

Some Causes and Consequences of the Loss of Biodiversity: Ten Years of Plant Ecological Research in the Yukon

Abstract

This article introduces the new Biodiversity Research Centre at UBC and reviews the nature and importance of biodiversity research in a changing world with rapidly expanding human population. Results from the Kluane Forest Boreal Forest Ecosystem Project have shown that nutrient availability is the main determinant of vegetation abundance rather than herbivory. However, with increasing nutrients and vegetation abundance there was a correlated loss of species diversity. Planned experiments in the same area are described which aim to remove species and functional groups from the vegetation (Biological Knock Out). These experiments are expected to give further insights into the functioning of this ecosystem. (abstract prepared by journal)

Introduction

Biological diversity, or biodiversity, is a general term referring to the variety of the world's organisms, including their genetic diversity, their populations, and the assemblages they form. Biologists have described over one and a half million species, but there are perhaps as many as fifteen million. Natural changes in communities, such as succession, have been occurring as long as communities have existed, but today human development, resource extraction, population pressure, habitat destruction, and global warming are speeding the rate of change and altering the types of change. Rates of species extinction are between one hundred to one thousand times greater than in pre-human history. Biodiversity loss is an early warning of a deteriorating environment but it is also a social, cultural and economic loss. If we wish to retain a rich biota in fully functioning ecosystems and sustain the resources required to maintain a growing global population, it is critical to slow the rate of biodiversity loss.

Roy Turkington

Dept. of Botany and Biodiversity Research Centre, University of British Columbia,
Vancouver, BC, V6T 1Z4

I. The Biodiversity Research Centre at UBC

The UBC Biodiversity Research Centre was founded in 1966. The mandate of the Centre includes:

1. *Research* - to understand the impacts of the loss of genes and species on the normal function of ecosystems. Specifically we address such questions as:
 - a. What are species and what is their role?
 - b. How are ecosystems changed when species are lost?
 - c. How will climate change affect Canada's biodiversity?
 - d. How is genetic diversity maintained in populations?
 - e. Where are the hotspots of species diversity?
 - f. Topics of conservation biology including invasive [exotic] species, endemism, rarity, small populations, extinction, bottlenecks, habitat fragmentation
 - g. Strategies to conserve biodiversity.
2. *Assessment* - of the biodiversity of western Canada with a goal to determine reference areas for preservation and to develop a predictive science of ecological management.
3. *Guidance* - to provide independent advice to government, the private sector, and the public, and provide a scientific basis or conservation and management of populations, communities and ecosystems.
4. *Training* - of experts in identification and categorization of species.
5. *Education* - to promote public understanding of issues related to biodiversity and the consequences of biodiversity loss.

Biodiversity is a synthetic concept that lies at the junction of many disciplines and requires an integrative approach – genetics, ecology, evolutionary theory, biogeography, bioinformatics, and systematics. The Centre has more than forty researchers actively involved in diverse areas of research. In this paper I will provide a glimpse into biodiversity research, illustrated by some of my own work over this past number of years at Kluane in southwestern Yukon. The focus of this article is not on detailed results, rather on providing a glimpse into the types of questions we ask and the

types of methodology we use to address those questions. Specifically I will relate a few case studies related to the loss of biodiversity in Yukon, and then describe a study designed to consider the consequences of such losses.

Much of the early research effort devoted to plant ecology was essentially descriptive. It is natural that the first stage in the growth of any discipline, or individual study, should consist of a description of the material that is to be studied. The next stage is to search for correlations between, and causes of, what has been described. This frequently involves the implementation of well-designed, replicated, manipulative field experiments, which typically will test hypotheses. Such studies allow us to understand how populations and communities are structured, and how their components interact, and which processes contribute to the patterns we have described. This then permits us to make predictions about how the community and its component species and populations might change in the face of perturbations, either human-induced or natural. My many colleagues and I have made a bold attempt to implement a large manipulative field experiment designed to understand the organization of the entire ecosystem. After explaining the broad scope of this project, I will describe in more detail our research on the understory herbaceous vegetation and finally I will present an overview of new research into the consequences of biodiversity loss.

