CHANGES IN TROPHIC STRUCTURE ALONG A GRADIENT OF WATER AVAILABILITY IN TEMPERATE MONTANE GRASSLANDS

by

William Laughton Harrower

Dipl. Environmental Technology Camosun College, 1998
B.Sc. (Honors) The University of British Columbia, 2002
M.Sc. The University of Victoria, 2007

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF

THE REQUIREMENTS FOR THE DEGREE OF

Doctor of Philosophy

in

THE FACULTY OF GRADUATE AND POSTDOCTORAL STUDIES

(Botany)

THE UNIVERSITY OF BRITISH COLUMBIA

(Vancouver)

February 2017

Abstract

Predators and plants are inextricably linked by the flow of energy in ecosystems. However, we still lack good descriptions of how predators affect the diversity, function, and stability of ecosystems under different environmental conditions. If water availability to plants modifies the interactions between predators and plants, and changes in these species interactions lead to a modification of trophic structure, then the direction and strength of trophic cascades must depend on the availability of water to plants. I use the unifying concept of the trophic cascade and an underlying gradient of water availability to investigate how species interactions in a montane grassland influence the diversity and function of these ecosystems. Firstly, I examine the distribution, abundance, and community composition of grassland songbirds. I show that as water becomes more abundant, the number of species increases more slowly than the number of songbird individuals. Second, I manipulate the presence of vertebrate predators along the gradient. I found that changes in the abundance of both songbirds, small mammals and their prey alters feeding behavior and restructures communities. These changes in intraguild predation work in conjunction with the metabolic demands of consumers to determine trophic structure and alter the strength of the trophic cascade in response to water availability. Finally, I show that predators mediate apparent competition between herbivore and detritivore food chains. In the montane grassland I studied, an apparent trophic cascade becomes established as detritus food chains emerge with increasing water availability. I show that the reversal of trophic control typical of ecosystems with allochthonous external subsidies does not occur with autochthonous detritus subsidies in my system. The direction of trophic control in the grazing food chain remains bottom-up, but the detritus food chain is instead controlled by generalist predators. These interactions between predators and plants regulate the diversity of plants and arthropod functional groups, and affect ecosystem functions such as plant biomass production and decomposition. My results show that as water availability to plants increases in semi-arid and temperate grasslands, food webs become shorter, broader, more reticulate, and are more resistant to the effect of species losses and drought.

Preface

All chapters were written by me with input by Roy Turkington and Diane Srivastava. The identification and design of the initial experiments was the result of discussions between Lauchlan Fraser, Roy Turkington, Cameron Carlyle, and myself. I performed the experiments, conducted the research, collected the data, organized the database, supervised research staff, designed and performed the analysis and wrote the manuscripts.

I envisioned, designed, and presented the ideas and structure of the dissertation. Diane Srivastava provided extensive and valuable input into the analysis, writing, and presentation for the three main chapters. Charlie Krebs provided valuable input to all stages of analysis and writing. Roy Turkington provided input on the first drafts of the manuscripts. To a large extent this work was the result of lectures and conversations with Diane Srivastava, Roy Turkington, Charlie Krebs, and Tony Sinclair. My supervisory committee Roy Turkington, Lauchlan Fraser, Gary Bradfield and Diane Srivastava provided editorial input. Jake Goheen, John Shurin, and Mark Vellend were all members of the supervisory committee in the early stages. Cindy McCallum assisted in the design and implementation of avian surveys and obtained some instrumental capture permits. She taught me to hold little birds. Cindy provided editorial comments on Chapter 2.

Permits for live trapping and handling wildlife were provided by BC Government (KA09-55644), Park Use permits (102724) were provided by BC Parks as part of Lauchlan Fraser's parallel research program. Songbird capture permits were provided by Environment Canada; Animal Capture permits were provided and overseen by UBC (A09-0434). Both William Harrower (10758 A) and Cindy McCallum (10277 H) held sub-banding permits from the Environment Canada Banding office under the primary permit (BC-11-0045) held by Roy Turkington and overseen by the University of Alberta.

Table of contents

List of tables

List of figures

List of abbreviations

a.s.l. = above sea level

BC = British Columbia

NDVI = Normalized Difference Vegetation Index

NMDS = Non-metric Multidimensional Scaling

Glossary

Abiotic resources: a resource is any substance or object that is required to meet the basic needs of growth, maintenance and reproduction of an organism. It is any substance over which an organism can compete. Abiotic resources are those not composed of organic materials such as water, nutrients, carbon dioxide, and light. Resources can be consumed.

Allochthonous subsidy: not formed in situ. A subsidy of net primary productivity that came from photosynthesis that occurred outside the ecosystem. Primary production that comprises this subsidy was supported by abiotic resources that are different from those of the ecosystem receiving the subsidy.

Alpha (α) diversity: number of species in a defined area and the distribution of abundance and biomass between species. Includes the number of species (richness) and the degree of similarity in species abundance (evenness).

Apparent competition: negative correlation between the abundance of two species mediated by shared predator and unrelated to resource abundances

Apparent trophic cascade: negative correlation between the abundance of two consumers in a food web mediated by a shared predator and affecting the abundance, diversity, or function of lower trophic levels. The negative interaction between consumers with a shared generalist predator results in top-down control in one path to plants and bottom-up control in the other path to plants.

Autochthonous subsidy: formed in the place it is found. A subsidy of net primary productivity that arose from photosynthesis that occurred in the same ecosystem that receives the subsidy, and that was supported by abiotic resources such as water, nutrients, etc. that are the same as those that support the ecosystems that receives the subsidy.

Beta (β) diversity: spatial or temporal turnover of species from one place to another or one time to another, turnover can include both co-occurrence of species or shared absence (beta = gamma/alpha).

Biodiversity: the variety and variability of life on earth; all of the genes species and ecosystems within a region.

Bottom-up: see resource control

Community structure: the number, identity and abundance occupying a particular area.

Connection web: a representation of the feeding relationships between species in an ecosystem where connections between species are represented with little or no regard to the flow of energy through ecosystems.

Consumer control: control of ecosystems occurs when predators or herbivores determine the distribution, abundance, and community composition of species occupying lower trophic levels in the ecosystem. Also called top-down control.

Detritivore: heterotrophic organisms that feed primarily on dead organisms. Detritivores mostly feed on decomposing plant material but also animal parts and feces.

Disturbance: a temporary event that changes the distribution and abundance of organisms in an ecosystem. Disturbances can be abiotic (e.g., fire, flood, drought) or biotic (e.g., herbivore, invasion or loss of key species).

Ecosystem function: interaction and distribution of the structural components of an ecosystem. Components include the physical, (e.g., rocks) chemical (e.g., nitrogen), and biological processes (e.g., predation) that contribute to the flow of energy, cycling of nutrients and regulation of populations in ecosystems.

Ecosystem service: benefits received by humans from ecosystems; supporting, provisioning, regulating and cultural. Examples include: food production, pollination, clean water, and flood control.

Energy channel or pathway: a component of a food web that contains a subset of species whose feeding relationships derive energy from a single basal resource. Can be top-down or bottom-up.

Energy web: a map of species interactions (e.g., food web) depicting the feeding relationships between species as the directional flow of energy through the ecosystems from basal resources to upper trophic levels. Arrows generally point from plants to top predators.

Food web: a map depicting feeding relationships between species in an ecosystem (i.e., an antagonistic network).

Functional group: a subset of organisms in an ecosystem based on some characteristic that describes their similar effect on major ecosystem processes or similar response to environmental conditions.

Gamma diversity: the number and evenness of species in a community, a community is defined arbitrarily but is generally all organisms inhabiting a particular area, interacting (either directly or indirectly), and sharing a common resource base.

Interaction strength: a measure of how much a predator alters population size, biomass, or production of its prey. The link between species sharing some sort connection (e.g., facilitation, mutualism, predation, competition), which can be direct, or indirect (through an intermediate species).

Interaction web: a representation of the feeding relationships between species in an ecosystem where connections between species represent the direction and sometimes magnitude of the largest impact. For example, in a top-down ecosystems arrows point from predators to plants.

Intraguild predation: a special case of omnivory where the consumer feeds on potential competitors. Thus the intraguild predator feeds on both intraguild prey and a shared common resource.

Mesopredator: a secondary consumer when a tertiary consumer is present in an ecosystem. A particular trophic level whose presence extends the length of typical food webs and produces a four-level trophic cascade.

Omnivory: when consumers feed on organisms from multiple trophic levels.

Primary Consumer: heterotrophic organisms that feed primarily on autotrophs. Herbivore.

Primary producer (autotrophs): organisms that convert energy from the sun and inorganic compounds to organic molecules through photosynthesis. Form the base of the food web, but are often limited by the availability or inorganic compounds or abiotic resources. Plant.

Primary productivity: rate at which energy from the sun in converted to organic molecules by plants using photosynthesis.

Primary production: the mass of organic material that plants produce over a given period of time. Can be gross primary production which is all biomass produced, or net primary production which is gross primary production minus the energy consumed by plants during respiration and thus unavailable to produce biomass. Standing stock.

Resource control: the nutrient supply to the primary producers that ultimately controls the distribution, abundance, and community composition of species in the ecosystem. Also called bottom-up control.

Secondary Consumer: heterotrophic organism that feeds primary on herbivores. Predator or can be a mesopredator if a tertiary consumer is present.

Semi-arid climate (steppe): an ecosystem that receives precipitation below the potential evapotranspiration. Often dependent on temperature. Group B as per the Koppen-Geiger climate classification (Kottek et al. 2006).

Stability: measure of the ability and/or speed with which a food web regains its structure following a disturbance (resilience) or a measure of how strongly an ecosystem resists change following a disturbance (resistance). Can be measured by a change in biomass, change in species distribution, or change in rates of ecological processes.

Temperate climate: an ecosystem with cool winters and warm summers. Can be maritime or continental and generally occurs between tropics and the poles.

Tertiary consumer: heterotrophic organism that feeds primary on other predators. Top-predator.

Top-down: see consumer control

Top-predator (apex predator): a species in an ecosystem that is not eaten by any other consumer while it is alive. As a result, its distribution and abundance are controlled by its prey.

Trophic cascade: the pattern of change in each successive trophic level that occurs when the feeding links between a top predator and prey are severed. Results from the indirect effect of predators on plants that occurs through intermediate consumers.

Trophic position: location an organism occupies in a food web based on its feeding behavior. Is defined as the number of feeding links an organism is away for the primary producer. For example, producers, consumers, and detritivores. Previously categorical but not typically defined by stable isotope analysis. Food chain length.

Trophic structure: the distribution of species as biomass or abundance within an ecosystem. Could include number of species in each functional group (predators, herbivores, legumes, grasses) at particular trophic levels, or the number of species occupying each trophic level. Has been described as a pyramid of biomass or a pyramid of abundance, suggesting there is always a greater abundance of producers than consumers.

Acknowledgements

Departure, oil paints on canvas, 149 cm x 149 cm,

Chapter 1: Introduction

Predation is a fundamental process structuring ecological systems. Its effects can cascade through ecosystems structuring food webs, regulating diversity, and controlling the stability of populations and the function of ecosystems (McCann 2000, Duffy 2002, Cardinale et al. 2006, 2012, Schmitz 2008b, Estes et al. 2011, Thompson et al. 2012, Sergio et al. 2014). The cascading effects of predators through ecosystems is governed by the amount of abiotic resources available to plants (Krebs et al. 1995, Shurin et al. 2002, Borer et al. 2005, Letnic and Dickman 2006, Gruner et al. 2008, Turkington 2009, Hopcraft et al. 2010, Piovia-Scott et al. 2011). These abiotic resources provide the foundation for plant productivity and govern the amount of energy entering the base of the food web. Thus, although they normally do not directly interact, predators and plants are inextricably linked by the flow of energy through ecosystems. These links between predators and plants occur through a series of generally complicated species interactions that ultimately structure communities. Community structure is usually defined by counting the number and type of species, determining the abundance of each species, or describing species geographic distributions (Krebs 2009). Ecologists typically examine community structure in only a single trophic level (Moore et al. 2004, Srivastava et al. 2009). Trophic means food or feeding, and a trophic level describes the level or position an organism occupies in the food chain. Although ecologists generally describe community structure at only one trophic level (e.g., plants), examining more than one level can provide new insights into both the structure and function of ecosystems (e.g., Sinclair et al., Fraser et al. 2015, Turkington and Harrower 2016).

Trophic structure derives from the feeding relationships between primary producers, herbivores, primary consumers, secondary consumers, tertiary consumers, and detritivores. Trophic structure helps determine the diversity of species, the function of ecosystems, how quickly ecosystems respond following disturbance (i.e., resilience), or how large a disturbance is needed to transform ecosystems (i.e., resistance). For example, a disturbance such as the extirpation or extinction of a top predator often has

profound effects on ecosystems. This type of disturbance is normally described as a strong trophic cascade (Schmitz et al. 2000, Shurin et al. 2002, Borer et al. 2005). Trophic structure is not static, and is dependent on the amount of abiotic resource available to primary producers (plants), the number and composition of species inhabiting the ecosystem, and behavior (particularly feeding behavior) of species. These processes dictate how energy moves through a community and ultimately how much biomass resides at each trophic level (Trebilco et al. 2013). Understanding how predation, and the resulting trophic structure of ecosystems, changes when different amounts of abiotic resources are available will help people respond when changes to our climate alter the ecosystems upon which we depend.

The central thesis of my dissertation is that the amount of abiotic resources available to plants modifies the interactions between predators and plants in such a way as to change trophic structure and thus alter diversity, function, and stability in ecosystems. I use the unifying concept of the trophic cascade to investigate the feeding relationships in temperate grassland ecosystems along a gradient of water availability to plants. Water is a key limiting resource in many semi-arid and temperate grassland ecosystems and large changes in its availability are predicted worldwide (Chase et al. 2000). My objective is to develop a better understanding of what structures communities and how predators and plants interact. I also hope my research helps people understand how changes in the trophic structure, and thus diversity, function, and stability, will be altered by changing climate conditions by providing one example in temperate grasslands. Worldwide, species that occupy higher trophic levels are disproportionately threatened with extinction (Estes et al. 2011, Sergio et al. 2014). Losing these and other species will undoubtedly affect ecosystems (Bruno and Cardinale 2008, Hooper et al. 2012). Changes in species interactions brought about by species losses will interact with the shifting effects of climate on resource availability. As ecologists we need to understand and explain this interaction better so that we can inform policies that will help people mitigate the negative and interacting effects of the biodiversity and climate crises.

In the temperate grasslands of western Canada, persistent and long-term drought threatens biodiversity and the provision of many ecosystem services provided to humans by ecosystems. Many grassland and insectivorous birds have declined in abundance by up to 50% since 1970 (North American Bird Conservation Initiative Canada. 2012, Davidson et al. 2015). One third of all semi-arid and grassland bird species are on the Environment and Climate Change Canada Watch List, and birds that overwinter in the Chihuahua region of northern Mexico, but breed in southern Canada and the north plains of the United States have seen declines in abundance of up to 70% since 1970 (North American Bird Conservation Initiative 2016). This includes the dominant grassland birds in this study. Persistent drought also restricts plant growth, impacts wildlife, and threatens forage availability to livestock (George et al. 1992, Milstead et al. 2007, Frank et al. 2014, Briske et al. 2015). In the montane grasslands of Montana changes in rainfall have led to a 50% reduction in the production of C_3 grasses (Brookshire and Weaver 2015). A collapse of the traditional ranching industry in the west would transform many human communities (Harrower 2016) and lead to the destruction of much of the remaining natural grasslands. Conversion of these lands would further reduce biodiversity, limit air and water filtering services, reduce carbon sequestration, and reduce the provision of food. Through time, humans have change political and social structures in response to both the heterogeneity and scarcity of water (Harrower 2008). How humans respond to water scarcity can produce tremendous social upheaval. Thus, solving fundamental ecological questions such as how predators and plants interact under different resource conditions have direct and tangible conservation and management applications for human societies (Angert et al. 2013). Only by understanding how ecosystems work can humans hope to adopt activities that mitigate the effects of rapidly changing resource availability.

1.1 Trophic cascades

Trophic cascades are particular cases of strong consumer control, whereby high-level predator effects propagate down the food web to lower trophic levels. A simple version of a trophic cascade was described

by Paine (1980) and since then the concept of a trophic cascade has become a key unifying concept linking community and ecosystem ecology. The trophic cascade concept typically describes a pattern of systematic changes in the biomass of organisms at different trophic levels that results from the addition or removal of a predator (Hairston et al. 1960). In the classic cascade model, when primary consumers are added or removed there can be predictable changes in the biomass of plants because changes in predator occurrence result in altered herbivore effects (Sinclair and Krebs 2000). If predators are removed from ecosystems with top-down control herbivores typically increase in abundance. More herbivores consume more plants and thus the amount of plant biomass declines (e.g., the green, brown, or black world hypothesis; see summary in Turkington 2009). It is these alternating changes in abundance cascading from declines in predators, to increases in herbivores, to declines in plants that typifies the pattern of a trophic cascade (Power 2000, Polis et al. 2000, Holt 2000).

The response of plants to the removal of top predators is dependent on the type of species in the community. For example, adding an additional consumer trophic level such as mesopredators can alter the response of plants to predator removals. Mesopredators are secondary consumers that are eaten by top predators (i.e., tertiary consumers). The presence of a mesopredator can dramatically alter trophic cascades (Prugh et al. 2009). When mesopredators are present, the alternating effects of predator removals on the abundance of each subsequent trophic level results in an increase in plant biomass. This is termed a four-level trophic cascade, as opposed to the classic three-level trophic cascade typified by predators, herbivores, and plants.

An additional way in which the type of species can alter cascades occurs when the diet of predators changes. Omnivory occurs when predators feed at more than one trophic level (Kratina et al. 2012). Intraguild predation is a specific case of omnivory where a top predator feeds its competitor (Polis and Holt 1992, Holt and Polis 1997). This creates a food web with an intraguild predator (i.e., top predator),

intraguild prey (i.e., mesopredator), a shared resource (i.e., herbivores or detritivores), and plants. Here, the response of plants to the removal of the intraguild predator will depend on the composition of the predator's diet. If the intraguild predator feeds mostly on herbivores, their removal would result in an increase in plant biomass. If the intraguild predator feeds mostly on intraguild prey their removal would result in a decrease in intraguild prey abundance. A third case could also occur where a balanced intraguild predator diet results in the limited response of plants to predator removals. Thus, omnivory can dampen trophic cascades (Borer et al. 2005, Finke and Denno 2005, Gruner et al. 2008).

The indirect effect of predator removals on plants can be seen in ways other than simple changes in the abundance of plants and herbivores (Polis et al. 2000). Until now I have described the classic example of a community-level cascade. A community-level cascade occurs when the distribution of abundance or biomass between trophic levels changes in response to predator removals. However, the presence of a predator can change the composition, diversity or behavior or herbivores and result in changes in the biomass, diversity, or composition of the producer community. This is a species-level cascade in which the presence of predators results in changes in diversity in the lower trophic levels. A third way that predators can exert control on communities occurs is by changing the function of ecosystems. There is growing recognition that predators can exert control on ecosystems by altering processes such as decomposition rates, nutrient storage (including carbon), primary productivity, and water cycling (Moore et al. 2005, Strickland et al. 2013, Leroux and Schmitz 2015). This ecosystem-level cascade would demonstrate altered ecosystem function with predator removal without necessarily showing obvious changes in the herbivore community. As ecologists, we are beginning to broaden our views and include not only measures of biomass, but also measures of diversity and ecosystem function when examining the cascading effects of predators (Dyer and Letourneau 2002, Moore et al. 2004, Duffy et al. 2007, Srivastava et al. 2009, Estes et al. 2011, Sergio et al. 2014).

Thus, predators can have large indirect effects on plants through a series of complex species interactions. These indirect effects are pervasive and can help regulate the diversity and function of ecosystems. We typically observe the indirect effect of predators on plants through disturbances or experimental manipulations. The extirpation of top predators or the experimental exclusion of species provides insight into how the myriad of interactions between predators and plants changes with the presence or absence of predators. However, a number of processes underlie the pattern of cascading changes with disturbances when we remove predators. In particular, altered plant productivity arising from changes in the availability of abiotic resources will alter food webs, thereby altering the role of predators (Hairston et al. 1960, Fretwell 1977, Oksanen et al. 1981, Menge and Sutherland 1987, Oksanen and Oksanen 2000). Temperature can also influence food webs, especially aquatic ones (Boyce et al. 2015). Thus, the indirect effects between predators and plants are not static and are often driven by the availability of abiotic resources to primary producers.

1.2   Gradients

I used an environmental gradient as a tool to better understand how changes in abiotic resources interact with predation to influence trophic structure. The use of environmental gradients has a long history in ecology (Whittaker 1956, Keddy 1991), and they have been used primarily to determine how the community structure of a single trophic level is altered by environmental conditions (Rahbek 2005, Colwell et al. 2008). More recently gradients have been used as a space-for-time substitute to test how climate change might influence the distribution of species (Moritz et al. 2008). Using spatial variability in natural ecosystems to understand ecological process is key tool for ecologists. Gradients can provide powerful tools to examine community and ecosystem responses to environmental change that have occurred on scales larger and longer than experiments can provide (Sundqvist et al. 2013). Gradients can provide a way of testing how biodiversity will response to changing climate conditions (Fukami and Wardle 2005, McCain and Colwell 2011). Although experiments along gradients can isolate the relative

roles of abiotic conditions and biotic interactions in structuring communities and ecosystems, few of these studies have been performed (Sundqvist et al. 2013).

I examined trophic structure along a single mountainside. This location is unique because it is one of the only places in western North America where there are large changes in the water availability to plants occurring over a short distance. Thus, nearly every species found at the bottom of the gradient also occurs at or can disperse to the top; however, the relative abundances of these species change dramatically. The differences in water availability are caused by the orographic or rain shadow effect of the Coast Mountains. Changes in the relative abundance of species are ultimately the result of differences in the availability of water to plants along the gradient, but the proximate causes are unknown. Thus, the gradient I examined had hot dry valley bottoms and wetter moist upper elevations. These rapid changes in water availability occur over such short distances (~10 km) I was able to examine how the differences in water availability to plants influenced the role of predation in structuring temperate grassland food webs with relatively consistent species pools (i.e., gamma diversity).

I use this gradient as an experimental treatment in two ways (Fukami and Wardle 2005). First, I use the gradient as a treatment to control water availability to plants. The use of the gradient in this way assumes that variables such as temperature, altitude, and plant communities that are confounded with the gradient in water availability are not strongly correlated with the role predation plays in establishing trophic structure. Thus, using this gradient allowed me to examine how a location that has developed a particular food web with a consistent level of water availability over time will respond to loss of predators. Second, I used the gradient as an indirect space-for-time substitution that has no relationship to the age of the ecosystem. This assumes that changes in water availability due to climate will alter temperate montane grasslands in the same way as changes in water availability due to elevation (Dunne et al. 2004).

Although factors such as temperature, altitude, soil type, etc. may influence the role above ground primary production and vertebrate predator removals, water is likely the largest determinant on above ground net primary productivity in the system I studied. Generally, temperate grassland above ground net primary productivity is often determined by water availability to plants (Sala et al. 1988, Lauenroth and Sala 1992, Knapp and Smith 2001, Knapp 2002, Frank 2007). Co-limitation can occur especially with temperature, CO2, or nitrogen (Reich et al. 2014); however, these effects often confounded with water as plants compensate by changing water use efficiency (the amount of water required to produce one unit of plant dry matter) or nutritional content. For example, high rainfall during cool moist seasons can lead to increase nitrogen limitation and reduce the influence of increased CO2 levels on above ground net primary productivity (Hovenden et al. 2014). Likewise, temperature can cause reductions in above ground net primary productivity, this happens only at high elevations and on gradients with large changes in temperature (Han et al. 2013). The gradient I work on is relatively short and low (~10km distance and 700m elevation; max elevation >1000m a.s.l) and thus the difference in the number of growing degree days between the top and bottom of the gradient is limited. In contrast, there are large differences in the amount annual precipitation. Thus, I estimate aboveground net primary productivity using remotely sensed images and calculating the Normalized Difference Vegetation Index (NDVI) and generally assume water availability to plants is the primary determinant of differenced in NDVI between different locations.

1.3   Resource subsidies

Similar to gradients, I used subsidies in resource abundance to isolate the effect of plant productivity on food web structure. Changes in resource abundance typically measured on gradients are examples of ecosystems at equilibrium where species and communities have had the time to adjust to the local conditions. In contrast, subsidies generally demonstrate how species interactions in food webs respond to short-term, immediate, or pulses in resource abundances. The term subsidy means assistance and it is typically used in terms of economic policies (e.g., a government subsidy). In ecological terms, a resource

subsidy adds energy in excess of what is normal for a particular ecosystem. This energy could be increased prey abundance for predators or increased plant biomass for herbivores. Both provide increased food that translates into greater consumer abundance. I am interested in two types of subsidies, allochthonous and autochthonous. Both types of subsides add plant primary productivity to the base of the food web and thus should increase productivity and diversity at all trophic levels.

Allochthonous resource subsidies arise from abiotic conditions different than those that occur in the ecosystem they subsidize. They are typified by cross-ecosystem inputs of primary production and can dramatically change food web dynamics (Polis et al. 1997a). When ecosystems rely exclusively on allochthonous inputs they are called donor-controlled ecosystems. Allochthonous inputs come from either the movement of productivity or from the movement of animals. For example, marine subsidies of island ecosystems changed trophic structure in Bahaman islands (Piovia-Scott et al. 2011, Wright et al. 2013). The subsidy was marine plants washed up on shore following hurricanes and other large storms. An example of allochthonous subsidies from animal movements comes from the migration of wildebeest in the semi-arid grasslands of the Serengeti. Wildebeest survive periods of resource shortage in the southern plains by moving to more productive grasslands further north (Fryxell et al. 1988). However, trophic structure of the southern plains benefits from plant production further north because migratory wildebeest are able to reach high abundance and support larger populations of large predators on the southern plain (Hopcraft et al. 2014). Southern and northern ecosystems have different levels of water availability. Thus, primary production from outside the ecosystem can have profound effects on trophic structure.

A second type of subsidy arises from the same abiotic resources that support the ecosystem it subsidizes. Autochthonous subsidies arise with slow consistent increases in primary production. These types of subsidies generally arise as limiting resources such as water or nitrogen increase in supply more slowly than allochthonous subsidies. Often ecologists are interested in the balances of allochthonous and

autochthonous inputs in freshwater streams and lakes (Allen et al. 2012, Bartels et al. 2012). The dichotomy between different types of subsidies helps freshwater ecologists determine if food webs are supported by their own primary production or rely on the donation of production from outside ecosystems. Autochthonous subsides effect food webs in complex ways that are not completely understood, but like allochthonous subsides do provide subsidies to higher trophic levels as more primary production becomes available. We must know how allochthonous or autochthonous subsides influence the abundance of different animals in upper trophic levels in order to determine the indirect interactions between predators and plants (Polis and Strong 1996).

In the case of my research, autochthonous inputs come from the slow and consistent increase in primary productivity resulting from incremental increase in water availability to plants. An analogy to autochthonous subsidies could be a space-for-time substitution on a gradient. In this case, an autochthonous subsidy would occur when moving incrementally up or down the mountain. In time, the analogous subsidy would be the consistent increase in water availability to plants from climate change such as (Brookshire and Weaver 2015). As a distinction, periodic events or pulses of resources arising from phenomenon such as El Nino Southern Oscillation and affect trophic structure (e.g., Polis et al. 1997b, Meserve et al. 2003, Stapp and Polis 2003, Letnic and Dickman 2006, Sinclair et al. 2013) would be considered allochthonous inputs. These periodic events may have different effects on food webs than the autochthonous subsides I examine, although seasonality in resource supply begins to bridge these boundaries as animals adapt to seasonal resource shortages (McMeans et al. 2015). Increases in growing season water availability to plants arising from increased spring rain or reduced winter snow melt would be considered autochthonous subsidies.

1.4   Dissertation overview

The primary objective of my research was to determine how predation, and subsequently trophic structure, was influenced by the availability of water to plants. The foundation of this research is one large observational data set and two experiments linked by common treatments. The dataset I collected and experiments I performed, all occurred in a montane gradient of water availability to plants in Lac du Bois Protected Grasslands near Kamloops British Columbia, Canada. The observational data set documented the abundance of songbird, small mammal, arthropod, and plants along the gradient. This data set was used to not only document 'typical' abundances of all these functional groups along the gradient, but also to examine how the abundance and community composition of predators changes along the gradient. In particular, the songbird monitoring component allowed me to understand how communities of songbird predators change in both abundance and type (Chapter 2). This knowledge formed the foundation from which I interpreted the experimental results.

The experimental data came from two experiments that each ran for four years. In the first experiment (Chapter 3) I attempted to elicit trophic cascades at different points along the gradient of water availability to plants. By doing so, I could determine the extent of predator control of trophic structure, and later identify the primary consumer at different points along the gradient. I tested the hypothesis that small vertebrate predators such as songbirds and small mammals could exert top-down control in montane grasslands, especially when water was scarce. I speculated that the effects of predators were transmitted through arthropods, but did not understand how these complicated interactions within the various arthropod function groups could influence plant abundance or species number. To increase the realism of my study, I distributed my experimental treatments throughout the Lac du Bois Protected Area. This ensured that each 9 m x 9 m experimental unit determined the effect of different individual predators (e.g., songbird breeding pair) on local plant communities. I felt that this design, as opposed to single large treatments was both more appropriate to my study system and question, but also allowed me to draw

11

broad inferences because of increased replication. This experiment is most similar to the projects running in Chile (Gutiérrez et al. 2010) and Arizona (Thibault et al. 2010) that examine the effect of small mammals on desert ecosystems, and experiments on Caribbean islands that examine how subsidies effect food web structure (Spiller and Schoener 1998, Piovia-Scott et al. 2011) or Pacific islands that examine the effects of introduced predators on food web structure (Rogers et al. 2012).

The second experiment was designed to isolate how two separate sources of primary production influenced the upper trophic levels. In many ecosystems worldwide, dead plant material (detritus or litter) is an important energy source for upper trophic levels (Wolkovich et al. 2014). However, in semi-arid and temperate grassland ecosystems either most detritus is consumed by herbivores or vaporizes under high amounts of ultraviolet radiation or photo degradation (Austin and Vivanco 2006, Brandt et al. 2007). Since decomposer food webs often control nutrient cycling and can also link to and subsidize plant-herbivore-predator food webs, I sought to determine how detritus influenced the above ground food web (Chapter 4). I built another series of 9 m x 9 m predator exclosures along the gradient, but in this subset I doubled and removed detritus from 3 m x 3 m plots inside each predator treatment. This split plot design allowed me to isolate the effects of energy transferred to predators by grazing and detritus sources. In each of the subsequent chapters I used the two data sets in specific investigations of trophic structure along the gradient of water availability to plants. I describe the specific objectives of each chapter below.

In Chapter 2, *Temperate grassland songbird species accumulate incrementally along a gradient of water availability to plants*, I explored how grassland songbird communities changed along the gradient. I report the results of five years of occupancy surveys, and a single year of territory mapping of songbirds. My objective was to describe how the abundance of individual birds, the composition of songbird communities, and the number of species in any one location changed along the gradient. I use my observations to test two hypotheses about how patterns of species accumulate on resource gradients.

Simply put, the *more individuals hypothesis* predicts species should accumulate slower than the number of individuals as plant productivity rises, but that the identity of species and their relative abundances should remain unchanged. In contrast, the *more specialization hypothesis* suggests that the number of individuals and species will also increase with plant productivity, but that we should see very different species and different patterns of relative abundance at different levels of plant production. In the context of my larger research objectives, my hope was that this work would allow me to describe how the abundance and type of predators differed along the gradient.

In Chapter 3, *Intraguild predation is mediated by the availability of water in temperate grassland ecosystems*, I present the results of my four-year predator exclusion experiment. I did this experiment to determine how the degree of omnivory in temperate montane grasslands changes along the gradient. I predicted changes in the direction and strength of trophic control depending on the amount of water available to plants. This top-down control would be transmitted from songbird and small mammal predators through arthropod predators, herbivores and decomposers to plants. However, songbirds and small mammals consume all three of these arthropod functional groups. I speculated that predation on different functional groups would change along the gradient. Because the degree of intraguild predation changes on the gradient, the responses of plants and arthropods to predator removals should also be different. The differential response of plants to the cascading effect of predator exclusions allowed me to infer changes in trophic structure along the gradient.

