habitat restoration will help some functional plant types persist under climate change in fragmented landscapes. *Glob. Change Biol.*, 18, 2057–2070.

Resasco, J., Haddad, N.M., Orrock, J.L., Shoemaker, D., Brudvig, L.A., Damschen, E.I., *et al.* (2014). Landscape corridors can increase invasion by an exotic species and reduce diversity of native species. *Ecology*, 95, 2033–2039.

Reyer, C.P.O., Rammig, A., Brouwers, N. & Langerwisch, F. (2015). Forest resilience, tipping points and global change processes. *J. Ecol.*, 103, 1–4.

Rietkerk, M., Dekker, S. tefanC., Wassen, M.J., Verkroost, A.W.M. & Bierkens, M.F.P. (2004). A putative mechanism for bog patterning. *Am. Nat.*, 163, 699–708.

Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., *et al.* (2014). Status and ecological effects of the world's largest carnivores. *Science*, 343, 1241484.

Rist, L., Felton, A., Samuelsson, L., Sandström, C. & Rosvall, O. (2013). A new paradigm for Adaptive Management. *Ecol. Soc.*, 18.

Rondinini, C., Stuart, S. & Boitani, L. (2005). Habitat suitability models and the shortfall in conservation planning for African vertebrates. *Conserv. Biol.*, 19, 1488–1497.

Rudnick, D., Ryan, S.J., Beier, P., Cushman, S.A., Dieffenback, F., Epps, C., *et al.* (2012). The role of landscape connectivity in planning and implementing conservation and restoration priorities. *Issues Ecol.*, 16, 1–16.

Sahrawat, K.L. (2003). Organic matter accumulation in submerged soils. *Adv. Agron.*, 81, 169–201.

Sala, O.E., Chapin, F.S.I., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., *et al.* (2000). Global biodiversity scenarios for the year 2100. *Science*, 287, 1770–1774.

Sanderson, E.W., Jaiteh, M., Levy, M.A., Redford, K.H., Wannebo, A.V. & Woolmer, G. (2002). The human footprint and the last of the wild. *BioScience*, 52, 891–904.

Saunders, D.A., Hobbs, R.J. & Margules, C.R. (1991). Biological consequences of ecosystem fragmentation: A review. *Conserv. Biol.*, 5, 18–32.

Scheffer, M. (2009). *Critical Transitions in Nature and Society*. Princeton University Press.

Scheffer, M., Bascompte, J., Brock, W.A., Brovkin, V., Carpenter, S.R., Dakos, V., *et al.* (2009). Early-warning signals for critical transitions. *Nature*, 461, 53–59.

Scheffer, M., Carpenter, S., Foley, J.A., Folke, C. & Walker, B.H. (2001). Catastrophic shifts in ecosystems. *Nature*, 413, 591–596.

Scheffer, M. & Carpenter, S.R. (2003). Catastrophic regime shifts in ecosystems: Linking theory to observation. *Trends Ecol. Evol.*, 18, 648–656.

Scheffer, M., Carpenter, S.R., Dakos, V. & van Nes, E.H. (2015). Generic indicators of ecological resilience: Inferring the chance of a critical transition. *Annu. Rev. Ecol. Evol. Syst.*, 46, 145–167.

Scheffer, M., Carpenter, S.R., Lenton, T.M., Bascompte, J., Brock, W., Dakos, V., *et al.* (2012). Anticipating critical transitions. *Science*, 338, 344–348.

Scheffer, M., Hosper, S.H., Meijer, M.-L., Moss, B. & Jeppesen, E. (1993). Alternative equilibria in shallow lakes. *Trends Ecol. Evol.*, 8, 275–279.

Scheu, K.S.-C.R.-S. & Maraun, M. (2004). Feeding biology of oribatid mites: A minireview. *Phytophaga*, XIV, 247–256.

Scheu, S. (2002). The soil food web: Structure and perspectives. *Eur. J. Soil Biol.*, 38, 11–20.

Schmalholz, M. & Hylander, K. (2011). Microtopography creates small-scale refugia for boreal forest floor bryophytes during clear-cut logging. *Ecography*, 34, 637–648.

Schneider, K., Migge, S., Norton, R.A., Scheu, S., Langel, R., Reineking, A., *et al.* (2004). Trophic niche differentiation in soil microarthropods (Oribatida, Acari): Evidence from stable isotope ratios (15N/14N). *Soil Biol. Biochem.*, 36, 1769–1774.

Schröder, A., Persson, L., Roos, A.M. de & Lundbery, P. (2005). Direct experimental evidence for alternative stable states: A review. *Oikos*, 110, 3–19.

Seip, D.R. (1992). Factors limiting woodland caribou populations and their interrelationships with wolves and moose in southeastern British Columbia. *Can. J. Zool.*, 70, 1494–1503.

Selwood, K.E., Thomson, J.R., Clarke, R.H., McGeoch, M.A. & Mac Nally, R. (2015). Resistance and resilience of terrestrial birds in drying climates: Do floodplains provide drought refugia? *Glob. Ecol. Biogeogr.*, 24, 838–848.

SER. (2004). The SER International Primer on Ecological Restoration. *Wwwserorg Tucson Soc. Ecol. Restor. Int.*

Shackelford, N., Hobbs, R.J., Heller, N.E., Hallett, L.M. & Seastedt, T.R. (2013). Finding a middle-ground: The native/non-native debate. *Biol. Conserv.*, 158, 55–62.

Shackelford, N., Starzomski, B.M., Banning, N.C., Battaglia, L., Becker, A., Bellingham, P.J., *et al.* (2016). Isolation predicts compositional change after discrete disturbances in a global meta-study. *Ecography*, n/a-n/a.

Shackelford, N., Starzomski, B.M., Banning, N.C., Battaglia, L.L., Becker, A., Bellingham, P.J., *et al.* (2017). Isolation predicts compositional change after discrete disturbances in a global meta-study. *Ecography*, 40, 1256–1266.

Shapiro, S.S. & Wilk, M.B. (1965). An analysis of variance test for normality (complete samples). *Biometrika*, 52, 591–611.

Simberloff, D. (2014). Biological invasions: What's worth fighting and what can be won? *Ecol. Eng.*, Sustainable Restoration, 65, 112–121.

Slater, F.M. & Agnew, A.D.Q. (1977). Observations on a peat bog's ability to withstand increasing public pressure. *Biol. Conserv.*, 11, 21–27.

Smit, B. & Spaling, H. (1995). Methods for cumulative effects assessment. *Environ. Impact Assess. Rev.*, 15, 81–106.

Soulé, M.E. (1985). What is conservation biology? *BioScience*, 35, 727–734.

Sousa, W.P. (1984). The role of disturbance in natural communities. *Annu. Rev. Ecol. Syst.*, 15, 353–391.

Spaling, H. & Smit, B. (1993). Cumulative environmental change: Conceptual frameworks, evaluation approaches, and institutional perspectives. *Environ. Manage.*, 17, 587–600.

Staddon, P., Lindo, Z., Crittenden, P.D., Gilbert, F. & Gonzalez, A. (2010). Connectivity, non-random extinction and ecosystem function in experimental metacommunities. *Ecol. Lett.*, 13, 543–552.

Standish, R.J., Hobbs, R.J., Mayfield, M.M., Bestelmeyer, B.T., Suding, K.N., Battaglia, L.L., *et al.* (2014). Resilience in ecology: Abstraction, distraction, or where the action is? *Biol. Conserv.*, 177, 43–51.

Starzomski, B.M. & Srivastava, D.S. (2007). Landscape geometry determines community response to disturbance. *Oikos*, 116, 690–699.

Stoffels, R.J. (2015). Physiological trade-offs along a fast-slow lifestyle continuum in fishes: What do they tell us about resistance and resilience to hypoxia? *PLOS ONE*, 10, e0130303.

Studlar, S.M. (1983). Recovery of trampled bryophyte communities near Mountain Lake, Virginia. *Bull. Torrey Bot. Club*.

Suding, K.N. (2011). Toward an era of restoration in ecology: Successes, failures, and opportunities ahead. *Annu. Rev. Ecol. Evol. Syst.*, 42, 465–487.

Suding, K.N., Gross, K.L. & Houseman, G.R. (2004). Alternative states and positive feedbacks in restoration ecology. *Trends Ecol. Evol.*, 19, 46–53.

Suding, K.N. & Hobbs, R.J. (2009). Threshold models in restoration and conservation: A developing framework. *Trends Ecol. Evol.*, 24, 271–279.

Suding, K.N., Lavorel, S., Chapin, F.S., Cornelissen, J.H.C., Díaz, S., Garnier, E., *et al.* (2008). Scaling environmental change through the community-level: A trait-based response-and-effect framework for plants. *Glob. Change Biol.*, 14, 1125–1140.

Svendsen, E. & Campbell, L. (2008). Urban ecological stewardship: Understanding the structure, function and network of community-based urban land management. *Cities Environ. CATE*, 1.

Swenson, N.G. & Howard, D.J. (2005). Clustering of contact zones, hybrid zones, and phylogeographic breaks in North America. *Am. Nat.*, 166, 581–591.

Tagawa, H., Suzuki, E., Partomihardjo, T. & Suriadarma, A. (1985). Vegetation and succession on the Krakatau Islands, Indonesia. *Vegetatio*, 60, 131–145.

Talbot, J., Richard, P. j. h., Roulet, N. t. & Booth, R. k. (2010). Assessing long-term hydrological and ecological responses to drainage in a raised bog using paleoecology and a hydrosequence. *J. Veg. Sci.*, 21, 143–156.

Taylor, P.D., Fahrig, L., Henein, K. & Merriam, G. (1993). Connectivity is a vital element of landscape structure. *Oikos*, 68, 571–573.

Therivel, R. & Ross, B. (2007). Cumulative effects assessment: Does scale matter? *Environ. Impact Assess. Rev.*, Special issue on Data Scale Issues for SEA, 27, 365–385.

Thomas, C.D. & Palmer, G. (2015). Non-native plants add to the British flora without negative consequences for native diversity. *Proc. Natl. Acad. Sci.*, 112, 4387–4392.

Thrush, S.F., Hewitt, J.E., Lohrer, A.M. & Chiaroni, L.D. (2013). When small changes matter: The role of cross-scale interactions between habitat and ecological connectivity in recovery. *Ecol. Appl.*, 23, 226–238.

Timpane-Padgham, B.L., Beechie, T. & Klinger, T. (2017). A systematic review of ecological attributes that confer resilience to climate change in environmental restoration. *PLOS ONE*, 12, e0173812.

Tingley, M.W. & Beissinger, S.R. (2009). Detecting range shifts from historical species occurrences: new perspectives on old data. *Trends Ecol. Evol.*, 24, 625–633.

Toews, M. (2016). Managing human footprint with respect to its effects on large mammals: Implications of spatial scale, divergent responses and ecological thresholds. University of Victoria.

Turner, M.G., Baker, W.L., Peterson, C.J. & Peet, R.K. (1998). Factors influencing succession: Lessons from large, infrequent natural disturbances. *Ecosystems*, 1, 511–523.

Turner, M.G., Gardner, R.H. & O'Neill, R.V. (1995). Ecological dynamics at broad scales. *BioScience*, 45, S29–S35.

Turner, W.R., Brandon, K., Brooks, T.M., Costanza, R., Fonseca, G.A.B. da & Portela, R. (2007). Global conservation of biodiversity and ecosystem services. *BioScience*, 57, 868–873.

Twidwell, D., Fuhlendorf, S.D., Taylor, C.A. & Rogers, W.E. (2013a). Refining thresholds in coupled fire–vegetation models to improve management of encroaching woody plants in grasslands. *J. Appl. Ecol.*, 50, 603–613.

Twidwell, D., Rogers, W.E., Fuhlendorf, S.D., Wonkka, C.L., Engle, D.M., Weir, J.R., *et al.* (2013b). The rising Great Plains fire campaign: Citizens' response to woody plant encroachment. *Front. Ecol. Environ.*, 11, e64–e71.