II. Understanding a Functioning Ecosystem: The Kluane Boreal Forest Ecosystem Project¹

The Study Site

These studies were done near Kluane Lake in the Shakwak Trench, a wide glacial valley in southwestern Yukon in northern Canada, and described by John & Turkington (1995, 1997), Turkington *et al.* (1998) and Krebs *et al.* (2001). The area is in the rain shadow of the St. Elias Mountains and receives a mean annual precipitation of ca. 230 mm, mostly falling as rain during the summer months, but including an average annual snowfall of about one hundred cm. The region is a closed to open spruce forest community and the dominant tree is *Picea glauca* (Moench) Voss (white spruce), interspersed

¹The principal Investigators were C.J. Krebs, K. Martin, J. N. M. Smith, A.R.E. Sinclair, R. Turkington (University of British Columbia), S. Boutin, M.R.T. Dale (University of Alberta), R. Boonstra (University of Toronto, Scarborough).

with stands of *Populus tremuloides* Michx. (trembling aspen) and *Populus balsamifera* L. (balsam poplar). The understory is dominated by *Salix glauca* (L.) and other *Salix* spp. (shrub willows), *Betula glandulosa* Michx. (dwarf birch), *Shepherdia canadensis* (L.) Nutt. (soapberry), and a well developed ground layer, chiefly *Lupinus arcticus* S. Wats. (arctic lupine) (back cover), *Festuca altaica* Torr. (Northern rough fescue), *Linnaea borealis* L. (twin flower) (Figure 5), *Arctostaphylos uva-ursi* (L.) Spreng. (bearberry), *Mertensia paniculata* (Aiton) G. Don (bluebells), *Achillea millefolium* L. var. *borealis* (Bong.) Farwell (yarrow), and *Epilobium angustifolium* L. s.l. (fireweed) (Figure 6). Snowshoe hares are the primary herbivore and they undergo a regular 10 to 12-year population cycle. Many other small mammals include herbaceous vegetation in their diet but these were quite infrequent at our sites. The first major impacts of an outbreak of spruce bark beetle were observed in 1995.

The Study

This study was designed to understand the structure and dynamics of the Boreal Forest ecosystem in southwestern Yukon with a special emphasis on the vertebrate communities. This was a bold program and we considered the system to have four trophic levels – predators, herbivores, plants (mostly shrubs available as winter food supply), and soil nutrients. To answer these questions we imposed seven treatments (Table 1) that manipulated the levels of one trophic level, and then monitored the responses, usually abundance,

Trophic Level	Manipulations	Plot Sizes	Monitored Responses
Soil nutrients	Add nutrients as fertilizer	1 km ² & 5 m ²	Plant populations
Plants	Remove vegetation	1 m ²	Soil nutrients
Herbivores	Increase herbivores by feeding with rabbit chow	1 km ²	Predator, and plant populations
Herbivores	Exclude herbivores	4 ha & 5 m ²	Plant populations
Predators	Exclude predators	1 km ²	Herbivore populations
Multi-level	Exclude predators, add rabbit chow	1 km ²	Herbivores and plants
Multi-level	Exclude herbivores and add fertilizer	4 ha & 5 m ²	Plant populations

Table 1. A summary of the seven treatment combinations used in the Kluane Boreal Forest Ecosystem Project.

in other trophic levels. The principle is straightforward – if we think that a community is structured by herbivore populations, then we would manipulate the level of herbivory and monitor the responses in both the predator and plant populations. These experiments were designed to test hypotheses pertaining to the regulation of abundance at the various trophic levels (I will detail the vegetation level below), and when considered as a whole, to provide insight about the factors influencing community organization.

There are two general sets of models and many variations of them – ‘bottom-up’ (nutrient limitation) and ‘top-down’ (predator control). Bottom-up hypotheses assume that systems are regulated by nutrient flow from below and they assume a shortage of suitable resources. There are various top-down hypotheses with different implications for population regulation at all levels, but pure ‘top-down’ proposes that each trophic level is regulated by the one above with the top predators being self-regulated.

There were 5 different treatments, which when combined, resulted in that resulted in seven different perturbations (Table 1). These systematically removed or supplemented trophic levels, and made predictions about the direction of change in abundance (mostly biomass) at other trophic levels (Boutin *et al.* 2001).

Treatment 1: Fertilizer was applied from the air to two 1 km² plots of forest. Fertilizer (N:P:K 35:10:5) was applied in granular form most years between mid-May and early June after snow melt at a rate of 17.5 g N/m²/yr, 5 g P/m²/yr and 2.5 g K/m²/yr (55 metric tons per plot annually).

Treatment 2: Commercial rabbit food (chow) was applied *ad libitum* to three areas. The amounts applied varied between 3000 – 7000kg of food per plot per year.

Treatment 3: Carnivores were excluded from two 1 km² plots of forest by electrified wire fencing to a height of 2.2m. A 10 ha subplot of one of these fenced areas was covered with an overhead monofilament screen to deter birds of prey.