In Chapter 4, *Apparent trophic cascades are mediated by the availability of water to plants in temperate montane grasslands*, I present the results a four-year predator exclusion and detritus manipulation experiment. I did this experiment to isolate the role of two separate food chains on the trophic structure of montane grasslands. Detritus food chains can supplement generalist top predator abundance and could, in theory, change the direction of trophic control in grazing food chains. Along a gradient that varies from

low amounts to high amounts of detritus, such as the one I examined, there should be a change in trophic structure from a food web based on a single grazing food chain to one with both grazing and detritus food chains. I sought to document if this change occurred, and determine if the original grazing food chain reversed trophic control with the addition of the detritus food chain. Autochthonous detritus subsides to generalist predators could increase their abundance and switch the direction of control in the grazing food chain from bottom-up to top-down. Again, I used the concept of the trophic cascade to reveal trophic structure, and concurrently manipulated detritus to isolate how these three factors –predators, detritus, and water – combined to structure temperate grassland food webs.

Chapter 5 summarizes the results and my interpretation of the previous three chapters. I discuss some of the implications of the methods I used, and discuss the broader implications of my work. I discuss some recommendations for future work and in conclusion outline some of the conservation implications of the results of my research.

Chapter 2: Temperate grassland songbird species accumulate incrementally along a gradient of water availability to plants

2.1 Introduction

Across North America, grassland songbirds have been declining in abundance for almost 40 years (Brennan and Kuvlesky 2005 State of Canada's Birds 2012). Recovery of these species will depend on maintaining and restoring high-quality breeding grounds. Presumably, increases in the availability of resources such as water and nutrients lead to increases in the abundance of organisms at all trophic levels in an ecosystem (Hamilton and Wright 1983, Bonn et al. 2004) and would improve the quality of breeding grounds. However, there is still strong debate about the mechanisms by which environmental gradients in resource availability affect the number of species of either plants (Adler et al. 2011) or higher trophic levels such as songbirds (Rahbek 1997, Hawkins and Porter 2003, McCain 2009).

In temperate grasslands, changes in the availability of abiotic resources such as water have been linked to changes in the richness, abundance, and reproductive success of many grassland bird species (Cody 1968, Rotenberry and Wiens 1980a, Wiens and Rotenberry 1981, Wiens et al. 1987, Fisher and Davis 2010). Effects of resources on birds is often thought to be mediated by vegetation change (Jankowski et al. 2013). Certainly, plant characteristics such as live plant biomass, the mass or cover of plant detritus, and shrub abundance have often emerged as predictors of grassland songbird abundance and species number (Fisher and Davis 2010). However, when gradients in resource availability occur over large spatial scales (e.g. latitudinal gradients), the effect of resources can be confounded by other factors, such as the spatial turnover in species identity. Examining changes in grassland songbird communities along local gradients such as a single mountainside provides an ideal opportunity to test the mechanisms of how grassland songbirds accumulate species with increases in water or nutrient availability to plants. Local gradients allow us to isolate these mechanisms while maintaining consistent species pools, disturbance patterns, and evolutionary histories (Fukami and Wardle 2005, Sundqvist et al. 2013). Consequently, examining

patterns of diversity on local gradients can provide insight into how diversity changes along broad latitudinal or continental-scale variation in water and nutrient abundance (Hawkins and Porter 2003, McDonald et al. 2012, Coristine and Kerr 2015).

Elevation gradients are particularly useful local gradients because they provide some of the most rapid spatial changes in abiotic resources. Along most elevation gradients, climatic variables have strong correlations with avian species richness and the abundance of individual birds (Rahbek 1997, McCain 2009). However, although elevation gradients can circumvent some of the limitations of larger-scale environmental gradients, there are additional confounding factors to consider. Locations along elevation gradients typically become drier and colder with altitude (Sanders and Rahbek 2012) resulting in fewer species at higher elevation. In such cases, it is challenging to determine if a low number of species at high elevations is due to low plant productivity or the fact that montane species are less widely distributed (i.e., geometric constraints). However, in some areas orographic precipitation produces an effect that results in dry warm valley bottoms (i.e., deserts) and wet cool mountain tops (i.e., grasslands), resulting in an increasing number of species at higher elevation. By using such an elevation gradient in this study, I was able to isolate the effects of resource availability from the otherwise confounding effects of elevation and geometric constraints.

I examined the distribution of temperate grassland songbirds along an elevation gradient to determine if and how species number accumulates with plant productivity. I then tested two hypotheses that could explain how songbird diversity changes along this gradient. By examining how songbirds accumulate species along this gradient I provide insight into how these species will respond to changing climates and which management strategies could be used to recover declining populations.

Two alternative hypotheses propose mechanisms to account for changes in songbird abundance and species number under different levels of resource availability to plants (Rahbek 1997, McCain 2009). Both hypotheses predict that as abiotic resources such as water increase, the number of songbird species will also rise. However, each hypothesis provides a different mechanism for the accumulation of species. Both provide a series of predictions for how the abundance of individuals, number of species, and structure of communities (identity and abundance of species) should change along a resource gradient (Figure 2.1). I use these predictions to provide evidence supporting or refuting each hypothesis.

The *more individuals hypothesis* asserts that the number of individuals increases linearly as a function of resource availability, and this increase in individuals is associated with more species through simple sampling effects (Srivastava and Lawton 1998). Applied to our grassland birds, this hypothesis implies that an increase in water availability will increase with plant productivity and therefore the number of birds supported per unit area will also increase. Because of the positive relationship between water availability and the number of songbird species is due solely to increased abundances, there will be little difference in the types or identity of grassland songbirds species along the gradient ("turnover" in Anderson et al. 2011) and adjacent locations will have similar species identity and relatives abundances ("variability" in Anderson et al. 2011). The increase in bird abundance along the gradient may also be achieved through an accompanying decline in territory size in all species: at high resource availability, smaller areas are required to obtain sufficient energy.

Alternatively, the *more specialization hypothesis* predicts that one songbird species will replace another as resource availability changes (Whittaker 1960, 1972). When resources are scarce, only generalists or species that consume a broad range of resources can obtain sufficient resources to persist (Srivastava and Lawton 1998). As water availability increases, rare resource types will become sufficiently abundant to support specialist songbird species. Consequently, increasing water results in more species as a few

generalist species consuming multiple resource types are replaced by multiple specialist species each consuming few resource types. In particular, there should be a greater variation in songbird community structure within particular vegetation communities, especially in vegetation communities with low productivity. Assuming that resources are always heterogeneously distributed, then dry locations occupied by generalist species are expected to have lower beta diversity than wetter locations which are occupied by specialist species that show fine-scale spatial segregation.

To test if either of these hypotheses applies to grassland songbirds, I asked specific questions about the factors that structure grassland songbird communities at particular points along a local gradient of water availability to plants in south-central British Columbia, Canada (Figure 2.1). Firstly, does the number of individual grassland songbirds and number of songbird species change along the gradient? If I do detect patterns of change in the number of species and the number of individuals, are these changes associated with water availability? Second, what is the mechanism by which the number of species accumulates along the gradient? Are there changes in the number of species related to the abundance of songbird individuals, are there compositional changes in songbird communities (e.g., species turnover), and do territory sizes of individual species change along the gradient?

Each of the hypotheses I tested has different implications for conservation. If the number of species increases with water availability in a manner consistent with the more specialization hypothesis, grassland managers interested in promoting songbird species must provide for the specific habitat requirements of each individual species. If the number of species increases in a manner consistent with the more individuals hypothesis, grassland managers can provide general habitat requirements that benefit many species simultaneously. Thus, if species accumulate via the more individuals hypotheses, grassland managers interested in recovering songbirds can avoid intensive and expensive species specific management approaches and instead focus on practices that promote the broad-scale health of grasslands.

2.2   Methods

I conducted songbird surveys and described vegetation characteristics in the Lac du Bois Provincial park near Kamloops, British Columbia, Canada (50°39'59'' N, 120°19'09'' W). Mean monthly precipitation at the Kamloops weather station (345 m a.s.l.) between 1981 and 2010 averaged 23.15 mm (range = 12.4 mm.an^{-1} - 37.4 mm.an^{-1}). June and July have historically been the wettest months and February and March the driest. Mean daily temperatures over the same period averaged 9.2 °C (range -2.8 °C to 21.5 °C). July and August are the hottest months and December and January the coldest (Canada 2015). Lac du Bois Provincial Park is a protected shortgrass and shrub-steppe ecosystem that occurs in the rain shadow of the British Columbia Coast Mountains. The entire region is characterized by a strong orographic effect having dry hot valley bottoms. With increasing elevation, the dry valley vegetation transitions across a series of benches to wet, cool grasslands at the upper elevation forest boundary. This is the reverse of the elevation gradient typically seen in other studies.

Local differences in precipitation, temperature, soil depth and texture, soil parental material, topography, and aspect contribute to the structure and composition of local plant and animal communities (Schmidt et al. 2012, Carlyle et al. 2014, Lee et al. 2014). Dominant grasses include bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Love) and rough fescue (*Festuca scabrella* Rydb.). Common shrubs include big sagebrush (*Artemisia tridentata* Nutt.), rabbit brush (*Chrysothamnus nauseosa* (Pallas ex Pursh) Britton.), rose shrubs (*Rosa acicularis* Lindl.) and grey horsebrush (*Tetradymia canescens* Nutt.) (Lee et al. 2014). The study area has been used extensively for livestock grazing, homesteading, and recreation for over 150 years (McLaren et al. 1981), but currently it is primarily used for cattle grazing at low to moderate stocking rates (Evans 2011).

To identify patterns of songbird diversity along the gradient, I counted grassland songbirds during the breeding season (mid-May to early July) using two methods: occupancy surveys and territory mapping. Occupancy surveys were conducted annually from 2008 to 2012 at 96 point locations over 5 years. Locations were grouped into six blocks, with 16 locations in each block. Locations were separated by at least 250 m and the six blocks were distributed across and along the gradient. Occupancy surveys consisted of visiting a location within 4 hours of sunrise and counting all grassland songbirds seen or heard within 100 m of the location during a 5-minute period. Each location was visited between three and five times during each breeding season. Abundances were determined by using the maximum number of individuals detected in a single count (i.e., singing males) and correcting this value using estimates of detectability (Jankowski and Rabenold 2007). I estimated detectability by year and species only for the five most common species using function gdistsamp in package unmarked v. 0.10-4 (Fiske and Chandler 2011) in R 3.1.1. For species with less than five records, I pooled records from all years and species and estimated detectability using function pcount in package unmarked v. 0.10-4 in R 3.1.1 (R Development Core Team 2011) .

To estimate territory sizes of individual species I surveyed 12 areas five times during the breeding season of 2008. Two mapping areas were associated with each of 6 blocks used for occupancy surveys. Each mapping location consisted of four adjacent, 100 m wide transects, each 500 m long, for a total of 20 ha. Each survey started at sunrise and for 3 hours all visual or auditory observations of birds were recorded as the observer slowly traversed the 20 ha area. To delineate territories, I combined sightings for all five visits for individual birds, and then estimated the minimum convex polygon (MCP) for each individual songbird using the Minimum Bounding Geometry Tool in ArcGIS 10.2.2 for Desktop software (ESRI 2013).

To determine the distribution and abundance of plants, I surveyed plant functional groups (grasses, forbs, shrubs, trees) and the amount of bare ground at each of the 96 locations used in the songbird occupancy surveys. I estimated cover of each functional group using 20 m diameter circular plots, and measured the amount of living herbaceous plant material (live biomass) and dead herbaceous plant material (detritus mass) at each location using a destructive harvest of two 0.5 m x 0.5 m plots. I ranked survey blocks into cover classes from 1 (121.1 g.m^{-2}) to 6 (326.3 g.m^{-2}) based on the average amount of live biomass plus detritus mass collected at each location.

I summarized data at both the block (n=6) and location (n=96) scales. At each location I counted the number of individual singing males by species. Species richness was determined with a simple count of the number of species, and rarefied richness was calculated using function::rarefy in package VEGAN in R 3.1.1 (Oksanen et al. 2015). I rarefied to standardize species number along the entire gradient. I calculated two measures of α-diversity to account of the effect of abundance on species richness. To estimate songbird evenness, I used the Probability of Interspecific Encounter (PIE), as 1-D, where D = Simpson's Diversity (*D = sum p_i^2*). All calculations were performed using function Diversity in package VEGAN in R 3.1.1 (Oksanen et al. 2015). I calculated and tested rarefied richness (Colwell et al. 2012) using package VEGAN.

I tested for relationships between songbird species abundance, richness, rarefied richness, and evenness using generalized linear mixed models (GLMMs). I determined the most appropriate random effect structure by comparing the full model with different random effect structures using Akaike Information Criteria (AIC). The most parsimonious random effects structure allows only the intercept to vary between both blocks and years. Analyses were done using the function lmer or function glmer in package lme4 (Bates et al. 2015) in R 3.1.1. I specified Gaussian errors in GLMMs for abundance and evenness relationships and Poisson errors for richness relationships. The strength of these relationships was

assessed by examining whether the slopes of the regression lines were different than zero or different than other treatments. I assessed the existence of a hump-shaped relationship with abundance, richness or evenness by testing if a quadratic form of the statistical model fit the data better than the simpler linear form.

To test for changes in community composition and species composition along the gradient, I calculated β-diversity in two ways following Anderson et al. (2011). First, I tested for turnover in songbird communities along the gradient of either live biomass or detritus mass by first calculating a Bray-Curtis distance matrix to estimate the distance between songbird communities (Sorensen's Dissimilarity) at each of the 96 points as well as another distance matrix measuring dissimilarity as the difference in pair-wise comparisons of the amount of live biomass or detritus mass (T3, T4 in Anderson et al. 2011). These two matrices were compared using Mantel tests and generalized linear mixed models. Detrended Correspondence Analysis (DCA) was applied to the pair-wise matrix of live biomass and detritus mass to remove any bias the distance matrix calculations may have imposed on the linear nature of the gradient. I did not perform a similar analysis with shrub cover because a large number of locations had no shrubs and fitting a simple statistical model was not possible.

As a second way of calculating beta diversity, I tested for a consistent change in the variability in community composition within blocks along the gradient (V4 in Anderson et al. 2011). I ranked blocks based on their mean NDVI (n=16/block), and then calculated how different the community composition of songbirds at each point was from the group mean (i.e., dispersion within blocks). The function BETADISP in package VEGAN was used to calculate the amount of dispersion in songbird communities from the typical community (the centroid) of that block. By comparing values at each of the six blocks ranked in order of mean biomass, I estimated variability of songbird communities within blocks. I fit generalized linear models (GLMs) or GLMMs to test for the relationship between vegetation descriptors

and variability in songbird community composition within blocks. I assessed the nature of this relationship by examining the parameters in the statistical models I had fit.

2.3   Results

The abundance, richness, and evenness of grassland songbird communities changed along the gradient of water availability to plants (Figure 2.2). As elevation increased, so did bird abundance and species richness, although this relationship was unimodal with peak individual abundance at 783 m a.s.l. and a corresponding peak in the number of species at 783 m a.s.l. My proxy of water availability (NDVI) increases as a curvilinear function of elevation ($R^2 = 59\%$, quadratic regression $F_{4,6} = 27.3$, p <0.001), so abundance and species richness also increased with NDVI (Figure 2.3). However, the linear relationships were as good a descriptor of the pattern (difference between linear and polynomial models: abundance χ^2 = 0.01, p = 0.916, richness $\chi^2 = 0.11$, p =0.734). Water availability changes plant resources in terms of shrub abundance, ground cover, live plant biomass and detritus mass. There was no relationship between the abundance of birds and shrubs ($\chi^2_{4,5} = 0.49$, p = 0.480), but bird abundance did increase with increasing ground cover ($\chi^2_{4,5} = 12.1$, p <0.001; Figure 2.4C), live plant biomass ($\chi^2_{4,5} = 7.78$, p = 0.005) and detritus mass ($\chi^2_{4,5} = 17.05$, p < 0.001; Figure 2.4B). Species richness similarly was unrelated to shrub cover ($\chi^2_{3,4} = 2.13$, p = 0.150), but increased with ground cover ($\chi^2_{3,4} = 11.9$, p < 0.001; Figure 2.4F), live plant biomass ($\chi^2_{3,4} = 5.0$, p = 0.026; Figure 2.4D) detritus mass ($\chi^2_{3,4} = 6.57$, p = 0.010; Figure 2.4E). All told, both live plant and detritus biomass provide the best predictors of songbird abundance and richness along the gradient and this relationship is roughly linear.

To distinguish if songbird communities increased in abundance and richness following either the more individual or more specialization hypothesis I first examined relationships between individual abundance and the number of species. Along the gradient, the number of individuals increased more quickly than the number of species (Figure 2.3). Rarefaction allows us to correct species richness for plot variation in

abundance. The more individuals hypothesis predicts that all plot difference in richness are due to sampling different numbers of individuals, so under this hypothesis rarefaction should remove differences in the number of species. While rarefied species richness still significantly increased with NDVI, rarefaction greatly diminished the magnitude of the NDVI effect (Figure 2.2C). Rarefaction removed the significant association of species number with plant live biomass (Figure 2.4). Thus, in general when I account for the increase in abundances the number of species per location (rarefied richness) remains relatively constant along the gradient.

The more specialization hypothesis predicts that community composition will change along the gradient, with a few dominant and widespread generalist species being replaced by a number of specialist species that partition the resources and habitat at a finer scale. Therefore, the more specialization hypothesis would be supported by changes in species identity, and increases in spatial variability in community composition and species evenness along the gradient. Mantel tests did not show any association between changes in songbird communities and resource availability (Table 2.1). Likewise, GLMMs showed no change in species identity along the gradient of either live biomass ($F_{4, 5} = 0.42$, $p = 0.52$) or detritus mass ($F_{4, 5} = 0.01$, $p = 0.91$). There was also no strong spatial variability in songbird communities along the gradient when I ranked blocks based on either live biomass, detritus mass, or bare ground ($F_{5,90} = 1.51$, $p = 0.194$). Finally, although evenness did decrease with NDVI ($\chi^2_{4, 5} = 31.9$, $p < 0.001$), live biomass ($\chi^2_{4, 6} = 13.88$, $p < 0.001$) and detritus mass ($\chi^2_{4,5} = 8.61$, $p = 0.003$), this relationship was opposite to the increase in evenness predicted by the more specialization hypothesis. Songbird communities did not change in composition or increase in their variability along the gradient. More individuals of the same species were present as the amount of live plant or detritus mass increased along the gradient. Likewise, community composition changed little between adjacent locations. If anything, dominant species became slightly more dominant, and evenness was reduced with increasing water availability and plant production.

To determine how the distribution of resources in each block was influencing foraging behavior and the number of species, I estimated the territory size of 203 individual birds from four common species along the gradient. Vesper Sparrows (n=102), Western Meadowlarks (n=31), Chipping Sparrows (n=55) and Savannah Sparrows (n=15) each had three or more sightings over the five days of survey at each location. The size of Vesper Sparrow ($F_5 = 0.93$, $p = 0.464$) and Savannah Sparrow ($F_5 = 0.96$, $p = 0.444$) territories did not change along the gradient. However, territory sizes for Western Meadowlark ($F_5 = 4.31$, $p = 0.005$) and Chipping Sparrow ($F_5 = 5.79$, $p < 0.001$) were lower in areas where water was abundant than in areas where water was scarce. Territory size for individual species did not change with the amount of live biomass, detritus mass, shrub or bare ground cover. Generally, territory size declines with increased live plant biomass, detritus mass, and increases with the amount of bare ground, but this relationship is highly variable (Figure 2.5).

2.4   Discussion

I show that songbird species accumulate along a gradient of water availability to plants consistent with the more individuals hypothesis. My data show that there is a linear and generally consistent increase in both the number of individuals and number of species of grassland songbirds with increasing water availability to plants. This occurred because common birds either had smaller territories or greater territory overlap at high water availability. It did not occur because resource generalists were supplanted by specialists. Specifically, the identity of the dominant species in songbird communities did not change along the gradient, nor did beta diversity at locations along the gradient increase with water availability. Taken together, these data provide much stronger support for the more individuals hypothesis than for the more specialization hypothesis, and suggest that songbird species in temperate grasslands might accumulate diversity on gradients of abiotic resources in ways different than songbirds in other biomes. Semi-arid ecosystems experience periodic resource abundance interspersed with long periods of resource shortages

or drought (Meserve et al. 2003, Letnic and Dickman 2006, 2010, Greenville et al. 2014). When resources are in short supply or resource availability is periodic, consumers must be opportunistic when choosing prey especially in time of resource shortage (Ostfeld and Keesing 2000). This makes specialization difficult for species occupying ecosystems at the lower end of their resource tolerance. These results are important for two reasons. First, by providing contrasting results to tropical systems (Terborgh 1977, Rahbek 1997, Parra et al. 2011, Acharya et al. 2011, Jankowski et al. 2013). I demonstrate that the mechanisms driving species accumulation along resource gradients may be dependent on the patterns of resource abundance and shortage in the ecosystem. Second, I examined not only the shape of the richness-productivity relationship in upper trophic levels, but provided a concrete approach to test why these patterns occur.

I suggest that despite large changes in water availability and plant community structure along the gradient, songbird species accumulate along gradients in temperate grasslands by first adding new species at low abundances. New rare species were added to songbird communities incrementally as water availability to plants increased, and these species generally remained rare as water availability increased. Thus, the richness-productivity relationship in grassland songbirds relies on the addition of less common species through simple probability. When abiotic resources such as water increase, plant growth increases and there is a corresponding increase in the number of songbird individuals because more plant growth can support an abundance of arthropods on which songbirds forage. As the number of songbird individuals supported at a particular location increases, it is likely that some of these species will be not be the same as the species already present. Thus, species richness increases. In areas where water is scarce, very few individuals occur and either sampling or priority effects favour species that are more common in the regional species pool.

One key pattern supporting the more individuals hypothesis is that the same two songbird species (Western Meadowlark and Vesper Sparrow) remained dominant along the entire gradient. Although some rarer species such as the Brewer's Sparrow or Savannah Sparrow do not occur along the whole gradient, other rare species such as Western and Mountain Bluebirds and Warbling Vireo have a broad distribution on the gradient. Thus, I conclude that similar to studies in other grassland bird communities (Wiens 1973) there is no strong specialization of birds with respect to particular resources in the temperate grasslands I examined, and that the number of species increases primarily as a function of ecosystem-level productivity. This is in contrast to other bird communities (Terborgh 1977, Parra et al. 2011, Acharya et al. 2011, Jankowski et al. 2013) and other vertebrate species (Cadena et al. 2012) which typically show strong changes in species identity along gradients.

The mechanisms that regulate avian diversity along resource gradients may depend on the nature of the gradient. I speculate that dry ecosystems, with variable or uncertain resource availability, may accumulate diversity in a manner consistent with the more individuals hypothesis. This may occur because interspecific competition for specific resources is limited along the gradient (Rotenberry and Wiens 1980b, Wiens and Rotenberry 1981, Wiens et al. 1985). Strong competition for resources at this local scale would be unlikely in ecosystems with periodic or uncertain resource availability (May and MacArthur 1972, Ostfeld and Keesing 2000). Conversely, wetter ecosystems that are less prone to resource shortage accumulate diversity in a manner consistent with the more specialization hypothesis.

The distribution of grassland songbirds I observed does not match the change in species identity and increasing species richness with plant productivity typically described in tropical songbirds (Terborgh 1977, Rahbek 1997, Acharya et al. 2011, Jankowski et al. 2013), but the patterns of changing species identity and species richness with plant productivity I observed do match results from dry grassland communities (Wiens and Rotenberry 1981, 1987). In tropical forests there are often large changes in

species identity along the gradient linked to marked changes in vegetation structure (Terborgh 1977, Rahbek 1997, Jankowski et al. 2013). Additionally, tropical gradients often demonstrate declining plant productivity with elevation which places geometric constraints on the number of species. Since the ecosystem I examined has the reverse trend in resource availability to tropical gradients, it may be that the patterns of changing species identity on gradients seen in tropical systems arises from geometric constraints on species number placed by decreasing productivity at higher elevations. Geometric constraints may require changes in species identity on gradients as individuals must have different traits to occur in areas with a different distribution of resources. Removing geometric constraints could allow the same species to exist but these species would simply change the area over which they forage. For example, in eastern Oregon, the number of species of shortgrass prairie and shrub-steppe songbirds was also found to be dependent on the abundance of peripheral or wide-ranging species rather than resident species that dominate local communities (Wiens and Rotenberry 1981), and in my study we observed declining territory sizes in the dominant songbirds with increased plant productivity.

Another reason my results may differ from those in tropical ecosystems other than geometric constraints is that scarce and periodically available resources could change species traits in semi-arid ecosystems. Interspecific competition for specific resources by grassland birds is limited in similar semi-arid ecosystems (Rotenberry and Wiens 1980b, Wiens and Rotenberry 1981, Wiens et al. 1985), and my results are also consistent with this more detailed habitat and behavioral work on songbird communities. Although few studies relate abundance or community structure of songbirds to particular vegetation characteristics (Winter et al. 2005), songbird abundance in these semi-arid systems is generally positively associated with prey abundance (Wiens 1973) or increased vegetation structure (Harrison et al. 2010, 2011). In studies covering larger areas across the Great Basin of the western United States, songbird species are associated with the density of shrubs and woody vegetation or more open vegetation (Knick et al. 2003). However, despite these associations, grassland songbirds consistently fail to show large

differences in species composition between habitat types (Rotenberry and Wiens 1980b, Wiens and Rotenberry 1981). Thus, grassland songbird communities appear dependent on broad factors, such as the overall productivity of the ecosystem, and not local scale differences in vegetation characteristics. This is again consistent with the more individuals hypothesis being better supported in dry ecosystems. Future studies should focus on isolating the effects of geographic constraints and the availability or periodicity of resource availability to plants in determining patterns of species accumulation in songbirds.

My findings aid in our understanding of the factors that determine community structure in grassland songbirds, but also inform conservation efforts and management actions (Davis et al. 1999, Knick et al. 2003). Both the number of species and the abundance of individual songbirds in temperate grasslands could be increased by promoting processes that lead to greater plant productivity. Plant productivity can be increased by allowing detritus to accumulate. Detritus accumulation can be promoted by reducing the frequency of disturbances such as prescribed fire and livestock grazing. This would be especially true in areas with low to moderate water availability. Tall grass prairie studies have found that the accumulation of songbirds peaks at 3 to 4 years following disturbances such as fire or other disturbance (Swengel and Swengel 2001, Grant et al. 2006, 2010, Richardson 2012). It may be that increasing grazing intensity but extending periods of no grazing could allow the recovery of both plant species and higher trophic levels through the accumulation of detritus. Following from the more individuals hypothesis, increased detritus may allow upper trophic levels, such as arthropods and songbirds, to reach higher levels of abundance and promote the accumulation of species. At drier locations, during periodic drought, or to mitigate climate change effects, grassland managers could promote the accumulation of detritus to increase the number of songbird species.

2.5   Conclusion

These findings point to different mechanisms that underlie general increases in the number of songbird species with ecosystem productivity that are dependent on resources availability. Semi-arid and temperate grasslands such as the one I studied often have periodic resource shortages that can dictate characteristics of species accumulation at both the plant and higher trophic levels (Dickman et al. 2001, Meserve et al. 2003, Letnic and Dickman 2010, Greenville et al. 2014). I suggest that persistent resource shortage can lower plant productivity and reduce the availability of resources to species in upper trophic levels. In the grasslands I examined, this reduces the number of songbird species. Wetter ecosystems such as tropical forest, have more consistent patterns of resource abundance and in these ecosystems species could accumulate through different mechanisms than in the semi-arid ecosystems I studied. Determining the mechanism through which diversity accumulates is important because knowing the mechanism can provide both a prediction for how changes in diversity will occur when the climate changes, but also provide guidance for how to manage ecosystems to promote diversity. If diversity accumulates through processes such as the more individuals hypothesis, we may be able to manage many species simultaneously and thus reduce management costs and efforts. In semi-arid and temperate grasslands, managing with ecosystem-wide techniques that promote plant productivity may also allow managers to mitigate the effects of climate change by proactively improving habitat quality for a broad range of species.
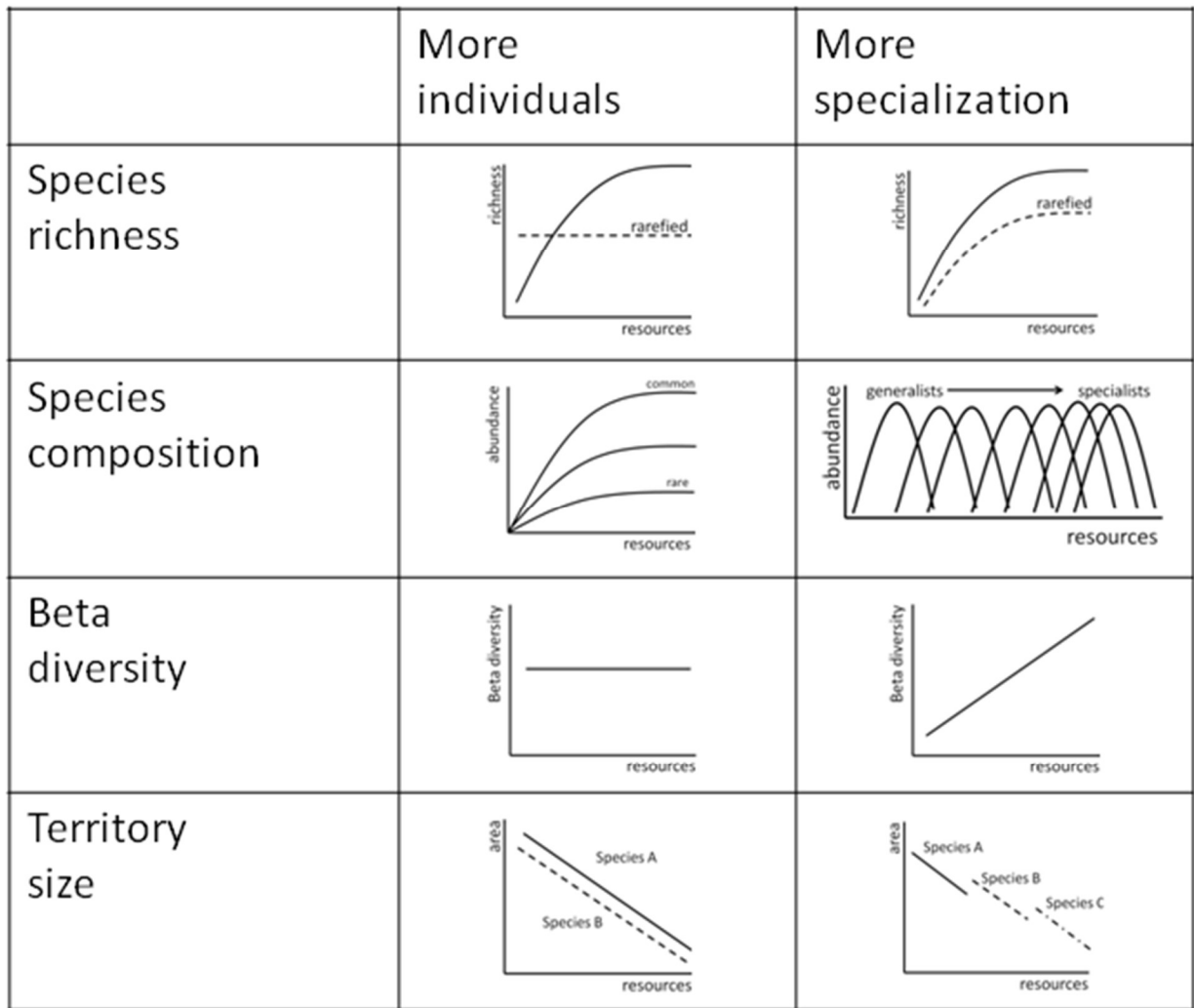
Figure 2.1. Predictions for mechanisms behind richness-productivity relationships in semi-arid and temperate grassland bird communities of south-central British Columbia, Canada. Each row represents predictions for how species richness, species composition, beta diversity, or territory size will change on a gradient of resources under either the *more individuals hypothese*s or the *more specialization hypotheses*.
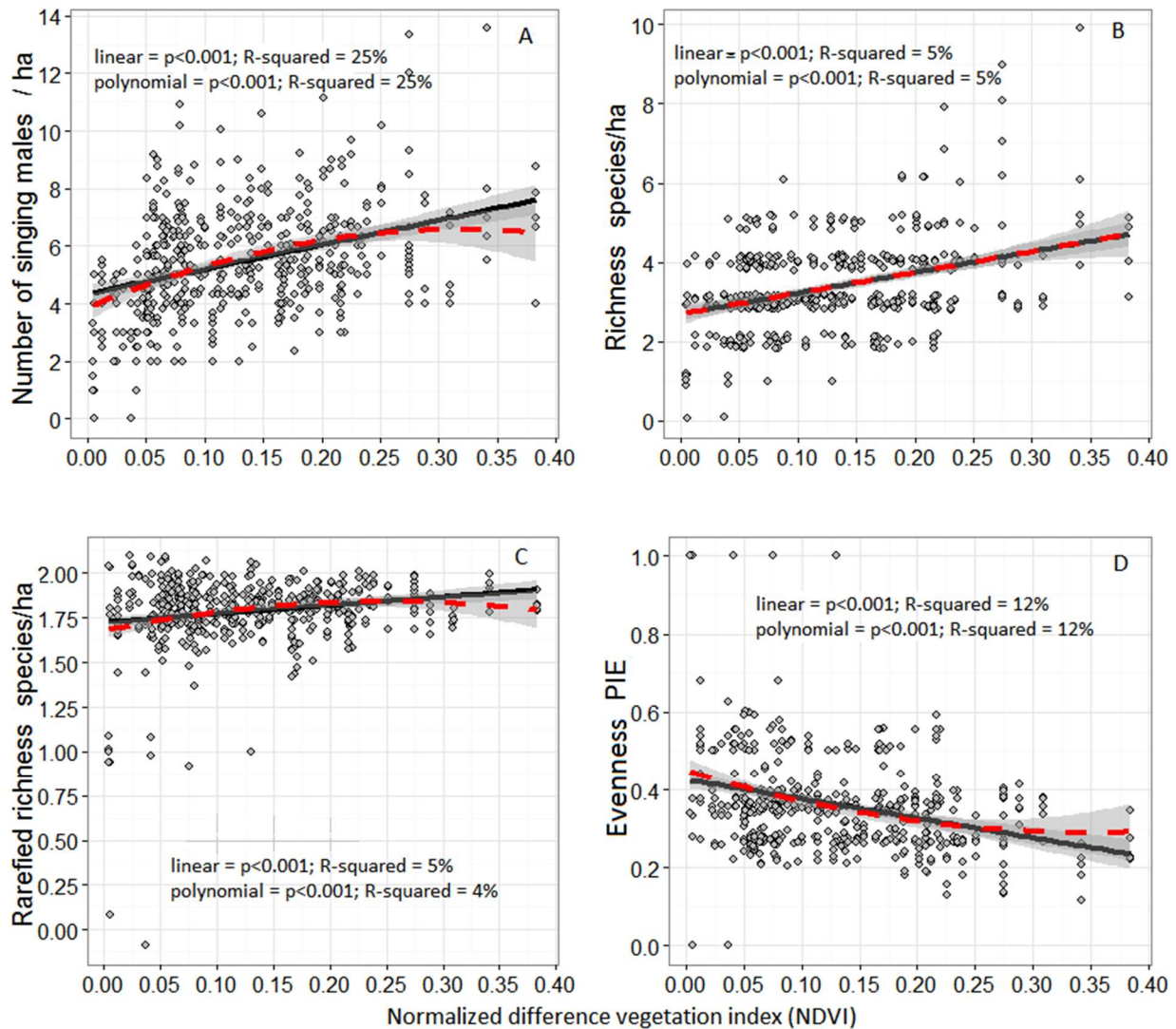
Figure 2.2 Avian abundance as the number of singing males (A), richness (B), rarefied richness (C), and species evenness (PIE) along a gradient of plant productivity (NDVI). Songbird communities were surveyed during the breeding season from 2008 - 2012 at 96 locations. Solid lines represent the fitted values of generalized linear models with a single term, and dotted red lines represent a similar fitted but polynomial (curved) model. Generalized linear mixed models were used to test for goodness of fit of models to data and whether straight or curved lines fit the data better. In all cases the straight line model fit (solid black lines) the data better than the curved ones (dotted red lines). Shaded areas represent 95% confidence intervals.