Van Auken, O.W. (2009). Causes and consequences of woody plant encroachment into western North American grasslands. *J. Environ. Manage.*, 90, 2931–2942.

Veraart, A.J., Faassen, E.J., Dakos, V., van Nes, E.H., Lürling, M. & Scheffer, M. (2012). Recovery rates reflect distance to a tipping point in a living system. *Nature*, 481, 357–359.

Verheyen, K., Vellend, M., Van Calster, H., Peterken, G. & Hermy, M. (2004). Metapopulation dynamics in changing landscapes: A new spatially realistic model for forest plants. *Ecology*, 85, 3302–3312.

Vilà, M., Espinar, J.L., Hejda, M., Hulme, P.E., Jarošík, V., Maron, J.L., *et al.* (2011). Ecological impacts of invasive alien plants: A meta-analysis of their effects on species, communities and ecosystems. *Ecol. Lett.*, 14, 702–708.

Waddington, J.M., Morris, P.J., Kettridge, N., Granath, G., Thompson, K.D. & Moore, P.A. (2015). Hydrological feedbacks in northern peatlands. *Ecohydrology*, 8, 113–127.

Wahren, C.H.A., Williams, R.J. & Papst, W.A. (2001). Vegetation change and ecological processes in alpine and subalpine Sphagnum bogs of the Bogong High Plains, Victoria, Australia. *Arct. Antarct. Alp. Res.*, 33, 357–368.

Walker, B., Holling, C.S., Carpenter, S. & Kinzig, A. (2004). Resilience, adaptability and transformability in social-ecological systems. *Ecol. Soc.*, 9.

Walker, B.H. (1992). Biodiversity and ecological redundancy. *Conserv. Biol.*, 6, 18–23.

Walker, B.H. (2008). A resilience perspective on landscape dynamics. In: *Managing and Designing Landscapes for Conservation: Moving from Perspectives to Principles* (eds. Lindenmayer, D.B. & Hobbs, R.J.). John Wiley & Sons.

Walker, B.H. & Salt, D. (2012). *Resilience Practice: Building Capacity to Absorb Disturbance and Maintain Function*. Island Press.

Wallén, B., Falkengren-Grerup, U. & Malmer, N. (1988). Biomass, productivity and relative rate of photosynthesis of Sphagnum at different water levels on a south Swedish peat bog. *Holarct. Ecol.*, 11, 70–76.

Walters, C.J. (1986). *Adaptive Management of Renewable Resources*. MacMillam Publishing Company, New York.

Walters, C.J. & Holling, C.S. (1990). Large-scale management experiments and learning by doing. *Ecology*, 71, 2060–2068.

Watson, J.E.M., Dudley, N., Segan, D.B. & Hockings, M. (2014). The performance and potential of protected areas. *Nature*, 515, 67–73.

Weir, R.D. (2003). *Status of the fisher in British Columbia*. Ministry of Water, Land and Air Protection Biodiversity Branch and Ministry of Sustainable Resource Management Conservation Data Centre, Province of British Columbia.

Weir, R.D. & Corbould, F.B. (2006). Density of fishers in the Sub-Boreal Spruce Biogeoclimatic Zone of British Columbia. *Northwest. Nat.*, 87, 118–127.

Westoby, M., Walker, B. & Noy-Meir, I. (1989). Opportunistic management for rangelands not at equilibrium. *J. Range Manag.*, 42, 266–274.

Whittaker, R.H. (1967). Gradient analysis of vegetation. *Biol. Rev.*, 42, 207–264.

Wiens, J.A. & Milne, B.T. (1989). Scaling of 'landscapes' in landscape ecology, or, landscape ecology from a beetle's perspective. *Landsc. Ecol.*, 3, 87–96.

Wilcove, D.S., Rothstein, D., Dubow, J., Phillips, A. & Losos, E. (1998). Quantifying threats to imperiled species in the United States. *BioScience*, 48, 607–615.

Williamson, M. & Fitter, A. (1996). The varying success of invaders. *Ecology*, 77, 1661–1666.

Wilson, D.E. & Ruff, S. (1999). *The Smithsonian Book of North American Mammals*. University of British Columbia Press.

Wissel, C. (1984). A universal law of the characteristic return time near thresholds. *Oecologia*, 65, 101–107.

Wittmer, H.U., McLellan, B.N., Seip, D.R., Young, J.A., Kinley, T.A., Watts, G.S., *et al.* (2005). Population dynamics of the endangered mountain ecotype of woodland caribou (Rangifer tarandus caribou) in British Columbia, Canada. *Can. J. Zool.*, 83, 407–418.

Wood, S. (2016). *mgcv: Mixed GAM Computation Vehicle with GCV/AIC/REML Smoothness Estimation*.

Zalasiewicz, J., Williams, M., Steffen, W. & Crutzen, P. (2010). The new world of the Anthropocene. *Environ. Sci. Technol.*, 44, 2228–2231.

Zhang, D. & Pearse, P.H. (1996). Differences in silvicultural investment under various types of forest tenure in British Columbia. *For. Sci.*, 42, 442–449.

Zuur, A., Ieno, E.N., Walker, N., Saveliev, A.A. & Smith, G.M. (2009). *Mixed Effects Models and Extensions in Ecology with R*. Springer Science & Business Media.

Appendices

Appendix 1.A: Average oribatid species or genera richness

Average oribatid species or genera richness per plug for each treatment by time (second column from far right) and average richness by time over all treatments (far right).

	Oribatid richness	
Treatment	Average by treatment and time	Average by time
	0 months	
P - U	3.7	
P - D	3.5	3.7
I	3.8	
	3 months	
P - U	5	
P - D	5.2	5
I	4.9	
	6 months	
P – U	6.5	
P – D	5.9	6.3
I	6.4	
	9 months	
P – U	6.4	
P – D	5.2	6
I	6.4	

Connected with undisturbed (P – U)

Connected with disturbed (P – D)

Isolated (I)

Average oribatid species or genera abundance per plug for each treatment by time. The average control abundance is listed followed by the average disturbed abundance in parentheses. Only oribatid species or genera are shown that represented more than 1% of the total oribatid individuals over the full study. Species or genera are listed from the most abundant (far left) to the least (far right).

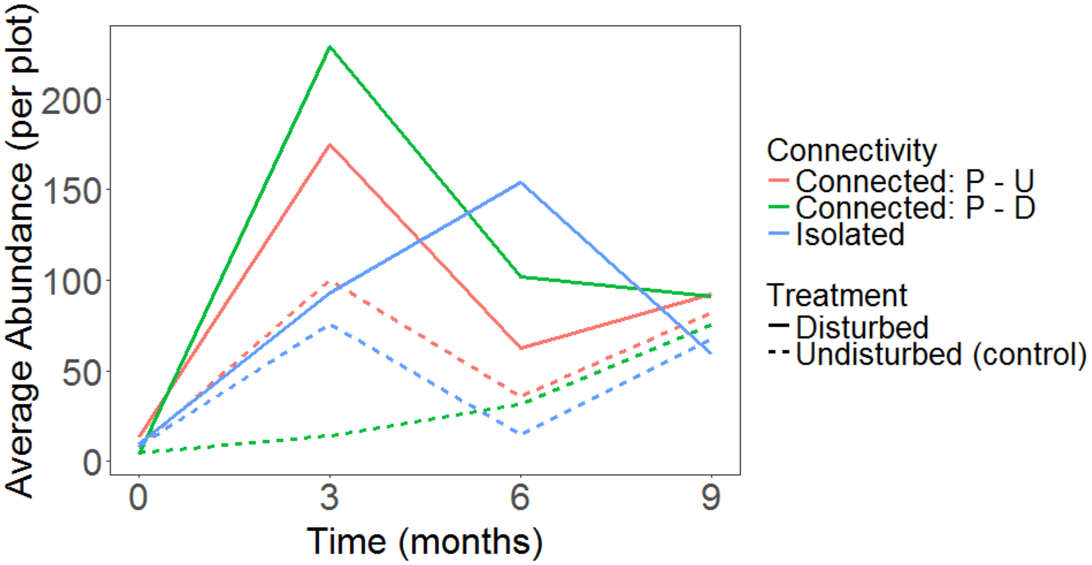
	Average Oribatid Abundance								
Treatment	Unknown immatures	*Trihypocthonius tectorum*	*Autogneta* nr. *longilamellata*	*Quadroppia quadricarinata*	*Propelops canadensis*	*Eueremaeus chiatous*	*Pilogalumna* sp.	*Scheloribates* sp.	*Oribatula* sp.
0 months									
P - U	7.67 (2.2)	0.83 (2.37)	0 (0.17)	0.83 (1.4)	0.83 (0.47)	0 (0.43)	0 (0)	0.17 (0)	0.17 (0.37)
P - D	3.17 (4.96)	0.33 (1.96)	0 (0.18)	0.5 (0.61)	4.17 (0.57)	0 (0.5)	0 (0.11)	0 (0)	0 (0.14)
I	6.83 (5.72)	0.17 (1.38)	0 (0.03)	1.17 (1.03)	7.5 (1.69)	0 (1.59)	0.17 (0.03)	0 (0)	2 (0.16)
3 months									
P - U	6.67 (6.9)	9.67 (5.77)	0.17 (0.53)	2 (1.13)	0.33 (0.9)	0.33 (0.3)	0 (0.13)	0 (0.73)	1.17 (1.03)
P - D	16.5 (5.57)	20.33 (6.27)	0 (0.13)	2.33 (0.8)	1.17 (0.53)	0 (0.3)	0 (0.13)	0 (0.73)	0.17 (0.53)
I	5.17 (12.7)	34.67 (2.73)	0.17 (0.03)	2.17 (0.33)	0.5 (0.87)	0.33 (0.17)	0.17 (0.17)	0.33 (1.3)	0.83 (0.07)
6 months									
P – U	9 (19.73)	45.33 (15.57)	3.67 (14.1)	0 (1.6)	0.67 (0.73)	0 (0.3)	0.33 (0.33)	0 (0.07)	0 (0)
P – D	13 (11.13)	4.5 (11.28)	0 (3)	0.5 (1.25)	1.25 (1.31)	1.5 (0.16)	0 (0.09)	0 (0.13)	0 (0.09)
I	3.83 (13.87)	13 (12.9)	0.83 (0.8)	0.83 (0.43)	0.17 (0.83)	0 (0.47)	0.17 (0.2)	0 (0.33)	0.33 (0.27)
9 months									
P – U	4.17 (5.1)	6.5 (4.77)	0.17 (3.3)	0.83 (3.23)	0 (0.27)	0.67 (0.1)	0.33 (0.53)	0 (0.2)	0 (0.17)
P – D	1.17 (16.37)	4.5 (1.6)	0.17 (16.6)	1.33 (1.8)	0 (0.27)	0 (0.07)	0 (0.6)	0 (0.07)	0 (0.07)
I	128.17 (6.57)	0.17 (1.87)	19.5 (1.47)	9.17 (0.53)	0.83 (0.33)	0 (0.27)	2.17 (1.47)	0 (0.2)	0 (0)

Connected with undisturbed (P – U)
Connected with disturbed (P – D)
Isolated (I)

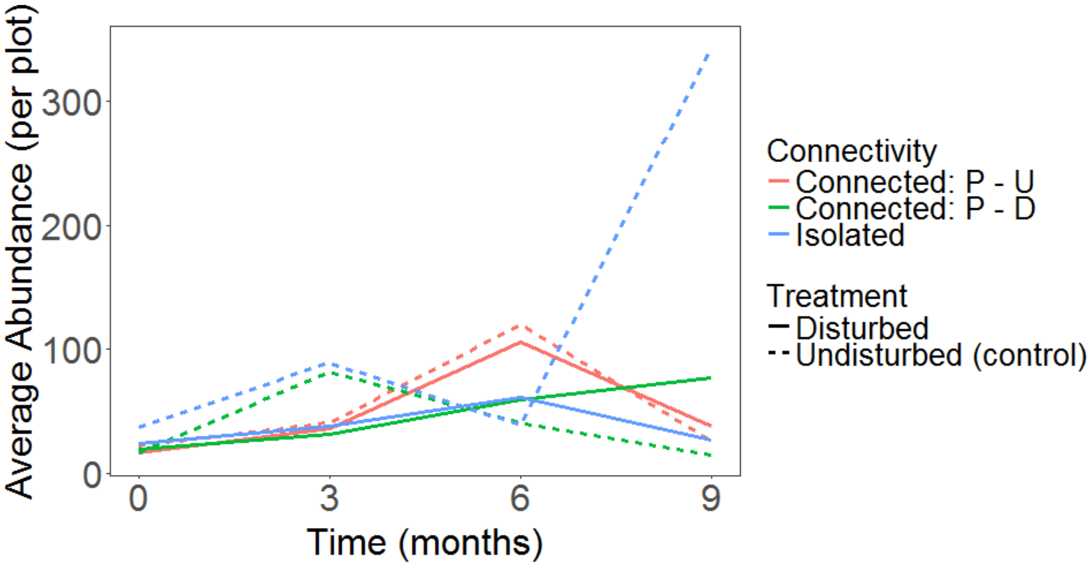
Appendix 1.B: Average abundance of major organism groups through time

Abundance of each major lifeform through time in disturbed and undisturbed treatments. All three landscape treatments are shown, where P–U is connected to an undisturbed landscape, P–D is connected to a disturbed landscape, and I is isolated.