Treatment 4: Hares were excluded from two areas of 4 ha each, using heavy grade 5 cm mesh plastic fencing to a height of 3m.

Treatment 5: In ten 1m² plots at each of five sites, vegetation was killed by herbicide and left *in situ*.

This major set of experiments ran for 10 years from 1986 – 1996. The results have been published in about thirty graduate theses, more than one hundred peer-reviewed articles, as a book (Krebs *et al.* 2001), and as a major summary paper (Sinclair *et al.* 2000, 2001). In general, the direct effect of each treatment produced strong bottom-up and top-down changes in biomass. At both the vegetation (mostly shrubs) and herbivore levels, top-down effects were stronger than bottom-up, but the combined results from all treatments showed a strong interaction of both models acting at all trophic levels.

III. The Understory Herbaceous Vegetation: Investigating Causes of Species Loss

This study was done in the same general area as the previous one. As botanists, naturally we focused on the plants in the system. Plants in the boreal forest are an important component of the ecosystem for two main reasons. First, the plants as vegetation form the physical surroundings for both herbivores and carnivores and are the basis of the physical structure of the community. Second, as primary producers, they provide the energy and nutrients to the herbivores on which higher trophic levels depend. Therefore, understanding the factors that limit the quantity and the quality of plants is fundamental. The previous “major” study focused on shrubs as winter food supply. These studies focused on the herbaceous vegetation, the grasses and herbs, which are relatively abundant in the forest understory and are the primary summer food supply. These plants provide a source of relatively high quality food to the herbivores. Soil nutrients, especially nitrogen, often limit the productivity of boreal forest vegetation, and may control vegetation

Hypothesis	Fertilizer Added	Herbivores Excluded	Fertilizer Added & Herbivores Excluded
1. Bottom-up, donor control	+	0	+
2. Top-down control	0	+	+
3. Interactive control	+	+	+

Table 2. Predictions of the direction of change in plant biomass, or standing crop, from each of the three experimental treatments according to the three hypotheses. + = biomass increase, and 0 = no change.

standing crop. Plants differ in their abilities to respond to raised nutrient levels, and community composition usually changes following fertilization as more competitive species begin to dominate. Conversely, herbivory may have a direct effect of vegetation quantity and quality. Herbivory has long been known to influence species composition in some plant communities due to differential plant palatability and differences in plants' abilities to tolerate herbivory.

To understand some of the inter-trophic level linkages between components of the system, three hypotheses regarding the vegetation were tested: that vegetation was controlled by (i) nutrient availability alone (bottom-up, or donor control), (ii) by herbivores alone (top-down control), and (iii) by both nutrient availability and herbivores. This involved three major experimental treatments - fertilization, herbivore exclusion, and fertilization plus herbivore exclusion. These treatments allow us to make specific predictions about changes in plant biomass, or standing crop, under the three different hypotheses (Table 2). In addition to the direct predictions in Table 2, some subsequent predictions are also made; these predictions are formalized below.

Hypothesis 1: Vegetation is controlled by nutrient availability alone.

This hypothesis leads to four predictions:

1. There will be an overall increase in the abundance of vegetation in fertilized plots (Arii & Turkington ; John & Turkington 1995; Turkington *et al.* 1998, 2001, 2002)
2. Herbivore exclusion alone will not lead to an increase in vegetation abundance (Dlott & Turkington 2000).
3. Community composition will change in response to fertilization according to species differences in the ability to respond to raised nutrient levels. Specifically we predict that grasses and most of the taller herbaceous dicots will increase, while prostrate species and groups such as woody vines, mosses, and lichens will decline (John & Turkington 1997; Turkington *et al.* 1998, 2002).
4. Species number and diversity will decline in fertilized plots because of increasing dominance by a few species (Turkington *et al.* 2002).

Hypothesis 2: Vegetation is controlled by herbivores alone (top-down or consumer control).

This hypothesis leads to three predictions:

1. There will be no increase in vegetation abundance when plots are fertilized but unfenced (Arii & Turkington; John & Turkington 1995; Turkington *et al.* 1998, 2001, 2002)
2. Vegetation abundance will increase in exclosures (John & Turkington 1995; Dlott & Turkington).
3. Species number and diversity will decline inside exclosures because removal of herbivores will permit competitively dominant plant species to exclude some less competitive species (Dlott & Turkington 2000).

Hypothesis 3: Vegetation is controlled by both nutrient availability and herbivory (interaction control).