Figure 2.3. Relationship between the richness of grassland songbird species and the abundance of grassland songbirds. Each data point represents the number of songbird species and their estimated number of individual birds at a single location in one year. The estimated relationship is shown with shading representing the 95% confidence interval. For simplicity, I do not show error in estimating the number of individuals or species in this figure.

Figure 2.4. Relationship between abundance, number of species (richness), and species evenness (PIE) with live biomass, detritus mass, and ground cover. Points indicate observations of songbird communities at 96 locations made from 2008 - 2012. Lines are linear model fits with shaded 95% confidence intervals.
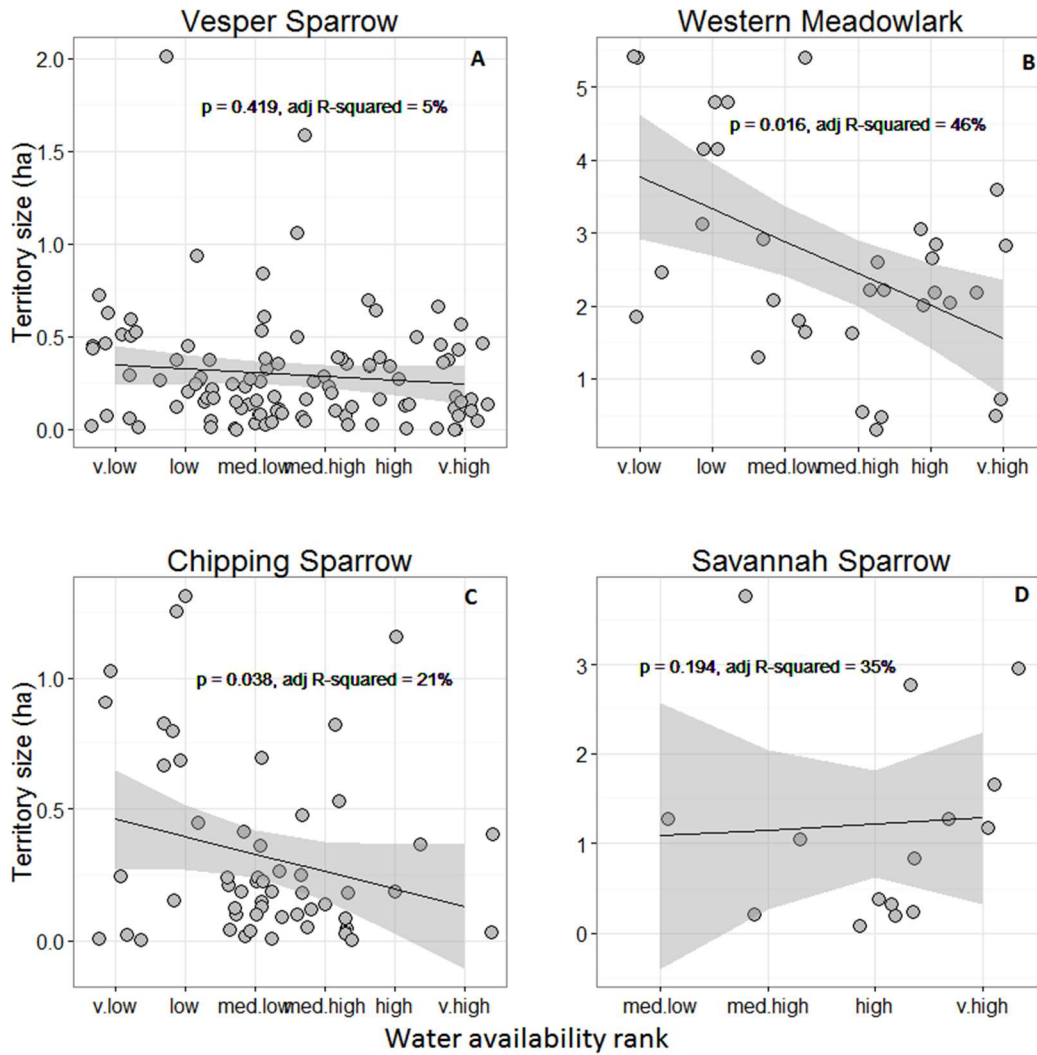
Figure 2.5. Territory size estimates for the four most common species of grassland birds observed during the breeding season of 2008. Observations were made over a range of grassland types. Each point represents the size of an individual territory measured at one of two 20 ha sites in ranked categories of water availability. Ranks run from where water is scarce (v.low) to where water is abundant (v.high). Points are offset over productivity ranks to show overlapping points. Relationships are shown as generalized additive models with shading representing 95% confidence intervals.

Table 2.1. Results of Mantel tests examining the relationship between change in community composition of songbirds between sites on the gradient and change in either live biomass or detritus mass between sites for each of five years in which we did surveys.

Correlation r (p-value)	Live Biomass	Detritus mass
2008	-0.08 (0.921)	0.07 (0.122)
2009	-0.09 (0.934)	0.10 (0.055)
2010	-0.03 (0.714)	-0.04 (0.726)
2011	-0.15 (0.997)	0.07 (0.081)
2012	-0.10 (0.944)	0.14 (0.017)

Chapter 3: Intraguild predation is mediated by the availability of water in temperate grassland ecosystems

3.1 Introduction

Trophic control in many of the world's ecosystems is being altered by global environmental change (Estes et al. 2011, IPCC 2014). Predators can affect the distribution of biomass between lower trophic levels (Pace et al. 1999, Schmitz et al. 2000, Polis et al. 2000, Shurin et al. 2002). Predators can also have either diversity-enhancing or diversity-depleting effects on lower trophic levels (Spiller and Schoener 1998, Fraser and Grime 1999, Schmitz 2003) and they have been shown to influence ecosystem functions such as biomass production, carbon sequestration, and nutrient cycling (Terborgh et al. 2001, Strickland et al. 2013). However, for these top-down processes to occur, ecosystems must have adequate levels of resource availability and subsequently primary production to support herbivorous prey, their predators, and sometimes tertiary consumers. Thus, the amount and distribution of limiting abiotic resources can have a profound influence on the strength of top-control in ecosystems (see reviews by Turkington 2009, O'Connor et al. 2015, Shurin 2015). Increasing resource availability could strengthen consumer control in ecosystems by increasing consumer biomass, by changing the intensity of intraguild predation, and by altering the relative abundance of endotherm (vertebrate) and ectotherm (arthropod) consumers.

Classic trophic theory (e.g., Fretwell 1977, Oksanen et al. 1981) focuses primarily on how shifts in resource availability alter top-down control by changing consumer biomass. Increases in resource availability are predicted to permit the appearance of, and increased abundance in, a higher trophic level, which exerts increasingly strong top-down effects on lower trophic levels. This theory assumes that predator and herbivore consumers have fixed diets and that changes in trophic structure arise from the addition and removal of whole species or functional groups (see reviews by Turkington 2009, O'Connor et al. 2015, Shurin 2015). However, food webs are complex, omnivory is ubiquitous, and species removal

or additions are transferred through food webs in complicated ways (Polis et al. 1989, Kratina et al. 2012).

Intraguild predation is a specific form of omnivory in which top predators (i.e., intraguild predators) compete for a shared food source with their prey (i.e., intraguild prey). Thus, intraguild predators feed at two trophic levels. Changes in feeding behavior of top predators can alter the strength of species interactions between intraguild predators, intraguild prey, and the shared resource. When the impacts of intraguild predators are spread between both the intraguild prey and the shared resource, food webs should be relatively stable: when top predators are removed there should be no strong trophic cascade because the positive and negative effects of predator removals on plants are balanced. However, when intraguild predator and prey interactions are unequal we should see strong cascading effects, and predator removal on plants should demonstrate either a three- or a four-level trophic cascade dependent, respectively, on whether the top predator consumes largely the shared resource or the intraguild prey. As resource availability increases, we predict the food web to shift from the dominance of the three-level pathway, to a balance between the three- and four-level pathways, to dominance of the four-level pathway (Figure 3.1).

Finally, the metabolic traits of predators can also be impacted by the flow of energy from basal resources, and such changes in predator traits can subsequently influence the strength and direction of top-down control (Yodzis 1984, Borer et al. 2005). Ectothermic species (e.g., arthropods, reptiles) have much higher assimilation efficiency than endotherms (e.g., bird and mammals), and thus ectotherms have lower basal metabolic rates (Humphreys 1979). Ectotherms are also able to survive periods of resource shortage better than their endothermic counterparts (Ayal 2007). Depending on the dominant prey type, ectotherms may also be better adapted to match physiologically restricted foraging times to the periods of highest prey availability (Yodzis 1984, Ewers et al. 2015). Because of these traits, ectothermic predators may be

able to persist in sites where basal resource availability is too low to support endothermic counterparts. However, when resource availability is high enough to support either ectothermic or endothermic predators of herbivores, top-down effects could be on average stronger with endothermic predators (Borer et al. 2005). Thus, changes in resource availability at the bottom of the food web can alter the abundance of ectothermic herbivores, change the relative abundance of ectothermic versus endothermic predators, and result in very different patterns of intraguild predation. If ectothermic predators become more abundant, intraguild predation could favour predation by intraguild predators on intraguild prey rather than herbivores, and a four-level trophic cascade would result. Conversely, if there are enough ectothermic herbivores to support large populations of endothermic predators, predation by intraguild predators on herbivores will dominant and a three level-trophic cascade would result.

The role of resource availability in determining the top-down effects of predators can be experimentally determined by excluding predators along gradients in resource availability and monitoring subsequent changes in the abundance of organism in lower trophic levels. Such an experimental approach can thus provide insight into food web structure that is not apparent without experiments (Borer et al. 2006, Turkington 2009, Turkington and Harrower 2016). In the temperate grasslands of western North America, gradients in water availability produce ecosystems that range from dry desert through shrub-steppe to productive savannah each with a corresponding increase in primary productivity. These changes can occur over only a few tens of kilometers and can result in very different food web structure in ecosystems drawing from relatively similar species pools (i.e., gamma diversity).

If we remove top, endothermic predators from areas of temperate grasslands that receive varying amounts water, and thus have very different amounts of primary productivity, we would expect the response of plants to be dependent on resource (i.e., water) availability. The role of either consumer biomass (i.e., bottom-up) or intraguild predation (i.e., top-down) in mediating the effect of predator removals on trophic

structure can be inferred by determining how the response of plants changes over the resource gradient (Figure 3.1). Consumer biomass effects predict a strengthening positive effect of predator removals on live plant biomass, and intraguild predation predicts a switch from positive to negative effects on live plant biomass. In addition, intraguild predation predicts a decrease in the trophic position and reduction in diet breadth of the top predator as resources increase and preferred prey becomes more abundant.

3.2   Methods

To decipher trophic control of grassland plants by birds and small mammals, and determine if the degree of intraguild predation changed along the gradient of water availability to plants, I excluded songbirds and small mammals in a factorial design from areas of temperate grasslands for four years. I conducted this study in Lac du Bois Grasslands Protected Area near Kamloops, British Columbia, Canada (50°39'59''N, 120°19'09''W). Lac du Bois Protected Area encompasses approximately 15,500 ha of grassland that occurs in the rain shadow of the British Columbia Coast Mountains. The region is characterized by a strong orographic effect having dry hot valleys with shrub-steppe vegetation rising through a series of benches to wet, cooler grass-dominated plant communities at a forest boundary. Local differences in precipitation, temperature, soil depth and texture, soil parental material, topography, and aspect all contribute to the structure and composition of local plant and animal communities. Dominant grasses include bluebunch wheatgrass (*Pseudoroegneria spicata*) and rough fescue (*Festuca scabrella*). The dominant shrubs include big sagebrush (*Artemisia tridentata*), rabbit brush (*Chrysothamnus nauseosa*), rose shrubs (*Rosa acicularis*) and grey horsebrush (*Tetradymia canescens*) (Lee et al. 2014). The area has been used extensively for livestock grazing, homesteading, and recreation for over 150 years (McLaren et al. 1981), but is currently primarily used for cattle grazing at low to moderate stocking rates (Evans 2011).

Water generally limits plant productivity in Lac du Bois Protected Grasslands. Low elevation grasslands experience less precipitation and warmer temperatures than upper elevation grasslands (Lee et al. 2014). More frequent spring watering is associated with increased soil carbon respiration (Sapozhnikova 2012), and a decrease in available nitrogen n (NO3 - and NH4 +) in the soil (McCulloch 2013) suggesting water limits plant growth. However, watering and warming treatments had variable effects on the gradient. Areas with low rainfall are more likely to experience extremes of temperature and moisture, and have the largest response to watering (Carlyle et al. 2011, Carlyle 2012). I assume areas with limited precipitation and higher temperatures, low on the gradient receive insufficient water relative to areas high on the gradient. Water availability to plants, particularly during the spring growing season, most likely limits long-term site productivity in my study area.

3.2.1   Consumer trophic position and diet

To assess food web structure, I calculated the trophic position of all major taxa (arthropods and vertebrates), and estimated the proportion of major food sources in the diet of vertebrate consumers (i.e., songbirds and small mammals) using stable isotopes of carbon and nitrogen. I measured stable isotope ratios of carbon and nitrogen (δ^{13}C and δ^{15}N isotopes) by sampling the tissue of organisms during the breeding season. Songbird blood was extracted after birds had spent a minimum of one month on the breeding grounds so isotope levels in their blood would reflect their breeding season diet (Inger and Bearhop 2008). For arthropods, individual animals were sacrificed, ground and crushed prior to loading into tin capsules. For plants, I ground mixed samples of whole plant communities collected at similar locations to where animal samples were obtained. Samples (vertebrate blood, whole insect, or plant communities) were measured and weighed into tin capsules following procedures outlined by the Cornell Stable Isotope Laboratory and stable isotope analysis was performed by that facility.

3.2.2 Experimental effects of bird and small mammal removals on plants

The four-year experiment consisted of a 2 x 2 factorial design with 2 treatment levels of songbirds (control/removal), 2 treatment levels of small mammals (control/removal), and 12 replicates of each treatment pair, for a total of 48 plots. From 2009 to 2012 I excluded songbirds and small mammals from 48 temperate grassland sites along a gradient of rainfall, and measured the response of arthropods and plants to these removals. Each exclosure was 81 m^2 surrounded by a 9 m X 9 m barbed wire fence to eliminate grazing by domestic livestock and wildlife. A galvanized 6 mm steel mesh, 1.5 m high, was placed on the perimeter of half (24) of the exclosures and buried in the ground below the plant rooting depth (~ 30 cm) to prevent small mammals including (*Peromyscus sp.*) and voles (*Microtus sp.*) from burrowing under the wire. To exclude small birds from the plots, half (24) of the exclosures were covered with 20 mm extruded polypropylene mesh. The remaining 12 exclosures had only barbed wire fencing so that birds and small mammals could come and go but the majority of large grazing vertebrates were excluded. I dismantled the exclosures in the late fall of 2013.

To measure changes in plant community composition over time, I surveyed the abundance of plant species within each exclosure every year from 2010 to 2013. During the growing season I estimated the visual percent cover of each species in eight, 0.5 m^2 plots placed systematically within each of the 48 experimental plots. In the fall of 2013, I destructively sampled vegetation in the exclosures. I collected plant material from each of the 384, 0.5 m^2 plots where I had previously estimated the abundance of plants by species. All standing dead plant material (detritus) was collected. Any plant material that was decomposed to the point that it could not be identified to species was left at the site. Following the removal of detritus I harvested all remaining live plant biomass. All samples of both live biomass and detritus mass were air dried for at least two weeks, dried in an oven at ~60ºC for >48 hours, and then weighed. To estimate the mass of plant species after four years of treatments, I standardized total cover estimates from 2013 to 1.0 for each plot and then divided this proportional abundance into the total mass

of live plants collected. This assumed that the cover of a species was proportional to its live biomass, and that dominant plants were the two species of dominant bunchgrass, bluebunch wheatgrass and rough fescue.

I used the Normalized Difference Vegetation Index (NDVI) as a proxy for primary productivity in areas that were larger than my experimental units. In my study area NDVI correlates well with elevation, temperature and precipitation (measured at point locations). The NDVI measures also correlate well with live plant biomass and detritus mass. I calculated NDVI off seamless Landsat Thematic Mapper Images obtained from the British Columbia Government Geographic Data Warehouse. The grid cell size of these images was 30 m square.

3.2.3 Experimental effects on arthropods

To estimate arthropod responses to predator removals, I destructively sampled the abundance of foliar and ground dwelling arthropods inside exclosures in the spring and fall of 2013. I used two methods to do this: pitfall traps to capture primarily ground dwelling arthropods, and vacuum samples to capture primarily arthropods living on vegetation. All samples from pitfalls and vacuum sampling were sorted and identified to order, genus, or species depending on the taxonomic group. Arthropods were sorted and preserved in 95% ethanol in individual vials unique to the taxonomic group, time, and location of collection. I then determined the mass of subsamples of arthropod taxa after oven drying specimens for 48 hours at 60°C.

To estimate the prevalence of different arthropod prey in the diet of songbirds and small mammals, and estimate changes in diet breath of these vertebrate consumers along the gradient of water availability, I used Bayesian stable isotope mixing models (SIMM), and stable isotope Bayesian ellipses (SIBER) to determine the most likely proportion of each source item in the diet of vertebrate consumers, I developed

Bayesian isotopic mixing models in SIAR v4.0 (Stable Isotope Analysis in R; Parnell et al. 2010). I calculated trophic position following methods outlined in Post (2002). I used different trophic enrichment factors of 0.5‰ (sd = 0.5) for carbon and 2.5‰ (sd = 1.0) for nitrogen (Caut et al. 2010), and ran models for 500,000 iterations with a 50,000 iteration burn in. Diet breadth was estimated by determining the area of the ellipse surrounding all isotope samples.

To assess the significance of songbird and small mammal exclusion on live plant, detritus, and arthropod abundance and diversity, I used generalized linear mixed models. I determined the most appropriate random effect structure by comparing the full model with different random effect structures using Akaike Information Criteria (AIC). Analyses were done using the function lmer or function glmer in package lme4 (Bates et al. 2015). I specified Gaussian errors in GLMMs for abundance and evenness relationships and Poisson errors for richness relationships. Biomass was log transformed in GLMM. The strength of these relationships was assessed by examining whether the slope of the regression was different than zero or different than another treatment. I assessed the existence of a hump-shaped relationship by testing if a quadratic form of the statistical model fit the data better than the simpler linear form. I used vegan metaMDS for non-metric multidimensional scaling with Morisita-Horn distance matrix to create the NMDS plot in Figure 3.6. Canonical correspondence analysis (CCA) was used to test both for the change in plant community (species identity and relative abundance) after four years of experiment and for changes in the plant community over time. I used a PERMANOVA with Type III effects for all tests and when testing for the effect on plant communities over time I conditioned the models on grassland type (high, medium, or low water availability). All analyses were performed in R 3.1.1 (R Development Core Team 2011).

3.3 Results

3.3.1 Consumer trophic position and consumer diet

The length of the trophic chain declined as water availability increased along the gradient for almost all taxonomic and trophic groups (Figure 3.2) although declines were only significant for sparrows and small mammals. All birds, small mammals and arthropods (except detritivore beetles) showed patterns of declines in trophic position with increased water availability, calculated from stable isotopes of nitrogen, suggesting that consumers consistently ate prey from lower trophic positions at wetter sites. However, these declines were generally small (Table 3.1). Herbivores tended not to decline along the gradient.

Using isotopic tissue samples collected from plants and animals along the gradient I was able to examine how the diet of different species of vertebrate varied. During the nesting period, songbirds demonstrate a much smaller diet breath than small mammals, both in terms of trophic level (omnivory; $\delta^{15}N$) and food type (breadth; $\delta^{13}C$). In particular, bird stable isotope values clustered closer to and extended between spider and ant sources (Figure 3.3A & C), suggesting that spiders represent ~10% - 30% of the diet of songbirds. The range of $\delta^{15}N$ values for deer mice are larger (Figure 3.3) than for birds suggesting they ate more different types of prey. Likewise, variation in deer mice $\delta^{13}C$ values are larger than other species suggesting they feed on a wider range of food items when feeding at a single trophic level. At drier sites (Figure 3.3A), values of $\delta^{15}N$ and $\delta^{13}C$ in two individual deer mice were outside the range of the sources I sampled. This suggests that although I sampled what I thought was a comprehensive set of deer mouse prey, deer mice fed on prey that I did not sample.

Deer mouse diet breadth, represented by the size of the ellipse, declined as water became more abundant. Conversely, songbird diet breadth increased slightly. However, the greatest change in songbird diet appeared to be the shift to sources with lower $\delta^{15}N$ values and to isotopic values closer to those of beetles as water availability and plant productivity rose. At wetter sites (Figure 3.3C), it appears I sampled all

45

food items, but diet breadth of birds and small mammals is much more variable than at drier sites and so my sampling was incomplete. The *Sorex* spp. I examined were always higher in $\delta^{15}N$ values than *Microtus* species. *Sorex* sp. values of both $\delta^{15}N$ and $\delta^{13}C$ were typically within the range of values exhibited by spiders suggesting species fed on other consumers.

3.3.2 Experimental effects of bird and small mammal removals on plants

Songbirds and small mammals had significant indirect effects on plant biomass, and the nature of those indirect effects was dependent on the amount of water available to plants (Figure 3.4; Table 3.2). The exclusion of birds and small mammals together had a larger effect on plant biomass along the gradient of water availability than either the exclusion of birds or the exclusion of mammals independently although mammals had a larger effect at drier sites and birds had a larger effect at wetter sites. Likewise, there was a non-additive effect of predator exclusions on plant species number (Figure 3.5, Table 3.3).

The mean composition of plant communities changed over the gradient. Canonical correspondence analysis (CCA) with two terms, grassland type (high, medium and low water availability) and treatment type (Exclude Birds and Mammals, Exclude just birds, Exclude just mammals and controls), suggested plant community composition changes along the gradient (Figure 3.6A; PERMANOVA: $F_{2, 42} = 5.5$, p <0.001, $R^2 = 0.25$), but after four years of predator exclusions treatment type had little effect on plant species composition (PERMANOVA: $F_{3, 42} = 1.1$, p = 0.591, $R^2 = 0.25$). However, plant communities were changing over time and this change depended on the type of predator exclusion treatment. When I control for the differences between grassland types (high, medium, and low water availability) by using partial ordination, both year (PERMANOVA: $F_{1, 41} = 2.2$, p <0.001, $R^2 = 0.17$) and predator treatment (PERMANOVA: $F_{3, 41} = 1.5$, p <0.001, $R^2 = 0.17$) had a significant impact on plant community composition. Because of the continued directional change of treatments over time (Figure 3.6B → D) this experiment may have ended too early to see dramatic effects on plant functional groups.

3.3.3   Experimental effects on arthropods

The abundance of arthropods generally increased as water and subsequently plants became more abundant along the gradient (Table 3.5). This was primarily the result of increasing numbers of herbivores along the gradient (Figure 3.7A --> D, solid lines). Herbivores included species from leaf suckers (Hemiptera, Heteroptera), and leaf chewers (Orthoptera, Coleoptera).

Carnivorous arthropods responded to vertebrate predator removals in different ways depending on the availability of water. When all endothermic predators were removed at drier sites, carnivorous arthropods declined in abundance (Figure 3.7A; Table 3.5). When all endothermic predators were removed at wetter sites, carnivorous arthropod increased in abundance. Carnivorous arthropods were mostly spiders (Araneae), although there were many carnivorous carabid beetles at drier sites. Orthoptera and Hemiptera taxonomic groups were the only other functional groups to have an interaction effect of predators along the gradient (Figure 3.7B → D; Table 3.5). Herbivore abundance generally declined when predators were removed, but the magnitude of this response was larger at the drier end of the gradient (Figure 3.7; Table 3.5).

3.4   Discussion

I present some of the first evidence of the cascading effects of small predatory vertebrates in montane temperate grasslands. The cascading effects of small predatory vertebrates are dependent on water availability to plants in temperate montane grasslands. There are good examples of the effects of herbivores on plants, and predators of these animals can elicit trophic cascades (McLaren and Peterson 1994, Krebs et al. 1995, Ripple et al. 2001, Beschta and Ripple 2009, Sinclair et al. 2013). There is also mounting evidence that small predators can have strong effects on ecosystem structure and function (Meserve et al. 2003, Schmitz 2003, Mäntylä et al. 2011, Spiller et al. 2016). However, few if any studies

simultaneously examine these types of tri-trophic effects over a range of abiotic resource conditions (Schmitz et al. 2000, Shurin et al. 2002, Borer et al. 2005). Most studies focus on either a single level of abiotic resource availability, or on temporal changes in ecosystems (Meserve et al. 2007, Spiller and Schoener 2008). When water is scarce, predatory vertebrates as a group appear to depress plant biomass, whereas under abundant water predatory vertebrates have little impact on plant biomass. Since birds and mammals are primarily consumers, rather than herbivores, their effect on plants must be indirect rather than direct. That is, it must be mediated by the intervening arthropod trophic levels. The first step in understanding these context-dependent effects of predatory vertebrates on plants is to differentiate between the individual and combined effects of birds and mammals.

Birds and mammals differ in their impact on lower trophic levels over the gradient. These differences are likely more related to changes in the relative abundance of birds versus mammals rather than changes in their composition. At the dry end of the gradient, removing mammals has similar impact on plants as removing both birds and mammals. This is consistent with numerical effects of the high densities of small mammals and low densities of birds in these sites. However, at the wet end of the gradient, results of removals are not consistent with pure numerical effects. Specifically, at the wet end, densities of birds are high and small mammals low, but effects of removing birds are not similar to those of removing both birds and mammals. Here, non-additive effects of birds and mammals are required to explain patterns in plant biomass, as indicated by the three-way interaction term between birds, mammals and NDVI in my experiment.

This increase in the non-additive effects of birds and mammals along the gradient is similarly seen in a number of arthropod groups, such as Coleoptera consumers, Hemiptera consumers, and Orthoptera herbivores. These plant and arthropod non-additive effects are consistent with birds and mammals having greater than additive suppression of spiders at the wet end of the gradient, which indirectly benefits

herbivores. Such non-additive effects on spiders could originate from changes in the behaviour of spiders in the presence of one predator in a way that makes it more vulnerable to the other predator (Schmitz et al. 1997, Preisser et al. 2007). Thus, I suggest that the strong synergistic effects of birds and small mammals on arthropod carnivores reverses the direct negative effects of predatory vertebrates on herbivores that occurs at drier sites. This mechanism could occur if vegetation structure, especially the presence of abundant plant detritus affects the behaviour of spiders in relation to the presence of vertebrate predators.

The effects of vertebrates on herbivores and live plant biomass do not conform to the established theories of how trophic cascades change with productivity. I predicted that the changing effect of predators with water availability would occur through either changes in diet (i.e., consumer biomass) or through changing species composition due to metabolic requirements (i.e., metabolic trait). In order for intraguild predation to reverse the cascade itself we would need to see a shift in trophic position of almost a full trophic level in both birds and small mammals, but not the arthropods. This does not occur. Birds decline by only about one third of a trophic level over the gradient. Small mammal trophic position declines but this is partially due to an increase in the relative abundance of a more herbivorous species, the montane vole, as plant productivity increases. Furthermore, arthropods also show a tendency to decline in trophic position over the gradient, suggesting that diet changes in these groups may actually underlie the small declines in bird trophic level. Small mammals as a group decline by approximately one half a trophic level, not because of intraspecific diet shifts but because of an increasing prevalence of omnivorous voles at wetter sites. Thus, although some change in diet does occur along the gradient as the most abundant and likely most important predatory vertebrate changes from small mammals to song birds, changes in diet are not enough in isolation to explain the responses of plants to predator removals I observed.

Likewise, metabolic theory predicts a shift in the relative abundance of invertebrates and vertebrates with increases in net primary productivity. Predatory invertebrates should dominate drier sites that have less primary production, whereas predatory vertebrates should dominate at wetter sites. However, I saw no such shift in the relative abundance of vertebrates and invertebrates over the gradient. Rather, changes in relative abundance tend to be between different groups of invertebrates or between different groups of vertebrates. Therefore, although metabolic demands must affect energetic limitations of trophic structure, metabolic demands are not the sole determinant of food web structure.