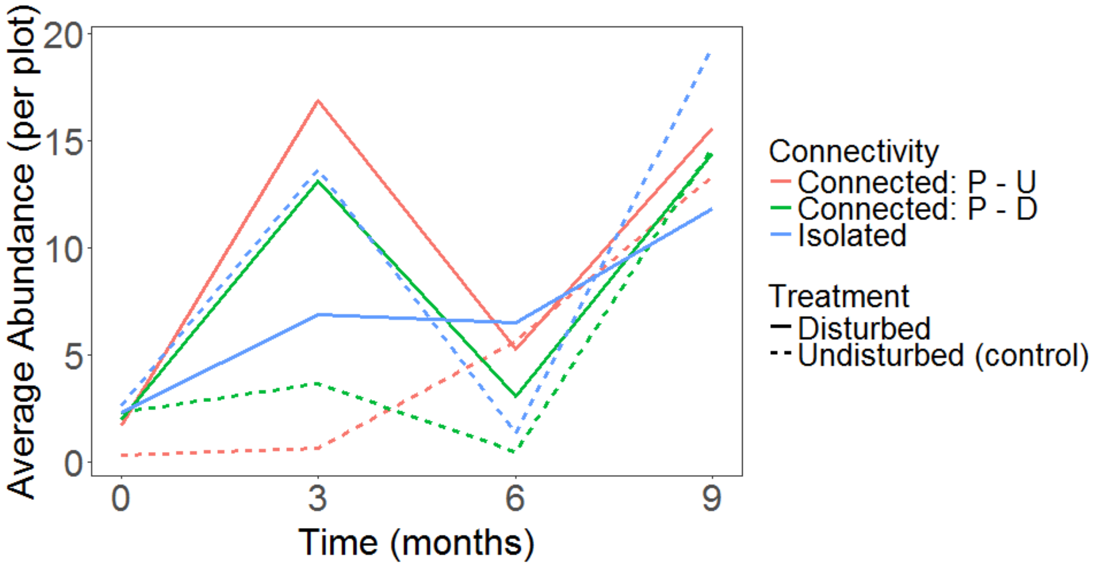
Springtails



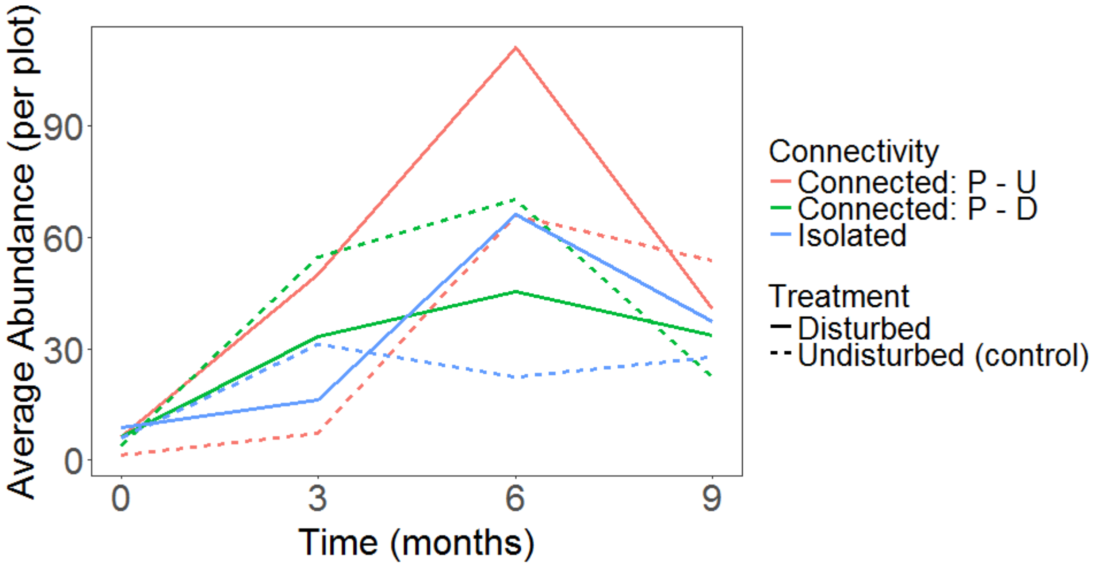
Oribatid mites



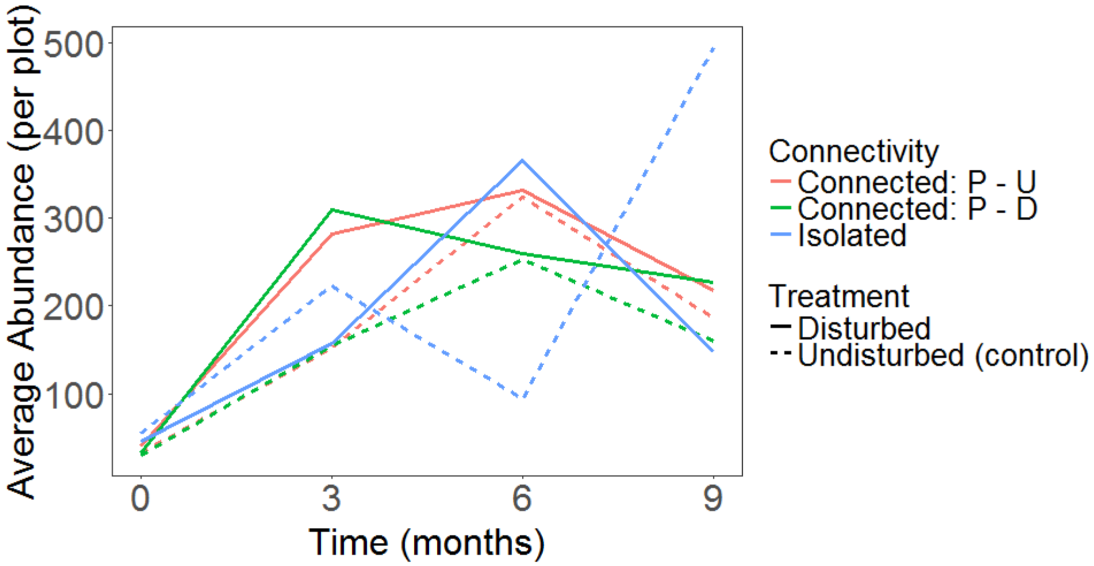
Mesostigmatid mites



Prostigmatid mites

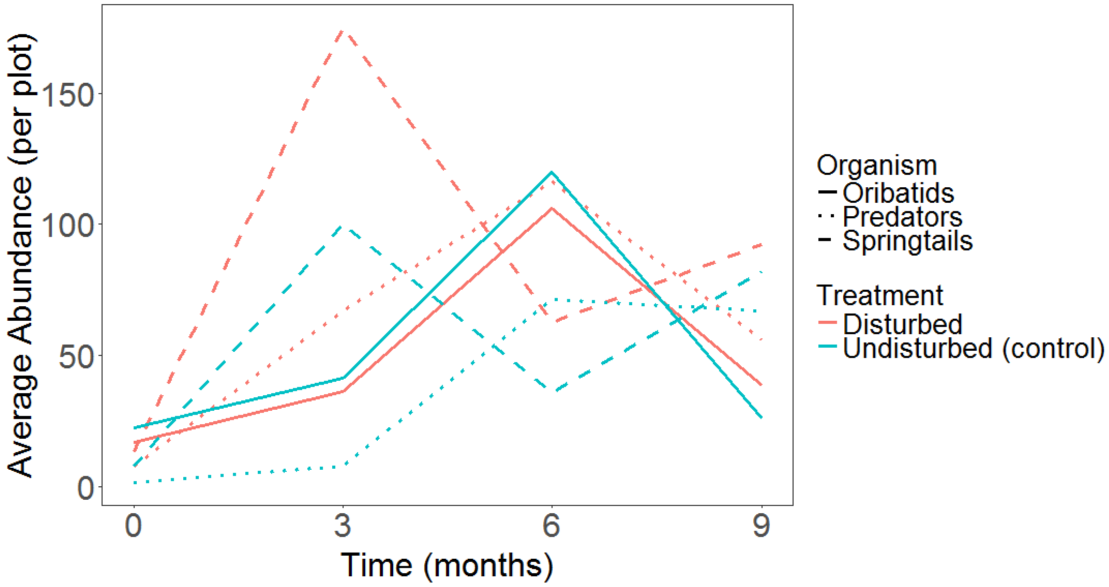


Total microarthropod abundance

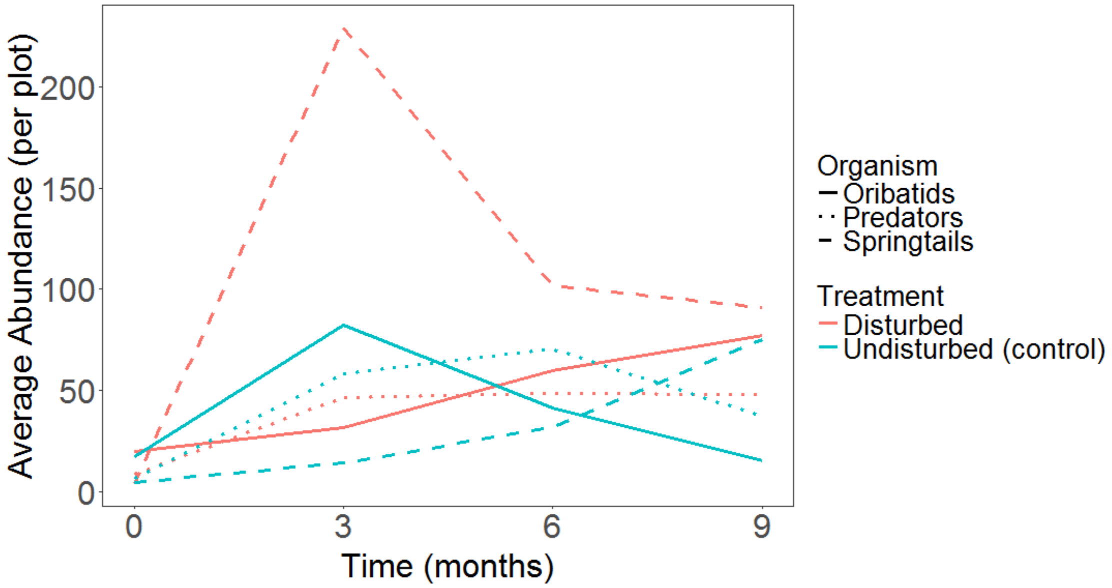


Abundance through time of three groups (oribatids, springtails, and 'predators' which includes the sum of mesostigmatid and prostigmatid mites). Plots are split by connectivity treatment.