This hypothesis leads to four predictions:

1. There will be an increase in plant growth in fertilized plots but there will be an interaction between the exclosure and fertilizer treatments as herbivores remove some of the additional growth due to fertilizer (Sharam 1997; Graham & Turkington 2000).
2. In herbivore exclosures, vegetation abundance will increase.
3. Plots that have been both fertilized and fenced will have the lowest species number and diversity because both treatments lead to the exclusion of some plant species (Dlott & Turkington 2000).
4. Grazing intensity will be increased on fertilized plots due to increased quality of forage (Sharam 1997; Dlott & Turkington 2000; Hicks & Turkington 2000).

Between 1990 and 2003 most of these hypotheses were directly tested in the field. Here I will describe only the methods for the major study, and present a few of the major findings, mostly from Turkington *et al.* (1998, 2001, 2002).

The Study

This experiment was replicated at two sites in areas of moderately open spruce forest (Figure 9) with a well developed (>90% cover) herbaceous understorey. Both sites were probably last burned in 1872. Sixteen 5 m x 5 m plots were selected in small meadows at each site. At each site, the plots were randomly divided among four treatments: control (no treatment), fence only, fertilizer only, and fence with fertilizer. Fences were 1m high and made

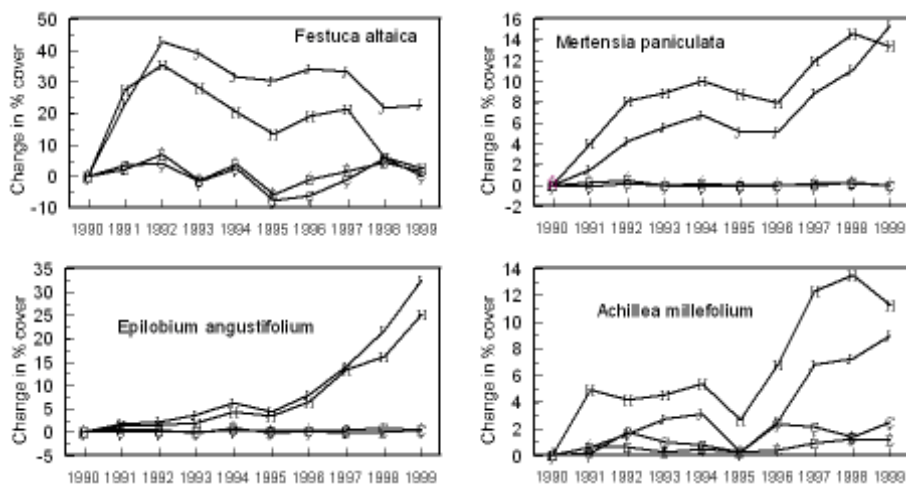


Figure 1. Change in percent cover of four species that increased in response to the fertilizer treatment. Solid symbols show fertilized treatments, open symbols unfertilized. Triangles show fenced treatments, circles unfenced.

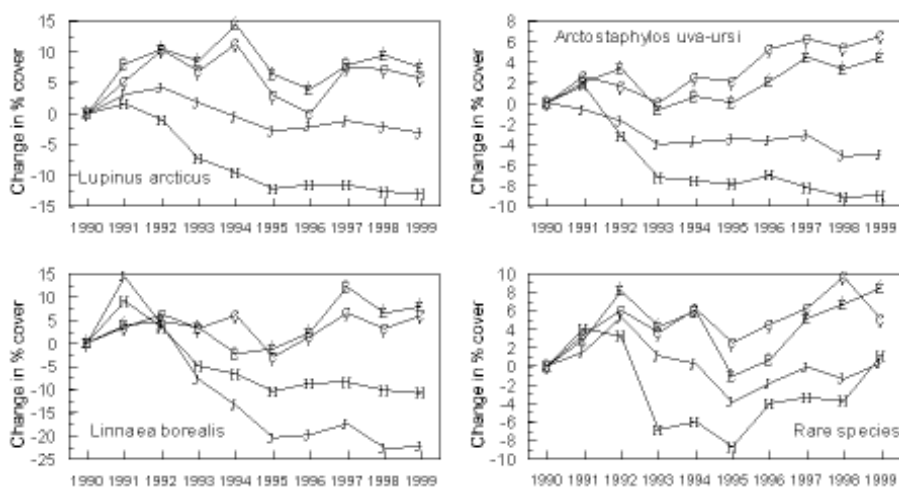


Figure 2. Change in percent cover of four species that decreased in response to the fertilizer treatment. Solid symbols show fertilized treatments, open symbols unfertilized. Triangles show fenced treatments, circles unfenced.