Instead of mechanisms driven by shifts in diet or metabolism, I suggest that the reason for the change in trophic structure, revealed here by difference in the trophic cascades along the gradient, can be better understood in terms of two factors. First, birds and mammals have different and non-additive effects because of the type of predators they are. These two groups of vertebrates forage in different ways and potentially on different taxonomic groups. This results in changes in the behavioural and numerical responses of arthropods. Thus, when birds and mammals are excluded separately their effects are different than when they are excluded together. Second, the relative proportion of prey in the diet of vertebrate predators may not reflect the net impact this predator has on arthropod prey abundance. For example, the isotopic analysis reveals predators receive most of their energy from arthropod herbivores rather than arthropod carnivores; however, the removals show that vertebrates normally depress arthropod carnivores such as spiders but have variable effects on herbivorous arthropods.

A mismatch between diet and impact could occur if spiders have much stronger consumptive effects on grasshoppers than the predatory vertebrates do (Belovsky and Joern 1995). Even small decreases in spider densities could have large positive impacts on grasshopper densities that offset the direct negative effect of vertebrate predation leading to no net effect of vertebrates on grasshoppers. Since the joint, synergistic effect of birds and mammals in depressing spiders strengthens over the gradient, it is likely that any

50

indirect effects mediated by spiders also strengthen over the gradient. Therefore, at the wet end of the gradient, vertebrates have little net impact on herbivores and subsequently plants. Likewise, a mismatch between diet and impact could occur because of thermal differences along the gradient. Cooler temperatures where water was abundant could change arthropod herbivore or arthropod predator feeding behaviour or could change phenology (Chase 1996, Schmitz et al. 1997) or ontological (Belovsky et al. 1990, Belovsky and Slade 1993) of these insect or arachnids further altering the functional response between predators and prey(Ritchie 2000) .

Together, the mechanisms described above result in an alteration in the strength of trophic control over the water availability gradient. Previous work also supports my conclusion that trophic cascades can be elicited simply by altering the abundance of abiotic resources, rather than changing the presence of top predators. For example, the relative abundance of vertebrate and arthropod consumers in tropical forests can be altered by changes to ecosystem size (Terborgh et al. 2001). Similarly, migratory behaviour of wildebeest in the Serengeti allows wildebeest to escape top down regulation (Sinclair et al. 2003) and reach much higher population densities than resident populations (Fryxell et al. 1988). In the Serengeti, an expansion of wildebeest foraging areas allows animals to escape seasonally unsuitable areas (Harris et al. 2009) and hence escape the top-down effects of predators.

In contrast, other studies have shown little effect of ecosystem primary productivity on the strength of trophic cascades. For example, in forests re-establishing on tropical islands, arthropod predator abundance increased only with the exclusion of avian predators and not with fertilization, whereas arthropod herbivores and plants responded only to fertilizer treatments (Gruner 2004). Similarly, fertilizing Spartina plants did not strengthen top-down control of plant hoppers in salt marshes (Denno et al. 2002). It may be that additions in abiotic resources in ecosystems may reduce the prevalence of cascades where, restricting

resource abundance helps elicit them; or it could also be that experiments performed in a single location are unlikely to detect changes in trophic structure with ecosystem productivity.

3.5   Conclusion

My results show that predatory effects of small vertebrates can have large effects in temperate grassland ecosystems. Thus, dramatic declines in the abundance of grassland birds could have large and widespread effects on North American grasslands. These small predators can control the outbreak of pests, such as grasshoppers, but also in maintaining ecosystems functions such as plant biomass production. Additionally, my results suggest that changes in climate could alter trophic dynamics. If predictions for increased intensity and frequency of drought in western North America (Cook et al. 2004, Brookshire and Weaver 2015) are correct, dry conditions in temperate grassland of this region could experience large changes in trophic structure. My study demonstrates one mechanism by which climate, not invasions or extirpation of predators, can elicit trophic cascades. I used trophic cascades to reveal trophic structure in grasslands and show predators and resources maintain the structure, function, and diversity. If my results are general, it may mean that there are no simple generalizations of food web structure that are independent of climate.
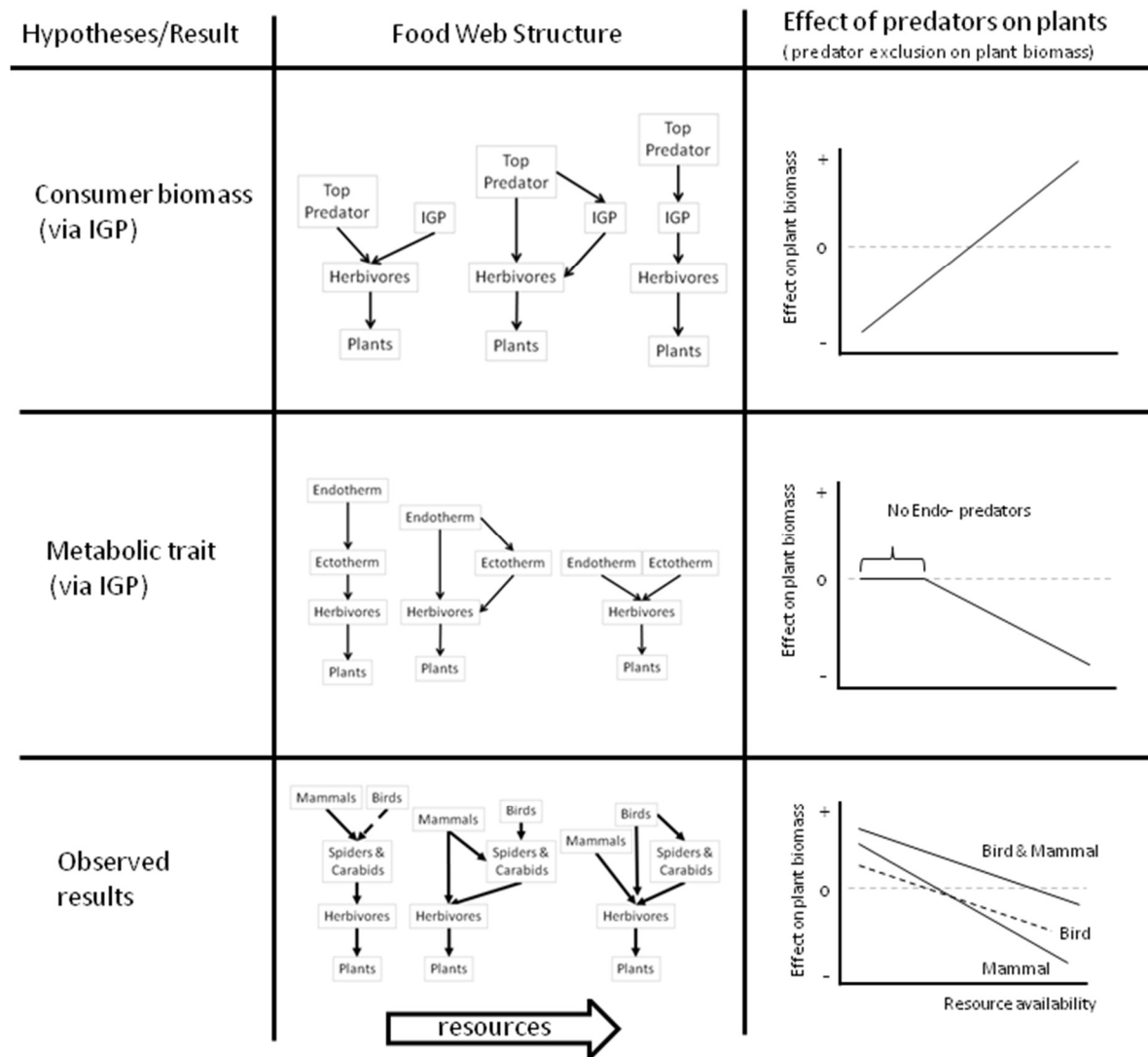
Figure 3.1. Alternative models of species interactions in areas with different levels of water availability to plants. Rows represent predictions from either the consumer biomass hypothesis, metabolic traits hypothesis, or for comparison observed results. All models transition through a state with balanced intraguild predation as the effect of predator removal on plants changes from a three-level to four-level trophic cascade. Columns represent responses along the gradient of water availability in predator abundance, they show either changes in food webs structure or changes in the magnitude of predator effects. Under the metabolic trait hypothesis, the effect of predator removal on plants illustrates a condition where endothermic predators are nearly absent, and thus a four-level cascade (positive effect of predator removal on plants) does not occur.
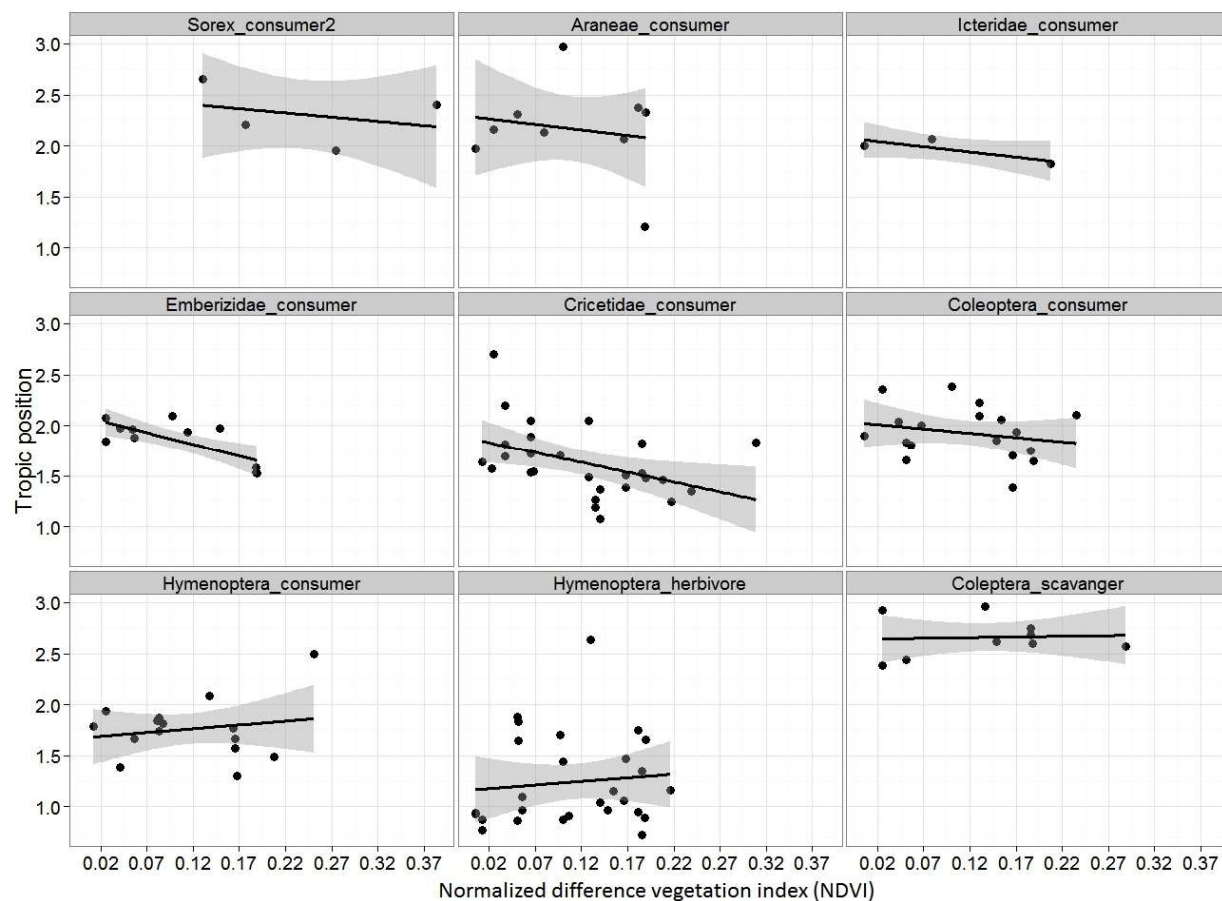
Figure 3.2. Trophic position estimated from stable isotopes of nitrogen and carbon taken from blood and tissue of seven taxa sampled along a gradient of plant productivity (NDVI - normalized difference vegetation index). Each point represents a value for one individual animal and individual animals were sampled at a range of water availability in each category. Lines represent generalized linear mixed model fits for each family_trophic position group with genera as a random effect. The 95% confidence intervals are shaded. Significance levels from linear models are provided in the Table 3.1.
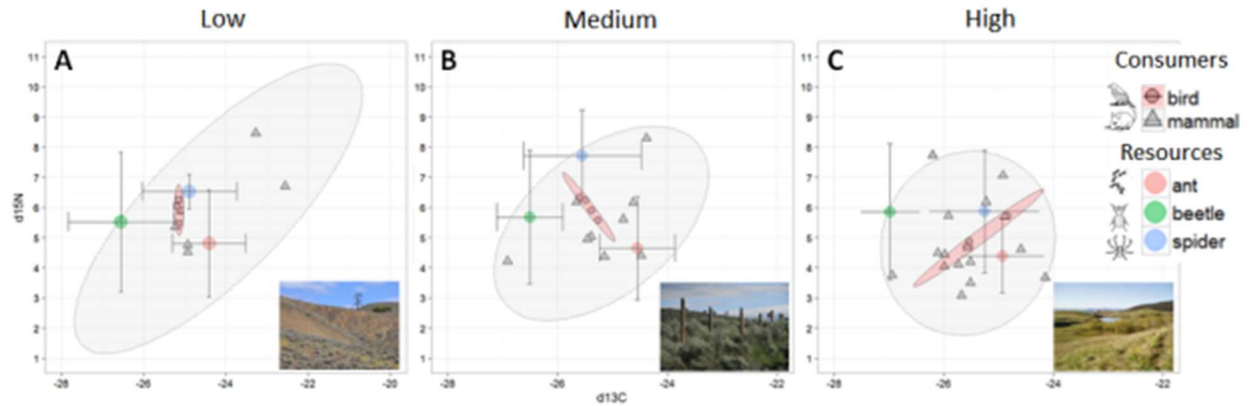
Figure 3.3. Values for stable isotopes of carbon and nitrogen obtained from small mammals and songbirds during the growing season at three levels of relative water availability to plants (Low, Medium, High). Each point represents the δ^{13}C and δ^{15}N values from a single animal sampled between 2010 and 2013. Values for consumers (songbirds and small mammals) are plotted relative to their three most abundant arthropod food resources (ants, beetles, and spiders). Ellipses represent 90% confidence intervals on songbirds (dark/red) and mammals (light grey). The closer a bird or small mammal value is to the source the more likely it is to consume that prey. The closer an individual point is to a source is suggestive of the proportion of that source in the diet of the consumer. The size of ellipse approximates diet breadth.
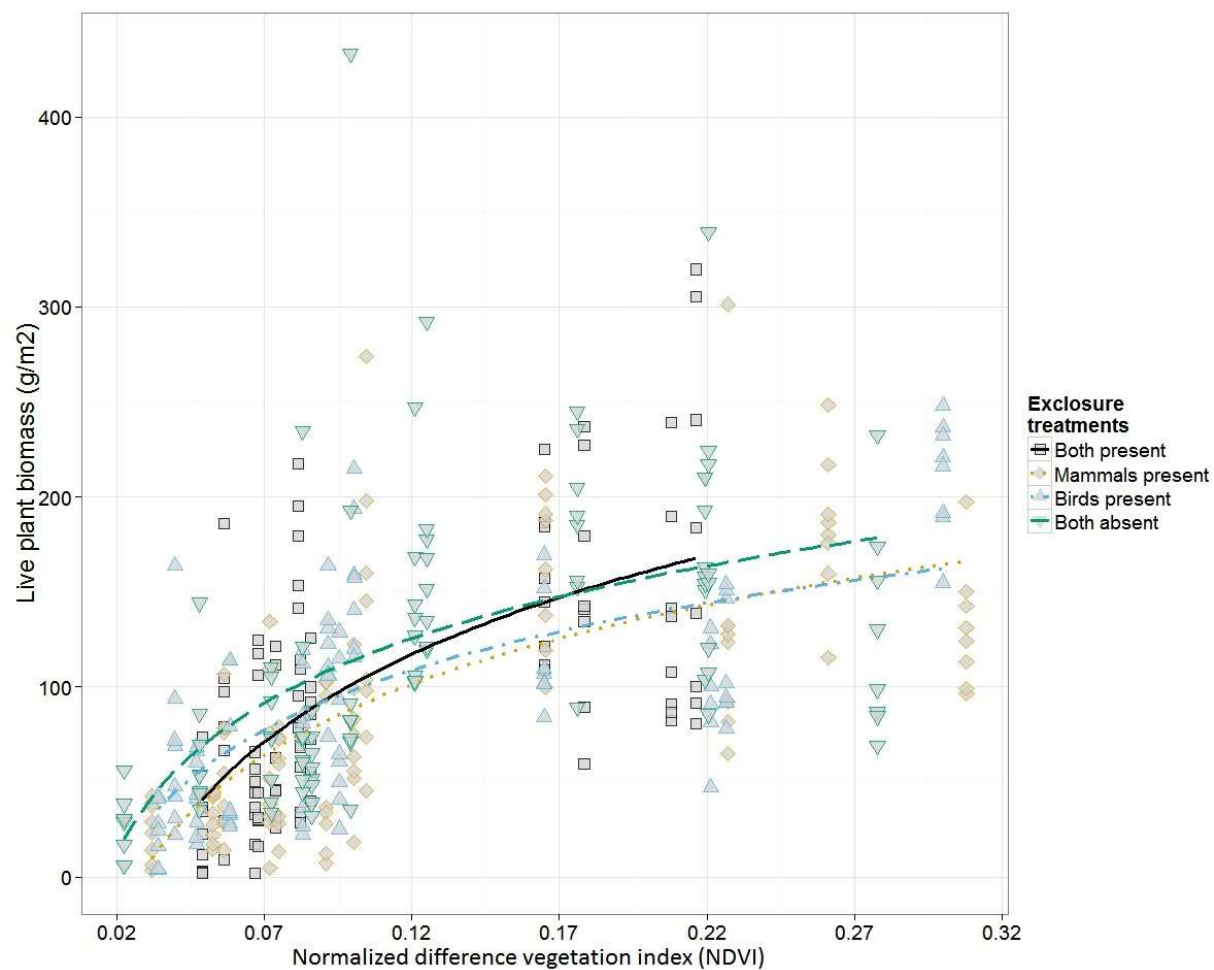
Figure 3.4. Live plant biomass response to the exclusion of songbirds and small mammals from temperate grasslands from 2009 to 2013 along a gradient plant productivity (NDVI). Songbirds and small mammals were excluded from 48, 9m x 9m plots for four years prior to the measurement of biomass. Lines show the generalized linear models for change in live biomass with NDVI. The results of generalized linear mixed models are provided in the text. Significance values are provided in Table 3.2.
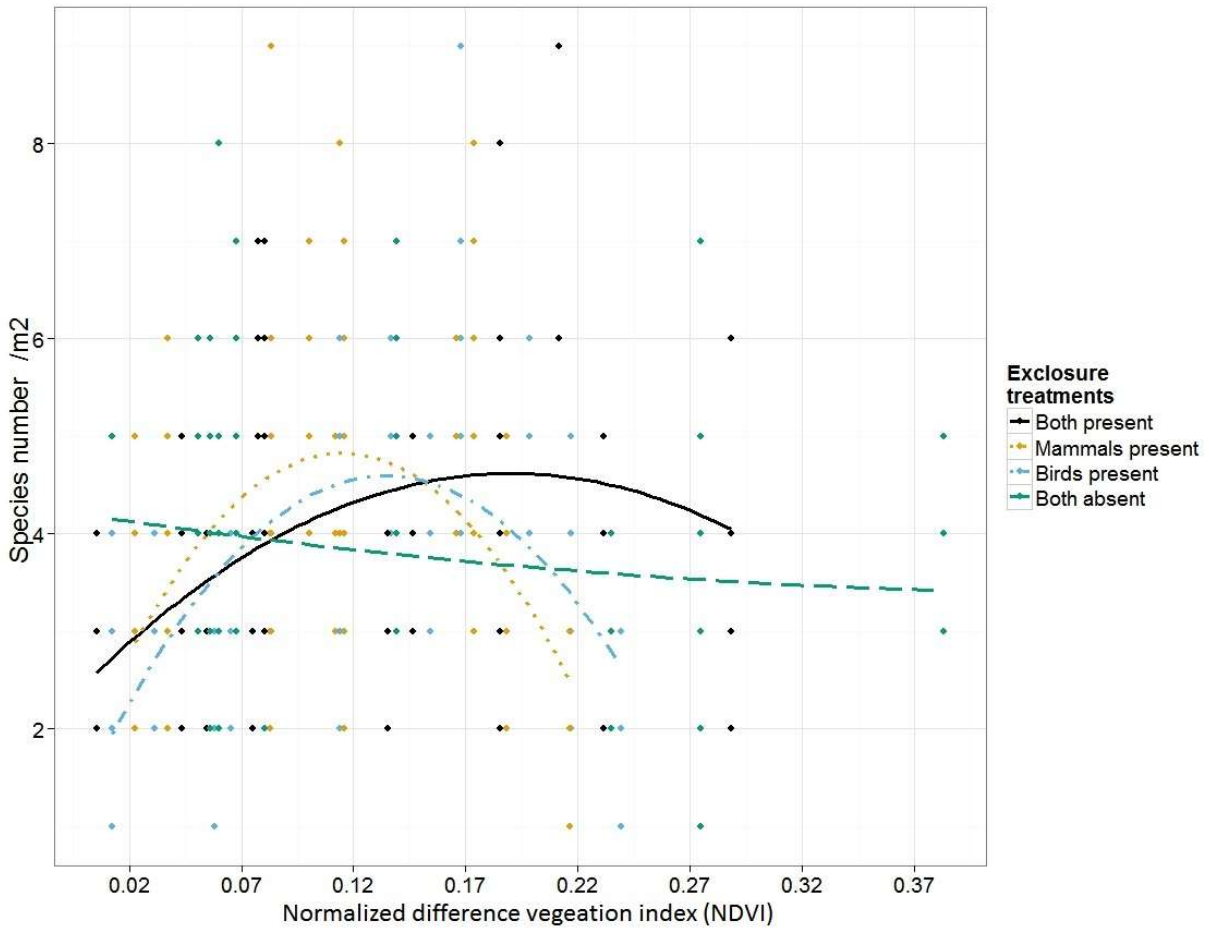
Figure 3.5: The response of in the number of plant species to the exclusion of songbirds and small mammals from temperate grasslands from 2009 to 2013 along a gradient of plant productivity (NDVI). Songbirds and small mammals were excluded from 48, 9m x 9m plots for four years prior to the measurement of species richness. Lines show the generalized linear mixed models (Poisson errors) for change in species number with NDVI. The results of generalized linear mixed models are provided in the text. Significance values are provided in Table 3.3.
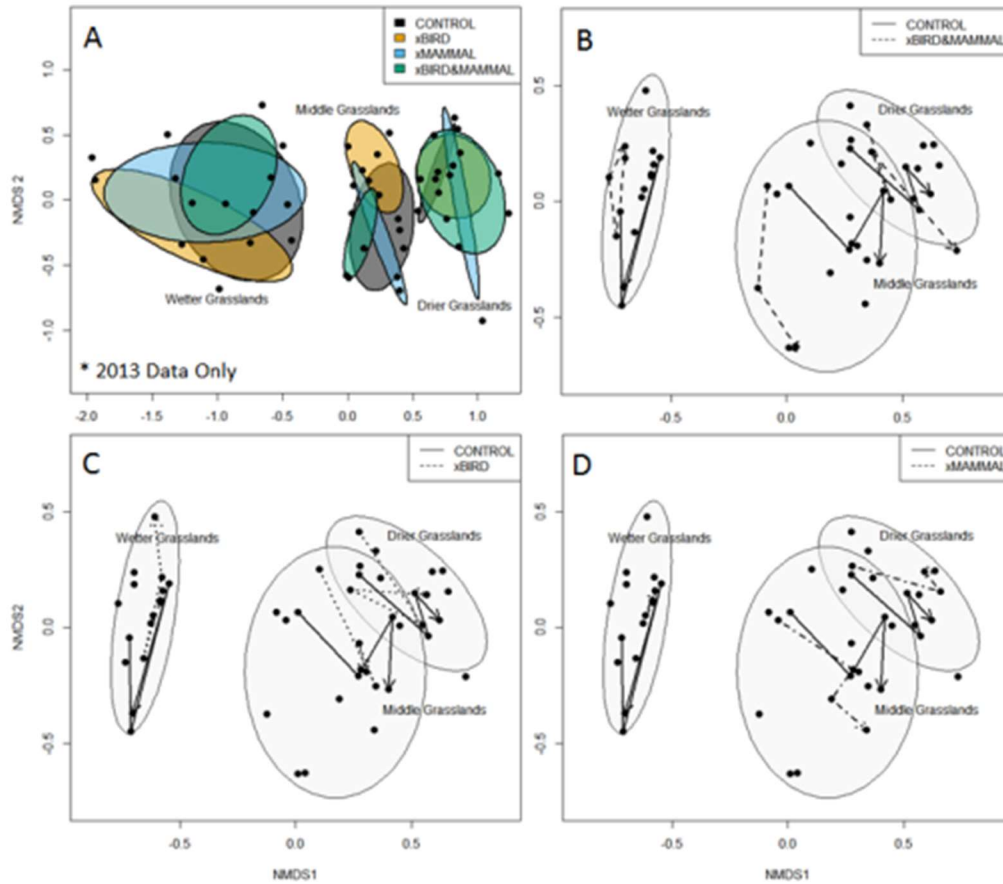
Figure 3.6. Non-metric multidimensional scaling (NMDS) plot of plant community composition based on visual percent cover. Panel A shows the composition of plant communities at three levels of water availability to plants after four years of treatment (2013 data only). Ellipses are based on 95% standard errors. Panels B, C, and D show the dispersion of values in each plant community for each level of water availability, and show the trajectory of change in each plant community with predator exclusions from 2010 to 2013. The change in community composition over time is shown for songbirds and small mammal exclusion plots (Panel B) and for only songbird exclusions (Panel C) and small mammal exclusions (Panel D). Each point represents the mean percent cover value for species by cases averaged over four sites. Arrows represent trajectory of community change from 2010 to 2013 in each level of water availability and predator exclosure treatment. Ellipses in panels B, C, and D are 90% confidence intervals based on standard deviations. The results of PERMANOVA statistical tests are provided in Table 3.4.
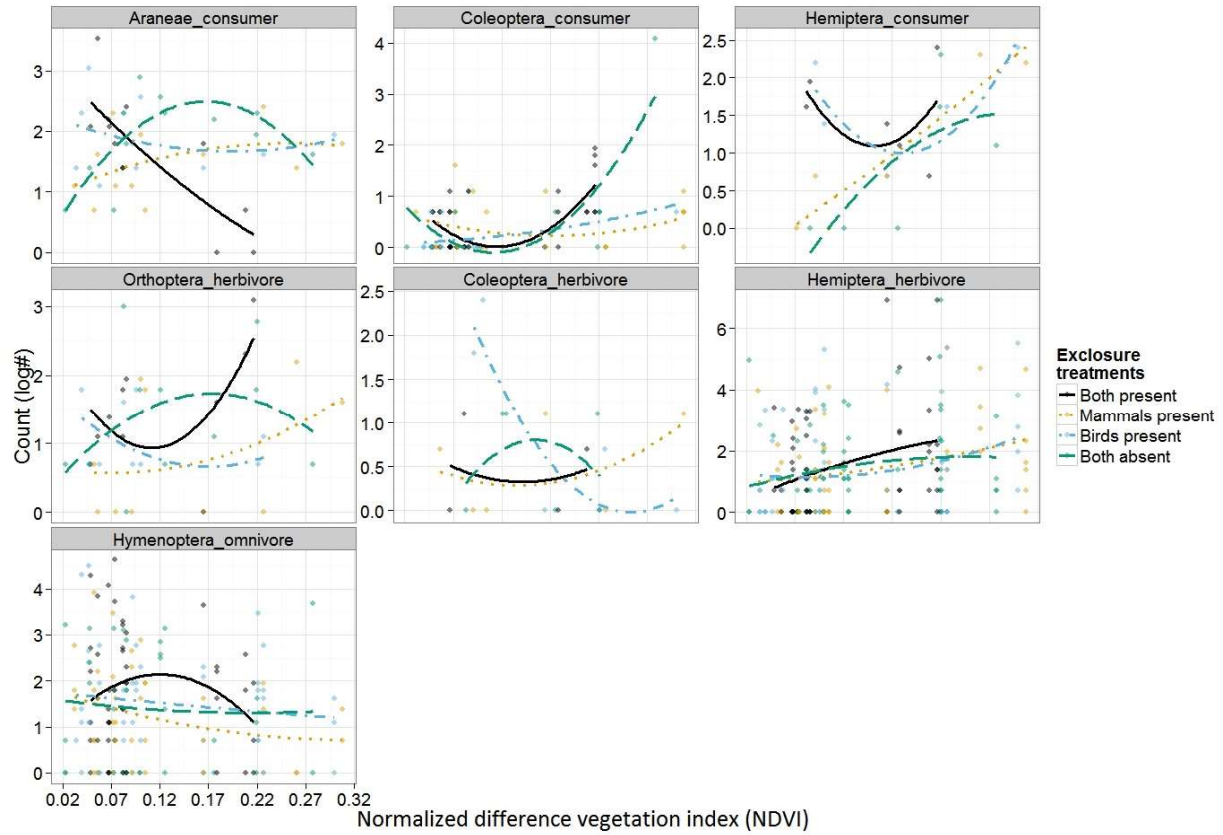
Figure 3.7. Number of individuals within different arthropod functional groups in each experimental treatment along a gradient plant productivity (NDVI). Each point represents the collection of 4 pitfall traps open for 6 days twice (spring and fall) of 2013. Treatments excluded birds and small mammals, for both together from 2009-2013. Lines represent fitted results of generalized linear models. Results of statistical tests are provided in Table 3.5.

Table 3.1. Estimated trophic position (TP) and slope of relationship (with NDVI) generalized linear mixed models (GLMM) with genus as random effect to remove the variability due to multispecies groups. For each group trophic level tropic Position (TP) at low elevation, the slope coefficient and their standard errors (SE) are reported. Trophic positions were estimated with methods outlined in Post (2000) and categorical tropic levels assigned with the delta15N values from the lowest values of water availability (i.e., min(NDVI)).

Common Name	Family_trophiclevel	TP(SE)	Slope	X²	p-value	R²
Shrews	Soricinae_consumer2	2.5 (0.46)	-0.8 (1.8)	0.2	0.640	0.068
Carrion beetles	Silphidae_consumer2	2.6 (0.23)	0.1 (0.84)	0.0	0.877	0.002
Meadowlarks	Icteridae_consumer	2.1 (0.09)	-1.0 (0.72)	2.0	0.158	0.499
Sparrows	**Emberizidae_consumer**	**2.1 (0.15)**	**-2.3 (0.70)**	**11.0**	**<0.001**	**0.400**
Voles and mice	**Cricetidae_consumer**	**1.9 (0.20)**	**-1.9 (0.82)**	**5.7**	**0.017**	**0.147**
Spiders	Araneae_consumer	2.3 (0.53)	-1.1 (2.3)	0.2	0.641	0.015
Ants	Formicidae_consumer	1.7 (0.16)	0.7 (1.1)	0.4	0.502	0.029
Ground beetles	Carabidae_consumer	2.0 (0.20)	-0.9 (0.94)	0.8	0.364	0.034
Ants	Formicidae_herbivore	1.2 (0.24)	0.20 (1.1)	0.0	0.851	<0.001

Table 3.2. Results of Type III ANOVA on nested mixed effects model examining the effect of water availability to plants (NDVI) and bird and mammal exclusions on live plant biomass and detritus mass. The amount of live biomass in treatments relative to controls was assessed by excluding songbirds and small mammals for four years. The normalized difference vegetation index (NDVI) and biomass where log transformed, and random effects are exclosures (n=8) nested in blocks (n=6). The three way interaction was never significant and thus omitted. In the detritus model all interactions were non-significant and thus omitted.