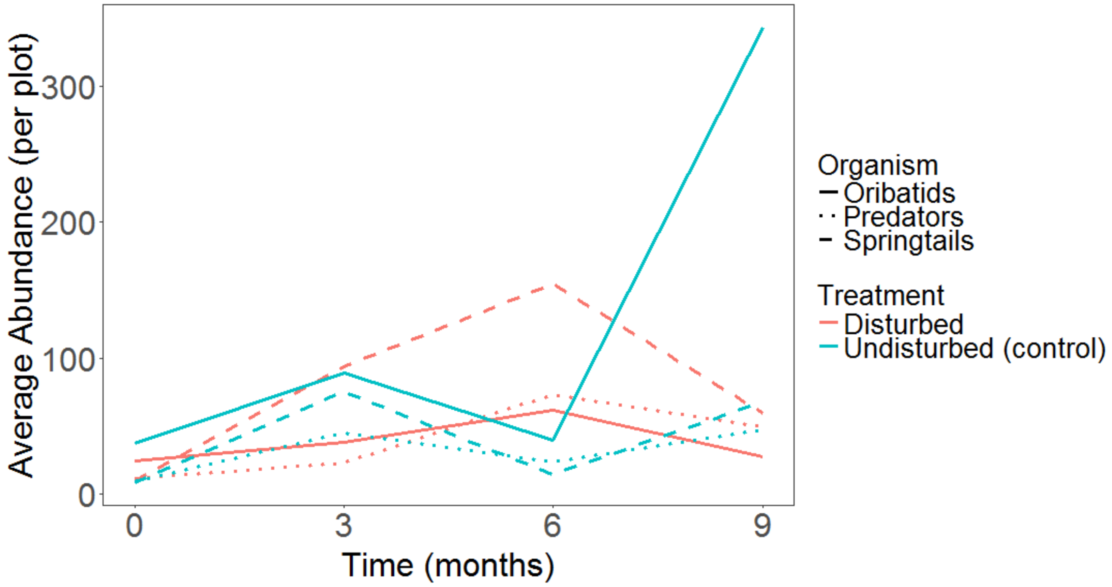
P–U: Connected to an undisturbed landscape



P–D: Connected to a disturbed landscape



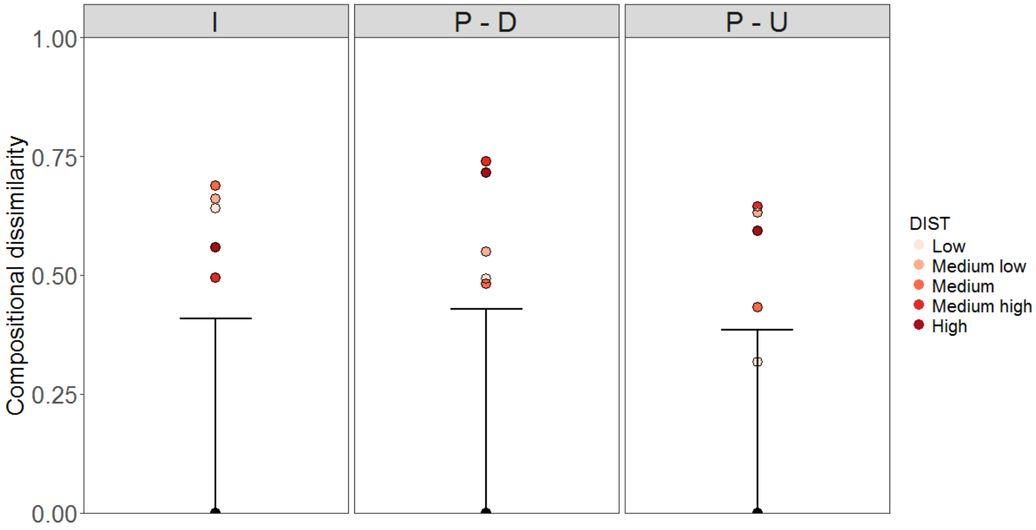
I: Isolated



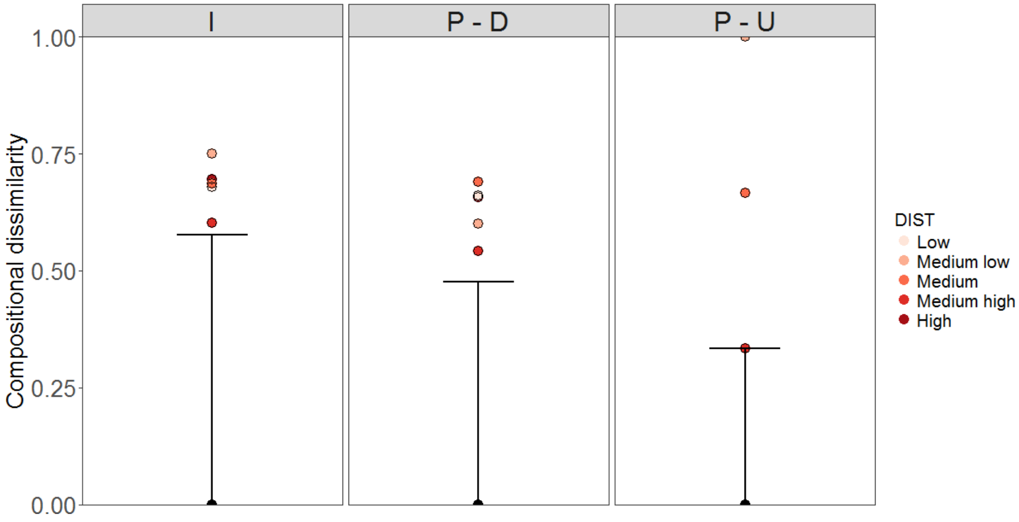
Appendix 1.C: Breakdown of resistance by lifeform

Overall, the only significant finding within lifeforms for resistance was that springtails had lowest resistance in the P–D treatment. However, both mesostigmatid and prostigmatid mites had the opposite relationship, where resistance was highest in the P–D treatment. Though neither was significant individually, when combined into the full community dataset, the response of mesostigmatid and prostigmatid mites drove a significant relationship with higher resistance in the P–D treatment at the community level.

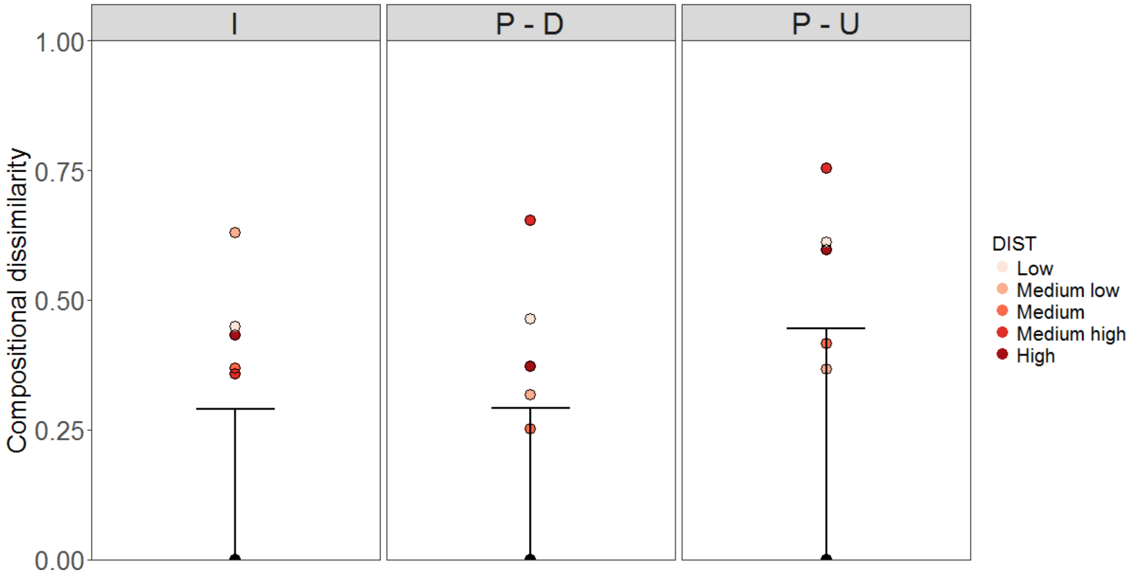
Oribatid mite results



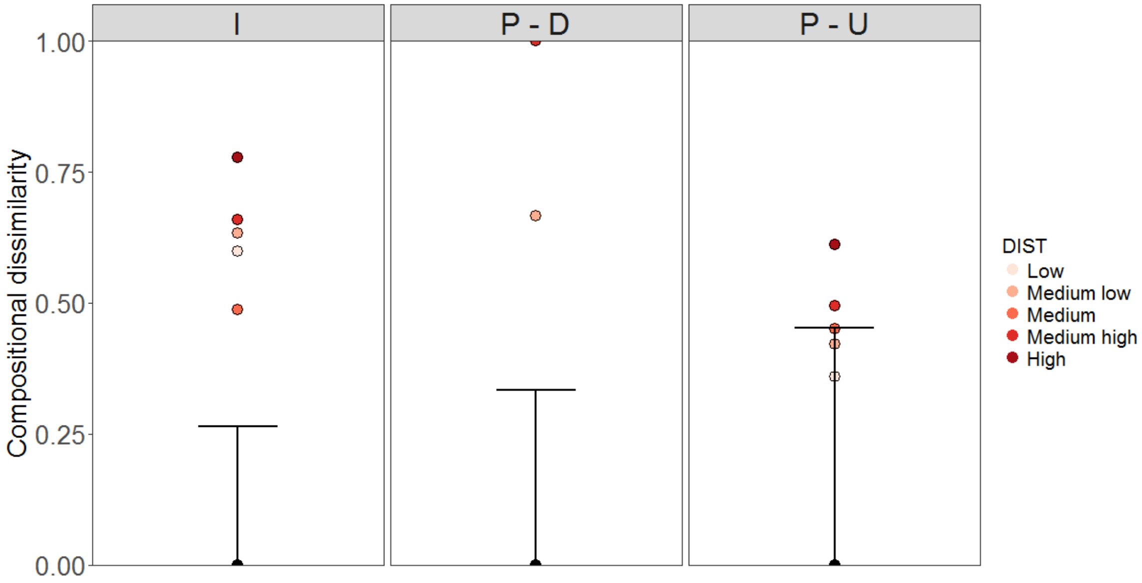
Mesostigmatid mite results



Prostigmatid mite results



Springtail results

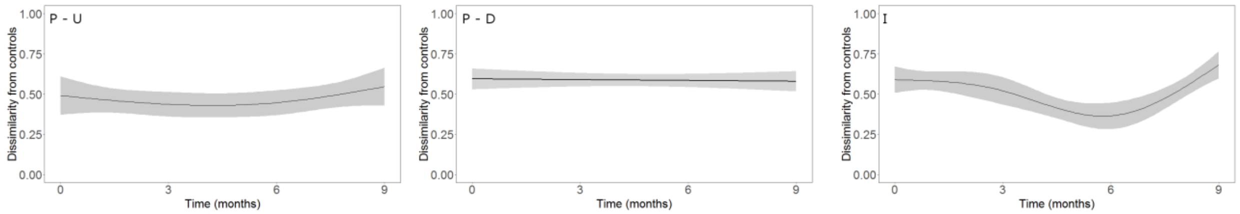


Appendix 1.D: Breakdown of recovery by lifeform

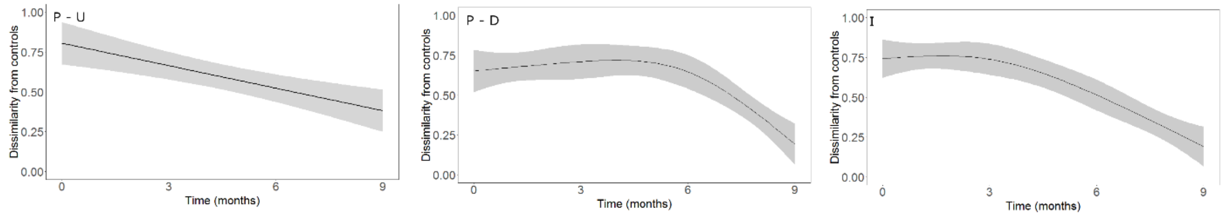
Each lifeform recovered on different trajectories. The oribatid mite communities showed little to no recovery, and in the isolated treatment became more dissimilar than previous timesteps by month nine. Springtails showed linear recovery over all treatments. Mesostigmatid and prostigmatid mite communities showed relatively rapid, linear recovery in P–U treatments. Mesostigmatid mite communities showed delayed recovery in the P–D and isolated treatments, while prostimatid mite communities showed slowed but linear recovery in the isolated treatment, and a hump shaped recovery pattern in the P–D treatment.