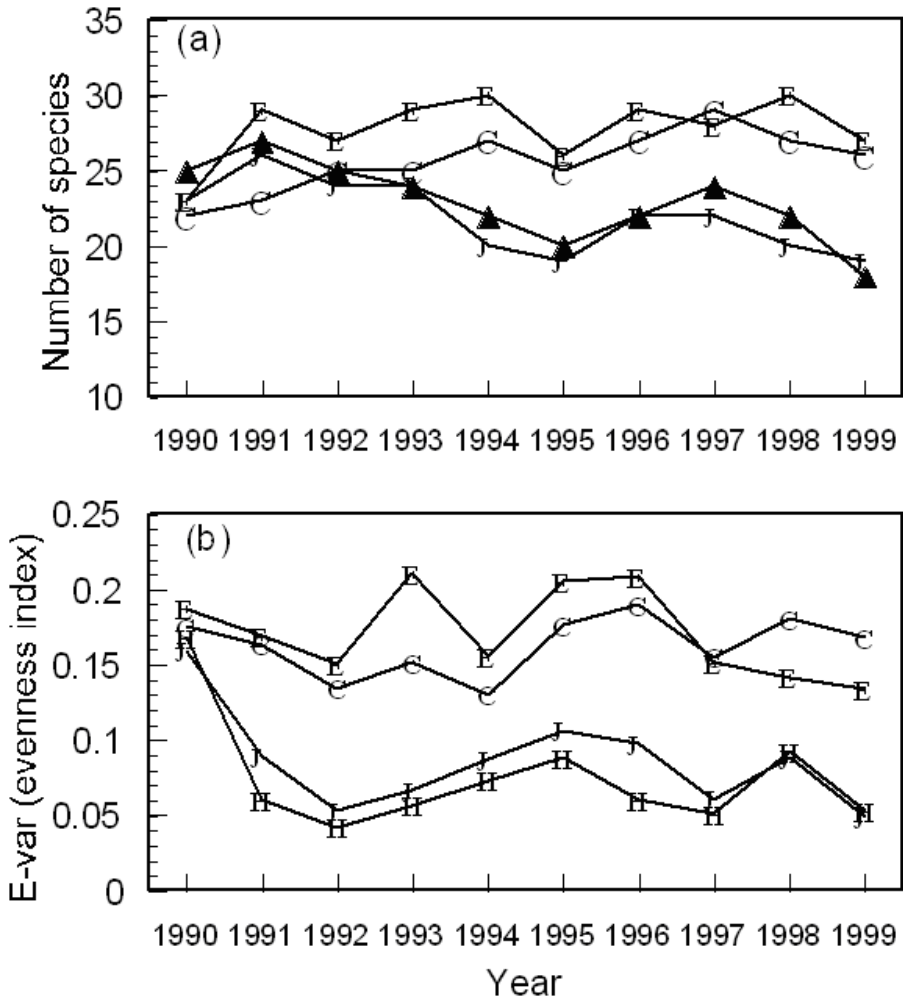


Figure 3. (a) The number of species, and (b) evenness (calculated using the E_{var}) of species, in plots subjected to treatments from 1990 to 1999. Solid symbols show fertilized treatments, open symbols unfertilized. Triangles show fenced treatments, circles unfenced.

of galvanized chicken wire with 2.5 cm mesh, supported by 2 m steel T-bars, and firmly stapled to the ground to prevent animals intruding under the fence; there was no obvious evidence of any herbivory inside fenced plots. Fertilizer (N:P:K 35:10:5) was applied in granular form each year between mid-May and early June after snow melt at a rate of 1.25 kg per 5

m x 5 m plot per year, resulting in an addition of 17.5 g N/m²/yr, 5 g P/m²/yr and 2.5 g K/m²/yr. This application rate was used to be consistent with other studies being done in our area (Boutin *et al.* 2001 p60). Because of the on-going nature of the project we could not use destructive sampling procedures and therefore percentage cover was measured to represent abundance.

The majority of the data presented support the bottom-up hypothesis that herbaceous vegetation standing crop is controlled by nutrient availability alone. With fertilization there was an overall increase in the amount of herbaceous vegetation (Figures 7 and 8); the grass *Festuca*, and the herbs *Mertensia*, *Epilobium*, and *Achillea* (Figure 1) showed the most dramatic increases in abundance while *Lupinus*, and the two low-growing woody ground cover species (*Arctostaphylos* and *Linnaea* (Figure 2)) consistently declined in abundance when fertilized. It is likely that the declines following fertilizer addition for some species are due to competition from the more rapidly growing species. The studies also indicate that the summer herbaceous vegetation is not under top-down control and that the impact of mammalian herbivory, primarily by hares, on the vegetation is minimal.