Response	Variable	Chisq	df	p-value
Live biomass	**Intercept**	**316.01**	**1**	**<0.001**
R^{2}m = 0.391	**Log(NDVI)**	**20.19**	**1**	**<0.001**
R^{2}c = 0.507	Bird	0.03	1	0.858
	Mammal	1.27	1	0.260
	log(NDVI):bird	0.26	1	0.455
	log(NDVI) x mammal	**5.71**	**1**	**0.017**
	Bird x mammal	**3.80**	**1**	**0.051**
Detritus mass	**Intercept**	**356.18**	**1**	**<0.001**
R^{2}m = 0.388	**log(NDVI)**	**47.91**	**1**	**<0.001**
R^{2}c = 0.509	Bird	0.05	1	0.830
	Mammal	**4.23**	**1**	**0.040**

Table 3.3. Results of Type III ANOVA on nested mixed effects model with Poisson errors examining the effect of water availability to plants (NDVI) and bird and mammal exclusion on plant species number. The normalized difference vegetation index (NDVI) was log transformed and random effects are exclosures nested in blocks.

Model	Term	Chisq	df	p-value
Full Model	**Intercept**	**335.62**	**1**	**<0.001**
R^{2}m = 0.101	Poly(**NDVI**,2)	0.99	2	0.609
R^{2}c = 0.145	Bird	2.35	1	0.125
	Mammal	1.84	1	0.175
	Poly(NDVI,2) x Bird	**10.44**	**2**	**0.005**
	Poly(NDVI,2) x Mammal	**8.97**	**2**	**0.011**
	Poly(NDVI,2) x Bird x Mammal	**4.87**	**1**	**0.027**
	Poly(NDVI,2) x Bird x Mammal	**10.59**	**2**	**0.005**

Table 3.4. Results of PERMANOVA testing for the differences in plant species composition of the plant community with treatments and along a gradient of water availability to plants. The abundance of live plants was determined by measuring species cover in each year and correlating this with the total live plant biomass per plot. Grassland types include areas with high, moderate, and low water availability to plants. Predator treatments include the exclusion of birds and small mammals, exclusion of only birds, and exclusion of only mammals.

Term	df	F-value	p-value	R^2
Grassland Type	2	63.7	<0.001	0.635
Year	1	9.7	<0.001	0.048
Predator treatment	3	3.5	<0.001	0.053
Grassland Type x Year	2	2.1	0.030	0.021
Grassland Type x Predator	6	2.6	<0.001	0.079
Residuals	33	--	---	0.164
Total	47	--	---	1.000

Table 3.5. Results of Type III ANOVA on nested mixed effects model with Poisson errors examining the effect of water availability to plants (NDVI) and bird and mammal exclusion on arthropod functional group abundance. Random effects include genus nested in 6 experimental blocks. Models were all reduced by omiting non-significant interaction.

Functional Group	Taxonomic Group	Term	LR Chisq	df	p-value
Primary consumer	Araneae R^2m = 0.422 R^2c = 0.422	Intercept	260.5	1	<0.001
		Poly(NDVI,2)	**26.9**	**2**	**<0.001**
		Bird	**4.0**	**1**	**0.045**
		Mammal	0.4	1	0.547
		Poly(NDVI,2) x Bird	**39.5**	**2**	**<0.001**
		Poly(NDVI,2) x Mammal	**15.5**	**2**	**<0.001**
	Coleoptera R^2m = 0.414 R^2c = 0.414	Intercept	8.3	1	0.004
		Poly(NDVI,2)	**156.8**	**2**	**<0.001**
		Bird	1.1	1	0.294
		Mammal	0.2	1	0.621
		Poly(NDVI,2) x Bird	**33.2**	**2**	**<0.001**
		Poly(NDVI,2) x Mammal	**92.9**	**2**	**<0.001**
		Bird x Mammal	3.3	1	0.069
		Poly(NDVI,2) x Bird x Mammal	**24.8**	**2**	**<0.001**
	Hemiptera R^2m = 0.733 R^2c = 0.733	Intercept	9.3	1	0.002
		Poly(**NDVI**,2)	6.0	2	0.051
		Bird	**4.4**	**1**	**0.035**
		Mammal	0.1	1	0.712
		Poly(NDVI,2) x Bird	**11.7**	**2**	**0.003**
		Poly(**NDVI**,2) x Mammal	2.3	2	0.314
		Bird x Mammal	0.08	1	0.772
Herbivore	Orthoptera R^2m = 0.063 R^2c = 0.482	Intercept	38.9	1	<0.001
		Poly(NDVI,2)	**49.6**	**2**	**<0.001**
		Bird	**29.2**	**1**	**<0.001**
		Mammal	2.6	1	0.108
		Poly(NDVI,2) x Bird	**73.1**	**2**	**<0.001**
		Poly(NDVI,2) x Mammal	**46.6**	**2**	**<0.001**
		Bird x Mammal	**1.6**	**1**	**0.019**
	Coleoptera R^2m = 0.387 R^2c = 0.414	Intercept	2.5	1	0.116
		Poly(**NDVI** ,2)	0.6	2	0.731
		Bird	0.9	1	0.337
		Mammal	0.0	1	0.858
		Poly(**NDVI**,2) x Bird	3.2	2	0.202
		Poly(**NDVI**,2) x Mammal	2.3	2	0.317
		Bird x Mammal	1.2	1	0.281
	Hemiptera R^2m = 0.074	Intercept	62.5	1	<0.001
		Poly(NDVI,2)	**327.7**	**2**	**<0.001**

	R²c = 0.648	Bird	129.9	1	<0.001
		Mammal	231.4	1	<0.001
		Poly(NDVI,2) x Bird	323.5	2	<0.001
		Poly(NDVI,2) x Mammal	267.3	2	<0.001
		Bird x Mammal	153.9	1	<0.001
		Poly(NDVI,2) x Bird x Mammal	382.5	2	<0.001
Omnivore	Hymenoptera R²m = 0.339 R²c = 0.464	Intercept	50.0	1	<0.001
		Poly(NDVI,2)	0.9	2	0.636
		Bird	5.4	1	0.020
		Mammal	13.1	1	<0.001
		Poly(NDVI,2) x Bird	12.1	2	0.002
		Poly(NDVI,2) x Mammal	14.4	2	<0.001
		Bird x Mammal	24.2	1	<0.001

3.6   Supplemental figures

Figure S3.8. The proportion of small mammal traps filled at 96 survey sites sampled along a gradient of plant productivity (NDVI). Trapping occurred using four traps over a single trapnight following and six day prebaiting period in the fall of 2009, spring and fall of 2010, and spring summer and fall of 2011 and 2012. Water availability to plants along the gradient was estimated using the Normalized Difference Vegetation Index (NDVI) calculated from Landsat TM data.
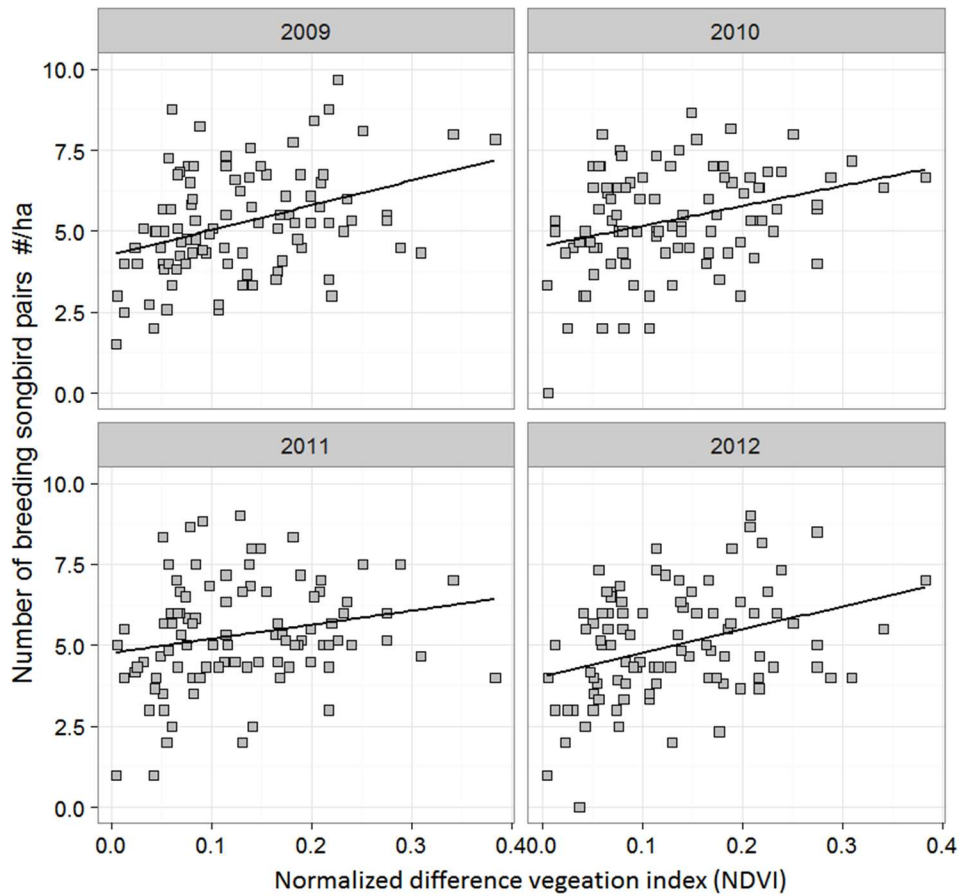
Figure S3.9. The songbird breeding pairs at 96 survey sites sampled along a gradient of plant productivity (NDVI). Occupancy surveys for songbirds were done 3 -5 times per year and songbird density estimated using distance sampling methods (see chapter 2). Water availability to plants along the gradient was estimated using the Normalized Difference Vegetation Index (NDVI) calculated from Landsat TM data.

Chapter 4: Apparent trophic cascades are mediated by the availability of water to plants in temperate montane grasslands

4.1   Introduction

Predators and plants are inextricably linked by the flow of energy through ecosystems. However, it is still difficult to predict how the indirect interactions between predators and plants will influence the fate of primary production and maintenance of diversity in complex natural systems with changing climates. To date, much of the theory of trophic dynamics has either focused on whether ecosystems are controlled by predators (top-down or consumer controlled) or plants (bottom-up or resource controlled). More recently, focus has shifted to identifying factors that determine the strength of trophic cascades in different ecosystems and differences in the strength of top-down control between ecosystems (Schmitz et al. 2000, Shurin et al. 2002, Borer et al. 2005, Turkington 2009). Despite this change in focus and a rich theoretical history (Hairston et al. 1960, Paine 1966, 1980, Menge and Sutherland 1976, 1987, Fretwell 1977, Oksanen et al. 1981), few studies have examined how trophic control in particular ecosystems is altered when the availability of abiotic resources change. With climate change, the distribution of abiotic resources such a nutrients and water will change in many ecosystems and we need examples of how such changes alter trophic control. Understanding the balance of top-down and bottom-up control with changing resources will help develop management and conservation approaches to mitigate the effects of climate change.

Gradients of abiotic resources can provide a foundation for investigations of how trophic dynamics respond to incremental increases in the availability of nutrients or water. Increasing the amount of abiotic resources at the base of food webs is known to affect biodiversity (Duffy et al. 2007, Hillebrand et al. 2009), food web structure (Elton 1927, Lindeman 1942, Odum 1969, White 1978) and ecosystem stability (Paine 1966, DeAngelis et al. 1989, Huxel and McCann 1998, Moore et al. 2004). These effects often manifest themselves in unexpected ways (Halaj and Wise 2002, Moore et al. 2004, Srivastava et al. 2009,

Wolkovich et al. 2014). For example, changes in the feeding behavior of generalist predators resulting from differences in prey availability could change which species interactions dominate food webs. If the strongest impact of predators switches from herbivores to detritivores this could alter the indirect effects of predators on plants (i.e., trophic cascades). Local-scale environmental gradients, such as those on particular mountainsides, allow us to determine how changes in resources abundance influences particular ecosystems (Fukami and Wardle 2005, Sundqvist et al. 2013). In contrast, large disturbances such as El Nino events, hurricanes, or severe drought, produce pulses in abundance and periodic shortages of resources that may affect trophic structure differently than incremental changes in availability. When severe, these disturbances can reset ecosystems (Bond et al. 2005). In this study, I attempt to determine how gradual spatial changes in abiotic resources effects trophic dynamics on a local gradient ranging from semi-arid to temperate grasslands.

Resources can increase through space and time with subsidies. Subsidies that increase plant productivity in ecosystems can occur when slow change in abiotic conditions influences plant production (autochthonous subsidies), or when subsidies offer new resources from outside the ecosystems (allochthonous or cross-ecosystem subsidies) (Knight et al. 2005). One way in which subsidies can produce complicated changes in trophic control is through the establishment of additional energy channels between predators and plants (Wolkovich 2016) (Figure 4.1). New energy channels can provide additional food to generalist predators (Holt and Lawton 1993), cause reversals in the direction of trophic control (Huxel et al. 2002), and result in unanticipated cascading effects on biomass distributions, diversity, and ecosystem function (Loreau et al. 2001, Cardinale et al. 2006, Estes et al. 2011). If additional energy channels establish with increasing plant productivity, and generalist predators receive additional food from this subsidy, then how will the cascading effects of predators on lower trophic levels be affected? Here, I experimentally test the combined effects of generalist predators and abiotic resource

availability on the trophic structure of temperate montane grassland food webs and isolate the effects of live plant productivity from those of detritus.

As resource subsidies increase along abiotic gradients, an apparent cascades may result. Apparent trophic cascades result from the coalescence of the top-down effects of trophic cascades with the lateral indirect effects of apparent competition (Polis and Strong 1996, Polis et al. 1997a). Trophic cascades arise when predators indirectly influence plant abundance or diversity through intermediate consumers (Polis et al. 2000). In a three-level trophic cascade, with a single consumer level between predators and plants, removing predators will reduce plant biomass, whereas in a four-level trophic cascade (two consumer levels) plant biomass will increase when top predators are removed. Apparent competition (Holt 1977, Abrams et al. 1998) describes a situation where negative interactions between primary consumers are regulated by common predators rather than competition for common resources. In an apparent trophic cascade, unlike a classic trophic cascade, generalist predators feed from more than one energy pathway (Figure 4.1.A). Consequently, in an apparent trophic cascade, more bottom-up control in one energy channel results in an increase in top-down control in another (Wollrab et al. 2012, Ward et al. 2015).

As with classic trophic theory, the appearance and strength of apparent trophic cascades should depend on the amount of abiotic resources available at the base of the food web (Hairston et al. 1960, Menge and Sutherland 1976, Oksanen et al. 1981). However, the fate of primary production in multichannel food webs will depend on which energy channel is controlled by predators (top-down control) and which is controlled by resources (bottom-up control). Consider, for example, a grassland food web with a live plant energy channel (i.e., grazing channel) and a detritus energy channel (Figure 4.1.A). If top-down control occurs primarily through the grazing channel (i.e., the classic apparent trophic cascade, abbreviated here as ATCH), we can infer a traditional four-level trophic cascade in which the exclusion of predators results in increased plant growth. Alternatively, if top-down control occurs primarily through

the detritus channel and the original grazing channel remains primarily bottom-up, we have a reverse apparent trophic cascade (r-ATCH). In this situation we could infer a different form of the four-level trophic cascade where the effect of predators on live plants occurs primarily through top-down effects in the detritus channel (Figure 4.1.A). Thus, we can determine which channel experiences top-down control by excluding predators and examining the cascading changes on live plants and detritus.

In addition to affecting the fate of primary production, these types of complicated cascading effects can have large impacts on the diversity and function of ecosystems (Dyer and Letourneau 2002, 2013, Schmitz 2003, 2006, 2008a). For example, when resources are low there may be only enough live plant production to support herbivores, or herbivores and very small populations of secondary consumers. In this case, herbivores are regulated by resources and consume all edible plant biomass. When herbivores consume the majority of live plant production there is little or no plant detritus available to support decomposer communities. As plant productivity rises, it can support large populations of secondary consumers and eventually these generalist consumers begin to regulate herbivore populations. Once regulated by generalist predators, herbivores can no longer consume all live plant production. The uneaten portion of plant biomass become detritus and begins to support decomposer communities (intrinsic factors such as density dependent reproduction could also regulate herbivore numbers but that is beyond consideration here). Generalist predators subsidized by high herbivore abundance could consume more detritivores, subsequently inhibiting decomposition, and ultimately nutrient additions to soil.

We can test for the presence of these complicated trophic structures using experiments that exclude predators or change the abundance of detritus. Excluding predators can signal top-down control by eliciting trophic cascades that change plant biomass through grazing channels, and removing detritus may induce resource limitation of the detritivores, thereby reducing the cascading effects of predators through this channel (Figure 4.1.B). If we add detritus and see no response in detritivores this could also indicate

top-down control of detritivores. In this way we can test the presence of complicated trophic structures (i.e., reticulate food webs) that often stabilize food webs and promote biodiversity.

Because of the importance of understanding reticulate interactions in food webs, and because we have few empirical examples of these systems derived from experiments (Wolkovich 2016), I asked two specific questions about the nature of apparent trophic cascades. First, is the appearance of multiple energy channels, and hence the existence of apparent trophic cascades, dependent on the amount of water availability to plants in temperate montane grasslands? Second, if I detect a version of apparent trophic cascade (alternating top-down and bottom-up control in different channels), does trophic control in the original grazing channel switch from bottom-up to top-down with increased water availability to plants (i.e., an ATCH), or is there simply top-down control in the newly established energy channel (i.e., a reverse apparent trophic cascade or r-ATCH).

The existence of apparent trophic cascades, as opposed to multichannel cascades, is indicated by two patterns. First, exclusion of predators should affect only one of live plant biomass and detritus accumulation. Predator exclusion effects on live plant biomass indicate top-down control of the grazing channel, and predator exclusion effects of detritus accumulation suggest top-down control in the detritus channel. The one exception that might occur here is if there is direct causal link between live plant biomass and detritus mass: greater live plant production may result in more leaf material to senesce or greater detritus accumulation could provide nutrients fueling plant production. Second, negative correlations between herbivores and detritivores would indicate apparent competition and the possibility of multiple energy channels, especially if one channel is top-down controlled.

We can further distinguish between types of apparent cascades (ACTH vs. r-ACTH) by using gradients to examine how predator exclusion and the manipulation of detritus mass changes live plant biomass,

detritus accumulation, and abundances of herbivores and detritivores. Cascading effects of predator exclusion on either live plant biomass or detritus accumulation suggest top-down control on the grazing (ACTH) or detritus (r-ACTH) channels, respectively. Top-down control should coincide with decreases in either herbivore or detritivore abundance. For example, if top-down control occurs in the detritus channel, predator exclusion should result in both an increase in detritivores and a decrease in detritus accumulation with predator exclusion if songbirds and small mammals control detritivore abundance. In this case, if we double detritus in the presence of predators, we should have no effect on detritivore abundance as detritivores are primarily limited by predation (Figure 4.1.B). However, if we remove detritus we may induce food limitation of the detritivores, thereby reducing the cascading effects of predators through this channel. The effects of detritus manipulations will reveal top-down control in the detritus channel if it exists because excluding birds and small mammals would allow spiders and predatory beetles to control detritivores. If this occurs, determining top-down control would rely on the combined response of vertebrate predator removals and detritus manipulations.

4.2   Methods

I tested for the existence and direction of consumer control in a montane grassland with a gradient of water availability to plants in south-central British Columbia. Lac du Bois Grasslands Protected Area near Kamloops, British Columbia, Canada (50°39'59'' N, 120°19'09'' W) encompasses approximately 15,500 ha of grassland that occurs in the rain shadow of the British Columbia Coast Mountains. The entire region is characterized by strong orographic effects with dry hot valleys with shrub-steppe vegetation leading to wetter, colder grasslands at higher elevations. Local differences in precipitation, temperature, soil depth and texture, soil parental material, topography, and aspect all contribute to the structure and composition of local plant and animal communities (Lee et al. 2014).

To assess the existence and direction of trophic control arising from multiple energy channels and changes in resource availability to plants, I manipulated both predators and detritus along a gradient of water availability. The elevation of experimental sites ranged from 400 m to 900 m a.s.l. with lower elevations receiving less rainfall, lower snowfall, and more snow melts before the spring growing season. The presence and persistence of snow during the winter increased with elevation, and the spring melt of this accumulated snow combined with a similar gradient in growing season precipitation with elevation to create a strong gradient of water availability to plants.

To exclude vertebrate predators, I established twelve 9 m X 9 m exclosures (81 m^2) along the gradient of water availability to plants. These exclosures were grouped into six pairs. Each exclosure in a pair was within 100 m of the other, and pairs were always greater than 3 km apart. From 2009 to 2012, I excluded birds and small mammals from one randomly chosen exclosure of each pair. Regardless of this predator treatment, livestock and wild ungulates were always excluded and therefore all twelve plots are referred to as exclosures.

One of each pair of exclosures (6 total) was fenced and netted to exclude vertebrate predators of arthropods. To exclude small mammals, I placed galvanized steel mesh fencing on the perimeter of exclosures to prevent the entry of deer mice (*Peromyscus sp.*), voles (*Microtus sp.*) and shrews (*Sorex sp.*). The mesh fence was 1.0 m – 1.5 m high, had a mesh size of 6 mm, and it was buried in the ground below the plant rooting depth (~ 30 mm). To exclude all birds, I covered the 6 predator exclosures (i.e., those with small mammal fencing) with 20 mm extruded polypropylene mesh netting. I began building the exclosures in the autumn of 2009 and dismantled them in the autumn of 2013.

All twelve exclosures was divided into four quarters (3 x 3 m, or 9 m^2 square plots), each of which received a different detritus treatment. In each of the four years the experiment ran, I manipulated the

amount of detritus in plots nested inside each exclosure. In three of the four quarters, all dead plant material (detritus) was removed. The remaining square was left untouched as a control. As a treatment control, I returned the detritus collected in one plot back to that site. Then, the remaining detritus from the other two quarters was combined and returned to a single square. This left one quarter with no detritus, and one quarter with twice the amount of natural detritus present at this location. This procedure resulted in four randomly placed treatments: (1) no change (Control), (2) the complete removal of detritus (No Detritus), (3) replacement of natural amount of detritus (Treatment Control), and (4) double the natural amount of detritus (2x Detritus).

4.2.1   Experimental effects on plant abundance

To assess the response of live plants to predator and detritus treatments I estimated the visual percent cover of plants by species in eight, 50 cm x 50 cm (0.25 m^2) subplots placed systematically in each exclosure (N = 2 per detritus plot or quarter). I did this during each growing season from 2010 to 2013. At the end of the experiment (autumn of 2013) I cut, collected, and weighed all vegetation in the 96 plots, and correlated these samples with visual cover estimates to estimate changes in plant communities over time. I collected all living and dead plant material from each of the 96, 0.25 m^2 plots. Any plant material that was decomposed to the point that it could not be identified as a species of plant was left at the site. All samples of both live plant and detritus were air dried for at least two weeks, dried in an oven at ~60°C for >48 hours, and then the mass was determinate to the nearest gram. As I could not collect live plant biomass throughout the experiment without affecting the results, I instead used visual cover estimates from 2010 through 2012 to predict live plant biomass measured in 2013. I standardized the percent cover estimates from 2013 to 1.0 and correlated these with dry mass of living biomass on the plots.

4.2.2   Experimental effects on plant diversity

To measure how predators and detritus treatments impact plant species number, I surveyed the abundance of plant species within each exclosure and detritus treatment every year from 2010 to 2013. At the peak of the growing season I estimated the visual percent cover of each plant species in two, 0.25 m^2 subplots placed systematically within each of the detritus treatments. This resulted in eight subplots in each exclosure and two subplots in each detritus treatment.

4.2.3   Experimental effects on arthropods

Arthropod species' abundance and community composition was surveyed after four years of predator and detritus treatments. During the final year of the experiment (2013), I determined the relative abundance of foliar and ground dwelling arthropods inside detritus treatments at two time periods. Surveys were performed only at the end of the experiment to avoid influencing the response of arthropods with sampling. Two methods were used to count arthropods: pitfall traps (N=1) were used to estimate primarily ground dwelling arthropods, and vacuum sampling (9 m^2) was used to estimate arthropods living on vegetation. Sampling occurred in the summer and autumn to ensure insects were captured emerging at different times during the growing season. All samples from pitfalls and vacuum sampling were sorted and identified to order, genus, or species dependent upon the difficulty of identifying a particular taxonomic group; predatory beetles were identified to genus and ants were identified to species because feeding habits of ants differed broadly between species not genus. Arthropods were sorted and preserved in 95% alcohol in individual vials unique to the taxonomic group, time, and location of collection. I determined the mass of a subsample of arthropods sorted generally to taxonomic group after oven drying specimens for 48 hours at 60°C. Arthropods were classified as either predators, herbivores, or detritivores based either on natural history information on taxonomic groups, or the trophic position calculated from stable isotopes of nitrogen (see Chapter 3).

I used generalized linear mixed models to assess the significance of bird and small mammal exclusions, and detritus manipulations on live plant mass, detritus mass, plant abundance and species number, and arthropod abundance and diversity. All analyses were performed in R 3.1.1 (R Development Core Team 2011). I determined the most appropriate random effect structure by comparing the full model with different random effect structures using Akaike Information Criteria (AIC). The most parsimonious random effects structure allows only the intercept to vary between both blocks and years and so I retained these as random effects. Analyses were done using the function lmer or function glmer in package lme4 (Bates et al. 2015). I specified Gaussian errors in GLMMs for abundance and evenness relationships and Poisson errors for richness relationships. The strength of these relationships was assessed by examining whether the slope of the regression was different than zero or different than another treatment. I assessed the existence of a hump-shaped relationship between NDVI and species richness or biomass using Likelihood Ratio tests to determine if a quadratic form of the statistical model fit the data better than the simpler linear form. I tested the response of live biomass and detritus mass in each detritus treatment with separate linear models.

4.3   Results

4.3.1   Experimental effects on plant abundance

There was no cascading effect of predator removals on live plant biomass across the gradient and only a limited effect of manipulating detritus on live plant biomass. As water availability increased, live plant biomass increased and supported a greater abundance of organisms at all trophic levels (Figure 4.2 - top row). The removal of predators resulted in an increase in live plant biomass in areas where water was abundant (Figure 4.2B, Table 4.1). When water was scarce and birds and small mammals excluded, there was a small reduction in live plant biomass when detritus was removed (Figure 4.2A). When water was abundant, there was a small increase in plant biomass along the entire gradient when detritus was doubled (Figure 4.2C).

There were large cascading effects of predator removals on the amount of detritus that remained after four years, and the presence of the cascading effects was dependent on detritus treatments. The amount of detritus was also dependent on water availability to plants as amount of detritus increased with increasing water availability to plants along the entire gradient (Figure 4.2 - bottom row). The cascading effect of predator removal on detritus mass occurred when water was abundant (Figure 4.2E; Table 4.1). When detritus was removed, there was no cascading effect of predator removals on detritus (Figure 4.2D). However, there was an interacting effect of predator additions along the gradient that occurred when detritus was doubled (Table 4.2). Here, sites where predators were present became more like sites where predators were removed. This occurred both in detritus control plots and in doubling treatments (Figure 4.2F). In general, doubling detritus caused more detritus to accumulate especially in areas where water was abundant. Doubling detritus did not change the top-down cascading effect on predators. Thus, removing detritus appeared to stop the cascading effects of predator exclusions.

4.3.2   Experimental effects on plant diversity

The cascading effects of predator exclusion on the number of plant species was also mediated by water availability to plants (Table 4.3). There was an underlying hump-shaped relationship between the number of plant species with availability of water to plants (**Error! Reference source not found.** - solid lines). The shape of this richness-productivity relationship was dependent on both the presence of predators and the presence of detritus, although the effect of predator removals was greater than the effect of detritus manipulations. When predators were present, the doubling of detritus flattened the hump-shaped relationship (Figure 4.3A, dashed line). When predators were excluded, the addition and removal of detritus increased the number of plant species, especially at wetter sites (Figure 4.3B, dashed and dotted lines). Neither of these trends were significant. I also separated wetter and drier sites to examine only the effect of predators and detritus (Table 4.3). At drier sites, the exclusion of predators decreased plant

species by approximately 0.8 species/m^2. When water was abundant, the exclusion of predators increased species richness by about 1.7 species/m^2. Again, there changes in plant species number were non-significant.

4.3.3 Experimental effects on arthropods

To determine if apparent competition occurred between arthropod herbivores and detritivores I looked for correlated changes in their abundance along the gradient. Herbivore and detritivore numbers were always negatively correlated (Figure 4.4; Tables 4.4 and 4.5) although this correlation was weak (detritivore ~ herbivore: $\chi^2 = 3.3$, p = 0.067 overall). Herbivore abundance increased along the gradient with plant abundance and water availability to plants, and despite large increases in the amount of plant detritus, detritivore abundance decreased on the gradient. These declines were not significant (Table 4.4). When detritus was removed, detritivore number was dependent both on herbivore number but not the predator treatment (Figure 4.4A, Table 4.4). This was especially true when water was abundant (predator x herbivore: $\chi^2 = 4.2$, p = 0.040). When detritus was doubled, there remained correlations between herbivores and detritivores (Figure 4.4C, Table 4.4) and an interaction with predator treatments. Detritivore number was not dependent on predator treatment or position on the gradient.

The abundance of arthropod functional groups was generally dependent on the gradient, but the effects of predator removals were seen mostly in carnivorous and omnivorous arthropod abundance. The exclusion of birds and small mammals allowed carnivore abundance to increase when water was abundant, and caused omnivore numbers to increase especially when detritus was available (Table 4.5). When detritus was removed and birds and mammals excluded, omnivores began to respond strongly to the gradient (NDVI: $\chi^2 = 18.9$, p = <0.001; NDVI x predator: $\chi^2 = 14.1$, p = <0.001) and increase in abundance in areas were water and detritus were abundant. Detritivores responded positively to predator removals but

declined along the gradient. In contrast herbivores were unaffected by the predators or detritus although they generally increase on the gradient.

4.4   Discussion

My data provide the first experimental test of the apparent trophic cascade hypothesis in terrestrial ecosystems with varying resource abundance and autochthonous input of detritus. I show that with increasing water availability to plants, plant production eventually reaches a level that can support a multichannel food web without the input of primary production or pulsed abiotic resources from outside the ecosystem. Of the proposed hypotheses, my results are most consistent with a reverse apparent trophic cascade (r-ATCH), where there is bottom-up control in the original grazing energy channel and top-down control in supplemental detritus channel. The support for the r-ACTH relies on the following observations. Firstly, there were top-down effects of predatory vertebrates effects on both live plants and detritus, arguing against a purely bottom-up multichannel food web. Second, these effects of vertebrate predators on live plants and detritus only occurred when there was sufficient water available to living plants, suggesting strong bottom-up effects of live plants enabled top-down effects on the food web as predicted by r-ATCH. Third, there were also strong negative correlations between herbivores and detritivores in the presence of vertebrates, consistent with some type of trophic coupling between the green and brown food webs. In fact, herbivores appeared to be more affected by water (a bottom-up effect) and detritivores by vertebrates (a top-down effect), suggesting that the direction of this trophic coupling is herbivores->vertebrate predators -> detritivores as predicted by r-ATCH. Finally, although detritus manipulations often affected invertebrates and live plants, such effects were not monotonic. Therefore, the enhancement of the detritus channel did not reverse trophic control in the original grazing energy channel as suggested by the ACTH (Polis and Strong 1996, Ward et al. 2015).

I propose the following trophic dynamics that largely follow the r-ATCH. Live plant production increases with increasing water availability faster than this could be converted to herbivore biomass. As plant production increases, detritus begins to accumulate. At the same time, increasing plant production results in more herbivores, bolstering numbers of predatory invertebrates and birds in the grazing channel. Arthropod predators such as spiders may have also benefited from detritus additions because detritus increased their food sources and their preferred habitat (Schmitz et al. 1997, Wise et al. 1999, Schmitz 2008a, Buchkowski and Schmitz 2015). The consequence of this series of events is that both vertebrate and arthropod predators, supported by an increasing number of herbivores at the wet end of the gradient, will suppress detritivore abundance, increasing the amount of detritus (an r-ACTH).