All relationships were significant except recovery through time in the oribatid communities in the P–U and P–D treatments.

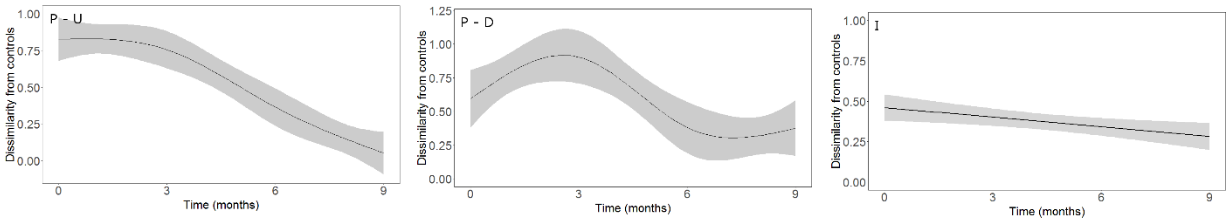
Oribatid mite results



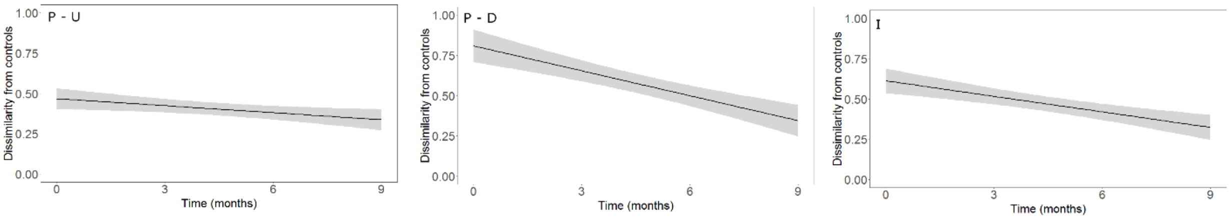
Mesostigmatid mite results



Prostigmatid mite results



Springtail results



Appendix 1.E: Statistical analysis of oribatid richness and total microarthropod abundance by area

Methods

Oribatid richness was calculated by totaling the number of oribatid species and genera in each plug. Total abundance of all microarthropods was also calculated for each plug.

We then ran a series of linear models to test whether there was a significant effect of area:

response ~ Area

response ~ Area + Time

response ~ Area + Time + Disturbance

Results

Model	**p-value of predictor “area”**
Microarthropod abundance	
~ Area	0.53
~ Area + Time	0.55
~ Area + Time + Disturbance	0.53
Oribatid richness	
~ Area	0.62
~ Area + Time	0.55
~ Area + Time + Disturbance	0.54

Appendix 2.A: Model details

The upslope experiment was established in 2013 as a pilot treatment to ensure that high survival of vegetation was consistent across the control and drawdown treatments. In 2014, the downslope experiment was established. Each model was fit to a different subset of data, with those combining the up- and downslope data having temporally disjoint data points. The below table details the data used for each model. All models had plot included as a random variable.

Trend	Model	Data	Time	Replicates	n
Slow change	Moss cover ~ Year	Untrampled control plots upslope Untrampled drawdown plots upslope	2013 - 2017	5	25
		Control plots downslope with no tree seedlings Drawdown plots downslope with no tree seedlings	2014 - 2017	5	20
	Woody cover ~ Year	Untrampled control plots upslope Untrampled drawdown plots upslope	2013 - 2017	5	25
		Control plots downslope with no tree seedlings Drawdown plots downslope with no tree seedlings	2014 - 2017	5	20
	Grass cover ~ Year	Untrampled control plots upslope Untrampled drawdown plots upslope	2013 - 2017	5	25
		Control plots downslope with no tree seedlings Drawdown plots downslope with no tree seedlings	2014 - 2017	5	20
	Forb cover ~ Year	Untrampled control plots upslope Untrampled drawdown plots upslope	2013 - 2017	5	25
		Control plots downslope with no tree seedlings Drawdown plots downslope with no tree seedlings	2014 - 2017	5	20
	Sedge cover ~ Year	Untrampled control plots upslope Untrampled drawdown plots upslope	2013 - 2017	5	25
		Control plots downslope with no tree seedlings Drawdown plots downslope with no tree seedlings	2014 - 2017	5	20
Tree - drawdown feedbacks	Moss cover ~ Year	Control plots downslope with tree seedlings Drawdown plots downslope with tree seedlings	2014 - 2017	5	20
	Woody cover ~ Year	Control plots downslope with tree seedlings Drawdown plots downslope with tree seedlings	2014 - 2017	5	20

	Grass cover ~ Year	Control plots downslope with tree seedlings Drawdown plots downslope with tree seedlings	2014 - 2017	5	20
	Forb cover ~ Year	Control plots downslope with tree seedlings Drawdown plots downslope with tree seedlings	2014 - 2017	5	20
	Sedge cover ~ Year	Control plots downslope with tree seedlings Drawdown plots downslope with tree seedlings	2014 - 2017	5	20
Autocorrelation	Compositional dissimilarity (lag1) ~ Treatment	Untrampled upslope plots: 2014 to 2013; 2015 to 2014; 2016 to 2015; 2017 to 2016 (4 consecutive measurements) Downslope plots with no tree seedlings: 2015 to 2014; 2015 to 2015; 2017 to 2016 (3 consecutive measurements)	Upslope: 2014 - 2017 Downslope: 2015 - 2017	10	70
	Compositional dissimilarity (lag2) ~ Treatment	Untrampled upslope plots: 2014 to 2013; 2016 to 2014; 2017 to 2015 (3 consecutive measurements) Downslope plots with no tree seedlings: 2016 to 2014; 2017 to 2015 (2 consecutive measurements)	Upslope: 2015 - 2017 Downslope: 2016 - 2017	10	50
	Compositional dissimilarity (lag3) ~ Treatment	Untrampled upslope plots: 2015 to 2013; 2017 to 2014 (2 consecutive measurements) Downslope plots with no tree seedlings: 2017 to 2014 (1 consecutive measurements)	Upslope: 2016 - 2017 Downslope: 2017	10	30
Recovery	Moss cover ~ Year	Trampled control plots Trampled drawdown plots	2014 (post-trampling) - 2017	5	20
	Woody cover ~ Year	Trampled control plots Trampled drawdown plots	2014 (post-trampling) - 2017	5	20
	Grass cover ~ s(Year) Grass cover ~ Year	Trampled control plots Trampled drawdown plots	2014 (post-trampling) - 2017	5	20
	Forb cover ~ Year Forb cover ~ s(Year)	Trampled control plots Trampled drawdown plots	2014 (post-trampling) - 2017	5	20
	Sedge cover ~ Year	Trampled control plots Trampled drawdown plots	2014 (post-trampling) - 2017	5	20
	Compositional dissimilarity (to avg of untrampled in same year) ~ s(Year)	Trampled control plots Trampled drawdown plots	2014 (post-trampling) - 2017	5	20

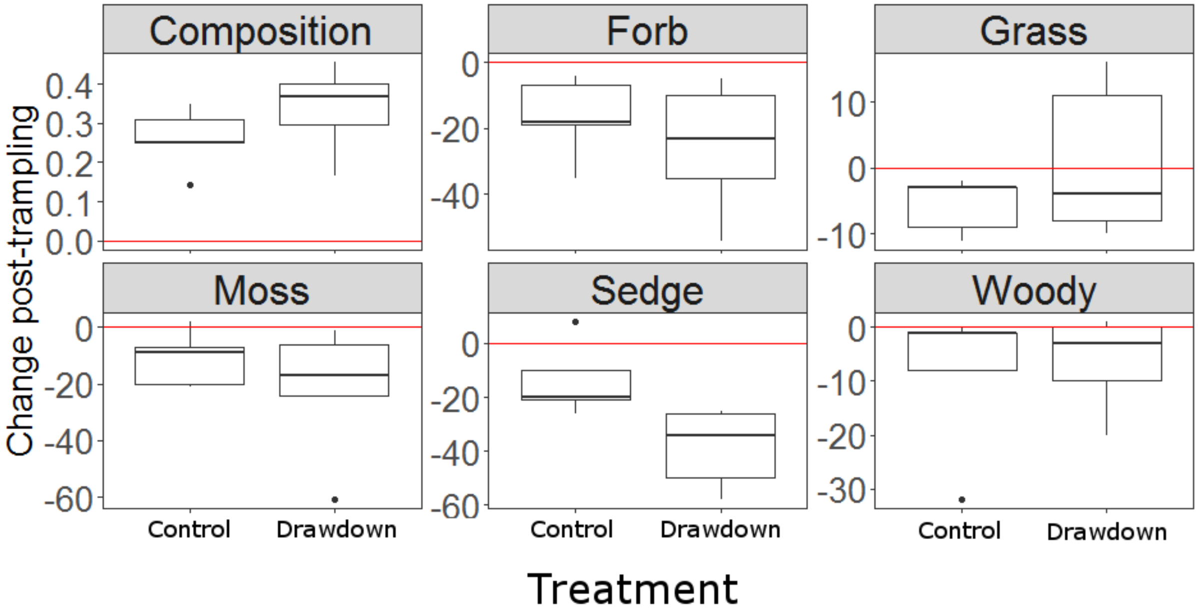
Appendix 2.B: Additional results

Autocorrelation

Model results for auto-correlation, where first-order is the dissimilarity between a plot and the same plot one year prior; second-order is the dissimilarity between a plot and itself two years prior; and third-order is the dissimilarity between a plot and itself three years prior. The table shows the co-efficient estimate for the drawdown treatments ± the 95% CI, the p-value for the co-efficient, and the marginal- and conditional-R^2 for the model.

Level	**Coefficient estimate**	**p-value**	**Marginal-R^2**	**Conditional-R^2**
Lag-1	0.08 ± 0.05	0.008	0.19	0.46
Lag-2	0.12 ± 0.08	0.009	0.24	0.63
Lag-3	0.18 ± 0.09	0.002	0.36	0.55

Discrete disturbance



Change in post-trampled communities from pre-trampled. The plot represents a comparison between a single plot post-disturbance and itself pre-disturbance, with untrampled control plots excluded from this information. The red line in each plot represents zero change; *i.e.* the instance of no change happening in lifeform cover due to trampling. The top left panel shows compositional dissimilarity, with positive values indicating larger changes. The remaining five panels show changes in the cover of each lifeform, with larger negative values representing greater loss of cover (in %).

Appendix 3.A: Trait description and data sources

Trait, trait type (effect: E or response: R), description of each trait, range of values each trait took in the data, and the primary sources of information for each trait.