From 1990 – 1999 there were two major responses to the annual application of fertilizer - we recorded a loss of seven species from our fertilized plots (Figure 3a), and the evenness² of the fertilized plots declined quite markedly (Figure 3b). A low value of evenness indicates that some of the species are of much lower abundance than others. The repeated application of fertilizer will therefore drive many of the species to low abundance (reflected in low evenness values) and ultimately exclude some of the species (those labeled “rare” in Figure 2) from the plots. In the next section I will address the relevance of nitrogen application to northern forests.

Global Warming and Biodiversity

As global warming occurs it will have two direct effects - the growing season will be extended at both ends, and it will be warmer. It has been suggested that the application of nutrients to northern communities may stimulate some of the same effects in the plant community that might be

² Evenness is a measure of the relative abundances of the component species in a community such that evenness is high when all species are equally represented.

produced by global environmental change. Global changes such as increasing CO₂ concentrations, increasing deposition of nitrogen and sulphur pollutants, and rising temperatures will have crucial impacts on nutrient cycles consequently leading to changes in primary production and species composition. It has been argued that climate change will increase the supply of nutrients (both nitrogen and phosphorus), by stimulating decomposition processes, and increase the rate of soil carbon accumulation. Additionally, anthropogenic impacts on the global nitrogen cycle are occurring via combustion of fossil fuels, production of nitrogen fertilizers and cultivation of nitrogen fixing legumes. Industrial nitrogen fixation has increased exponentially since the 1940s and there is increased anthropogenic nitrogen deposition due to vehicle exhaust, petrochemical refining, power and heat production and forest fires. These changes will of course be modified by the interactions between plants and their environment. We can predict that some species will respond strongly to an increased nutrient supply at the expense of others leading to an increase in biomass but a loss of diversity. In our system we might initially expect that bryophytes, lichens, prostrate growth forms, and low nutrient-requiring species will be suppressed or eliminated by faster-growing, more upright clonal species such as the graminoids, *Mertensia paniculata* and *Achillea millefolium*. Clearly species, and vegetation types, with low nutrient uptake demands will be the most sensitive to the predicted changes.

The Value of Long-term Experiments

Initial responses to fertilizer and fencing treatments are species-specific, and transient. The short-term responses measured over the first few years were poor indicators of longer term changes in community composition, and perhaps the current 10 years will be a poor indicator of longer-term trends. Conclusions would have differed had the data been collected after 1 year (beginning of the hare decline), 5 years (during a hare low), or 10 years (during a hare peak) but the general trends identified may be important. It is quite likely that ecosystems such as the boreal forest understory, where the herbaceous community is characterized by slow-growing long-lived plants, never attain equilibrium because the density of hares fluctuates, forests burn and climate changes constantly and slowly. This means that transient responses may be the only ones we have to work with, because permanent shifts in vegetation composition may not be evident until many years later, or may never be attained.

Another particular value of long-term studies is their potential to provide insight into rare events or episodic phenomena. In 1995 we observed the first major signs of an outbreak of spruce bark beetle. As mature trees die and the canopy becomes more open to light penetration this will undoubtedly influence processes at ground level. *Achillea* and *Epilobium* were both minor components of the understory vegetation of our plots until this time, but in 1996, both of these species showed dramatic increases in the fertilized plots. Both species are more typically associated with open areas and the opening of the canopy in combination with increased soil fertility probably stimulated their increase.

IV. Consequences of Species Loss (Biological Knock-Out Experiment)³

The Study Site

The study area is a relatively dry grassland near Kluane Lake about fifteen km north of the previously described sites. This study is being done in an open grassland surrounded by a closed to open spruce forest community dominated by *Picea glauca*. The grassland is dominated by *Poa glauca* Vahl and *Carex stenophylla* Wahlenb. subsp. *eleocharis* (Bailey) Hultén, and also contains many non-leguminous forbs (dominated by *Erigeron caespitosus* Nutt., *Artemisia frigida* Willd. (pasture sage), *Penstemon gormanii* Greene, and *Pulsatilla ludoviciana* (Nutt.) Heller (pasque-flower) and legumes (dominated by *Oxytropis campestris* (L.) DC. (late yellow locoweed).