Although the majority of my results appear to agree with r-ACTH pathways, there are additional complexities in the food web. Most strikingly, the r-ATCH predicts that the live plants cause changes in predatory vertebrates rather than the other way around. While birds and mammals undoubtedly changed in relative abundance over the gradient in water availability to plants (see Chapter 3), I also found evidence that vertebrates depressed live plant and detritus biomass when water was abundant. Thus, there are both top-down and bottom-up links between plants and predatory vertebrates. In order for birds and small mammals to depress live and dead plants, there must be an even number (presumably two) trophic levels between them: predatory invertebrates and their detritivore or herbivore prey.

I did not see strong cascading effects of vertebrates on abundance of predatory invertebrates or herbivores. This could be because I did not have experimental treatments large enough to demonstrate population level changes in arthropod abundance, because I sampled arthropod abundance in only a single year, or because arthropods were allowed to come and go freely from our plots. Alternatively, changes in arthropod species composition or per capita feeding rates might be more important: vertebrates did shift the composition of predatory invertebrates from beetles to spiders and bugs. Finally, an unexplored

possibility is that top-down effects of vertebrates on detritus biomass affected soil nutrition, and therefore live plant production. Regardless of the precise details, live plant and detritus biomass did respond to the combination of: a) water availability; b) manipulations of detritus quantity; and c) vertebrate exclusion, so the mechanism must involve a combination of bottom-up effects of water coupled with trophic dynamics within the arthropod food web.

Unlike previous work with multichannel systems and allochthonous resource subsidies (Polis and Hurd 1996, Halaj and Wise 2002, Schoener et al. 2004, Spiller and Schoener 2008, Tunney et al. 2012, Wright et al. 2013), the establishment of multiple energy channels in my system did not change the direction of trophic control in the grazing channel. Multiple channels between predators and plants should become established when either: 1) there are edible and inedible portions of primary production (Chase et al. 2000, Olff et al. 2009), 2) there are multiple habitats in which generalist predators feed (Ahrens et al. 2012, Tunney et al. 2012), or 3) when energy flow is dominated by keystones (Smith and Knapp 2003, Duffy 2003, Wollrab et al. 2012). My detritus additions could be seen as an autochthonous subsidy because the detritus underpinning the detritus food web comes from primary production occurring within this ecosystem. In other words, the source of abiotic resources, in this case water, for both energy channels is the same and detritus does not arise from a far away source. Unlike previous work, there was no effect of detritus additions or removals on live plant biomass, and thus little support for the supposition that detritus provides a subsidy to predators that drives top-down control of herbivores in the temperate grasslands I studied. This supports my conclusion that a r-ATCH occurs on the wetter parts of my study area.

Detritus inputs arising from uneaten portions of live plants provides new food sources and habitat for arthropods. These arthropods in turn feed generalist vertebrate predators such as birds and small mammals. The inherently internal source of the detritus subsidy suggests and the failure of this subsidy to

reverse the apparent cascade from bottom-up to top-down in the original grazing channel suggests such reversals may be dependent of the source of the resource subsidy. Here, the autochthonous source contrasts with the allochthonous input of detritus that drives the subsidy of predators typically described in other studies (Huxel et al. 2002, Leroux and Loreau 2008). For example, the majority of multichannel studies examined in aquatic systems were combinations of benthic and pelagic systems where predators were able to couple separate habitats (Ward et al. 2015), reversals occurred when subsidies of primary production were transported into ecosystems (Polis and Hurd 1995, Spiller et al. 2010). With the autochthonous subsidy, increases in live plant production outweigh any novel species interactions that occur because one or both energy channels receive increasing energy input from outside the ecosystem.

There is evidence that allochthonous resource subsidies can change the direction of trophic control in ecosystems. However, there are few studies that examine autochthonous inputs especially in terrestrial ecosystems. At the interface of marine and terrestrial systems, spider abundance can increase with marine subsidies to coast beaches (Polis and Hurd 1996, Spiller et al. 2010). Likewise, there is experimental evidence of apparent cascades in German grasslands where subsides to spiders from adjacent riparian areas increase predation on terrestrial arthropod herbivores and increase plant growth (Henschel et al. 2001). Similar effects occur in vertebrates where bird activity was 5 - 7 times higher in riparian areas with aquatic prey subsides (Murakami and Nakano 2002). Thus, cross-ecosystem subsidies can have large effects on trophic structure of adjacent ecosystems. Here, I examine a system with an autochthonous subsidy that has been speculated to change trophic structure (Polis and Strong 1996). I show that despite increasing input of water the direction of trophic control does not change. A new energy channel arises when primary productivity becomes sufficient to support additional prey for generalist predators, but this new energy channel is not sufficient to become the primary prey supporting greater predation by generalist vertebrate predators. Thus, the food web becomes more complex as resource become more

abundant, but the direction of trophic control does not reverse as in other ecosystems where subsidized by allochthonous resources and novel species interactions occur.

There is also evidence that climate can mediate the effect of predators in multichannel systems. In a multi-predator systems with an allochthonous input of marine detritus, ant and lizard effects on herbivores were reduced with the addition of detritus as they switched from their preferred prey to detritivores subsidies by marine inputs (Piovia-Scott et al. 2011). A number of studies have also examined the detritus chains within larger food webs and found both top-down (Halaj and Wise 2002, Lawrence and Wise 2004) and bottom-up control (Chen and Wise 1999, Lawrence and Wise 2004). However, there is emerging evidenced that these interactions are mediated by climate (e.g., Chapter 3) and affect not only food web structure, but also ecosystem function (Lensing and Wise 2006, Liu et al. 2015). Thus, trophic rearrangement in multichannel food webs can occur with changes in resource availability arising from climate change. Here, I show that this can occur even without external input of resources. Ecosystems composed of similar species have a very different trophic structure depending on the availability of water, but autochthonous inputs typical of gradual climatic change does not produce widely different and novel species interactions. These changes could occur at particular sites as water becomes scarce. In temperate grasslands such as the one I study, prolonged drought can reduce plant productivity (Brookshire and Weaver 2015). Reduced productivity from prolonged drought could produce a rearrangement of trophic structure in multichannel grassland food webs.

My results demonstrate how changes in the availability of water can result in rearrangements to trophic structure and changes in trophic control when water availability to plants is either increased or decreased. Presumably, conditions such as persistent drought could reverse the trends towards the establishment of multichannel webs with increasing elevation (Brookshire and Weaver 2015). Additionally, any land use change, such as fire or livestock grazing, that alters the amount of detritus can interact with climate to

exacerbate negative changes in trophic structure brought on by resource shortage such as drought in temperate grasslands. In contrast, any action that promotes the accumulation of detritus could mediate negative effects on climate on plant production and subsequently trophic structure.

4.5 Conclusion

I show that increased primary productivity transferred to higher trophic levels could produce changes in trophic structure without the need to have new sources of plant production arising from outside the ecosystem. Increases in plant growth arising from changes in abiotic resources such as water from climate change could produce increases in plant productivity and rearrangements of trophic structure. Thus, incremental change in abiotic resources could produce large structural changes in food webs without the need for dramatic events such as hurricanes, floods, or even El Nino conditions (e.g., Spiller 1998, Terborgh et al. 2001, De La Maza et al. 2009). Experiments manipulating abiotic conditions support my findings on gradients (Suttle et al. 2007, Spiller and Schoener 2008). They show that food webs can restructure with changes in abiotic conditions predicted by climate change scenarios, and that the restructuring of food webs can produce unexpected cascading effects on biomass distributions, diversity, and ultimately ecosystem function. My manipulations of predators and detritus on a gradient of abiotic conditions demonstrate one plausible mechanism of how these changes could unfold. Multichannel food webs can develop or subside with the predicted changes in resource availability with climate such as persistent drought. These changes in food web structure could have profound implications for the diversity and function of ecosystems.
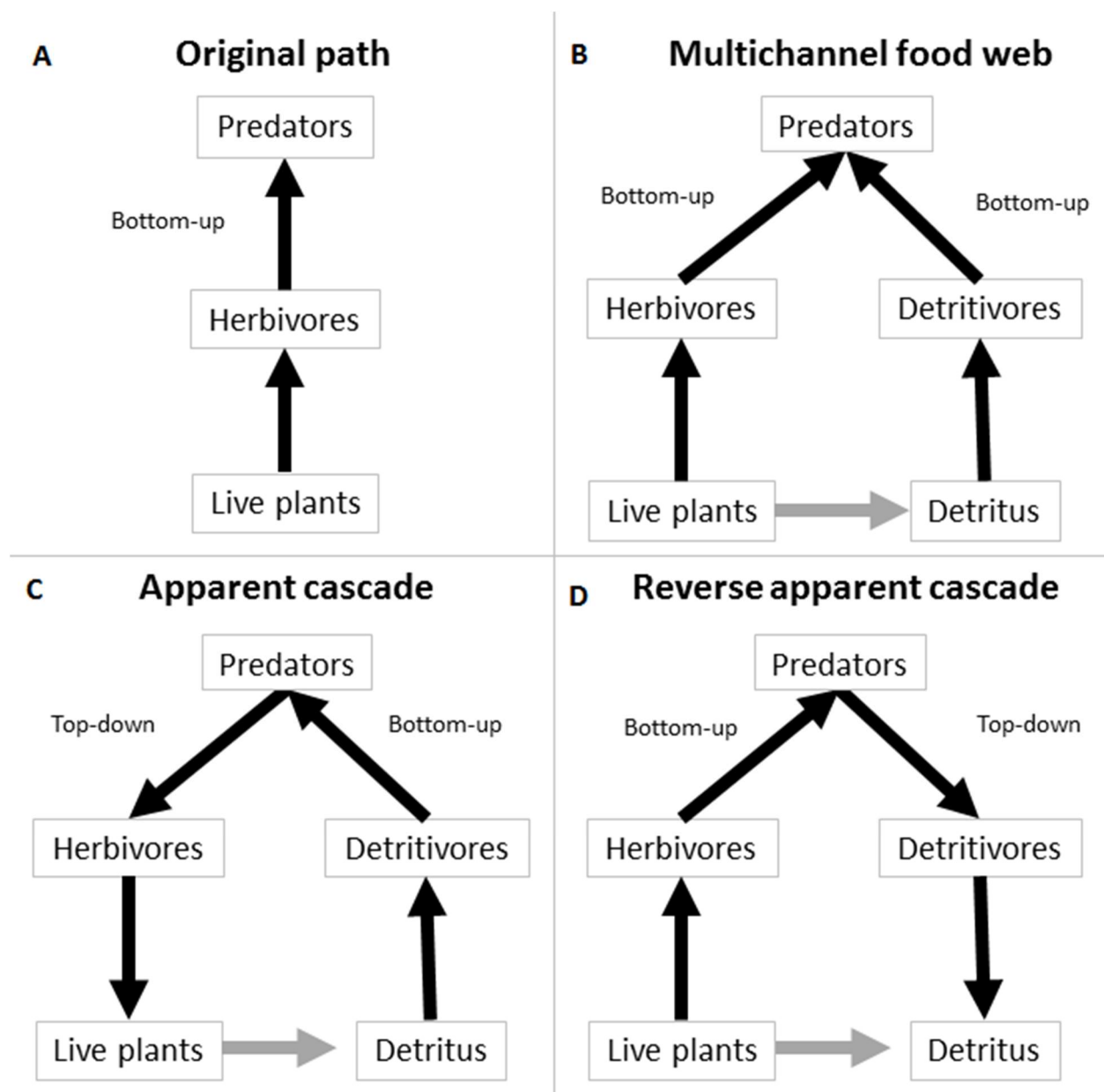
Figure 4.1. Generalized food web relationships and predicted primary consumer responses where a multichannel food web develops. Four possible food webs for ecosystems that change from one resource to two resources systems with increasing primary productivity. Black arrows indicate direction of dominant causal effect, grey arrows show direction of donor control of new energy channel. The case where both channels are top-down controlled suggests strong trophic cascades and is not shown.
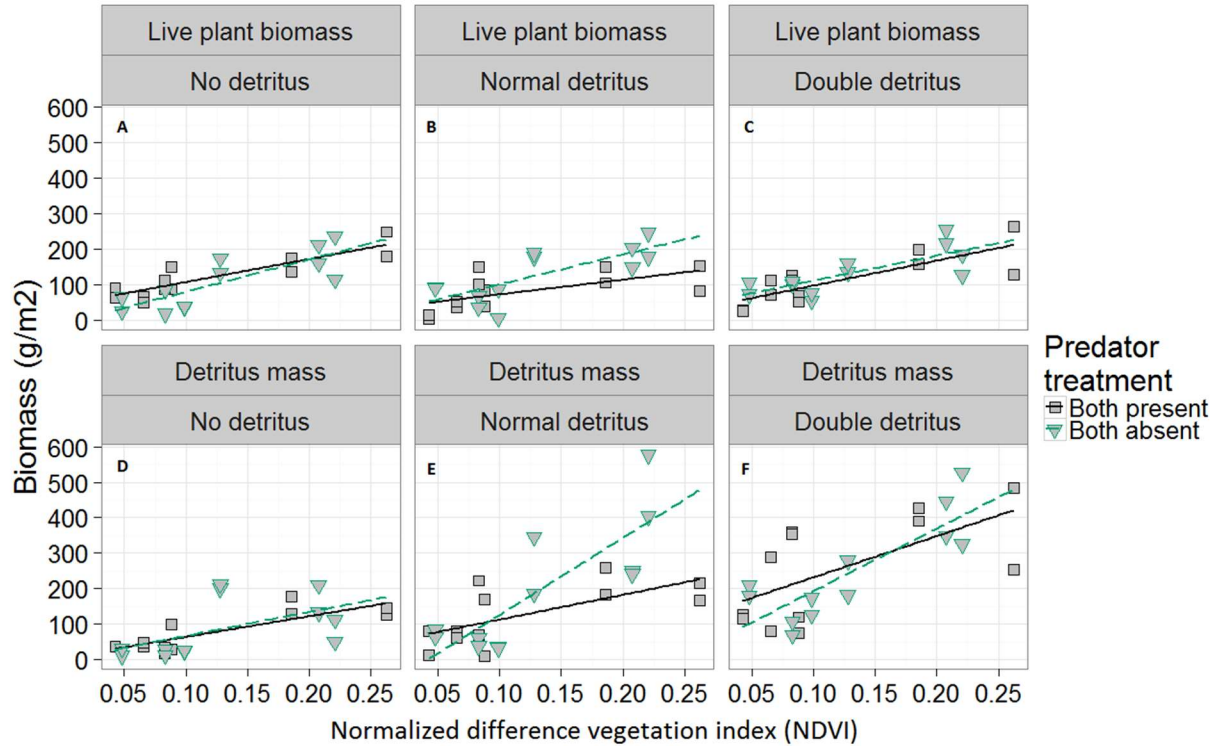
Figure 4.2. The amount of live plant biomass and detritus mass remaining on after four years of excluding songbirds and small mammals along a gradient of plant productivity (NDVI). Points represent the mass of dried plant material either live or detritus counted inside 3 m x 3 m detritus treatment plots nested within 9 m x 9 m predator exclusions. Panels represent areas with different detritus treatments. Detritus was either removed completely (No detritus), doubled (Double detritus), or left untouched (Normal detritus) in the fall of each year. Lines represent fitted values from polynomial least squares regressions from predator removal treatments. Birds and small mammals were either excluded for four years (Both absent, triangles and dotted lines) or allowed to enter and leave plots freely (Both present, squares and solid lines).
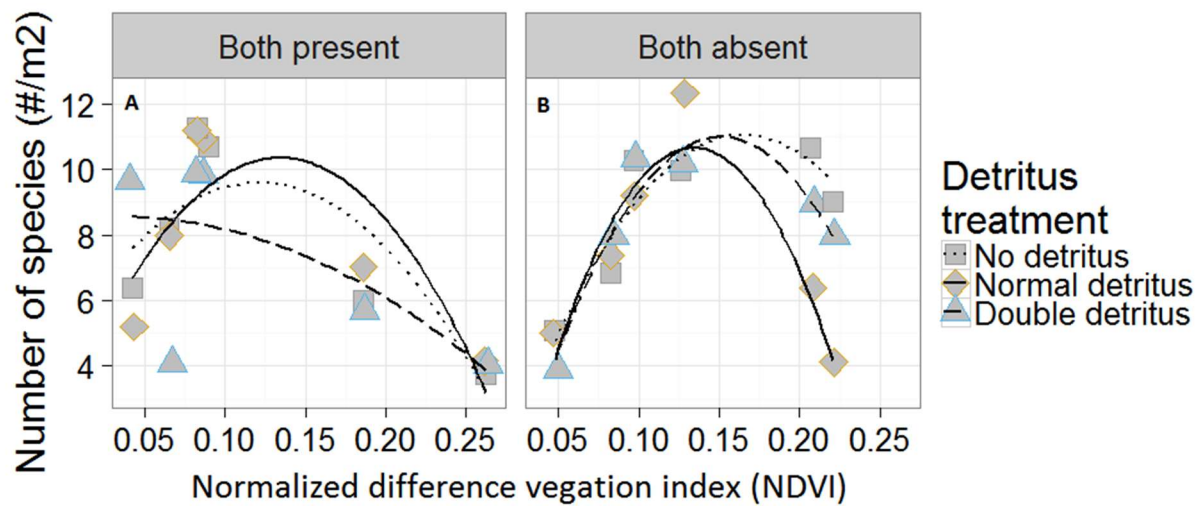
Figure 4.3. The number of plant species present after four years of excluding songbirds and small mammals along a gradient of plant productivity (NDVI). Points represent the number of species counted inside 3 m x 3 m detritus treatment plots nested within 9 m x 9 m predator exclusions. Detritus was either removed completely each fall (No detritus), doubled (Double detritus), or left untouched (Normal detritus) in the fall of each year. Panels represent areas open to birds and small mammals (Both present) and areas where birds and small mammals were excluded for four years (Both absent). Lines represent fitted values from polynomial least squares regressions. Detailed statistical tests are provided in Table 4.3.
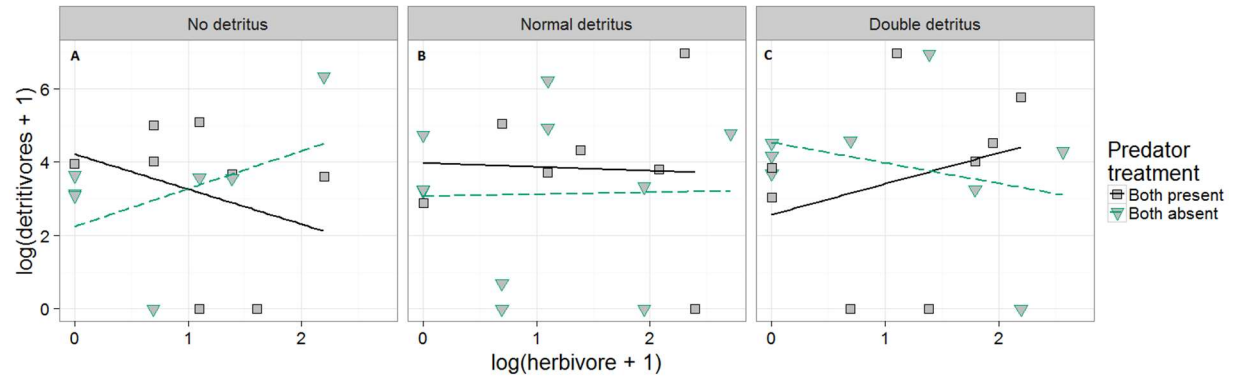
Figure 4.4. Correlation between arthropod detritivores and arthropod herbivore abundance with and without songbirds and small mammals present for three detritus treatments. Each panel represents one of three detritus treatments performed along a gradient of water availability to plants, and hence a gradient in herbivore and detritivore abundance. All detritus was removed each fall for four years (No detritus), and doubled each fall for four years (Double detritus), or plots were left undisturbed (Normal detritus). Detritus treatments were nested inside predator exclusions where songbirds and small mammals were either absent (dotted lines, diamonds) or present (solid lines, squared). Points represent the log+1 transformed counts.
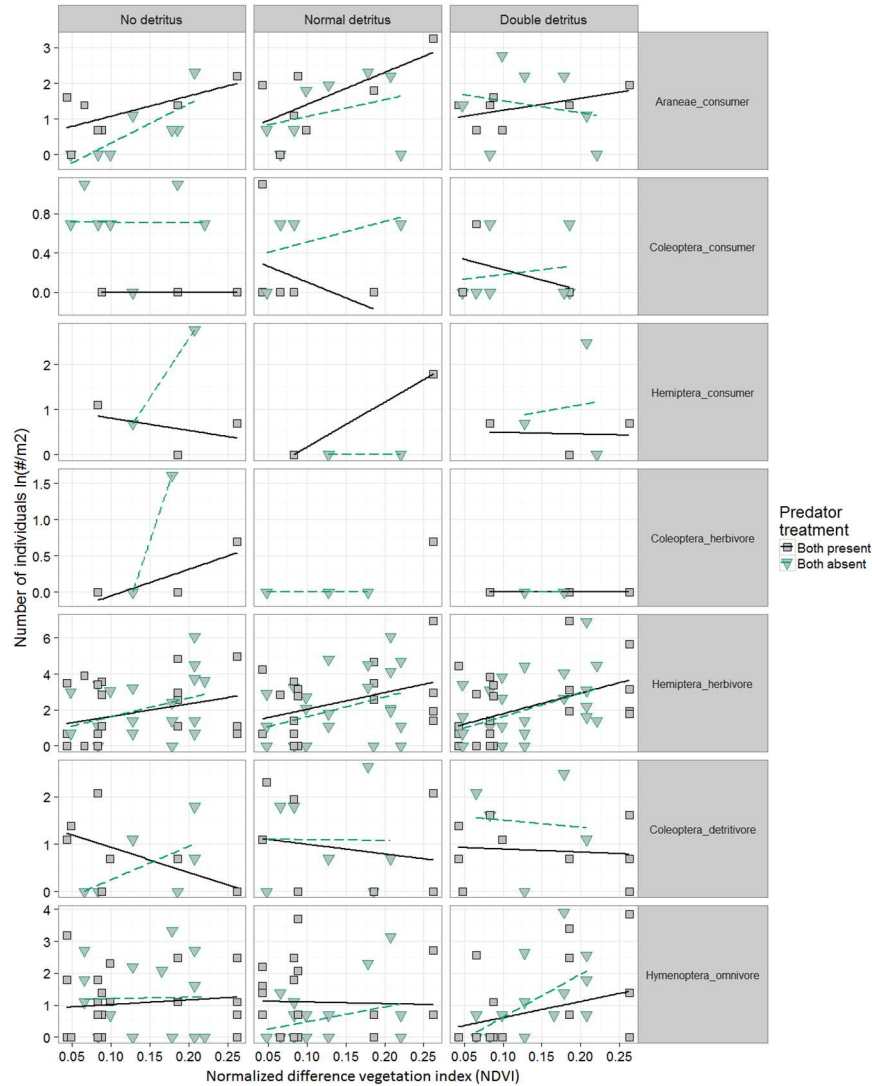
Figure 4.5. Arthropod functional group response to four years of songbirds and small mammal exclusion along a gradient of plant productivity (NDVI). Each panel represents a single family - functional group combination. Response and indicates when songbirds and small mammals were absent for four years (dotted lines, triangles) or present (solid lines, squared). Each point represents spring and fall count from both pitfall traps and vacuum sampling over a 3 X 3 m area combined. Statistical tests are provided in Table 4.5

Table 4.1. The response of live plant biomass and detritus mass to the exclusion of songbird and small mammal (Predator), and the doubling or removal of plant detritus (Detritus) along a gradient of water availability to plants. Water availability to plants was estimated using the normalized difference vegetation index (NDVI). Songbird and small mammal predators (Predator) were excluded for four years, and plant detritus (detritus) was either removed or added within plots nested in predator exclosures. Result are from a type three ANOVA on generalize linear mixed models. Highlighted areas have p-values <0.05.

Response	Exclusion Type	Term	df	LR Chisq	p-value
Live plant biomass	Full Model $mR^2 = 0.588$ $cR^2 = 0.751$	**Intercept**	1	**58.9**	**<0.001**
		Poly(NDVI,2)	2	**15.3**	**<0.001**
		Predator	1	0.1	0.706
		Detritus	3	5.8	0.124
		Poly(NDVI,2) x Predator	2	4.3	0.119
		Poly(NDVI,2) x Detritus	3	7.2	0.066
		Predator x Detritus	6	**15.3**	**0.018**
	Water Scarce $mR^2 = 0.058$ $cR^2 = 0.199$	**Intercept**	1	**12.4**	**<0.001**
		Predator	3	3.3	0.068
		Detritus	4	3.2	0.369
		Predator x Detritus	4	3.0	0.386
	Water Abundant $mR^2 = 0.061$ $cR^2 = 0.141$	Intercept	1	**16.7**	**<0.001**
		Predator	3	0.1	0.786
		Detritus	4	1.9	0.589
		Predator x Detritus	4	3.6	0.302
Detritus mass	Full Model $mR^2 = 0.600$ $cR^2 = 0.675$	**Intercept**	1	**80.0**	**<0.001**
		Poly(NDVI,2)	2	**24.6**	**<0.001**
		Predator	1	0.6	0.435
		Detritus	3	**27.7**	**<0.001**
		Poly(NDVI,2) x Predator	2	5.0	0.083
		Poly(NDVI,2) x Detritus	3	3.5	0.326
		Predator x Detritus	6	9.8	0.131
	Water Scarce $mR^2 = 0.268$ $cR^2 = 0.658$	**Intercept**	1	**13.9**	**<0.001**
		Predator	3	1.9	0.167
		Detritus	4	7.7	0.053
		Predator x Detritus	4	6.3	0.096
	Water Abundant $mR^2 = 0.250$ $cR^2 = 0.662$	**Intercept**	1	**22.8**	**<0.001**
		Predator	3	0.4	0.535
		Detritus	4	**22.1**	**<0.001**
		Predator x Detritus	4	2.4	0.335

Table 4.2. The response of live plant biomass and detritus mass to the exclusion of birds and small mammals (predator) for four years along a gradient of water availability to plants. Water availability to plants was estimated using the normalized difference vegetation index (NDVI) from Landsat TM data. Responses were determined for three types of detritus treatments. Detritus was either left untouched (Detritus Control), was removed in the fall of each year (No Detritus), or was doubled in the fall of each year (2x Detritus). Result are from a type three ANOVA on generalize linear mixed models. Highlighted areas have p-values <0.05.

Response	Exclusion Type	Term	df	LR Chisq	p-value
Live plant biomass	**No detritus** mR^2 = 0.648 cR^2 = 0.660	**Intercept**	**1**	**61.2**	**<0.001**
		Poly(NDVI,2)	**2**	**23.1**	**<0.001**
		Predator	1	1.5	0.220
		Poly(NDVI,2) x Predator	2	1.1	0.574
	Normal detritus mR^2 = 0.574 cR^2 = 0.801	**Intercept**	**1**	**48.9**	**<0.001**
		Poly(NDVI,2)	**2**	**11.7**	**0.003**
		Predator	**1**	**5.9**	**0.015**
		Poly(NDVI,2) x Predator	**2**	**6.2**	**0.046**
	Double detritus mR^2 = 0.549 cR^2 = 0.783	**Intercept**	**1**	**52.6**	**<0.001**
		Poly(NDVI,2)	**2**	**6.5**	**0.038**
		Predator	1	0.1	0.751
		Poly(NDVI,2) x Predator	2	2.8	0.250
Detritus mass	**No detritus** mR^2 =0.507 cR^2 = 0.699	**Intercept**	**1**	**12.0**	**<0.001**
		Poly(NDVI,2)	**2**	**12.2**	**<0.001**
		Predator	1	0.9	0.340
		Poly(NDVI,2) x Predator	2	1.7	0.429
	Normal detritus mR^2 = 0.609 cR^2 = 0.797	**Intercept**	**1**	**28.7**	**<0.001**
		Poly(NDVI,2)	**2**	**18.7**	**<0.001**
		Predator	1	3.5	0.061
		Poly(NDVI,2) x Predator	**2**	**10.1**	**<0.001**
	Double detritus mR^2 = 0.534 cR^2 = 0.645	**Intercept**	**1**	**54.4**	**<0.001**
		Poly(NDVI,2)	**2**	**12.7**	**0.002**
		Predator	1	0.2	0.649
		Poly(NDVI,2) x Predator	2	4.6	0.100

Table 4.3. The response of plant species richness along a gradient of water availability to plants (NDVI) in response to the exclusion of songbirds and small mammals (Predator), and the doubling or removal of plant detritus (Detritus). I estimated the water availability to plants using the normalized difference vegetation index (NDVI). Songbird and small mammal predators were excluded for four years, and plant detritus was either removed or added within plots nested in predator exclosures. Result are from a type three ANOVA on generalize linear mixed models. The interaction between predators and detritus when water is abundant suggests top down control of detritus energy channel when water availability to plants is high. Highlighted areas have p-values <0.05.

Model Type	Term	df	LR Chisq	p-value
Full Model	**Intercept**	**1**	**289.0**	**<0.001**
$mR^2 = 0.432$	**Poly(NDVI,2)**	**1**	**8.3**	**0.016**
$cR^2 = 0.432$	Predator	1	0.3	0.559
	Detritus	2	0.4	0.804
	Poly(NDVI,2) x Predator	1	4.0	0.135
Water Scarce	**Intercept**	**1**	**85.9**	**<0.001**
$mR^2 = 0.025$	Predator	1	0.2	0.661
$cR^2 = 0.330$	Detritus	2	0.0	0.986
	Detritus x Predator	2	0.0	0.993
Water Abundant	**Intercept**	**1**	**61.3**	**<0.001**
$mR^2 = 0.121$	Predator	1	1.6	0.209
$cR^2 = 0.330$	Detritus	2	0.1	0.953
	Detritus x Predator	2	0.8	0.657
No Detritus	**Intercept**	**1**	**170.1**	**<0.001**
$mR^2 = 0.488$	Poly(NDVI,2)	2	3.2	0.202
$cR^2 = 0.488$	Predator	1	0.0	0.963
	Poly(NDVI,2) x Predator	2	2.6	0.277
Normal Detritus	**Intercept**	**1**	**178.5**	**<0.001**
$mR^2 = 0.526$	Poly(NDVI,2)	2	3.6	0.167
$cR^2 = 0.526$	Predator	1	1.2	0.264
	Poly(NDVI,2) x Predator	2	0.6	0.728
Double detritus	**Intercept**	**1**	**146.7**	**<0.001**
$mR^2 = 0.420$	Poly(NDVI,2)	2	2.3	0.317
$cR^2 = 0.420$	Predator	1	0.0	0.964
	Poly(NDVI,2) x Predator	2	2.8	0.246

Table 4.4. Correlations between arthropod herbivores and detritivores along a gradient of water availability to plants in response to the exclusion of birds and small mammals for four years. Data are the combined abundance of each functional group measured in the spring and fall in the year after four years using pitfall traps and vacuum sampling of 3 x 3 m square plots. Results are generalized linear models (GLMs) with Poisson distributed errors.