Function	Type	Description	Values	Primary sources
Invasive	E	Is it characterized as invasive in this region? Non-traditional effect trait, but heavily influences ecosystem management activities	0/1	Invasive Species Council of British Columbia
Growth form	E	As per Pérez-Harguindeguy *et al.* 2013	Herbaceous rosette, herbaceous rhizomatous, stemmed herb, tussock, scrambler, succulent, bambusoid, prostrate shrub, dwarf shrub, shrub, excurrent tree, deliquescent tree, parasite, hydrophyte	eFlora: Electronic Atlas of the Flora of British Columbia
Life history	E		Annual, biennial, herbaceous monocarpic perennial, herbaceous polycarpic perennial, woody perennial	USDA Plants Database
Raunkiaer	E		Geophyte, phanerophyte, therophyte, hemicryptophyte, epiphyte	FEIS: Fire Effects Information System Online Atlas of the British and Irish Flora
Leaf size (length X width)	E		Continuous: cm^2	eFlora: Electronic Atlas of the Flora of British Columbia eFlora: Flora of North America
Height (average maximum)	E		Continuous: cm	eFlora: Electronic Atlas of the Flora of British Columbia
Number of growth seasons	E		1 – 4	USDA Plants Database
Season growth starts	E		Ordinal: 1 (spring), 2 (summer), 3 (fall), 4 (winter)	USDA Plants Database Calflora plants database
Evergreen	E	Are photosynthetic leaves retained in all seasons?	0/1	FEIS: Fire Effects Information System PFAF: Plants for a Future database USDA Plants Database
Nitrogen fixing	E/R		0/1	USDA Plants Database
Palatability	E/R		Ordinal: 1 (low), 2 (medium), 3 (high)	USDA Plants Database
Defense	E/R	Is there some mechanism of grazing defense? Either	0/1	eFlora: Electronic Atlas of the Flora of British Columbia

		chemical (*e.g.* toxins) or physical (*e.g.* thorns)?		PFAF: Plants for a Future database USDA Plants Database
Growth Rate	E/R		Ordinal: 1 (slow), 2 (moderate), 3 (rapid)	USDA Plants Database
Hermaphrodite	R		0/1	PFAF: Plants for a Future database
Clonal	R	Is a major reproductive strategy through vegetative reproduction?	0/1	FEIS: Fire Effects Information System PFAF: Plants for a Future database USDA Plants Database Calflora plants database
Pollination method	R		0/1 each for wind, self, insect, animal	PFAF: Plants for a Future database
Dispersal method	R		0/1 each for wind, water, animal, explosive, none	FEIS: Fire Effects Information System PFAF: Plants for a Future database USDA Plants Database
Precipitation envelope (range maximum – range minimum)	R		Continuous: cm	Calflora plants database
Drought tolerance	R		Ordinal: 1 (low), 2 (medium), 3 (high)	USDA Plants Database
Shade tolerance	R		Ordinal: 1 (low), 2 (medium), 3 (high)	USDA Plants Database
Minimum root depth	R		Continuous: cm	Calflora plants database
Seed weight	R		Continuous: seeds/lb	USDA Plants Database Kew SID: Seed Information Database

Appendix 3.B Patch results

These are the patch results for 2006, 2009, and 2017. From left to right: patch code, level of invasive species management, connectivity, area of the patch (2006 / 2017), total species richness of the patch (2006 / 2017), species found in 2006 and not in 2017 (number of NIS in parentheses), species found in 2017 and not in 2006 (number of NIS in parentheses), total species richness within the NI functional groups (2006 / 2017), proportion of total species richness that was NIS (2006 / 2017), average functional redundancy within functional groups in each patch (2006 / 2017), average response diversity within functional groups in each patch (2006 / 2017), average functional redundancy per square meter (2009 / 2017), and average response diversity per square meter (2009 / 2017).

Patch	Manage-ment	Road density	Connectivity	Area (ha)	Species richness	Species missing	Species gained	Species richness NI Functions	NIS Prop.	FR within groups	RD within groups	FR_all per m^2	RD_all per m^2
Albert Head	Low	8.44	109130.2	1.173 / 1.068	84 / 83	15 (8)	13 (6)	14 / 14	0.51 / 0.51	3.18 / 3.24	0.19 / 0.2	0.47 / 0.52	0.29 / 0.25
Bear Hill (A)	None	3.64	50181.04	2.146 / 1.824	78 / 92	7 (2)	22 (11)	6 / 11	0.4 / 0.42	3 / 3.29	0.18 / 0.22	0.58 / 0.53	0.28 / 0.3
Bear Hill (B)	Low	3.93	28970.14	4.477 / 3.639	96 / 95	15 (7)	16 (9)	10 / 11	0.35 / 0.34	3.58 / 3.42	0.21 / 0.2	0.54 / 0.42	0.29 / 0.28
Boulderwood (E)	None	4.52	25283.02	1.73 / 1.68	94 / 119	11 (4)	38 (19)	11 / 12	0.44 / 0.46	3.46 / 4.42	0.15 / 0.21	0.61 / 0.57	0.3 / 0.27
Boulderwood (W)	None	10.17	27006.47	1.113 / 1.067	79 / 94	13 (4)	28 (17)	5 / 15	0.37 / 0.45	3.08 / 3.39	0.18 / 0.21	0.58 / 0.56	0.29 / 0.24
Camrose	Low	1.97	69018.49	1.477 / 1.104	66 / 63	25 (17)	42 (13)	15 / 8	0.7 / 0.68	3 / 2.94	0.18 / 0.19	0.47 / 0.53	0.29 / 0.29
Cedar Hill	High	3.58	77929.92	2.766 / 2.369	68 / 87	7 (2)	27 (18)	11 / 16	0.62 / 0.66	2.59 / 3.23	0.15 / 0.22	0.55 / 0.43	0.29 / 0.3
Chatterton	Med	2.14	15888.79	1.223 / 1.089	84 / 93	11 (11)	20 (11)	17 / 18	0.64 / 0.58	2.68 / 3	0.16 / 0.18	0.57 / 0.51	0.3 / 0.28
Christmas Hill	High	3.44	65270.2	8.721 / 8.721	112 / 129	16 (10)	37 (18)	19 / 21	0.55 / 0.53	3.17 / 3.48	0.19 / 0.22	0.59 / 0.44	0.3 / 0.27
Francis King (N)	None	1.74	409167.9	1.355 / 0.987	80 / 90	10 (2)	19 (9)	5 / 10	0.33 / 0.38	3.33 / 3.67	0.18 / 0.18	0.59 / 0.56	0.29 / 0.28
Francis King (S)	None	2.58	2171374	1.202 / 1.202	81 / 102	4 (1)	27 (17)	8 / 14	0.36 / 0.4	3.26 / 3.48	0.19 / 0.21	0.62 / 0.42	0.28 / 0.28

Garibaldi	None	1.08	82461.15	5.89 / 5.86	95 / 96	19 (3)	18 (7)	5 / 10	0.28 / 0.34	3.04 / 3.67	0.18 / 0.22	0.52 / 0.42	0.18 / 0.26
Gonzales	Low	2.22	28234.75	1.312 / 1.101	95 / 93	22 (12)	20 (12)	12 / 14	0.61 / 0.61	3.91 / 3.65	0.19 / 0.16	0.53 / 0.39	0.24 / 0.28
Gore	High	6.1	39619.77	1.548 / 1.34	101 / 116	10 (4)	25 (12)	10 / 14	0.39 / 0.41	3.46 / 3.43	0.21 / 0.18	0.68 / 0.51	0.28 / 0.29
Horth Hill	None	2.89	22215.26	1.216 / 0.871	82 / 90	10 (1)	17 (8)	4 / 4	0.4 / 0.44	3.79 / 4.17	0.2 / 0.21	0.65 / 0.6	0.28 / 0.28
John Dean (P)	High	7.95	17421.59	0.725 / 0.725	82 / 91	12 (4)	18 (9)	6 / 6	0.33 / 0.36	3.39 / 3.52	0.19 / 0.19	0.52 / 0.6	0.28 / 0.3
John Dean (E)	High	9.85	17872.01	0.769 / 0.769	85 / 99	17 (5)	30 (14)	5 / 10	0.29 / 0.35	3.76 / 4	0.2 / 0.2	0.5 / 0.51	0.29 / 0.3
Knockan (N)	Med	5.79	49476.64	3.185 / 2.88	111 / 111	22 (11)	23 (14)	17 / 15	0.51 / 0.52	3.32 / 3.58	0.18 / 0.18	0.57 / 0.55	0.26 / 0.26
Knockan (S)	Low	4.35	62155.21	1.27 / 1.109	97 / 101	19 (13)	25 (17)	14 / 15	0.6 / 0.57	2.91 / 3.05	0.19 / 0.2	0.55 / 0.54	0.26 / 0.27
Konuckson (A)	None	8.31	70719.17	0.595 / 0.565	73 / 79	16 (11)	19 (5)	9 / 11	0.55 / 0.48	2.86 / 2.38	0.21 / 0.19	0.45 / 0.37	0.28 / 0.27
Konuckson (B)	None	2.27	72684.95	0.178 / 0.134	72 / 59	24 (22)	10 (5)	12 / 8	0.63 / 0.49	3.83 / 3.67	0.21 / 0.21	0.54 / 0.5	0.29 / 0.28
Layritz	None	2.08	42008.72	4.431 / 3.491	107 / 104	20 (11)	19 (10)	15 / 16	0.51 / 0.51	3.72 / 3.8	0.2 / 0.2	0.6 / 0.62	0.28 / 0.29
Little Mt Doug	High	0.79	254285.7	8.815 / 8.815	106 / 111	14 (3)	19 (11)	13 / 16	0.42 / 0.48	2.91 / 3.52	0.22 / 0.23	0.54 / 0.44	0.29 / 0.29
Moss Rock	Med	7.64	51199.58	2.032 / 1.978	82 / 97	15 (9)	27 (15)	15 / 15	0.7 / 0.67	2.85 / 3.4	0.19 / 0.24	0.43 / 0.43	0.3 / 0.28
Peacock	Low	9.92	65664.79	1.146 / 1.034	71 / 88	6(4)	23 (16)	14 / 17	0.7 / 0.72	3.6 / 4.24	0.19 / 0.22	0.5 / 0.58	0.29 / 0.29
Summit	High	11.26	33108.48	5.882 / 4.961	92 / 102	17 (14)	28 (14)	18 / 15	0.73 / 0.65	2.88 / 3.08	0.2 / 0.2	0.64 / 0.5	0.28 / 0.28
Mt Stewart	None	0.69	476104.7	6.524 / 5.833	105 / 125	7 (0)	28 (14)	9 / 16	0.33 / 0.39	3.96 / 4.57	0.22 / 0.21	0.54 / 0.35	0.28 / 0.29
Scafe (E)	Low	5.43	881894	5.028 / 5.028	99 / 118	5 (2)	23 (9)	9 / 12	0.35 / 0.36	3.84 / 4.36	0.2 / 0.22	0.59 / 0.56	0.29 / 0.3
Scafe (W)	None	8.33	533719.8	1.843 / 1.649	76 / 82	11 (2)	12 (6)	7 / 8	0.38 / 0.41	3.08 / 3.58	0.17 / 0.22	0.72 / 0.42	0.27 / 0.28
Seymour	None	3.44	2342245	3.267 / 3.022	106 / 123	8 (4)	17 (13)	15 / 16	0.39 / 0.41	3.72 / 4.5	0.19 / 0.22	0.59 / 0.4	0.28 / 0.28

Appendix 3.C Functional groups

Species within each functional group, status (native: N or non-indigenous: NIS), description of the functional group, total number of species over all sites found in that functional group, percentage of total species that were NIS, and response diversity of the functional group over all species. Groups with ≥75% NIS were considered non-indigenous functional groups for the purposes of this study. They are at the bottom of the table in grey.