The Study

As global warming continues, and biodiversity declines, there are concerns that species-poor systems will perform less well or less efficiently than species rich systems. The idea that decreased species diversity can result in decreased ecosystem function has recently received much attention. Ecosystem function is defined as “the activities, processes or properties of ecosystems that are influenced by its biota” and although commonly productivity is the ecosystem function examined other ecosystem functions such as nutrient cycling and litter decomposition have also been examined. A variety of relationships between biodiversity and ecosystem function have been pro-

³ This is the PhD program of Jennie McLaren at the Botany Dept., UBC.

posed, the two most common being the rivet model and the redundancy model. The rivet model is a verbal analogy relating species in an ecosystem to rivets on an airplane wing: the wing may lose a number of rivets (or an ecosystem may lose a number of species) without consequence, but the loss of an additional rivet beyond a certain number could result in the loss of the wing and a serious accident (or the loss of an additional species could result in large changes in ecosystem function). Similarly, the redundancy hypothesis assumes that the loss of a species can be compensated for by other species, and that there will be no decline in ecosystem function until a threshold number of species are lost.

The overall objective of this research is to use a removal experiment to examine the roles of different plant functional groups (graminoids, leguminous forbs, and non-leguminous forbs) in determining ecosystem function. The approach is identical in principle to genetic knock-out experiments where a specific known gene is “knocked-out” from an organism. The consequent development of that organism without the gene is compared to specimens retaining the gene, and the difference in development is an indication of the role of that gene in development. In our system, genes are replaced by functional groups, the organism is replaced by the ecosystem, and the functioning of a community with, and without, a functional group is a measure of the influence of that functional group on the functioning of the community. The objective is to (i) remove biota in a way that might occur naturally, (ii) apply a disturbance in a fashion that has some resemblance to real impacts (e.g. add fertilizer, and remove mycorrhizae), and (iii) monitor the response of the ecosystem to these removals and applied disturbances.

In the treatments, plants were removed from 80 - 1m² plots using Round-up™ glyphosate non-selective herbicide. This method was used so as to minimize soil disturbance and prevent re-growth that may occur with clipping. Herbicide was applied selectively to the leaves and stems of plants using a small paintbrush. Application of herbicide was precise with minimal non-target effects to neighbours. The measures of ecosystem function are:

Above and below-ground decomposition rates: Decomposition rates are measured using litter bags (4 x 8cm, made of 2mm nylon window screening). Each above-ground litter bag contained 0.5 g of dried leaf material and is stapled to the ground surface. Each below-ground litter bag

contains 0.25 g of dried root material and was inserted into the soil to 7 cm depth. One replicate bag of each type will be collected at the end of each growing season and the amount of decomposed material assessed.

Nutrient supply rates: Nutrient supply rates are measured using ion exchange membranes (Plant Root Simulator (PRS)TM-probes). The PRSTM-Probe consists of either a cation- or anion-exchange resin membrane. Two anion and two cation-probes are inserted into each plot and left in place for the duration of the growing season. The PRSTM-probes are left in the soil to measure *in situ* nutrient supply rates for the duration of a growing season.

Soil moisture: Soil moisture (%) is measured using a water content sensor at 10 cm depth.

Mycorrhizal colonization rate: Mycorrhizal colonization rate will be measured in a random sample of roots taken from each plot. Roots will be stained in trypan blue and analyzed microscopically for percent root colonization.

Soil Extractable Ions: Using chemical extractions, we will measure mineral available nitrogen (NO_3^- , NH_4^+) and phosphate (PO_4^{3-}). Soil cores will be extracted using 0.5 M K_2SO_4 and analyzed using a colorimetric analyzer.

Microbial biomass nitrogen and phosphorus: Microbial biomass N will be measured using the chloroform fumigation method. The chloroform fumigation lyses microbial cell walls and releases the nutrients within. Thus, total microbial N can be calculated by subtracting the nitrogen in unfumigated soils from the nitrogen in fumigated soils.

Soil microbial community: Jennie McLaren plans on examining the effects of the treatments on the belowground microbial community using both BIOLOG EcolplatesTM (BIOLOG Inc., Hayward, CA, USA) and phospholipids fatty acid (PLFA) analysis. These permit an assessment of the diversity, density and composition of the microbial community.

Conclusion

The United Nations recently estimated that the world's human population will reach 9.1 billion by 2050. Human demands on natural resources are rising rapidly resulting in habitat fragmentation and an alarming rate of loss



Photo: Roy Turkington

Figure 4. Emerald Lake exemplifies the boreal forest ecosystems of the Yukon Territory.