Model Type	Term	df	LR Chisq	p-value
No detritus	**Poly(NDVI,2)**	**1**	**27.0**	**<0.001**
Pseudo R^2 = 0.778	**Predator**	**1**	**56.9**	**<0.001**
	Herbivore	**1**	**5.9**	**0.015**
	Poly(NDVI,2) x Herbivore	**1**	**55.2**	**<0.001**
	Predator x Herbivore	1	0.1	0.744
Normal Detritus	**Poly(NDVI,2)**	**1**	**490.5**	**<0.001**
Pseudo R^2 = 0.345	Predator	1	0.8	0.377
	Herbivore	1	1.3	0.262
	Poly(NDVI,2) x Herbivore	**1**	**24.7**	**<0.001**
	Predator x Herbivore	**1**	**3.8**	**0.050**
Double detritus	**Poly(NDVI,2)**	**1**	**2269.3**	**<0.001**
Pseudo R^2 = 0.773	**Predator**	**1**	**705.3**	**<0.001**
	Herbivore	**1**	**101.1**	**<0.001**
	Poly(NDVI,2) x Herbivore	**1**	**134.4**	**<0.001**
	Predator x Herbivore	**1**	**171.4**	**<0.001**

Table 4.5. The response of arthropod functional groups to the exclusion of birds and small mammals for four years (Predator) along a gradient of water availability to plants (NDVI). Water availability (NDVI) was fit as a quadratic term in subsequent generalized linear mixed models (Poly(ndvi,2)). Models were fit with Poisson errors and experimental family nested in experimental blocks as random effects. Responses were determined for three types of detritus treatments. Detritus was either left untouched (Normal detritus), was removed in the fall of each year (No detritus), or was doubled in the fall of each year (Double detritus). Result are from a type three ANOVA on generalize linear mixed models. Highlighted values p-values <0.05

Group	Term	Df	No detritus		Normal detritus		Double detritus	
			LR Chisq	p-value	LR Chisq	p-value	LR Chisq	p-value
Consumer	Intercept	1	5.0	0.026	28.7	<0.001	12.3	<0.001
	Poly(NDVI,2)	2	0.1	0.949	5.4	0.069	0.1	0.938
	Predator (1/0)	1	1.2	0.275	1.8	0.180	0.2	0.623
	NDVI x Predator	2	6.5	0.038	16.0	<0.001	9.8	0.008
			mR^2=0.124; cR^2=0.381		mR^2=0.364; cR^2=0.407		mR^2=0.264; cR^2=0.381	
Herbivore	Intercept	1	24.0	<0.001	6.5	<0.001	9.6	0.002
	Poly(NDVI,2)	2	0.1	0.930	3.7	0.155	1.5	0.470
	Predator (1/0)	1	3.8	0.050	0.4	0.536	0.7	0.395
	NDVI x Predator	2	0.4	0.836	5.2	0.074	4.4	0.112
			mR^2=0.255; cR^2=0.255		mR^2=0.238; cR^2=0.238		mR^2=0.369; cR^2=0.524	
Detritivore	Intercept	1	8.1	<0.001	13.4	<0.001	21.6	<0.001
	Poly(NDVI,2)	2	1257.3	<0.001	81.8	<0.001	211.7	<0.001
	Predator (1/0)	1	344.8	<0.001	60.1	<0.001	56.9	<0.001
	NDVI x Predator	2	46.7	<0.001	9.7	0.008	31.9	<0.001
			mR^2=0.141; cR^2=0.881		mR^2=0.140; cR^2=0.735		mR^2=0.174; cR^2=0.797	
Omnivore	Intercept	1	28.6	<0.001	15.9	<0.001	30.6	<0.001
	Poly(NDVI,2)	2	16.4	<0.001	4.9	0.088	1.6	0.445
	Predator (1/0)	1	5.8	0.016	5.1	0.023	1.1	0.291
	NDVI x Predator	2	7.1	0.029	27.2	<0.001	2.8	0.242
			mR^2=0.292; cR^2=0.321		mR^2=0.127; cR^2=0.127		mR^2=0.021; cR^2=0.021	

Chapter 5: Conclusion

The study of the inextricable links between predators and plants bridges the divide between community and ecosystem ecology and provides a unifying theme to determine how changing climate conditions affect species interactions. Predators and plants are inextricably linked by the flow of energy through ecosystems, and energy flow is primarily governed by specific species interactions. Thus, examining changes in species interactions under different abiotic conditions should provide insight into how predators and plants jointly affect the diversity, function, and stability of ecosystems. In my dissertation, I used the concept of the trophic cascade and an underlying environmental gradient to investigate the feeding relationships of species in the semi-arid and temperate grassland ecosystems of south-central British Columbia, Canada. I did this to understand how interactions between species and the subsequent trophic structure of ecosystems are influenced by abiotic resources. I showed that:

    i.   the accumulation of grassland songbird abundance and species number is dependent on water availability to plants, but that new species are added to more productive locations incrementally at low abundances;

    ii.   small predatory vertebrates cause trophic cascades in grasslands dependent on water availability to plants.

These non-additive indirect effects could arise because of either: differences in the predatory traits of birds and mammals (i.e., birds feed on different prey than mammals), or they could arise from differences in magnitude of indirect effects resulting from changes in prey behaviour. Autochthonous subsidies to generalist predators does not necessarily produce rearrangements in trophic structure and a reversal of trophic control typical of subsidies of primary production from far off ecosystems. Thus, the impact of extreme events climate events in the system I studied is likely to be different from changes arising from slow incremental change.

In particular, I have shown that grassland songbirds are key predators that influence both the number of plant and arthropod species and their abundance. The number of grassland songbird individuals increases more dramatically than the number of songbird species along a gradient of water availability to plants. This suggests a bottom-up process regulates diversity in the upper trophic levels of semi-arid and temperate grassland ecosystems. I also tested two mechanisms by which species diversity could increase with plant productivity. I show that in ecosystems with low or variable resource abundance, such as temperate grasslands, accumulate bird species incrementally. This is in contrast to wetter or more productive ecosystems where accumulation of species may occur by adding more specialized species with increasing primary production. My work provides the basis for future investigations of the mechanisms that underlie the richness-productivity hypothesis in higher trophic levels.

At a smaller scale, I have shown that grassland songbirds and small mammals elicit strong top-down control on semi-arid and temperate grassland ecosystems. The strength and nature of this top-down control changes with the increase in the availability of water to plants and the ecosystem restructures from having four to three trophic levels. Because birds and small mammals have different behavioral and numerical impacts on arthropods, together they have a non-additive effect on plants. The presence of one vertebrate predator may cause changes in the behavior of arthropod mesopredators and thus alter the cascading effects seen when only a single vertebrate predator is present. Additionally, predation on the most abundant prey may not cause the largest ecological effect. When water is abundant, leaf sucking prey, such as Hemiptera, may not have large negative effects on plants as less abundant leaf chewing prey, such as Orthoptera. Thus, the indirect effect on plants of bird and mammal predation on arthropods may not be reflected in the abundance of different prey items in their diet.

As plant productivity increases, detritus provides the energy and physical structure to support new energy pathways (i.e., food chains) between predators and plants. This new detritus energy source supplements

songbird and small mammal diets and broadens the food web. However, the new detritus energy pathway and its subsidy to generalist top predators does not fundamentally change trophic control in the original grazing pathway from bottom-up to top-down or vice versa. In the semi-arid and temperate grasslands I examined, the new energy pathway broadens the food web and increases the stability to the ecosystem by reducing the strength of the trophic cascade.

The strength of a trophic cascade is a key measure of stability of an ecosystem in response to species extinctions (McCann 2012). If we take the strength of the trophic cascade to be the change in plant biomass with predator removal, and this change to be one measure of how resistant ecosystems are to disturbance, then stability in the ecosystem I examined is greater when water is abundant than when water is scarce. If grassland songbirds and small mammals decline in abundance or even disappear, the effect on the ecosystem may be smaller in wetter grasslands than in grasslands where water is scarce. However, these community-wide effects, the species- or ecosystem-wide effect of predator extirpations could be profound. I was able to show that songbirds and small mammals play a large role in determining the diversity of plants and arthropods, and that they can influence both the amount of live plant biomass and decomposition of detritus.

My findings are important because they demonstrate that viewing ecosystems as either being controlled by predators or by plants is too simplistic. As climate changes, we must adopt a perspective that simultaneously incorporates both consumers and resources into our ideas about what controls trophic structure, diversity, and function. My findings are also important because changes in the supply of abiotic resources to primary producers, such as reduced water availability arising from climate change, can elicit trophic cascades in a manner similar to that of species losses. Typically, cascades are only associated with the loss of top predators. I show that if the amount of abiotic resources such as water supporting the food web changes, there could be rearrangements of trophic structure that result in differences in the strength

or even direction of trophic control. These rearrangements of trophic structure have consequences for diversity and function in ecosystems, including determining the ultimate fate of primary production (i.e., the world is green, brown, black, or somewhere in between). Finally, my results are important because they demonstrate how the complexity and stability of ecosystems change with resource availability.

In my study, when water was scarce, food chains were less complex and demonstrated stronger trophic cascades. When water was abundant, food chains were shorter, more reticulate, and the effects of removing predators dampened. Thus, if the decline in North American grassland songbirds continues (North American Bird Conservation Initiative Canada. 2012, North American Bird Conservation Initiative 2016), we can expect a greater effect on the diversity and function of drier ecosystems that experience more severe, more persistent, and more frequent droughts. However, in the wettest grasslands we still require grazing or fire disturbance to prevent the excess accumulation of detritus and a decline in plant diversity. Thus, human caused disturbance such as grazing or prescribed fire must be tailored to the abiotic conditions of the ecosystem, promote trophic structure, and prevent the over dominance of single species. This knowledge should extend debates around trophic cascades beyond simply asking if they occur, or if they are top-down or bottom-up, towards deeper questions and a more holistic view of how predators help regulate the diversity, function, and stability of ecosystems in changing environments.

My study applies specifically to semi-arid and temperate grassland ecosystems. These types of ecosystems often have stronger trophic control than other terrestrial ecosystems (Chase et al. 2000, Bond 2008, Veldman et al. 2015) and are similar to tropical savannas. I use gradients to revel the changes in species interactions and subsequently trophic structure that arise from incremental changes in abiotic conditions. The changes I describe might only occur in these and other savanna ecosystems; however, the concepts I describe may be more far reaching. If I had unlimited resources I would have built exclosures that influenced populations of arthropods and plants, and I would have monitored plant abundance and

species composition outside exclosures. The semi-arid grasslands I examined are primarily composed of C3 perennial plants and thus the four-year timeframe of my study only monitored changes in the relative abundance of these perennials without livestock and large vertebrate herbivore grazing. Also, the size of my experimental treatments (predator exclosures and detritus treatments) was presumably not large enough to affect the population size of arthropods. Although my treatments were relatively large (9 m x 9 m), the movement of arthropods in and out of exclosures could have influenced experimental results. Additionally, if exclosures were larger I could have documented changes in arthropod abundance over time.

My investigation should be repeated in other ecosystems or at different scales to confirm that the responses I describe are more general. It may be appropriate to test if the patterns I describe occur in marine systems, forests, or large vertebrate food webs. Looking for the cascading effects of predators on plants that occur through multiple energy pathways and determining how these interactions are dependent on abiotic resources will provide valuable insight into how predators help shape ecosystems. Although these effects may not change the fate of biomass in these systems, they may regulate diversity or change ecosystem functions. These data may continue to inform actions regarding the role of predators and predation in restoration projects (Sinclair et al. in review).

5.1   Chapter summaries

Each major chapter of my dissertation (Chapters 2 to 4) provides its own unique insights into the role of predators in semi-arid and temperate grassland ecosystems. The study of abundance and diversity of grassland songbirds (Chapter 2) suggests that the mechanism behind the accumulation of species with plant productivity may be different in semi-arid and temperate ecosystem than in wetter tropical ecosystems. Richness-productivity patterns in birds are typically described on broad elevation or productivity gradients in more productive ecosystems. Here, I show that when water availability to plants

is scarce, the number of songbird species appears to accumulate more slowly than abundance. Many studies examine richness-productivity relationships, but few examine the mechanisms behind these common patterns or their effect on upper trophic levels (Grace et al. 2014). I asked how species identity, the number of species, and individual abundance of grassland songbirds changes along a gradient of water availability to plants.

Species are often thought to change identity along environmental gradients (Whitaker 1956, 1960, Rahbek 2005, Colwell et al. 2008, Sundqvist et al. 2013). However, in Chapter 2 I show that there is more evidence to support an alternative mechanism for how the number of grassland songbird species changes on gradients. On the gradient I examined, the number of individuals rose faster in response to increases in water availability than did the number of species. However, the relative abundance of species did not change, and territory sizes were relatively invariant. Thus, the identity of the dominant songbird does not change with plant productivity; their population size simply becomes larger. My measure of the number of songbird species increases along the gradient because there are more chances each individual encountered will be a new and different species. Because there are more individuals there are more chances a non-dominant species from the regional species pool will occur in that location. In the context of my dissertation, this work shows that the nature of predators does not change dramatically along the gradient. Western meadowlarks and vesper sparrows remain the dominant predators as water availability increases and any change in predation intensity should come either from: a) these species altering their diet, or b) the abundance of these species declining dramatically.

By experimentally excluding predators along a gradient of water availability, I was able to show in Chapter 3 that neither intraguild predation nor metabolic requirements alone explain changes in trophic structure with increasing water availability. Small vertebrates can have large effects in temperate montane grasslands through predation on arthropods. When water is scarce, predatory vertebrates depress plant

101

biomass. When water is abundant water predatory vertebrates have little impact on plant biomass. The predator effects of birds and mammals on lower trophic levels also differ over the gradient. These differences are likely more related to changes in the relative abundance of birds versus mammals rather than changes species composition. Small mammals were abundant when water was scarce and birds abundant when water abundant. The non-additive effects of vertebrates on plant and arthropod are consistent with birds and mammals having greater than additive suppression of spiders when water is abundant. I suggest that the strong synergistic effect of birds and small mammals on arthropod carnivores reverses the direct negative effects of predatory vertebrates on herbivores that occur at drier sites. Abundant plant detritus affects the behaviour of spiders in relation to the presence of vertebrate predators.

There has been much speculation of energy subsidies at the base of food webs influencing the strength of top-down controls (Polis and Strong 1996, Polis et al. 1997a, Leroux and Loreau 2008). Until now this has mostly been explored by examining subsidies from primary productivity external to the ecosystem (Huxel and McCann 1998, Halaj and Wise 2002, Huxel et al. 2002). However, because of the nature of grasslands and the structure of the gradient I examined, there is a spatial pattern that results in an increase in heterogeneity as water availability to plants increases. As primary production of live plants increase, herbivores cannot eat all the production. Live plants die and become the detritus food source in donor-controlled food webs. However, the addition of this subsidy is directly dependent on the same input of water that determines live plant production. Detritus increases with plant productivity in a way that subsidizes arthropod communities and establishes a parallel food chain. Detritus provides both the physical habitat and food resources to support this additional food chain. The complexity of the ecosystem increases because it has multiple food chains and more interactions between species. Manipulating detritus provides a mechanism to isolate the effect of primary production on the trophic structure of the grassland food webs I examined, and allowed me to examine how autochthonous subsidies influenced food webs.

Recently, some of the most fruitful work on trophic theory has investigated the role of subsides and cross-ecosystem coupling of food chains (Rooney et al. 2006, Spiller et al. 2010, Tunney et al. 2012, Piovia-Scott et al. 2013, Sinclair et al. 2013, Wright et al. 2013). By manipulating detritus from within the ecosystem, I provide a new aspect to this debate in Chapter 4. First, I used the concept of the trophic cascade to isolate the role of different sources of energy (live plants or detritus) in structuring ecosystems along a gradient of abiotic conditions. Past research has typically examined how predators couple energy channels in adjacent ecosystems (benthic and limnetic, marine or terrestrial) or examined subsidies arising from primary productivity outside the ecosystems (streams from upstream or upland, marine subsidies). I examined subsidies arising from detritus and coupling of energy pathways within the same ecosystem. Grassland food webs become increasingly heterogeneous with increasing water availability. Detritus abundance increase supporting both new habitats for predators like spiders and new food for detritivores. Increasing heterogeneity in the ecosystem resulted in a reduced effect of predators on plants and did not replace top-down control of predators on plants. Although predators did not have strong effects on plant biomass, their top-down effects on the detritus pathway altered the outcome of plant competitive interactions and changed the number of coexisting plant species. Thus, predators and plants are inextricably linked in ecosystems even when top-down control may not be the predominant force controlling ecosystem structure.

Furthermore, by investigating the existence and direction of an apparent trophic cascade, I was able to show that when subsidies arise from within an ecosystem, an apparent cascade develops but does not change the overall direction of trophic control. Other studies show subsidies can change trophic control from bottom-up to top-down in the original grazing pathway, but the subsides are always from primary productivity external to the system (i.e., cross ecosystem boundaries). For example, apparent trophic cascades arise when primary production in the primary food chain, in this case grazing chain from green

plants to herbivores to songbirds and mammals, results in enough surplus primary production to support a second food source for songbird and mammals, in this case detritivores (Ward et al. 2015). Thus, the negative relationships between competitors for the same primary production (i.e., apparent competition between herbivores and detritivores) result in one pathway with top-down control and a second with bottom-up control. Whether the grazing or detritus pathway has top-down or bottom-up control appears dependent on the source of the subsidy. In my system, the local source produces a reverse apparent trophic cascade where the grazing pathway is controlled by live plant production and the detritus pathway is controlled by predators.

5.2   Conclusion

Predators have been the focus of many conservation efforts because of their vulnerability to extinction, the charismatic nature of these species, their need for large relatively undisturbed protected areas, and their ability to affect ecosystem diversity, function and stability. Here, I provide evidence that small vertebrates regulate the diversity, function, and stability of ecosystems even when biomass distributions are thought to be controlled by resources. I show with data and experiments that predation, even by small animals can alter the diversity, function, and stability of ecosystems. Additionally, I show that the effect of predators in ecosystems is mediated by the availability of abiotic resources. Thus, predators and plants are inextricably linked with the abundance and diversity of each determined by the other. Because of the similarity of my results to those described in other large vertebrate systems my results likely scale up to systems with larger animals. The type of experiments I did are exceedingly difficult in large vertebrate systems, but the processes I describe are likely similar whether we are examining the role of songbirds and small mammals or the role of lions and hyenas or lynx and goshawks. I demonstrate two mechanisms through which predators can influence ecosystems under varying environmental conditions: intraguild predation and apparent competition. I suggest that knowing how climate change alters resource availability is useful because changes in resource availability will determine how trophic structure is

modified by climate. We can use this knowledge to develop management strategies to mitigate climate change impacts. For example, slow incremental change in resource availability in spring resulting from the premature melting of winter snow or the absence of spring rains could have very different impacts on grassland trophic structure than increases in summer thunderstorms. Additionally, the migration of animals into grasslands from other ecosystems as they attempt to escape unfavorable conditions elsewhere could dramatically change trophic structure. Again, these changes will be different from those that arise from slow incremental changes in water availability. Distinguishing between these different types of climate impacts will be essential as people attempt to develop conservation and management practices that slow the rate of change in ecosystems, and maintain the services ecosystems provide humans.

References

Abrams, P. A., R. D. Holt, and J. D. Roth. 1998. Apparent competition or apparent mutualism? Shared predation when populations cycle. Ecology 79:201–212.

Acharya, B. K., N. J. Sanders, L. Vijayan, and B. Chettri. 2011. Elevational gradients in bird diversity in the Eastern Himalaya: An evaluation of distribution patterns and their underlying mechanisms. PloS ONE 6:e29097.

Adler, P. B., E. W. Seabloom, E. T. Borer, H. Hillebrand, Y. Hautier, A. Hector, W. S. Harpole, L. R. O'Halloran, J. B. Grace, T. M. Anderson, J. D. Bakker, L. A. Biederman, C. S. Brown, Y. M. Buckley, L. B. Calabrese, C.-J. C.-J. Chu, E. E. Cleland, S. L. Collins, K. L. Cottingham, M. J. Crawley, E. I. Damschen, K. F. Davies, N. M. DeCrappeo, P. A. Fay, J. Firn, P. Frater, E. I. Gasarch, D. S. Gruner, N. Hagenah, J. Hille Ris Lambers, H. Humphries, V. L. Jin, A. D. Kay, K. P. Kirkman, J. A. Klein, J. M. H. Knops, K. J. La Pierre, J. G. Lambrinos, W. Li, A. S. MacDougall, R. L. McCulley, B. A. Melbourne, C. E. Mitchell, J. L. Moore, J. W. Morgan, B. Mortensen, J. L. Orrock, S. M. Prober, D. A. Pyke, A. C. Risch, M. Schuetz, M. D. Smith, C. J. Stevens, L. L. Sullivan, G. Wang, P. D. Wragg, J. P. Wright, and L. H. Yang. 2011. Productivity is a poor predictor of plant species richness. Science 333:1750–3.

Ahrens, R. N. M., C. J. Walters, and V. Christensen. 2012. Foraging arena theory. Fish and Fisheries 13:41–59.

Allen, D. C., C. C. Vaughn, J. F. Kelly, J. T. Cooper, and M. H. Engel. 2012. Bottom-up biodiversity effects increase resource subsidy flux between ecosystems. Ecology 93:2165–2174.

Anderson, M. J., T. O. Crist, J. M. Chase, M. Vellend, B. D. Inouye, A. L. Freestone, N. J. Sanders, H. V. Cornell, L. S. Comita, K. F. Davies, S. P. Harrison, N. J. B. Kraft, J. C. Stegen, and N. G. Swenson. 2011. Navigating the multiple meanings of β diversity: A roadmap for the practicing ecologist. Ecology Letters 14:19–28.

Angert, A. L., S. L. LaDeau, and R. S. Ostfeld. 2013. Climate change and species interactions: Ways forward. Annals of the New York Academy of Sciences 1297:1–7.

Austin, A. T., and L. Vivanco. 2006. Plant litter decomposition in a semi-arid ecosystem controlled by photodegradation. Nature 442:555–8.

Ayal, Y. 2007. Trophic structure and the role of predation in shaping hot desert communities. Journal of Arid Environments 68:171–187.

Bartels, P., J. Cucherousset, K. Steger, P. Eklov, L. J. Tranvik, and H. Hillebrand. 2012. Reciprocal subsidies between freshwater and terrestrial ecosystems structure consumer resource dynamics. Ecology 93:1173–1182.

Bates, D., M. Mächler, B. Bolker, Walker, S. Walker, and M. M. B. B. S. W. Douglas Bates. 2015. Fitting Linear Mixed-Effects Models using lme4. Journal of Statistical Software 67:27–30.

Belovsky, G. E., and J. B. Slade. 1993. The Role of Vertebrate and Invertebrate Predators in a Grasshopper Community. Oikos 68:193.

Belovsky, G. E., J. B. Slade, and B. A. Stockhoff. 1990. Susceptibility to predation for different grasshoppers: an experimental study. Ecology 71:624–634.

Belovsky, G., and A. Joern. 1995. The dominance of different regulating factors for rangeland grasshoppers. Pages 359–386 *in* N. Cappucino and P. W. Price, editors. Population dynamics. San Diego, CA.

Beschta, R. L., and W. J. Ripple. 2009. Large predators and trophic cascades in terrestrial ecosystems of the western United States. Biological Conservation 142:2401–2414.

Bond, W. J., F. I. Woodward, and G. F. Midgley. 2005. The global distribution of ecosystems in a world without fire. New Phytologist 165:525–538.

Bonn, A., D. Storch, and K. J. Gaston. 2004. Structure of the species-energy relationship. Proceedings of the Royal Society B: Biological Sciences 271:1685–1691.

Borer, E. T., B. S. Halpern, and E. W. Seabloom. 2006. Asymmetry in community regulation: Effects of predators and productivity. Ecology 87:2813–2820.

Borer, E. T., E. W. Seabloom, J. B. Shurin, K. E. Anderson, C. A. Blanchette, B. Broitman, S. D. Cooper, and B. S. Halpern. 2005. What determines the strength of a trophic cascade? Ecology 86:528–537.

Boyce, D. G., K. T. Frank, B. Worm, and W. C. Leggett. 2015. Spatial patterns and predictors of trophic control in marine ecosystems. Ecology Letters 18:1001–1011.

Brandt, L. A., J. Y. King, and D. G. Milchunas. 2007. Effects of ultraviolet radiation on litter decomposition depend on precipitation and litter chemistry in a shortgrass steppe ecosystem. Global Change Biology 13:2193–2205.

Brennan, L. A., W. P. Kuvlesky, C. Kleberg, and A. Texas. 2005. North American grassland birds: An unfolding conservation crisis? Journal of Wildlife Management 69:1–13.

Briske, D. D., L. A. Joyce, H. W. Polley, J. R. Brown, K. Wolter, J. A. Morgan, B. A. McCarl, and D. W. Bailey. 2015. Climate-change adaptation on rangelands: Linking regional exposure with diverse adaptive capacity. Frontiers in Ecology and the Environment 13:249–256.

Brookshire, E. N. J., and T. Weaver. 2015. Long-term decline in grassland productivity driven by increasing dryness. Nature Communications 6:7148.

Bruno, J. F., and B. J. Cardinale. 2008. Cascading effects of predator richness. Frontiers in Ecology and the Environment 6:539–546.

Buchkowski, R. W., and O. J. Schmitz. 2015. Detritivores ameliorate the enhancing effect of plant-based trophic cascades on nitrogen cycling in an old-field system. Biology Letters 11.

Cadena, C. D., K. H. Kozak, J. P. Gomez, J. L. Parra, C. M. McCain, R. C. K. Bowie, a. C. Carnaval, C. Moritz, C. Rahbek, T. E. Roberts, N. J. Sanders, C. J. Schneider, J. VanDerWal, K. R. Zamudio, and C. H. Graham. 2012. Latitude, elevational climatic zonation and speciation in New World vertebrates. Proceedings of the Royal Society B: Biological Sciences 279:194–201.

Canada, E. 2015. Canadian Climate Normals 1981-2010, Kamloops A Station. http://climate.weather.gc.ca/climate_normals/results_1981_2010_e.html?stnID=1275&autofwd=1.

Cardinale, B. J., J. E. Duffy, A. Gonzalez, D. U. Hooper, C. Perrings, P. Venail, A. Narwani, G. M. Mace, D. Tilman, D. A. Wardle, A. P. Kinzig, G. C. Daily, M. Loreau, J. B. Grace, A. Larigauderie, D. S. Srivastava, and S. Naeem. 2012. Biodiversity loss and its impact on humanity. Nature 486:59–67.

Cardinale, B. J., D. S. Srivastava, J. E. Duffy, J. P. Wright, A. L. Downing, M. Sankaran, and C. Jouseau. 2006. Effects of biodiversity on the functioning of trophic groups and ecosystems. Nature 443:989–92.

Carlyle, C. N. 2012. Interacting effects of climate change and disturbance on grassland plants and plant communities. University of British Columbia.

Carlyle, C. N., L. H. Fraser, and R. Turkington. 2011. Tracking Soil Temperature and Moisture in a Multi-Factor Climate Experiment in Temperate Grassland: Do Climate Manipulation Methods Produce their Intended Effects? Ecosystems 14:489–502.

Carlyle, C. N., L. H. Fraser, and R. Turkington. 2014. Response of grassland biomass production to simulated climate change and clipping along an elevation gradient. Oecologia 174:1065–1073.

Caut, S., E. Angulo, F. Courchamp, and J. Figuerola. 2010. Trophic experiments to estimate isotope discrimination factors. Journal of Applied Ecology 47:948–954.

Chase, J. M. 1996. Abiotic controls of trophic cascades in a simple grassland food chain. Oikos 77:495–506.

Chase, J. M., M. A. Leibold, A. L. Downing, and J. B. Shurin. 2000. The effects of productivity, herbivory, and plant species turnover in grassland food webs. Ecology 81:2485–2497.

Chen, B., and D. H. Wise. 1999. Bottom-up limitation of predaceous arthropods in a detritus-based terrestrial food web. Ecology 80:761–772.

Cody, M. L. 1968. On the methods of resource division in grassland bird communities. The American Naturalist 102:107–147.

Colwell, R. K., G. Brehm, C. L. Cardelus, A. C. Gilman, and J. T. Longino. 2008. Global warming,

elevational range shifts, and lowland biotic attrition in the wet tropics. Science 322:258–261.

Colwell, R. K., A. Chao, N. J. Gotelli, S. Y. Lin, C. X. Mao, R. L. Chazdon, and J. T. Longino. 2012. Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. Journal of Plant Ecology 5:3–21.

Cook, E., C. Woodhouse, C. Eakin, D. Meko, and D. Stahle. 2004. Long-term aridity changes in the western United States. Science 306:1015–1018.

Coristine, L. E., and J. T. Kerr. 2015. Temperature-related geographical shifts among passerines: Contrasting processes along poleward and equatorward range margins. Ecology and Evolution 5:5162–5176.

Davidson, P. J. ., R. J. Cannings, A. R. Coutrurier, D. Lepage, and C. M. Di Corrado, editors. 2015. Atlas of the Breeding Birds of British Columbia, 2008-2012. Bird Studies Canada, Delta, BC.

Davis, S. K., D. Duncan, and M. Skeel. 1999. Distribution and habitat associations of three endemic grassland songbirds in southern Saskatchewan. The Wilson Bulletin 111:389–396.

DeAngelis, D. L., P. J. Mulholland, A. V. Palumbo, A. D. Steinman, M. A. Huston, and J. W. Elwood. 1989. Nutrient dynamics and food-web stability. Annual Review of Ecology and Systematics 20:71–95.

Denno, R. F., C. Gratton, M. Peterson, G. A. Langelloto, D. L. Finke, and A. F. Huberty. 2002. Bottom-up forces mediate natural-enemy impact in a phytophagous insect community. Ecology 83:1443–1458.

Dickman, C. R., A. S. Haythornthwaite, G. H. Mcnaught, P. S. Mahon, B. Tamayo, and M. Letnic. 2001. Population dynamics of three species of dsyurid marsupials in arid central Australia: A 10-year study. Wildlife Research 28:493–506.

Duffy, J. E. 2002. Biodiversity and ecosystem function: The consumer connection. Oikos 99:201–219.

Duffy, J. E. 2003. Biodiversity loss, trophic skew and ecosystem functioning. Ecology Letters 6:680–687.

Duffy, J. E., B. J. Cardinale, K. E. France, P. B. McIntyre, E. Thébault, and M. Loreau. 2007. The functional role of biodiversity in ecosystems: Incorporating trophic complexity. Ecology Letters 10:522–538.

Dunne, J. A., S. R. Saleska, M. L. Fischer, and J. Harte. 2004. Integrating experimental and gradient methods in ecological climate change research. Ecology 85:904–916.

Dyer, L. a., and D. Letourneau. 2002. Top-down and bottom-up diversity cascades in detrital vs. living food webs. Ecology Letters 6:60–68.

Dyer, L. a., and D. K. Letourneau. 2013. Can climate change trigger massive diversity cascades in terrestrial ecosystems? Diversity 5:479–504.

Elton, C. S. 1927. Animal Ecology. Page Animal Ecology. The Macmillan Company, New York.

ESRI. 2013. ArcGIS Desktop: Release 10.2. Environmental Systems Research institute.

Estes, J. A., J. Terborgh, J. S. Brashares, M. E. Power, J. Berger, W. J. Bond, S. R. Carpenter, T. E. Essington, R. D. Holt, J. B. C. Jackson, R. J. Marquis, L. Oksanen, T. Oksanen, R. T. Paine, E. K. Pikitch, W. J. Ripple, S. a Sandin, M. Scheffer, T. W. Schoener, J. B. Shurin, A. R. E. Sinclair, M. E. Soulé, R. Virtanen, and D. A. Wardle. 2011. Trophic downgrading of planet Earth. Science (New York, N.Y.) 333:301–306.

Evans, C. W. 2011. A comparison of the effects of 20 and 30 years of grazing on grassland soil properties in southern British Columbia. University of British Columbia, Vancouver BC.

Ewers, R. M., M. J. W. Boyle, R. A. Gleave, N. S. Plowman, S. Benedick, H. Bernard, T. R. Bishop, E. Y. Bakhtiar, V. K. Chey, A. Y. C. Chung, R. G. Davies, D. P. Edwards, P. Eggleton, T. M. Fayle, S. R. Hardwick, R. Homathevi, R. L. Kitching, M. S. Khoo, S. H. Luke, J. J. March, R. Nilus, M. Pfeifer, S. V Rao, A. C. Sharp, J. L. Snaddon, N. E. Stork, M. J. Struebig, O. R. Wearn, K. M. Yusah, and E. C. Turner. 2015. Logging cuts the functional importance of invertebrates in tropical rainforest. Nature Communications 6:6836.

Finke, D. L., and R. F. Denno. 2005. Predator diversity and the functioning of ecosystems: The role of intraguild predation in dampening trophic cascades. Ecology Letters 8:1299–1306.

Fisher, R. J., and S. K. Davis. 2010. From Wiens to Robel: A review of grassland bird habitat selection. Journal of Wildlife Management 74:265–273.

Fiske, I. J., and R. B. Chandler. 2011. unmarked: An R package for fitting hierarchical models of wildlife occurrence and abundance. Journal of Statistical Software 43:1–23.

Frank, A. S. K., G. M. Wardle, C. R. Dickman, and A. C. Greenville. 2014. Habitat- and rainfall-dependent biodiversity responses to cattle removal in an arid woodland - Grassland environment. Ecological Applications 24:2013–2028.

Frank, D. A. 2007. Drought effects on above- and belowground production of a grazed temperate grassland ecosystem. Oecologia 152:131–139.

Fraser, L. H., and J. P. Grime. 1999. Interacting effects of herbivory and fertility on a synthesized plant community. Journal of Ecology 87:514–525.