Genus	**Species**	**Status**	**Notes**	**Richness**	**NIS Percent**	**RDiv**
Abies	*grandis*	N	Large, slow growing, native trees.			
Arbutus	*menziesii*	N				
Picea	*sitchensis*	N				
Pinus	*contorta*	N				
Pseudotsuga	*menziesii*	N				
Quercus	*garryana*	N				
Taxus	*brevifolia*	N				
Thuja	*plicata*	N		8	0%	0.23
Acer	*macrophyllum*	N	Early blooming, woody, phanerophytes			
Ceanothus	*sanguineus*	N				
Gaultheria	*shallon*	N				
Lonicera	*hispidula*	N				
Oemleria	*cerasiformis*	N				
Paxistima	*myrsinites*	N				
Rubus	*parviflorus*	N				
Sorbus	*sitchensis*	NIS		8	13%	0.18
Achillea	*millefolium*	NIS	Early blooming, hemicryptophyte herbs, with moderate to low palatability, and defensive traits			
Alliaria	*petiolata*	NIS				
Angelica	*genuflexa*	N				
Anthoxanthum	*odoratum*	NIS				
Cirsium	*brevistylum*	N				
Conium	*maculatum*	NIS				
Digitalis	*purpurea*	NIS				
Elymus	*elymoides*	N				
Holcus	*lanatus*	NIS				
Stellaria	*media*	NIS				
Tanacetum	*parthenium*	NIS				
Veratrum	*viride*	N		12	67%	0.3
Achnatherum	*lemmonii*	N	Hemicryptophyte rosettes with moderate palatability			
Crepis	*capillaris*	NIS				
Dodecatheon	*pulchellum*	N				
Goodyera	*oblongifolia*	N				
Hieracium	*albiflorum*	N				
Hypochaeris	*radicata*	NIS				
Koeleria	*macrantha*	NIS				
Piperia	*unalascensis*	N				
Plantago	*lanceolata*	NIS				
Platanthera	*aquilonis*	N		10	40%	0.23
Agoseris	*grandiflora*	N	Geophyte or hemicryptophyte, polycarpic herbs rosettes,			
Bellis	*perennis*	NIS				
Iris	*germanica*	NIS		9	45%	0.23

Muscari	*armeniacum*	NIS	with low to medium palatability, and a moderate growth rate			
Olsynium	*douglasii*	N				
Plantago	*major*	NIS				
Triteleia	*hyacinthina*	N				
Woodsia	*scopulina*	N				
Zigadenus	*veneosus*	N				
Agrostis	*scabra*	N	Rapid growing, geophyte or hemicryptophyte, polycarpic herbs			
Anisocarpus	*madioides*	N				
Arabis	*nutalli*	N				
Brodiaea	*coronaria*	N				
Callitriche	*heterophylla*	N				
Cardamine	*nuttallii*	N				
Carex	*hoodii*	N				
Cerastium	*arvense*	N				
Clinopodium	*douglasii*	N				
Elymus	*glaucus*	N				
Epilobium	*ciliatum*	N				
Eriophyllum	*lanatum*	N				
Galium	*triflorum*	N				
Grindelia	*integrifolia/hirsuta/stricta*	N				
Juncus	*bufonius*	N				
Lepidium	*heterophyllum*	NIS				
Lomatium	*dissectum*	N				
Luzula	*multiflora*	NIS				
Luzula	*subsessilis*	N				
Lychnis	*coronaria*	NIS				
Moehringia	*macrophylla*	N				
Potentilla	*recta*	NIS				
Sanicula	*bipinnatifida*	N				
Taraxacum	*officinale*	NIS				
Trientalis	*borealis*	N				
Veronica	*filiformis*	NIS		26	23%	0.23
Aira	*caryophyllea*	NIS	Early blooming, smaller, extra stemmed, annual herbs, with a short growing season, and a moderate to rapid growth rate			
Aira	*praecox*	NIS				
Arenaria	*serpyllifolia*	NIS				
Bromus	*sitchensis*	N				
Bromus	*sterilis*	NIS				
Clarkia	*amoena*	N				
Collinsia	*parviflora*	N				
Cynosurus	*echinatus*	NIS				
Epilobium	*foliosum*	N				
Eshscholzia	*californica*	NIS				
Juncus	*tenuis*	N				
Linanthus	*bicolor*	N				
Lunaria	*annua*	NIS				
Madia	*sativa*	NIS				
Mimulus	*alsinoides*	N				
Minuartia	*tenella*	N				
Myosotis	*discolor*	NIS				
Nemophila	*parviflora*	N				
Parentucellia	*viscosa*	NIS				
Plagiobothrys	*scouleri*	N		28	54%	0.25

Poa	*annua*	NIS				
Polypogon	*monspeliensis*	NIS				
Rhinanthus	*minor*	N				
Sagina	*decumbens*	N				
Sherardia	*arvensis*	NIS				
Silene	*gallica*	NIS				
Thlaspi	*arvense*	NIS				
Triphysaria	*pusilla*	N				
Allium	*acuminatum*	N	Fast growing, spring blooming, geophyte, polycarpic herbs, rosettes, with short growing seasons, and defensive characteristics			
Allium	*amplectans*	N				
Allium	*cernuum*	N				
Allium	*vineale*	NIS				
Hyacinthoides	*hispanica*	NIS				
Narcissus	*pseudonarcissus*	NIS				
Rumex	*acetosella*	NIS		7	57%	0.24
Amelanchier	*alnifolia*	N	Geophyte or phanerophyte, woody shrubs, with a moderate growth rate			
Arctostaphylos	*columbiana*	N				
Holodiscus	*discolor*	N				
Ligustrum	*vulgare*	NIS				
Lonicera	*ciliosa*	N				
Lonicera	*involucrata*	N				
Philadelphus	*lewisii*	N				
Ribes	*sanguineum*	N				
Sambucus	*racemosa*	N				
Spiraea	*douglasii*	N				
Syringa	*vulgaris*	NIS		11	18%	0.19
Arabis	*glabra*	NIS	Smaller, fast growing, hemicryptophytes			
Barbarea	*orthoceras*	N				
Bromus	*carinatus*	N				
Cerastium	*fontanum*	NIS				
Daucus	*carota*	N				
Lactuca	*muralis*	NIS				
Lathyrus	*nevadensis*	N				
Ranunculus	*occidentalis*	NIS				
Spergularia	*rubra*	NIS				
Spiranthes	*romanzoffiana*	N				
Tragopogon	*porrifolius*	NIS		11	55%	0.22
Asplenium	*viride*	NIS	Early blooming, evergreen, polycarpic herbs with lower palatability			
Cryptogramma	*acrostichoides*	N				
Heuchera	*micrantha*	N				
Lycopodium	*clavatum*	N				
Pentagramma	*triangularis*	N				
Polystichum	*imbricans*	N				
Polystichum	*lonchitis*	N				
Sedum	*album*	NIS				
Sedum	*reflexum*	NIS				
Sedum	*spathulifolium*	N				
Selaginella	*wallacei*	N		11	27%	0.21
Aster	*curtus*	N	Early blooming, hemicryptophyte polycarpic herbs, with a slow growth rate			
Cichorium	*intybus*	NIS				
Foeniculum	*vulgare*	NIS				
Hesperis	*matronalis*	N		7	29%	0.19

Lomatium	*nudicaule*	N				
Mimulus	*guttatus*	N				
Prunella	*vulgaris*	N				
Avena	*fatua*	NIS	Highly palatable annuals with a moderately long growth season and a rapid growth rate			
Bromus	*hordeaceus*	NIS				
Centaurea	*cyanus*	NIS				
Erodium	*cicutarium*	NIS				
Lotus	*micranthus*	N				
Montia	*dichotoma*	N				
Plectritis	*congesta*	N				
Valerianella	*locusta*	NIS		8	63%	0.19
Brassica	*juncea*	NIS	Fast growing, annuals, with medium palatability			
Bromus	*rigidus*	NIS				
Castilleja	*attenuata*	N				
Epilobium	*minutum*	N				
Geranium	*dissectum*	NIS				
Geranium	*molle*	NIS				
Geranium	*robertianum*	NIS				
Hordeum	*murinum*	NIS				
Lamium	*amplexicaule*	NIS				
Lamium	*purpureum*	NIS				
Lapsana	*communis*	NIS				
Matricaria	*discoidea*	N				
Moenchia	*erecta*	NIS				
Montia	*fontana*	N				
Plectritis	*macrocera*	N				
Sisymbrium	*officinale*	NIS				
Torilis	*japonica*	NIS				
Vulpia	*bromoides*	NIS				
Vulpia	*myuros*	NIS		19	74%	0.2
Brassica	*kaber*	NIS	Annuals, with medium to low palatability, and defensive characteristics.			
Calandrinia	*ciliata*	N				
Capsella	*bursa-pastoris*	NIS				
Lupinus	*bicolor*	N				
Lupinus	*polycarpus*	N				
Navarretia	*squarrosa*	N				
Senecio	*vulgaris*	NIS				
Sonchus	*asper*	NIS				
Sonchus	*oleraceus*	NIS		9	56%	0.21
Calypso	*bulbosa*	N	Slower growing, short seasoned, geophytes			
Camassia	*leichtlinii*	N				
Camassia	*quamash*	N				
Cardamine	*oligosperma*	N				
Corallorhiza	*striata*	N				
Crocus	*longiflorus*	NIS				
Dodecatheon	*hendersonii*	N				
Erythronium	*oregonum*	N				
Lilium	*columbianum*	N				
Lithophragma	*parviflorum*	N				
Monotropa	*uniflora*	N				
Orobanche	*uniflora*	N				
Perideridia	*gairdneri*	N		16	13%	0.22

Phalaris	*arundinacea*	NIS				
Pteridium	*aquilinum*	N				
Triteleia	*howellii*	N				
Carex	*inops*	N	Highly palatable, early blooming, geophyte polycarpic herbs, with a short growing season			
Elymus	*repens*	NIS				
Fritilaria	*affinis*	N				
Lomatium	*utriculatum*	N				
Poa	*compressa*	NIS				
Poa	*pratensis*	NIS		6	50%	0.25
Claytonia	*exigua*	N	Rapid growing, annuals, with medium or low palatability			
Daucus	*pusillus*	N				
Draba	*verna*	NIS				
Galium	*aparine*	NIS				
Hypochaeris	*glabra*	NIS				
Plantago	*elongata*	N		6	50%	0.24
Crataegus	*douglasii*	N	Spring blooming, woody perennials, with moderate to fast growth rate, and short growth season			
Crataegus	*monogyna*	NIS				
Laburnum	*anagyroides*	NIS				
Malus	*fusca*	N				
Prunus	*emarginata*	N				
Rosa	*gymnocarpa*	N				
Rosa	*nutkana*	N				
Rubus	*ursinus*	N				
Symphoricarpos	*albus*	N		9	22%	0.2
Cynosurus	*cristatus*	NIS	Highly palatable, hemicryptophyte herbs, with moderate to fast growth rate, and medium to high palatability			
Dactylis	*glomerata*	NIS				
Danthonia	*californica*	N				
Festuca	*occidentalis*	N				
Festuca	*rubra*	N				
Luzula	*comosa*	N				
Malva	*sylvestris*	NIS				
Osmorhiza	*berteroi*	N				
Poa	*bulbosa*	NIS				
Poa	*secunda*	N				
Trifolium	*repens*	NIS		11	45%	0.24
Cystopteris	*fragilis*	N	Low palatable, geo/hemicryptophyte herbs, with a spring bloom period			
Lamiastrum	*galeobdolon*	NIS				
Melica	*harfordii*	N				
Melica	*subulata*	N				
Sanicula	*crassicaulis*	N				
Sanicula	*graveolens*	N				
Saxifraga	*caespitosa*	N				
Saxifraga	*rufidula*	N				
Saxifrage	*integrifolia*	N		9	11%	0.2
Delphinium	*menziesii*	N	Fast growing geo/hemicryptophytes			
Epilobium	*angustifolium*	N				
Equisetum	*arvense*	N				
Lotus	*corniculatus*	NIS		4	25%	0.23
Medicago	*arabica*	NIS	Nitrogen fixing annuals			
Medicago	*lupulina*	NIS				
Trifolium	*dubium*	NIS				
Trifolium	*microcephalum*	N		11	55%	0.18