Photo: Roy Turkington

Figure 5. *Linnaea borealis*.



Figure 6. *Epilobium angustifolium*.



Photo: Roy Turkington

Figure 7. A 5 × 5 meter plot after one year of fertilizing.



Photo: Roy Turkington

Figure 8. A 5 × 5 meter plot after five years of fertilizing.

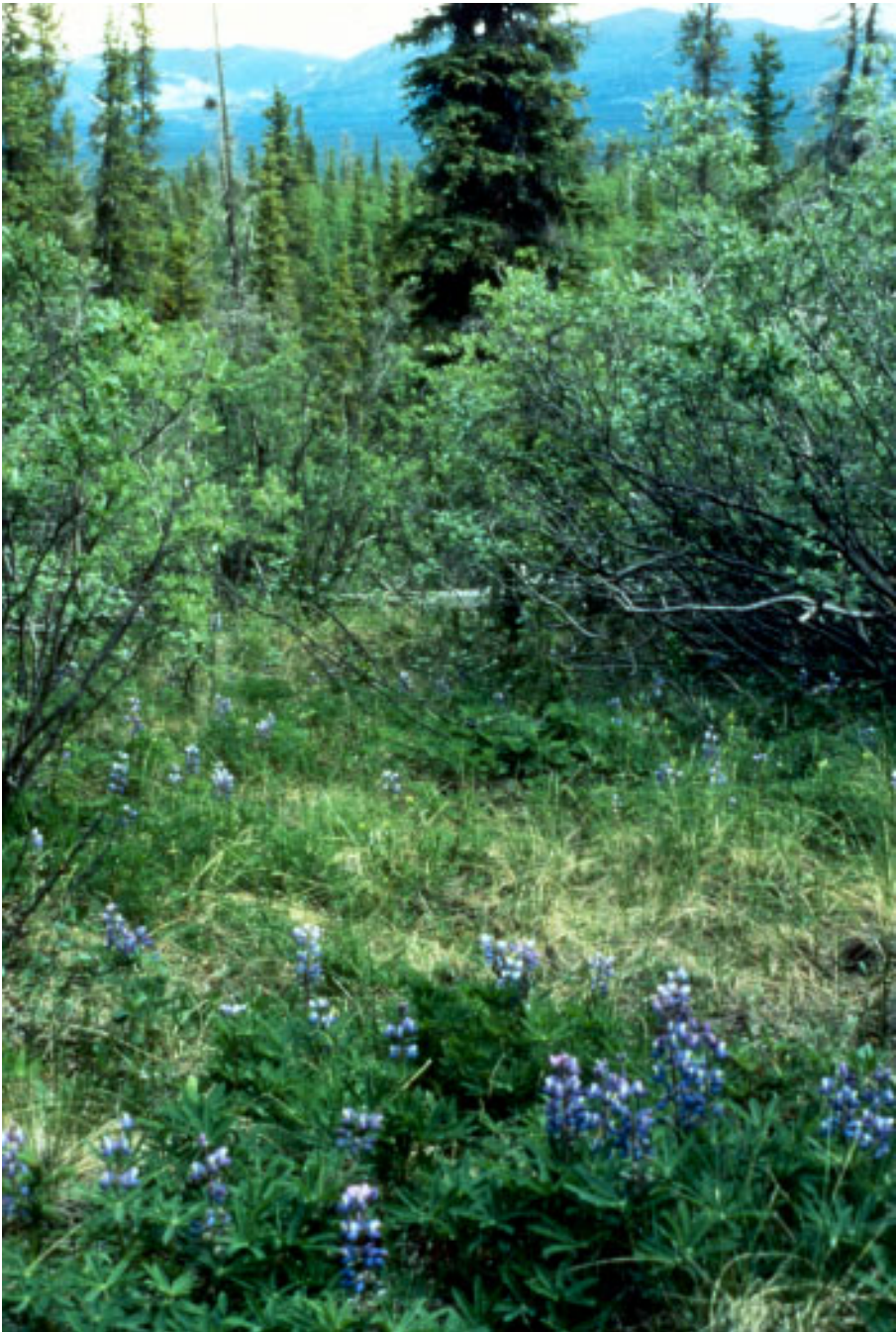


Figure 9. General view of an open understory.

of plant and animal habitat around the world. Species loss is accelerating globally and the inexorable conclusion is that the study and understanding of natural systems, and the protection of biodiversity must become a national and international priority.

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