Fraser, L. H., W. L. Harrower, H. W. Garris, S. Davidson, P. D. N. Hebert, R. Howie, A. Moody, D. Polster, O. J. Schmitz, A. R. E. Sinclair, B. M. Starzomski, T. P. Sullivan, R. Turkington, and D. Wilson. 2015. A call for applying trophic structure in ecological restoration. Restoration Ecology 23:503–507.

Fretwell, S. D. S. D. 1977. The regulation of plant communities by the food chains exploiting them. Perspectives in Biology and Medecine 20:169–185.

Fryxell, J. M., J. Greever, and A. R. E. Sinclair. 1988. Why are migratory ungulates so abundant? American Naturalist 131:781–798.

Fukami, T., and D. A. Wardle. 2005. Long-term ecological dynamics: Reciprocal insights from natural and anthropogenic gradients. Proceedings of The Royal Society B. Biological sciences 272:2105–15.

George, T. L., A. C. Fowler, R. L. Knight, and L. C. McEwen. 1992. Impacts of a severe drought on grassland birds in western North Dakota. Ecological Applications 2:275–284.

Grant, T. A., E. M. Madden, T. L. Shaffer, and J. S. Dockens. 2010. Effects of prescribed fire on vegetation and passerine birds in northern mixed-grass prairie. Journal of Wildlife Management 74:1841–1851.

Grant, T. A., E. M. Madden, T. L. Shaffer, P. J. Pietz, G. B. Berkey, and N. J. Kadrmas. 2006. Nest survival of Clay-Colored and Vesper Sparrows in relation to woodland edge in mixed-grass prairies. Journal of Wildlife Management 70:691–701.

Greenville, A. C., G. M. Wardle, B. Tamayo, and C. R. Dickman. 2014. Bottom-up and top-down processes interact to modify intraguild interactions in resource-pulse environments. Oecologia 175:1349–1358.

Gruner, D. S. 2004. Attenuation of top-down and bottom-up forces in a complex terrestrial community. Ecology 85:3010–3022.

Gruner, D. S., J. E. Smith, E. W. Seabloom, S. a. Sandin, J. T. Ngai, H. Hillebrand, W. S. Harpole, J. J. Elser, E. E. Cleland, M. E. S. Bracken, E. T. Borer, and B. M. Bolker. 2008. A cross-system synthesis of consumer and nutrient resource control on producer biomass. Ecology letters 11:740–55.

Gutiérrez, J. R., P. L. Meserve, D. A. Kelt, A. Engilis, M. Andrea Previtali, W. B. Milstead, and F. M. Jaksic. 2010. Long-term research in Bosque Fray Jorge National Park: Twenty years studying the role of biotic and abiotic factors in a Chilean semiarid. Revista Chilena de Historia Natural 83:69–98.

Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. American Naturalist 94:421–425.

Halaj, J., and D. H. Wise. 2002. Impact of a detrital subsidy on trophic cascades in a terrestrial grazing food web. Ecology 83:3141–3151.

Hamilton, D., and D. H. Wright. 1983. Species-energy theory: An extension of species-area theory. Oikos 41:496–506.

Han, Q., G. Luo, C. Li, H. Ye, and Y. Chen. 2013. Modeling grassland net primary productivity and

water-use efficiency along an elevational gradient of the Northern Tianshan Mountains. Journal of Arid Land 5:354–365.

Harris, G., S. Thirgood, J. Hopcraft, J. Cromsight, and J. Berger. 2009. Global decline in aggregated migrations of large terrestrial mammals. Endangered Species Research 7:55–76.

Harrison, M. L., N. A. Mahony, P. Robinson, A. Newbury, and D. J. Green. 2010. Vesper Sparrows and Western Meadowlarks show a mixed response to cattle grazing in the intermountain region of British Columbia. Avian Conservation and Ecology 5:1–17.

Harrison, M. L., N. A. Mahony, P. Robinson, A. Newbury, and D. J. Green. 2011. Nest-site selection and productivity of Vesper Sparrows breeding in grazed habitats. Journal of Field Ornithology 82:140–149.

Harrower, M. J. 2008. Hydrology, ideology, and the origins of irrigation in ancient southwest Arabia. Current Anthropology 49:497–510.

Harrower, M. J. 2016. Water histories and spatial archaeology: Ancient Yemen and the American West. Cambridge University Press, Cambridge UK.

Hawkins, B. A., and E. E. Porter. 2003. Relative influences of current and historical factors on mammal and bird diversity patterns in deglaciated North America. Global Ecology and Biogeography 12:475–481.

Henschel, J. R., D. Mahsberg, and H. Stumpf. 2001. Allochthonous aquatic insects increase predation and decrease herbivory in river shore food webs. Oikos 93:429–438.

Hillebrand, H., E. T. Borer, M. E. S. Bracken, B. J. Cardinale, J. Cebrian, E. E. Cleland, J. J. Elser, D. S. Gruner, W. Stanley Harpole, J. T. Ngai, S. Sandin, E. W. Seabloom, J. B. Shurin, J. E. Smith, M. D. Smith, W. S. Harpole, J. T. Ngai, S. Sandin, E. W. Seabloom, J. B. Shurin, J. E. Smith, M. D. Smith, W. Stanley Harpole, J. T. Ngai, S. Sandin, E. W. Seabloom, J. B. Shurin, J. E. Smith, and M. D. Smith. 2009. Herbivore metabolism and stoichiometry each constrain herbivory at different organizational scales across ecosystems. Ecology letters 12:516–527.

Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. Theoretical population biology 12:197–129.

Holt, R. D. 2000. Trophic cascades in terrestrial ecosystems. Reflections on Polis et al. Trends in Ecology and Evolution 15:444–445.

Holt, R. D., and J. H. Lawton. 1993. Apparent competition and enemy-free space in insect host-parasitoid communities. The American Naturalist 142:623–645.

Holt, R. D. R., and G. A. Polis. 1997. A theoretical framework for intraguild predation. The American Naturalist 149:745–764.

Hooper, D. U., E. C. Adair, B. J. Cardinale, J. E. K. Byrnes, B. a. Hungate, K. L. Matulich, A. Gonzalez, J. E. Duffy, L. Gamfeldt, M. I. O'Connor, and M. I. O'Connor. 2012. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. Nature 486:105–108.

Hopcraft, J. G. C., J. M. Morales, H. L. Beyer, M. Borner, E. Mwangomo, A. R. E. Sinclair, H. Olff, and D. T. Haydon. 2014. Competition, predation, and migration: Individual choice patterns of Serengeti migrants captured by hierarchical models. Ecological Monographs 84:355–372.

Hopcraft, J. G. C., H. Olff, and A. R. E. Sinclair. 2010. Herbivores, resources and risks: Alternating regulation along primary environmental gradients in savannas. Trends in Ecology and Evolution 25:119–128.

Hovenden, M. J., P. C. D. Newton, and K. E. Wills. 2014. Seasonal not annual rainfall determines grassland biomass response to carbon dioxide. Nature 511:583–586.

Humphreys, W. F. 1979. Production and respiration in animal populations. Journal of Animal Ecology 48:427–453.

Huxel, G. R., and K. McCann. 1998. Food web stability: The influence of trophic flows across habitats. The American Naturalist 152:460–469.

Huxel, G. R., K. McCann, and G. A. Polis. 2002. Effects of partitioning allochthonous and autochthonous resources on food web stability. Ecological Research 17:419–432.

Inger, R., and S. Bearhop. 2008. Applications of stable isotope analyses to avian ecology. Ibis 150:447–461.

IPCC. 2014. Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II,III, to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change.

Jankowski, J. E., C. L. Merkord, W. F. Rios, K. G. Cabrera, N. S. Revilla, and M. R. Silman. 2013. The relationship of tropical bird communities to tree species composition and vegetation structure along an Andean elevational gradient. Journal of Biogeography 40:950–962.

Jankowski, J. E., and K. N. Rabenold. 2007. Endemism and local rarity in birds of neotropical montane rainforest. Biological Conservation 138:453–463.

Keddy, P. A. 1991. Working with Heterogeneity: An Operator's Guide to Environmental Gradients. Pages 181–200*in* J. Kolasa and S. T. A. Pickett, editors.Environmental Heterogeneity. Springer-Verlag, New York.

Knapp, A. K. 2002. Rainfall Variability, Carbon Cycling, and Plant Species Diversity in a Mesic Grassland. Science 298:2202–2205.

Knapp, A. K., and M. D. Smith. 2001. Variation Among Biomes in Temporal Dynamics of Aboveground Primary Production. Science 291:481–484.

Knick, S. T., D. S. Dobkin, J. T. Rotenberry, M. A. Schroeder, W. M. Vander Haegen, and C. van Riper. 2003. Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. Condor 105:611–634.

Knick, S. T., and J. T. Rotenberry. 2000. Ghosts of habitats past: Contribution of landscape change to current habitats used by shrubland birds. Ecology 81:220–227.

Knight, T. M., M. W. McCoy, J. M. Chase, K. A. McCoy, and R. D. Holt. 2005. Trophic cascades across ecosystems. Nature 437:880–883.

Kottek, M., J. J. Grieser, C. Beck, B. Rudolf, and F. Rubel. 2006. World Map of the Köppen-Geiger climate classification uppdated 2006. Meteorologische Zeitschrift 15:259–263.

Kratina, P., R. R. M. LeCraw, T. Ingram, and B. R. Anholt. 2012. Stability and persistence of food webs with omnivory: Is there a general pattern? Ecosphere 3:1–18.

Krebs, C. J. 2009. Ecology: The Experimental Analysis of Distribution and Abundance. 6th edition. Benjamin Cummings, San Francisco.

Krebs, C. J., S. Boutin, R. Boonstra, A. R. E. E. Sinclair, J. N. M. N. M. Smith, M. R. T. R. T. Dale, K. Martin, and R. Turkington. 1995. Impact of food and predation on the snowshoe hare cycle. Science 269:1112–1115.

De La Maza, M., M. Lima, P. L. Meserve, J. R. Gutiérrez, and F. M. Jaksic. 2009. Primary production dynamics and climate variability: ecological consequences in semiarid Chile. Global Change Biology 15:1116–1126.

Lauenroth, W. K., and O. E. Sala. 1992. Long-term forage production of North American shortgrass steppe.

Lawrence, K. L., and D. H. Wise. 2004. Unexpected indirect effect of spiders on the rate of litter disappearance in a deciduous forest. Pedobiologia 48:149–157.

Lee, R. N., G. E. Bradfield, M. Krzic, R. F. Newman, and W. F. P. Cumming. 2014. Plant community – soil relationships in a topographically diverse grassland in southern interior British Columbia , Canada. Botany 92:837–845.

Lensing, J. R., and D. H. Wise. 2006. Predicted climate change alters the indirect effect of predators on an ecosystem process. Proceedings of the National Academy of Sciences of the United States of America 103:15502–15505.

Leroux, S. J., and M. Loreau. 2008. Subsidy hypothesis and strength of trophic cascades across ecosystems. Ecology Letters 11:1147–1156.

Leroux, S. J., and O. J. Schmitz. 2015. Predator-driven elemental cycling: The impact of predation and risk effects on ecosystem stoichiometry. Ecology and Evolution 5:4976–4988.

Letnic, M., and C. R. Dickman. 2006. Boom means bust: Interactions between the El Nino Southern

Oscillation (ENSO), rainfall and the processes threatening mammal species in arid Australia. Biodiversity and Conservation 15:3847–3880.

Letnic, M., and C. R. Dickman. 2010. Resource pulses and mammalian dynamics: Conceptual models for hummock grasslands and other Australian desert habitats. Biological Reviews 85:501–521.

Lindeman, R. L. R. 1942. The trophic-dynamic aspect of ecology. Ecology 23:399–417.

Liu, S., J. Chen, W. Gan, S. Fu, D. Schaefer, J. Gan, and X. Yang. 2015. Cascading effects of spiders on a forest-floor food web in the face of environmental change. Basic and Applied Ecology 17:527–534.

Loreau, M., S. Naeem, P. Inchausti, J. Bengtsson, J. P. Grime, A. Hector, D. U. Hooper, M. A. Huston, D. Raffaelli, B. Schmid, D. Tilman, and D. A. Wardle. 2001. Biodiversity and Ecosystem Functioning: Current Knowledge and Future Challenges. Science 294:804–808.

Mäntylä, E., T. Klemola, and T. Laaksonen. 2011. Birds help plants: A meta-analysis of top-down trophic cascades caused by avian predators. Oecologia 165:143–151.

May, R. M., and R. H. MacArthur. 1972. Niche overlap as a function of environmental variability. Proceedings of the National Academy of Sciences of the United States of America 69:1109–1113.

McCain, C. M. 2009. Global analysis of bird elevational diversity. Global Ecology and Biogeography 18:346–360.

McCain, C. M., and R. K. Colwell. 2011. Assessing the threat to montane biodiversity from discordant shifts in temperature and precipitation in a changing climate. Ecology Letters 14:1236–1245.

McCann, K. S. 2000. The diversity–stability debate. Nature 405:228–233.

McDonald, K. W., C. J. W. McClure, B. W. Rolek, and G. E. Hill. 2012. Diversity of birds in eastern North America shifts north with global warming. Ecology and Evolution 2:3052–3060.

McLaren, B. E., and R. O. Peterson. 1994. Wolves, moose, and tree rings on isle royale. Science (New York, N.Y.) 266:1555–1558.

McLaren, K., K. Cartwright, and A. McLean. 1981. Treasures of Lac du Bois. Peerless Printers, Kamloops, B.C.

McMeans, B. C., K. S. McCann, M. Humphries, N. Rooney, and A. T. Fisk. 2015. Food web structure in temporally-forced ecosystems. Trends in Ecology and Evolution 30:662–672.

Menge, B. A., and J. P. Sutherland. 1976. Species diversity gradients: Synthesis of the roles of predation, competition, and temporal heterogeneity. The American Naturalist 110:351.

Menge, B. A., and J. P. Sutherland. 1987. Community regulation: Variation in disturbance, competition, and predation in relation to environmental stress and recruitment. The American Naturalist 130:730.

Meserve, P. L., J. R. Gutiérrez, J. a Yunger, L. C. Contreras, F. M. Jaksic, and N. Jan. 2007. Role of Biotic Interactions in a Small Mammal Assemblage in Semiarid Chile. Ecology 77:133–148.

Meserve, P. L., D. A. Kelt, W. B. Milstead, and J. R. Gutierrex. 2003. Thirteen years of shifting top-down and bottom-up control. BioScience 53:633.

Milstead, W. B., P. L. Meserve, A. Campanella, M. A. Previtali, D. A. Kelt, J. R. Gutiérrez, and M. Andrea. 2007. Spatial ecology of small mammals in north-central Chile : Role of precipitation and refuges. Journal of Mammalogy 88:1532–1538.

Moore, J. C., E. L. Berlow, D. C. Coleman, P. C. Ruiter, Q. Dong, A. Hastings, N. C. Johnson, K. S. McCann, K. Melville, P. J. Morin, K. Nadelhoffer, A. D. Rosemond, D. M. Post, J. L. Sabo, K. M. Scow, M. J. Vanni, D. H. Wall, P. C. De Suiter, Q. Dong, A. Hastings, N. C. Johnson, K. S. McCann, K. Melville, P. J. Morin, K. Nadelhoffer, A. D. Rosemond, D. M. Post, J. L. Sabo, K. M. Scow, M. J. Vanni, and D. H. Wall. 2004. Detritus, trophic dynamics and biodiversity. Ecology Letters 7:584–600.

Moore, J. C., K. McCann, and P. C. De Ruiter. 2005. Modeling trophic pathways, nutrient cycling, and dynamic stability in soils. Pedobiologia 49:499–510.

Moritz, C., J. Patton, C. Conroy, and J. Parra. 2008. Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. Science 322:261–4.

Murakami, M., and S. Nakano. 2002. Indirect effect of aquatic insect emergence on a terrestrial insect population through predation by birds. Ecology Letters 5:333–337.

North American Bird Conservation Initiative. 2016. The State of North America's Birds 2016. Ottawa, ON, Canada.

North American Bird Conservation Initiative Canada. 2012. The State of Canada's Birds. Page Environment Canada. Environment Canada, Ottawa, Canada.

O'Connor, M. I., J. R. Bernhardt, and N. C. Caulk. 2015. Food Webs. Page *in* D. Gibson, editor. Oxford Bibliographies. Oxford University Press, NY.

Odum, E. P. 1969. The strategy of ecosystem development. Science (New York, N.Y.) 164:262–270.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O. Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and H. Wagner. 2015. vegan: Community Ecology Package. CRAN.

Oksanen, L., S. D. Fretwell, J. Arruda, and P. Niemela. 1981. Exploitation ecosystems in gradients of primary productivity. The American Naturalist 118:240–261.

Oksanen, L., and T. Oksanen. 2000. The logic and realism of the hypothesis of exploitation ecosystems. The American Naturalist 155:703–723.

Olff, H., D. Alonso, M. P. Berg, B. K. Eriksson, M. Loreau, T. Piersma, P. T. R. S. B, and N. Rooney. 2009. Parallel ecological networks in ecosystems. Philosophical transactions of the Royal Society of London. Series B, Biological sciences 364:1755–79.

Ostfeld, R. S., and F. Keesing. 2000. Pulsed resources and community dynamics of consumers in terrestrial ecosystems. Trends in Ecology and Evolution 15:232–237.

Pace, M. L. M., J. J. J. Cole, S. R. S. Carpenter, and J. J. F. Kitchell. 1999. Trophic cascades revealed in diverse ecosystems. Trends in Ecology & Evolution 14:483–488.

Paine, R. T. 1966. Food web complexity and species diversity. The American Naturalist 100:65.

Paine, R. T. 1980. Food webs: Linkage, interaction strength and community infrastructure. Journal of Animal Ecology 49:667–685.

Parnell, A. C., R. Inger, S. Bearhop, and A. L. Jackson. 2010. Source partitioning using stable isotopes: Coping with too much variation. PLoS ONE 5:1–5.

Parra, J. L., C. Rahbek, J. A. Mcguire, and C. H. Graham. 2011. Contrasting patterns of phylogenetic assemblage structure along the elevational gradient for major hummingbird clades. Journal of Biogeography 38:2350–2361.

Piovia-Scott, J., D. A. Spiller, and T. W. Schoener. 2011. Predation in an island food web. Science 331:461–463.

Polis, G. A., W. B. Anderson, and R. D. Holt. 1997a. Toward an integration of landscape and food web ecology: The dynamics of spatially subsidized food webs. Annual Review of Ecology and Systematics 28:289–316.

Polis, G. A., and R. D. Holt. 1992. Intraguild predation: The dynamics of complex trophic interactions. Trends in Ecology & Evolution 7:151–154.

Polis, G. A., and S. D. Hurd. 1995. Extraordinarily high spider densities on islands: Flow of energy from the marine to terrestrial food webs and the absence of predation. Proceedings of the National Academy of Sciences of the United States of America 92:4382–4386.

Polis, G. A., and S. D. Hurd. 1996. Linking marine and terrestrial food webs: Allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. The American Naturalist 147:396.

Polis, G. A., S. D. Hurd, C. T. Jackson, and F. S. Pińero. 1997b. El Nino effects on the dynamics and control of an island ecosystem in the gulf of California. Ecology 78:1884–1897.

Polis, G. A., A. L. . W. Al Sears, G. R. G. Huxel, D. R. D. Strong, and J. Maron. 2000. When is a trophic cascade a trophic cascade? Trends in Ecology & Evolution 15:473–475.

Polis, G. A., and D. R. Strong. 1996. Food web complexity and community dynamics. The American Naturalist 147:813–846.

Polis, G. a, C. a Myers, and R. D. Holt. 1989. The ecology and evolution of intraguild predation: Potential competitors that eat each other. Annual Review of Ecology and Systematics 20:297–330.

Post, D. M. 2002. Using stable isotopes to estimate trophic position: Models, methods, and assumptions.

Ecology 83:703–718.

Power, M. E. 2000. What enables trophic cascades? Commentary on Polis et al. Trends in Ecology and Evolution 15:443–444.

Preisser, E. L., J. L. Orrock, and O. J. Schmitz. 2007. Predator hunting mode and habitat domain alter nonconsumptive effects in predator-prey interactions. Ecology 88:2744–2751.

Prugh, L. R., C. J. Stoner, C. W. Epps, W. T. Bean, W. J. Ripple, A. S. Laliberte, and J. S. Brashares. 2009. The Rise of the Mesopredator. BioScience 59:779–791.

R Development Core Team, R. 2011. R: a language and environment for statistical computing.

Rahbek, C. 1997. The relationship amoung area, elevation, and regional species richness in neotropical birds. The American Naturalist 149:875–902.

Rahbek, C. 2005. The role of spatial scale and the perception of large-scale species-richness patterns. Ecology Letters 8:224–239.

Reich, P. B., S. E. Hobbie, and T. D. Lee. 2014. Plant growth enhancement by elevated CO2 eliminated by joint water and nitrogen limitation. Nature Geoscience 7:920–924.

Richardson, A. N. 2012. Changes in Grassland Songbird Abundances through Time in Response to Burning and Grazing in the Northern Mixed-grass Prairie. University of Manitoba.

Ripple, W. J., E. J. Larsen, R. A. Renkin, and D. W. Smith. 2001. Trophic cascades among wolves, elk and aspen on Yellowstone National Park's northern range. Biological Conservation 102:227–234.

Ritchie, M. E. 2000. Nitrogen limitation and trophic vs. abiotic influence on insect herbivores in a temperate grassland. Ecology 81:1601–1612.

Rogers, H., J. Hille Ris Lambers, R. Miller, and J. J. Tewksbury. 2012. "Natural experiment" demonstrates top-down control of spiders by birds on a landscape level. PloS one 7:e43446.

Rotenberry, J. T., and J. A. Wiens. 1980a. Temporal variation in habitat structure and shrubsteppe bird dynamics. Oecologia 47:1–9.

Rotenberry, J. T., and J. A. Wiens. 1980b. Habitat structure, patchiness , and avian communities in North American steppe vegetation: A multivariate analysis. Ecology 61:1228–1250.

Sala, O. E., W. J. Parton, L. A. Joyce, and W. K. Lauenroth. 1988. Primary production of the central grassland region of the united states. Ecology 69:40–45.

Sanders, N. J., and C. Rahbek. 2012. The patterns and causes of elevational diversity gradients. Ecography 35:1–3.

Schmidt, A. C., L. H. Fraser, C. N. Carlyle, and E. R. L. Bassett. 2012. Does cattle grazing affect ant abundance and diversity in temperate grasslands? Rangeland Ecology & Management 65:292–298.

Schmitz, O. J. 2003. Top predator control of plant biodiversity and productivity in an old-field ecosystem. Ecology Letters 6:156–163.

Schmitz, O. J. 2006. Predators have large effects on ecosystem properties by changing plant diversity, not plant biomass. Ecology 87:1432–1437.

Schmitz, O. J. 2008a. Effects of predator hunting mode on grassland ecosystem function. Science (New York, N.Y.) 319:952–4.

Schmitz, O. J. 2008b. Herbivory from individuals to ecosystems. Annual Review of Ecology, Evolution, and Systematics 39:133–152.

Schmitz, O. J., A. P. Beckerman, and K. M. O'Brien. 1997. Behaviorally mediated trophic cascades: Effects of predation risk on food web interactions. Ecology 78:1388–1399.

Schmitz, O. J., P. A. Hambäck, and A. P. Beckerman. 2000. Trophic Cascades in Terrestrial Systems: A Review of the Effects of Carnivore Removals on Plants. The American Naturalist 155:141–153.

Schoener, T. W., D. A. Spiller, and J. B. Losos. 2004. Variable ecological effects of hurricanes: The importance of seasonal timing for survival of lizards on Bahamian islands. Proc Natl Acad Sci U S A 101:177–181.

Sergio, F., O. J. Schmitz, C. J. Krebs, R. D. Holt, M. R. Heithaus, A. J. Wirsing, W. J. Ripple, E. Ritchie, D. Ainley, D. Oro, Y. Jhala, F. Hiraldo, and E. Korpimäki. 2014. Towards a cohesive, holistic view of top predation: A definition, synthesis and perspective. Oikos 123:1234–1243.

Shurin, J. B. 2015. Top-down and bottom-up regulation of communities. Page *in* G. D., editor. Oxford Bibliographies. Oxford University Press, NY.

Shurin, J. B., E. T. Borer, E. W. Seabloom, K. Anderson, C. A. Blanchette, B. Broitman, S. D. Cooper, and B. S. Halpern. 2002. A cross-ecosystem comparison of the strength of trophic cascades. Ecology Letters 5:785–791.

Sinclair, A. R. E., S. Mduma, and J. S. Brashares. 2003. Patterns of predation in a diverse predator-prey system. Nature 425:288–290.

Sinclair, A. R. E., K. L. Metzger, J. M. Fryxell, C. Packer, A. E. Byrom, M. E. Craft, K. Hampson, T. Lembo, S. M. Durant, G. J. Forrester, J. Bukombe, J. McHetto, J. Dempewolf, R. Hilborn, S. Cleaveland, A. Nkwabi, A. Mosser, and S. A. R. Mduma. 2013. Asynchronous food-web pathways could buffer the response of Serengeti predators to El Nino Southern Oscillation. Ecology 94:1123–1130.

Sinclair, A. R. E., R. P. Pech, J. M. Fryxell, M. K., A. E. Byrom, C. J. Savory, J. S. Brashares, R. Turkington, R. Beyers, W. L. Harrower, and R. Beyers. (n.d.). Assessing the success of rewilding using a quantitative index x:x.

Smith, M. D., and A. K. Knapp. 2003. Dominant species maintain ecosystem function with non-random species loss. Ecology Letters 6:509–517.

Spiller, D. A., J. B. Losos, and T. W. Schoener. 1998. Impact of a catastrophic hurricane on island populations. Science 281:695–697.

Spiller, D. A., J. Piovia-scott, A. N. Wright, L. H. Yang, G. Takimoto, T. W. Schoener, T. Iwata, S. Url, and N. Wright. 2010. Marine subsidies have multiple effects on coastal food webs. Ecology 91:1424–1434.

Spiller, D. A., and T. W. Schoener. 1998. Lizards reduce spider species richness by excluding rare species. Ecology 79:503–516.

Spiller, D. A., and T. W. Schoener. 2008. Climatic control of trophic interaction strength: The effect of lizards on spiders. Oecologia 154:763–771.

Spiller, D. A., T. W. Schoener, and J. Piovia-Scott. 2016. Predators suppress herbivore outbreaks and enhance plant recovery following hurricanes. Ecology 97:2540–2546.

Srivastava, D. S., B. J. Cardinale, A. L. Downing, J. E. Duffy, C. Jouseau, M. Sankaran, and J. P. Wright. 2009. Diversity has stronger top-down than bottom-up effects on decomposition. Ecology 90:1073–83.

Srivastava, D. S., and J. H. Lawton. 1998. Why more productive sites have more species: An experimental test of theory using tree-hole communities. The American Naturalist 152:510–529.

Stapp, P., and G. A. Polis. 2003. Influence of pulsed resources and marine subsidies on insular rodent populations. Oikos 102:111–123.

Strickland, M. S., D. Hawlena, A. Reese, M. A. Bradford, and O. J. Schmitz. 2013. Trophic cascade alters ecosystem carbon exchange. Proceedings of the National Academy of Sciences of the United States of America 110:11035–8.

Sundqvist, M. K., N. J. Sanders, and D. A. Wardle. 2013. Community and ecosystem responses to elevational gradients: Processes, mechanisms, and insights for global change. Annual Review of Ecology, Evolution, and Systematics 44:261–280.

Suttle, K. B., M. A. Thomsen, and M. E. Power. 2007. Species interactions reverse grassland responses to changing climate. Science 315:640–642.

Swengel, S. R., and A. B. Swengel. 2001. Relative effects of litter and management on grassland bird abundance in Missouri, USA. Bird Conservation International 11:113–128.

Terborgh, J. 1977. Bird Species Diversity on an Andean Elevational Gradient. Ecology 58:1007–1019.

Terborgh, J., L. Lopez, P. Nun, P. Nuñez, M. Rao, G. Shahabuddin, G. Orihuela, M. Riveros, R. Ascanio, G. H. Adler, T. D. Lambert, and L. Balbas. 2001. Ecological meltdown in predator-free forest fragments. Science 294:1923–6.

Thibault, K. M., S. K. M. Ernest, E. P. White, J. H. Brown, and R. Jacob. 2010. Long-term insights into

the influence of precipitation on community dynamics in desert rodents. Journal of Mammalogy 91:787–797.

Thompson, R. M., U. Brose, J. a. Dunne, R. O. Hall, S. Hladyz, R. L. Kitching, N. D. Martinez, H. Rantala, T. N. Romanuk, D. B. Stouffer, and J. M. Tylianakis. 2012. Food webs: Reconciling the structure and function of biodiversity. Trends in Ecology and Evolution 27:689–697.

Trebilco, R., J. K. Baum, A. K. Salomon, N. K. Dulvy, R. Trebilco, J. K. Baum, A. K. Salomon, and N. K. Dulvy. 2013. Ecosystem ecology: Size-based constraints on the pyramids of life. Trends in Ecology and Evolution 28:423–431.

Tunney, T. D., K. S. McCann, N. P. Lester, and B. J. Shuter. 2012. Food web expansion and contraction in response to changing environmental conditions. Nature communications 3:1105.

Turkington, R. 2009. Top-down and bottom-up forces in mammalian herbivore – vegetation systems: An essay review. Botany 87:723–739.

Turkington, R., and W. L. Harrower. 2016. An experimental approach to addressing ecological questions related to the conservation of plant biodiversity in China. Plant Diversity 1:1–10.

Ward, C. L., K. S. McCann, and N. Rooney. 2015. HSS revisited: Multi-channel processes mediate trophic control across a productivity gradient. Ecology Letters 18:1190–1197.

White, T. C. R. 1978. Importance of a relative shortage of food in animal ecology. Oecologia 33:71–86.

Whittaker, R. 1956. Vegetation of the great smoky mountains. Ecological Monographs.

Whittaker, R. H. 1960. Vegetation of the Sisiyou mountains, Orgeon and California. Ecological Monographs 30:279–338.

Whittaker, R. H. 1972. Evolution and measurement of species diversity. Taxon 21:213–251.

Wiens, J. A. 1973. Pattern and process in grassland bird communities. Ecological Monographs 43:237–270.

Wiens, J. A. A., J. T. T. Rotenberry, and B. Van Horne. 1985. Territory size variations in shrubsteppe birds. Auk 102:500–505.

Wiens, J. A., and J. T. Rotenberry. 1987. Shrub-steppe birds and the generality of community models: A response to Dunning. Amerincan Naturalist 129:920–927.

Wiens, J. A., J. T. Rotenberry, and B. Van Horne. 1987. Habitat occupancy patterns of North America shrubsteppe birds: The effects of spatial scale. Oikos 48:132–147.

Wiens, J. A., and J. T. J. Rotenberry. 1981. Habitat associations and community structure of birds in shrubsteppe environments. Ecological Monographs 51:21–42.

Winter, M., D. H. Johnson, and J. A. Shaffer. 2005. Variability in Vegetation Effects on Density and Nesting Success of Grassland Birds. The Journal of Wildlife Management 69:185–197.

Wise, D. H., W. E. Snyder, P. Tuntibunpakul, and J. Halaj. 1999. Spiders in decomposition food webs of agroecosystems: Theory and evidence. The Journal of Arachnology 27:363–370.

Wolkovich, E. M. 2016. Reticulated channels in soil food webs. Soil Biology and Biochemistry:4–7.

Wolkovich, E. M., S. Allesina, K. L. Cottingham, J. C. Moore, S. A. Sandin, and C. De Mazancourt. 2014. Linking the green and brown worlds: The prevalence and effect of multichannel feeding in food webs. Ecology 95:3376–3386.

Wollrab, S., S. Diehl, and A. M. De Roos. 2012. Simple rules describe bottom-up and top-down control in food webs with alternative energy pathways. Ecology Letters 15:935–946.

Wright, A. N., J. Piovia-Scott, D. A. Spiller, G. Takimoto, L. H. Yang, and T. W. Schoener. 2013. Pulses of marine subsidies amplify reproductive potential of lizards by increasing individual growth rate. Oikos 122:1496–1504.

Yodzis, P. 1984. Energy flow and the vertical structure of real ecosystems. Oecologia 65:86–88.

Departure - Installation view, oil paints on canvas, 149 cm x 149 cm
© 2016 Marion Landry, by permission