Trifolium	*microdon*	N				
Trifolium	*oliganthum*	N				
Trifolium	*subterraneum*	NIS				
Trifolium	*variegatum*	N				
Trifolium	*willdenovii*	N				
Vicia	*hirsuta*	NIS				
Vicia	*sativa*	NIS				
Leucanthemum	*vulgare*	NIS	Moderate to slow growing, medium to low palatability ELR polycarpic herbs with a short growing season			
Maianthemum	*racemosum*	N				
Maianthemum	*stellatum*	N				
Montia	*parvifolia*	N				
Polypodium	*glycyrrhiza*	N				
Viola	*praemorsa*	N		6	17%	0.26
Arctostaphylos	*uva-ursi*	N	Native woody evergreens with defensive characteristics			
Mahonia	*aquifolium*	N				
Mahonia	*nervosa*	N		3	0%	0.2
Lathyrus	*latifolius*	NIS	Nitrogen fixing perennials			
Trifolium	*pratense*	NIS				
Vicia	*americana*	N				
Vicia	*cracca*	NIS		4	75%	0.22
Agrostis	*capillaris*	NIS	Highly palatable, early blooming, hemicryptophyte polycarpic herbs, with moderate to fast growth rates, and short growth season			
Arrhenatherum	*elatius*	NIS				
Fragaria	*vesca*	NIS				
Fragaria	*virginiana*	N				
Phleum	*pratense*	NIS		5	80%	0.24
Anthriscus	*caucalis*	NIS	Smaller, late blooming, annuals, with two growth seasons			
Aphanes	*arvensis*	NIS				
Cardamine	*hirsuta*	NIS				
Cerastium	*glomeratum*	NIS				
Claytonia	*perfoliata*	N				
Teesdalia	*nudicaulis*	NIS				
Veronica	*arvensis*	NIS				
Agrostis	*stolonifera*	NIS		8	75%	0.24
Convolvulus	*arvensis*	NIS	Medium palatable, early blooming, geo/hemicryptophyte herbs, with a rapid growth rate, and short growth season			
Convolvulus	*sepium*	NIS				
Lolium	*perenne*	NIS				
Rumex	*aquaticus*	NIS				
Rumex	*crispus*	NIS				
Cirsium	*arvense*	NIS		6	100%	0.23
Cirsium	*vulgare*	NIS	Invasive perennials with defensive characteristics			
Hedera	*helix*	NIS				
Hypericum	*perforatum*	NIS				
Ranunculus	*repens*	NIS				
Senecio	*jacobaea*	NIS				
Sonchus	*arvensis*	NIS		7	100%	0.29
Cytisus	*scoparius*	NIS	Invasive woody perennials with defensive characteristics			0.25
Daphne	*laureola*	NIS				
Ilex	*aquifolium*	NIS				
Rubus	*discolor*	NIS		7	100%	

Rubus	*laciniatus*	NIS
Ulex	*europaeus*	NIS
Vinca	*major*	NIS

Appendix 4.A: Land-use datasets and descriptions

List of datasets and details of use. The 'Status' column details the currency of the information: ongoing datasets are maintained on a daily, weekly, monthly, or quarterly basis; other datasets were compiled and uploaded a single time in the year listed. The last two columns detail which attribute we used to determine the land use properties of each shape where some of the data needed was irrelevant to our interests. The actual attribute we used and all categories within that attribute are listed in the 'Attributes' column, while the subset of categories we chose to use in the analysis are listed in the 'Subset' column. For example, the Developed Mineral Occurrence shapefile contained data on whether the mineral had been or is currently being actively extracted. We discarded all points that had not been developed and analyzed only those points that had or are under current development. Data came as polygons and lines. We analyzed polygons as provided, and we transformed all lines into 250-m-wide polygons to match raster cell size.

Data	Map file	Source	Description	Year	Shape	Attribute	Subset
Land classification	GeoBC: BTM_PLU_V1	BC Ministry of Environment, Lands, and Parks	Land use polygons as determined by a combination of analytic techniques, mostly using Landsat 5 image mosaics	1992	polygon	PLU_LABEL: Agriculture; Residential Agriculture Mixes; Alpine; Subalpine Avalanche Chutes; Barren Surfaces; Recently Burned; Estuaries; Old Forest; Young Forest; Glaciers and Snow; Recently Logged; Selectively Logged; Mining; Rangelands; Recreation Activities; Shrubs; Urban; Wetlands; Fresh Water; Salt Water	Conservation interests:Alpine; Subalpine Avalanche Chutes; Barren Surfaces; Old Forest; Young Forest (includes Recently Burned, Recently Logged, and Selectively Logged); Glaciers and Snow; Shrubs; Wetlands; Fresh Water Impact interests: Agriculture; Residential Agriculture Mixes; Urban; Mining; Rangelands
Conservancies	GeoBC: TA_CONSERVANCY_AREAS_SVW	BC Ministry of Forests, Lands, and Natural	Conservancy areas designated under the Park Act or by the	ongoing	polygon	N/A	None

		Resource Operations: Tantalis Spatial database	Protected Areas of British Columbia Act				
National parks	GeoBC: CLAB_NATPK	Canada Legal Surveys Division	Canada Lands which includes Indian Reserves, Cree-Naskapi Category 1A and 1A-N Lands, Yukon First Nations Settlement Lands, Kanesatake Mohawk Interim Land Base, National Parks, National Park Reserves, National Marine Conservation Areas and Aboriginal Land Claims Settlement Areas	2005	polygon	N/A	None
Provincial parks	GeoBC: TA_PARK_ECORES_PA_SVW	BC Ministry of Forests, Lands, and Natural Resource Operations: Tantalis Spatial database	BC Parks, Ecological Reserves, and Protected Areas	ongoing	polygon	N/A	None
Wildlife management areas	GeoBC: TA_WILDLIFE_MGMT_AREAS_SVW	BC Ministry of Forests, Lands, and Natural Resource Operations: Tantalis Spatial database	Areas for which administration and control has been transferred to the Ministry of Environment (MoE) via the Land Act due to the significance of their wildlife/fish values and designated as Wildlife Management Areas under the Wildlife Act	ongoing	polygon	N/A	None

Forest tenure tracks	GeoBC:FTN_C_B_PL	BC Forest Tenures Section	Operational activities for cutblocks contained within harvesting authorities	ongoing	polygon	LIFE_ST_CD: Retired; Pending; Active	Impact interests: Active; Retired
Vegetation age	GeoBC: VEG_COMP_LYR_R1_POLY	BC Ministry of Forests, Lands and Natural Resource Operations - Forest Analysis and Inventory	Geospatial forest inventory dataset updated for depletions, such as harvesting, and projected annually for growth. Sample attributes in this dataset include: age, species, volume, height. The Vegetation Resources Inventory (VRI) determines both where a resource is located and how much of a given vegetation resource (for example, timber or coarse woody debris) is within an inventory unit.	ongoing	polygon	N/A	0 - 10 years old; 10 - 60 years old; 60 - 120 years old
Agricultural Land Reserve locations	GeoBC: TSLRPLS_polygon	BC Land Reserve Commission	Boundaries of designated ALR locations	ongoing	polygon	N/A	None
BC roads	GeoBC: DGTL ROAD ATLAS DPAR SP	BC Digital Road Atlas program	Partial information about roads in British Columbia, restricted to publically available data	ongoing	line	N/A	None
Developed mineral occurrence	GeoBC: MINFILE	BC Geological Survey Branch	All bodies of rock containing, or thought to contain, ore minerals or potential ore minerals; point depicts most physical reference point to the mineralization	ongoing	point	STAT_DESC: Anamoly; Developed Prospect; Past Producer; Producer; Prospect; Showing	Impact interests: Developed Prospect; Past Producer; Producer

Oil and gas: facility sites	GeoBC: OG_FAC_ST	BC Oil and Gas Commission	Facilities containing any grouping of equipment where water and hydrocarbon liquids are processed, measured, upgraded (i.e., remove impurities or other constituents to meet contact specifications), or stored prior to the point of custody transfer; or where natural gas is processed, measured, upgraded, or stored prior to entering the natural gas transmission and storage source category		polygon	N/A	None
Oil and gas: seismic lines	GeoBC: OG_GEOPHY_ line	BC Oil and Gas Commission	Geophysical programs study the physical characteristics and properties of subsurface formations relating to oil and gas deposits, derived artificially by explosives or other means to map subsurface structure. Spatial data is collected through the Oil and Gas Commission's electronic Petroleum Application Submission System (ePASS). ePass submissions for geophysical applications became mandatory October 30, 2006 and so this dataset contains spatial data for applications submitted on or after this date. All approved	ongoing	line	N/A	None

			final plan geophysical applications with are included.				
Oil and gas: waste disposal locations	GeoBC: OG_WASTE_DISPOSAL_SITES_SP	BC Oil and Gas Commission	Drilling waste disposal sites from upstream oil and gas operations. Drilling waste disposal areas include portions of the wellsite or remote sump where drilling wastes have been buried, spread on land, or mixed into soil	ongoing	polygon	N/A	None
Oil and gas: well sites	GeoBC: OG_WELL_SITES_PUB_SP	BC Oil and Gas Commission	The location of clearing or well pads	ongoing	polygon	N/A	None
Oil and gas: pipelines	GeoBC: OG_PIPELINE_RW_PUB_SP	BC Oil and Gas Commission	Area over which a right-of-way exists for the purposes of constructing, maintaining or decommissioning a pipeline	ongoing	polygon	N/A	None
Oil and gas: access roads	GeoBC: OG_PETRLM_ACCESS_ROADS_PUB_SP	BC Oil and Gas Commission	Location data for all road applications received by the Commission, including access roads for wellsites and prescribed roads, received on or after October 30, 2006.	ongoing	line	N/A	None
Oil and gas: development roads	GeoBC: OG_DEVRD	BC Oil and Gas Commission	Location data for all petroleum development road applications received by the Commission, including access roads for wellsites and prescribed roads, received on or after October 30, 2006.	ongoing	line	N/A	None

Oil and gas: sump locations	GeoBC: OG_SUMP_LC	BC Oil and Gas Commission	Locations of sump sites used for drilling waste disposal	ongoing	point	N/A	None

Appendix 4.B: Species range estimates

British Columbia has 32 native terrestrial carnivore and ungulate species (Eder & Pattie 2001). We did not consider wildlife that are known to respond neutrally or positively to land-use (cougars: Carter & Linnell 2016; e.g. white-tailed deer and coyote: Toews 2016), mimicking management prioritizations that consider sensitive species first. Additionally, we were not able to consider species with too little data to confirm range loss despite recorded declines in abundance. Some species such as Roosevelt elk (*Cervus canadensis roosevelti*) and badger (*Taxidea taxus*) have limited distribution in BC but historic ranges are poorly understood. For others (e.g. small mustelids: Zielinski et al. 2004; and wolverines: Lofroth & Krebs 2007), sensitivity to human development has been documented and range contractions are probable (Stewart et al. 2016) but cannot be mapped with confidence. Their exclusion is an unfortunate, but unavoidable, result of the difficulties in understanding the ecology and distribution of cryptic species.

Historic ranges were based on The Mammals of North America (Hall & Kelson 1959) and captured species' distributions before Euro-American settlement as per field sightings from the 18th and 19th centuries. Current ranges were based on The Smithsonian Book of North American Mammals (Wilson & Ruff 1999) and Mammals of North America (Kays & Wilson 2009) and updated with information from the BC Ministry of the Environment. Ministry data are a combination of habitat information, field survey data, recent harvest data, and expert opinion.

After editing, we were able to check the distributions for a subset of species through personal communication with experts at the BC Ministry of Forests, Lands, and Natural Resources. Of the seven species selected, we conferred with experts on current distributions of caribou, mountain goat, and grizzly bears. For the remaining four species, we matched our distribution maps with the last status reports from the BC Ministry of Forests, Lands, and Natural Resources (bighorn sheep and elk: Blood 2000a, b; fisher: Weir 2003; wolves: Ministry of Forests, Lands and Natural Resource Operations 2014).